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1 Evolution and extinction of Maastrichtian (Late Cretaceous) cephalopods from the  
2 López de Bertodano Formation, Seymour Island, Antarctica  
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8 ABSTRACT

9 One of the most expanded records to contain the final fortunes of ammonoid cephalopods is within  
10 the López de Bertodano Formation of Seymour Island, James Ross Basin, Antarctica. Located at ~65°  
11 South now, and during the Cretaceous, this sequence is the highest southern latitude onshore outcrop  
12 containing the Cretaceous-Paleogene (K–Pg) transition. We present comprehensive new  
13 biostratigraphic range data for 14 ammonite and one nautiloid species based on the collection of >700  
14 macrofossils from high-resolution sampling of parallel sedimentary sections, dated Maastrichtian to  
15 earliest Danian in age, across southern Seymour Island. We find evidence for only a single, abrupt  
16 pulse of cephalopod extinction at the end of the Cretaceous when the final seven ammonite species  
17 disappeared, consistent with most evidence globally. In the lead up to the K–Pg extinction in the  
18 James Ross Basin, starting during the Campanian, ammonite diversity decreased overall, but the  
19 number of endemic taxa belonging to the family Kossmaticeratidae actually increased. This pattern  
20 continued into the Maastrichtian and may be facies controlled, linked to changes in sea level and  
21 seawater temperature. During the early Maastrichtian, ammonite diversity dropped significantly with  
22 only two species recorded from the basal López de Bertodano Formation on Seymour Island. The  
23 subsequent diversification of endemic taxa and reappearance of long-ranging, widespread species into  
24 the basin resulted in an increase in ammonite diversity and abundance during the mid-Maastrichtian.  
25 This was coincident with an apparent period of warming temperatures and sea level rise interpreted  
26 from palynology and sedimentology, perhaps reflecting a high latitude expression of the Mid-  
27 Maastrichtian Event. Late Maastrichtian diversity levels remained stable despite reported climatic and  
28 environmental variation. Ammonite diversity patterns during the Maastrichtian parallel those of  
29 microfossil species such as nannofossil and planktonic foraminifera, suggesting that dynamic climatic  
30 and environmental changes affected many planktonic and nektonic organisms during the latest  
31 Cretaceous. However, we suggest that these perturbations had a minimal effect on overall diversity  
32 prior to the catastrophic extinction event at the K–Pg boundary.

33

34 *Key words:* Cretaceous; palaeoenvironments; ammonite; extinction; Antarctica; diversity.

35

## 36 **1.Introduction**

37           The final demise of the ammonoid cephalopods at the end of the Cretaceous is a key  
38 component of the ongoing debate about the nature of the Cretaceous – Paleogene (K–Pg) boundary  
39 mass extinction event of 66 Ma (Gallagher, 1991; Ward et al., 1991; Marshall and Ward, 1996).  
40 Whether this event was caused by the devastating impact of an extra-terrestrial object (Alvarez et al.,  
41 1980; Schulte et al., 2010; Renne et al., 2013), or was drawn out through the final few million years of  
42 the Cretaceous, with other factors such as climate and sea level changes or the environmental effects  
43 of large scale flood basalt volcanism playing a primary role (Archibald et al., 2010; Courtillot and  
44 Fluteau, 2010; Keller et al., 2010).

45           Latest Cretaceous (Maastrichtian, 72–66 Ma) cephalopod faunas are known from every  
46 continent and palaeolatitude, although these faunas have traditionally been difficult to correlate to the  
47 international timescale due to lack of a global biostratigraphic framework (e.g. Ward, 1990; Landman  
48 et al., 2014). This has led to debate about the timing of ammonoid extinction associated with the K–  
49 Pg transition, as well as diversity changes throughout the Maastrichtian (e.g. Kennedy, 1989; Marshall  
50 and Ward, 1996; Stinnesbeck et al., 2012), a geological age with well-studied climatic and  
51 oceanographic changes (e.g. Barrera, 1994; Barrera and Savin, 1999; Miller et al., 2003; Thibault et  
52 al., 2010; Voigt et al., 2012).

53           Despite being prominent victims of the end-Cretaceous catastrophe, the actual cause of  
54 ammonite extinction remains largely unclear. With a planktonic larval stage (Shigeta, 1993; Landman  
55 et al., 1996; Tajika and Wani, 2011), and probable reliance of some groups on plankton as a primary  
56 food source (Kruta et al., 2011; Tanabe, 2011), ammonites may have been victims of a mass  
57 extinction of marine calcifying organisms and associated productivity or food chain collapse related to  
58 the impact event (Hsü et al., 1985; D’Hondt, 2005; Schulte et al., 2010; Robertson et al., 2013).  
59 However, some doubt has recently been cast upon the general model of catastrophic productivity  
60 collapse at the K–Pg (Sepulveda et al., 2009; Hull et al., 2011; Alegret et al., 2012; Sogot et al.,

61 2013). Other extinction scenarios focus on an alleged long-term decline in ammonite diversity  
62 through the Late Cretaceous (Wiedmann and Kullmann, 1996; Zinsmeister and Feldmann, 1996;  
63 Stinnesbeck et al., 2012) and the subsequent effects of Maastrichtian sea level, climate, and  
64 oceanographic changes on an already diminished group (Stinnesbeck et al., 2012). In support of this  
65 argument, ammonites appear to have been particularly sensitive to environmental change throughout  
66 their long evolutionary history (e.g. House, 1989; O'Dogherty et al., 2000; Whiteside and Ward,  
67 2009; Korn and Klug, 2012). Ultimately only high-resolution stratigraphic data from well-dated K–Pg  
68 boundary successions can provide insights into the fate of the group during the last few million years  
69 of the Cretaceous.

70         The López de Bertodano Formation, which crops out on Seymour Island, James Ross Basin,  
71 Antarctica (Fig. 1) is a key unit for assessing biotic change at this time, primarily because it is the  
72 highest latitude onshore record available in the Southern Hemisphere (~65°S presently and during the  
73 Late Cretaceous; Lawver et al., 1992; Hathway, 2000). Further, the expanded nature of the  
74 sedimentary sequence provides excellent temporal resolution (Crame et al., 1999; Crame et al., 2004;  
75 Olivero, 2012a). In this paper we present new data based on collections of Maastrichtian cephalopods  
76 (ammonites and nautiloids) from measured sections through the López de Bertodano Formation on  
77 Seymour Island (Fig. 2). We provide a detailed assessment of high latitude ammonoid diversity  
78 throughout the Maastrichtian from Seymour Island, discuss diversity trends and extinction patterns  
79 with an emphasis on the K–Pg boundary, and assess our record within the longer term context of other  
80 changes taking place during the Late Cretaceous in the James Ross Basin.

81         The López de Bertodano Formation has become an important section for calibrating  
82 ammonite extinction through the use of statistical methods (e.g. Marshall, 1995; Wang and Marshall,  
83 2004) based on early ammonite range data (Macellari, 1986). However, these data came from  
84 collections made before the precise location of the K–Pg boundary on Seymour Island was known  
85 (Elliot et al., 1994). Whilst previous studies (e.g. Macellari, 1986; Zinsmeister, 1998; Zinsmeister,  
86 2001) have also illustrated cephalopod range data from this succession, our study involves systematic  
87 high-resolution sampling tied to measured sedimentary sections in the field, allowing for accurate

88 stratigraphic location of individual fossils. In addition, we have undertaken a taxonomic review of the  
89 fauna (see Appendix 1) and compared our data to newly developed age models (e.g. Tobin et al.,  
90 2012; Bowman et al., 2013a), which enable us to accurately place this important record in a global  
91 context for the first time. The new data also allow the terminal ammonite extinction to be considered  
92 in the context of their Late Cretaceous record in the region and the controls on diversity to be  
93 assessed.

## 94 **2. Geological Setting**

95         During the Late Cretaceous the James Ross Basin was located adjacent to an active volcanic  
96 island arc (Fig. 1), now represented by the Antarctic Peninsula (Hathway, 2000; Crame et al, 2004;  
97 Olivero et al, 2008; Olivero, 2012a). The principal basin fill is subdivided into three lithostratigraphic  
98 groups: Gustav Group (Aptian–Coniacian), Marambio Group (Santonian–Danian), and Seymour  
99 Island Group (Paleocene–Eocene) (Crame et al, 1991; Scasso et al, 1991; Pirrie et al, 1997; Crame et  
100 al, 2004; Crame et al, 2006; Olivero, 2012a). Samples used in this study were collected from the  
101 López de Bertodano Formation, which forms the upper part of the ~3000m thick Marambio Group  
102 (Olivero, 2012a) and crops out over ~70 km<sup>2</sup> of southern Seymour Island and neighbouring Snow Hill  
103 Island (Fig. 1; Pirrie et al, 1997; Crame et al, 2004; Olivero et al, 2007; 2008; Bowman et al, 2012).

104         The lithostratigraphy and sedimentology of the López de Bertodano Formation have been  
105 described by a number of authors (Macellari, 1988; Crame et al, 1991; Pirrie et al, 1997; Crame et al,  
106 2004; Olivero et al, 2007; 2008; Olivero, 2012a). The dominant lithology of the ~1100 m thick  
107 section exposed on Seymour Island is a mix of fine-grained clayey-silts and silty-clays with occasional  
108 clay-rich layers and sand, demonstrating little lithological variation (Fig. 2) (Macellari, 1988; Crame  
109 et al, 2004; Olivero et al, 2007; Olivero et al, 2008). Although largely homogenous, the sediment also  
110 contains occasional sandstone beds interspersed with the dominant finer-grained lithologies, as well as  
111 many discrete layers of early diagenetic concretions – some containing well-preserved mollusc and  
112 crustacean fossils. Regional dip is 8 to 10° to the southeast, and varies little throughout the sequence.

113 Differing palaeoenvironmental interpretations have been proposed for the López de  
114 Bertodano Formation. Macellari (1988) favoured deposition in a shallow water, nearshore setting for  
115 the basal portion (~300 m), an interpretation elaborated upon by Olivero (1998) and Olivero et al.,  
116 (2007; 2008), who suggested that large, shore-parallel channels at this level formed within a large  
117 estuary or embayment. In contrast, Crame et al., (2004) suggested that a slight decrease in grain size  
118 above the underlying Haslum Crag member of the Snow Hill Island Formation (also noted by Pirrie et  
119 al., 1997), together with the poorly fossiliferous nature of this portion of the succession, represented  
120 deep water shelf conditions. Stratigraphically higher, the mid-upper portion of the formation  
121 represents overall transgression and the establishment of mid-outer shelf environments (Macellari,  
122 1988; Crame et al., 2004; Olivero et al., 2008; Olivero, 2012a).

123 The upper part of the sequence on Seymour Island the monotonous bioturbated siltstones also  
124 contain a succession of glauconite-rich horizons, often topped with fossiliferous 'lags' containing  
125 many molluscs and other fossils. These layers suggest periods of sediment starvation (Crame et al.,  
126 2004). Previous authors have suggested that this upper portion of the succession across the K–Pg  
127 boundary represents a regressive phase and loss of accommodation space (Macellari, 1988; Crame et  
128 al., 2004; Olivero, 2012a). The base of a prominent series of glauconite horizons ~1000 m above the  
129 base of the sequence coincides with a distinct change in both macro and microfossil faunas and floras  
130 (Elliot et al., 1994; Zinsmeister, 1998; Crame et al., 2004; Stilwell et al., 2004; Bowman et al., 2012),  
131 and is interpreted as being equivalent to the 'K–T glauconite' succession of Zinsmeister (1998) (Fig.  
132 2). The base of this glauconite-rich interval contains a small iridium (Ir) spike and the first  
133 appearance (FA) and acme of the dinoflagellate cyst *Senegalinium obscurum*, markers used by  
134 previous authors to locate the K–Pg boundary on Seymour Island (Elliot et al., 1994; Crame et al.,  
135 2004; Bowman et al., 2012). This horizon is also the contact between informal mapping units 'K1b9'  
136 and 'K1b10' of Macellari (1988) and Sadler (1988). Above this the 50–70 m thick unit 'K1b10' is  
137 made up of brown-grey mudstones and siltstones with scattered concretions and a distinctive  
138 macrofossil fauna dominated by the large bivalve *Lahillia* and the gastropod *Struthiochenopus*  
139 (Macellari, 1988; Crame et al., 2004; Montes et al., 2010).

140           There is no sedimentological or palaeontological evidence for any major hiatuses in the López  
141 de Bertodano Formation on Seymour Island and most estimates of the rate of sediment accumulation  
142 are high at 10 – 30 cm ka<sup>-1</sup> (McArthur et al., 1998; Crame et al., 1999; McArthur et al., 2000; Dutton  
143 et al., 2007; Tobin et al., 2012).

### 144 **3. Age model**

145           Recent work has allowed the construction of an integrated age model for the López de  
146 Bertodano Formation (Fig. 3) based on strontium isotope stratigraphy (McArthur et al., 1998; Crame  
147 et al., 2004), ammonite and dinoflagellate cyst biostratigraphy (Olivero, 2012a; Bowman et al., 2012;  
148 Bowman et al., 2013a) and magnetostratigraphy (Tobin et al., 2012). Tobin et al., (2012) identified  
149 chrons C31R through to C29N on Seymour Island, indicating an early Maastrichtian–Danian age for  
150 the sequence, which agrees with strontium isotope data from macrofossil shell material (McArthur et  
151 al., 1998; Crame et al., 2004), the presence of an Ir anomaly marking the K–Pg boundary (Elliot et al.,  
152 1994) and dinoflagellate cyst biostratigraphy (Elliot et al., 1994; Bowman et al., 2012). Correlation of  
153 the magnetostratigraphy of Tobin et al, (2012) to our composite section was achieved using GPS  
154 coordinates provided in that study, and the location of our measured section lines accurately plotted  
155 using field GPS data and the published topographic map of Seymour Island (Fig. 1; Brecher and  
156 Tope, 1988). The timescale of Gradstein et al. (2012) has been added to the age model using linear  
157 interpolation between the known ages of chron reversal boundaries. Published ammonite  
158 biostratigraphy is useful for correlation within the James Ross Basin but is of limited use for dating  
159 purposes due to the presence of primarily endemic taxa (Fig. 3; Macellari, 1986; Olivero and Medina,  
160 2000; Crame et al., 2004; Olivero, 2012a). In addition, strontium isotope stratigraphy applied to other  
161 Maastrichtian successions supports this age model when compared to existing data (Vanhof et al.,  
162 2011).

163           Recent updates to the astronomical (Husson et al., 2011; Batenburg et al., 2014) and  
164 geochronological (Gradstein et al., 2012; Voigt et al., 2012; Renne et al., 2013) calibrations of the  
165 Maastrichtian timescale suggest the C31R–C31N chron reversal can be dated at 69.2 Ma, with the

166 Campanian–Maastrichtian boundary at 72.2 Ma and the K–Pg boundary at ~66 Ma. A large portion of  
167 the succession can thus be considered late Maastrichtian in age, which is in agreement with  
168 dinoflagellate biostratigraphy (Bowman et al., 2012). Previous workers placed the Campanian–  
169 Maastrichtian boundary in Antarctica in the lowermost Cape Lamb Member of the Snow Hill Island  
170 Formation as exposed on nearby Vega Island, stratigraphically ~200 m below the base of the  
171 succession described here (McArthur et al., 1998; Crame et al., 1999; McArthur et al., 2000; Olivero,  
172 2012a).

## 173 **4. Material and Methods**

### 174 *4.1 Macrofossil range data*

175 More than 700 cephalopod macrofossils were collected and examined during this study, with  
176 over 550 identified to species level (See Appendix 1 and Supplementary Data). Collection occurred as  
177 part of a multi-field season stratigraphic study of the López de Bertodano Formation on Seymour  
178 Island (Crame et al., 2004; Bowman et al., 2012; Bowman et al., 2013a; Bowman et al., 2014). The  
179 fossils are stored and curated at the British Antarctic Survey (BAS), Cambridge, UK. All fossils are  
180 precisely located on two composite measured sections across the southern part of the island (Fig. 1).  
181 The first is 470 m thick and comprises sub-sections DJ.959, 957, 952, and 953 (Crame et al., 2004).  
182 This section encompasses the mid to upper portion of the López de Bertodano Formation up to the  
183 contact with the overlying Sobral Formation (Fig. S1). The second section (composite section  
184 D5.251) is along strike to the south and is ~1100 m thick comprising sub-sections D5.212, D5.215,  
185 D5.218, D5.219, D5.220, D5.222, and D5.229. This extends through the Haslum Crag Member of the  
186 Snow Hill Island Formation and the entire López de Bertodano Formation, terminating at the  
187 lowermost Sobral Formation (Fig. S2; Thorn et al., 2007; Bowman et al., 2012; Bowman et al., 2013a;  
188 Bowman et al., 2014).

