



A SMALL YET OCCASIONAL MEAL: PREDATORY DRILL HOLES IN PALEOCENE OSTRACODS FROM ARGENTINA AND METHODS TO INFER PREDATION INTENSITY

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Abstract: Ostracods are common yet understudied prey item in the fossil record. We document drill holes in Paleocene (Danian) ostracods from central Argentina using 9025 specimens representing 66 species. While the percentage of drilled specimens at assemblage-level is only 2.3%, considerable variation exists within species (0.3–25%), suggesting prey preference by the drillers. This preference is not determined by abundance because no significant correlation is found between species abundance and drilling percentages. Seven methods were used, some of which are new, to quantify drilling percentages for the abundant and commonly drilled *Togoina argentinensis*. The resulting range, from 9.9% to 14.6%, suggests that drilling percentages are fairly insensitive to the method used, implying that comparisons across studies are possible. This information, combined with data from the literature, suggests the Cretaceous–Palaeogene mass extinction may have had a limited effect on drilling intensity

in ostracods. The cylindrical (*Oichnus simplex*) and parabolic (*O. paraboloides*) drill holes from Argentina may have been caused primarily by naticid and possibly muricid gastropods. Two oval drill holes (*O. ovalis*) are morphologically similar to octopod drill holes, but their small size, the fact that extant octopods are not known to drill ostracods and the absence of such holes in co-occurring gastropods, preclude ascription to a predator clade. Drill holes are located preferentially in the median and dorsal regions, where most soft tissue, including the adductor muscle, is located. Drilled specimens are statistically taller than non-drilled specimens for *T. argentinensis* and larger predators selected larger ostracods. The drilling percentage does not significantly differ in ornamented ostracods.

Key words: predation, ostracod, gastropod, octopod, Danian, palaeoecology.

OSTRACODS are microcrustaceans that are a food source for various groups, including carnivorous bivalves (Leal 2008), gastropods (Reyment 1963, 1966a, b; Bhatia *et al.* 1989; Ruiz *et al.* 2011a), fish (Vaske Júnior *et al.* 2008), turbellarians (Smith & Kamiya 2008), annelids (Fidalgo *et al.* 2006), scaphopods (Glover *et al.* 2003), echinoids (Neale 1983), octopods (Nigmatullin & Ostapenko 1976), amphibians (Hogan 2008) and even other ostracods (Campbell 1995). As the presence of drill holes is the most abundant direct evidence of predator–prey interactions in the fossil record (Kabat 1990; Kowalewski *et al.* 1998; Kelley & Hansen 2003; Huntley & Kowalewski 2007; Bardhan *et al.* 2012; Mallick *et al.* 2014; Harper

2016; Klonpmaker *et al.* 2017) it is no surprise that drilled ostracods are also known. Drill holes in fossil ostracods attributed to predators were first figured by Livan (1937) based on a drilled ostracod from the Oligocene of the Mainz Basin in Germany. Subsequently, drilled ostracods have been recorded from the Carboniferous (one specimen, Vannier *et al.* 2003), Triassic (one specimen, Forel *et al.* 2018), Cretaceous (Reyment *et al.* 1987; Maddocks 1988), Eocene (Maddocks 1988; Bhatia *et al.* 1989), Miocene (Elewa 2007; Ruiz *et al.* 2010a), Pliocene (Aranki 1987; Ruiz *et al.* 2010a), Pleistocene (Maddocks 1988; Ruiz 1997; Kihn *et al.* 2011; Kihn & Gómez 2015) and Holocene (Hussain *et al.* 2004; Ruiz

et al. 2010*b*, 2011*a*, *b*; Kihn *et al.* 2011). From the Paleocene, we know of only three detailed studies identifying drilling predation in Danian ostracods: one from North America (Maddocks 1988) and the others from Nigeria (Reyment 1966*b*; Reyment *et al.* 1987).

Studies of extant marine invertebrates have identified flatworms, octopods, nematodes and principally gastropods as predatory drillers, and these are potential predators in the fossil record also (Kowalewski 1993, 2002; Klompmaker *et al.* 2017, in press). Ostracods are drilled primarily by naticid and muricid gastropods (Reyment & Elewa 2003) but flatworms and octopods have also been mentioned as potential predators (Maddocks 1988). Studies on fossil drilled ostracods are restricted principally to European, Indian, North American and African deposits thus far (Reyment *et al.* 1987; Maddocks 1988; Bhatia *et al.* 1989; Hussain *et al.* 2004; Ruiz *et al.* 2011*a*, *b*; Forel *et al.* 2018). For South America, we only know of the studies carried out by Kihn *et al.* (2011) and Kihn & Gómez (2015), documenting drill holes in Quaternary marine and freshwater ostracods of central Argentina. Recently, we have found drill holes in ostracods from the Danian of the Jagüel and Roca formations (Neuquén basin) of Argentina. The goals of this paper are to: (1) quantify the prevalence of drill holes found in the Danian ostracods using some methods not used previously for ostracods; (2) evaluate the cause of these drill holes; (3) determine if there is any size or site-selectivity; (4) assess whether ornamentation is functional against drilling predation; and (5) compare and contrast predation to previous studies of drilled ostracods.

GEOLOGICAL AND GEOGRAPHICAL CONTEXT

The specimens described herein originate from the Cerro Azul section (38°50'48"S, 67°52'20"W) of the Jagüel and Roca formations (Villegas-Martín *et al.* 2019, table S1), which is a relatively new site in the eastern sector of Lake Pellegrini, General Roca province, Argentina (Fig. 1A). The Jagüel and Roca formations are part of the infill of the Neuquén sedimentary basin, a foreland basin located in west-central Argentina. The sediments of both formations belong to the same sedimentary cycle (Uliana & Dellapé 1981). In the Cerro Azul section, the Jagüel Formation deposits are overlain by sediments from the Roca Formation (Fig. 1B). The environment for this sequence has been interpreted principally as an open marine setting varying from an offshore facies (not deeper than 150 m) for the upper part of Jagüel Formation (*sensu* Uliana & Dellapé 1981) to a shoreface environment affected by wave action for the Roca

Formation (Bertels 1970, 1975; Barrio 1991). The presence of *Palmoconcha similis* (Bertels, 1973) (458 specimens) and *Cytherella terminopunctata* Holden, 1964 (71 specimens) as the most abundant ostracod species in the Roca Formation indicates the shallower character of the Roca Formation compared to the Jagüel Formation (Malarkodi *et al.* 2010).

Jagüel Formation

The marine sediments of the Jagüel Formation are part of Malargüe Group deposited during the first transgression of the Atlantic Ocean (Casadío *et al.* 1998; Gasparini *et al.* 2007). This formation is assigned to the late Maastrichtian to early Danian (Rodríguez 2011); the same age was suggested for the Cerro Azul section based on its calcareous nannofossil and ostracod associations (Musso *et al.* 2012; Ceolin *et al.* 2015, 2016).

The deposits of the Jagüel Formation consist mainly of a homogeneous grey calcareous mudstone (Musso *et al.* 2012), containing principally fish teeth (Bogan & Agnolin 2010), bivalves (Casadío 1998; Casadío *et al.* 2005; del Río *et al.* 2008), echinoids (Parma & Casadío 2005), ammonoids (Casadío & Leanza 1991) and decapod crustaceans (Feldmann *et al.* 1995). Additionally, bioerosion structures (borings) attributed to polychaete annelids have been documented on oysters from the Maastrichtian part of the unit (Brezina *et al.* 2014).

Micropaleontological studies have reported on ostracods (Bertels 1973, 1974; Ceolin *et al.* 2015), foraminifers (Bertels 1980), nannofossils (Concheyro 1995) and paly-nomorphs (Barreda *et al.* 2004). Studies at the Cerro Azul section have focused principally on micropalaeontology. The section represents a marine environment of low energy and good circulation (Concheyro 1995; Parma & Casadío 2005). The ostracod samples used herein originate from the Danian upper part of the Jagüel Formation (Ceolin *et al.* 2015, 2016).

Roca Formation

The deposits of the Roca Formation cover an extensive area of Septentrional Patagonia and are considered to be shallow-water deposits. The lithology is more variable compared to the Jagüel Formation (Bertels 1980; Nañez & Concheyro 1996) and varies from carbonates to intercalated sandstones, and limestone and mudstones of a greyish-green colour depending on the region in which the formation is exposed (del Río *et al.* 2011). At the Cerro Azul section, the Roca Formation is defined by an alternation of carbonate rocks and greenish grey calcareous mudstones. The base of the formation is defined by the first

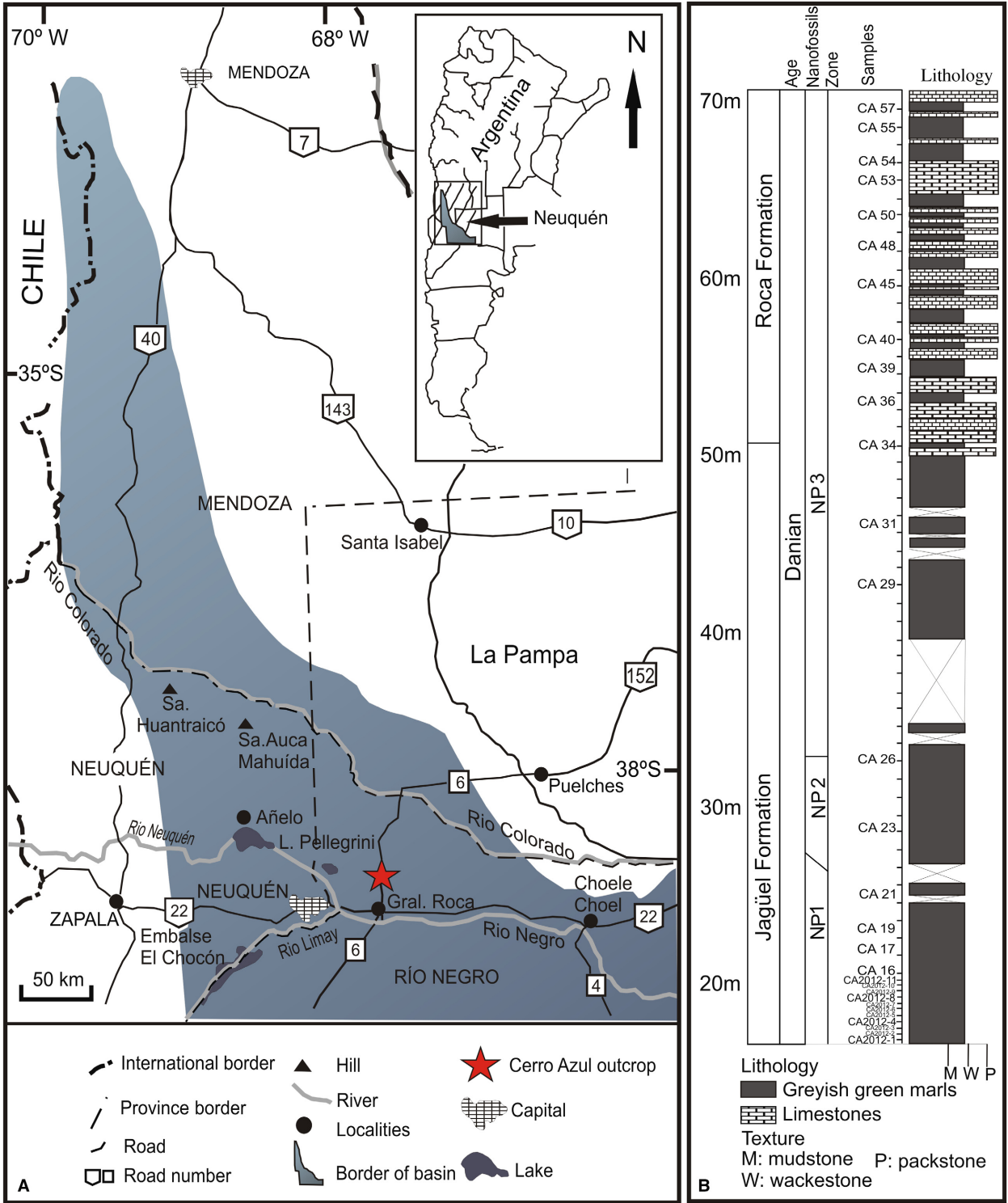


FIG. 1. A, geographical location of the study area Cerro Azul (star) in the General Roca province, Argentina (modified from Ceolin *et al.* 2015). B, schematic profile of a part of the sedimentary succession of the Jagüel and Roca formations (Cerro Azul section), with the distribution of the samples with ostracods used in this study. Colour online.

appearance of organogenic limestones (Uliana & Dellapé 1981). This formation is assigned to the late Danian (Rodríguez 2011; del Río *et al.* 2011), which is corroborated by calcareous nannofossils (Musso *et al.* 2012).

