1   **'Business as usual': drilling predation across the K-Pg mass extinction event in Antarctica**

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12   **ABSTRACT**

13   A survey of 759 predatory drill holes in Late Cretaceous and Paleogene molluscan and

14   serpulid worm prey from Seymour Island (Antarctica) has allowed exploration of the effects

15   of the K-Pg mass extinction on predator-prey dynamics at this high latitude site. Circular

16   holes (0.62 - 6.41 mm in diameter), suggesting a large gastropod predator, most probably

17   *"Vanikoropsis" arktowskiana*, occur throughout the study interval. Analysis suggests that

18   the driller was a catholic predator capable of attacking a range of prey types, showing some

19   degree of size and stereotypic handling behaviour. Although there were changes in prey

20   choice across the extinction event, these reflect changes in available prey, and in particular

21   limited options immediately post extinction. There were no significant changes in failure

22   rate (Prey Effectiveness) over the mass extinction. Our findings suggest that at this site, for

23   this particular predator, aside from menu choice, predation dynamics post-extinction was

24   'business as usual'.

25   **1. Introduction**

26   Predators are thought to have played a fundamental role in shaping the course of

27   evolution of their prey (Vermeij, 1987; Stanley 2008). It is clear that the dynamics between

28   predators and prey have not been constant over the Phanerozoic. Vermeij (1987)

29   hypothesised that mass extinctions perturb these dynamics and, in particular, predicted that

30   these events selectively remove more escalated (i.e. better defended) prey. These ideas

31   have been tested for post-Palaeozoic extinction events, most notably the Cretaceous-

32   Paleogene (K-Pg) and Eocene-Oligocene events, based on patterns of drilling predation in

33   molluscan prey from the US Coastal Plain (Hansen and Kelley, 1995; Hansen et al. 1999;

34   Hansen et al 2004; Kelley and Hansen, 1993, 1996a,b, 2006; Kelley et al., 2001; Reinhold and

35   Kelley, 2005). These studies show a series of escalation cycles from the Cretaceous onwards

36   punctuated by significantly higher frequencies of drilling after mass extinction events. These

37   authors follow Vermeij (1987) in proposing that an increase in the frequency of drilling

38   predation in recovery faunas is due to the selective removal of escalated prey taxa, but

39   supporting evidence for this hypothesis, as expressed by prey morphology, is limited

40   (Hansen *et al.*, 1999; Reinhold and Kelley, 2005). In addition, specific studies of the metrics

41   of prey effectiveness have not supported the notion that predators were more successful in

42   the immediate aftermath of extinction events (Kelley et al., 2001; 2006).

43   Mallick et al. (2014, p. 227) suggest that the effects of mass extinction on the

44   dynamics of drilling predation 'should be global'.   However, this seems unlikely to be true.

45   Mass extinctions are widespread phenomena to which there are local responses. The US

46   Coastal Plain faunas are relatively low latitude, mixed carbonate - clastic shelf communities,

47   which were sited in close proximity to the Chicxulub impact site, the postulated cause of the

48   K-Pg event (Schulte et al., 2010). There have been few other detailed studies which have

49   attempted to test the effects of mass extinction at different sites, although two recent

50   papers examine drilling predation associated with the K-Pg event in India (Mallick et al.,

51   2013; Mallick et al., 2014), another low latitude, subtropical site in close proximity to the

52   Deccan Traps, which is another possible extinction trigger (Keller, 2005). These studies

53   demonstrated high frequencies of drilling predation in turritellid prey below the boundary

54   but found no evidence of any drill holes in the relatively small sample from the sparse fauna

55   above it, although it seems unclear what the significance of the latter is.

56   Not all regions exhibited similar levels of extinctions in the wake of the K-Pg event,

57   with higher latitudes apparently least affected (Zinsmeister et al., 1989; Keller, 1993; Raup

58   and Jablonski, 1993). It is possible that environmental variation associated with a strongly

59   seasonal climate may have less influence at higher latitudes, where more generalist faunas

60   prevail (Alegret et al., 2012). Additionally, following the meteorite impact or Deccan

61   volcanism hypotheses, the effects of such an event are likely to be more significant closest

62   to the site of impact/eruption (Raup and Jablonski, 1993; Schulte et al., 2010). It is also

63   evident that patterns of predator-prey interactions are naturally highly variable on both

64   temporal and spatial scales in both modern (Schmidt, 1989; Cadée et al., 1997; Harper and

65   Peck 2016) and fossil faunas (Hansen and Kelley, 1995; Harries and Schopf, 2007). Clearly,

66   additional studies are needed which investigate a broader range of environments and

67   palaeolatitudes in order for us to capture a full sense of the variability between sites and so

68   to fully unravel the role of mass extinction events in predator- prey relationships.

69   Recognising and measuring the activities of predators from the fossil record is highly

70   problematic (Bromley, 1981; Harper, 2016). However, predators, such as gastropods or

71   octopods, which leave sharp-sided circular drill holes provide less ambiguous and more

72   preservable evidence of their activities than do many other predators, and offer the

73   opportunity to examine frequency, success and prey selectivity (Kelley and Hansen, 2003;

74   Harper, 2003). As such they have been a key method of assessing various predation-based

75   hypotheses (Leighton and Aronowsky, 2003; Huntley and Kowalewski, 2007; Klompmaker et

76   al., 2017).   In this paper we investigate drilling predation on a range of molluscan and

77   serpulid worm prey over the K-Pg boundary at a high palaeolatitude (~65˚S) site on Seymour

78   Island near the northern end of the Antarctic Peninsula. Our aim is to survey a variety of

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79   prey taxa, consider possible culprits, and use various analyses of the drill holes themselves

80   to test the following hypotheses based on the predctions of Vermeij (1987, 1995) and Kelley

81   *et al.* (2001):

82   -   Prey effectiveness decreases after mass extinction events as indicated by a decrease

83   in both incomplete drill holes and multiply drilled individuals.

84   -   Predators become less selective after mass extinction as evidenced by reduced