189 Sedimentary sections were measured using traditional field methods (Jacob's staff and Abney  
190 level, with some intervals then sub-divided using a tape measure), which yielded a high-resolution  
191 stratigraphy (e.g. Crame et al., 1991; Pirrie et al., 1997; Crame et al., 2004). Correlation between the

192 two composite sections was made using stratigraphic tie-points, including the K–Pg boundary, the  
193 unconformity between the López de Bertodano and Sobral formations, and a prominent glauconite  
194 horizon 174 m below the K–Pg that can be traced laterally across the island (Fig. 2). Based on our  
195 field knowledge we have assumed planar bedding along strike and no significant hiatuses. Although  
196 identification of tie points in the lower portion of the sequence is challenging, our section lines show  
197 little lateral facies or structural variation in the field that would impede the use of one main composite  
198 section for biostratigraphic purposes. This is particularly evident when first and last appearances of  
199 different macrofossil species are compared across section lines because in many cases these occur at  
200 approximately (within ~10 m) the same stratigraphic height (e.g. last appearance (LA) of *Maorites* cf.  
201 *weddelliensis* and first appearance (FA) *Grossouvrites johare* (Fig. 4). Macrofossil collections were  
202 made either every metre or in binned intervals several metres thick and of considerable lateral extent  
203 along strike (binned intervals were on average 10 m thick in sections DJ.959-953 and 5 m thick in  
204 D5.251). In such thick stratigraphic sections and with a high sedimentation rate (e.g. McArthur et al.,  
205 1998; Crame et al., 1999; McArthur et al., 2000; Dutton et al., 2007; Tobin et al., 2012) these are high  
206 resolution collections for assessing key biostratigraphic patterns. Effort was also made to ensure that  
207 all section lines were collected uniformly with a similar amount of time spent collecting within each  
208 binned interval and no increase in sampling intensity close to the K–Pg boundary (Figs. S1 and S2).

209 Taxonomic analysis of the Antarctic ammonite fauna was conducted using the monograph of  
210 Macellari (1986), supplemented by earlier works such as those of Spath (1953) and Howarth (1958,  
211 1966) as well as studies of other Maastrichtian faunas (e.g. Henderson and McNamara, 1985;  
212 Kennedy and Henderson, 1992a; Klinger and Kennedy, 2003; Ifrim et al., 2004; Salazar et al., 2010).  
213 Nautiloid taxonomic analysis used the work of Cichowolski et al. (2005) and Nielsen and Salazar  
214 (2011). Systematic nomenclature of Maastrichtian ammonoids follows the Treatise of Invertebrate  
215 Paleontology (Wright et al., 1996) to sub-generic level. Taxonomic comments on the cephalopod  
216 fauna can be found in Appendix 1. Representative ammonite taxa from the López de Bertodano  
217 Formation are illustrated in Figs. 5 and 6.

218           Following taxonomic identification (Appendix 1), stratigraphic ranges were compiled for  
219 each composite section (Figs. S1 and S2) using data from all sub-sections and amalgamated into a  
220 single range chart (Fig. 4), with care taken to ensure repetition of fossil-bearing horizons was avoided.  
221 For illustration purposes, each fossil occurrence is placed at the mid-point of the binned interval in  
222 which it was collected. Species diversity indices are illustrated in Fig. 7. Raw species richness is the  
223 number of species present at any given horizon, and standing species richness is the number of species  
224 that first appear or last appear at any given horizon, plus those that range through the horizon.

#### 225 *4.2 Statistical analysis*

226           To assess the ‘Signor-Lipps effect’ (i.e. that the final stratigraphic occurrence of any given  
227 taxon in a particular stratigraphic section is unlikely to be the true final occurrence of that taxon in the  
228 basin) (Signor and Lipps, 1982) within our dataset, we have applied the stratigraphic abundance  
229 method of Meldahl (1990). The last occurrence of a taxon is plotted against their stratigraphic  
230 abundance (the percent of stratigraphic sample intervals in which the species occurs, S) (Fig. 8). Only  
231 species with an S value greater than 15% are generally considered reliable indicators of extinction (i.e.  
232 species occurring in more than 15% of all stratigraphic horizons, Meldahl, 1990; Rampino and Adler,  
233 1998; Song et al, 2013).

234           We also calculated 50% confidence intervals for all taxa, based on the stratigraphic  
235 distribution and the number of occurrences of each taxon in the composite section. These are  
236 illustrated as range extensions on the composite range chart using the method of Marshall (1995) (Fig.  
237 4). Range extensions were calculated for all taxa with > 1 fossil occurrence in the composite section.

### 238 **5. Results**

#### 239 *5.1 Antarctic macrofossil range data*

240           In total, fourteen ammonite species assigned to eight genera were identified from our samples,  
241 as well as a single species of nautiloid. Four species remain in open nomenclature or are unnamed  
242 (Figs. 5 and 6, Appendix 1). In terms of taxonomic composition, the fauna is numerically dominated  
243 by individuals belonging to members of the family Kossmaticeratidae (the genera *Maorites* and

244 *Grossouvrites*), as well as Desmoceratidae (*Kitchinites*), alongside rarer examples of the  
245 Lytoceratidae (*Zelandites*, *Anagaudryceras*, *Pseudophyllites*), Pachydiscidae (*Pachydiscus*  
246 (*Pachydiscus*)), and a single species of Diplomoceratidae (*Diplomoceras*).

247 The basal portion of the López de Bertodano Formation is poorly fossiliferous (Figs. 4 and 7).  
248 The first appearance of ammonites in our composite section is represented by examples of the large  
249 heteromorph *Diplomoceras cylindraceum* (DeFrance) (Fig. 5G) at 95 m in our composite section  
250 D5.251, followed by small fragmentary specimens of *Maorites tuberculatus* (Howarth) (Fig. 6C)  
251 which appear at 235 m, and similarly poorly preserved examples of *Pseudophyllites* cf. *loryi* (Killian  
252 and Reboul) (Fig. 5C) at 330m. A relatively sparse and poorly preserved benthic macrofossil  
253 assemblage is also present at these levels (Macellari, 1988; Crame et al, 2004; Olivero et al., 2007).  
254 Although not found in either of our section lines, a single horizon containing specimens of the  
255 belemnite *Dimitobelus* (*Dimitocamax*) *seymouriensis* (Doyle and Zinsmeister) was located 636 m  
256 below the K–Pg boundary (~370 m) (McArthur et al, 1998; Crame et al, 2004). No ammonites were  
257 found associated with the belemnites. There appears to be no change in the benthic fauna, which is  
258 dominated by serpulid worm tubes (*Rotularia*) and echinoid spines at this level (Doyle and  
259 Zinsmeister, 1988; Dutton et al, 2007).

260 *Maorites tuberculatus* has its last appearance datum (LAD) at 431 m and fragmentary  
261 specimens of the larger, coarse-ribbed *Maorites seymourianus* (Killian and Reboul) (Fig. 6D) were  
262 found at 437 m. A distinct change in the fauna is evident at 525 m above the base of the section (Figs.  
263 4 and 7); specimens of *Kitchinites* sp. (Fig. 6E) appear, alongside examples of another coarse-ribbed  
264 kossmaticeratid species: *Maorites* cf. *weddelliensis* (Macellari) (Fig. 6A). This horizon also contains  
265 the first example of the nautiloid *Eutrephoceras dorbignyanum* (Forbes in Darwin) (Fig. 5D). The  
266 base of sub-sections DJ.959 and D5.218 at ~615 m sees an increase in the abundance of large  
267 specimens of *Maorites seymourianus* and *Kitchinites* sp, along with several well-preserved examples  
268 of *Eutrephoceras dorbignyanum*. The LAD of *Maorites* cf. *weddelliensis* occurs within a short  
269 stratigraphic interval several metres thick at this level, which correlates well across the two section

270 lines. This level also contains the FAD of representatives of the kossmaticeratid *Grossouvrites johare*  
271 (Salazar) (Fig. 5E).

272 Overall, a steady increase in the diversity of the fauna is notable through the mid portion of  
273 the section (Fig. 4). The lytoceratid *Anagaudryceras seymouriense* (Macellari) (Fig. 5A) appears at  
274 659 m, followed by an occurrence of a single, poorly preserved pachydiscid resembling *Pachydiscus*  
275 (*Pachydiscus*) cf. *ootacodensis* (Stoliczka) as also identified by Macellari (1986) at 669 m. Several  
276 desmoceratid and kossmaticeratid taxa also exhibit turnover through this interval. Thus, *Kitchinites*  
277 sp. disappears at ~674 m and is replaced by *Kitchinites laurae* (Macellari) (Fig. 5F), and similarly  
278 *Maorites seymourianus* is replaced by the finer-ribbed, more compressed *Maorites densicostatus*  
279 (Killian and Reboul) (Fig. 6B). Macellari (1986) described three morphotypes of this species, but their  
280 stratigraphic and morphological ranges overlap and they are considered here as a single rather  
281 variable species (Appendix 1).

282 The upper portion of the succession is dominated by species belonging to long-ranging genera  
283 (*Pseudophyllites*, *Anagaudryceras*, and *Diplomoceras*) and kossmaticeratids (*Grossouvrites johare*,  
284 *Maorites densicostatus*) (Fig. 4). *Kitchinites laurae* also occurs sporadically, along with examples of  
285 *Eutrephoceras dorbignyanum*. At 809 m the large pachydiscid *Pachydiscus (Pachydiscus) riccardii*  
286 (Macellari) (Fig. 6G) appears and remains abundant for around 20 m before a return to the *Maorites*-  
287 *Grossouvrites-Anagaudryceras* fauna. A further influx of large pachydiscids occurs at 942 m  
288 (identified as *Pachydiscus (Pachydiscus) ultimus* (Macellari) (Fig. 6F) and, like *Pachydiscus*  
289 (*Pachydiscus*) *riccardii* they remain abundant for only a short stratigraphic interval until their  
290 disappearance at 976 m.

291 Four ammonite species are present in the five metres beneath the K–Pg boundary in our  
292 sections (Figs. 4 and 7). Specimens of *Diplomoceras cylindraceum* and *Maorites densicostatus*  
293 remain common, along with rare *Anagaudryceras seymouriense* until just below the base of the ‘K–T  
294 glauconite’. There are also several small ammonites similar to those identified by Macellari (1986) as  
295 *Zelandites varuna* (Forbes, 1846) (Fig. 5B) in this interval. A number of large examples of the

296 nautiloid *Eutrephoceras dorbignyanum* were also found directly below the boundary. Other common  
297 taxa in the upper portion of the López de Bertodano Formation (e.g. *Grossouvrites johare*, *Kitchinites*  
298 *laurae*) have LADs in the 40 m below the boundary in all of our section lines (Fig. 4).

299 No definitively *in situ* cephalopod fossils were found above the K–Pg boundary, although  
300 poorly preserved ammonites have been previously reported from this interval on Seymour Island  
301 (Sadler, 1988; Zinsmeister et al, 1989). Zinsmeister (1998) considered these to be the result of local  
302 inliers of Cretaceous-aged sediment in the broad dip-slopes of the Paleocene unit ‘K1b10’ but our  
303 recent observations indicate that their positions may be the result of recent transport due to glacial  
304 action, and they are therefore considered reworked.

305 Composite results suggest that six taxa (*Kitchinites* sp., *Maorites seymourianus*,  
306 *Grossouvrites johare*, *Maorites densicostatus*, *Eutrephoceras dorbignyanum*, and *Diplomoceras*  
307 *cylindraceum*) have a stratigraphic abundance (S) greater than/equal to 15% and should therefore give  
308 an accurate record of their true extinction horizon (e.g. Meldahl, 1990). A plot of LAD against  
309 stratigraphic height (Fig. 8) shows a cluster of last appearances close to the K–Pg boundary for three  
310 of these taxa (*Diplomoceras cylindraceum*, *Maorites densicostatus*, *Eutrephoceras dorbignyanum*)  
311 along with *Anagaudryceras seymouriense* (S value of 12), with *Grossouvrites johare* disappearing  
312 some 40 metres below in both section lines.

313 Analysis of 50% confidence intervals shows ranges are generally well sampled with the larger  
314 range extensions clearly being due to rare occurrences (Fig. 4). Five 50% range extensions extend  
315 above the K–Pg boundary, four of which belong to taxa with high stratigraphic abundance (S values >  
316 15% *Diplomoceras cylindraceum*, *Maorites densicostatus*, *Anagaudryceras seymouriense*,  
317 *Eutrephoceras dorbignyanum*). Confidence intervals for the remaining eight taxa all terminate within  
318 the Maastrichtian, below the K–Pg interval.

## 319 **6. Discussion**

320 The recently published magnetostratigraphy (Tobin et al, 2012) and updated palynological  
321 biostratigraphy (Bowman et al, 2012; Bowman et al., 2013a; Bowman et al., 2014) allow us to

322 accurately place the Maastrichtian ammonite record from Seymour Island in a global context for the  
323 first time. It is clear that revisions are required to the age models used in previous studies (e.g.  
324 Macellari (1986; Zinsmeister (2001) and subsequent comparisons to global events.

325 *6.1 K–Pg Mass extinction in . In addition, Pachydiscus (Pachydiscus) cf. Antarctica*

326 Previous studies of extinction patterns in the upper part of the López de Bertodano Formation  
327 have suggested that the K–Pg mass extinction may have been either a gradual or step-wise event in  
328 the southern high latitudes (Zinsmeister et al., 1989; Zinsmeister, 1998; Tobin et al., 2012), with  
329 extinction events in the late Maastrichtian preceding the K–Pg extinction event itself (Tobin et al.,  
330 2012). However, previous studies using statistical analysis of existing ammonite fossil range data  
331 (Macellari, 1986) were unable to rule out the possibility of a sudden extinction at the K–Pg boundary  
332 distorted by the Signor-Lipps effect (Marshall, 1995; Marshall and Ward, 1996).

333 Our new data add support to the hypothesis of a sudden extinction event for ammonites  
334 associated with the K–Pg boundary. The largest concentration of last appearances in our composite  
335 section occurs between 1 and 5 m below the base of the glauconitic interval containing the K–Pg  
336 boundary (Fig. 8). The extinction level is not associated with any major changes in sedimentology but  
337 coincides with benthic losses (Macellari, 1988; Crame et al., 2004; Stilwell et al., 2004), the  
338 disappearance of marine reptiles (Martin, 2006; Martin and Crame, 2006) and turnover in the  
339 palynological record (Elliot et al., 1994; Bowman et al., 2012).

340 Zinsmeister (1998) reported six ammonite species as having their final occurrence < 2m  
341 below the K–Pg boundary on Seymour Island. His records of *Maorites densicostatus* and  
342 *Diplomoceras cylindraceum* are consistent with our data, as is the restricted occurrence of *Zelandites*  
343 *varuna*, (Fig. 4) but Zinsmeister also reported the presence of *Kitchinites laurae*, *Pseudophyllites loryi*  
344 and *Grossouvrites gemmatus* (probably *Grossouvrites johare* – see Appendix 1 and Salazar et al.,  
345 2010), which were not found during our study. In Zinsmeister’s (1998) range data the final  
346 occurrences of *Kitchinites laurae* and *Pseudophyllites loryi* are also the only records of these species  
347 in a 16 m interval beneath the boundary. Similarly, examples of *Grossouvrites* only occur twice in the

348 same interval. This suggests that, in addition to four common species, several rare species were  
349 present in the latest Maastrichtian. In support of this hypothesis several small external moulds of  
350 *Anagaudryceras seymouriense* were discovered ~5 m below the K–Pg in one of our section lines, a  
351 species not previously recorded from this interval.

