Cretaceous Research (2000) **21**, 269–279
doi: 10.1006/cres.1999.0192, available online at http://www.idealibrary.com on IDEAL®

Patterns of Late Cretaceous ammonite biogeography in southern high latitudes: the family Kossmaticeratidae in Antarctica[1]

***Eduardo B. Olivero and †Francisco A. Medina**

**Centro Austral de Investigaciones Científicas (CADIC-CONICET), Avda. Malvinas Argentinas s/n, 9410 Ushuaia, Tierra del Fuego, Argentina; e-mail: eolivero@satlink.com*
†Centro de Investigaciones en Recursos Geológicos (CIRGEO-CONICET); R. de Velasco 847; 1414 Buenos Aires, Argentina.

Revised manuscript accepted 29 April 1999

A refined biostratigraphy of the Antarctic kossmaticeratids from the James Ross Basin is contrasted against other Upper Cretaceous sections around southern Gondwana to inspect for possible biogeographic patterns. In the 3-km-thick Marambio Group two major unconformities are recognized at the base of the upper Campanian and Maastrichtian, respectively. The unconformities divide the succession into a Santonian–lower Campanian Sequence (NS); an upper Campanian–lower Maastrichtian Sequence (NGS); and a Maastrichtian–Danian Sequence (MGS). *Natalites* in the NS; *Neograhamites-Gunnarites* in the NGS; and *Maorites-Grossouvrites* in the MGS are the most abundant kossmaticeratid ammonites, represented in parts by hundreds or thousands of specimens. Comparison of the Antarctic fauna with that of eastern South Africa, Madagascar, southern India, Australia, New Zealand and southern South America suggests three diversification phases for the Kossmaticeratinae and Brahmaitinae, occurring in different places at different times in southern Gondwana. Early diversification of the Kossmaticeratinae started in the Santonian of eastern Gondwana and continued into the early Campanian of southern high latitudes. Five kossmaticeratid genera, including the relatively long-ranging *Maorites* and *Grossouvrites*, and a low-endemic ammonite fauna are recorded. The NS/NGS unconformity marks a major faunal change and the early disappearance in Antarctica of several mollusc groups that are known to range into the Maastrichtian in lower latitudes. Within the NGS, a new late Campanian–early Maastrichtian diversification phase took place in southern high latitudes and five Kossmaticeratinae, mostly endemic to the Weddellian Province, were added. Finally, the Maastrichtian NGS/MGS unconformity marks a drastic reduction of Weddellian Kossmaticeratinae, with only *Grossouvrites* and *Maorites* reaching the topmost Maastrichtian in Antarctica. By contrast, the Maastrichtian of eastern Gondwana saw a final diversification phase, with three new Brahmaitinae (present also in the Northern Hemisphere) and the persistence of five Campanian–early Maastrichtian Weddellian Kossmaticeratinae. The pattern of successive low endemism in the early Campanian NS, earlier exclusion of lower latitude Maastrichtian groups and higher endemism in the late Campanian–Maastrichtian NGS, and drastic diversity decrease in the Maastrichtian MGS, is consistent with known calcareous microfossil biogeography and long-term cooling in southern high latitudes. During the final Maastrichtian diversification, the kossmaticeratids spread toward lower latitudes as a stenothermal group of ammonites moving toward their preferred seawater temperature.

Key Words: Late Cretaceous; Santonian; Campanian; Maastrichtian; ammonites; Kossmaticeratidae; biogeography; biostratigraphy; southern Gondwana; Antarctica; James Ross Basin.

1. Introduction and methods

Late Cretaceous kossmaticeratids are known as distinct biogeographic elements of southern Gondwana, including eastern South Africa, Madagascar, southern India, Australia, New Zealand, Antarctica, and southern South America. The progressive opening of the Indian and South Atlantic oceans and accompanying palaeoceanographic and palaeoclimatic changes, severed the biotic links among southern parts of Gondwana and by the Campanian–Maastrichtian two broad biogeographically distinct areas existed: South Africa-Madagascar-India (eastern Gondwana) and Antarctica-New Zealand-Patagonia (Weddellian Province) (cf. Kaufman, 1973; Zinsmeister, 1982). However, detection and tracking of changing

---

[1] Contribution to IGCP Project 381: South Atlantic Mesozoic correlations.