The Roca Formation contains a diverse and abundant fauna of invertebrates, mainly dominated by molluscs (Casadío 1998; del Río *et al.* 2007, 2008; Griffin *et al.* 2008; Pérez & del Río 2017), followed by decapod crustaceans (Feldmann *et al.* 1995), echinoids (Parma & Casadío 2005; Martínez *et al.* 2011) and nautiloids (Casadío *et al.* 1999). The micropalaeontological record consists of planktonic and benthonic foraminifers, ostracods (Bertels 1969*a, b*, 1970, 1973, 1980) and calcareous nannofossils (Concheyro & Nañez 1994). The ostracod samples used herein originate from the lower part (upper Danian) of the Roca Formation (Ceolin *et al.* 2015, 2016).

The deposits are interpreted as a shallowing sequence that can vary from a platform hardly affected by waves to shallow deposits representing a high energy regime (Casadío 1998; Bona *et al.* 2009). These deposits represent the final part of the Atlantic transgressive–regressive phase of the sea that flooded Patagonia during the Cretaceous–Palaeogene interval (Uliana & Dellapé, 1981; del Río *et al.* 2007, 2011).

MATERIAL AND METHOD

The studied material is housed in the palaeontological collection of Museu de História Geológica do Rio Grande do Sul, Universidade do Vale do Rio dos Sinos, Brazil, under the prefix ULVG. The specimens were extracted from 30 sediment samples collected randomly from Danian-aged beds (Jagüel and Roca formations) along the Cerro Azul section (Villegas-Martín *et al.* 2019, table S1). Each sample consisted of 20 g of sediments prepared according to a standard method to obtain ostracods (methodology of Sohn *et al.* 1965, detailed in Slipper 1997): samples were washed through 63 and 180 µm sieves and then dried at 60°C. All ostracods were hand-picked under a stereomicroscope for each size fraction (63–180 and >180 µm).

The material consists of 9025 ostracod specimens composed of (nearly complete and complete) left valves, right valves and carapaces (valves still connected). The specimens consist principally of adults and last juvenile instars. A specimen was considered an adult depending its size (length and height of the shell), which varies somewhat for each species; when exhibiting a maximum development of characters such as the thickness of the inner lamella and shell and the development of ornamentation. These last characters are equally well-expressed in adults and A1 instars, so valve size was used as the diagnostic

character to separate the two ontogenetic stages. The Danian ostracods were attributed to 66 species described previously by Ceolin *et al.* (2015, 2016).

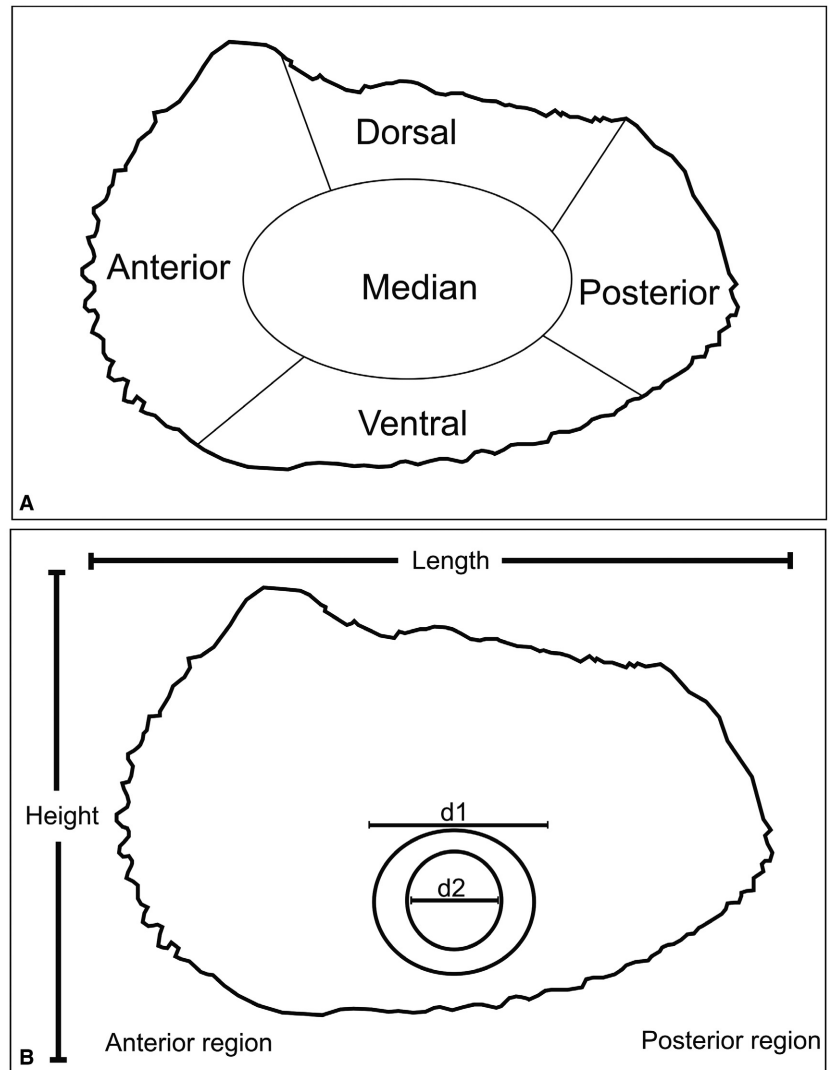
For drilled specimens, the following data were collected for each drill hole: (1) maximum outer diameter; (2) maximum inner diameter; (3) the number of drill holes per valve; and (4) position of each perforation, also relative to the adductor muscle scar area (Fig. 2). To determine the drill-hole position, the location of the centre of each drill hole was used to assign each hole to the anterior, posterior, median, ventral or dorsal part (Fig. 2A) following Bhatia (1968). The cross-sectional profiles of the drill holes were determined using a microscope. For the ichnotaxonomy of the drill holes, we follow Bromley (1981, 1993) and Wisshak *et al.* (2015). Drill holes were categorized as predatory using the following criteria: morphology, single perforations, penetration from the exterior, penetration axis perpendicular to the shell surface, holes positioned non-randomly on the shell (stereotypy) and a lack of widely-ranging sizes (Baumiller 1990; Kowalewski 2002; Harper 2003; Kelley & Hansen 2003; Daley 2008; Klompmaker *et al.* 2016).

Using the program PAST (v. 3.15; Hammer *et al.* 2001), a rarefaction curve (number of species vs the number of specimens) was constructed to determine whether most species were collected by combining data from all samples. A χ^2 -test was used to determine whether there was a preference to drill a particular region of the shell. All regions are of about the same area.

The length and height of each drilled ostracod shell were measured using digital calipers accurate to *c.* 0.03 mm to determine whether there is a relationship between drill-hole size, as a proxy for predator size (Kitchell *et al.* 1981; Kowalewski 2004; Klompmaker *et al.* 2017), and prey size. We also assessed whether there is a significant relationship between drilling percentage and specimen abundance per species for the entire assemblage and also for the Jagüel and Roca formations separately.

Using (nearly) complete shells, the drill-hole predation percentages for the entire ostracod assemblage and per species in the assemblage were calculated, as well as for each formation and for each sample. Right and left valves as well as carapaces (= connected valves) of adult and juveniles (all the instars found were used) are considered to be single specimens herein. It is unlikely that two separated valves of the same specimen are present in the sample due to post-mortem transport and potential time-averaging. The juvenile specimens may represent moults of the same organism but were counted because it is impossible to distinguish between moults and corpses. Additionally, juveniles are known to be drilled from both fossil and extant ostracods (Reyment 1966*a*; Ruiz 1997; Ruiz *et al.* 2010*a*, 2011*a, b*; Kihn & Gómez 2015, and

FIG. 2. A, the different lateral regions of ostracods used to determine the location of the centre of drill holes. B, biometric measurements used in this study for the drill holes in ostracods: maximum outer drill-hole diameter (d1); maximum inner drill-hole diameter (d2).



references therein) and thus constitute potential prey. In many previous studies this particular method seems to have been used, but these studies often do not explain precisely how specimens were counted. The authors mentioned that the material (drilled or non-drilled) was composed of single valves and carapaces attributed to adults and juveniles (Reyment 1966a; Ruiz 1997; Ruiz *et al.* 2010a, b, 2011b; Kihn *et al.* 2011). Some studies did not include fragmented or abraded valves (Ruiz 1997; Ruiz *et al.* 2010a).

To explore the influence of the choice of method in determining drilling percentages for the first time for ostracods, seven methods were used to determine the drilling percentage for drill holes interpreted as being produced by predators of the abundant, commonly drilled and well-preserved species *Togoina argentinensis* from the Jagüel Formation. One (Method 1) was the used for the entire ostracod assemblage and per species

in the assemblage. For the other six methods, only adult specimens and last juvenile instars were used (specimens with lengths of at least 0.7–0.8 mm were considered to be adult, and last juvenile instars were those with lengths of at least 0.6–0.7 mm). The total number of specimens was determined as follows: (Method 2) left and right valves and carapaces were all considered as single specimens; (Method 3) the number of left and right valves was divided by two, as for bivalves (Kowalewski 2002), while carapaces were counted as single specimens; (Method 4) carapaces and only the left valves were used; (Method 5) carapaces and only the right valves were used; (Method 6) only carapaces were used; (Method 7) only adult specimens (carapace, left and right valves) were used. The specimens of *T. argentinensis* were also used to test for size-selectivity by the predator using the Mann–Whitney test. For all statistical tests, a 5% significance level was used.

RESULTS

Characteristics of the drill holes

In the studied assemblage, 211 ostracod valves contain 214 drill holes (Villegas-Martín *et al.* 2019, table S1; Tables 1, 2). The maximum outer drill-hole diameter ranges from 0.02 to 0.46 mm (mean = 0.20 mm) and nearly all are oriented approximately perpendicular to the shell surface. Circular to subcircular drill holes dominate (205/214, 95.8%). Most are parabolic in profile and completely penetrate the shell, thus representing the ichnospecies *Oichnus paraboloides* Bromley, 1981 (123/214, 57.5%), with sizes ranging from 0.03 to 0.44 mm and a mean of 0.24 mm (Fig. 3A–I). Some specimens with complete (sub)circular drill holes have walls oriented perpendicular to the shell surface (cylindrical), and are ascribed to *Oichnus simplex* Bromley, 1981 (55/214, 25.7%; outer diameter range 0.02–0.41 mm, mean = 0.14 mm) (Fig. 3J–O). Other (sub)circular drill holes were assigned to *Oichnus* isp. (22/214, 10.3%; diameters 0.11–0.32 mm, mean = 0.20 mm), including: (1) those for which the completeness and cross-sectional shape could not be determined due to sediment infill (18/22, Fig. 4A–I); and (2) those that are complete, but the poor preservation does not permit ascription to an ichnospecies (4/22). Incomplete circular drill holes (*Oichnus* isp. (incomplete), 5/214, 2.3%) are rare (Table 1; Fig. 4J–L, O). The ichnospecies cannot be determined because sediments cover most of the shell bottom of the drill hole so that the presence of a central boss cannot be identified clearly. Two drill holes (2/214, 0.8%) exhibit an oval shape and have a conical profile in cross-section representing *Oichnus ovalis* Bromley, 1993, with diameters of 0.09 mm by 0.04 mm and 0.03 mm by 0.02 mm (Fig. 5). These drill holes have somewhat irregular outer margins, one of which is more irregular and contains a lip or gutter (Fig. 5A, B) (Villegas-Martín *et al.* 2019, table S1).

Valves usually contain a single drill hole, except for three valves exhibiting two drill holes each, ascribed to *O. paraboloides* (2), *Oichnus* isp. (4) (Fig. 4M–O). All remaining holes (7/214, 3.3%) were not assigned to *Oichnus* because they appear highly abraded and/or dissolved, and are very irregular in outline (Fig. 6).