85   stereotyped handling patterns and poor size selectivity

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87   **2. Geological setting**
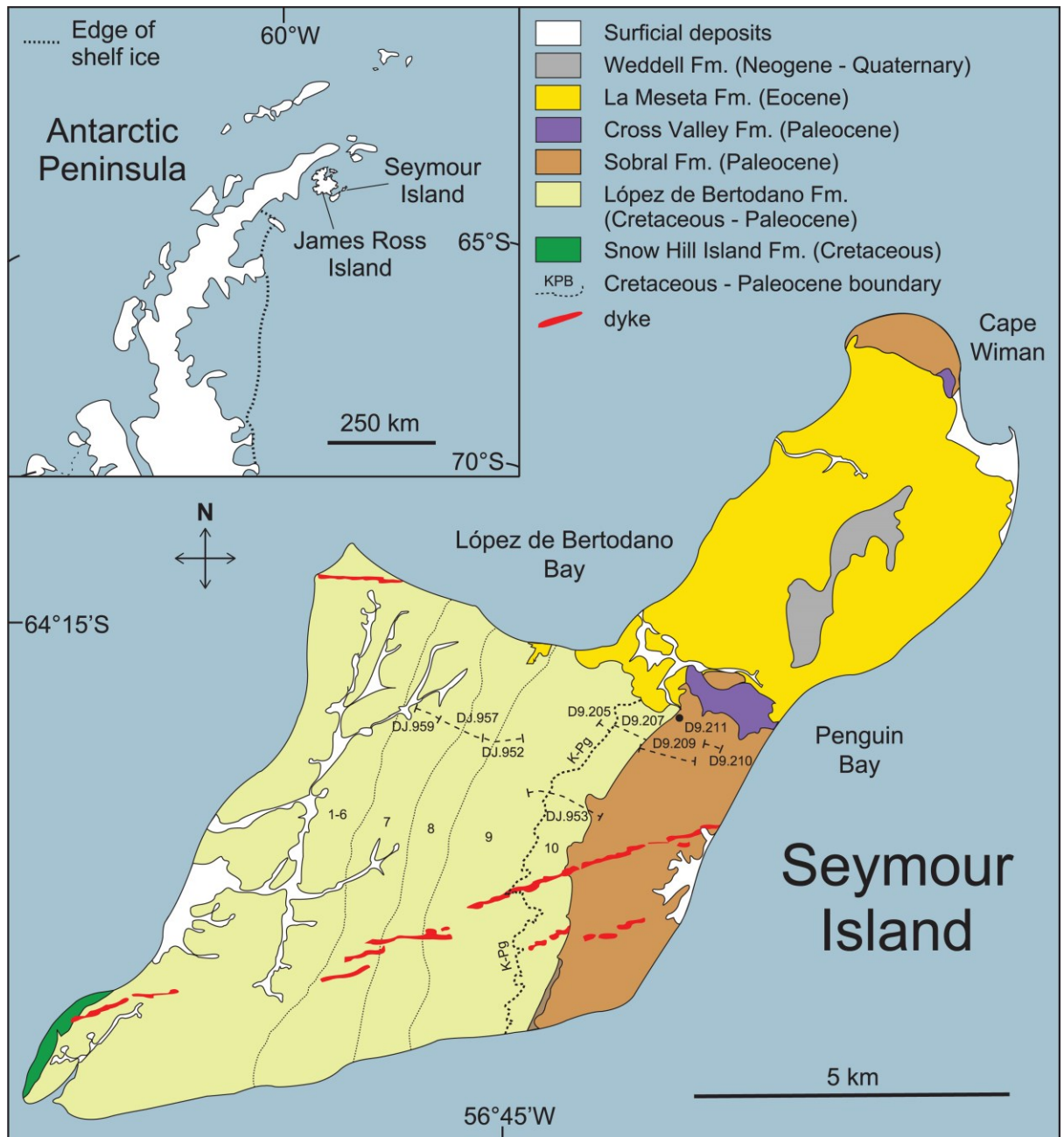
Fig. 1. Geological and locality map for Seymour Island, north-eastern Antarctic Peninsula. Key section lines are marked, together with localities that are prefixed by the letters "D" or "DJ". Also shown are the main informal lithostratigraphical divisions for the López de Bertodano Formation. 1-9 refer to units Klb 1-9 within the Cretaceous López de Bertodano Formation and 10 to unit Kplb 10 above the K-Pg boundary.   Based on Crame et al. (2014, fig. 1), with minor modifications

The Seymour Island K–Pg sedimentary succession is part of an extensive back-arc

basin exposed on the north-eastern flank of the Antarctic Peninsula (Hathway, 2000) (Fig. 1).

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98   In the central and southern parts of the island, a 950m-thick sequence of uppermost

99   Cretaceous (Maastrichtian) silty mudstones, siltstones, and fine- to coarse-grained

100   sandstones dips gently eastwards beneath a 300m-thick sequence of very similar Paleocene

101   lithologies (Sadler, 1988; Montes et al., 2010; Bowman et al., 2012). As it has so far proved

102   impossible to subdivide the Maastrichtian succession into meaningful lithostratigraphic

103   units, we have retained the use of the informal mapping divisions proposed by Sadler

104   (1988). The most fossiliferous intervals occur in units Klb 7-9, i.e. approximately the

105   uppermost 500 m of Maastrichtian sediments, where there is a rich ammonite – bivalve

106   assemblage, together with other macrofossil taxa such as gastropods, echinoids, decapod

107   crustaceans and serpulid worms (Fig. 1) (Macellari, 1988; Zinsmeister et al., 1989; Feldman

108   et al., 1993; Zinsmeister, 2001; Olivero, 2012). The Maastrichtian stratigraphy of Antarctica

109   is definitively defined in Crame et al. (2004) and detailed stratigraphic columns for the K –

110   Pg succession are shown in Crame et al. (2004), Bowman et al. (2014), Kemp et al. (2014)

111   and Witts et al. (2015, 2016), including the locality information and assignment to

112   biostratigraphic zone for the samples used in the current study (Crame et al. 2004; Figures 2

113   and 4).

114   The base of section DJ. 959 occurs in the lower levels of unit Klb 7, approximately

115   450m beneath the K–Pg boundary. It is marked by the sudden incoming of the ammonites

116   *Kitchinites darwini* and *Grossouvrites gemmatus*, together with a prolific benthic

117   macrofauna (Crame et al., 2004). The boundary between units Klb 7 and Klb 8 is transitional

118   but at a level of approximately 200m beneath the K–Pg boundary the base of Klb 9 is

119   marked by the sudden appearance of medium – large pachydiscid ammonites attributable

120   to *Pachydiscus riccardi* and *Pachydiscus ultimus.* These two species have been referred to an

121   informal *P. riccardi – P. ultimus* horizon (or zone) which overlies a *Pachydiscus ootacodensis*

122   horizon (Olivero and Medina, 2000; Crame et al., 2004). Locality DJ. 957 is equivalent to the

123   upper levels of Klb 7 and the greater part of Klb 8; DJ. 952 is equivalent to most of Klb 9, but

124   the uppermost levels, including the K – Pg boundary, are included in DJ. 953, which extends

125   into the basal Paleocene Sobral Formation (Fig. 1).

126   The K–Pg boundary occurs at the junction between units Klb 9 and Kplb 10 and is

127   marked by a prominent 5-6 m scarp of greenish-weathering glauconitic sandstones that can

128   be traced for some 7 km across the island. At the crest of the scarp is a 1 m-thick, sharp-

129   based concretionary glauconite that is equivalent to Zinsmeister's (1998) Lower Glauconite;

130   it is the base of this bed that corresponds to the last ammonite occurrence and a small

131   Iridium anomaly (Elliot *et al*., 1994), and is here taken as the K – Pg boundary (Fig. 1).

132   Directly above the Lower Glauconite is a 2-3 m sequence of yellowish to tan-weathering

133   siltstones and fine sandstones devoid of any obvious macrofossils apart from scattered fish

134   fragments, including various aggregations of scales, bones and teeth. This is the so-called

135   fish-kill horizon and is directly overlaid by a second prominent glauconitic sandstone

136   identified as the Upper Glauconite (Zinsmeister, 1998). Detailed macrofossil investigations

137   across the K–Pg boundary indicate species level extinctions in the region of 60% and genus

138   levels of 30 – 40% (Witts et al., 2015, 2016). Such levels are similar to those seen at much

139   lower latitudes and attest to a rapid and severe global extinction event.

140   Directly overlying the Upper Glauconite there is a subtle change in lithologies to

141   massive grey – brown mudstones and muddy siltstones containing numerous small

142   concretions. But what is even more striking is the change in benthic faunas. Serpulid worm

143   tubes and cidaroid spines, both abundant throughout the latest Maastrichtian, are

completely absent and the molluscan macrofauna is dominated by a small number of

extremely abundant species; the shallow-burrowing bivalves *Lahillia larseni* and *Cucullaea*

ellioti, and epifaunal gastropod, *Struthiochenopus hurleyi,* are particularly abundant (Crame

et al., 2004; Stilwell et al., 2004). These appear to be opportunist species in the wake of the

mass extinction, and this 55 – 60 m thick interval (unit Kplb 10 of the López de Bertodano

Formation) is referred to informally as the "recovery interval" (localities DJ. 953 and D9.

207, Fig. 1).

A low-angle but distinct unconformity separates the top of unit Kplb 10 from the base of

the overlying Sobral Formation (Fig. 1). The latter comprises approximately 300 m of

mudstones, silty mudstones and sandstones with a characteristic greenish weathering tinge

(localities D9. 209 and D9. 210, Fig. 1). Macrofossils reoccur in some abundance at the 48 –

120 m level in the Sobral Formation and are dated as earliest Danian (i.e. ~65 Ma; Bowman

et al., 2012, 2016). Thereafter the relative scarcity of macrofossils is related to a marked

change in sedimentary facies, with a distinctive set of sandstones between 185 – 230 m

showing the characteristic features of tidal sandbars. A sparse macrofauna from the very

highest levels of the Sobral Formation is dated as Danian – Selandian boundary (i.e. ~61 Ma;

Montes et al. 2010; Bowman et al., 2016)**.**

3. Materials and methods

This study used specimens that were collected over three field seasons by BAS staff

and their collaborators in a comprehensive programme to investigate the biostratigraphy

and palaeoecology of the Antarctic K-Pg sections on Seymour Island. The sampling strategy

is as given in Witts et al. (2016). In brief, very detailed macrofossil collections were made up

the various stratigraphic sections. In practice this involved the use of some 377 individual

167   sampling stations where work continued at each one until a representative collection, i.e.