0195–6671/00/020269+11 $35.00/0

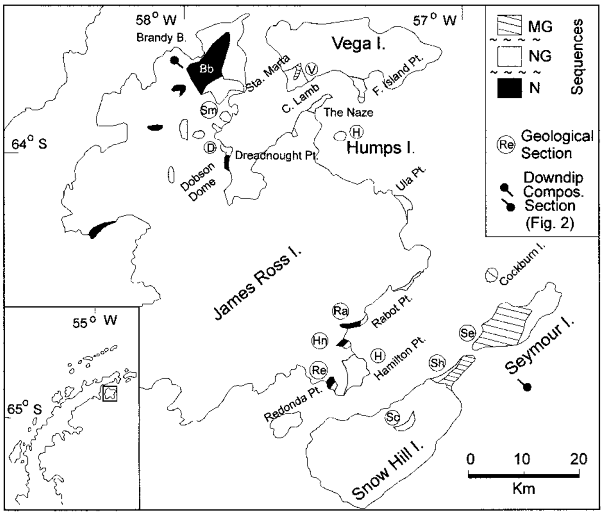

Figure 1. Location map and areal distribution of Santonian–Maastrichtian outcrops of the *Natalites* Sequence (N, Santonian–early Campanian); *Neograhamites-Gunnarites* Sequence (NG, late Campanian–early Maastrichtian); and *Maorites-Grossouvrites* Sequence (MG, Maastrichtian) in the James Ross Basin, Antarctica. Key for local sections in Figure 2.

biogeographic patterns has been obscured by the lack of sound systematic and stratigraphic control on the ammonite faunas, especially in Antarctica. Based on new data from the James Ross Basin, Antarctic Peninsula (Figure 1), we present a refined biostratigraphy of the Antarctic kossmaticeratid genera, which is compared with other Upper Cretaceous sections around southern Gondwana to inspect for possible biogeographic patterns.

In the James Ross Basin the thick and highly fossiliferous Santonian–Maastrichtian Marambio Group is superbly exposed in three main areas: NW James Ross Island; N James Ross, Vega, and Humps islands; SE James Ross, Snow Hill and Seymour islands (Figure 1). The Kossmaticeratidae dominates the ammonite fauna. In several horizons, kossmaticeratid specimens can be counted by hundreds or thousands and largely outnumber the rest of the fauna. Dominance of fine-grained rocks, mostly silty-sandy mudstones, tuffaceous mudstones, and very fine muddy sandstones, with subordinate medium sandstones, conglomerates, and coquinas, makes lithostratigraphic division of the group difficult. As a consequence there is no general agreement on the stratigraphic division and nomenclature below the group level. For the purpose of this study and to avoid conflicts of stratigraphic nomenclature, we use a different approach, dividing the Santonian–Maastrichtian succession into three main sequences. This is based on correlation of similar ammonite successions across the basin and recognition of two basin-wide unconformities. Using mainly kossmaticeratid taxa as biostratigraphic markers, the correlation of 12 combined local sections situated in a downdip direction across the basin resulted in a 3 km thick composite section for the Marambio Group (Figures 1, 2). Two major unconformities indicated by erosional surfaces, significant faunal changes, and marked shifts of sedimentary facies (Olivero *et al.*, 1992; Olivero & Scasso, 1992) are recognized at the basal upper Campanian and Maastrichtian, respectively. These unconformities divide the succession into a Santonian–lower Campanian sequence (NS); an upper Campanian–lower Maastrichtian sequence (NGS); and a Maastrichtian–Danian sequence (MGS) (Figure 2). The names of the sequences are derived from their most abundant kossmaticeratid genera: *Natalites* in the NS; *Neograhamites-Gunnarites* in the NGS; and *Maorites-Grossouvrites* in the MGS.