Ostracod taxa drilled

A rarefaction curve indicates that most species were collected (Fig. 7). At least 27 species (211 specimens) contain drill holes, of which 22 are ornamented and 5 are smooth (Tables 1, 2, Villegas-Martín *et al.* 2019, table S1).

A total of 19 ostracod species exhibit both cylindrical (*O. simplex*) and parabolic (*O. paraboloides*) drill holes (Table 1). However, *Hysterothereis coinotes* and *Keijia*

huantraicoensis only have cylindrical drill holes. Conversely, four species exhibit only parabolic drill holes (Table 1). *Oichnus paraboloides* is found principally in *Huantraiconella prima* (22), *Actinocythereis indigena* (15) and *Cytherella saraballentae* (14), a pattern that is non-random ($\chi^2 = 372.87$, $p < 0.0001$). *Oichnus simplex* is found primarily in *K. huantraicoensis* (6), whereas *O. ovalis* is found in single specimens of *T. argentinensis* and *K. kratis-tos* (Table 1; Villegas-Martín *et al.* 2019, table S1). Incomplete drill holes are found only in *Henryhowella* (*Henryhowella*) *nascens*, *Paracypris bertelsae*, *C. saraballentae* and *Huantraiconella prima* (Table 2; Villegas-Martín *et al.* 2019, table S1). Valves with multiple drill holes are found in one specimen each of *A. biposterospinata*, *H. prima* and *C. saraballentae* (Fig. 4M–O).

Drill hole predation percentages

The drilling percentage for the entire Danian assemblage is 2.3% (204/9025). The Jagüel Formation has a drilling percentage of 2.5% (185/7445), whereas this percentage is only 1.2% (19/1580) for the Roca Formation, which is a significant difference ($\chi^2 = 9.9$; $p < 0.001$). The percentages are different among species (Table 2). Higher than average (2.3%) drilling percentages are found in *Togoina argentinensis*, *Munseyella costaevermiculatus*, *Orthrocosta phantasia*, *Hysterothereis paredros* and *Togoina semiinornata*, whereas *Cytherella terminopunctata*, *C. semicatillus*, *C. trajectiones*, *H. coinotes* and *Petalocythereis shilleri* exhibit lower drilling percentages. *Actinocythereis biposterospinata*, *Huantraiconella prima*, *Henryhowella* (*Wichmannella*) *meridionalis* and *Neoveenia argentinensis* are species found to have been drilled in both formations (Table 2). When comparing sample-based drilling percentages per formation for samples with at least 30 specimens available, drilling frequencies remain significantly different (Mann–Whitney $U = 17.5$, $p = 0.005$; median Jagüel = 3.5%, median Roca = 0.7%).

Relative abundance per species (ranging from 0.2% to 8.3%, see Villegas-Martín *et al.* 2019, table S2) is not significantly correlated with their respective predation percentages for species with at least 30 specimens ($R = -0.04$, $p = 0.81$) (Fig. 8), implying that common species are not drilled more frequently than uncommon species and vice versa for the entire sample. A similar result is also obtained when analysing data separately for the Jagüel (relative abundance per species 0.2–7.7%, predation percentages 0.4–25%) ($R = -0.10$, $p = 0.58$) and Roca (relative abundance per species 1.08–27.9%, predation percentages 0.9–25%) ($R = -0.76$, $p = 0.06$) formations. Also, the relative abundance of ostracods in each sample (ranging from 1.6% to 25.1%, see Table 3) is not significantly correlated with their respective predation percentages ($R = 0.16$, $p = 0.44$), for samples with >30 specimens.

TABLE 1. Measurements of the drilled ostracod species and their drill holes from the Danian part of the Jagüel and Roca formations, Argentina.

Taxon	Length (mm)– range (mean)	Height (mm)– range (mean)	Ichnotaxon of drill hole	No. drill holes per ichnotaxon	Maximum outer drill-hole diameter per ichnotaxon (mm)
<i>Actinocythereis</i>	0.693–0.853 (0.769)	0.358–0.852 (0.486)	<i>O. paraboloides</i>	3	0.161–0.260
<i>biposterospinata</i>			<i>O. simplex</i>	4	0.118–0.208
Bertels, 1973			<i>Oichnus</i> isp.	5	0.114–0.199
<i>A. indigena</i> Bertels, 1969a	0.696–0.882 (0.817)	0.398–0.496 (0.453)	<i>O. paraboloides</i>	15	0.162–0.305
			<i>O. simplex</i>	3	0.082–0.236
<i>A. rex</i> Bertels, 1973	0.833–0.896 (0.871)	0.493–0.496 (0.495)	<i>O. paraboloides</i>	2	0.214, 0.274
			<i>Oichnus</i> isp.	1	0.185
<i>Bairdoppilata?</i> sp.	0.771	0.442	<i>Oichnus</i> isp.	1	0.195
<i>Castillocythereis</i>	0.696–0.832 (0.738)	0.420–0.503 (0.453)	<i>O. paraboloides</i>	2	0.087–0.273
<i>multicastrum</i> Ceolin & Whatley, 2015			<i>O. simplex</i>	2	0.041–0.127
<i>Cythereis stratioides</i> Ceolin & Whatley in Ceolin et al., 2015	0.641–0.973 (0.823)	0.308–0.517 (0.445)	<i>O. paraboloides</i>	11	0.044–0.351
			<i>O. simplex</i>	2	0.081, 0.221
			<i>Oichnus</i> isp.	2	0.236, 0.251
<i>C. trajectiones</i> Ceolin & Whatley, 2015	0.598–0.933 (0.801)	0.354–0.504 (0.431)	<i>O. paraboloides</i>	1	0.231
			<i>O. simplex</i>	2	0.116, 0.405
<i>Cythereis?</i> sp.	0.634–0.709 (0.662)	0.380–0.403 (0.391)	<i>O. paraboloides</i>	3	0.173–0.204
			<i>O. simplex</i>	1	0.124
			<i>Oichnus</i> isp.	2	0.214, 0.234
<i>Cytherella saraballentae</i> Ceolin & Whatley, 2015	0.700–0.874 (0.755)	0.391–0.527 (0.454)	<i>O. paraboloides</i>	14	0.167–0.319
			<i>O. simplex</i>	2	0.219, 0.289
			<i>Oichnus</i> isp. (incomplete)	1	0.150
<i>C. semicatillus</i> Ceolin & Whatley, 2015	0.760	0.40	<i>O. paraboloides</i>	1	0.197
<i>C. terminopunctata</i> Holden, 1964	0.715, 0.814	0.452, 0.520	<i>O. paraboloides</i>	2	0.224, 0.236
<i>Henryhowella (Wichmannella)</i> <i>meridionalis</i> (Bertels, 1969b)	0.868–1.057 (0.943)	0.475–0.577 (0.538)	<i>O. paraboloides</i>	5	0.196–0.456
			<i>O. simplex</i>	1	0.110
			<i>Oichnus</i> isp.	1	0.201
<i>H. (Henryhowella) nascens</i> (Bertels, 1969b)	1.101, 1.129	0.600, 0.621	<i>O. paraboloides</i>	1	0.272
			<i>Oichnus</i> isp. (incomplete)	1	0.230
<i>Huantraiconella prima</i> Bertels, 1973	0.658–1.270 (1.006)	0.102–0.740 (0.620)	<i>O. paraboloides</i>	22	0.150–0.376
			<i>O. simplex</i>	6	0.136–0.331
			<i>Oichnus</i> isp.	6	0.143–0.329
			<i>Oichnus</i> isp. (incomplete)	2	0.173, 0.206
<i>Hysterocythereis coinotes</i> Ceolin & Whatley, 2015	0.729	0.407	<i>O. simplex</i>	1	0.233
<i>H. diversotuberculatus</i> Ceolin & Whatley, 2015	0.765, 0.838	0.456, 0.468	<i>O. paraboloides</i>	2	0.248, 0.352
<i>H. paredros</i> Ceolin & Whatley, 2015	0.626–1.016 (0.813)	0.370–0.525 (0.454)	<i>O. paraboloides</i>	5	0.191–0.307
			<i>O. simplex</i>	3	0.040–0.264
			<i>Oichnus</i> isp.	1	0.035
<i>Keijia huantraicoensis</i> (Bertels, 1969a)	0.387–0.457 (0.413)	0.189–0.244 (0.217)	<i>O. simplex</i>	6	0.024–0.111
<i>K. kratistos</i> Ceolin & Whatley, 2015	0.402–0.536 (0.448)	0.196–0.276 (0.240)	<i>O. paraboloides</i>	1	0.034
			<i>O. simplex</i>	5	0.019–0.196
			<i>O. ovalis</i>	1	0.033

(continued)

TABLE 1. (Continued)

Taxon	Length (mm)– range (mean)	Height (mm)– range (mean)	Ichnotaxon of drill hole	No. drill holes per ichnotaxon	Maximum outer drill-hole diameter per ichnotaxon (mm)
<i>Munseyella costaevermiculatus</i> Ceolin & Whatley, 2015	0.386–0.400 (0.393)	0.203–0.221 (0.210)	<i>O. paraboloides</i>	2	0.024, 0.048
			<i>O. simplex</i>	2	0.020, 0.118
<i>Neoveenia argentinensis</i> Bertels, 1969b	0.685–1.040 (0.848)	0.394–0.637 (0.503)	<i>O. paraboloides</i>	12	0.148–0.345
			<i>O. simplex</i>	1	0.181
			<i>Oichnus</i> isp.	1	0.174
<i>Orthrocosta atopos</i> Ceolin & Whatley, 2015	0.787, 0.815	0.382, 0.439	<i>O. paraboloides</i>	1	0.173
<i>Orthrocosta phantasia</i> Ceolin & Whatley, 2015	0.677–0.837 (0.770)	0.360–0.457 (0.388)	<i>O. simplex</i>	1	0.149
			<i>O. paraboloides</i>	1	0.209
			<i>O. simplex</i>	2	0.218, 0.313
<i>Paracypris bertelsae</i> Ceolin & Whatley, 2015	0.912, 1.209	0.446, 0.478	<i>Oichnus</i> isp.	2	0.181, 0.205
			<i>O. simplex</i>	1	0.182
			<i>Oichnus</i> isp. (incomplete)	1	0.224
<i>Petalocythereis shilleri</i> (Bertels, 1973)	0.805–0.961 (0.875)	0.492–0.528 (0.515)	<i>O. paraboloides</i>	3	0.322–0.392
<i>Phelocyprideis acardomesido</i> Ceolin & Whatley, 2015	0.502–0.509 (0.505)	0.309–0.322 (0.314)	<i>O. paraboloides</i>	2	0.184, 0.203
			<i>O. simplex</i>	1	0.105
<i>Togoina argentinensis</i> Bertels, 1975	0.653–0.912 (0.751)	0.413–0.540 (0.451)	<i>O. paraboloides</i>	9	0.170–0.234
			<i>O. simplex</i>	5	0.129–0.264
			<i>O. ovalis</i>	1	0.087
<i>T. semiinornata</i> Bertels, 1975	0.726, 0.757	0.472, 0.476	<i>O. paraboloides</i>	1	0.258
<i>Trachyleberis weiperti</i> Bertels, 1969a	1.057, 1.130	0.615, 0.755	<i>O. simplex</i>	1	0.096
			<i>O. paraboloides</i>	1	0.224
			<i>O. simplex</i>	1	0.114

Drilled shells are absent in numerous samples. In the samples with specimens drilled, predation percentages are low (0.4–4.9%, usually <4%). Within the Roca Formation, in which both limestones and mudstones are present, the drilling percentages do not significantly differ between rock types based on a limited number of samples (Mann–Whitney $U = 6.5$, $p = 0.40$), although the number of samples is low and no minimum number of specimens was specified for each sample to be able to run the test.

The drilling percentage for ornamented ostracods is 2.3% (180/7765), whereas only 1.9% (24/1258) of the smooth ostracods are drilled, which is not significantly different ($\chi^2 = 0.79$, $p = 0.3743$). The drilling percentage of incomplete drill holes is 0.04% (3/7767) for ornamented ostracods and 0.16% (2/1258) for smooth ostracods, which is not significantly different ($\chi^2 = 2.75$, $p = 0.097$).