168   when all the obvious macrofossil types had been obtained. Stratigraphic sections across

169   Seymour Island were correlated using a variety of palaeontological and lithological criteria

170   (Crame et al., 2004; Bowman et al., 2012, 2016; Witts et al., 2015, 2016).

171   Accurate taxonomic identifications were made in the laboratories of the British Antarctic

172   Survey, Cambridge (BAS) and the University of Leeds (UK), and further material was

173   examined in the Zinsmeister Collection housed at Paleontological Research Institute (Ithaca,

174   USA) (Zinsmeister and Macellari 1988; Stillwell et al. 2004). Crame et al. (2014) provided a

175   detailed discussion of taxonomic affinities. As the field collections were made for a different

176   set of studies (Bowman et al. (2014), Kemp et al. (2014) and Witts et al. (2015, 2016)) with

177   different aims, specimens were collected without bias with regard of drill holes.

178   All molluscan specimens in the three repositories were screened for predatory drill holes

179   (around 8,000 specimens), and at BAS and Leeds all serpulid worms were also included

180   (around 2,500 individuals). In practice most of these specimens had been cleaned previously

181   and were largely free of matrix.   Each specimen was examined carefully, using a

182   stereomicroscope as required. Predatory drill holes were recognized using the criteria

183   developed by Baumiller (1990), though relaxing the need for evidence of stereotypic

184   positioning (Harper, 2003). All measurements were made with vernier calipers. In view of

185   the large sample size and the fact that we had chosen not to calculate drilling frequency

186   (see Discussion) we did not record data for undrilled specimens. For each drilled individual

187   specimen the following information was recorded: taxon, size of the prey (to the nearest 0.1

188   mm) according to taxon dependent parameters (length or height for bivalves as appropriate,

189   length for gastropods and width for serpulids) and, for bivalves, the state of articulation, and

190   the number of drill holes present. A conservative approach was adopted such that doubtful

191   drill holes, which may have been genuine but altered by taphonomic processes, were

192   discounted from the analysis. For each drill hole, outer diameter (measured to the nearest

193   0.01 mm), shape and positioning were recorded and an assessment made as to whether

194   they were complete (i.e., penetrate the full thickness of the shell) or incomplete (i.e.,

195   terminating within the thickness of the shell rather than fully peforating it). Following the

196   objection laid out by Harper (1994), no attempt was made to distinguish between functional

197   and non-functional drill holes using the ratio of outer and inner diameters as advocated by

198   Kitchell et al. (1986). Drill hole positioning was plotted on a master diagram for each prey

199   taxon using the centre of the hole. For bivalves, holes were recorded as penetrating either

200   left or right valves and also which of four approximately equal area sectors on each valve

201   (dividing each valve into posterior and anterior sections, each themselves divided into

202   dorsal and ventral areas). Similarly, drill hole positioning on gastropod prey was recorded as

203   either dorsal or ventral, with note made of the position of perforation relative to the

204   aperture, and also position along the spire, while those on serpulid worms were recorded as

205   puncturing one of 8 even area radial sectors relative to the aperture and also dorsal or

206   ventral halves. The coiled nature of both gastropods and serpulids gives a measure of

207   uncertainty in spatial analysis where the aperture is damaged and also where an incomplete

208   drill hole's relative position may have changed markedly if it significantly pre-dated the

209   death of the prey. All spatial analyses were assessed by chi- squared test, and null

210   hypotheses which predicted random siting of drill holes leading to equal distribution over all

211   sectors.

212   Relative values of prey defence were calculated using the Prey Effectiveness (PE) metric

213   proposed by Vermeij (1987), defined as the number of incomplete drill holes in a sample

214   divided by the total number of drill holes present. Where it was not possible to determine

215   whether the hole was complete or not (because they were filled with indurated sediment),

216   these specimens were not included. PE was calculated for individual species in instances

217   where the number of holes exceeded 10. We also calculated an index for multiple drill holes

218   used by Kelley and Hansen (1993) and subsequently defined as MULT by Kelley et al. (2001)

219   as a complementary measure of prey effectiveness. MULT is determined by the number of

220   holes in multiply drilled specimens divided by the total number of attempted drill holes in a

221   particular taxon. It is difficult to make meaningful estimates of MULT for bivalve taxa where

222   there is a tendency for valves to be disarticulated. Nevertheless, most *Lahillia* and arcoids

223   were articulated and the tendency for drilling left valves of oysters makes some estimates

224   feasible from the material available. Additionally for each multiple-drilled individual we

225   tabulated the complete/incomplete status of each hole within the multiple set.

226   Data were split into four consecutive time intervals. Below the K-Pg event we used the

227   ammonite zones recognised by Crame et al. (2004) namely, the *ootacodensis* Zone

228   (equivalent to Klb 7 and 8) and the *ultimus/riccardi* Zones (Klb 9), to divide the top part of

229   the López de Bertodano Formation. Above the boundary data were split between unit Kplb

230   10 (the recovery interval), and the succeeding Sobral Formation. Where data permitted we

231   tested for differences between the four identified intervals but where insufficient we

232   amalgamated the *ootacodensis* and *ultimus/riccardi* Zones (i.e. Klb 7-9) to provide a single

233   pre-extinction dataset.

234   **4. Results**

In total we recorded 759 drill holes in a range of molluscan and serpulid worm prey taxa (Fig. 2) and distributed throughout the sequence. A summary of these data is presented in Table 1. As discussed in Section 5.4, we chose not to calculate drilling frequencies for the molluscan prey taxa because of the nature of the samples available. These data were available for the serpulid taxa where the frequencies of individuals with at least one drill hole were 5.7% (N = 1663 individuals) and 6.6% (N=786 individuals) for Klb 7 and 8 and Klb 9 respectively.
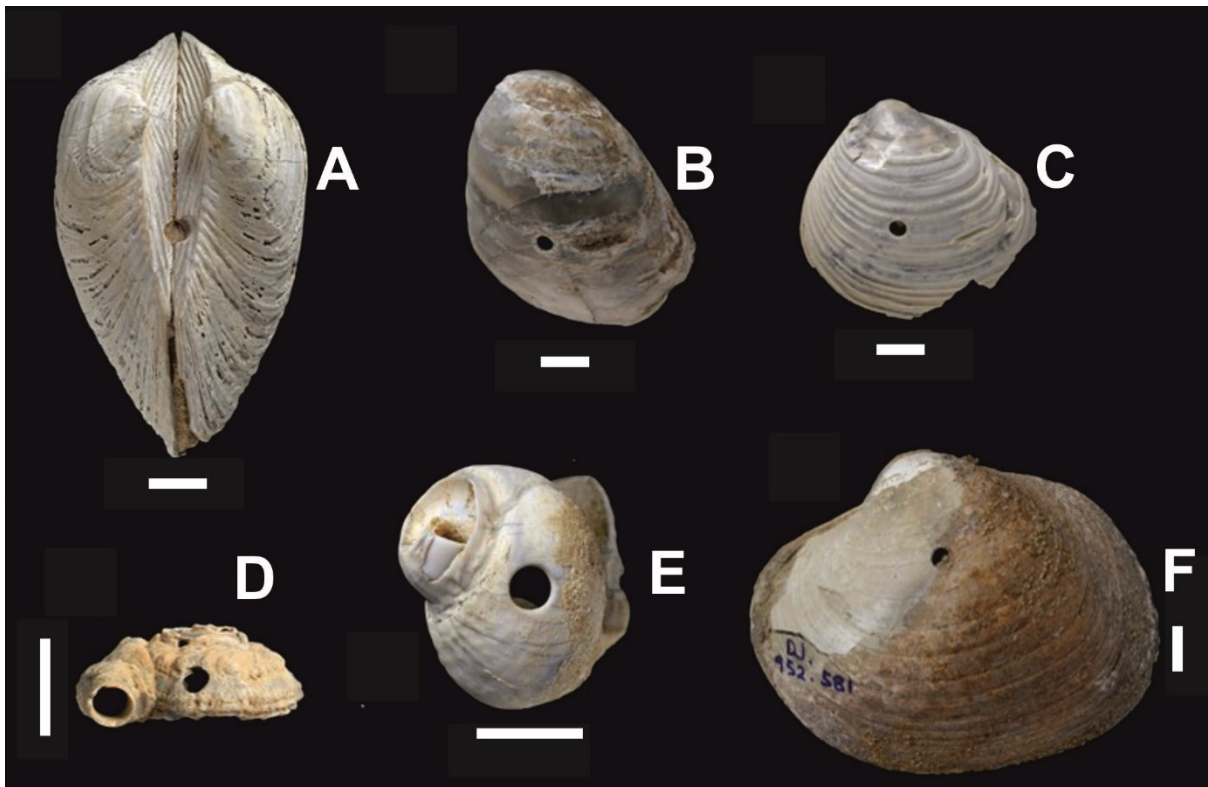
Fig. 2. Examples of drilled prey. A, *Cucullaea antarctica* (DJ.959.141, Klb 7 and 8); B. *Pycnodonte vesicularis* (DJ.953.627, Klb 9); C. *Eselaevitrigonia regina* (DJ.957.365, Klb 8); D. *Rotularia* sp. (DJ.952. A2, Klb 9); E. *"Vanikoropsis" arktowskiana* (DJ.951.28, Klb 8) and F, *Lahillia larseni* (DJ.952.581, Klb 9). All scale bars represent 10 mm. All specimens in BAS Collections, Cambridge UK.