352 Including Zinsmeister’s (1998) records with those from this study, a total of seven ammonite  
353 species have now been reported from the 5 m interval directly beneath the K–Pg boundary on  
354 Seymour Island (Fig. 4) (*Maorites densicostatus*, *Diplomoceras cylindraceum*, *Zelandites varuna*,  
355 *Grossouvrites johare*, *Kitchinites laurae*, *Pseudophyllites loryi*, *Anagaudryceras seymouriense*).  
356 Using the age model described herein and published sedimentation rates for the López de Bertodano  
357 Formation, a conservative estimate would suggest this 5 m interval could represent as little as ~15  
358 kyrs, or as much as ~50 kyrs (McArthur et al., 1998; Crame et al., 1999; McArthur et al., 2000; Tobin  
359 et al., 2012). The highest ammonite occurrence is less than 50 cm below the base of the glauconite  
360 sandstone containing the iridium anomaly and K–Pg boundary (Zinsmeister, 1998).

361 The seven species present in this interval represent three of the four suborders of post-Triassic  
362 ammonites (Wright et al., 1996) and are a mixture of taxa endemic to the southern high latitudes  
363 (presumably cool-temperate Austral specialists, e.g. kossmaticeratids *Maorites* and *Grossouvrites*,  
364 *Kitchinites laurae*) and long-ranging cosmopolitan taxa (e.g. *Diplomoceras*, *Pseudophyllites*,  
365 *Anagaudryceras*, *Zelandites*). We suggest that these ammonites persisted through the late  
366 Maastrichtian but became extinct at the K–Pg boundary. The remaining seven species present in the  
367 López de Bertodano Formation are therefore likely victims of background turnover during the  
368 Maastrichtian rather than of any sudden extinction event at or before the K–Pg boundary. The high  
369 stratigraphic abundance values for two of these species (*Maorites seymourianus* and *Kitchinites* sp.)  
370 and lack of distinct clusters of LAD at any other portion of the section besides the K–Pg interval  
371 provide supportive evidence (Fig. 8). In addition, the nautiloid *Eutrephoceras dorbignyanum*  
372 disappears from Antarctica at the K–Pg boundary, raising the total number of cephalopod taxa lost in  
373 this interval to eight. This genus exhibits a global distribution in the Maastrichtian (Landman et al.,  
374 2014), and although Paleogene representatives are known from lower latitude locations (e.g. Teichert

375 and Glenister, 1959; Stilwell and Grebneff, 1996; Darragh, 1997; Casadio et al., 1999), it failed to  
376 recolonize Antarctica.

377         Having established the sudden nature of the ammonite extinction event, it is also important to  
378 compare the record of ammonite extinction from Antarctica with lower latitudes. Extensive study of  
379 Maastrichtian sedimentary successions worldwide suggests that although many macrofossil-bearing  
380 shallow water K–Pg successions often contain a hiatus between the upper Maastrichtian and Danian  
381 (e.g. Machalski, 2005), a conservative estimate suggests 30 to 35 species of ammonite belonging to 31  
382 genera were present in the final few 100 kyrs prior to the K–Pg boundary at a variety of sites around  
383 the globe (Landman et al., 2007; Landman et al., 2014). In the most complete successions, ammonites  
384 extend to within a few cm of the boundary (as defined by impact debris and/or microfossil turnover,  
385 e.g. Birkelund, 1993; Ward and Kennedy, 1993; Landman et al., 2004a; 2004b; Machalski, 2005;  
386 Landman et al., 2014). The taxonomic composition of many of these faunas indicates that all four  
387 suborders of post-Triassic ammonites (Phylloceratina, Lytoceratina, Ammonitina, and  
388 Ancyloceratina) survived into the latest Maastrichtian (Birkelund, 1993; Landman et al., 2007).  
389 Below we review the records from several of the most complete K–Pg successions, which also  
390 contain palaeoenvironmental information, in order to compare with our new data from Antarctica.

391         Several localities along the Biscay coast of Spain and France contain complete deep-water  
392 (100–500 m) K–Pg successions (Ward et al., 1991; Ward and Kennedy 1993).-A total of 31 species in  
393 19 genera are known from the Maastrichtian, with nine, possibly 10, species belonging to 10 genera  
394 ranging to within the final metre beneath the K–Pg boundary (Ward and Kennedy, 1993). The onset  
395 of a basin-wide regression is recognised ~20 m below the boundary, coinciding with the  
396 disappearance of many other ammonite species (Ward and Kennedy, 1993). No ammonite fossils are  
397 found in an interval 8–1.5 m below the boundary corresponding to the peak of this regression  
398 (Marshall and Ward, 1996). The K–Pg boundary itself is within a period of rising sea level (Pujalte et  
399 al., 1998) coincident with the reappearance of ammonites 1.5 m below, and suggesting a strong facies  
400 control on ammonite diversity in these sections.

401           A number of localities in the Danish chalk also contain Maastrichtian successions with little  
402 or no hiatus present at the K–Pg boundary (Hart et al., 2005; Hansen and Surlyk, 2014) and with  
403 diverse ammonite faunas (Birkelund 1979; 1993). These faunas are of considerable interest as the  
404 only complete Maastrichtian record of ammonites in the Boreal Realm of the Northern Hemisphere  
405 (Birkelund, 1993). A total of 19 species belonging to 11 genera were present in the Danish  
406 successions during the Maastrichtian, with seven species in seven genera present directly beneath the  
407 K–Pg boundary (Birkelund, 1993; Machalski, 2005; Hansen and Surlyk, 2014). Sea level changes and  
408 palaeoenvironmental fluctuations prior to the K–Pg interval have been recorded from the basin (e.g.  
409 Surlyk, 1997; Hart et al., 2005; Hansen and Surlyk, 2014) but cephalopods do not appear to have  
410 suffered significant decline prior to the K–Pg boundary (Hansen and Surlyk, 2014). Records of two  
411 species indicate they may even have survived briefly into the early Danian (Surlyk and Nielsen, 1999;  
412 Machalski and Heinberg, 2005; Landman et al., 2014).

413           Elsewhere in Europe, North America, Africa and the Russian Far East, diverse ammonite  
414 faunas are also present in the latest Maastrichtian (e.g. Goolaerts et al., 2004; Machalski, 2005; Jagt et  
415 al., 2006; Landman et al., 2007; Ifrim et al., 2010; Jagt-Yazykova, 2012), although many of these  
416 records are from sites where uncertainties remain about the completeness of the K–Pg interval, or  
417 where ammonites are recorded from only part of the succession. Nevertheless, the majority of these  
418 low latitude records agree with the evidence from Seymour Island for abrupt ammonite extinction at  
419 the K–Pg boundary.

420           In contrast, Stinnesbeck et al. (2012) concluded that in South America ammonites declined  
421 during the Maastrichtian, and disappeared prior to the K–Pg boundary. They suggest a diachronous  
422 extinction for the group, beginning in the tropics and expanding towards high latitudes. However, the  
423 lack of abundant ammonites in the uppermost Maastrichtian of the Neuquén Basin, Argentina and at  
424 Quiriquina Island in Chile, where a diverse Maastrichtian assemblage is present (Salazar et al., 2010),  
425 could relate to unfavourable local palaeoenvironmental conditions for cephalopods at these localities  
426 where very shallow water environments were developed and possibly stressed by local volcanic  
427 activity (Keller et al., 2007).

428           Although compilations suggest an overall decline in ammonite diversity during the Late  
429 Cretaceous in many regions of the globe (Kennedy, 1989; Jagt-Yazykova, 2011; Olivero, 2012a), this  
430 may be due to a reduction in the number of short-lived and presumably specialist genera (Yacobucci,  
431 2005). Many of these genera were likely inhabitants of epeiric or epicratonic seaways, the majority of  
432 which were in retreat during the latest Cretaceous (e.g. Kennedy et al., 1998). Data compilations  
433 suggest Maastrichtian faunas were dominated by long-ranging multi-stage taxa (Yacobucci, 2005).  
434 Recent work has suggested however, that many ammonite genera that survived to the end of the  
435 Maastrichtian were geographically restricted (Landman et al., 2014), perhaps making them more  
436 vulnerable to extinction. Despite these observations, that reveal the complex pattern of diversity  
437 change during the Late Cretaceous, there is little evidence globally of ammonites becoming seriously  
438 impoverished prior to the latest Maastrichtian (but see section 6.2 below for discussion of regional  
439 variation). In addition, there does not appear to be evidence of significantly higher extinction rates for  
440 the group as a whole when the Maastrichtian record is placed in the context of the entire mid – Late  
441 Cretaceous, despite diversity fluctuations (Yacobucci, 2005; Jagt-Yazykova, 2011; Olivero, 2012a).  
442 The final extinction of the group therefore appears to have been abrupt and catastrophic, consistent  
443 with the idea of a bolide impact as the primary cause.

## 444 7.

445           Ammonite extinction at the K–Pg boundary was probably associated with marine food chain  
446 collapse and disruption to surface-water ecosystems resulting from the after-effects of the Chicxulub  
447 impact event (Alvarez et al., 1980; Hsü et al., 1985; D’Hondt, 2005; Schulte et al., 2010), primarily  
448 caused by a global dust-cloud that extinguished sunlight and suppressed photosynthesis (Robertson et  
449 al., 2013). Suggestion has also been made that a short-lived period of transient ocean acidification  
450 may have contributed to the mass extinction of calcifying planktonic organisms across the K–Pg  
451 which included embryonic ammonites (Alegret et al., 2012; Arkhipkin and Laptikhovsky, 2012) and  
452 their prey (Kruta et al., 2011).

### 453 *6.2 Late Cretaceous faunal diversity and environmental change in Antarctica*

454 Examination of our extended range data (Fig. 4) reveals patterns in the few million years  
455 leading up to the K–Pg extinction that helps to place this event in the context of longer-term changes  
456 (Fig. 9). Olivero and Medina (2000) identified three major sedimentary cycles in the James Ross  
457 Basin during deposition of the Marambio Group, each capped by regional unconformities and  
458 containing distinct facies and biota. The N (Santonian–early Campanian), NG (late Campanian–early  
459 Maastrichtian), and MG (early Maastrichtian–Danian) sequences are correlated across the basin by  
460 means of 14 distinct ammonite assemblages, based on the most common genus of the ammonite  
461 family Kossmaticeratidae found within each (N–*Natalites*, NG–*Neograhamites* and *Gunnarites*, MG–  
462 *Maorites* and *Grossouvrites*) (Fig. 9; see also Olivero, 2012a; 2012b).

463 To examine the picture of ammonite diversity on a longer timescale, ammonite ranges at the  
464 generic level through the Coniacian–Maastrichtian (~89–66 Ma) of the James Ross Basin have been  
465 plotted (Fig. 9), based primarily on ammonite assemblage data presented in Olivero (2012a; 2012b),  
466 supplemented by information from the Coniacian age Hidden Lake Formation from Kennedy et al.  
467 (2007). The generic level turnover through time has been calculated by plotting the difference  
468 between the number of generic FAD and LADs in each ammonite assemblage (e.g. O’Dogherty et al.,  
469 2000). The K–Pg interval forms the upper boundary of ammonite assemblage 14 and is marked by the  
470 disappearance of the final seven genera of ammonites, with one group (Pachydiscidae) disappearing  
471 before the boundary, still within assemblage 14. This is the only assemblage for which the accurate  
472 position of FADs and LADs within the assemblage is available; all other data are plotted at the mid-  
473 point of each assemblage. We have also included range data for belemnites, inoceramid bivalves, and  
474 nautilids at the order level based on separate stratigraphic data (see below) (Doyle, 1990; Crame et al.,  
475 1996; Crame and Luther, 1997; Olivero, 2012b; Cichowolski et al., 2005).

476 The low diversity in the López de Bertodano Formation contrasts markedly with the  
477 underlying formations (Figs. 5 and 9; Olivero, 1992; Zinsmeister and Feldmann, 1996; Crame et al.,  
478 1996; Olivero and Medina, 2000; Olivero, 2012a). Overall, a total of 43 genera were present in the  
479 basin during the Coniacian – Maastrichtian interval (Fig. 9; Zinsmeister and Feldmann, 1996;  
480 Kennedy et al., 2007; Olivero, 2012a; 2012b), with the highest diversities recorded in the Santonian–

481 Campanian Santa Marta Formation, followed by a general decline through the Campanian –  
482 Maastrichtian Snow Hill Island Formation (Fig. 9). The lower portion of the Santa Marta Formation  
483 (ammonite assemblages 1–4, Santonian to early Campanian) is an interval where originations and first  
484 appearances dominate over extinctions, whereas extinction rate appears to increase in assemblage 6 of  
485 the N sequence towards the top of the formation. This is followed by overall turnover and diversity  
486 decline within the NG sequence (late Campanian–early Maastrichtian) before a period of stability – at  
487 least at generic level – and then a pulse of extinction in assemblage 14 of the MG sequence (i.e. the  
488 K–Pg interval within the uppermost López de Bertodano Formation) (Fig. 9). These patterns are  
489 unlikely to be a result of sampling bias, as the key sections within the James Ross Basin have been  
490 extensively collected for over 100 years (see reviews in Zinsmeister, 1988; Crame et al., 1991).

491         Whilst the decline in diversity and disappearance of genera in the Santa Marta Formation  
492 could be due to the basin-wide regression at the top of the N sequence, the pattern in the overlying  
493 NG sequence in particular does not appear to correlate well with the contemporaneous transgressive-  
494 regressive cycle, suggesting other factors may be responsible for driving diversity changes during this  
495 period. In addition, the overall composition of the fauna underwent a series of changes during this  
496 interval. Notably, several groups of ammonites disappear from Antarctica during deposition of the N  
497 and NG sequences (e.g. scaphitids, baculitids) (Olivero and Medina, 2000; Olivero, 2012a), while  
498 remaining common components of younger Maastrichtian faunas at lower latitudes. As a result,  
499 whereas the Santa Marta Formation contains a mixture of cosmopolitan and endemic genera, faunas  
500 from the younger NG and MG sequences are numerically dominated by the largely endemic family  
501 Kosmaticeratidae, which shows distinct Austral affinities in its distribution pattern, being found in  
502 South America, South Africa, Australia, and New Zealand during the Campanian and Maastrichtian  
503 (Henderson, 1970; Henderson and MacNamara, 1985; Kennedy and Klinger, 1985; Olivero and  
504 Medina, 2000; Salazar et al., 2010).

505         Other macrofossil groups show similar divergent extinction patterns in the James Ross Basin  
506 compared to lower latitudes, in particular inoceramid bivalves and belemnites (Crame et al., 1996;  
507 Zinsmeister and Feldmann, 1996). Inoceramid bivalves disappeared from Antarctica during

508 deposition of the upper portion of the Santa Marta Formation (Crame et al., 1996; Crame and Luther,  
509 1997; Olivero and Medina, 2000) in the late Campanian (McArthur et al., 2000) (Fig. 9) earlier than  
510 their mid-Maastrichtian extinction elsewhere (e.g. McLeod et al., 1996). Belemnites disappeared even  
511 earlier, albeit temporarily, in the early Campanian, as recorded in the mid-portion of the Santa Marta  
512 Formation on James Ross Island (Doyle, 1990; Crame et al., 1996; McArthur et al., 2000), before a  
513 single species reappeared in the basin in the early Maastrichtian of Seymour Island (Fig. 9; Doyle and  
514 Zinsmeister, 1988; Dutton et al., 2007).

515         These diversity declines and regional extinctions have been linked to a global cooling trend  
516 that began during the mid-Campanian and culminated around the Campanian–Maastrichtian boundary  
517 (Barrera and Savin, 1999; Friedrich et al., 2012; Linnert et al., 2014). It is therefore probable that the  
518 diversity decline at the top of the N sequence, which continued into the NG sequence, was at least  
519 partly driven by high-latitude cooling during the Campanian–Maastrichtian transition (Crame et al.,  
520 1996; Olivero and Medina, 2000, Olivero, 2012a), recorded in Antarctica by both marine and  
521 terrestrial proxies (e.g. Ditchfield et al., 1994; Francis and Poole, 2002) and synonymous with the  
522 trend seen globally. Despite this, ammonites remain locally abundant and reasonably diverse in  
523 Antarctica close to the Campanian–Maastrichtian boundary when peak global cooling occurred, as  
524 shown by the occurrence of nine genera in the ‘*Gunnarites antarcticus* fauna’ (ammonite assemblage  
525 10) (Crame et al., 1999; Crame et al., 2004; Olivero, 2012a) stratigraphically below the base of the  
526 López de Bertodano Formation (Fig. 9). However, diversity did not return to levels attained during the  
527 Campanian.

