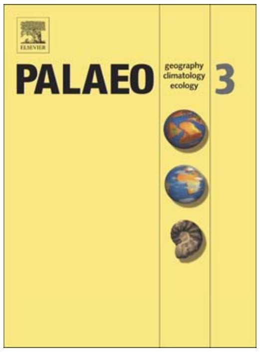

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Evolution and extinction of Maastrichtian (Late Cretaceous) cephalopods from the López de Bertodano Formation, Seymour Island, Antarctica

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ABSTRACT

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

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

1. Introduction

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

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

Despite being prominent victims of the end-Cretaceous catastrophe, the actual cause of ammonite extinction remains largely unclear. With a planktonic larval stage (Shigeta, 1993; Landman et al., 1996; Tajika and Wani, 2011), and probable reliance of some groups on plankton as a primary food source (Kruta et al., 2011; Tanabe, 2011), ammonites may have been victims of a mass extinction of marine calcifying organisms and associated productivity or food chain collapse related to the impact event (Hsü et al., 1985; D'Hondt, 2005; Schulte et al., 2010; Robertson et al., 2013). However, some doubt has recently been cast upon the general model of catastrophic productivity collapse at the K–Pg (Sepulveda et al., 2009; Hull et al., 2011; Alegret et al., 2012; Sogot et al., 2013). Other extinction scenarios focus on an alleged long-term decline in ammonite diversity through the Late Cretaceous (Wiedmann and Kullmann, 1996; Zinsmeister and Feldmann, 1996; Stinnesbeck et al., 2012) and the subsequent effects of Maastrichtian sea level, climate, and oceanographic changes on an already diminished group (Stinnesbeck et al., 2012). In support of this argument, ammonites appear to have been particularly sensitive to environmental change throughout their long evolutionary history (e.g. House, 1989; O'Dogherty et al., 2000; Whiteside and Ward, 2009; Korn and Klug, 2012). Ultimately only high-resolution stratigraphic data from well-dated K–Pg boundary successions can provide insights into the fate of the group during the last few million years of the Cretaceous.

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

The López de Bertodano Formation has become an important section for calibrating ammonite extinction through the use of statistical methods (e.g. Marshall, 1995; Wang and Marshall, 2004) based on early ammonite range data (Macellari, 1986). However, these data came from collections made before the precise location of the K–Pg boundary on Seymour Island was known (Elliot et al., 1994). Whilst previous studies (e.g. Macellari, 1986; Zinsmeister, 1998; Zinsmeister, 2001) have also illustrated cephalopod range data from this succession, our study involves systematic high-resolution sampling tied to measured sedimentary sections in the field, allowing for accurate stratigraphic location of individual fossils. In addition, we have undertaken a taxonomic review of the fauna (see Appendix 1) and compared our data to newly developed age models (e.g. Tobin et al., 2012; Bowman et al., 2013a), which enable us to accurately place this important record in a global context for the first time. The new data also allow the terminal ammonite extinction to be considered in the context of their Late Cretaceous record in the region and the controls on diversity to be assessed.

2. Geological Setting

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

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

Differing palaeoenvironmental interpretations have been proposed for the López de Bertodano Formation. Macellari (1988) favoured deposition in a shallow water, nearshore setting for the basal portion (~300 m), an interpretation elaborated upon by Olivero (1998) and Olivero et al., (2007; 2008), who suggested that large, shore-parallel channels at this level formed within a large estuary or embayment. In contrast, Crame et al., (2004) suggested that a slight decrease in grain size above the underlying Haslum Crag member of the Snow Hill Island Formation (also noted by Pirrie et al., 1997), together with the poorly fossiliferous nature of this portion of the succession, represented deep water shelf conditions. Stratigraphically higher, the mid-upper portion of the formation represents overall transgression and the establishment of mid-outer shelf environments (Macellari, 1988; Crame et al., 2004; Olivero et al., 2008; Olivero, 2012a). In the uppermost 300 m of the sequence on Seymour Island the monotonous bioturbated siltstones also contain a succession of glauconite-rich-rich horizons, often topped with fossiliferous 'lags' containing many molluscs and other fossils. These layers suggest periods of sediment starvation (Crame et al., 2004). Previous authors have suggested that this upper portion of the succession across the K–Pg boundary represents a regressive phase and loss of accommodation space (Macellari, 1988; Crame et al., 2004; Olivero, 2012a). The base of a prominent series of glauconite horizons ~1000 m above the base of the sequence coincides with a distinct change in both macro and microfossil faunas and floras (Elliot et al., 1994; Zinsmeister, 1998; Crame et al., 2004; Stilwell et al., 2004; Bowman et al., 2012), and is interpreted as being equivalent to the 'K–T glauconite' succession of Zinsmeister (1998) (Fig. 2). The base of this glauconite-rich interval contains a small iridium (Ir) spike and the first appearance (FA) and acme of the dinoflagellate cyst *Senegalinium obscurum*, markers used by previous authors to locate the K–Pg boundary on Seymour Island (Elliot et al., 1994; Crame et al., 2004; Bowman et al., 2012). This horizon is also the contact between informal mapping units 'Klb9' and 'Klb10' of Macellari (1988) and Sadler (1988). Above this the 50–70 m thick unit 'Klb10' is made up of brown-grey mudstones and siltstones with scattered concretions and a distinctive macrofossil fauna dominated by the large bivalve *Lahillia* and the gastropod *Struthiochenopus* (Macellari, 1988; Crame et al., 2004; Montes et al., 2010).

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

3. Age model

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

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

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

4. Material and Methods

4.1 Macrofossil range data

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

Sedimentary sections were measured using traditional field methods (Jacob’s staff and Abney level, with some intervals then sub-divided using a tape measure), which yielded a high-resolution stratigraphy (e.g. Crame et al., 1991; Pirrie et al., 1997; Crame et al., 2004). Correlation between the two composite sections was made using stratigraphic tie-points, including the K–Pg boundary, the unconformity between the López de Bertodano and Sobral formations, and a prominent glauconite horizon 174 m below the K–Pg that can be traced laterally across the island (Fig. 2). Based on our field knowledge we have assumed planar bedding along strike and no significant hiatuses. Although identification of tie points in the lower portion of the sequence is challenging, our section lines show little lateral facies or structural variation in the field that would impede the use of one main composite section for biostratigraphic purposes. This is particularly evident when first and last appearances of different macrofossil species are compared across section lines because in many cases these occur at approximately (within ~10 m) the same stratigraphic height (e.g. last appearance (LA) of *Maorites* cf. *weddelliensis* and first appearance (FA) *Grossouvrites johare* (Fig. 4).

Macrofossil collections were made either every metre or in binned intervals several metres thick and of considerable lateral extent along strike (binned intervals were on average 10 m thick in sections DJ.959-953 and 5 m thick in D5.251). In such thick stratigraphic sections and with a high sedimentation rate (e.g. McArthur et al., 1998; Crame et al., 1999; McArthur et al., 2000; Dutton et al., 2007; Tobin et al., 2012) these are high resolution collections for assessing key biostratigraphic patterns. Effort was also made to ensure that all section lines were collected uniformly with a similar amount of time spent collecting within each binned interval and no increase in sampling intensity close to the K–Pg boundary (Figs. S1 and S2).

Taxonomic analysis of the Antarctic ammonite fauna was conducted using the monograph of Macellari (1986), supplemented by earlier works such as those of Kilian and Reboul (1909), Spath (1953) and Howarth (1958, 1966) as well as studies of other Maastrichtian faunas (e.g. Henderson and McNamara, 1985; Kennedy and Henderson, 1992a; Klinger and Kennedy, 2003; Ifrim et al., 2004; Salazar et al., 2010). Nautiloid taxonomic analysis used the work of Cichowolski et al. (2005) and Nielsen and Salazar (2011). Systematic nomenclature of Maastrichtian ammonoids follows the Treatise of Invertebrate Paleontology (Wright et al., 1996) to sub-generic level. Taxonomic comments on the cephalopod fauna can be found in Appendix 1. Representative ammonite taxa from the López de Bertodano Formation are illustrated in Figs. 5 and 6.

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

4.2 Statistical analysis

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

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

5. Results

5.1 Antarctic macrofossil range data

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

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

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

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

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

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

Four ammonite species are present in the five metres beneath the K–Pg boundary in our sections (Figs. 4 and 7). Specimens of *Diplomoceras cylindraceum* and *Maorites densicostatus* remain common, along with rare *Anagaudryceras seymouriense* until just below the base of the 'K–T glauconite'. There are also several small ammonites similar to those identified by Macellari (1986) as *Zelandites varuna* (Forbes, 1846) (Fig. 5B) in this interval. A number of large examples of the nautiloid *Eutrephoceras dorbignyanum* were also found directly below the boundary. Other common taxa in the upper portion of the López de Bertodano Formation (e.g. *Grossouvrites johare, Kitchinites laurae*) have LADs in the 40 m below the boundary in all of our section lines (Fig. 4).