2. Upper Cretaceous stratigraphy of the James Ross Basin

N Sequence: Santonian–lower Campanian

In the Brandy Bay-Santa Marta Cove and Dreadnought Point areas the N Sequence includes the Alpha and Beta members of the Santa Marta Formation (Figures 1, 2, sections Bb, Sm, D; Olivero *et al.*, 1986; Scasso *et al.*, 1991; Strelin *et al.*, 1992) or the Lachman Crags and part of the Herbert Sound members (Pirrie, 1989; Pirrie *et al.*, 1997). At Rabot, Redonda and north Hamilton points it includes the lower-mid parts of the Rabot Formation (Figure 2, sections Ra, Hn, Re; Marenssi *et al.*, 1992); or partly the Rabot Point Member (Pirrie *et al.*, 1997).

Time-lines used for correlation in Figure 2 are mainly based on the ammonite assemblages delineated by Olivero (1992) in which, except for the lowermost assemblage, the lower boundaries were traced at the first record of a characteristic kossmaticeratid species. These include the following: (1) *Baculites* aff. *kirki* Assemblage, Santonian; (2) *Natalites rossensis* Assemblage, basal lower Campanian; (3) *Natalites* spp. group 1 Assemblage, lower Campanian; (4) *Grossouvrites occultus-Maorites* sp. Assemblage, lower Campanian; (5) *Natalites* aff. *morenoi-N. taylori* Assemblage, lower Campanian; and (6) *Karapadites* aff. *centinelaensis-Natalites* spp. group 2 Assemblage, topmost lower Campanian.

Assemblage 2 is dominated by a single species of *Natalites*, with an important presence of scaphitids, nostoceratids, baculitids, and pachydiscids. Within