For *Togoina argentinensis*, the drilling percentage is 9.9% (15/151, Method 1). The total number of carapaces and left and right valves of adult and last instars (A1) is only 150 specimens, yielding a drilling percentage of 10.0% (15/150, Method 2). Dividing the number of left and right valves by two yields 80 specimens, resulting in a drilling percentage of 11.2% (14/125) (Method 3). The total number of carapaces and left valves is 114, yielding a maximum drilling percentage of 12.3% (14/114)

(Method 4). Using right valves only in addition to carapaces yields a drilling percentage of 11.2% (14/125, Method 5). The total number of drilled carapaces (13) divided by the total number of carapaces (89) results in a drilling percentage of 14.6% (Method 6). Finally, using carapaces and left and right valves of adults only (101) yields a maximum drilling percentage of 9.9% (10/101, Method 7). Thus, despite using seven methods, the range of drilling percentages (9.9–14.6%) is limited (Table 4).

Site stereotypy

The drill holes are located in all regions of the valve, but the dorsal (41/207, 19.8%) and median (103/207, 49.8%) regions are preferentially drilled, whereas the anterior (16/207, 7.7%), posterior (17/207, 8.2%), ventral (22/207, 10.6%) and between-valve (8/207, 3.9%) regions are less commonly drilled ($\chi^2 = 180.9$, $p < 0.0001$; Fig. 9). A similar result is obtained when *O. paraboloides* and *O. simplex* are analysed separately: the median (59/120, 49.2%) and dorsal (27/120, 22.5%) regions are primarily drilled for *O. paraboloides* ($\chi^2 = 92.7$, $p < 0.0001$); the median region (27/55, 49.1%) is preferentially drilled for *O. simplex* ($\chi^2 = 56.1$, $p < 0.0001$; Fig. 9).

TABLE 2. Total number of specimens, number of specimens drilled and the drilling percentage per ostracod species from the Danian Jagüel and Roca formations, Argentina.

Taxon	No. specimens	No. specimens drilled	No. juvenile specimens drilled	No. specimens with complete drill holes	No. specimens with incomplete drill holes	Drilling percentage (%)
Jagüel Formation						
<i>Actinocythereis biposterospinata</i>	200	8		4		4.0
<i>Actinocythereis indigena</i>	353	18		18		5.1
<i>Actinocythereis rex</i>	43	3		3		6.1
<i>Castillocythereis multicastrum</i>	221	4	1	4		1.8
<i>Cythereis?</i> sp.	188	6		6		3.2
<i>Cythereis stratioides</i>	288	15		13		5.2
<i>Cythereis trajectiones</i>	322	3		3		0.9
<i>Cytherella saraballentae</i>	355	16		16	1	4.5
<i>Cytherella semicatillus</i>	258	1		1		0.4
<i>Henryhowella (Wichmannella) meridionalis</i>	326	6		5		1.8
<i>Henryhowella (Henryhowella) nascens</i>	55	2		1	1	3.6
<i>Huantraiconella prima</i>	595	32	1	24	2	5.4
<i>Hysteroocythereis coinotes</i>	193	1		1		0.5
<i>H. diversotuberculatus</i>	79	2		2		2.5
<i>H. paredros</i>	209	9		9		4.3
<i>Keijia huantraicoensis</i>	377	6		6		1.6
<i>K. kratistos</i>	575	7		7		1.2
<i>Munseyella costaevermiculatus</i>	16	4		4		25
<i>Neoveenia argentinensis</i>	390	7	2	7		1.8
<i>Orthrocosta atopus</i>	28	2		2		7.1
<i>O. phantasia</i>	105	5		3		4.8
<i>Paracypris bertelsae</i>	156	2		1	1	1.3
<i>Petalocythereis shilleri</i>	325	3		3		0.9
<i>Phelocyprideis acardomesido</i>	83	3		3		3.6
<i>Togoina argentinensis</i>	151	15		15		9.9
<i>Trachyleberis weiperti</i>	52	2		2		3.8
Roca Formation						
<i>Actinocythereis biposterospinata</i>	26	3		3		11.5
<i>Bairdoppilata?</i> sp.	23	1		1		4.3
<i>Cytherella terminopunctata</i>	113	2		2		1.8
<i>Huantraiconella prima</i>	127	3		3		2.4
<i>Henryhowella (Wichmannella) meridionalis</i>	112	1		1		0.9
<i>Neoveenia argentinensis</i>	200	7		7		3.5
<i>Togoina semiornata</i>	17	2		2		11.8

Non-drilled taxa are not shown (see Villegas-Martin *et al.* 2019, table S3).

Size selectivity

The drilled specimens have a length range of 0.40–1.27 mm (mean = 0.80 mm) and a height range of 0.10–0.85 mm (mean = 0.47 mm) (Table 1; Villegas-Martín *et al.* 2019, table S1). The maximum outer drill-hole diameter ranges from 0.02 to 0.44 mm and is significantly correlated with shell length ($R = 0.54$; two-tailed t -test $p < 0.001$) and height ($R = 0.49$; two-tailed t -test $p < 0.001$) (Fig. 10). For the Jagüel Formation separately, the maximum outer drill-hole diameter (0.02–0.41 mm) is significantly correlated with shell length ($R = 0.57$;

two-tailed t -test $p < 0.001$) and shell height ($R = 0.54$; two-tailed t -test $p < 0.001$). Conversely, the maximum outer drill-hole diameter (range = 0.10–0.46 mm, mean = 0.23 mm) is not significantly correlated with shell length ($R = 0.22$; two-tailed t -test $p = 0.38$) and height ($R = 0.06$; two-tailed t -test $p = 0.82$) for the Roca Formation.

For *Togoina argentinensis*, the 15 drilled specimens have a length range of 0.65–0.91 mm (mean = 0.75 mm) and a height range of 0.41–0.54 mm (mean = 0.45 mm) (Table 1; Villegas-Martín *et al.* 2019, table S2), whereas the 151 non-drilled specimens of the entire Danian have

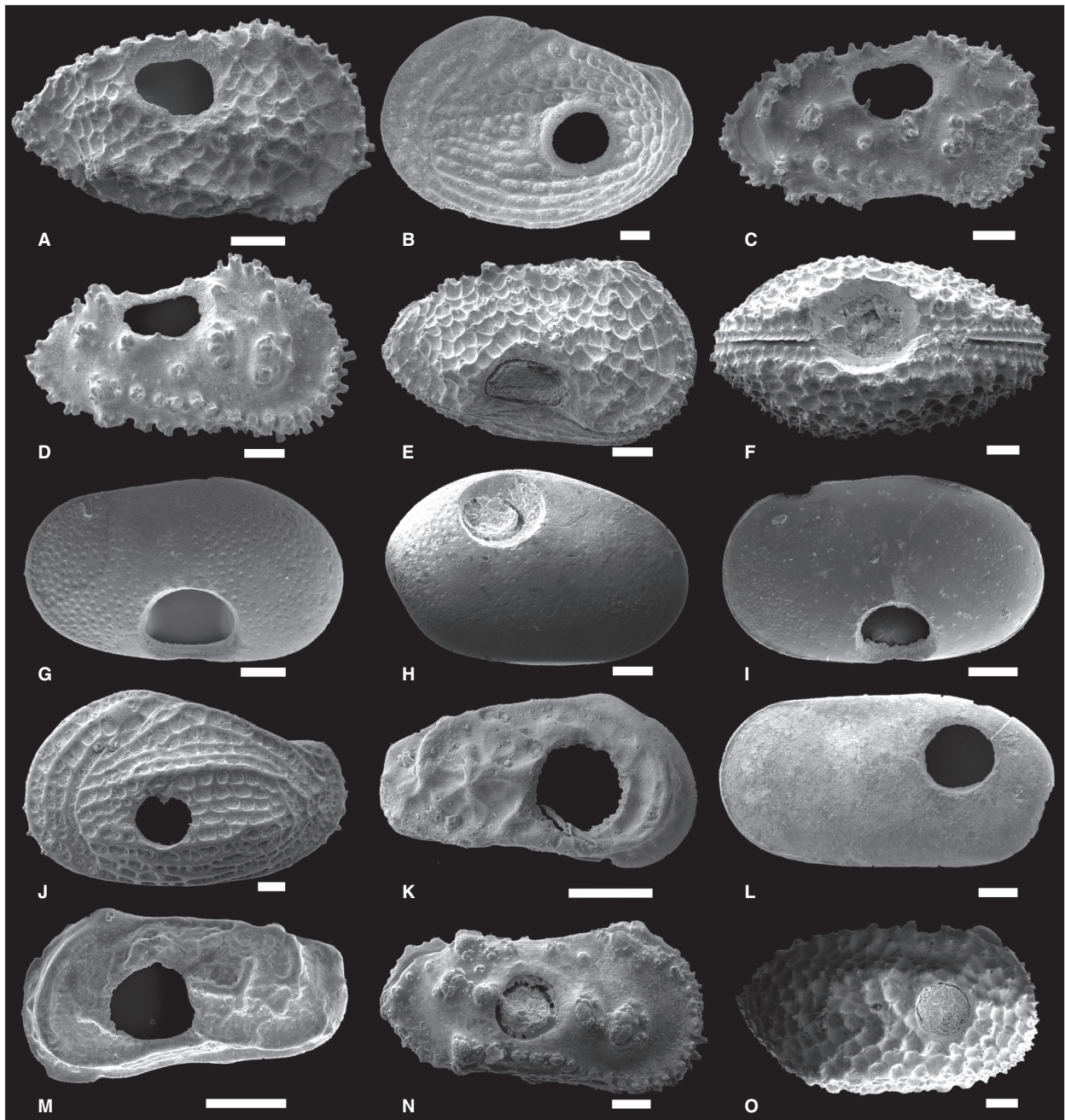


FIG. 3. A sample of ostracods from the Danian of Argentina inferred to be preyed upon by drilling gastropods. A–I, parabolic drill holes (*O. paraboloides*) attributed to naticids in the ornamented species *Cythereis stratos* (A, ULVG-12419), *Huantraiconella prima* (B, ULVG-12420), *Actinocythereis indigena* (C, ULVG-12421; D, ULVG-12422), *Hysterothereis paredros* (E, ULVG-12423), *Henryhowella* (*Wichmannella*) *meridionalis* (F, ULVG-12424) and in the smooth species *Cytherella saraballentae* (G, ULVG-12425; H, ULVG-12426; I, ULVG-12427). J–O, cylindrical drill holes assigned to *O. simplex* attributed to possible muricid predation in *Huantraiconella prima* (J, ULVG-12428), *Keijia huantraicoensis* (K, ULVG-12429; M, ULVG-12430), *Cytherella saraballentae* (L, ULVG-12431), *Actinocythereis biposterospinata* (N, ULVG-12432) and *Neoveenia argentinensis* (O, ULVG-12433). Scale bars represent 100 μ m.

a length range of 0.58–0.88 mm (mean: 0.74 mm) and a height of 0.25–0.56 mm (mean = 0.42 mm) (Villegas-Martín *et al.* 2019, table S2). The drilled specimens are

statistically larger in height (Mann–Whitney $U = 588.5$; $p = 0.005$), but not in length (Mann–Whitney $U = 860.5$; $p = 0.32$) (Fig. 11).