No definitively *in situ* cephalopod fossils were found above the K–Pg boundary, although poorly preserved ammonites have been previously reported from this interval on Seymour Island (Sadler, 1988; Zinsmeister et al., 1989). Zinsmeister (1998) considered these to be the result of local inliers of Cretaceous-aged sediment in the broad dip-slopes of the Paleocene unit 'Klb10' but our recent observations indicate that their positions may be the result of recent transport due to glacial action, and they are therefore considered reworked.

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

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

6. Discussion

The recently published magnetostratigraphy (Tobin et al., 2012) and updated palynological biostratigraphy (Bowman et al., 2012; Bowman et al., 2013a; Bowman et al., 2014) allow us to accurately place the Maastrichtian ammonite record from Seymour Island in a global context for the first time. It is clear that revisions are required to the age models used in previous studies of the Antarctic Maastrichtian successions (e.g. Macellari, 1986; Zinsmeister, 2001) and subsequent comparisons to global events.

6.1 K–Pg Mass extinction in Antarctica

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

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

Zinsmeister (1998) reported six ammonite species as having their final occurrence < 2m below the K–Pg boundary on Seymour Island. His records of *Maorites densicostatus* and *Diplomoceras cylindraceum* are consistent with our data, as is the restricted occurrence of *Zelandites varuna*, (Fig. 4) but Zinsmeister also reported the presence of *Kitchinites laurae*, *Pseudophyllites loryi* and *Grossouvrites gemmatus* (probably *Grossouvrites johare* – see Appendix 1 and Salazar et al., 2010), which were not found during our study. In Zinsmeister's (1998) range data the final occurrences of *Kitchinites laurae* and *Pseudophyllites loryi* are also the only records of these species in a 16 m interval beneath the boundary. Similarly, examples of *Grossouvrites* only occur twice in the same interval. This suggests that, in addition to four common species, several rare species were present in the latest Maastrichtian. In support of this hypothesis several small external moulds of *Anagaudryceras seymouriense* were discovered ~5 m below the K–Pg in one of our section lines, a species not previously recorded from this interval.

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

The seven species present in this interval represent three of the four suborders of post-Triassic ammonites (Wright et al., 1996) and are a mixture of taxa endemic to the southern high latitudes (presumably cool-temperate Austral specialists, e.g. kossmaticeratids *Maorites* and *Grossouvrites, Kitchinites laurae*) and long-ranging cosmopolitan taxa (e.g. *Diplomoceras, Pseudophyllites, Anagaudryceras*, *Zelandites*). We suggest that these ammonites persisted through the late Maastrichtian but became extinct at the K–Pg boundary. The remaining seven species present in the López de Bertodano Formation are therefore likely victims of background turnover during the Maastrichtian rather than of any sudden extinction event at or before the K–Pg boundary. The high stratigraphic abundance values for two of these species (*Maorites seymourianus* and *Kitchinites* sp.) and lack of distinct clusters of LAD at any other portion of the section besides the K–Pg interval provide supportive evidence (Fig. 8). In addition, the nautiloid *Eutrephoceras dorbignyanum* disappears from Antarctica at the K–Pg boundary, raising the total number of cephalopod taxa lost in this interval to eight. This genus exhibits a global distribution in the Maastrichtian (Landman et al., 2014), and although Paleogene representatives are known from lower latitude locations (e.g. Teichert and Glenister, 1959; Stilwell and Grebneff, 1996; Darragh, 1997; Casadio et al., 1999), it failed to recolonize Antarctica.

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

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

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

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

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

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

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

6.2 Late Cretaceous faunal diversity and environmental change in Antarctica

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

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

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

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

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

Other macrofossil groups show similar divergent extinction patterns in the James Ross Basin compared to lower latitudes, in particular inoceramid bivalves and belemnites (Crame et al., 1996; Zinsmeister and Feldmann, 1996). Inoceramid bivalves disappeared from Antarctica during deposition of the upper portion of the Santa Marta Formation (Crame et al., 1996; Crame and Luther, 1997; Olivero and Medina, 2000) in the late Campanian (McArthur et al., 2000) (Fig. 9) earlier than their mid-Maastrichtian extinction elsewhere (e.g. McLeod et al., 1996). Belemnites disappeared even earlier, albeit temporarily, in the early Campanian, as recorded in the mid-portion of the Santa Marta Formation on James Ross Island (Doyle, 1990; Crame et al., 1996; McArthur et al., 2000), before a single species reappeared in the basin in the early Maastrichtian of Seymour Island (Fig. 9; Doyle and Zinsmeister, 1988; Dutton et al., 2007).

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

6.3 Maastrichtian faunal diversity and environmental change on Seymour Island

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

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

Most studies of environmental changes during the MME focus on extinction and/or reduction in diversity of groups such as inoceramid bivalves (Macleod, 1994; Macleod et al., 1996) and rudist bivalve-dominated tropical reefs (Johnson and Kauffman, 1996), but our data suggest that in Antarctica this event saw an increase in the diversity and abundance of ammonites. A similar mid-Maastrichtian radiation event has been noted for planktonic foraminifera (MacLeod and Huber, 2001). A radiation event for ammonites at this time has also been recorded in the northwest Pacific (Jagt-Yazykova, 2011; 2012) and diversity increases in Mexico (Ifrim et al., 2004; Ifrim et al., 2010) suggest a global event. Ammonites seemed to have flourished during the mid-Maastrichtian, just a few million years before their extinction.

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

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

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

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

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

6.4 Comparison to patterns seen in other faunal groups

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

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

7. Conclusions

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

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

Bertodano Formations indicate a long-term global cooling trend which began during the Campanian and reached its peak across the Campanian–Maastrichtian boundary, appears to have led to the exclusion of a large number of common cosmopolitan ammonite genera from the James Ross Basin. This faunal change was coincident with the rise to dominance of endemic Austral ammonite taxa, and regional extinction events and temporary disappearances recorded by other molluscan groups such as inoceramid bivalves and belemnites.

4. Ammonites appear to have suffered a crisis in the early Maastrichtian of the James Ross Basin, with a low diversity assemblage in the basal López de Bertodano Formation on Seymour Island comprising just two species, and coincident with evidence for both shallow waters and low temperatures. Diversity increased during the mid-Maastrichtian, a period of climatic warming and sea level rise, which correlates with evidence from lower latitudes for a distinct 'Mid-Maastrichtian Event' at this time. Despite its apparent global nature, the effect of this event appears to vary according to taxonomic group, whereas some (inoceramid and rudist bivalves) suffer extinction, others such as ammonites and planktonic foraminifera appear to radiate and diversify. In Antarctica this event coincides with an influx of cosmopolitan ammonite taxa and proliferation of endemic kossmaticeratids.
5. Short term environmental changes during the late Maastrichtian (chrons C31N–29R) may be responsible for the brief stratigraphic appearances of a number of ammonite species in the Seymour Island succession prior to the K–Pg extinction event. These fluctuations show intriguing similarities with short-term changes recorded globally by microfossil groups such as calcareous nannofossil and planktonic foraminifera during the Campanian–Maastrichtian, suggesting a common cause – most likely dynamic short-term climate changes which allowed biotic exchange between low and high latitude assemblages. These oscillations do not appear to have had a deleterious effect on the overall diversity of ammonite faunas prior to the K–Pg extinction event.

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Appendix 1: Identification and taxonomy of Antarctic Maastrichtian Cephalopoda

Stratigraphic notes

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

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

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

For tabulated raw field data for each section line, reference should be made to Supplementary data tables S1999 and S2006 available online.

Systematic notes

Order AMMONOIDEA von Zittel, 1884

Suborder LYTOCERATINA Hyatt, 1900

Superfamily TETRAGONITOIDEA Hyatt, 1900

Family GAUDRYCERATIDAE Spath, 1927

Genus ANAGAUDRYCERAS Shimizu, 1934

Anagaudryceras seymouriense Macellari, 1986

Fig. 5A

Material: 14 specimens (Tables S1, S2).

Despite varying degrees of preservation, all specimens in the present study compare favourably with previous descriptions of the genus (e.g. Howarth, 1965; Kennedy and Klinger, 1979; Hoffman, 2010), and specimens assigned to the species *Anagaudryceras seymouriense* from Antarctica by Macellari (1986) (e.g. PRI# 58197, 58222, 60882, 58052, and 58743) and from the NW Pacific by Maeda et al. (2005). A number of internal moulds show ontogenetic change typical for this genus from small evolute juveniles with a depressed whorl section to larger, more involute adults with a slightly more compressed whorl outline. Evolute juveniles show gaudryceratid ornament of very fine ribbing on the flanks, which changes to smoother ornamentation comprising fine flexuous lirae and occasional fold-like ribs or undulations in larger (D > 65 mm) sub-adult and adult examples. Constrictions are apparent on juvenile examples but disappear on specimens greater than ~130 mm in diameter (Macellari, 1986). Rare fragments of very large individuals (D > 200 mm) containing well-preserved septal lobes and sutures are found associated with glauconite sandstone horizons in the upper López de Bertodano Formation (Zinsmeister, 2001) (e.g. DJ.952.1, DJ.952.335, DJ.952.423,). This species is found throughout the mid-upper (~650 – 1003 m in our sections) Maastrichtian on Seymour Island, with the stratigraphically highest recorded occurrence a number of external moulds of small evolute examples found in a 5m interval below the K–Pg boundary (DJ.953.689).