249 **Table 1.** Incidence of drill holes in molluscan and serpulid prey.

Prey	Number of drill holes	Number of failed drill holes	Prey Effectiveness^	Range of drill hole diameters (mm)	Number of multiply drilled individuas [MULT]†
Sobral Fm					
Gastropods *Struthiochenopus nordenskjoldi /hurleyi**	25	5	0.200	0.71-4.13	5 (11) [0.44]
"Vanikoropsis" arktowskiana	4	0	-	1.10-2.77	1 (2)
Bivalves *Cucullaea ellioti*	1	0	-	2.92	0
Pycnodonte seymourensis	7	5	-	1.79-4.68	2(6) [0.86]
Venerid indet.	3	0	-	2.14-3.15	0
Lahillia huberi	2	0	-	3.26-4.35	1 (2)
Saxolucina antarctipleura	2	0	-	0.96-1.04	0
Paleogene (UKplb 10) (López de Bertodano Fm)					
Gastropods *Struthiochenopus nordenskjoldi /hurleyi**	14	1	0.071	1.01-2.89	1(2) [0.143]
Bivalves *Cucullaea ellioti*	3	2	-	2.46-2.91	0
Lahillia larseni	27	4	0.148	2.09-4.98	5 (10) [0.370]
Serpulids *Rotularia (Austrorotularia) sp.**	6	3	-	0.63-1.26	2(6) [1.00]
K-Pg boundary here					
Cretaceous (Klb 9)					
Amberleya spinigera	3	0	-	1.80-3.50	0

Austroaporrhais larseni	1	0	-	2.34	0
"Cassidaria" mirabilis	13	3	0.231	1.54-3.88	3(7) [0.539]
Cryptorhytis philippiana	3	0	-	2.57-2.76	1 (3) [1.000]
Heteroterma? sp.	2	0	-	1.47-2.78	0
Taioma charcotiana	7	0	-	2.35-4.68	0
"Vanikoropsis" arktowskiana	3	1	-	1.90-3.08	0
Bivalves *Cucullaea antarctica*	5	0	-	3.16-4.60	0
Pycnodonte vesicularis	115	55	0.478	1.13-5.54	17 (35) [0.304]
Eselaevitrigonia regina	34	13	0.382	1.92-5.78	1(2) [0.059]
Oistotrigonia pygoscelium	2	0	-	2.94-3.68	0
Lahillia larseni	30	4	0.133	2.29-5.61	3 (6) [0.200]
Annelids *Rotularia (A.)* sp.*	67	22	0.328	0.87-2.42	12(27) [0.403]
Klb 7 and 8					
Gastropods *Amberleya spinigera*	14	1	0.071	0.91-6.03	3 (7) [0.500]
Austroaporrhais larseni	2	0	-	2.26-3.08	0
"Cassidaria" mirabilis	32	10	0.313	1.06-4.00	6(12) [0.375]
Struthiochenopus hurleyi	2	0	0	1.05-1.65	1(2) [0.500]
Taioma charcotiana	10	1	0.100	1.77-4.82	3(6) [0.600]
"Vanikoropsis" arktowskiana	16	1	0.063	1.58-4.27	0 [0.00]
Perissoptera nordenskjoldi	4	0	0	1.05-2.88	0 [0.000]
Cryptorhytis philippiana	5	1		1.26-3.61	0
Bivalves *Nucula suboblonga*	3	0	-	3.80-3.96	0
Nodenskjoldia nordenskjoldi	14	2	0.143	2.69-4.57	1(2) [0.143]

Cucullaea antarctica	31	6	0.194	1.67-5.78	2(4) [0.129]
Pycnodonte vesicularis	78	42	0.538	0.91-5.56	14 (35) [0.449]
Pulvinites antarcticus	1	0			
Eselaevitrigonia regina	31	11	0.355	1.88-6.41	3(7) [0.226]
Oistotrigonia pygoscelium	15	7	0.467	0.47-2.87	0 [0.000]
Dozyia drygalskiana	10	0	0.000	1.61-3.45	0 [0.000]
Lahillia larseni	2	0	-	3.17-4.42	0
Surobula nucleus	1	0	-	1.00	0
Serpulids *Rotularia (A.)* sp.*	109	19	0.174	0.62-3.80	1.0 11(26) [0.239]

250

251   ^Prey Effectiveness (defined as the number of incomplete drill holes divided by the total number of

252   drill holes observed in any sample) is calculated for all taxa where there were 10 or more drill holes;

253   † MULT defined as number of holes in multiply drilled specimens over total number of attempted

254   drill holes- = insufficient data; * data for *Struthiochenopus nordenskjoldi* and *S. hurleyi* are pooled

255   and although Macellari (1984) recognises 5 different species of *Rotularia (Austrorotularia)* from

256   Seymour Island, they are pooled herein.

257

258   *4.1 Drill hole characteristics*

259   Unaltered drill holes were circular in plan view with sharp outer edges. There was a

260   continuous range of diameters, from 0.62 to 6.41 mm, across the interval studied. Most

261   drill holes were straight-sided but a few, most notably those on curved shells such as the

262   smaller tubes of *Rotularia,* were more countersunk (i.e., holes with a bevelled edges).

263   Incomplete holes had flat bases. All holes recorded were through shell or tube walls and

264   none of the bivalves attacked were 'edged drilled' (i.e., drilled at the commissure between

265   the valves) in the manner described by Vermeij (1980). None of the drill holes observed

266 showed signs of having been drilled from the internal surface of the shell or tube (and thus

267 obviously post-mortem). There were no obvious changes in drill hole characteristics over

268 the K-Pg boundary.

269 *4.2 Prey selection*

270   A total of 24 taxa (15 species of bivalves, 8 species of gastropods and 1 genus of

271 serpulid worm) were found to be perforated by at least one drill hole (either complete or

272 incomplete) over the whole study period (Table 1). Some taxa which are well represented in

273 the collections (e.g. the bivalves *Pinna, Seymourtula, Leionucula, Entolium,* and *Panopea,*

274 and gastropods such as *Leptomaria* and *Mesalia*) were apparently not drilled.