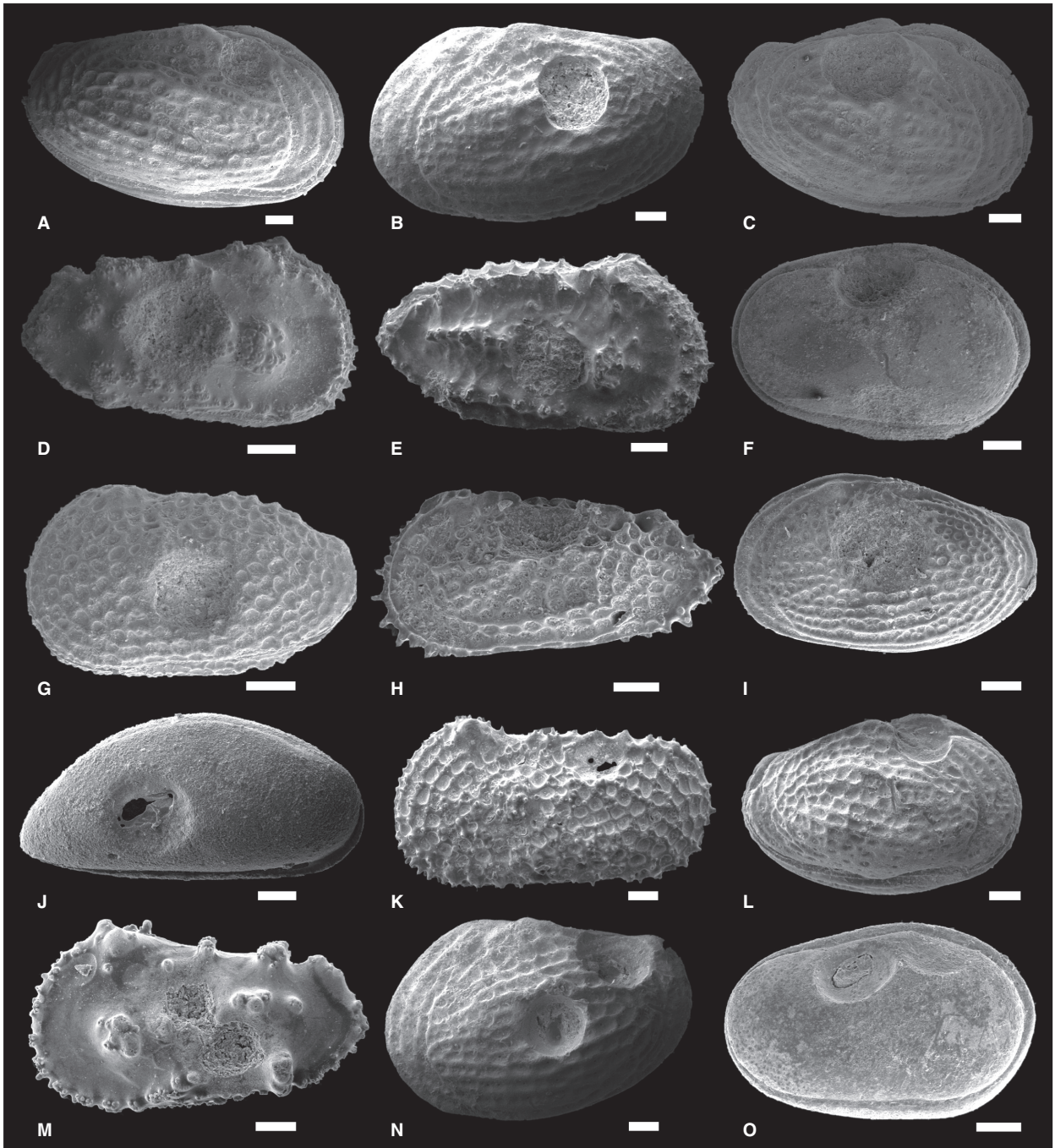


FIG. 4. A sample of drilled ostracods from the Danian of Argentina. A–I, drill holes infilled with sediment (*Oichnus* isp.) in *Huantraiconella prima* (A, ULVG-12434; B, ULVG-12435; C, ULVG-12436), *Actinocythereis biposterospinata* (D, ULVG-12437), *Cythereis stratius* (E, ULVG-12438), *Cytherella saraballentae* (F, ULVG-12439), *Neoveenia argentinensis* (juvenile) (G, ULVG-12440), *Orthrocosta atopus* (H, ULVG-12441) and *Togoina argentinensis* (I, ULVG-12442). J–L, incomplete drill holes in *Paracypris bertelsae* (J, ULVG-12443), *Henryhowella* (*Wichmannella*) *meridionalis* (K, ULVG-12444) and *Huantraiconella prima* (L, ULVG-12445). M–O, specimens exhibiting multiple drill holes in the same valve: *Actinocythereis biposterospinata* (M, ULVG-12446), *Huantraiconella prima* (N, ULVG-12447) and *Cytherella saraballentae* (O, ULVG-12448). In the specimen of *C. saraballentae* (O), one of the drill holes is incomplete. Scale bars represent 100 μm .

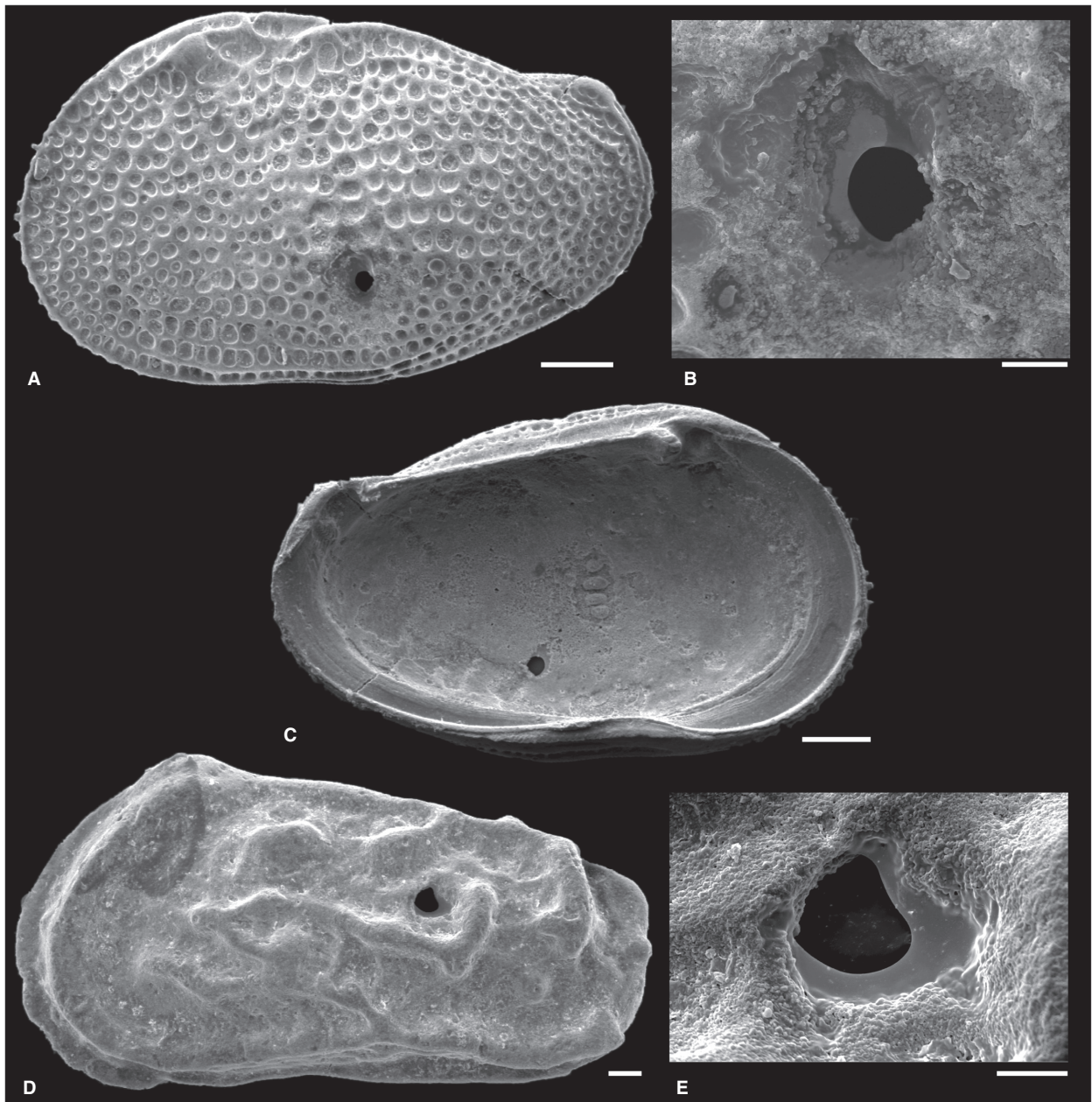


FIG. 5. A, D, Ostracods from the Jagüel Formation of Argentina exhibiting oval drill holes attributed to *Oichmus ovalis*, located near the adductor muscle: A, *Togoina argentinensis* (ULVG-12449); D, *Keijia kratistos* (ULVG-12450). C, inner surface of the valve of *T. argentinensis* showing the short distance from the drill hole to the central muscle scar. B, E, close-ups of the oval drill holes in both ostracods. Scale bars represent 100 μm (A, C); 20 μm (B, D); 10 μm (E).

DISCUSSION

The origin of the drill holes in the Danian ostracods

Although Ceolin (2015) speculated that the drill holes in the Danian ostracods from the Jagüel and Roca formations were caused by naticid and muricid gastropods, drill holes were not studied in detail nor were alternative

causes considered. We here discuss four potential causes: (1) abrasion; (2) dissolution holes; (3) non-predatory organisms such as spionids and parasites; and (4) predatory drillers.

Abrasion. Oval and circular drill holes in invertebrate shells may be caused by abiotic factors such as abrasion (see Gorzelak *et al.* 2013). This hypothesis cannot be

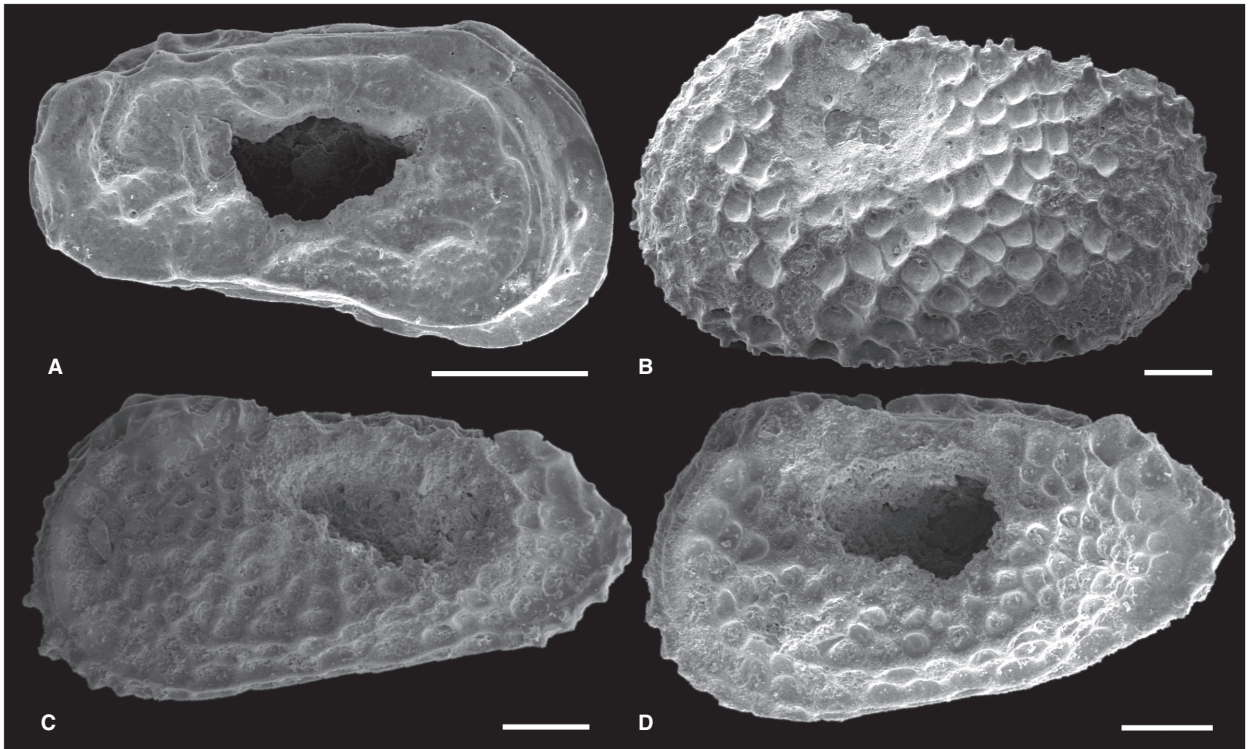


FIG. 6. A sample of ostracods with possible dissolution holes from the Danian of Argentina. A, *Keijia huantraicoensis* (ULVG-12451). B, *Henryhowella* (*Wichmannella*) *meridionalis* (ULVG-12452). C–D, *Orthocosta phantasia*: C, ULVG-12453; D, ULVG-12454. Holes show irregular outlines, walls sloping gently and an outer edge that is more or less abraded or dissolved (C, D). Scale bars represent 100 μm .