Genus ZELANDITES Marshall, 1926

Zelandites varuna (Forbes, 1846)

Fig. 5B

Material: 2 specimens.

These two specimens include one poorly preserved internal mould and cast embedded in well-cemented glauconitic sandstone layer, and one well-preserved internal mould retaining phragmocone and portion of body chamber as well as external ornament. Although both appear to be juveniles, they are very similar to those collected by previous workers (e.g. PRI# 61169) and described by Macellari (1986). *Zelandites varuna* is characterised by a compressed whorl section (Wb/Wh ratio of ~0.7

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

Family TETRAGONITIDAE Hyatt, 1900

Subfamily TETRAGONITINAE Hyatt, 1900

Genus PSEUDOPHYLLITES Kossmat, 1895

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

Fig. 5C

Material: 14 specimens.

Many of these specimens are rather small and poorly preserved examples commonly found embedded within well-cemented glauconite-rich sandstone layers in the mid – upper (700 – 830 m) portion of the López de Bertodano Formation hence why they are left in open nomenclature. Nonetheless, a number of these specimens contain identifiable sutures (e.g. D5.1164.2; DJ.957.529) and morphological features which compare favourably with material described from the James Ross Basin by previous workers as *Pseudophyllites loryi* and its synonyms such as *Pseudophyllites peregrinus* (e.g. Spath, 1953; Macellari, 1986) (PRI# 58284, 58728, 60434, 58193). Several large (>100 mm) but deformed internal moulds with the suture visible were found in the basal portion (330 – 350 m) of the López de Bertodano Formation (D5.855.2, D5.875.2). *Pseudophyllites loryi* is separated from other species of *Pseudophyllites* by to its evenly rounded whorl section, broader venter, and vertical rather than inclined umbilical wall. At least one of our specimens (DJ.957.189) also preserves evidence of extremely fine ribbing/lirae as noted by Macellari (1986). Differentiation between the various species of *Pseudophyllites* present in the Late Cretaceous is challenging and many have passed into synonymy. Generally speaking three species are recognised: *Pseudophyllites indra* (Forbes, 1846), which ranges from the Santonian to the latest Maastrichtian and has a virtually pandemic distribution (Kennedy and Klinger, 1977; Kennedy and Summesberger, 1986; Ward and Kennedy, 1993; Kennedy and Hancock, 1993), *Pseudophyllites loryi* (Kilian and Reboul, 1909) and its junior synonyms *Pseudophyllites latus*, *Pseudophyllites whangaroaensis* (Marshall, 1926), *Pseudophyllies peregrinus* (Spath, 1953) and *Pseudophyllites skoui* (Birkelund, 1965), which range from the Santonian - Campanian to the latest Maastrichtian of Antarctica, New Zealand, Australia, and Greenland, and finally *Pseudophyllites teres* (van Hoepen, 1920), known only from the Santonian - Campanian of South Africa and Madagascar (Kennedy and Klinger, 1977). *Pseudophyllites loryi* is clearly quite a rare taxon on Seymour Island, which coupled with the generally small size of the majority of our specimens perhaps indicates why our records do not match those of Zinsmeister (1998) in terms of the highest stratigraphic occurrence of this genus in Antarctica.

Suborder AMMONITINA Hyatt, 1889

Superfamily DESMOCERATACEAE von Zittel, 1895

Family DESMOCERATOIDEA von Zittel, 1895

Subfamily PUZOSIINAE Spath, 1922

Genus KITCHINITES Spath, 1922

Kitchinites sp.

Fig. 6E

Material: 53 specimens

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

Kitchinites laurae Macellari, 1986

Fig. 5F

Material: 13 specimens

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

Family KOSSMATICERATIDAE Spath, 1922

Subfamily KOSSMATICERATINAE Spath, 1922

Genus MAORITES Marshall, 1926

Maorites densicostatus (Kilian and Reboul, 1909)

Fig. 6B

Material: 194 specimens.

A full description of this species and its various synonyms is provided by Macellari (1986) and Macellari (1988). Typically for the genus, *Maorites densicostatus* appears to exhibit a large degree of morphological variation, but is easily seperated from other species of the genus. Specimens from Seymour Island were separated into three morphotypes by Macellari (1986), α, β, and γ, based mainly on patterns of external shell ornament such as ribbing density and number of constrictions. The stratigraphic ranges of these morphotypes appear to overlap, so for our purposes we refer to them as a single species which occurs between 730 and 1006 m in the composite section. As hypothesised by Macellari (1986), we suggest these morphotypes may relate to sexual dimorphism; certainly there are places in the upper Maastrichtian portion of the López de Bertodano Formation on Seymour Island where adult specimens of *Maorites densicostatus* exhibit a wide range of different sizes and external ornament at the same stratigraphic horizon. All morphotypes of this species are characterised by an involute shell, compressed whorl section (typical Wb/Wh ratio of ~0.45 – 0.57), and the presence of fine ribbing and constrictions in both adult and juvenile examples, often forming small nodes when several ribs meet at the umbilical margin. Morphotype α (e.g. DJ.952.144) typically shows 10 – 12 ribs in 1 cm at a whorl height of 3 cm, whereas morphotypes β (e.g. DJ.952.252) is characterised by 12 – 14 ribs, and γ typically only shows 6 – 7 ribs per 1 cm at an equivalent whorl height. *Maorites* *densicostatus* shows potential as a good stratigraphic marker for the upper Maastrichtian in the Southern Hemisphere, with occurrences in Australia (Henderson and McNamara, 1985), South America (Macellari, 1988; Olivero et al., 2009), South Africa (Kennedy and Klinger, 1985), and New Zealand (Henderson, 1970). Small specimens are also present in the Sandwich Bluff Member of the López de Bertodano Formation on Vega Island, and indicate at least a portion of this deposit to be of late Maastrichtian age (Pirrie et al, 1991).

Maorites seymourianus (Kilian and Reboul, 1909)

Fig. 6D

Material: 70 specimens.

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

Maorites tuberculatus Howarth, 1958

Fig.6C

Material: 17 specimens.

All our specimens compare favourably with the descriptions by Howarth (1958) and Macellari (1986) (e.g. PRI# 58278). Examples of *Maorites tuberculatus* are generally small, with rounded flanks and exhibit somewhat tighter coiling of the shell than is seen in *Maorites seymourianus* or *Maorites densicostatus*. The combination of prominent and numerous umbilical tubercles (up to 16 per whorl), numerous and flexuous constrictions (up to 9 per whorl), and fine ribbing also allow differentiation from other kossmaticeratids present on Seymour Island. This species has previously reported from the interval directly above the unconformable contact between the Haslum Crag Member of the Snow Hill Island Formation and the basal López de Bertodano Formation (Olivero et al, 2007; 2008; Olivero, 2012) where it is the marker species for the base of the MG stratigraphic sequence and ammonite assemblage 11 of Olivero (2012), but first appears in the composite section of the present study 235 m above this level..

Maorites cf. *weddelliensis* Macellari, 1986

Fig. 6A

Material: 6 specimens.

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

Genus: GROSSOUVRITES Kilian and Reboul 1909

Grossouvrites johare Salazar, 2010

Fig. 5E

Material: 100 specimens.

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

Family PACHYDISCIDAE Spath, 1922

Genus PACHYDISCUS von Zittel, 1895

Pachydiscus (*Pachydiscus*) *ultimus* Macellari, 1986

Fig. 6F

Material: 29 specimens.

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

Pachydiscus (*Pachydiscus*) *riccardii* Macellari, 1986

Fig. 6G

Material: 19 specimens.

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

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

Material: 1 specimen.

This specimen is a poorly preserved section of phragmocone with some shell material revealing external ornament, showing coarse radial ribbing on the ventral flank, an inflated whorl section, and overall morphology typical of many pachydiscids (compare Kennedy and Klinger 2006). The suture is not preserved. Similar specimens from Seymour Island were described by Macellari (1986) as *Pachydiscus* (*Pachydiscus*) *ootacodensis*, a species from the Pacific Northwest of the USA and Canada (Usher, 1952; Jones, 1963) where it is found in deposits of late Campanian – early Maastrichtian age (Mustard, 1994; Shigeta et al., 2010). No systematic revision of pachydiscids from these deposits has been undertaken since the work of Jones (1963), and this single sample from Antarctica is too poorly preserved to allow for a precise identification. *Pachydiscus* (*Pachydiscus*). *ootacodensis* has been used by previous authors to define a distinct biozone within the López de Bertodano Formation (Macellari, 1986; Olivero and Medina, 2000; Olivero, 2012), but as noted by Crame et al. (2004) and confirmed by the recovery of a single specimen in the present study, it is too rare on Seymour Island for this purpose.

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily TURRILITOIDEA Gill, 1871

Family DIPLOMOCERATIDAE Spath, 1926

Subfamily DIPLOMOCERATINAE Spath, 1926

Genus DIPLOMOCERAS Hyatt, 1900

Diplomoceras cylindraceum (Defrance, 1816)

Fig. 5G

Material: 44 specimens.