### 528 *6.3 Maastrichtian faunal diversity and environmental change on Seymour Island*

529         The low diversity in the species-level range data in the lowermost beds of the López de  
530 Bertodano Formation on Seymour Island (basal MG sequence of Olivero (2012a) is striking (Figs. 4  
531 and 7). Only *Maorites tuberculatus* and *Diplomoceras cylindraceum* were found despite consistent  
532 high-resolution sampling (Fig. S2). This diversity minimum is followed by a general increase starting  
533 around 500 m above the section base, up until a level ~50 m below the K–Pg boundary.

534           The main increase in diversity and species richness on Seymour Island appears to occur in  
535 several steps during the early–late Maastrichtian, encompassing magnetochrons 31R and 31N (Figs. 4  
536 and 7; Husson et al., 2011; Voigt et al., 2012). This coincides with a global environmental  
537 perturbation commonly referred to as the ‘Mid-Maastrichtian Event’ (MME) (Barrera, 1994;  
538 MacLeod, 1994; Barrera and Savin, 1999; MacLeod and Huber, 2001; Voigt et al., 2012; Jung et al.,  
539 2013), an interval that saw a eustatic high stand (Hancock, 1993; Dubicka and Peryt, 2012; Haq,  
540 2014) and changes in seawater temperatures and ocean circulation patterns (Thibault and Gardin,  
541 2006; Friedrich et al., 2012; Jung et al., 2013). The sedimentology of the lower portion of the López  
542 de Bertodano Formation appears to accord with a eustatic sea level rise prior to the MME high stand  
543 (Olivero et al., 2007; 2008; Olivero, 2012a). In addition, palaeotemperature estimates derived from  
544 oxygen isotope analysis of molluscan shell material from the lower portion of the López de Bertodano  
545 Formation, and correlated to chron C31R, are suggestive of cool ocean temperatures (Fig. 7; Barrera  
546 et al., 1987; Ditchfield et al., 1994; Dutton et al., 2007; Tobin et al., 2012). Abundance peaks of a  
547 particular species of dinoflagellate cyst, *Impletosphaeridium clavus* (Wrenn & Hart 1988) Bowman et  
548 al., 2013b, during this interval may even represent the appearance of seasonal sea ice and a stratified  
549 water column (Bowman et al., 2013a; 2013b). These same proxies show a warming trend through the  
550 middle portion of the sequence (400–600 m) coincident with the most prominent diversity increase  
551 seen in the cephalopod fauna (Tobin et al., 2012; Bowman et al., 2013a) indicating climate warming,  
552 which accords with evidence for global warming during the MME (Fig. 7; Thibault and Gardin, 2006;  
553 Friedrich et al., 2012; Jung et al., 2013).

554           Most studies of environmental changes during the MME focus on extinction and/or reduction  
555 in diversity of groups such as inoceramid bivalves (MacLeod, 1994; MacLeod et al., 1996) and rudist  
556 bivalve-dominated tropical reefs (Johnson and Kauffman, 1996), but our data suggest that in  
557 Antarctica this event saw an increase in the diversity and abundance of ammonites. A similar mid-  
558 Maastrichtian radiation event has been noted for planktonic foraminifera (MacLeod and Huber, 2001).  
559 A radiation event for ammonites at this time has also been recorded in the northwest Pacific (Jagt-  
560 Yazykova, 2011; 2012) and diversity increases in Mexico (Ifrim et al., 2004; Ifrim et al., 2010)

561 suggest a global event. Ammonites seemed to have flourished during the mid-Maastrichtian, just a  
562 few million years before their extinction.

563 In line with global temperature records (Li and Keller, 1998a; Barrera and Savin, 1999;  
564 Thibault and Gardin, 2006; Friedrich et al., 2012), temperature data from both marine and terrestrial  
565 proxies (Tobin et al., 2012; Bowman et al., 2013a, 2014; Kemp et al., 2014) in the upper López de  
566 Bertodano Formation indicate a renewed period of cooling, before a warming phase in the final two  
567 million years of the Maastrichtian (~830–980 m in composite section D5.251) (Fig. 7) which  
568 terminates prior to the K–Pg boundary in a further phase of cooling (Bowman et al., 2013a). A  
569 eustatic sea level fall just prior to the K–Pg boundary in other regions (Hancock, 1993; Surlyk, 1997;  
570 Hallam and Wignall, 1999; Kominz et al., 2008; Haq, 2014) is not clearly manifest in Antarctica,  
571 although abundance peaks of the dinoflagellate cyst genus *Manumiella* in the upper portion of the  
572 López de Bertodano Formation may record regional water depth changes (Thorn et al., 2009).

573 Despite the oscillations in temperature and sea level, late Maastrichtian ammonite diversity in  
574 Antarctica remained stable (Fig. 7). Shorter-term environmental changes may, however, be  
575 responsible for an intriguing feature in the late Maastrichtian interval on Seymour Island: notably the  
576 brief stratigraphic appearance of several ammonite species. Thus, *Pachydiscus (Pachydiscus)*  
577 *riccardii* occurs in large numbers between 780–830 m in our composite section and *Pachydiscus*  
578 *(Pachydiscus) ultimus* is abundant between 940–970 m ‘ootacodensis’ and *Zelandites varuna* are  
579 restricted to short intervals in the middle portion of C31N and directly beneath the K–Pg boundary  
580 respectively (Fig. 4) (Macellari, 1986; Zinsmeister, 2001).

581 The pachydiscid occurrences could be related to brief warming pulses; the appearance of  
582 *Pachydiscus (Pachydiscus) riccardii* coincides with the onset of climate warming recorded in the  
583 upper López de Bertodano Formation (Tobin et al., 2012; Bowman et al., 2013a), whilst *Pachydiscus*  
584 *(Pachydiscus) ultimus* appears in an interval where Tobin et al. (2012) record their most negative  
585 oxygen isotope values from macrofossil shell material, and therefore highest seawater temperatures  
586 (Fig. 7). This warming interval in chron C29R is seen globally (e.g. Stott and Kennett, 1990; Li and

587 Keller, 1998b; Wilf et al., 2003; Thibault et al., 2010; Tobin et al., 2012) and is often linked to the  
588 onset of the main eruptive phase of the Deccan Traps (Olsson et al., 2001; Chenet et al., 2009;  
589 Thibault and Gardin, 2010; Courtillot and Fluteau, 2010). *Pachydiscus* (*Pachydiscus*) cf.  
590 ‘*ootacodensis*’ is probably closely related to taxa recorded from the Campanian – Maastrichtian of the  
591 Pacific northwest (Usher, 1952; Jones, 1963) and its appearance on Seymour Island within chron  
592 C31N appears to coincide with evidence from lower latitudes of changes in microfossil faunas and  
593 floras, perhaps linked to ocean circulation and/or climatic changes that promoted biotic exchanges  
594 between the Indo-Pacific/Tethyan and Austral regions (e.g. Thibault et al., 2010).

595         In terms of the appearance of *Zelandites varuna* in the very latest Maastrichtian, taxa assigned  
596 to this species also appear just below K–Pg boundary interval in the northwest Pacific (Jagt-  
597 Yazykova, 2011; 2012) and possibly the western Tethys (Ward and Kennedy, 1993), but the  
598 significance of these simultaneous occurrences and possible links to environmental change is unclear.  
599 A brief period of global cooling is recorded worldwide immediately prior to the K–Pg boundary  
600 following the global warming event in chron C29R (Li and Keller, 1998a; 1998b; Wilf et al., 2003)  
601 which we suggest could have influenced the distribution pattern of this wide-ranging taxon,  
602 considered a cool water specialist (e.g. Ifrim et al., 2004).

#### 603 *6.4 Comparison to patterns seen in other faunal groups*

604         The new ammonite diversity data and comparisons with evidence for established  
605 Maastrichtian environmental changes show intriguing similarities with patterns exhibited by other  
606 faunal groups during the Maastrichtian, which suggest a common cause. Calcareous nannofossil  
607 assemblages in the Southern Ocean during the Campanian are largely composed of cosmopolitan taxa  
608 with a low degree of endemism (Huber and Watkins, 1992). This pattern changes during the  
609 Campanian–Maastrichtian transition with the rise of a distinct Austral Province composed of  
610 primarily endemic taxa (Huber and Watkins, 1992), which appears to mirror the rise of the distinctly  
611 Austral kossmaticeratid-dominated ammonite fauna during the same time interval. This pattern is  
612 reversed during the Maastrichtian with a return to assemblages containing mostly cosmopolitan taxa

613 (Huber and Watkins, 1992), perhaps indicating a response to climate amelioration. Despite this, both  
614 nannofossil and planktonic foraminifera exhibit a series of pole- and equator-ward migrations  
615 throughout the Maastrichtian, linked to the climate changes described above (Huber, 1991; Huber and  
616 Watkins, 1992; MacLeod and Huber, 2001; Thibault and Gardin, 2006, 2010). Despite these  
617 fluctuations, diversity in both groups remains high during the latest Maastrichtian, before a sudden  
618 and catastrophic extinction event at the K–Pg boundary (e.g. Arenillas et al., 2000; Bown, 2005).

619           New high resolution sampling and stratigraphic range data of ammonoid and nautiloid  
620 cephalopods from the highly expanded Maastrichtian López de Bertodano Formation on Seymour  
621 Island, Antarctica allow a detailed examination of diversity changes in the few million years before  
622 the K–Pg extinction event. Comparison of this data with newly developed age models has also  
623 allowed us to place this unique high latitude record in a global context for the first time. In summary;

- 624           1. We confirm a sudden extinction of ammonites at the K–Pg boundary in Antarctica was  
625 coincident with extinctions seen in other macro and microfossil groups. In total seven  
626 ammonite species belonging to seven genera range to the final few meters below the  
627 boundary, with only a single genus disappearing prior to this in the late Maastrichtian.
- 628           2. On Seymour Island there is no evidence for a significant reduction in the diversity of the  
629 ammonite fauna prior to a sudden mass extinction at the K–Pg boundary, despite evidence  
630 for dynamic environmental fluctuations during this interval. These data from the high  
631 southern latitudes are in accordance with those from well-studied lower latitude sections  
632 in the Tethyan and Boreal regions, and indicate no evidence of elevated extinction rates  
633 for ammonites globally prior to the sudden K–Pg mass extinction event.
- 634           3. On a longer time-scale, ammonite diversity in the James Ross Basin during the Late  
635 Cretaceous was controlled by a combination of sea level and temperature change. During  
636 the Santonian–early Campanian sea level appears to have been the dominant control, but  
637 during the late Campanian–Maastrichtian, data from the Snow Hill Island and López de  
638 Bertodano Formations indicate a long-term global cooling trend which began during the  
639 Campanian and reached its peak across the Campanian–Maastrichtian boundary, appears

640 to have led to the exclusion of a large number of common cosmopolitan ammonite genera  
641 from the James Ross Basin. This faunal change was coincident with the rise to dominance  
642 of endemic Austral ammonite taxa, and regional extinction events and temporary  
643 disappearances recorded by other molluscan groups such as inoceramid bivalves and  
644 belemnites.

645 4. Ammonites appear to have suffered a crisis in the early Maastrichtian of the James Ross  
646 Basin, with a low diversity assemblage in the basal López de Bertodano Formation on  
647 Seymour Island comprising just two species, and coincident with evidence for both  
648 shallow waters and low temperatures. Diversity increased during the mid-Maastrichtian, a  
649 period of climatic warming and sea level rise, which correlates with evidence from lower  
650 latitudes for a distinct 'Mid-Maastrichtian Event' at this time. Despite its apparent global  
651 nature, the effect of this event appears to vary according to taxonomic group, whereas  
652 some (inoceramid and rudist bivalves) suffer extinction, others such as ammonites and  
653 planktonic foraminifera appear to radiate and diversify. In Antarctica this event coincides  
654 with an influx of cosmopolitan ammonite taxa and proliferation of endemic  
655 kossmaticeratids.

656 5. Short term environmental changes during the late Maastrichtian (chrons C31N–29R) may  
657 be responsible for the brief stratigraphic appearances of a number of ammonite species in  
658 the Seymour Island succession prior to the K–Pg extinction event. These fluctuations  
659 show intriguing similarities with short-term changes recorded globally by microfossil  
660 groups such as calcareous nannofossil and planktonic foraminifera during the  
661 Campanian–Maastrichtian, suggesting a common cause – most likely dynamic short-term  
662 climate changes which allowed biotic exchange between low and high latitude  
663 assemblages. These oscillations do not appear to have had a deleterious effect on the  
664 overall diversity of ammonite faunas prior to the K–Pg extinction event.

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678

679 **Appendix 1: Identification and taxonomy of Antarctic Maastrichtian Cephalopoda**

680 *Stratigraphic notes*

681 For the 1999 field season each individual specimen received its own unique code number (e.g.  
682 DJ.953.100). The first portion of the code refers to the section line itself, whilst the second is a  
683 numerical code unique to the individual specimen.

684 For the 2006 field season sample numbers refer to location and fossil sample number. E.g. D5.1132.2  
685 refers to sample 2 from site D5.1132. Each fossil has a unique number and GPS location record.

686 Reference is also made to specimens collected by earlier workers from Seymour Island (e.g.  
687 Macellari, 1986; Zinsmeister, 2001), currently housed at the Paleontological Research Institute (PRI),  
688 Ithaca, NY, USA. Each sample in the PRI database is assigned a unique catalogue number (e.g.  
689 60882). Images of these specimens and associated notes are available online via the PRI Collections  
690 Database – [www.pricollectionsdatabase.org](http://www.pricollectionsdatabase.org)

691 *Systematic notes*

692 Order AMMONOIDEA von Zittel, 1884

693 Suborder LYTOCERATINA Hyatt, 1900

694 Superfamily TETRAGONITOIDEA Hyatt, 1900

695 Family GAUDRYCERATIDAE Spath, 1927

696 Genus ANAGAUDRYCERAS Shimizu, 1934

697 *Anagaudryceras seymouriense* Macellari, 1986

698 Fig. 5A

699 *Material*: 14 specimens (Tables S1, S2).

700 Despite varying degrees of preservation, all specimens in the present study compare favourably with  
701 previous descriptions of the genus (e.g. Howarth, 1965; Kennedy and Klinger, 1979; Hoffman, 2010),

702 and specimens assigned to the species *Anagaudryceras seymouriense* from Antarctica by Macellari  
703 (1986) (e.g. PRI# 58197, 58222, 60882, 58052, and 58743) and from the NW Pacific by Maeda et al.  
704 (2005). A number of internal moulds show ontogenetic change typical for this genus from small  
705 evolute juveniles with a depressed whorl section to larger, more involute adults with a slightly more  
706 compressed whorl outline. Evolute juveniles show gaudryceratid ornament of very fine ribbing on the  
707 flanks, which changes to smoother ornamentation comprising fine flexuous lirae and occasional fold-  
708 like ribs or undulations in larger ( $D > 65$  mm) sub-adult and adult examples. Constrictions are  
709 apparent on juvenile examples but disappear on specimens greater than ~130 mm in diameter  
710 (Macellari, 1986). Rare fragments of very large individuals ( $D > 200$  mm) containing well-preserved  
711 septal lobes and sutures are found associated with glauconite sandstone horizons in the upper López  
712 de Bertodano Formation (Zinsmeister, 2001) (e.g. DJ.952.1, DJ.952.335, DJ.952.423,). This species  
713 is found throughout the mid-upper (~650 – 1003 m in our sections) Maastrichtian on Seymour Island,  
714 with the stratigraphically highest recorded occurrence a number of external moulds of small evolute  
715 examples found in a 5m interval below the K–Pg boundary (DJ.953.689).

716

717 Genus ZELANDITES Marshall, 1926

718 *Zelandites varuna* (Forbes, 1846)

719 Fig. 5B

720 *Material*: 2 specimens.