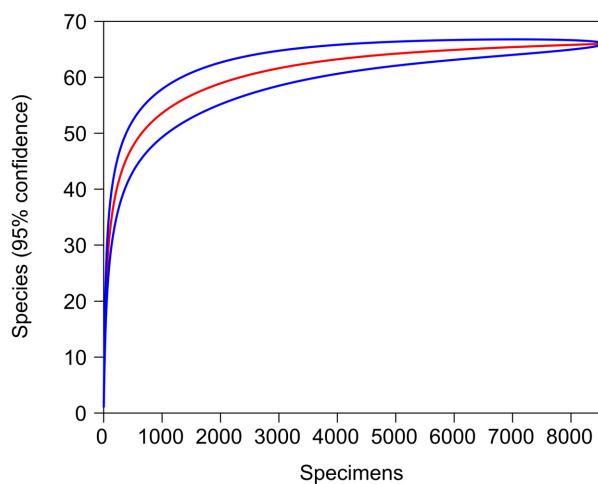


FIG. 7. Rarefaction curve with 95% confidence intervals of the ostracod species from the Danian of Argentina. Specimens for which the species could not be determined were excluded. $N = 8553$. Colour online.

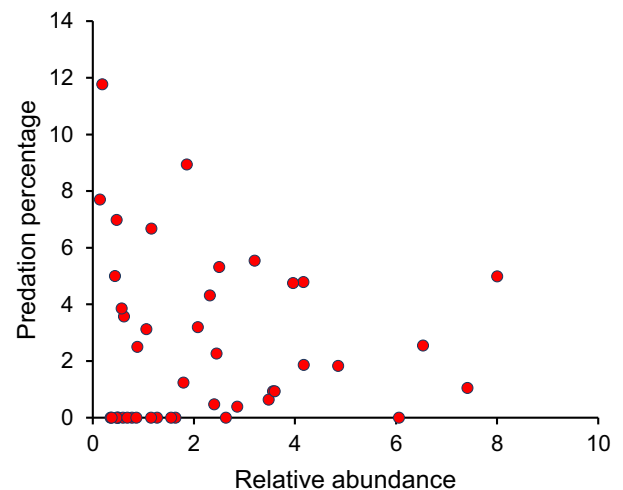


FIG. 8. Relative abundance (%) vs predation percentage for Danian ostracod species from Argentina. Linear trendline $R = -0.04$, $p = 0.81$ (not shown). Species with at least 30 specimens were included. Colour online.

supported here for several reasons (cf. Rojas *et al.* 2014, for a drill hole in a Pleistocene chiton plate). First, the fine-grained deposits in which the specimens of ostracods have been collected imply limited transport and

mechanical abrasion. Second, the characteristics of the ostracod shell such as the shape, the small size, thickness and the ratio between its size and thickness, suggests that the valve would be broken well before an abrasion-

TABLE 3. Total number of specimens, number of specimens drilled, relative abundance and the drilling percentage per sample from the Danian Jagüel and Roca formations, Argentina.

Formation	Sample	Lithology	No. specimens	No. specimens drilled	Relative abundance of ostracods	Drilling percentage (%)
Jagüel	CA 2012-1	Mudstones	224	4	3.0	1.8
Jagüel	CA 2012-2	Mudstones	202	7	2.7	3.5
Jagüel	CA 2012-3	Mudstones	22	0	0.3	0
Jagüel	CA 2012-4	Mudstones	193	7	2.6	3.6
Jagüel	CA 2012-5	Mudstones	120	1	1.6	0.8
Jagüel	CA 2012-6	Mudstones	230	8	3.1	3.5
Jagüel	CA 2012-7	Mudstones	306	15	4.1	4.9
Jagüel	CA 2012-8	Mudstones	604	10	8.1	1.7
Jagüel	CA 2012-9	Mudstones	181	7	2.4	3.9
Jagüel	CA 2012-10	Mudstones	125	5	1.7	4.0
Jagüel	CA 2012-11	Mudstones	309	15	4.2	4.9
Jagüel	CA 16	Mudstones	529	7	7.1	1.3
Jagüel	CA 17	Mudstones	187	4	2.5	2.1
Jagüel	CA 19	Mudstones	456	2	6.1	0.4
Jagüel	CA 21	Mudstones	581	3	7.8	0.5
Jagüel	CA 23	Mudstones	232	4	3.1	1.7
Jagüel	CA 26	Mudstones	436	13	5.9	3.0
Jagüel	CA 29	Mudstones	162	6	2.2	3.7
Jagüel	CA 31	Mudstones	307	11	4.1	3.6
Jagüel	CA 34	Mudstones	1596	66	21.4	4.1
Roca	CA 36	Mudstones	397	13	25.1	3.3
Roca	CA 39	Mudstones	283	0	17.9	0
Roca	CA 40	Limestones	64	1	4.1	1.6
Roca	CA 45	Mudstones	6	0	0.4	0
Roca	CA 48	Mudstones	23	0	1.5	0
Roca	CA 50	Mudstones	44	0	2.8	0
Roca	CA 53	Limestones	369	3	23.4	0.8
Roca	CA 54	Limestones	1	0	0.1	0
Roca	CA 55	Mudstones	96	0	6.1	0
Roca	CA 57	Mudstones	268	2	17.0	0.7

induced hole could be produced. Third, the specimens with ornamentation are well-preserved and show no evidence of substantial abrasion.

Dissolution holes. It has previously been hypothesized that holes may have been caused by dissolution in ostracods from the Cretaceous of Texas and Holocene of Spain (Maddocks 1988; Ruiz 1997). Some holes herein (7/214; Fig. 6) resemble those attributed to dissolution by Kornicker & Sohn (1971, pl. 1) and Maddocks (1988, pls 1–2). The holes herein exhibit irregular to more or less jagged outer edges and show some evidence of dissolution around the drill holes and vertical to unevenly curving walls as in some Cretaceous ostracods (Maddocks 1988). Dissolution holes produced in ostracods as a result of the ingestion by fish (solution by digestive fluids, Kornicker & Sohn 1971) have an irregular shape, but usually occur in clusters. Although there is evidence that these holes are caused by dissolution, we cannot exclude the possibility

that the irregular holes may have been produced by other biological processes and/or diagenetic alteration.

Domicile-commensal spionids. The small size of the holes completely penetrating the shell and their elliptical outline raises the possibility that the oval-shaped holes could be domiciles (commensalism) of spionid polychaetes (Cameron 1969; Zottoli & Carriker 1974; Kern *et al.* 1974; Kern 1979; Ishikawa & Kase 2007). However, holes attributed to spionids are principally circular in outline when they are small-sized (<1 mm), a difference previously identified by Bromley (1993). The outer opening in spionid-produced holes is basically a cylindrical hole in cross-section and it has a small, flat area beneath the hole opening (associated erosion on the shell) in gastropod shells (Cameron 1969; Kern *et al.* 1974; Ishikawa & Kase 2007). The holes herein have an irregular outline with occasional presence of a gutter, which is absent in drill holes produced by spionids. Finally, drill holes attributed

TABLE 4. A summary of the results of the seven methods used to estimate the drilling percentages for specimens of *Togoina argentinensis* from the Danian of Argentina.

	Total number of specimens in the sample	No. specimens drilled	Drilling percentage (%)
Method 1	151	15	9.9
Method 2	150	15	10.0
Method 3	125	14	11.2
Method 4	114	14	12.3
Method 5	125	14	11.2
Method 6	89	13	14.6
Method 7	101	10	9.9

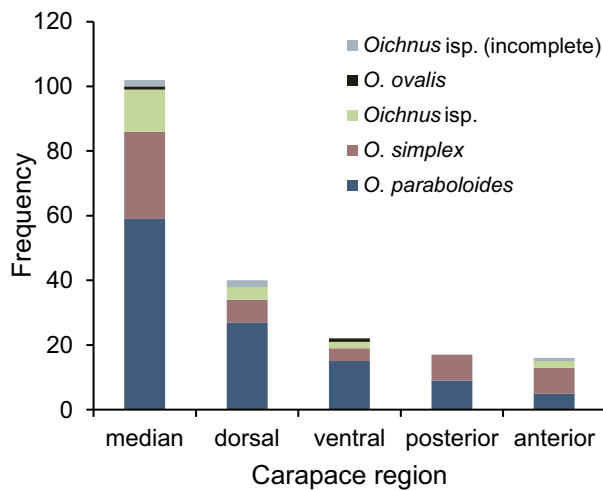


FIG. 9. The number drill holes per valve region split by ichnotaxon in the ostracod assemblage from the Danian of Argentina. *Oichnus* isp. (incomplete): incomplete drill holes, for which the ichnospecies cannot be determined because part of the bottom is covered with sediment. *Oichnus* isp.: (1) sediment infill precluded determining whether drill holes are complete or incomplete; and (2) when complete, the degree of preservation did not permit ascription to an ichnospecies.

to spionids have not been reported previously in ostracod shells, being only recorded in gastropods and other crustaceans thus far (Cameron 1969; Zottoli & Carriker 1974; Kern *et al.* 1974; Kern 1979; Ishikawa & Kase 2007).

Parasites. Drill holes attributed to parasitism can be small, circular and perpendicular to the shell surface (Daley 2008). The cylindrical holes could be attributed to foraminifers (Hallock & Talge 1994) and eulimid gastropods (Warén *et al.* 1994), whereas the parabolic drill holes could be attributed to capulid gastropods (Kowalewski & Nebelsick 2003). However, attachment scars commonly associated with prolonged attachment by parasites (eulimid and capulids) and repaired holes (Orr 1962;

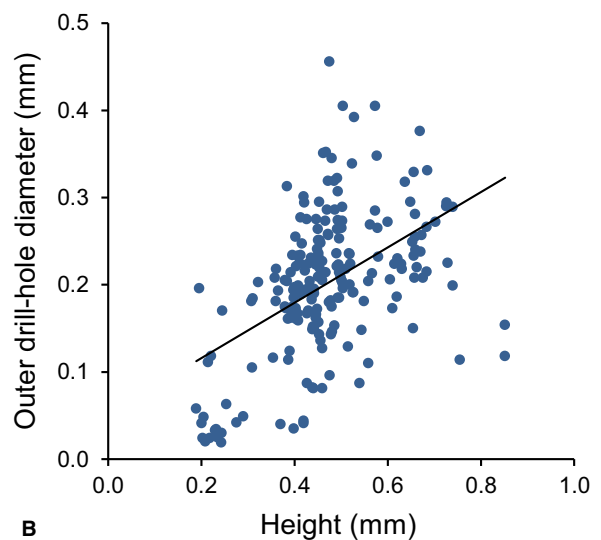
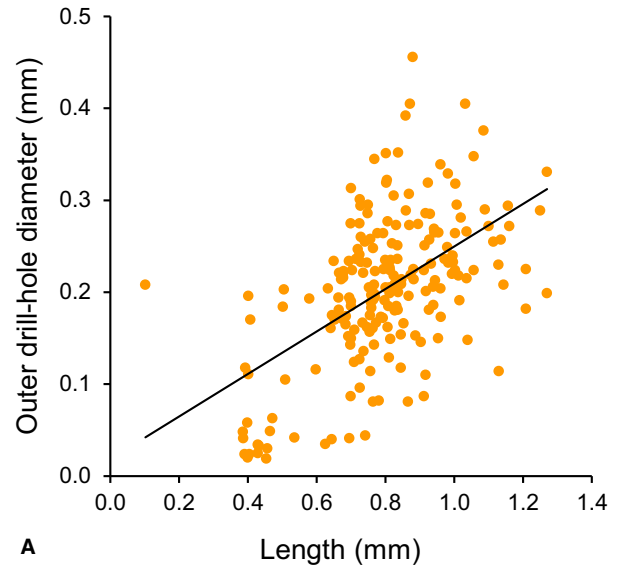


FIG. 10. Length vs outer drill hole diameter (A) and height vs outer drill-hole diameter (B) using the Danian ostracods from Argentina. A, trendline $R = 0.54$, $p < 0.001$; B, trendline $R = 0.49$, $p < 0.001$.