Specimens of this very large heteromorph are present throughout the López de Bertodano Formation, and include some of the most complete examples of the genus found anywhere in the world (e.g. Zinsmeister and Oleinik, 1995). The genus is characterised by a circular whorl section, uniform ribbing, distinctive suture, and development of 'paper clip-like' morphology. Species-level taxonomy has provoked some debate (Olivero and Zinsmeister, 1989; Kennedy and Henderson, 1992; Klinger and Kennedy, 2003; Machalski, 2012). Olivero and Zinsmeister (1989) assigned large specimens from the upper Maastrichtian (upper López de Bertodano Formation) of Antarctica to *Diplomoceras maximum* based mainly on changes in ribbing during ontogeny. Machalski (2012) noted that large specimens from the upper Maastrichtian of Europe also appear to conform to *Diplomoceras maximum*. However, differentiation of *Diplomoceras maximum* from *Diplmoceras cylindraceum* and its synonyms (e.g. *Diplomoceras lambi*) appears problematic, as pointed out by Kennedy and Henderson (1992), because specimens are extremely prone to *post-mortem* crushing. Here we follow Klinger and Kennedy (2003) and others in considering *Diplomoceras* monospecific, with *Diplomoceras cylindraceum* the single, often rather variable species. This species exhibits a pandemic distribution throughout the latest Campanian - Maastrichtian, and in common with lower latitudes first appears in Antarctica in the late Campanian Sanctuary Cliffs Member of the Snow Hill Island Formation (Pirrie et al., 1997; Olivero, 2012), remaining a common component of the ammonite fauna until directly beneath the K–Pg boundary (e.g. Landman et al., 2007).

Order NAUTILOIDEA de Blainville, 1825

Family NAUTILIDAE de Blainville, 1825

Genus EUTREPHOCERAS Hyatt, 1894

Eutrephoceras dorbignyanum (Forbes *in* Darwin, 1846)

Fig. 5D

Material: 16 specimens.

The taxonomy of Southern Hemisphere Late Cretaceous nautiloids has recently been reviewed (Cicholowski et al., 2005; Nielsen and Salazar, 2011). Specimens from the Maastrichtian of Antarctica and southern South America were united under the name *Eutrephoceras dorbignyanum*. All our specimens match the earlier descriptions, and are characterised by a globular shell, inflated whorl section, tiny umbilicus and extremely fine ornament most often seen in juvenile specimens. A number of large incomplete adult specimens are included in the BAS collections, often showing rather flattened flanks and fine growth lines. On Seymour Island *E. dorbignyanum* first appears in the middle of the López de Bertodano Formation, and remains an occasional component of the molluscan fauna until a final occurrence directly beneath the K–Pg boundary.

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Fig. 1

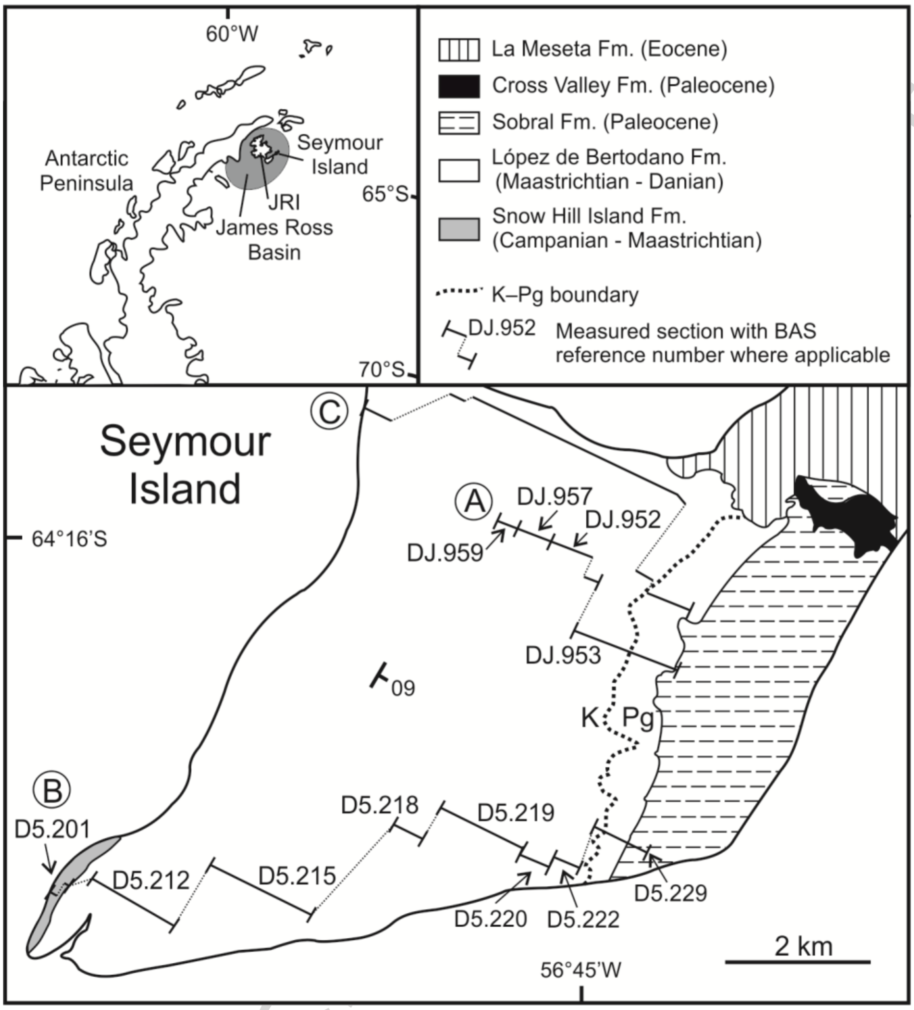

60°W
Antarctic Peninsula
Seymour Island
JRI
James Ross Basin
65°S
70°S
La Meseta Fm. (Eocene)
Cross Valley Fm. (Paleocene)
Sobral Fm. (Paleocene)
López de Bertodano Fm. (Maastrichtian - Danian)
Snow Hill Island Fm. (Campanian - Maastrichtian)
K–Pg boundary
DJ.952
Measured section with BAS reference number where applicable
Seymour Island
C
A
B
64°16'S
DJ.957
DJ.952
DJ.959
DJ.953
09
K
Pg
D5.201
D5.212
D5.215
D5.218
D5.219
D5.220
D5.222
D5.229
2 km
56°45'W

Figure 2

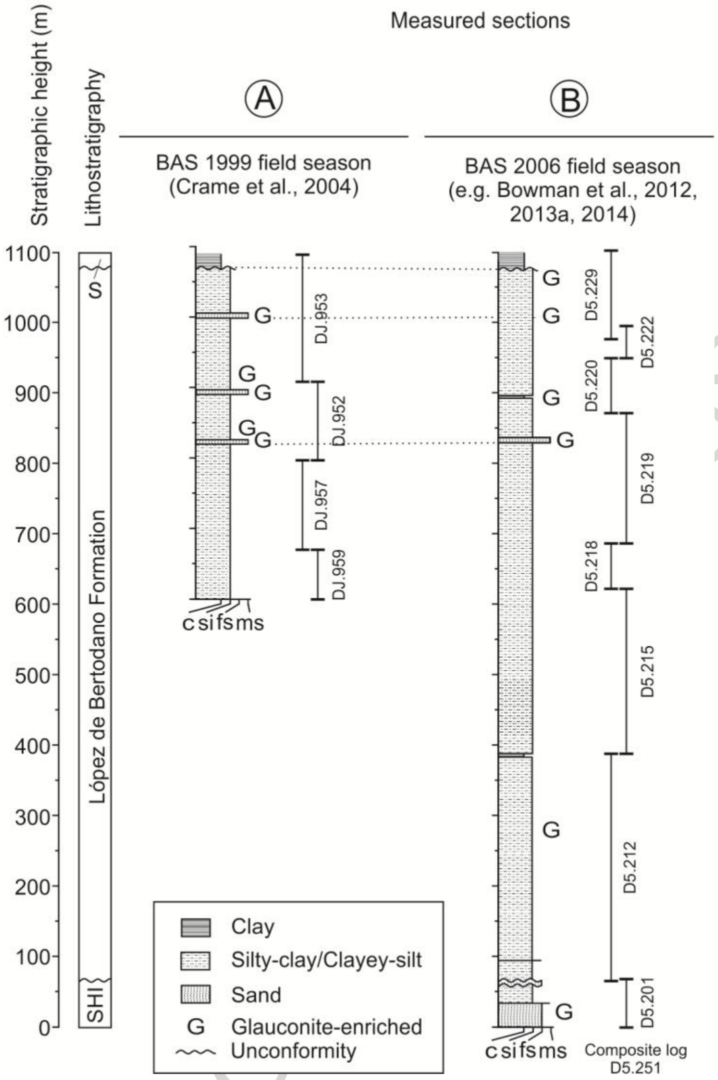

Stratigraphic height (m)
Lithostratigraphy
Measured sections
A
B
BAS 1999 field season (Crame et al., 2004)
BAS 2006 field season (e.g. Bowman et al., 2012, 2013a, 2014)
1100
1000
900
800
700
600
500
400
300
200
100
0
S
López de Bertodano Formation
SHI
G
DJ.953
DJ.952
DJ.957
DJ.959
D5.229
D5.222
D5.220
D5.219
D5.218
D5.215
D5.212
D5.201
c si fs ms
Composite log D5.251
Clay
Silty-clay/Clayey-silt
Sand
G Glauconite-enriched
Unconformity