721 These two specimens include one poorly preserved internal mould and cast embedded in well-  
722 cemented glauconitic sandstone layer, and one well-preserved internal mould retaining phragmocone  
723 and portion of body chamber as well as external ornament. Although both appear to be juveniles, they  
724 are very similar to those collected by previous workers (e.g. PRI# 61169) and described by Macellari  
725 (1986). *Zelandites varuna* is characterised by a compressed whorl section (Wb/Wh ratio of ~0.7  
726 (DJ.953.684)) with a narrow umbilicus and an initially evolute shell, become more involute through  
727 ontogeny. This species generally shows weak ornament consisting of very fine growth lines or lirae

728 and occasional prominent constrictions on the flanks – although these are absent in our specimens,  
729 perhaps because this feature is only present in larger examples, as noted by Macellari (1986) (e.g.  
730 PRI# 61262). All examples of this species found on Seymour Island appear to be from a short  
731 stratigraphic interval immediately below the K–Pg boundary (see also Zinsmeister, (2001). Salazar et  
732 al. (2010) suggested that specimens from Antarctica described by Macellari (1986) as *Zelandites*  
733 *varuna* differ from other examples of the species in terms of whorl breadth and whorl height  
734 (Wb/Wh) as well as changes during ontogeny. However, it appears this conclusion is based on an  
735 erroneous plot of data from Macellari (1986) who presented shell measurements in cm rather than mm  
736 (Compare Macellari, 1986 – Table 2, p.16 with Salazar et al., 2010 – Fig.12. p.197). Correcting this  
737 and comparing measurements of the best preserved of our samples (DJ.953.684) with those compiled  
738 by Salazar et al. (2010), indicates the Antarctic material sits comfortably within the ontogenetic  
739 growth curve expected for *Zelandites varuna* and should therefore remain assigned to this species.

740

741 Family TETRAGONITIDAE Hyatt, 1900

742 Subfamily TETRAGONITINAE Hyatt, 1900

743 Genus PSEUDOPHYLLITES Kossmat, 1895

744 *Pseudophyllites cf. loryi* (Kilian and Reboul, 1909)

745 Fig. 5C

746 *Material*: 14 specimens.

747 Many of these specimens are rather small and poorly preserved examples commonly found embedded  
748 within well-cemented glauconite-rich sandstone layers in the mid – upper (700 – 830 m) portion of  
749 the López de Bertodano Formation hence why they are left in open nomenclature. Nonetheless, a  
750 number of these specimens contain identifiable sutures (e.g. D5.1164.2; DJ.957.529) and  
751 morphological features which compare favourably with material described from the James Ross Basin  
752 by previous workers as *Pseudophyllites loryi* and its synonyms such as *Pseudophyllites peregrinus*  
753 (e.g. Spath, 1953; Macellari, 1986) (PRI# 58284, 58728, 60434, 58193). Several large (>100 mm)

754 but deformed internal moulds with the suture visible were found in the basal portion (330 – 350 m) of  
755 the López de Bertodano Formation (D5.855.2, D5.875.2). *Pseudophyllites loryi* is separated from  
756 other species of *Pseudophyllites* by to its evenly rounded whorl section, broader venter, and vertical  
757 rather than inclined umbilical wall. At least one of our specimens (DJ.957.189) also preserves  
758 evidence of extremely fine ribbing/lirae as noted by Macellari (1986). Differentiation between the  
759 various species of *Pseudophyllites* present in the Late Cretaceous is challenging and many have  
760 passed into synonymy. Generally speaking three species are recognised: *Pseudophyllites indra*  
761 (Forbes, 1846), which ranges from the Santonian to the latest Maastrichtian and has a virtually  
762 pandemic distribution (Kennedy and Klinger, 1977; Kennedy and Summesberger, 1986; Ward and  
763 Kennedy, 1993; Kennedy and Hancock, 1993), *Pseudophyllites loryi* (Kilian and Reboul, 1909) and  
764 its junior synonyms *Pseudophyllites latus*, *Pseudophyllites whangaroaensis* (Marshall, 1926),  
765 *Pseudophyllites peregrinus* (Spath, 1953) and *Pseudophyllites skoui* (Birkelund, 1965), which range  
766 from the Santonian - Campanian to the latest Maastrichtian of Antarctica, New Zealand, Australia,  
767 and Greenland, and finally *Pseudophyllites teres* (van Hoepen, 1920), known only from the Santonian  
768 - Campanian of South Africa and Madagascar (Kennedy and Klinger, 1977). *Pseudophyllites loryi* is  
769 clearly quite a rare taxon on Seymour Island, which coupled with the generally small size of the  
770 majority of our specimens perhaps indicates why our records do not match those of Zinsmeister  
771 (1998) in terms of the highest stratigraphic occurrence of this genus in Antarctica.

772

773 Suborder AMMONITINA Hyatt, 1889

774 Superfamily DESMOCERATACEAE von Zittel, 1895

775 Family DESMOCERATOIDEA von Zittel, 1895

776 Subfamily PUZOSIINAE Spath, 1922

777 Genus KITCHINITES Spath, 1922

778 *Kitchinites* sp.

779 Fig. 6E

780 *Material*: 53 specimens

781 This species is a common component of the ammonite fauna throughout the middle portion of the  
782 López de Bertodano Formation, occurring between 525 and 673 m in our composite section.  
783 Specimens generally show a relatively compressed whorl section (Wb/Wh ratio of 0.6), prominent  
784 prorsiradiate to rectiradiate constrictions on an otherwise smooth umbilical wall which become  
785 strongly projected forwards as they cross the venter, and coarse forwardly projected ribbing on the  
786 ventral margin. This species was previously described as *Kitchinites darwini* by Del Valle and Rinaldi  
787 (1976) and Macellari (1986), based on comparison with material from the Quiriquina Formation in  
788 Chile by Steinmann (1895) and subsequently Stinnesbeck (1986). Salazar et al. (2010) suggested  
789 separation of the Antarctic material from *Kitchinites darwini*, based on new collections from  
790 Quiriquina which showed differences in shell thickness and whorl outline; although it is clear that  
791 Maastrichtian examples of the genus from Chile and Antarctica are closely related. A comprehensive  
792 redescription of this species is beyond the scope of the present study so following Salazar et al. (2010)  
793 we prefer to leave our material as *Kitchinites* sp.

794 *Kitchinites laurae* Macellari, 1986

795 Fig. 5F

796 *Material*: 13 specimens

797 Although many of our specimens are fragmentary or rather poorly preserved, this taxon shows a  
798 number of morphological features which allow clear differentiation from *Kitchinites* sp. (compare  
799 PRI# 58669 (*Kitchinites* sp.) and PRI# 58309 (*Kitchinites laurae*). It typically exhibits a more inflated  
800 whorl section (Wb/Wh ratio of 0.7), much wider venter, more subdued constrictions, and the presence  
801 of fine prorsiradiate ribbing on the upper flanks which becomes subdued across the ventral margin.. It  
802 appears to be rare in the upper Maastrichtian on Seymour Island, occurring sporadically between 679  
803 and 987 m in our sections, and was previously recorded from a stratigraphic interval directly beneath  
804 the K–Pg boundary (e.g. Zinsmeister 1998).

805

806 Family KOSSMATICERATIDAE Spath, 1922

807 Subfamily KOSSMATICERATINAE Spath, 1922

808 Genus MAORITES Marshall, 1926

809 *Maorites densicostatus* (Kilian and Reboul, 1909)

810 Fig. 6B

811 *Material*: 194 specimens.

812 A full description of this species and its various synonyms is provided by Macellari (1986) and  
813 Macellari (1988). Typically for the genus, *Maorites densicostatus* appears to exhibit a large degree of  
814 morphological variation, but is easily separated from other species of the genus. Specimens from  
815 Seymour Island were separated into three morphotypes by Macellari (1986),  $\alpha$ ,  $\beta$ , and  $\gamma$ , based mainly  
816 on patterns of external shell ornament such as ribbing density and number of constrictions. The  
817 stratigraphic ranges of these morphotypes appear to overlap, so for our purposes we refer to them as a  
818 single species which occurs between 730 and 1006 m in the composite section. As hypothesised by  
819 Macellari (1986), we suggest these morphotypes may relate to sexual dimorphism; certainly there are  
820 places in the upper Maastrichtian portion of the López de Bertodano Formation on Seymour Island  
821 where adult specimens of *Maorites densicostatus* exhibit a wide range of different sizes and external  
822 ornament at the same stratigraphic horizon. All morphotypes of this species are characterised by an  
823 involute shell, compressed whorl section (typical Wb/Wh ratio of ~0.45 – 0.57), and the presence of  
824 fine ribbing and constrictions in both adult and juvenile examples, often forming small nodes when  
825 several ribs meet at the umbilical margin. Morphotype  $\alpha$  (e.g. DJ.952.144) typically shows 10 – 12  
826 ribs in 1 cm at a whorl height of 3 cm, whereas morphotypes  $\beta$  (e.g. DJ.952.252) is characterised by  
827 12 – 14 ribs, and  $\gamma$  typically only shows 6 – 7 ribs per 1 cm at an equivalent whorl height. *Maorites*  
828 *densicostatus* shows potential as a good stratigraphic marker for the upper Maastrichtian in the  
829 Southern Hemisphere, with occurrences in Australia (Henderson and McNamara, 1985), South

830 America (Macellari, 1988; Olivero et al., 2009), South Africa (Kennedy and Klinger, 1985), and New  
831 Zealand (Henderson, 1970). Small specimens are also present in the Sandwich Bluff Member of the  
832 López de Bertodano Formation on Vega Island, and indicate at least a portion of this deposit to be of  
833 late Maastrichtian age (Pirrie et al, 1991).

834 *Maorites seymourianus* (Kilian and Reboul, 1909)

835 Fig. 6D

836 *Material:* 70 specimens.

837 This species can easily be separated from *Maorites densicostatus* due to its wider umbilicus and thus  
838 more evolute shell, coarser ribbing in adult specimens (5 – 10 ribs in 1 cm at a whorl height of 3 cm),  
839 and more rounded whorl section (typical Wb/Wh ratio of 0.6 – 0.72). Separation from *M. tuberculatus*  
840 is mainly possible based on the absence of prominent umbilical tubercles, and straighter and less  
841 numerous constrictions. Changes between the three species of *Maorites* present in the López de  
842 Bertodano Formation appear to occur over narrow stratigraphic intervals, with little evidence of  
843 transitional forms present. As noted by Macellari (1986) specimens of *Maorites seymourianus* appear  
844 to exhibit a wide range of variation with regard to key morphological features such as shell ornament  
845 and size of adult specimens which like *Maorites densicostatus*, may be related to sexual dimorphism.  
846 This species is very common throughout the middle portion of the López de Bertodano Formation  
847 between 440 and 719 m in the composite section.

848 *Maorites tuberculatus* Howarth, 1958

849 Fig.6C

850 *Material:* 17 specimens.

851 All our specimens compare favourably with the descriptions by Howarth (1958) and Macellari (1986)  
852 (e.g. PRI# 58278). Examples of *Maorites tuberculatus* are generally small, with rounded flanks and  
853 exhibit somewhat tighter coiling of the shell than is seen in *Maorites seymourianus* or *Maorites*  
854 *densicostatus*. The combination of prominent and numerous umbilical tubercles (up to 16 per whorl),

855 numerous and flexuous constrictions (up to 9 per whorl), and fine ribbing also allow differentiation  
856 from other kossmaticeratids present on Seymour Island. This species has previously reported from the  
857 interval directly above the unconformable contact between the Haslum Crag Member of the Snow  
858 Hill Island Formation and the basal López de Bertodano Formation (Olivero et al, 2007; 2008;  
859 Olivero, 2012) where it is the marker species for the base of the MG stratigraphic sequence and  
860 ammonite assemblage 11 of Olivero (2012), but first appears in the composite section of the present  
861 study 235 m above this level..

862 *Maorites cf. weddelliensis* Macellari, 1986

863 Fig. 6A

864 *Material:* 6 specimens.

865 This species first identified by Macellari (1986) is separated from other examples of *Maorites* on  
866 Seymour Island based on the presence of coarse ribbing in both juvenile and adult examples, flat  
867 flanks, an evenly rounded venter, prominent tubercles on the umbilical margin, and incised  
868 constrictions with a thick adapical border. We tentatively assign several specimens which compare  
869 favourably with those presented by Macellari (1986) (e.g. PRI# 58731) to this species, but note that  
870 many of the features used to separate this from other species also assigned to *Maorites* in the López  
871 de Bertodano Formation appear to vary among individual specimens.

872

873 Genus: GROSSOUVRITES Kilian and Reboul 1909

874 *Grossouvrites johare* Salazar, 2010

875 Fig. 5E

876 *Material:* 100 specimens.

877 This distinctive taxon is abundant through most of the López de Bertodano Formation on Seymour  
878 Island and is easily separated from other species of kossmaticeratid. It exhibits a compressed whorl

879 outline (typical Wb/Wh ratio of 0.8), with vertical almost flat flanks ornamented by thick radial ribs,  
880 which arise in either pairs or threes from prominent tubercles at the umbilical margin. Juvenile  
881 specimens can also show constrictions. Several large and complete adult specimens containing the  
882 aperture are found among our samples (DJ.952.24, DJ.952.336, DJ.952.757, DJ.952.707, D5.1176.2  
883 (x3)). Specimens assigned to *Grossouvrites* are widely distributed in the Late Cretaceous of the  
884 Southern Hemisphere with records from the Campanian – Maastrichtian of Antarctica (Macellari,  
885 1986; Olivero, 1992, 2012), South America (Macellari, 1988; Salazar et al, 2010), New Zealand  
886 (Marshall, 1926; Henderson, 1970) and Australia (Henderson and McNamara, 1985; McNamara et al,  
887 1988), the majority of which have traditionally been assigned to the type species *Grossouvrites*  
888 *gemmatus* (Hupé, 1854). However, differences in shell outline and ornament as well as changes  
889 throughout ontogeny have led some authors to suggest several of these may represent distinct species  
890 (e.g. Macellari, 1988; Salazar et al, 2010). In their restudy of material from Quiriquina, Chile, Salazar  
891 et al. (2010) split *Grossouvrites* into two distinct species; *Grossouvrites gemmatus* and *Grossouvrites*  
892 *johare*, in the latter of which they included material described from Antarctica by Macellari (1986)  
893 and earlier authors (Kilian and Reboul, 1909; Howarth, 1958). Macellari (1986) claimed that  
894 specimens of *Grossouvrites* in the mid portion of the sequence on Seymour Island were characterised  
895 by flatter flanks and a more compressed whorl section than those found stratigraphically higher, but  
896 did not consider this grounds for separation into two species. Several of our specimens are crushed  
897 which can lead to difficulty in accurately ascertaining the range of variation in whorl outline. We  
898 follow Salazar et al. (2010) in identifying the Antarctic material as *Grossouvrites johare*. Previous  
899 authors have recorded this taxon (as *Grossouwrite gemmatus*) from the interval directly beneath the  
900 K–Pg boundary (Zinsmeister, 1998).

901

902 Family PACHYDISCIDAE Spath, 1922

903 Genus PACHYDISCUS von Zittel, 1895

904 *Pachydiscus (Pachydiscus) ultimus* Macellari, 1986

905 Fig. 6F

906 *Material*: 29 specimens.

907 This large pachydiscid is easily identified by its very involute shell, compressed whorl outline with  
908 flanks sloping gently from maximum width near the umbilicus, sparse ornament consisting of  
909 prominent forwardly projecting umbilical ribs and finer ribs across the venter which disappear  
910 towards mid-flank. Like other pachydiscids in the López de Bertodano Formation, it exhibits a rather  
911 restricted stratigraphic range; with large adult examples appearing suddenly some 62 m below the K–  
912 Pg boundary and persisting for only ~30 m before disappearing. There is no evidence that this or any  
913 other pachydiscid reaches the K–Pg boundary in any of our section lines.

914 *Pachydiscus (Pachydiscus) riccardii* Macellari, 1986

915 Fig. 6G

916 *Material*: 19 specimens.

917 As noted by Macellari (1986), this species can be differentiated from *Pachydiscus (Pachydiscus)*  
918 *ultimus* by its more inflated whorl section, the presence of rectiradiate nodes on the umbilicus, and  
919 radial ribbing which is conspicuous across the whole flank in juvenile specimens, but absent in adults.  
920 Like *Pachydiscus (Pachydiscus) ultimus* the suture is complex and typical for the genus. *Pachydiscus*  
921 *(Pachydiscus) riccardii* is abundant for a short (25 m) stratigraphic interval in the upper López de  
922 Bertodano Formation. Poorly preserved pachydiscids from the Haumurian (Campanian –  
923 Maastrichtian) of the Chatham Islands, New Zealand have also been tentatively assigned to this  
924 species (Consoli and Stilwell, 2005), which is otherwise only found in the López de Bertodano  
925 Formation on Seymour Island.