275   Analysing the relative numbers of drill holes in different taxa over the four study

276 intervals reveals that for both the pre-extinction zones and the recovery interval the

277 majority of holes were recorded in bivalve prey. Prior to the extinction serpulid worms were

278 also a significant proportion of the prey but not after; only 17 individuals were found in Kplb

279 10 (only 2 individuals of which were drilled) and it is even possible that these were derived

280 from lower units. Although gastropods were taken in all study intervals, only in the Sobral

281 Formation were they the dominant prey type. The number and variety of these different

282 taxa also changes markedly across the study intervals, with high levels of pre-extinction,

283 with 19 species (8 gastropod, 10 bivalve and 1 serpulid) in Klb 7and 8 and 13 species (7

284 gastropod, 5 bivalve and 1 serpulid) in Klb 9, but much fewer in both Kplb 10 (total of 4

285 species, 1 gastropod, 2 bivalve and 1 serpulid) and the Sobral Formation (total of 7, 2

286 gastropod and 5 bivalve). Prey taxa may be grouped according to family in order to gain

287 some insight into patterns across the study period where although a single species does not

288 span the total interval it may belong to either a genus or family which is represented in the

17

289   driller's diet over longer durations. Table 2 provides the life habit details of these higher

290   taxa which have at least 10 drill holes in the entire data set, and account for >96% of the

291   total number of drill holes studied. The taxa are believed to be either largely infaunal or

292   semi-infaunal inhabitants of soft sediments, and suspension feeders.

293   **Table 2.** Inferred life habits for major prey items (based on functional morphology and

294   knowledge of modern taxa; mostly after Macellari (1988).

Prey type	Inferred life habit
Bivalvia	
Oysters *Pycnodonte vesicularis, P. seymourensis*	Cemented to small hard substrata (often conspecifics) by part of the left valve, probably at full size, being partly submerged in soft sediment. Frequently found in aggregations
Arcoids *Cucullaea ellioti, Cucullaea antarctica, Nordenskjoldia nordenskjoldi*	Very shallow non-siphonate burrowers, living with posterior margin more or less parallel to sediment/water interface (Morton, 1981)
Cardioids *Lahillia larseni, L. huberi*	Very shallow siphonate burrower – some evidence to suggest that posterior margin was exposed above the sediment – water interface
Trigoniids *Eselaevitrigonia regina, Oistotrigonia pygoscelium*	Very shallow non-siphonate burrowers. Modern trigoniids are rapid burrowers with 'leaping' escape response (Tevesz, 1975)
Dozyia drygalskiana	Medium-sized astartid; likely shallow-burrowing suspension feeder
Gastropoda	
Aporrhaids: *Struthiochenopus nordenskjoldi* and *hurleyi, Austroapporhais larseni, Perissoptera*	Modern aporrhaids are sluggish grazers that live at least part of the year infaunally (Yonge, 1937; Perron, 1978)
Probable neogastropod *"Cassidaria" mirabilis*	Most likely an active predator (see Crame et al., 2014)
Probable neogastropod: *Taioma charcotianus*	Most likely an active predator (see Crame et al., 2014)
Amberleya spinigera	Likely epifaunal grazer
"Vanikoropsis" arktowskiana	Considered to be a soft-substrate burrower and inferred to be a drilling predator (Crame et al., 2014)
Serpulids	
Rotularia spp.	Juveniles attached to small hard substrata but there are conflicting suggestions that the adult may have been infaunal (Macellari, 1984) or epifaunal, reclining on a soft bottom (Savazzi, 1995)

295

296   *4.3 Incomplete drill holes and Prey Effectiveness*

297   Incomplete drill holes occurred throughout the section and were more common in

298   some prey taxa than others. For those taxa for which there were sufficient data to calculate

299   the Prey Effectiveness (PE) metric (Table 1), values ranged from 0.00 in the astartid *Dozyia*

300   *drygalskiana* in Klb 7 and 8 to 0.538 for the oyster *Pycnodonte vesicularis* from the same

301   interval. All failed drill holes recorded resulted from incomplete penetration; none were

302   observed to have been complete but repaired by subsequent shell deposition by a still living

303   prey as illustrated by Dietl (2000).

304   There were sufficient data for comparison of the diameter of complete and

305   incomplete drill holes within a particular taxon and time interval in 11 instances. In each of

306   these the mean diameter of incomplete drill holes was smaller than that of those that were

307   complete (Table 3). With a null hypothesis that the mean diameter of complete and

308   incomplete drillholes is equal, applying a one-tailed binomial test, the probability of

309   incomplete drill holes being smaller in 11 samples would be (0.5)11 or 0.0005.

310   **Table 3.** Comparison of the mean diameters of complete and incomplete holes

Unit	Prey Taxon	Mean diameter of Complete drill holes (mm) [N]	Mean diameter of Incomplete drill holes (mm) [N]
Sobral	*Struthiochenopus* spp	2.18 [20]	2.09[6]
Kplb 10	*Lahillia larseni*	3.50[21]	3.37[4]
Klb 9	*Lahillia larseni*	3.60[26]	3.12[5]

	Eselaevitrigonia regina	3.30[21]	3.05[13]
	Pycnodonte vesicularis	3.67[38]	2.85[34]
	Rotularia spp.	1.64[42]	1.46[25]
Klb 7 and 8	*Eselaevitrigonia regina*	3.67[20]	3.01[10]
	"Cassidaria" mirabilis	2.57[19]	1.89[10]
	Cucullaea antarctica	3.70[23]	2.86[6]
	Pycnodonte vesicularis	2.84[37]	2.50[42]
	Rotularia spp.	1.76[89]	1.50[19]

311   *Lahillia larseni* is the only taxon for which there were sufficient data to test whether

312   there was a change in PE over the K-Pg boundary. The PE is higher in the recovery interval

313   fauna, i.e. Kplb 10, (0.148) than in the pre-extinction beds (0.133) but this increase is not

314   statistically significant (p = 0.53 by chi –squared test). The aporrhaid, *Struthiochenopus* spp

315   was the only taxon for which there was a statistically significant change in PE between any

316   of the study intervals and with an increase between the Kplb 10 (PE = (0.071) and the Sobral

317   Formation (PE = 0.200) (p= 0.02 by Chi-squared).

318   *4.4 Multiple drill holes (MULT)*

319   Multiple drill holes (MULT) were recorded in a number of taxa across all the studied

320   stratigraphic intervals (Table 1). Although both MULT and PE may be seen as measures of

321   prey defence against a drilling predator, the two are not correlated in our data (p=0.744).

322   The only taxon/stratigraphic intervals for which there were more than 10 drill holes and a

323   MULT of zero were recorded for *Dozyia, Oistotrigonia* and *"Vanikoropsis" arktowskiana* (all

324   units Klb 7 and 8). MULT values of higher than 0.2 were recorded in the bivalves *Lahillia*

325   (units Klb 9 and Kplb 10)*, Eselaevitrigonia* (units Klb 7 and 8) and *Pycnodonte* (units Klb 7

326   and 8 and Klb 9, and Sobral Fm)*, the gastropods *Struthiochenopus* (Sobral Fm)*, "Cassidaria"*

327   (units Klb 7 and 8 and 9), *Amberleya* (units Klb 7 and 8) and *Taioma* (units Klb 7 and 8) and

328   also for serpulids in units Klb 7 and 8 and 9. MULT is generally high for molluscan taxa and

329   serpulids from unit Klb 9.

330   As with PE, *Lahillia larseni* was the only taxon with sufficient data for which it was

331   possible to investigate for differences in MULT on either side of the K-Pg boundary. In this

332   instance there was significant increase in the metric above the boundary (3% by chi-squared

333   test). There was also a significant increase in MULT between Unit 10 and Sobral in the

334   aporrhaid *Struthiochenopus* spp data (p = 0.01 by chi-squared test).