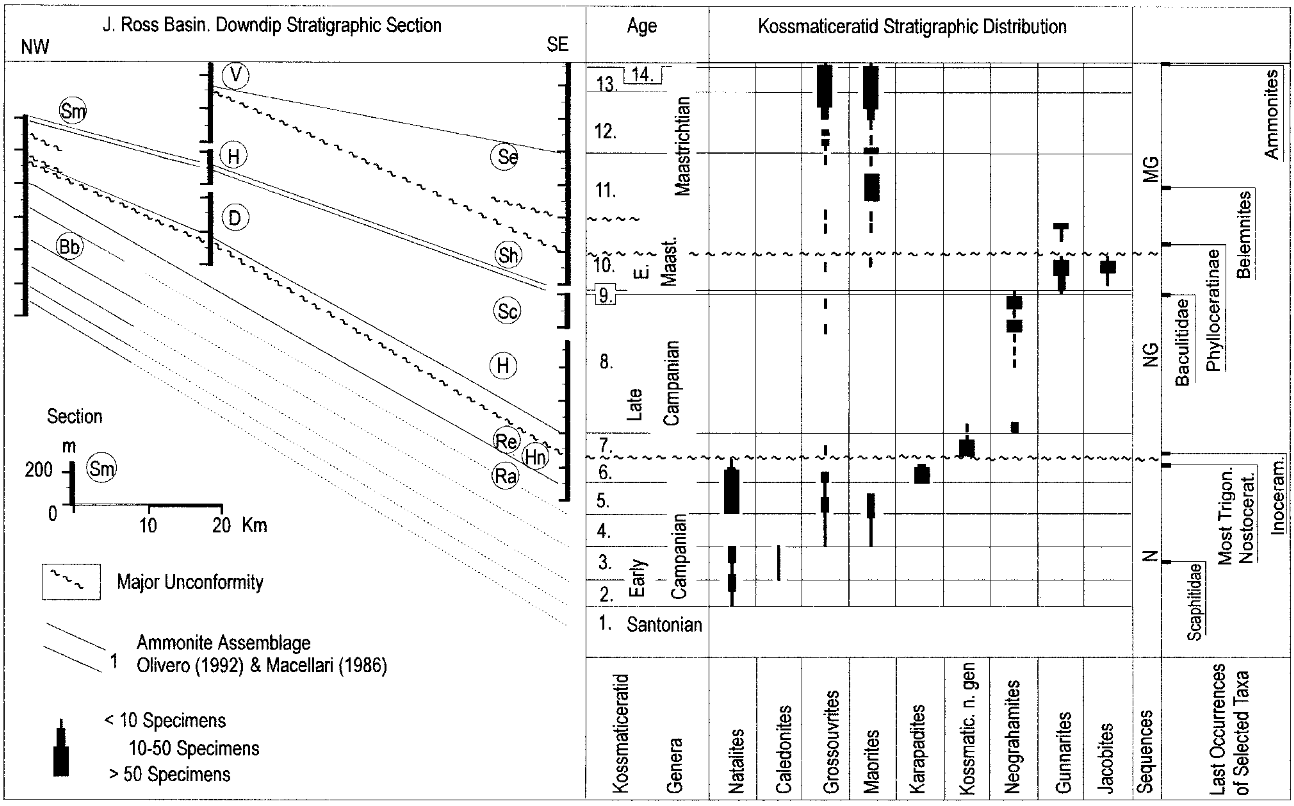

Figure 2. Left: downdip, composite stratigraphic section across the James Ross Basin (location in Figure 1); top datum line is approximately the K/T boundary; correlation and relative position of local sections based on ammonite assemblages 1–14 explained in the text. Right: stratigraphic distribution of Kossmaticeratidae genera in the James Ross Basin, with indication of relative abundance of specimens and stratigraphic position of last occurrences of selected non-kossmaticeratid taxa. Local sections: Brandy Bay (Bb); Santa Marta Cove (Sm); Vega (V) and Humps (H) islands; Dreadnought (D), Rabot (Ra), Redonda (Re), north Hamilton (Hn), and Hamilton (H) points; Sanctuary Cliffs (Sc); and Snow Hill (Sh) and Seymour (Se) islands.

the lower Campanian assemblages 2 to 6, the kossmaticeratids are dominated both in species richness and number of specimens by *Natalites*, with important representation in certain horizons of *Grossouvrites*, *Maorites*, and *Karapadites* (Figure 2). In the assemblages 5 and 6 part of the kossmaticeratids were previously accommodated either in *Neograhamites* or *Gunnarites* but they clearly belong to *Natalites* (cf. Olivero, 1992). Typical stephanoceratid-like *Neograhamites* or typically crenellated *Gunnarites* have all first records well above the unconformity at the top of the NS. For example, the first record of *Gunnarites* is more than 200 m or 700 m stratigraphically higher, respectively in proximal or distal parts of the basin, than the last record of *Natalites* (Figure 2). *Natalites* spp. group 2, include *Natalites rotundus* (Spath) and *N. pseudobhavani* (Spath) and this invalidates their proposed synonymy with *Gunnarites antarcticus* (Weller) and *G. kalika* (Stoliczka), respectively (Olivero, 1992).

In proximal parts of the basin (section Sm, Figure 2), the top of the NS is marked by a major unconformity defined by Olivero & Scasso (1992). Here, a single conglomerate horizon above the unconformity preserves a mixture of uppermost lower Campanian and basal upper Campanian ammonites (Olivero, 1992), representing parts of assemblages 6 and 7. In the distal parts of the basin (sections Ra, Re, Hn, Figure 2), these assemblages are recorded in a thickness in excess of 100 m, suggesting erosion or nondeposition of an important sedimentary package in the Brandy Bay-Santa Marta Cove area. In addition to this erosional episode, the unconformity is also expressed by a marked faunal change (cf. Scasso *et al.*, 1991, fig. 5; Olivero, 1992, fig. 3). The notable and abrupt changes in the ichnocenosis, sedimentary facies, and petrofacies of the sandstones below and above this unconformity at the boundary between the Beta and Gamma members, Santa Marta Cove area (cf. Scasso *et al.*, 1991; Pirrie, 1989), are also interpreted as related to this major unconformity. At Rabot, Hamilton, and Redonda points, the unconformity is marked by an abrupt change in the invertebrate fauna (Figure 2) and palynomorphs (Marenssi *et al.*, 1992, fig. 3). The unconformity between the NS and NGS could be of regional or even continental significance as its age approximately corresponds to a marked disconformity, detected in cores in the southern oceans (Huber & Watkins, 1992).