Kosuge & Hayashi 1967; Matsukuma 1978) have not been found. Additionally, although capulids originated in the Late Cretaceous or Cenozoic (Bandel 1993; Tracey *et al.* 1993), they have not been found in the Jagüel and Roca formations. Furthermore, their preferred prey are pectinids (Orr 1962; Kosuge & Hayashi 1967; Matsukuma 1978) and their drill holes tend to be predominantly larger (0.7–2.5 mm; see Orr 1962; Matsukuma 1978).

Eulimid-produced holes may be healed and can exhibit a circular groove around the hole (Neumann & Wisshak 2009), features that are both absent in the holes studied here. Eulimids (Warén *et al.* 1994) originated in the Cretaceous (Dockery 1993), but are unknown from the Jagüel

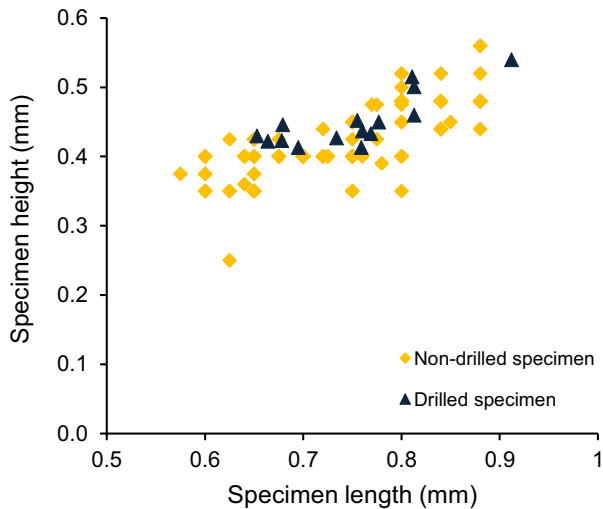


FIG. 11. Sizes of the drilled and non-drilled carapaces and valves of *Togoia argentinensis*. Colour online.

and Roca formations. Finally, drill holes attributed to eulimids are poorly documented and have been recorded principally from echinoids so far (Warén 1981; Kowalewski & Nebelsick 2003; Neumann & Wisshak 2009).

The drilled ostracods herein rarely exhibit multiple holes, which is untypical of predatory foraminifera that generally produce 2–10 holes per valve (Hallock & Talge 1994; Hallock *et al.* 1998). Additionally, the holes attributed to foraminifera are smaller (0.005–0.01 mm) than those holes found in ostracods (Hallock *et al.* 1998). Furthermore, their preferred prey are other foraminifera (Hallock & Talge 1994; Walker *et al.* 2017) and bivalves (Todd 1965). Although the work of parasites cannot be held responsible for the great majority of the holes in ostracods, it has been suggested that benthic foraminiferal tests from the Jagüel Formation contain parasitic holes (usually multiple per test, circular to oval or circular to conical and commonly perpendicular to the test surface) attributed to *Oichnus coronatus* Nielsen & Nielsen, 2001 and *Oichnus paraboloides* Bromley, 1981 (Malumián *et al.* 2007).

Predators

The majority of drill holes are single perforations; penetrations were made from the exterior; the penetration axis is nearly always perpendicular to the shell; they are almost always complete (207/214, 96.7%); drill holes do not have widely-ranging sizes and they show stereotypy. These characteristics suggest a predatory origin for most drill holes (Baumiller 1990; Kowalewski 2002; Harper 2003; Kelley & Hansen 2003; Daley 2008; Klompmaker *et al.* 2016). Below, we discuss the possible predators of the oval, cylindrical and parabolic drill holes.

Turbellarians (flatworms). The possibility of turbellarians being responsible for drill holes in ostracods was mentioned only by Maddocks (1988). The two oval holes herein may be attributed flatworms because their holes are oval in outline, very small in size (0.16 by 0.13 mm, 0.46 by 0.26 mm; 0.11 by 0.11 mm to 0.19 by 0.26 mm) and exhibit smooth outlines and sharp edges (Smith 1955; Woelke 1956). Additionally, it has been demonstrated experimentally that flatworms consume ostracods (Smith & Kamiya 2008), as specimens of *Darwinula stevensoni* (Brady & Robertson, 1870) were found in the gastrovascular cavity of turbellarian flatworms (their fig. 23), but these do not appear have been perforated and were still alive after being regurgitated (Smith & Kamiya 2008). Morphological features of the drill holes herein, such as the presence of a lip or gutter, are not known from flatworm-produced holes and argue against this predator. Finally, drill holes attributed to Turbellaria (*Pseudostylochus ostrepophagus* Hyman, 1955) were documented principally in oysters and occasionally in barnacles (Smith 1955; Woelke 1956).

Octopods. Modern octopods are voracious predators using their arms and interbranchial web to capture prey, followed by pulling apart shells, biting with the beak, or drilling (Nixon 1980; McQuaid 1994; Dodge & Scheel 1999; Voight 2000). In the fossil record, Bromley (1993) demonstrated that the presence of octopods can be inferred from the presence of oval drill holes in mollusc shells. The two small oval holes found herein preserve morphological features consistent with those produced by octopods: an oval shape, an irregular outline with occasional presence of a gutter and a conical profile tapering from a larger external opening to a much smaller internal opening (Fig. 5C, E). This morphology is comparable to that attributed to octopods in a variety of fossil and extant shells of decapods crustaceans, scallops, barnacles and molluscs (Arnold & Arnold 1969; Marliave 1981; Boyle & Knobloch 1981; Nixon 1985, 1987; Boucher-Rodoni *et al.* 1987; Nixon & Maconnachie 1988; Bromley 1993; Harper 2002; Todd & Harper 2011; Pasini & Garasino 2012; Klompmaker *et al.* 2013, 2014, 2015). Additionally, octopods had evolved by the Cretaceous (Strugnell *et al.* 2006; Fuchs *et al.* 2009; Kröger *et al.* 2011), while the ostracods herein are younger (Danian). Although octopod fossils are absent in the Cerro Azul section (Jagüel and Roca formations), this may be explained by the fact that soft tissues are not preserved here.

An important difference of the oval drill holes reported here is the small size (0.09 × 0.04 mm and 0.03 × 0.02 mm) compared to those made by modern octopods, with the smallest diameter known to us of

0.21 mm produced by a specimens of *Octopus vulgaris* Cuvier, 1797, of 270 g in the gastropod *Bittium reticulatum* (da Costa, 1778) (Nixon & Maconnachie 1988). The possibility of an octopod drilling ostracod shells was mentioned previously for some drill holes in fossil ostracods from Texas, USA (Maddocks 1988). We find morphological similarities of the oval drill holes reported here with some of the oval drill holes illustrated by Maddocks (1988) in *Cytherella* sp. (pl. 2.12) and *Haplocytheridea nanifaba* Crane, 1965 (pl. 2.6). Additionally, small holes identified as *Oichnus ovalis* (0.12 mm) were previously identified by Blissett & Pickerill (2007) on foraminifers from the middle Eocene of Jamaica, but they made no inferences on the possible predator. The dimensions of the hole may depend on the size of the octopod: hole size probably increases as has been noted for the buccal structures and the radula (Nixon 1973) so that larger octopuses produce bigger holes (Cortez *et al.* 1998). Furthermore, pelagic prey including ostracods and foraminifers were part of the diet of octopods based on stomach contents (Nigmatullin & Ostapenko 1976), particularly for juveniles (Laidig *et al.* 1995).

Young and paralarval octopods appear to be capable of drilling. For example, Boyle & Knobloch (1981) found that newly hatched specimens (5–15 days old) of the octopod *Eledone moschata* (Lamarck, 1798) have the ability to drill as soon as they begin to feed, while Mather (2008) mentioned that juvenile octopuses were able to learn positioning drill holes in a few trials. Nixon & Maconnachie (1988), citing Boletzky & Hanlon (1983), indicated that octopods attack prey of varying sizes from less than one-third to more than double their mantle length. Moreover, many species of juvenile and paralarval octopods are capable of eating benthic prey (Boletzky & Hanlon 1983).

Extant ostracods and octopods overlap in the littoral zone (Nigmatullin & Ostapenko 1976; Boyle & Rodhouse 2005), but reports on their trophic relationship remain poorly described, restricted only to the presence of ostracods as stomach contents in extant octopods (Nigmatullin & Ostapenko 1976; Boletzky & Hanlon 1983).

The holes are located near the adductor muscle scar of the ostracod (Fig. 4C), perhaps suggesting a focused attack by a predator to get access to the soft tissue or, in the case of octopods, to inject venom to relax the adductor muscles and thus open the ostracod valves (Nixon & Maconnachie 1988). Drill holes attributed to octopods near or over the adductor scar have been recorded in modern and Eocene bivalves (Cortez *et al.* 1998; Todd & Harper 2011). Predation on ostracods and other groups such as decapod crustaceans, polychaetes, isopods, amphipods, stomatopods and foraminifers has been mentioned as an incidental food source for octopods (Nigmatullin &

Ostapenko 1976), in line with the rare occurrence of oval drill holes. This observation was also expressed by Boletzky & Hanlon (1983), who mentioned ‘incidental food’ or ‘abnormal predation’ to occur in a trawl net during the course of a tow.

Although it is tempting to attribute the oval drill holes herein to octopods because they are similar in shape, and knowing that octopods had evolved by the Danian, the drill holes are much smaller than reported octopod drill holes, extant octopods are not known to drill ostracods and a preliminary survey of gastropod shells from the same formations does not yield any oval drill holes. A soft bodied, unknown driller is another possibility for these ‘octopodiform’ drill holes.

Gastropods. Spherical, parabolic drill holes with outer diameters exceeding the inner diameter (*O. paraboloides*) found on ostracods from the Jagüel and Roca formations closely resemble holes most often attributed to naticid gastropods (Bromley 1981; Carriker 1981; Kabat 1990; but see Klompmaker *et al.*, 2015). This drill-hole morphology has been inferred previously for extant and fossil ostracods (Reyment 1966a, Maddocks 1988; Kihn *et al.* 2011; Ruiz *et al.* 2011a, b; Kihn & Gómez 2015). Naticids have not been reported from the Jagüel Formation, but naticids attributed to the genus *Euspira* Agassiz in Sowerby, 1837 (*Euspira* sp.) have been identified in the Roca Formation (del Río 2012). Additionally, the drill-hole size range (0.03–0.41 mm) is similar to that found in ostracods that are suggested to have been preyed upon by primarily juvenile naticids (Table 2; Bhatia *et al.* 1989; Reyment & Elewa 2003; Ruiz *et al.* 2010a, 2011a).

The cylindrical drill holes (*O. simplex*) found in some species (Table 1) resemble those produced by muricid gastropods (Bromley 1981). The diameter of drill holes (0.02–0.41 mm) is also consistent with the size range of the drill holes (*O. simplex*) in extant and fossil ostracods produced by (juvenile) muricids (Table 2; Carriker 1955; Ruiz 1997; Reyment & Elewa 2003; Ruiz *et al.* 2010a, 2011a, b). However, muricids have not been reported from the Jagüel and Roca formations so far (del Río *et al.* 2011).

Thus, the morphological characteristics and the presence of naticids suggest that the parabolic drill holes were caused by naticids, while the predator of the cylindrical drill holes is somewhat enigmatic. The predominance of parabolic drill holes indicates that they were principally produced by naticids, as suggested by previous studies (Kihn *et al.* 2011; Ruiz *et al.* 2011a).

Given that the drill-hole diameter is correlated with the size of naticids and muricids (Kitchell *et al.* 1981; Kingsley-Smith *et al.* 2003) and the significant positive correlation between ostracod size and drill hole size herein,

gastropod predators may have fed on larger ostracods as they grew (Carriker & Yochelson 1968; Reyment & Elewa 2003).

Comparison between the drilling predation percentages

The low assemblage-level drilling percentage (2.3%) suggests that the Danian ostracods were probably not a preferred prey of gastropod predators in general, although individual ostracod species may have been targeted as percentages of 9.9% and 11.8% are known (Table 2). This preference is not related to taxon abundance given the lack of correlation between species abundance and drilling percentages. The low assemblage-level drilling percentage is probably an underestimation because the assemblage is likely to contain moults (instars are counted) and single valves were counted as specimens while the other valve may have contained a drill hole. However, similarly low drilling percentages have commonly been recorded in fossil (usually 1–8%; see Aranki 1987; Reyment *et al.* 1987; Maddocks 1988; Bhatia *et al.* 1989; Ruiz *et al.* 2010a) and extant ostracod assemblages (usually 1–5%; see Reyment, 1966a; Honnappa & Venkatachalapathy 1978; Ruiz 1997; Ruiz *et al.* 2010b, 2011a, b; Kihn *et al.* 2011; Kihn & Gómez 2015). The ostracod assemblage-level drilling percentages recorded herein are similar to those reported from the Cretaceous and Palaeogene (Table 5), suggesting that the Cretaceous–Palaeogene extinction had limited influence on the intensity of drilling predation on ostracods (contra a decrease right after the boundary for molluscs; Kelley & Hansen 1993, 1996; Mallick *et al.* 2014).