335   Most multiply drilled individuals had two holes, but three was not uncommon in

336   some individuals of *Pycnodonte* and a single individual had four. Most of the multiple holes

337   in the oysters were all in the left valve. For most taxa and individuals with multiple

338   attempts there was at least one incomplete one and in most of these instances the two or

339   more holes were of notably different diameter. There were, however, a number of

340   instances where a prey item was penetrated by more than one complete hole. This was

341   particularly common in *Struthiochenopus* where six out of eight multiply drilled individuals

342 (amalgamated from all stratigraphic intervals) had more than one complete hole, though it

343 was also frequent in the oyster *Pycnodonte.*

344 *4.5 Drill hole positioning and site selection*

345 As might be anticipated for equivalve orthothetic bivalves such as *Lahillia,* arcoids

346 and trigoniids, there were no statistically significant differences between numbers of drill

347 holes in right and left valves (chi-squared test - p >0.05 in all cases). However, for the

348 markedly inequivalve and pleurothetic oysters, there was a clear preference for drilling the

349 'lower' left valve (chi-squared test - p<0.001) in all units. The position of drill holes on most

350 bivalve taxa was not random. For *Lahillia larseni, Eselaevitrigonia regina* and all of the

351 arcoids there were statistically significant preferences for drilling the posterior dorsal sector

352 of the shell (chi-squared test - p<0.001 in all cases). Moreover, for the arcoids *Cucullaea*

353 *antarctica* and *Nordenskjoldia nordenskjoldi* there was a preference for drilling through the

354 ligament platform, often at the join between the two valves (Fig. 2A). Additionally, there

355 was a marked tendency for drilling the central region of oyster valves (chi-squared test -

356 p<0.0001 at all stratigraphic levels), though with no particular preference for the adductor

357 muscle scar itself.

358 Most drill holes in gastropod prey were placed in the most recently formed whorl

359 but with no clear sign of consistent placing in relationship to the aperture (although such a

360 pattern may be obscured by frequent damage to that region making aperture position hard

361 to establish for a complete animal). For the serpulid, *Rotularia,* drill holes were recorded in

362 all analysed sectors but there was a pronounced preference for drilling in that adjacent to

363 the aperture (chi-squared test- *p*<0.001) (Fig. 2D), but no statistically significant preference

364 between dorsal and ventral surfaces for each segment (chi-squared test - p>0.05).

365   *4.6 Drill hole size analysis*

366   The range of drill hole sizes recorded in individual prey type and stratigraphic units

367   are shown in Table 1. A 2-tailed Student's T test was used to compare the sizes of drill holes

368   in each time interval. Although the mean size of holes in the Sobral Formation (2.37 mm) is

369   significantly smaller ($p < 0.003$ in all instances) than those in all the other units, and the mean

370   size of those in Klb 7 and 8 (2.78 mm) is smaller than those in unit Klb 9 (3.25 mm)

371   ($p < 0.001$), the range of drill hole sizes in all units is similar. The minimum and maximum

372   diameters recorded in each unit is less than 0.9 mm and greater than 4.6 mm.

373   In order to explore whether there was any indication of size selection within a prey

374   taxon we examined the relationship between drill hole diameter and prey size   (length for

375   bivalves, height for gastropods and width of serpulids) in taxa for which there were

376   sufficient data (note that not all specimens were complete enough to measure prey size).

377   Because we had found that incomplete drill holes were frequently significantly smaller than

378   complete ones (see above), we restricted our analysis to complete holes. Firstly we

379   investigated data within the two Cretaceous intervals (Klb 7 and 8 and Klb 9). There was a

380   significant positive correlation between drill hole and individual prey size for only the unit

381   Klb 9 *Pycnodonte* (one tailed test, $p = 0.001$) and units Klb 7 and 8 *Rotularia* (one tailed test,

382    $p < 0.001$). There was insufficient data to test this relationship for *"Vanikoropsis"* in separate

383   time bins, but an amalgamation of the Cretaceous data revealed a positive correlation (one

384   tailed test, $p = 0.041$). Perhaps most surprising, there was a negative correlation for prey size

385   and drill hole diameter in *Nordenskjoldia nordenskjoldi* from units Klb 7 and 8 (one tailed

386   test, $p = 0.02$), although the sample size was low ($n = 10$ complete drill holes).

387   The size range of drilled individuals for each prey taxon was rather narrow. Because

388   of the size of the task and the incompleteness of many specimens no attempt was made to

389   measure the size of undrilled molluscan prey, but for *Rotularia* the mean sizes of drilled

390   individuals (19.1 mm, n = 146) was significantly larger than for undrilled (17.7 mm; n=2353)

391   (Mann-Whitney U test *p*<0.01). It is striking that *Rotularia* was a relatively small prey item

392   and was penetrated by drill holes at the lower end of the range of diameters recorded

393   across the study. These facts suggest an alternative way to explore the issue of prey size

394   selection by ranking prey. Although it is difficult to rank extinct prey in terms of their flesh

395   yield, a simplified approach of plotting the size of all prey items (length for bivalves, height

396   for gastropods and width for worms) against drill hole diameter within the four stratigraphic

397   intervals reveals for each of them that there is a significant positive relationship (Table 4).

398

399   **Table 4.** Correlation coefficients and significance levels for diameter of complete drill holes
400   vs largest dimension of each prey item in each of the stratigraphic intervals.

Stratigraphic Interval	N	r^2	p
Sobral Formation	26	0.3598	<0.001
Unit Kplb 10 –	31	0.2339	<0.0059
K-Pg Boundary			
Unit Klb 9	139	0.0385	<0.0001
Units Klb 7 and 8	179	0.0786	<0.00014

401

402   **5.   Discussion**

403   The highly distinctive trace fossils reported here are good evidence that predatory

404   drilling was not an uncommon fate for both shelly molluscs and serpulid worms in Antarctic

405   shallow water marine communities during both the end-Cretaceous and in the immediate

406   aftermath of the K-Pg mass extinction. As we have a comparatively large data set of some

407   759 drill holes effectively from a single site, they allow us to assess the impact of the K-Pg

408   event on the patterns of drilling predation in the immediate region and provide useful

409   comparison with previous studies of lower latitude localities over the same time interval.

410   *5.1 Likely driller*

411   It is a well known paradox that although the recognition of the predatory nature of

412   drill holes in both modern death assemblages and fossil material is relatively

413   uncontroversial, assigning a particular predatory taxon as responsible is highly equivocal

414   (Bromley, 1981). Several higher taxa, including a variety of gastropods, octopods,

415   nematodes and turbellarian worms, are known to drill holes in their shelly prey (Kabat,

416   1990; Kelley and Hansen, 2003). However, the drill holes described in this paper are

417   relatively large (diameters ranging from 0.62 to 6.41 mm), much bigger than those

418   associated to date with turbellarians, nematodes and most octopods (Carriker, 1981; Kabat,

419   1990; Todd and Harper, 2011) and penetrate sizeable prey. As such they conform well to the

420   expectations for those drilled by gastropods (Carriker, 1981; Bromley, 1981; Kabat, 1990).

421   The majority of victims of these drilling attacks were predominantly either sessile or

422   slow moving animals and mainly characterised as infaunal or semi-infaunal soft sediment

423   dwellers, mostly with suspension feeding life habits. Although most of the bivalves were

424   fully infaunal and there is a tendency for these to have been attacked at the posterior end

425   (i.e. closest to or even above the sea floor), nearly 25 % of all drill holes were in the

426   gryphaeid oysters, *Pycnodonte*. These oysters likely lived semi-submerged on their left

427   valves in the soft sediment and most holes were recorded on the 'lower' left valve which is

428   probably consistent with being attacked from underneath as noted by Dietl (2002) for

429   Paleocene congenerics from the USA. Together these observations point to a predominantly

430   shallow infaunal predator, perhaps capable of foraging at the surface as well.