926 *Pachydiscus (Pachydiscus) cf. ootacodensis* (Stoliczka, 1865)

927 *Material*: 1 specimen.

928 This specimen is a poorly preserved section of phragmocone with some shell material revealing  
929 external ornament, showing coarse radial ribbing on the ventral flank, an inflated whorl section, and

930 overall morphology typical of many pachydiscids (compare Kennedy and Klinger 2006). The suture is  
931 not preserved. Similar specimens from Seymour Island were described by Macellari (1986) as  
932 *Pachydiscus (Pachydiscus) ootacodensis*, a species from the Pacific Northwest of the USA and  
933 Canada (Usher, 1952; Jones, 1963) where it is found in deposits of late Campanian – early  
934 Maastrichtian age (Mustard, 1994; Shigeta et al., 2010). No systematic revision of pachydiscids from  
935 these deposits has been undertaken since the work of Jones (1963), and this single sample from  
936 Antarctica is too poorly preserved to allow for a precise identification. *Pachydiscus (Pachydiscus)*.  
937 *ootacodensis* has been used by previous authors to define a distinct biozone within the López de  
938 Bertodano Formation (Macellari, 1986; Olivero and Medina, 2000; Olivero, 2012), but as noted by  
939 Crame et al. (2004) and confirmed by the recovery of a single specimen in the present study, it is too  
940 rare on Seymour Island for this purpose.

941

942 Suborder ANCYLOCERATINA Wiedmann, 1966

943 Superfamily TURRILITOIDEA Gill, 1871

944 Family DIPLOMOCERATIDAE Spath, 1926

945 Subfamily DIPLOMOCERATINAE Spath, 1926

946 Genus DIPLOMOCERAS Hyatt, 1900

947 *Diplomoceras cylindraceum* (Defrance, 1816)

948 Fig. 5G

949 *Material:* 44 specimens.

950 Specimens of this very large heteromorph are present throughout the López de Bertodano Formation,  
951 and include some of the most complete examples of the genus found anywhere in the world (e.g.  
952 Zinsmeister and Oleinik, 1995). The genus is characterised by a circular whorl section, uniform  
953 ribbing, distinctive suture, and development of ‘paper clip-like’ morphology. Species-level taxonomy

954 has provoked some debate (Olivero and Zinsmeister, 1989; Kennedy and Henderson, 1992; Klinger  
955 and Kennedy, 2003; Machalski, 2012). Olivero and Zinsmeister (1989) assigned large specimens from  
956 the upper Maastrichtian (upper López de Bertodano Formation) of Antarctica to *Diplomoceras*  
957 *maximum* based mainly on changes in ribbing during ontogeny. Machalski (2012) noted that large  
958 specimens from the upper Maastrichtian of Europe also appear to conform to *Diplomoceras*  
959 *maximum*. However, differentiation of *Diplomoceras maximum* from *Diplomoceras cylindraceum* and  
960 its synonyms (e.g. *Diplomoceras lambi*) appears problematic, as pointed out by Kennedy and  
961 Henderson (1992), because specimens are extremely prone to *post-mortem* crushing. Here we follow  
962 Klinger and Kennedy (2003) and others in considering *Diplomoceras* monospecific, with  
963 *Diplomoceras cylindraceum* the single, often rather variable species. This species exhibits a pandemic  
964 distribution throughout the latest Campanian - Maastrichtian, and in common with lower latitudes first  
965 appears in Antarctica in the late Campanian Sanctuary Cliffs Member of the Snow Hill Island  
966 Formation (Pirrie et al., 1997; Olivero, 2012), remaining a common component of the ammonite  
967 fauna until directly beneath the K–Pg boundary (e.g. Landman et al., 2007).

968

969 Order NAUTILOIDEA de Blainville, 1825

970 Family NAUTILIDAE de Blainville, 1825

971 Genus EUTREPHOCERAS Hyatt, 1894

972 *Eutrephoceras dorbignyanum* (Forbes in Darwin, 1846)

973 Fig. 5D

974 *Material*: 16 specimens.

975 The taxonomy of Southern Hemisphere Late Cretaceous nautiloids has recently been reviewed  
976 (Cicholowski et al., 2005; Nielsen and Salazar, 2011). Specimens from the Maastrichtian of  
977 Antarctica and southern South America were united under the name *Eutrephoceras dorbignyanum*.  
978 All our specimens match the earlier descriptions, and are characterised by a globular shell, inflated

979 whorl section, tiny umbilicus and extremely fine ornament most often seen in juvenile specimens. A  
980 number of large incomplete adult specimens are included in the BAS collections, often showing rather  
981 flattened flanks and fine growth lines. On Seymour Island *E. dorbignyanum* first appears in the  
982 middle of the López de Bertodano Formation, and remains an occasional component of the molluscan  
983 fauna until a final occurrence directly beneath the K–Pg boundary.

984

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1554 **Figure captions**

1555

1556 **Fig. 1:** Locality and geology map of Seymour Island, James Ross Basin, Antarctic Peninsula. The  
1557 maps show modern geography. JRI, James Ross Island; BAS, British Antarctic Survey; K,  
1558 Cretaceous; Pg, Paleogene. The K–Pg boundary is shown by a dotted line and crops out within the  
1559 uppermost López de Bertodano Formation. A–B, measured sections discussed in this paper. A, BAS  
1560 1999 field season, sections DJ.959, DJ.957, DJ.952 and DJ.953 are stratigraphically continuous  
1561 (Crame et al., 2004). B, BAS 2006 field season, sub-sections D5.201, D5.212, D5.215, D5.218,  
1562 D5.219, D5.220, D5.222 and D5.229 comprise composite section D5.251 (Bowman et al., 2012,  
1563 2013a, 2014). C, Measured section trace from Tobin et al. (2012) based on GPS coordinates taken  
1564 from that study. Map after Montes et al (2010).

1565 **Fig. 2:** Lithostratigraphy, sedimentology and correlation of measured sections as located in Figure 1  
1566 (A – B), southern Seymour Island, Antarctic Peninsula. BAS, British Antarctic Survey; K,  
1567 Cretaceous; Pg, Paleogene. The K–Pg boundary horizon is identifiable using dinoflagellate cyst  
1568 biostratigraphy (Elliot et al., 1994; Askin and Jacobsen, 1996; Bowman et al., 2012), sedimentology  
1569 (the base of a prominent glauconite-rich bed, Zinsmeister, 1998) and the disappearance of ammonite  
1570 macrofossils. The age model is presented in Figure 3. The López de Bertodano Formation consists  
1571 predominantly of hundreds of metres of clayey-silts and silty-clays. In section B, the sub-section  
1572 overlap between D5.222 and D5.229 has been taken into account when interpreting the macrofossil  
1573 data.

1574 **Fig. 3:** Age model for the López de Bertodano Formation, southern Seymour Island, Antarctic  
1575 Peninsula. This sequence has been dated using biostratigraphy (palynology, micro- and macro-fossil,  
1576 e.g. Macellari, 1988; Elliot et al., 1994; Bowman et al., 2012; Olivero, 2012a; Bowman et al., 2013a),  
1577 magnetostratigraphy (Tobin et al., 2012) and strontium isotope stratigraphy (McArthur et al., 1998),  
1578 calibrated to Gradstein et al. (2012). SHI = Snow Hill Island Formation, S = Sobral Formation.

1579 **Fig. 4:** Composite range chart of cephalopod (ammonite and nautiloid) taxa from the López de  
1580 Bertodano Formation, southern Seymour Island, Antarctic Peninsula. Fossil occurrences have been  
1581 amalgamated from the DJ sections and section D5.251 to show the entire recorded range of each  
1582 taxon. Section correlation and the age model are illustrated in Figures 2 and 3, and discussed in the  
1583 text. Taxa are ordered by first appearance with 50% confidence intervals on ammonite ranges shown  
1584 as dashed red lines. Although ammonite confidence intervals span the K–Pg boundary, we believe  
1585 none survived into the Danian. Rare specimens collected above the boundary are not plotted as they  
1586 are considered reworked and their stratigraphic position probably the result of more recent glacial  
1587 drift. Tick marks are taxon occurrences plotted at the stratigraphic mid-point of sampling bins (refer  
1588 to Supplementary Figures 1 and 2). Refer to Appendix 1 for taxonomic notes. Ammonite species  
1589 names in black, nautiloid species name in grey; SHI, Snow Hill Island Formation; S, Sobral  
1590 Formation; \*, last appearance of taxa found beneath K–Pg boundary by Zinsmeister (1998).

1591 **Fig. 5:** A, *Anagaudryceras seymouriense* Macellari, 1986 (DJ.953.438); B, *Zelandites varuna* Forbes  
1592 1846 (DJ.953.684), B1– lateral view, B2 – apertural view; C, *Pseudophyllites cf. loryi* Kilian and  
1593 Reboul 1909 (DJ.957.189), C1 – lateral view, C2 – apertural view; D, *Eutrephoceras dorbignyanum*  
1594 Forbes in Darwin 1846 (D5.1011.2); E, *Grossouvrites johare* Salazar 2010 (DJ.952.756), E1 – lateral  
1595 view, E2 – ventral view; F, *Kitchinites laurae* Macellari 1986 (DJ.952.188), F1 – lateral view, F2 –  
1596 ventral view; G, *Diplomoceras cylindraceum* Defrance 1816 (D5.955.2). All figures are x 0.5 except  
1597 B and C which are x 2. Specimens were coated with ammonium chloride prior to photography.

1598 **Fig. 6:** A, *Maorites cf. weddelliensis* Macellari, 1986 (D5.691.2), A1 – lateral view, A2 – ventral  
1599 view; B, *Maorites densicostatus* Kilian and Reboul, 1909 (DJ.953.379), B1 – lateral view, B2 –  
1600 ventral view; C, *Maorites tuberculatus* Howarth, 1958 (D5.955.2); D, *Maorites seymourianus* Kilian  
1601 and Reboul 1909 (D5.1021.2); E, *Kitchinites* sp. (D5.1027.2); F, *Pachydiscus (Pachydiscus) ultimus*  
1602 Macellari, 1986 (DJ.953.404), F1 – lateral view, F2 – apertural view; G, *Pachydiscus (Pachydiscus)*  
1603 *riccardii* Macellari, 1986 (D5.251 – unlabelled). All figures are x 0.5. Specimens were coated with  
1604 ammonium chloride prior to photography.

1605 **Fig. 7:** Composite cephalopod diversity from the López de Bertodano Formation (southern Seymour  
1606 Island, Antarctic Peninsula) plotted against molluscan macrofossil oxygen isotope data (Dutton et al.,  
1607 2007; Tobin et al., 2012) regional palaeoclimate (Bowman et al., 2013a, 2014), and  
1608 sedimentological/sequence stratigraphic interpretations (Macellari, 1988; Olivero et al., 2007; Olivero  
1609 et al., 2008; Olivero, 2012a). Section correlation and the age model are illustrated in Figures 2 and 3,  
1610 and discussed in the text. Snowflake symbols indicate the possible occurrence of seasonal sea ice  
1611 based on palynological data (Bowman et al., 2013). Cephalopod diversity is represented as: (1) raw  
1612 species richness (number of species within sampling bin), circles; (2) Standing species richness:  
1613 (includes taxa that range through). See text for details of these indices and overall sampling strategy.  
1614 MME, Mid-Maastrichtian Event (e.g. Jung et al., 2013).

1615 **Fig. 8:** Composite stratigraphic abundance of uppermost Maastrichtian cephalopod taxa, López de  
1616 Bertodano Formation, southern Seymour Island, Antarctic Peninsula. Numbered squares correspond  
1617 to last appearance datum of taxa ordered stratigraphically. Red line indicates stratigraphic abundance  
1618 value of 15%, above which indicates a reliable last occurrence (Meldahl, 1990).

1619 **Fig. 9:** Stratigraphic distribution and faunal turnover of taxa present in the Late Cretaceous of the  
1620 James Ross Basin plotted against lithostratigraphy (not to scale) and biostratigraphy (ammonite  
1621 assemblages 1–14 taken from Olivero and Medina (2000) and Olivero (2012a; 2012b). Co. =  
1622 Coniacian, Sa. = Santonian, Gu. = Gustav Group, HL = Hidden Lake Formation. A = composite range  
1623 chart of taxa. Solid lines correspond to range through data; dashed lines indicate where taxon is not  
1624 recorded in two or more ammonite assemblages, i.e. temporarily absent from the basin. Horizontal  
1625 tick marks correspond to first and last appearances. Numbered ranges correspond to taxa as follows:  
1626 **1–43 = ammonite genera:** 1 = *Diplomoceras*; 2 = *Maorites*; 3 = *Anagaudryceras*; 4 = *Zelandites*; 5 =  
1627 *Kitchinites* (*Kitchinites*); 6 = *Pseudophyllites*; 7 = *Grossouvrites*; 8 = *Pachydiscus* (*Pachydiscus*); 9 =  
1628 *Gunnarites*; 10 = *Jacobites*; 11 = *Tetragonites*; 12 = *Gaudryceras* (*Gaudryceras*); 13 =  
1629 *Eupachydiscus*; 14 = *Anapachydiscus*; 15 = *Neograhamites*; 16 = *Baculites*; 17 = *Polyptychoceras*;  
1630 18 = *Astreptoceras*; 19 = *Phyllopachyceras*; 20 = *Neokossmaticeras*; 21 = *Metaplacenticeras*; 22 =  
1631 *Hoplitoplacenticeras*; 23 = *Neophylloceras*; 24 = *Natalites*; 25 = *Ryugasella*; 26 = *Parasolenoceras*;

1632 27 = *Karapadites*; 28 = *Oiphyllites*; 29 = *Hauriceras*; 30 = *Caledonites*; 31 = *Eubostriochoceras*; 32 =  
1633 *Yezoites*; 33 = *Hoploscaphites*; 34 = *Ainoceras*; 35 = *Vertebrites*; 36 = *Damesites*; 37 = *Placenticeras*;  
1634 38 = *Scaphites*; 39 = *Scalarites*; 40 = *Kossmaticeras* (*Kossmaticeras*); 41 = *Menuites*  
1635 (*Neopachydiscus*); 42 = *Perinoceras*; 43 = *Pseudoxybeloceras*. All first (FADs) and last appearance  
1636 datums (LADs) plotted at the mid-point of corresponding ammonite assemblage, except for ammonite  
1637 assemblage 14, where taxa 1–7 extend to the top of the assemblage (i.e. the K–Pg boundary). Genera  
1638 ordered based on last appearance, data from Kennedy et al., (2007) and Olivero (2012a; 2012b). **44 =**  
1639 **dimitobelid belemnites; 45 = inoceramid bivalves; 46 = nautilids** (*Eutrephoceras*). Data based on  
1640 Doyle, (1990), Crame et al., (1996), Crame and Luther, (1997), Cichowolski et al., (2005), Olivero  
1641 (2012b). B = Sedimentary cycles and relative sea-level changes identified by Olivero and Medina  
1642 (2000) and Olivero (2012a; 2012b) (N = *Natalites*; NG = *Neograhamites*–*Gunnarites*; MG =  
1643 *Maorites*–*Grossouvrites*). C = Faunal turnover data based on ammonite genera 1–43 calculated based  
1644 on difference between the number of FADs and LADs of ammonite genera in each ammonite  
1645 assemblage.