Figure 3

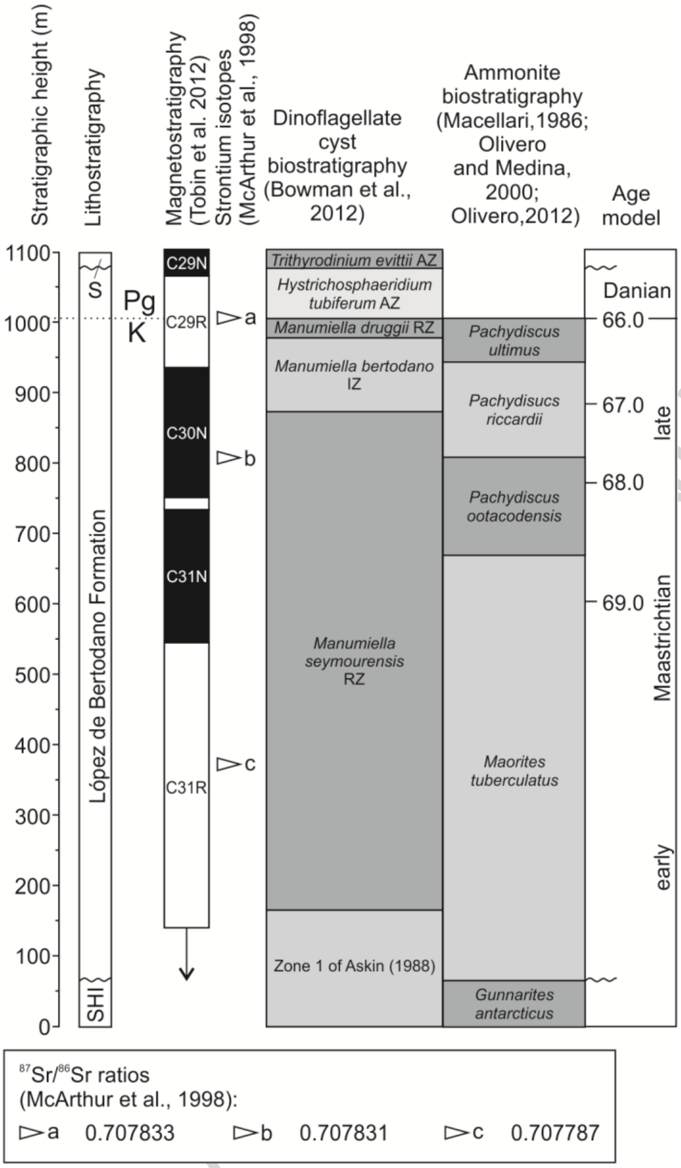
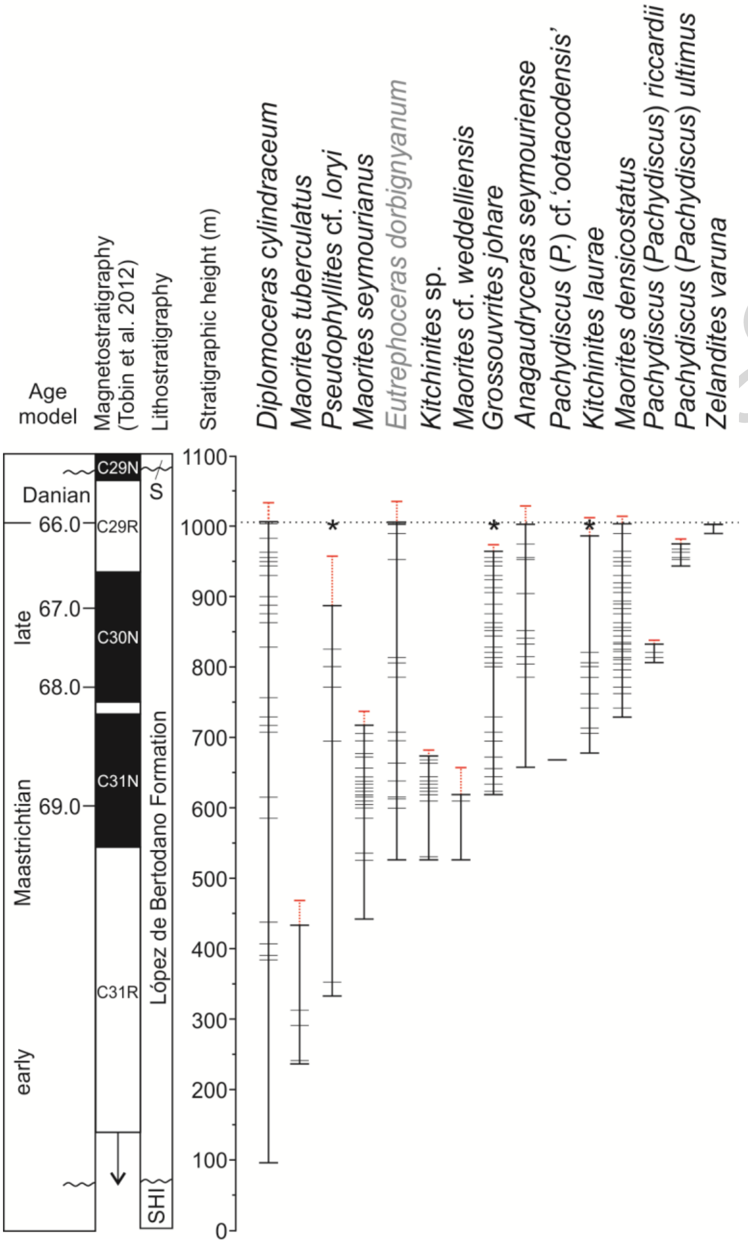
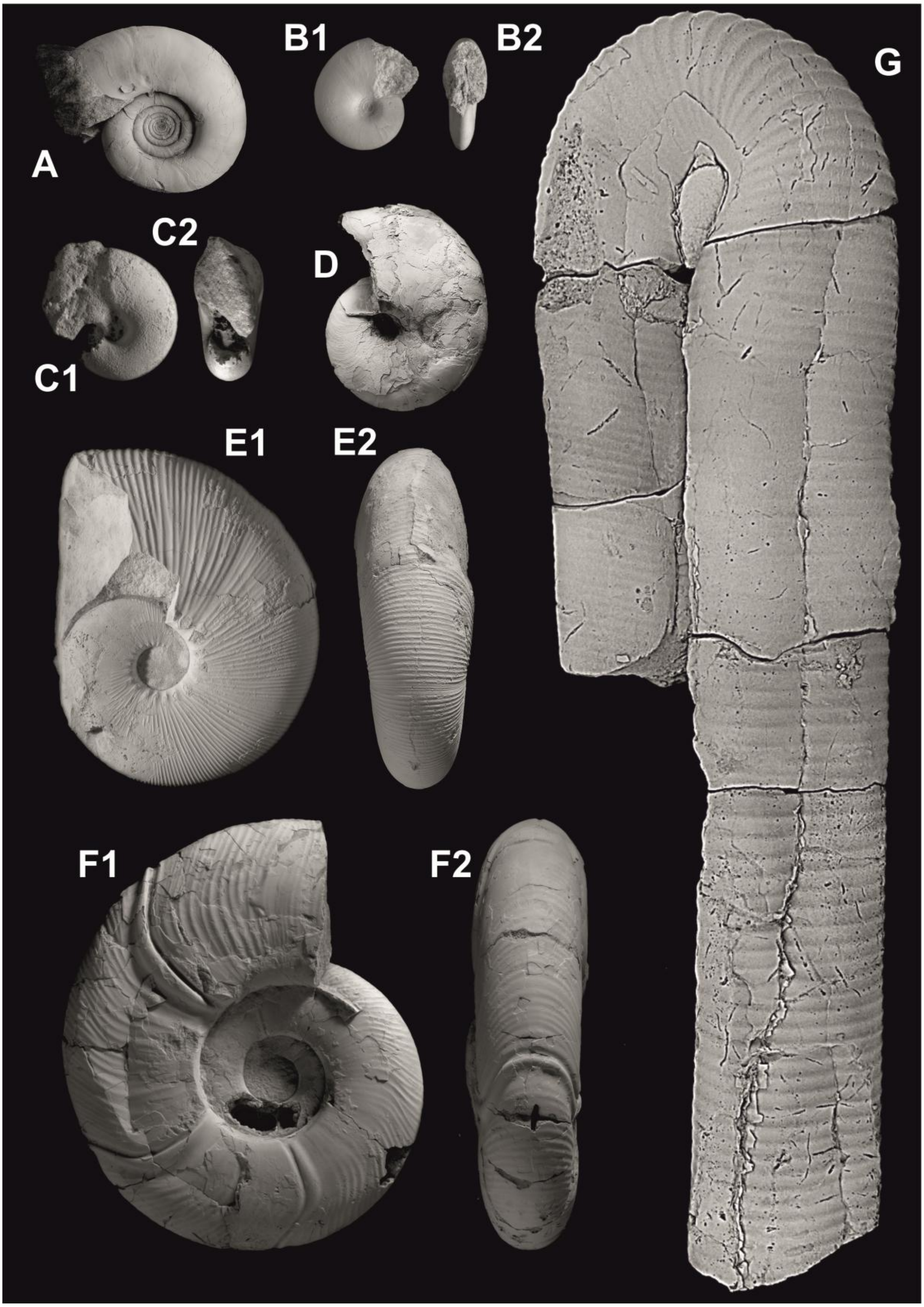