431   The predominantly infaunal/semi-infaunal nature of prey, the handling preferences

432   and several (but not all) aspects of the drill hole morphology suggest a naticid gastropod

433   driller (Carriker, 1981; Bromley, 1981; Kabat, 1990). Other studies of drilling predation from

434   either Late Cretaceous or early Paleogene sediments show that the holes are coeval with

435   well accepted naticid records elsewhere in the world (e.g. Kelley and Hansen, 1993; Harries

436   and Schopf, 2007; Mallick et al., 2013). However, despite the abundance of the naticids,

437   *Amauropisis* and *Euspira* higher up the geological sequence in the Eocene La Meseta

438   Formation (Crame et al., 2014), and whose predatory drill holes have been recognised in a

439   range of shelly prey (Aronson et al., 2009), there are no records, despite extensive collection

440   efforts, of unequivocal naticids at the stratigraphic levels studied here. However, following

441   Crame et al. (2014) we consider that the only plausible gastropod culprit is *"Vanikoropsis"*

442   *arktowskiana.* This enigmatic taxon has an exact temporal coincidence with the drill holes

443   ranging from the base of the López de Bertodano Formation (to the top of the Sobral

444   Formation on Seymour Island, including the recovery unit (Crame et al., 2014).   Stilwell *et*

445   *al* (2004) referred this taxon to *Vanikoropsis* Meek, 1876 of the caenogastropod family

446   Vanikoridae. Crame et al. (2014), however, revert to the original placement by Wilckens

447   (1910), partly on the basis of co-occurrence with drill holes, to favouring a naticid affinity

448   and suggest that in the future the taxon should be placed in a new genus of the family

449   Naticidae. Although the drill holes presented here do not share some of the well-

450   documented characteristics of classic naticid holes, such as having a central raised boss

451   (rather than flat) on the floor of incomplete holes and many are not properly countersunk,

452   our findings here support this view. It should be noted that there are no muricid gastropods

453   (the other major clade of gastropods which drill molluscs albeit largely on hard substrates)

454   in the fauna.

455   *5.2 Changes in potential prey over the K-Pg*

456   Regardless of the exact identity of the predator, our data provide an opportunity to

457   examine patterns in predator-prey interactions across this major biotic event. If we are

458   correct in identifying a single drilling predator on both sides of the boundary our analysis is

459   strengthened because there is no mixed signal conflating the activities of different predators

460   with different preferences and behaviours (Casey et al., 2015).   We preface the following

461   remarks with our considered opinion that there is only one mass extinction horizon within

462   the latest Cretaceous – earliest Paleogene succession of Seymour Island. Although the

463   possibility of a double extinction has been suggested by statistical analyses (Tobin et al.,

464   2012; Tobin, 2017), we could find no evidence for it in the field nor when the confidence

465   intervals on the range data are considered. As stated in Witts et al. (2016), the topography

466   of the boundary interval in our study area is such that exposure varies greatly in the

467   uppermost Maastrichtian. The last really good exposure beneath the K – Pg is a dip-slope at

468   approximately -45m, and very large collections have now been made from this. Thereafter

469   exposure is largely scarp-face up to the K-Pg and collections from this level are much more

470   restricted. But confidence interval analysis indicates that many taxa recorded from the -45m

471   level would in fact extend up to the K- Pg and there is no marked pre-extinction in either

472   benthic or pelagic taxa (Witts et al., 2016). The actual K – Pg boundary is quite clearly

473   marked by a stratigraphic hiatus at the base of the lower glauconite which can be traced,

474   albeit intermittently, along the 7 km of strike.

475   Our data demonstrate a sharp reduction in prey diversity across the K–Pg boundary

476   in Antarctica. Recent studies have shown that when benthic molluscan taxa from the

477   topmost 50 m of Maastrichtian strata (i.e. topmost unit Klb 9) are compared with unit Kplb

478   10 then there is a species level extinction of approximately 60% across the K–Pg (Witts et

479   al., 2016). However, if a comparison is made using the whole of unit Klb 9 (33 benthic

480   molluscan species) and unit Kplb 10 (8 species) then the extinction level rises to 75%; the

481   inclusion of three range-through taxa reduces these figures to 56% and 67%, respectively.

482   Regardless of which level is cited, the important point to emphasise is that prey choice is

483   drastically reduced in Kplb 10 (the recovery interval). Of the eight benthic molluscan species

484   recorded directly from it only three, the bivalves *Lahillia larseni* and *Cucullaea ellioti*, and

485   gastropod *Struthiochenopus hurleyi*, can be described as abundant (Witts et al., 2016). The

486   serpulid *Rotularia* is also almost completely absent from this interval (Zinsmeister et al.,

487   1989; Stilwell et al., 2004; Witts et al., 2016).

488   Although a 60% or even greater level of extinction across the K–Pg boundary might

489   prove fatal for a single predator such as "*Vanikoropsis*" *arktowskiana*, it is important to

490   emphasise that three of those taxa that remain, i.e. *Lahillia larseni, Cucullaea ellioti* and

491   *Struthiochenopus hurleyi*, are extremely abundant in unit Kplb 10 (Witts et al., 2016) and it

492   may well be that opportunistic taxa play an important role in maintaining the volume of

493   prey source following a mass extinction event (Hansen et al., 2004).

494   It also has to be borne in mind that the K–Pg boundary is a time of significant change

495   in the overall composition of benthic marine faunas, with bivalve-dominated ones

496   throughout the latest Cretaceous giving way to gastropod-dominated ones in the earliest

497   Paleocene (Hansen, 1988; Sepkoski, 2002; Stilwell, 2003). This is a truly global phenomenon

498   that is due to the rise of benthic marine predators in general and predatory neogastropods

499   in particular. The Seymour Island sedimentary succession documents a very steep rise in the

500   number of neogastropod taxa between the K–Pg boundary and the Middle Eocene (Crame

501   et al., 2014).

502   It might be predicted that potential prey taxa that survive or flourish after mass

503   extinctions will be less well armoured, as evidenced by the expression of morphological

504   features such as shell thickness and ornamentation (Vermeij, 1994). Although we have not

505   collected specific data on these traits, there is no obvious evidence of such morphological

506   differences between the post and pre-extinction faunas of Seymour Island, in particular

507   when comparing congenerics or conspecifics which traverse the extinction. In this respect

508   our findings echo those of Hansen et al. (1999) in their study of US Coastal Plain molluscs.

509   *5.3 Actual prey choice*

510   Our evidence suggests that at each stratigraphic level examined the driller had a

511   catholic diet. It must be emphasised that the range of prey taken may have been even

512   broader if it included soft-bodied taxa that have not been preserved or taxa that were

513   subdued without drilling. Prey types across the study interval are broadly similar, i.e. slow

514   moving/sedentary taxa living in or on soft bottoms. The exact nature of the prey varies

515   depending on stratigraphic level and probably also reflects patchiness within the

516   environment. This is particularly so in the latest Maastrichtian units Klb 8 and 9 where taxa

517   such as *Rotularia* and *Pycnodonte* occur locally in high numbers (Macellari (1984, 1988).

518   Slow moving gastropod predators might be expected to be strongly influenced by such

519   patchiness rather than having an ability to hunt out favoured prey (Harper, 2016).

520   Only a few species survive over the entire study interval (e.g. *Lahillia larseni,*

521   *Pycnodonte vesicularis* and *"Vanikoropsis" arktowskiana)* but for only *L. larseni* are there

522   sufficient data to analyse patterns in drilling behaviour in a single prey taxon over the K-Pg

523   event. Some prominent prey taxa before the mass extinction either disappear regionally in

524   that event (e.g. trigoniid bivalves are restricted to Australasia only following the mass

525   extinction; Darragh, 1986), or reduce dramatically in number (serpulid worms). Both

526   trigoniids and serpulids are prominent in the pre-extinction prey lists. Although the mass

527   extinction removes certain species, in some cases they are replaced in unit Kplb 10 and

528   Sobral Formation by congenerics and confamilials. It is striking that although drilled

529   aporrhaid gastropods were present throughout the study period, they are a much greater

530   proportion of the total number of drill holes in the two intervals succeeding the mass

531   extinction. This would seem to be a direct consequence of the very low availability of shallow –

532   burrowing infaunal bivalves in these levels.

533   *5.4 Frequency of attack*

534   Although other studies have determined drilling frequencies across mass extinction

535   events (Kelley and Hansen, 1993; Kelley et al., 2006) we have chosen not to do so because

536   although the Seymour Island fossils are well preserved, they are frequently not whole and

537   they were not collected as bulk samples. Another complication of such measures is that

538   they ignore the differential effect that extinction itself might have had on taphonomy.