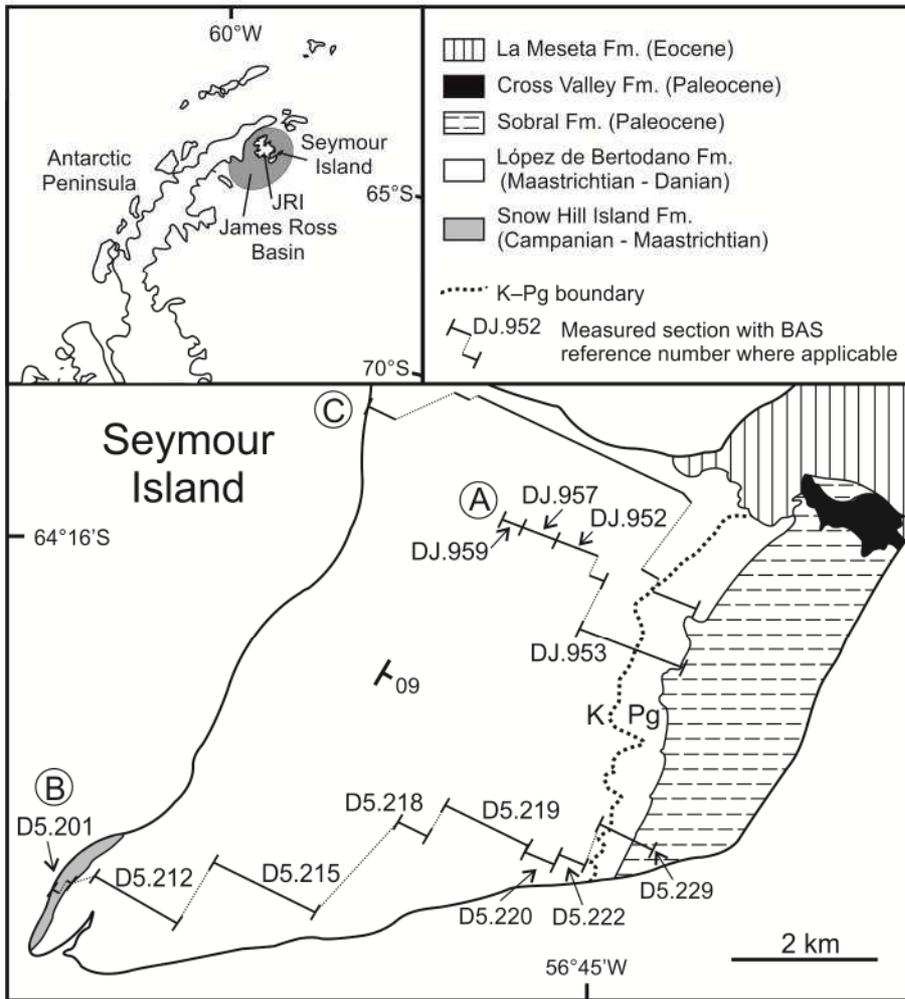
## 1646 **Supplementary figure captions**

1647 **Fig. S1:** Lithostratigraphy, sedimentology and stratigraphic range chart of cephalopod taxa from the  
1648 López de Bertodano Formation found in the 1999 BAS field season (sections DJ.959, 957, 952, 953  
1649 (see also Crame et al., 2004). See Fig. 1 (main text) for location of individual section lines and Fig. 2  
1650 for correlation with other sections. K = Cretaceous, Pg = Paleogene, S = Sobral Formation. Position of  
1651 the K–Pg boundary marked by dotted line at 398.5 m. Tick marks in stratigraphic range chart denote  
1652 individual fossil occurrences plotted at the stratigraphic mid-point of sampling bins as indicated on  
1653 the left of the figure by alternating grey squares. Sampling bins range in size from 1.5 m to 19.5 m  
1654 stratigraphic height. Taxa are ordered by first occurrence.

1655 **Fig. S2:** Lithostratigraphy, sedimentology and stratigraphic range chart of cephalopod taxa from the  
1656 López de Bertodano Formation found in the 2006 BAS field season (composite section D5.251 (see  
1657 also Bowman et al., 2012; Bowman et al., 2013; Bowman et al., 2014). See Fig. 1 (main text) for  
1658 location of individual section lines and Fig. 2 for correlation with other sections. K = Cretaceous, Pg =

1659 Paleogene, S = Sobral Formation. Position of the K–Pg boundary marked by dotted line at 1007.5 m.  
1660 Tick marks in stratigraphic range chart denote individual fossil occurrences plotted at the stratigraphic  
1661 mid-point of sampling bins as indicated on the left of the figure by alternating grey squares and lines.  
1662 Sampling bins range in size from 1 m to 7 m in stratigraphic height. Taxa are ordered by first  
1663 occurrence.  
1664

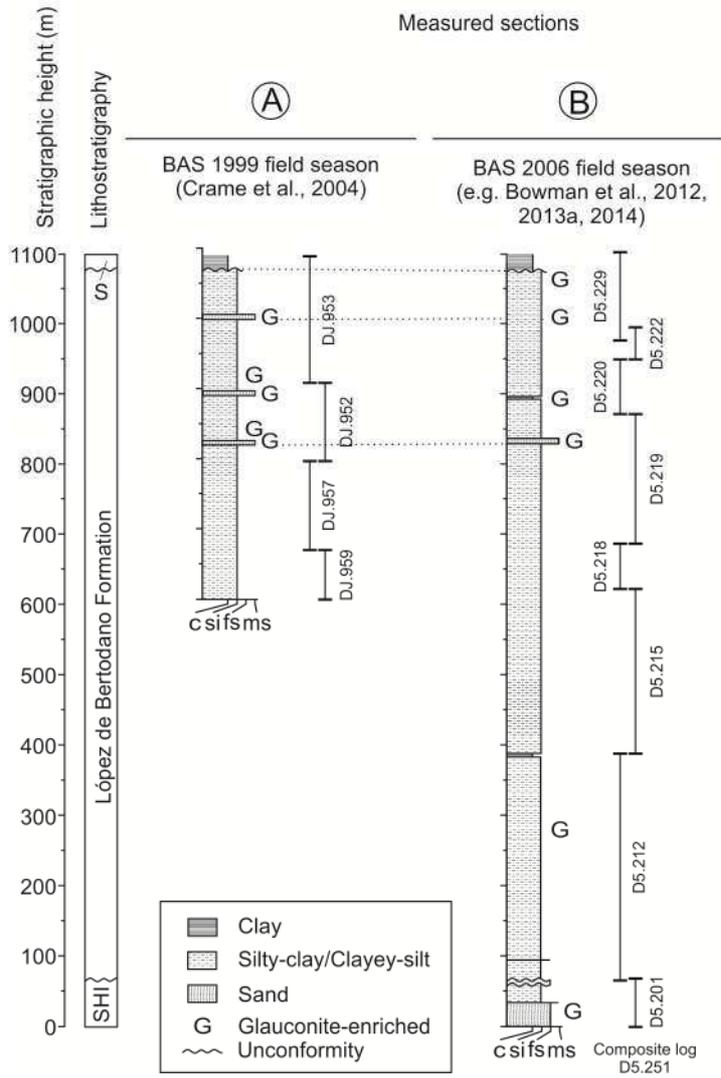
Fig. 1



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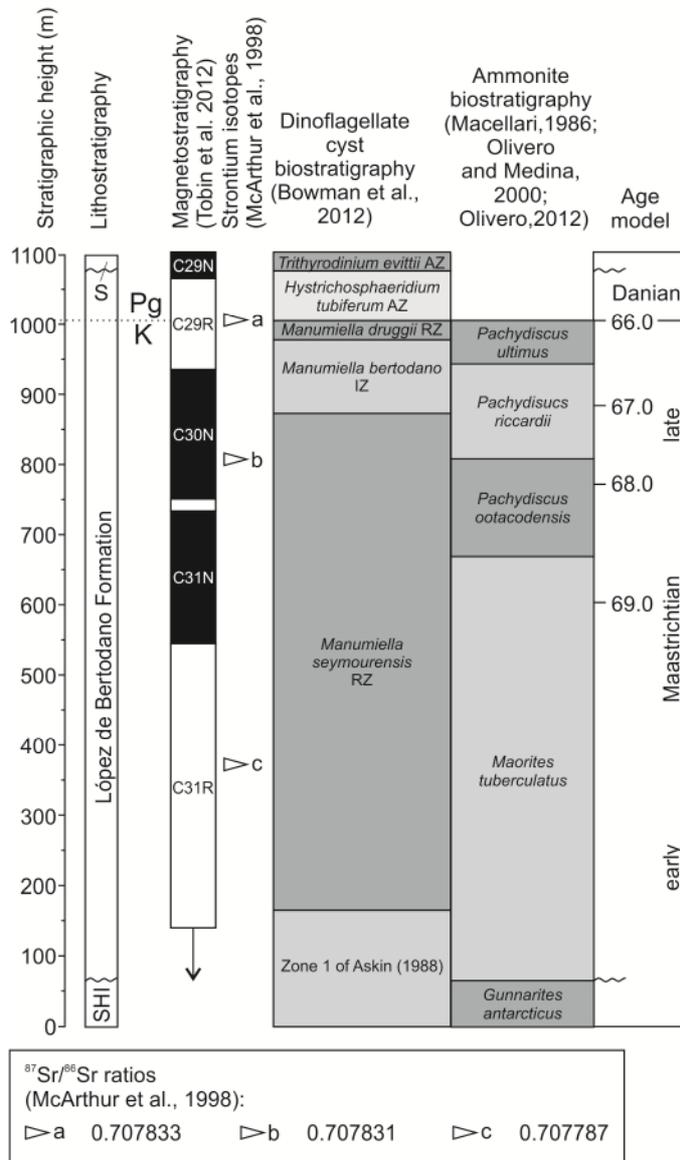
Figure 2



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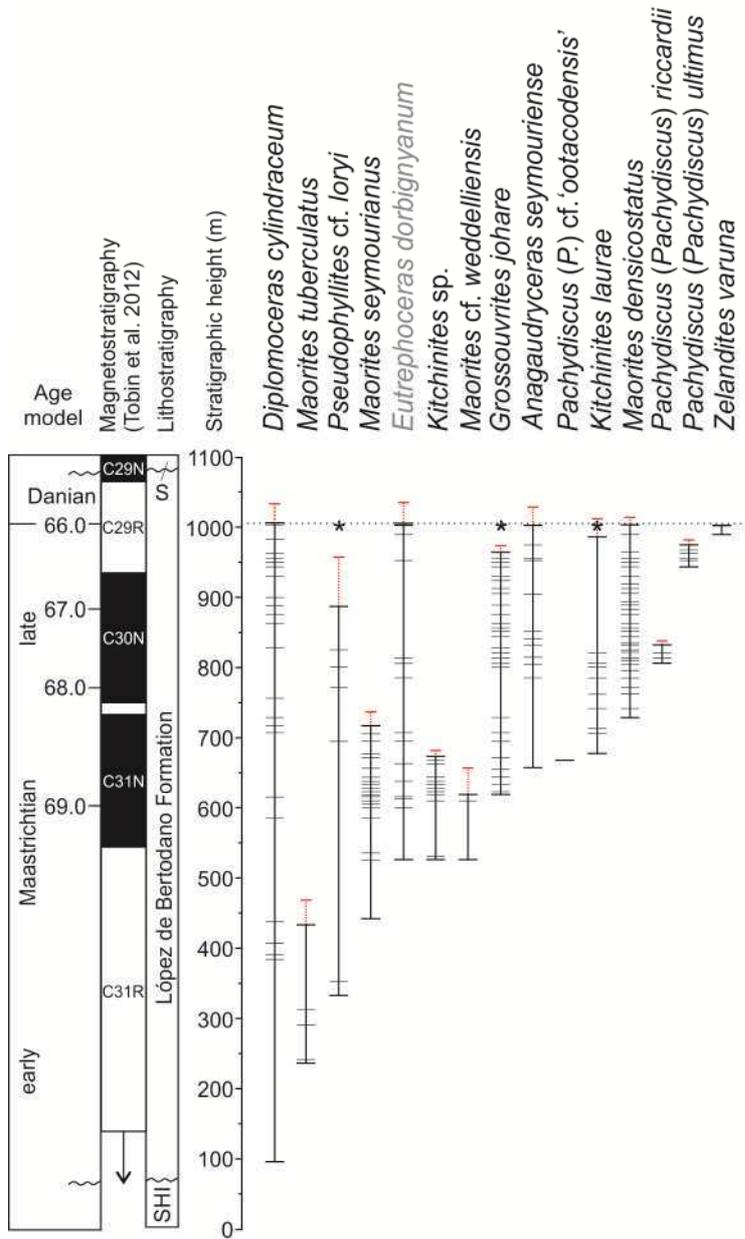
Figure 3



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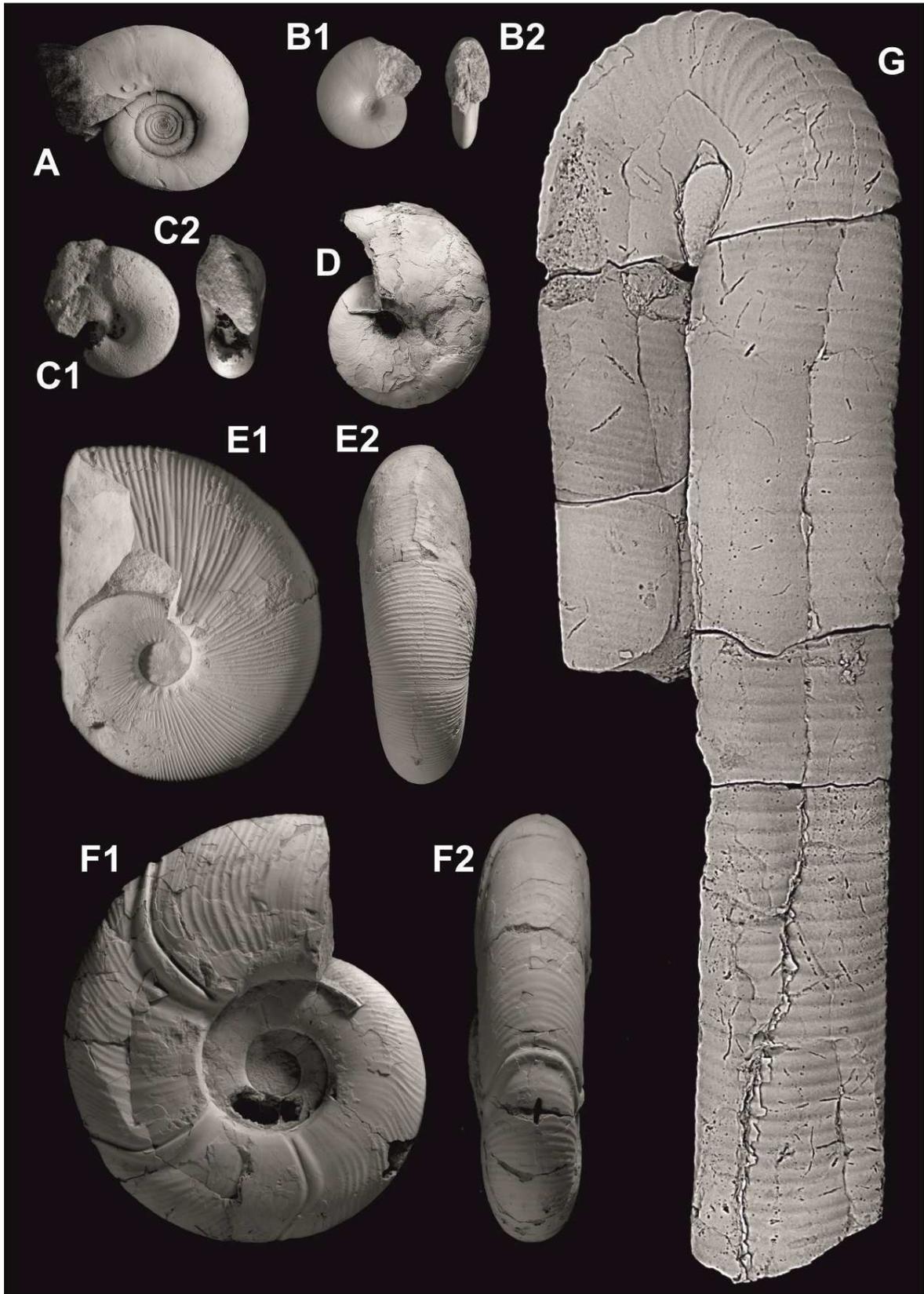
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Figure 4