Stratigraphic height (m)
Lithostratigraphy
Magnetostratigraphy (Tobin et al. 2012)
Strontium isotopes (McArthur et al., 1998)
Dinoflagellate cyst biostratigraphy (Bowman et al., 2012)
Ammonite biostratigraphy (Macellari,1986; Olivero and Medina, 2000; Olivero,2012)
Age model
1100
1000
900
800
700
600
500
400
300
200
100
0
S
López de Bertodano Formation
SHI
Pg
K
C29N
C29R
C30N
C31N
C31R
a
b
c
Trithyrodinium evittii AZ
Hystrichosphaeridium tubiferum AZ
Manumiella druggii RZ
Manumiella bertodano IZ
Manumiella seymourensis RZ
Zone 1 of Askin (1988)
Pachydiscus ultimus
Pachydisucs riccardii
Pachydiscus ootacodensis
Maorites tuberculatus
Gunnarites antarcticus
Danian
66.0
67.0
68.0
69.0
late
Maastrichtian
early
$^{87}Sr/^{86}Sr$ ratios (McArthur et al., 1998):
a 0.707833
b 0.707831
c 0.707787

Figure 4


Age model
Magnetostratigraphy (Tobin et al. 2012)
Lithostratigraphy
Stratigraphic height (m)
Diplomoceras cylindraceum
Maorites tuberculatus
Pseudophyllites cf. loryi
Maorites seymourianus
Eutrephoceras dorbignyanum
Kitchinites sp.
Maorites cf. weddelliensis
Grossouvrites johare
Anagaudryceras seymouriense
Pachydiscus (P.) cf. 'ootacodensis'
Kitchinites laurae
Maorites densicostatus
Pachydiscus (Pachydiscus) riccardii
Pachydiscus (Pachydiscus) ultimus
Zelandites varuna
Danian
66.0
67.0
68.0
69.0
late
Maastrichtian
early
C29N
C29R
C30N
C31N
C31R
S
López de Bertodano Formation
SHI
1100
1000
900
800
700
600
500
400
300
200
100
0
*
*
*