539   Vermeij et al. (1989) have persuasively pointed out that the co-occurrence of active crushing

540   predators at a site effectively removes undrilled dead individuals from any survey, thereby

541   inflating calculated drilling frequencies.   Major changes in either the crustacean or

542   vertebrate predator fauna at the K-Pg event may have significantly altered the proportions

543   of drilled and undrilled individuals in the fossil record. The Cretaceous sections of Seymour

544   Island yield frequent mosasaur material (Martin and Crame 2006) and it is not impossible

545   that for pre-extinction large molluscs (e.g. *Lahillia*) these would have been effective crushing

546   predators, thus perhaps over emphasizing the frequency of drill holes.   We did not

547   undertake a systematic survey of the collections for repaired breakage but noted that

548   repaired apertural breaks, similar to those seen in Allmon et al. (1990), indicate peeling

549   predation both pre- and post-extinction.

550   Recent evidence has suggested that the frequency of drilling predation by naticid

551   gastropods decreases with increasing latitude along the east coast of South America (Visaggi

552   and Kelley, 2015). Despite our lack of frequency data it is possible to demonstrate that at

553   this high latitude site (~ 65°S) predatory drilling appears to be not uncommon at this time,

554   as in the late Paleocene and Eocene (Aronson et al., 2009). Although the Neogene fossil

555   record of Antarctica is very incomplete, it is interesting to note that naticid genera such as

556   *Falsilunatia* and *Amauropsis* are relatively common in the Southern Ocean at the present

557   day (Dell, 1990).

558   *5.5 Patterns of prey handling*

559   Modern naticid species are known to be highly selective in terms of both prey size

560   and site of attack, which is prey taxon specific (Kitchell et al., 1981; Boggs et al., 1984).

561   These studies also demonstrate that drill hole diameter can be used as a proxy of predator

562   size.

563   Despite a varied diet, the Seymour Island driller showed consistent handling with

564   prey taxon-specific siting of drill holes in many instances. Much of the placement constancy

565   recorded here probably reflected the ease with which a shallow infaunal predator could

566   attack the prey, hence the preference for the posterior part of burrowing bivalves and the

567   underside of semi-infaunal oysters but stereotypic placement of drill holes also implies

568   familiarity of handling and drilling particular prey items. Interesting examples are the

569   apparent preference for drilling through the ligament platform in arcoids and next to the

570   aperture in *Rotularia.*

571   There is evidence of size selectivity by the driller. Smaller predators, as shown by

572   smaller diameter drill holes, took smaller prey types. A similar case of the drill holes in

573   serpulid prey being statistically smaller than those drilled in larger bivalves is reported by

574   Klompmaker (2012) for a Pliocene shallow marine fauna from the Netherlands. There is also

575   evidence in the Seymour Island *Rotularia* that a size refuge was reached whereby larger

576   individuals avoided drilling. Incomplete drill holes were significantly smaller than complete

577   ones suggesting that smaller, perhaps more inexperienced, drillers were more prone to

578   failure than larger ones. This can be taken as further evidence of size selectivity.

579   Both handling stereotypy and size selectivity may be taken as evidence of familiarity

580   by the predator and our data suggest that despite changing prey availability, the driller

581   maintained such patterns through the study interval. Thus there is no evidence at this site

582   to support the hypothesis that prey selectivity decreases after mass extinctions.

583   *5.6 Failure*

584   Failed predation attempts are common for most predator-prey systems and

585   unsuccessful predation is important in promoting defensive adaptations (Vermeij, 1982).

586   Our data show that incomplete drill holes occur throughout the section and in most prey

587   taxa. High levels of PE were found in taxa with notable defensive adaptations, such as

588   relatively thick shells (e.g. *Pycnodonte* and *Lahillia*) or those with active escape responses,

589   for example leaping in trigoniids (Tevesz, 1975). Failed drill holes were in all cases examined

590   smaller than complete holes in the same prey items, and in large enough data sets

591   significantly so thereby implying that perhaps over-ambition and mismatch of prey and

592   predator size.

593   Defensive adaptations which are active (such as leaping or swimming) or which may

594   involve laying down additional structures (such as thick shells or spines) have an additional

595   metabolic cost. Vermeij (1987) proposed that highly escalated, well defended prey are

596   more liable to extinction events associated with failures in food supply because of the

597   relative metabolic costs of their life styles. It might be predicted, consequently, that

598   predation success should increase in the aftermath of such events because surviving taxa

599   were less well-defended. In the context of this study then, one might expect to see a

600   reduction in Prey Effectiveness (PE) values over the K-Pg. Alternatively, a change in PE

601   across a mass extinction might suggest changes in competition and availability of prey (Dietl

602   et al., 2004; Hutchings and Herbert, 2013). However, similarly to Kelley et al. (2001) for the

603   US Coastal Plain, our data reveal no statistically significant change in PE over the mass

604   extinction at this site to be explained by either hypothesis. The only significant change in PE

605   recorded anywhere in our data set was for an increase in *Struthiochenopus* prey between

33

606   the recovery and the Sobral units.   While perhaps this supports the notion of better

607   defended prey emerging after the recovery, the data are limited to this taxon.

608   The phenomenon of multiple gastropod drill holes in prey items has been addressed

609   by several authors (Kitchell et al., 1986; Kelley and Hansen, 2007). It is evident that the

610   presence of several holes in any individual prey item may reflect a range of causes, for

611   example interruption and resumption of drilling by a single predator, group attacks by a

612   number of drillers (e.g. Brown and Alexander, 1994), or possession of highly effective prey

613   defences (for example the organic sheets in corbulid bivalves (Lewy and Samtleben, 1979).

614   MULT may be seen as a metric of prey effectiveness in only the last case. In our data high

615   values of MULT are associated with particular taxa, many of which have obvious defences;

616   however, there is no correlation between PE and MULT. One factor that may be important

617   here is that the frequency of MULT is likely to be in part controlled by prey longevity; the

618   longer a prey lives the more likely it is to be attacked on multiple occasions throughout its

619   life. Although longevities have not been determined for all the taxa concerned, it is well

620   known that high latitude taxa tend to be more long-lived (Moss et al., 2017). It is interesting

621   to note that the values of MULT recorded in our study are generally higher than those

622   recorded for the Cretaceous faunas on the US Coastal Plain (Kelley et al., 2001). Despite the

623   difficulty of interpreting MULT it is worth noting that for *Lahillia* there is a significant

624   increase over the mass extinction and also between unit Kplb 10 and the Sobral Formation

625   for aporrhaids.

626   *5.7 Cannibalism*

627   If we are correct that *"Vanikoropsis" arktowskiana* is the driller, then there is

628   evidence of cannibalism throughout the section with the exception of in unit Kplb 10.

629   Intraspecific predation is widespread across extant animal groups and may have profound

630   importance to both ecological relationships and evolution (Polis, 1981). Cannibalism, at

631   both family and species level, is well known in modern and fossil naticid gastropods

632   (Kitchell et al., 1981; Kelley, 1991; Kelley and Hansen, 2007; Chattopadhyay et al., 2014,

633   Brezina et al., 2016). Its significance is a matter of debate; while it may be interpreted as a

634   perfectly normal prey selection (Kitchell et al., 1981; Chattopadhyay et al., 2014; Brezina et

635   al., 2016), others have suggested it might be due to lack of other prey availability (Taylor,

636   1970), or predator ineptitude (Stanton and Nelson, 1980).

637   Our data on this interaction are limited, with drill hole numbers being highest pre-

638   extinction in Klb 7 and 8. They show good evidence of size selectivity and prey effectiveness

639   is relatively low and the range of drill hole diameters (1.10 to 4.27 mm) indicates that this

640   was a behaviour that was persistent over a range of ontogenetic ages and not necessarily

641   practiced by only older individuals as was found by Chattopadhyay *et al.* (2014).

642   **6. Conclusions**

643   Our data on predator-prey interactions over the K-Pg boundary in Antarctica show the

644   activities of a drilling predator, probably *"Vanikoropsis" arktowskiana,* was capable of

645   attacking a diverse range of molluscs and serpulid worms associated with soft sea floors.

646   Although the choice of prey items changed over the time interval studied, most notably

647   restricted after the mass extinction, various metrics of attack success and handling

648   behaviour suggest that, despite this major biotic crisis, it was 'business as usual'.

649   **Acknowledgments**

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