The significantly lower predation percentage in the Roca Formation relative to the Jagüel Formation could be

due to change in palaeoecological parameters because the Roca Formation is interpreted as a shallower setting. The high abundance of the ostracods *Palmoconcha* and *Cytherella* in the Roca Formation could also indicate fluctuations in the palaeoenvironment (Malarkodi *et al.* 2010) because these taxa have been identified in shallow marine deposits representing a wide range of temperatures and salinities from the Danian Rajahmundry intertrappean beds (India). The alternations in lithology between marls and limestones in the Roca Formation further support the hypothesis of palaeoenvironmental fluctuations. However, more detailed studies of the section are required to test whether palaeoenvironmental change is the cause of the difference in predation percentages between both units.

The seven methods used to estimate the predation percentage values for *Togoina argentinensis* came to very similar values within a narrow range of 9.9–14.6% (Table 4). One assumption for all methods is that drilled specimens are not more prone to breakage than non-drilled specimens, as discussed for bivalves and serpulids (Roy *et al.* 1994; Zuschin & Stanton 2001; Kelley 2008; Bardhan *et al.* 2012; Klompmaker 2012; Villegas-Martín *et al.* 2016). However, in this case, only a small portion of all specimens was broken, indicating that the effect of this potential bias is limited. Methods 1–6 include the last instars, which means that some may represent moults, in turn implying that the drilling percentages may be underestimations. For methods 1, 2, 4, 5 and 7, single valves are counted as specimens, whereas the other valve may also have contained a drill hole. For method 3, a left and right valve is considered to be a single individual, whereas they could constitute independent individuals. Again, drilling percentages may be underestimated. For methods

TABLE 5. Drilling percentages for Cretaceous and Palaeogene ostracod assemblages (specimens may constitute isolated valves and carapaces (two attached valves)).

Age	Country	Stratigraphic unit	Drilling percentage (%)	No. specimens drilled	Total no. specimens	References
Middle Albian	USA (Texas)	Walnut Formation	1.4	98	6842	Maddocks (1988)
Cenomanian	USA (Texas)	Del Rio Formation	0.6	11	1708	Maddocks (1988)
Late Santonian	Israel	<i>Limburgina miarensis</i> assemblage zone (S-3)	7.7	112	1446	Reyment <i>et al.</i> (1987)
Early–middle Campanian	USA (Texas)	Austin & Lower Taylor Groups	0.9	162	18099	Maddocks (1988)
Late Campanian	USA (Texas)	Middle & Upper Taylor Groups	0.6	64	9953	Maddocks (1988)
Maastrichtian	USA (Texas)	Navarro Group	2.3	220	9673	Maddocks (1988)
Danian	USA (Texas)	Midway Group	3.6	467	12868	Maddocks (1988)
Danian	Argentina	Jagüel Formation	2.6	192	7445	Herein
Danian	Argentina	Roca Formation	1.2	19	1580	Herein
Paleocene	Nigeria	Imo Shale	2.1	69	3364	Reyment <i>et al.</i> (1987)
Lutetian	USA (Texas)	Claiborne Group	6.8	259	3832	Maddocks (1988)

4 and 5, it is assumed that the driller had no preference for the left (1/25, 4%) or right (1/36, 2.8%) valve. For method 6, it is assumed that drilled valves do not disarticulate faster than non-drilled specimens. To our knowledge, there are no studies addressing this potential factor. For method 7, it is assumed that the juvenile instars are moults and were excluded from the analysis, but they may also have contained a drill hole. This method was used by Maddocks (1988) to determine 'mortality' in the ostracod fauna considering only adults, but adults were not defined. Maddocks (1988) indicated that this method might lead to an underestimation of the number of specimens.

Based on the seven methods used, the range for the estimated drill hole predation percentage in *T. argentinensis* is likely to be between 9.9% and 14.6% for this taxon with well-preserved specimens. The limited range of drilling percentage values suggests that: (1) the assemblage-level drilling percentage herein is likely to be fairly accurate; and (2) drilling percentages may be compared across various studies if specimens are well-preserved in general.

The Danian ostracods as prey

Our results suggest naticids and perhaps muricids were common predators of ostracods in this region during the Danian, as suggested for other modern and fossil ostracod assemblages (Reyment, 1966a; Bhatia *et al.* 1989; Ruiz 1997; Reyment & Elewa 2003; Ruiz *et al.* 2011a, b; Kihn & Gómez 2015). The high percentage of complete drill holes (187/207, 90.4%) and the rarity of multiple drill holes per ostracod valve (184/207, 88.9%) suggest a high success rate, as observed for other modern and fossil assemblages (Reyment *et al.* 1987; Ruiz *et al.* 2010a, 2011a, Kihn & Gómez 2015).

The presence of multiple drill holes in the same valve has been attributed to simultaneous attacks of two predators (Reyment *et al.* 1987). Reyment (1966a) suggested that the presence of drill holes located at the anterior and posterior ends of the same valve in *Bythocypris* Brady, 1880, may indicate drilling by two gastropods at the same time. Where multiple drill holes occur in the same valve in the Danian ostracods (Fig. 5), they are very close to each other indicating that simultaneous drilling is unlikely. Reyment (1966a, pl. 1 figs 15, 16, 26) also illustrated drill holes located side by side in mollusc and ostracod shells.

The drill holes in the specimens studied are located in all regions of the shell, but preferentially in the median and dorsal regions (Villegas-Martín *et al.* 2019, table S1; Fig. 6). Extant and fossil ostracods are also drilled preferentially in those regions by gastropods (Reyment 1963; Bhatia *et al.* 1989; Ruiz 1997; Ruiz *et al.* 2010a, b, 2011a, b). This preferred region could be due to the

presence of the greatest amount of soft tissue (Ruiz 1997) close to the adductor muscle scar (Ruiz *et al.* 2011b). This preference is most evident in drill holes attributed to naticids (68%), as has been documented in modern ostracods from Spain (Ruiz 1997). The anterior, anteroventral and posteroventral regions are rarely drilled in the Danian ostracods, consistent with patterns in Neogene and Holocene ostracods (Ruiz 1997). Furthermore, Ruiz (1997) identified the posterior region as a region that is not drilled frequently, but the anterior region has also been reported as being preferentially drilled (Ruiz *et al.* 2010a), while yet another study found no preferential drill-hole site (Aranki 1987). Only three complete drill holes (1.4%) are located in the dorsal and ventral regions between the valves (Fig. 6), again consistent with results from other studies (Ruiz & González-Regalado 1989; Ruiz 1997; Ruiz *et al.* 2010a). This low incidence may be due to the presence of the hinge. This structure connects both valves and represents a major functional character related to locomotion and carapace strength and stability (Park & Ricketts 2003). The dorsal region is possibly the strongest part of the ostracod according to Yamada (2007), as the calcification of the carapace commences from the dorsal and ventral marginal areas towards the central area. Drilling between the valves may also be dangerous because of the potential risk of amputation of the drilling apparatus, as suggested for bivalves (Burrell 1975; Dietl *et al.* 2004). Finally, the ventral region is the place where the less meaty appendages are located, which may explain the low incidence of drilling there.

Our results do not show a statistical difference in the drilling intensity of ornamented versus smooth specimens. Conversely, a possible preference of gastropods for smooth valves was identified for ostracods from the Holocene of Africa (Ruiz *et al.* 2011a), the Late Cretaceous and early Paleocene of Israel and Nigeria (Reyment *et al.* 1987) and the Eocene of India (Bhatia *et al.* 1989). Reyment (1963) suggested that predation affected the most abundant species regardless of ornamentation. However, our per-species results do not support the notion that more abundant species are more frequently drilled, and similar results were obtained for Quaternary ostracods (Ruiz *et al.* 2010a; Kihn *et al.* 2011).

Prey shell size and outer drill-hole diameter are significantly positively correlated (Fig. 10), suggesting that larger predators selected larger ostracod prey. Results are dissimilar to those found in extant and fossils ostracods from different countries (Reyment *et al.* 1987; Bhatia *et al.* 1989; Ruiz *et al.* 2010b, 2011a, b; Kihn *et al.* 2011; Kihn & Gómez 2015) but consistent with ostracod assemblages from Nigeria and Spain (Reyment 1966a; Aranki 1987). Positive correlations between predator size and drill-hole size are known for individual species (Kitchell

et al. 1981; Kowalewski 2004; Chiba & Sato 2012) and across species (Klompaker *et al.* 2017).

The interpretation of the Cerro Azul section suggests that the ostracods were probably living in a shallow marine paleoenvironment (Ceolin 2015). The predominance of drill holes attributed to naticids (Table 1) may indicate a predominantly infaunal life mode for many ostracods or that naticids were much more common than muricids. Indeed, naticids have been found at the Cerro Azul section, whereas muricids have not been encountered thus far. Naticids are predominantly infaunal predators, although subaerial hunting has also been observed (Savazzi & Reymont 1989; Pahari *et al.* 2016). Conversely, muricids hunt almost exclusively on the bottom (Carriker 1955). However, many species herein (20) exhibit drill holes that may be attributed to both naticids and muricids (parabolic and cylindrical, Table 1), perhaps suggesting that both gastropods had a partially overlapping diet. Some ostracod species may have lived both on and in the sea floor; some epifaunal ostracods seek refuge by burrowing in the sediment if local conditions suddenly change (De Deckker 2002) so that they were more readily available to naticids.

CONCLUSIONS

1. The predatory drill holes in the ostracods from the Danian of Argentina substantially increase our knowledge of predation by gastropods on ostracods in the Paleocene. The predominant morphology of the drill holes (*Oichnus paraboloides* and *O. simplex*) suggest that the predators were mostly naticid and perhaps muricid gastropods. Oval drill holes (*O. ovalis*) are morphologically close to those produced by octopods, but their relatively small size, the absence of octopod drill holes in extant ostracods and lack of oval drill holes in gastropods from the same formation preclude assignment to a specific predator.
2. The low assemblage-level drilling percentage (2.3%) in the Danian ostracods suggests that they may not have been a preferred prey of naticid and muricid gastropods. Conversely, the range of drilling percentages (0.4–25%) per species suggests that some individual ostracod species were preferred by certain predators, but not the most abundant species as there is no significant correlation between species abundance and drilling percentage. Drilling percentage is significantly lower within the Roca Formation compared to the Jagüel Formation based on combining all samples within each formation and when analysing data per sample; this may be related to environmental factors.
3. The limited range of drilling percentages in *Togoina argentinensis* based on seven different methods demonstrates that similar results may be obtained regardless of the method used and that the assemblage-level drilling percentage is likely to be fairly accurate. Thus, the use of these different methods suggests that drilling percentages for shells with two valves, such as ostracods and bivalves, can be estimated reasonably well if specimens of the assemblage are well preserved.
4. The strong site-selectivity for the median and dorsal regions of the ostracod valves suggests that predators aimed for a spot where most of the soft tissue is located within these carapaces, including the adductor muscle.
5. The significant correlation between drill-hole size and ostracod size suggests that larger predatory gastropods selected larger ostracod prey.
6. The drilled specimens of *Togoina argentinensis* are statistically larger in height than non-drilled specimens, suggesting size-selectivity by predatory gastropods.
7. The number of specimens with drill holes is dominated by ornamented ostracods, but they were also more common in the material studied. The percentage of drill holes in ornamented specimens is not significantly higher than in smooth specimens, indicating that ornamentation was probably not effective in deterring drilling predation in this case.
8. A comparison of Late Cretaceous and Palaeogene assemblage-level drilling predation percentages suggests that the Cretaceous–Palaeogene mass extinction may have had a limited effect on drilling intensities in ostracod prey.

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DATA ARCHIVING STATEMENT

Data for this study (three tables) are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.80df776>

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