A
B1
B2
G
C2
D
C1
E1
E2
F1
F2

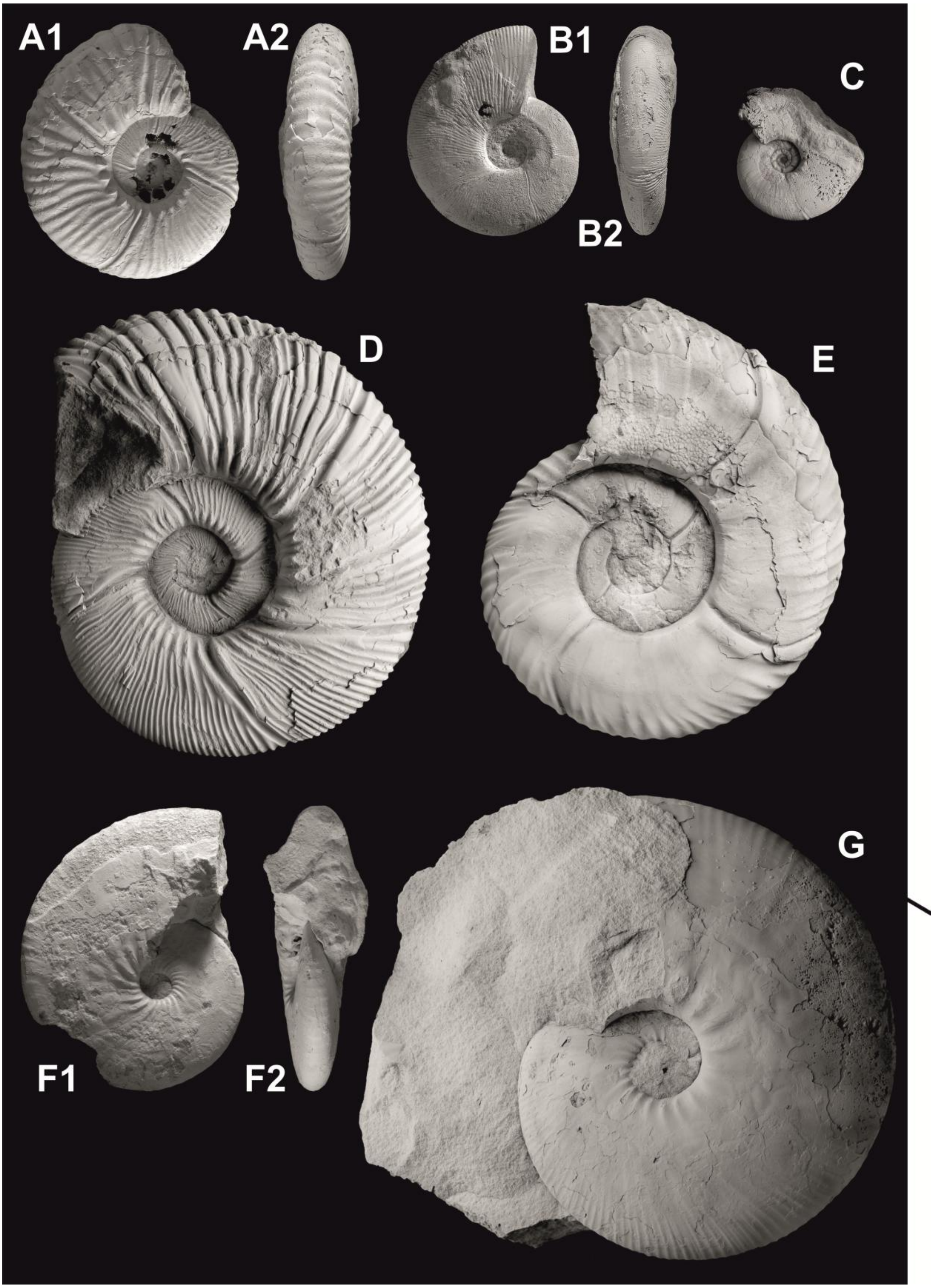

A1
A2
B1
B2
C
D
E
F1
F2
G

Figure 7

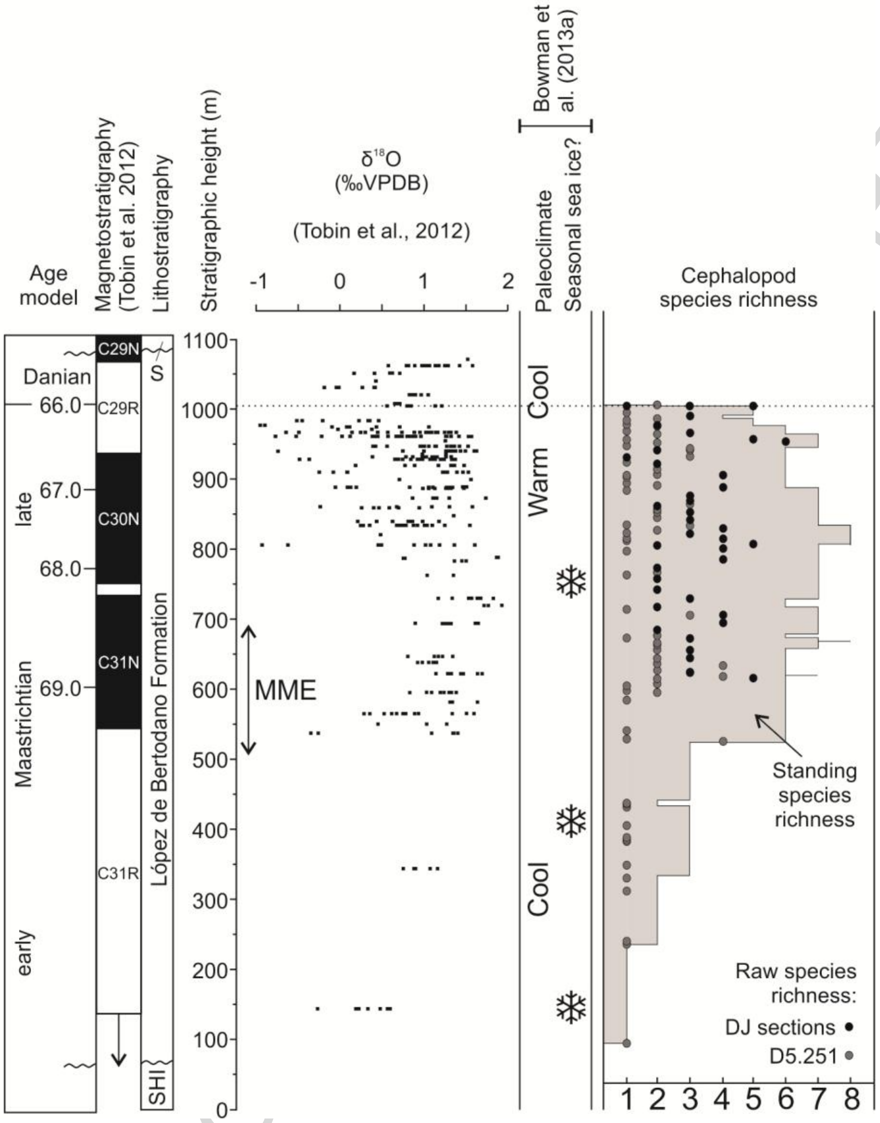

Age model
Magnetostratigraphy (Tobin et al. 2012)
Lithostratigraphy
Stratigraphic height (m)
δ18O (‰VPDB)
(Tobin et al., 2012)
-1
0
1
2
Paleoclimate
Seasonal sea ice?
Bowman et al. (2013a)
Cephalopod species richness
Danian
66.0
67.0
68.0
69.0
late
early
Maastrichtian
C29N
C29R
C30N
C31N
C31R
S
López de Bertodano Formation
SHI
1100
1000
900
800
700
600
500
400
300
200
100
0
MME
Cool
Warm
Cool
Standing species richness
Raw species richness:
DJ sections ●
D5.251 ●
1
2
3
4
5
6
7
8

Figure 8

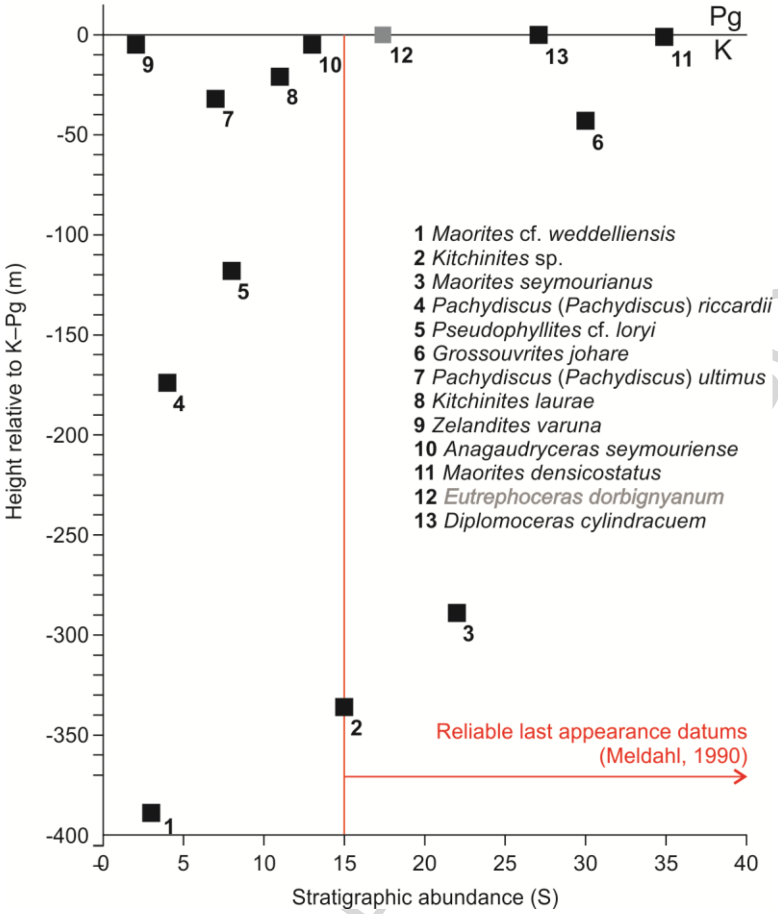

Pg
K
0
-50
-100
-150
-200
-250
-300
-350
-400
Height relative to K–Pg (m)
0
5
10
15
20
25
30
35
40
Stratigraphic abundance (S)
1
2
3
4
5
6
7
8
9
10
11
12
13
1 Maorites cf. weddelliensis
2 Kitchinites sp.
3 Maorites seymourianus
4 Pachydiscus (Pachydiscus) riccardii
5 Pseudophyllites cf. loryi
6 Grossouvrites johare
7 Pachydiscus (Pachydiscus) ultimus
8 Kitchinites laurae
9 Zelandites varuna
10 Anagaudryceras seymouriense
11 Maorites densicostatus
12 Eutrephoceras dorbignyanum
13 Diplomoceras cylindracuem
Reliable last appearance datums
(Meldahl, 1990)

Figure 9

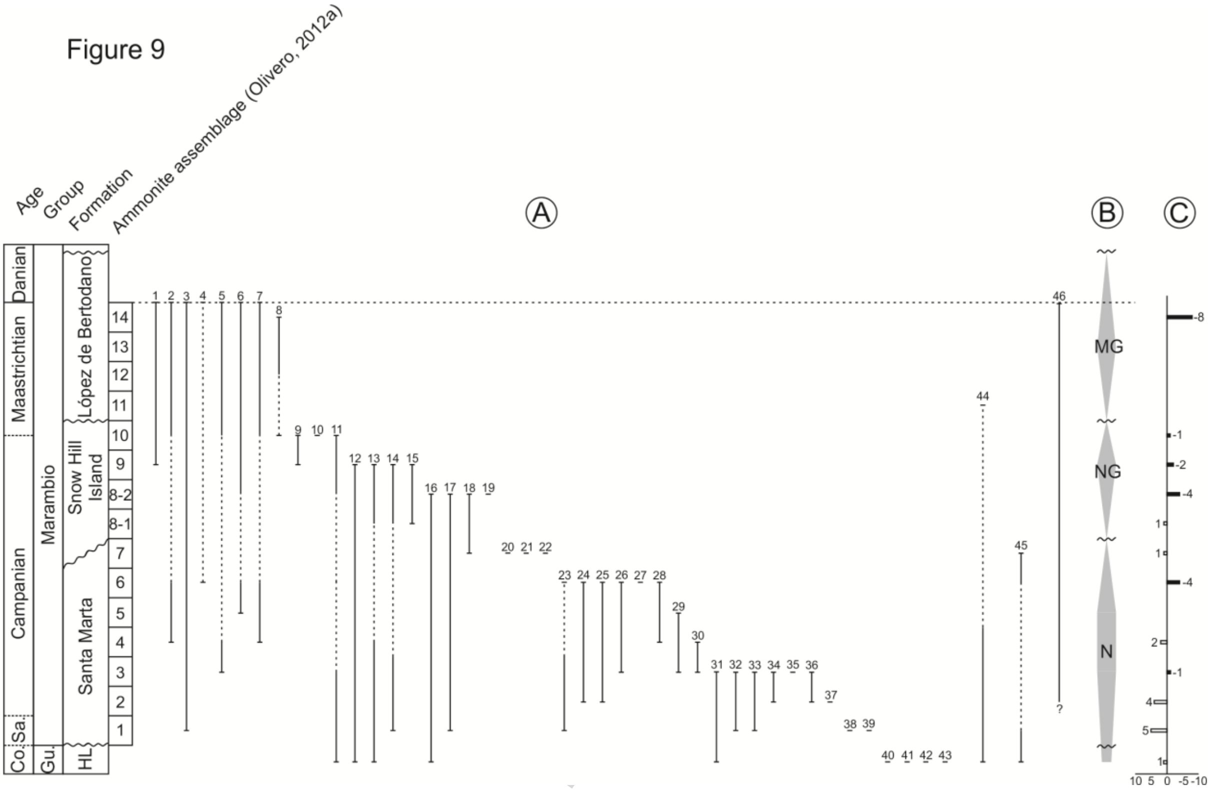

Age
Group
Formation
Ammonite assemblage (Olivero, 2012a)
Ⓐ
Ⓑ
Ⓒ
Danian
Maastrichtian
Campanian
Co.Sa.
Marambio
Gu.
López de Bertodano
Snow Hill Island
Santa Marta
HL
14
13
12
11
10
9
8-2
8-1
7
6
5
4
3
2
1
MG
NG
N
?
-8
-1
-2
-4
1
1
-4
2
-1
4
5
1
10 5 0 -5 -10