NG Sequence: basal upper Campanian–lower Maastrichtian

In the Brandy Bay-Santa Marta Cove, Dreadnought Point, and Dobson Dome areas the NG Sequence includes the Gamma Member of the Santa Marta Formation (Figures 1, 2, sections Sm and D; Olivero *et al.*, 1986; Scasso *et al.*, 1991; Strelin *et al.*, 1992); part of the Rabot Formation; and the López de Bertodano Formation at Humps and Vega islands (Informal Member A, Olivero *et al.*, 1992), Cape Hamilton, and Snow Hill Island (Figures 1, 2, sections Ra, Hn, Re, Sc, Sh; Marenssi *et al.*, 1992; Robles Hurtado & Concheyro, 1995). These strata are also referred to part of the Herbert Sound, Rabot Point, and Hamilton Point members (Santa Marta Formation); the Cape Lamb, Sanctuary Cliffs, and Karlsen Cliff members (Snow Hill Island Formation) (Pirrie *et al.*, 1997). The Campanian strata from Cockburn Island (Askin *et al.*, 1991) are also included in the NG Sequence

Times-lines used for correlation are the kossmaticeratid assemblages defined by Olivero (1992) with slight modifications, including the following: (7) Kossmaticeratidae n. gen. Assemblage, basal upper Campanian; (8) *Neograhamites* spp. Assemblage, upper Campanian; (9) *Gunnarites-Neograhamites* Assemblage, uppermost upper Campanian–lower Maastrichtian; (10) *Gunnarites-Jacobites* Assemblage, lower Maastrichtian.

Assemblage 7 (Kossmaticeratidae n. gen. Assemblage) corresponds to the *Neograhamites* Assemblage VII of Olivero (1992), including the diagnostic basal upper Campanian association of *Baculites* aff. *subanceps pacificus* Matsumoto and Obata, *Hoplitoplacenticeras* sp., and *Metaplacenticeras* aff. *subtilistriatum* (Jimbo). The basis for the *Neograhamites* Assemblage of Olivero (1992) was the first record of this genus in a single bed of reworked concretions at the boundary between the Beta and Gamma members in the Santa Marta Cove area. The interpretation of this horizon as a lag concentration of mixed faunas above a major erosional surface (Olivero, 1992; Olivero & Scasso, 1992) is fully supported by new data from the internal parts of the basin at Rabot, Hamilton and Redonda points. Here (Figure 2), the stratigraphic succession of the ammonite fauna is as follows: abundant *Grossouvrites*, *Maorites* and *Natalites* (NS, Assemblage 5); a declining abundance of *Natalites* spp. group 2 (NS, Assemblage 6); a sudden appearance of abundant Kossmaticeratidae n. gen., accompanied by *Metaplacenticeras* and *Hoplitoplacenticeras* (NGS, Assemblage 7); and a declining abundance of Kossmaticeratidae n. gen. together with the first occurrence of *Neograhamites* sp. (NGS, Assemblage 8). In an intermediate position within the basin a similar succession was found at Dreadnought Point, where this new kossmaticeratid genus was first identified as *Mesopuzosia* sp. (Strelin *et al.*, 1992). Although Kossmaticeratidae n. gen. superficially resembles *Mesopuzosia*, its association with, and morphological transition to, *Neograhamites* clearly support the assignment to the Kossmaticeratidae (Olivero, in preparation).