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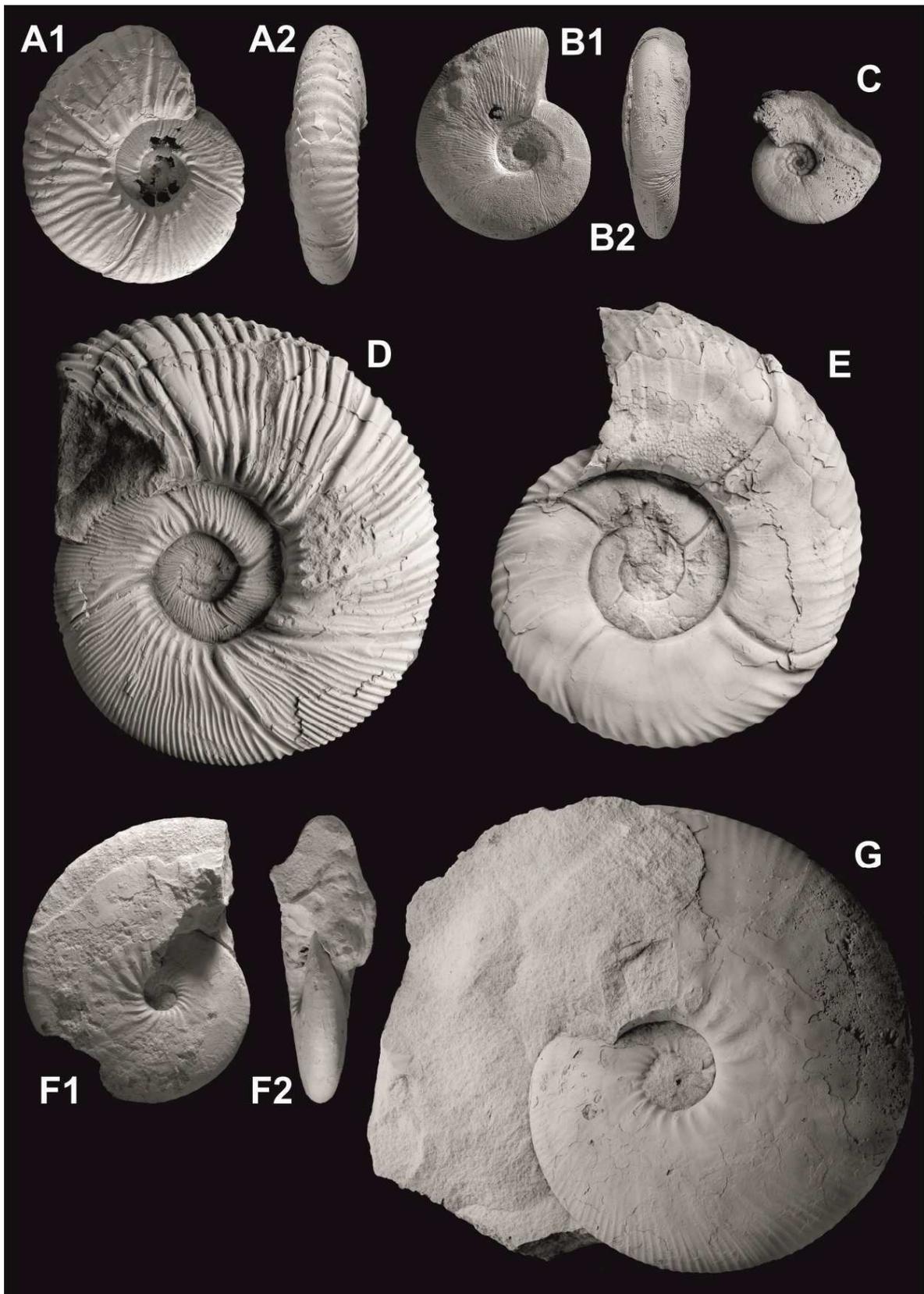
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1674 Figure 5

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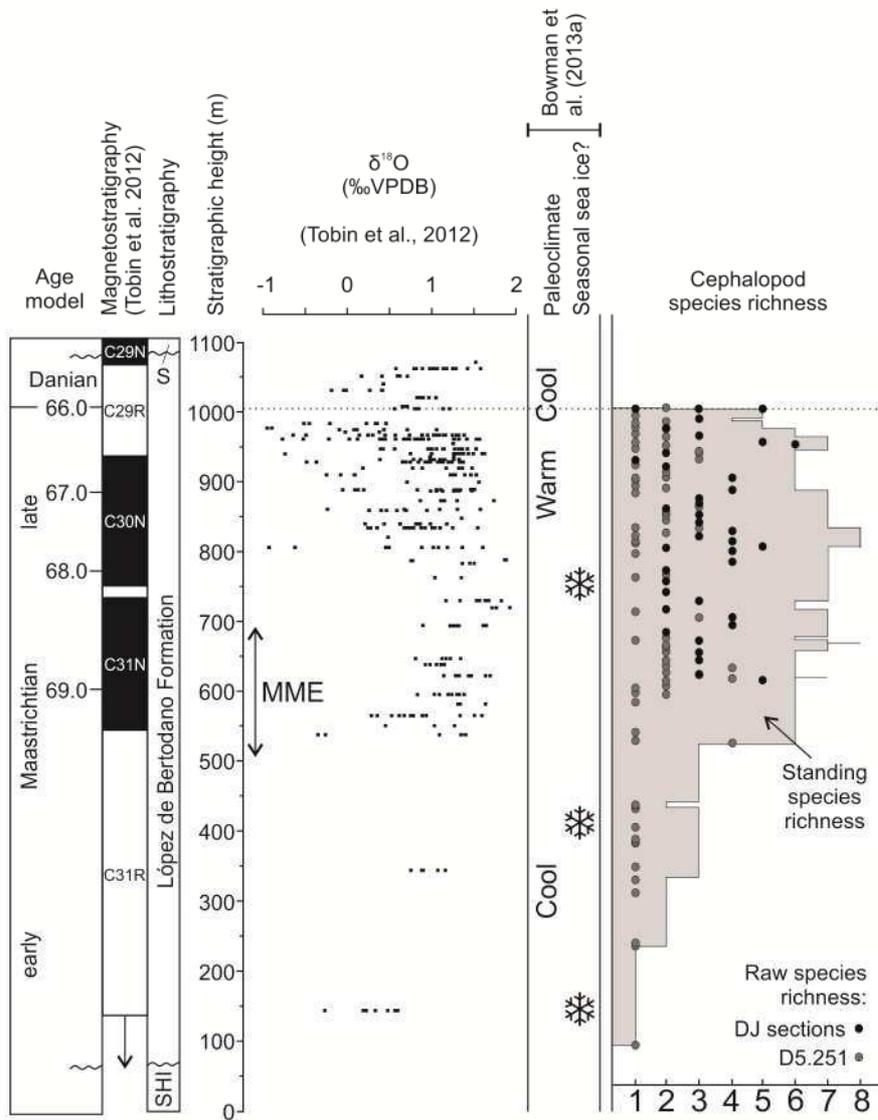


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1677 Figure 6

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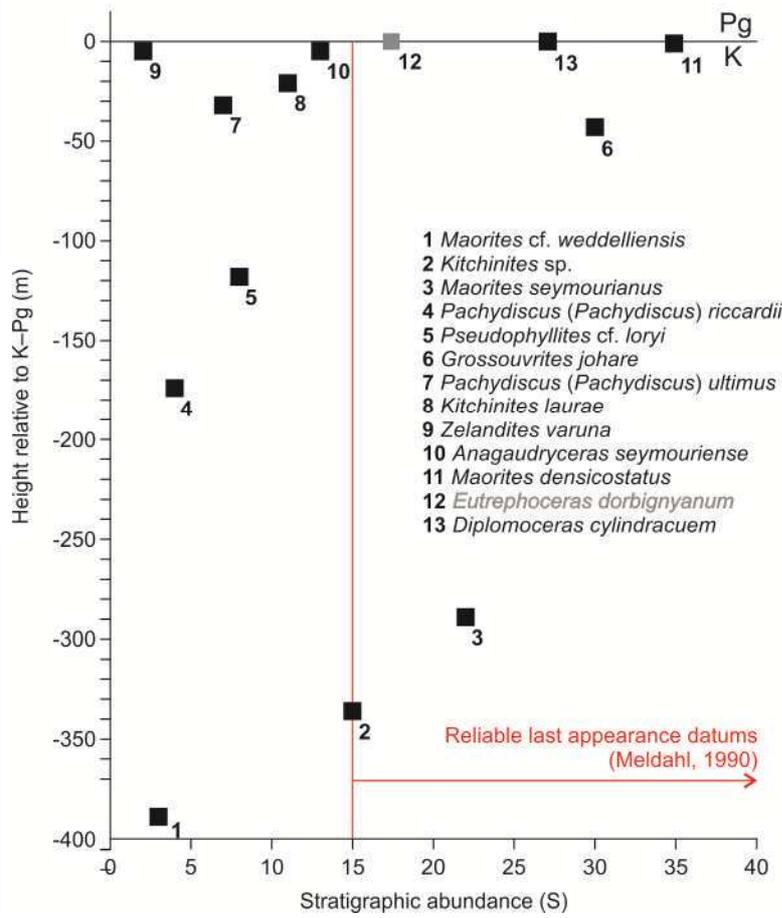
Figure 7



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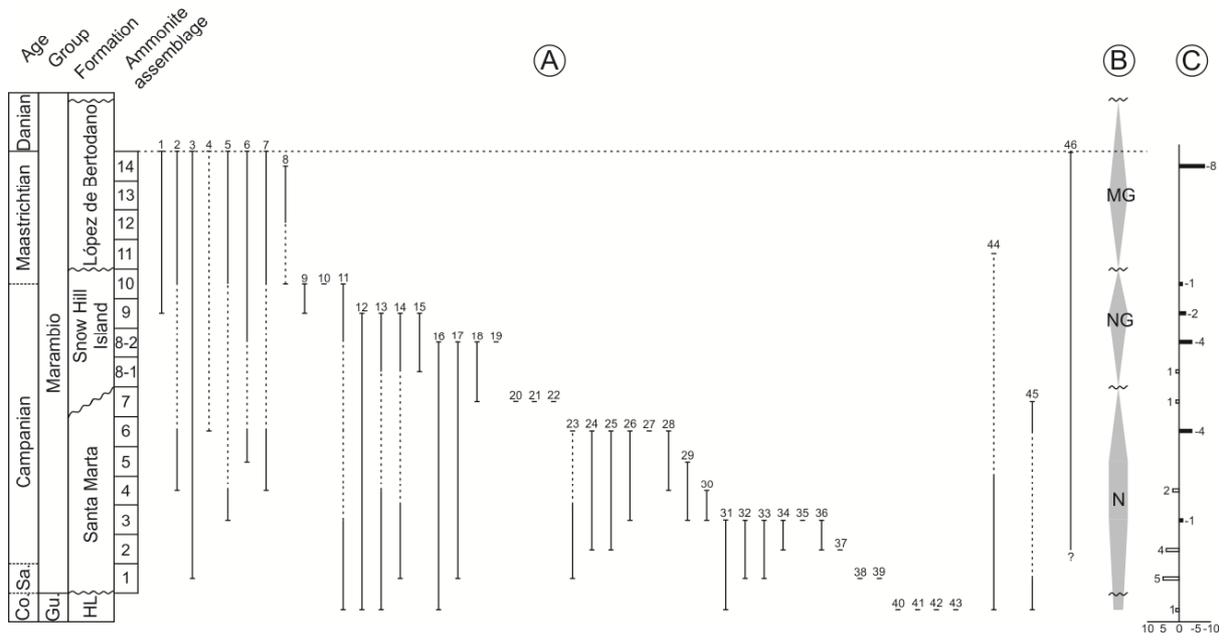
Figure 8



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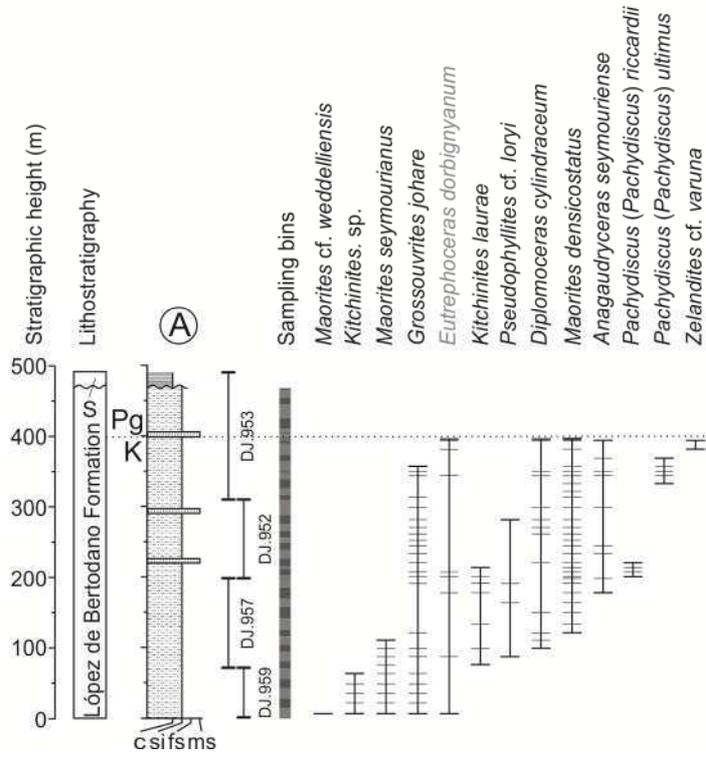
Figure 9



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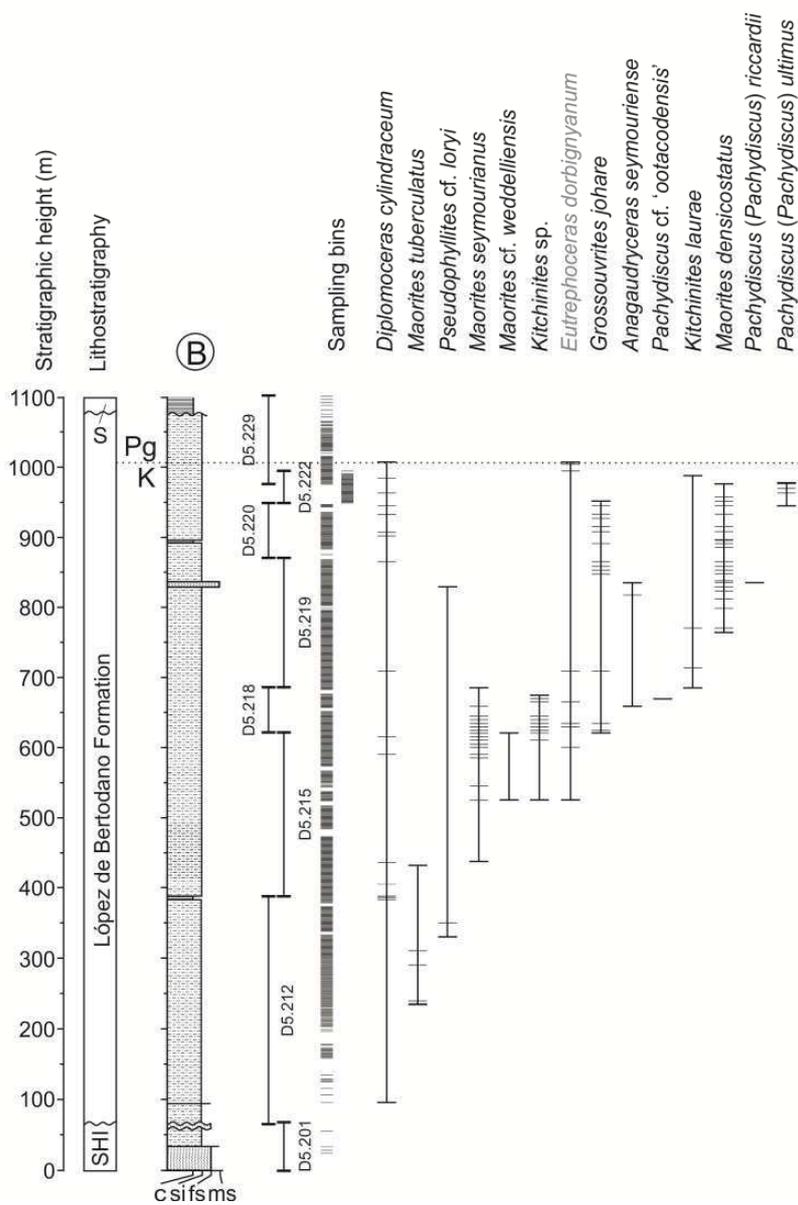
Supplementary Figure S1



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Supplementary Figure S2



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