Figure captions

Fig. 1: Locality and geology map of Seymour Island, James Ross Basin, Antarctic Peninsula. The maps show modern geography. JRI, James Ross Island; BAS, British Antarctic Survey; K, Cretaceous; Pg, Paleogene. The K–Pg boundary is shown by a dotted line and crops out within the uppermost López de Bertodano Formation. A–B, measured sections discussed in this paper. A, BAS 1999 field season, sections DJ.959, DJ.957, DJ.952 and DJ.953 are stratigraphically continuous (Crame et al., 2004). B, BAS 2006 field season, sub-sections D5.201, D5.212, D5.215, D5.218, D5.219, D5.220, D5.222 and D5.229 comprise composite section D5.251 (Bowman et al., 2012, 2013a, 2014). C, Measured section trace from Tobin et al. (2012) based on GPS coordinates taken from that study. Map after Montes et al (2010). [1.5 column width. Black and white]

Fig. 2: Lithostratigraphy, sedimentology and correlation of measured sections as located in Figure 1 (A – B), southern Seymour Island, Antarctic Peninsula. BAS, British Antarctic Survey; K, Cretaceous; Pg, Paleogene. The K–Pg boundary horizon is identifiable using dinoflagellate cyst biostratigraphy (Elliot et al., 1994; Askin and Jacobsen, 1996; Bowman et al., 2012), sedimentology (the base of a prominent glauconite-rich bed, Zinsmeister, 1998) and the disappearance of ammonite macrofossils. The age model is presented in Figure 3. The López de Bertodano Formation consists predominantly of hundreds of metres of clayey-silts and silty-clays. In section B, the sub-section overlap between D5.222 and D5.229 has been taken into account when interpreting the macrofossil data. [1.5 column width. Black and white]

Fig. 3: Age model for the López de Bertodano Formation, southern Seymour Island, Antarctic Peninsula. This sequence has been dated using biostratigraphy (palynology, micro- and macro-fossil, e.g. Macellari, 1988; Elliot et al., 1994; Bowman et al., 2012; Olivero, 2012a; Bowman et al., 2013a), magnetostratigraphy (Tobin et al., 2012) and strontium isotope stratigraphy (McArthur et al., 1998), calibrated to Gradstein et al. (2012). SHI = Snow Hill Island Formation, S = Sobral Formation. [1.5 column width. Black and white]

Fig. 4: Composite range chart of cephalopod (ammonite and nautiloid) taxa from the López de Bertodano Formation, southern Seymour Island, Antarctic Peninsula. Fossil occurrences have been amalgamated from the DJ sections and section D5.251 to show the entire recorded range of each taxon. Section correlation and the age model are illustrated in Figures 2 and 3, and discussed in the text. Taxa are ordered by first appearance with 50% confidence intervals on ammonite ranges shown as dashed red lines. Although ammonite confidence intervals span the K–Pg boundary, we believe none survived into the Danian. Rare specimens collected above the boundary are not plotted as they are considered reworked and their stratigraphic position probably the result of more recent glacial drift. Tick marks are taxon occurrences plotted at the stratigraphic mid-point of sampling bins (refer to Supplementary Figures 1 and 2). Refer to Appendix 1 for taxonomic notes. Ammonite species names in black, nautiloid species name in grey; SHI, Snow Hill Island Formation; S, Sobral Formation; *, last appearance of taxa found beneath K–Pg boundary by Zinsmeister (1998). [1.5 column width. For colour reproduction online, black and white in print]

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

Fig. 6: A, *Maorites* cf. *weddelliensis* Macellari, 1986 (D5.691.2), A1 – lateral view, A2 – ventral view; B, *Maorites densicostatus* Kilian and Reboul, 1909 (DJ.953.379), B1 – lateral view, B2 – ventral view; C, *Maorites tuberculatus* Howarth, 1958 (D5.955.2); D, *Maorites seymourianus* Kilian and Reboul 1909 (D5.1021.2); E, *Kitchinites* sp. (D5.1027.2); F, *Pachydiscus* (*Pachydiscus*) *ultimus* Macellari, 1986 (DJ.953.404), F1 – lateral view, F2 – apertural view; G, *Pachydiscus* (*Pachydiscus*)

riccardii Macellari, 1986 (D5.251 – unlabelled). All figures are x 0.5. Specimens were coated with ammonium chloride prior to photography. [Full page – black and white]

Fig. 7: Composite cephalopod diversity from the López de Bertodano Formation (southern Seymour Island, Antarctic Peninsula) plotted against molluscan macrofossil oxygen isotope data (Dutton et al., 2007; Tobin et al., 2012) regional palaeoclimate (Bowman et al., 2013a, 2014), and sedimentological/sequence stratigraphic interpretations (Macellari, 1988; Olivero et al., 2007; Olivero et al., 2008; Olivero, 2012a). Section correlation and the age model are illustrated in Figures 2 and 3, and discussed in the text. Snowflake symbols indicate the possible occurrence of seasonal sea ice based on palynological data (Bowman et al., 2013). Cephalopod diversity is represented as: (1) raw species richness (number of species within sampling bin), circles; (2) Standing species richness: (includes taxa that range through). See text for details of these indices and overall sampling strategy. MME, Mid-Maastrichtian Event (e.g. Jung et al., 2013). [1.5 column width. Black and white]

Fig. 8: Composite stratigraphic abundance of uppermost Maastrichtian cephalopod taxa, López de Bertodano Formation, southern Seymour Island, Antarctic Peninsula. Numbered squares correspond to last appearance datum of taxa ordered stratigraphically. Red line indicates stratigraphic abundance value of 15%, above which indicates a reliable last occurrence (Meldahl, 1990). [For colour reproduction online, black and white in print]

Fig. 9: Stratigraphic distribution and faunal turnover of taxa present in the Late Cretaceous of the James Ross Basin plotted against lithostratigraphy (not to scale) and biostratigraphy (ammonite assemblages 1–14 taken from Olivero and Medina (2000) and Olivero (2012a; 2012b). Co. = Coniacian, Sa. = Santonian, Gu. = Gustav Group, HL = Hidden Lake Formation. A = composite range chart of taxa. Solid lines correspond to range through data; dashed lines indicate where taxon is not recorded in two or more ammonite assemblages, i.e. temporarily absent from the basin. Horizontal tick marks correspond to first and last appearances. Numbered ranges correspond to taxa as follows: **1–43 = ammonite genera**: 1 = *Diplomoceras*; 2 = *Maorites*; 3 = *Anagaudryceras*; 4 = *Zelandites*; 5 = *Kitchinites* (*Kitchinites*); 6 = *Pseudophyllites*; 7 = *Grossouvrites*; 8 = *Pachydiscus* (*Pachydiscus*); 9 =

Gunnarites; 10 = *Jacobites*; 11 = *Tetragonites*; 12 = *Gaudryceras* (*Gaudryceras*); 13 = *Eupachydiscus*; 14 = *Anapachydiscus*; 15 = *Neograhamites*; 16 = *Baculites*; 17 = *Polyptychoceras*; 18 = *Astreptoceras*; 19 = *Phyllopachyceras*; 20 = *Neokossmaticeras*; 21 = *Metaplacenticeras*; 22 = *Hoplitoplacenticeras*; 23 = *Neophylloceras*; 24 = *Natalites*; 25 = *Ryugasella*; 26 = *Parasolenoceras*; 27 = *Karapadites*; 28 = *Oiphyllites*; 29 = *Hauriceras*; 30 = *Caledonites*; 31 = *Eubostrychoceras*; 32 = *Yezoites*; 33 = *Hoploscaphites*; 34 = *Ainoceras*; 35 = *Vertebrites*; 36 = *Damesites*; 37 = *Placenticeras*; 38 = *Scaphites*; 39 = *Scalarites*; 40 = *Kossmaticeras* (*Kossmaticeras*); 41 = *Menuites* (*Neopachydiscus*); 42 = *Perinoceras*; 43 = *Pseudoxybeloceras*. All first (FADs) and last appearance datums (LADs) plotted at the mid-point of corresponding ammonite assemblage, except for ammonite assemblage 14, where taxa 1–7 extend to the top of the assemblage (i.e. the K–Pg boundary). Genera ordered based on last appearance, data from Kennedy et al., (2007) and Olivero (2012a; 2012b). **44 = dimitobelid belemnites; 45 = inoceramid bivalves; 46 = nautilids** (*Eutrephoceras*). Data based on Doyle, (1990), Crame et al., (1996), Crame and Luther, (1997), Cichowolski et al., (2005), Olivero (2012b). B = Sedimentary cycles and relative sea-level changes identified by Olivero and Medina (2000) and Olivero (2012a; 2012b) (N = *Natalites*; NG = *Neograhamites–Gunnarites*; MG = *Maorites–Grossouvrites*). C = Faunal turnover data based on ammonite genera 1–43 calculated based on difference between the number of FADs and LADs of ammonite genera in each ammonite assemblage. [Full page – portrait orientation. Black and white]

Highlights

- High resolution sampling of a unique high latitude Maastrichtian cephalopod fauna.
- A single pulse of extinction in the cephalopod fauna occurs at the K–Pg boundary.
- Diversity increased during the Maastrichtian, linked to global environmental changes.
- Longer term diversity was controlled by dynamic Late Cretaceous sea level and climate changes.
- Despite these fluctuations ammonite diversity in Antarctica remained stable prior to the K–Pg extinction.