The base of Assemblage 8 is marked by the first occurrence of *Neograhamites* at Hamilton and Dreadnought points (Figure 2, sections H, D). The ammonite fauna in the lower and thicker part (about 500 m thick, section H, Figure 2) includes a sparse record of two *Neograhamites* species, a few specimens of *Kitchinites* and *Pachydiscus*, and the first record of *Diplomoceras lambi* Spath. The upper part (section Sc, Figure 2) records an explosive abundance of *Neograhamites* sp. and *N. kiliani* Spath.

The base of Assemblage 9 is defined by the first record of species of *Gunnarites*, which for a short stratigraphic interval are associated with *Neograhamites* sp. This association forms a relatively thin but highly distinctive horizon that can be followed across the basin from Sanctuary Cliffs and Humps Island to Santa Marta Cove (Figures 1, 2). The ammonite fauna is indicative of a latest late Campanian–early Maastrichtian age (Olivero, 1992) and this is confirmed by calcareous nannofossils indicative of the NC21-NC22 or CC23-CC24 Biozones (Robles Hurtado & Concheyro, 1995).

The base of Assemblage 10 is loosely set near the first record of species of *Jacobites* at Snow Hill Island. This is the typical horizon described by Kilian & Reboul (1909) from Snow Hill Island and it is characterized by *Jacobites* and the explosive abundance of *Gunnarites*. It is also recorded at Vega (Cape Lamb and False Island Point) and James Ross islands (The Naze and Ula Point) (Spath, 1953; Olivero *et al.*, 1992).

The top of the NG Sequence is a marked unconformity that can be seen in the upper part of the sea cliff near Nordenskjöld's Hut on Snow Hill Island. Here, the fine-grained rocks containing the *Gunnarites-Jacobites* Assemblage are erosively cut by a series of deep channels filled with poorly fossiliferous, glauconitic sandstones. At Vega Island, a similar erosional surface at the top of Assemblage 10 lies below a conglomerate bed and is associated with important changes in the invertebrate fauna, palynomorphs, and lithology (Olivero *et al.*, 1992; Pirrie *et al.*, 1997).

MG Sequence: Maastrichtian–Danian

Outcrops of this sequence are restricted to Snow Hill, Seymour, and Vega (Cape Lamb) islands (Figure 1), including part of the Snow Hill Island and the López de Bertodano formations (Rinaldi *et al.*, 1978; Macellari, 1988a; Olivero *et al.*, 1992; Pirrie *et al.*, 1997).

In the lower part of the sequence, including the informal units 1–3 of the López de Bertodano Formation (Macellari, 1988a) and the upper member of the Snow Hill Island Formation (Pirrie *et al.*, 1997), the biostratigraphic distribution of the ammonite fauna is not well known. Previous data and recent fieldwork by the authors in the area suggest the following kossmaticeratid succession. The basal glauconitic sandstones are poorly fossiliferous, except for a concretionary horizon with abundant small *Gunnarites* sp. (Figure 2) recorded both at Snow Hill and Seymour islands. Associated ammonites include a few specimens of *Anagaudryceras*, *Diplomoceras lambi*, *Neophylloceras*, *Pseudophyllites*, and one *Maorites tuberculatus* Howarth (only on Snow Hill Island). From an apparently similar concretionary horizon Pirrie *et al.* (1997) recorded abundant specimens of *Maorites* spp. Above this horizon we found on Snow Hill and Seymour islands an association of *Diplomoceras lambi*, *Grossouvrites gemmatus* (Huppé), *Maorites densicostatus* (Kilian & Reboul), and *M. tuberculatus*. In the following mudstone-dominated succession, forming the rest of the Rotularia units of Macellari (1988a), ammonites are scarce except for a few horizons with abundant *Maorites tuberculatus*. We tentatively included all the ammonite fauna recorded in the stratigraphic interval between the basal unconformity of the MGS and the top of the Rotularia units of Macellari (1988a) in a single *Maorites tuberculatus* Assemblage (11) named after its most common kossmaticeratid species (Figure 2). For the following mollusc-bearing informal units we use the ammonite zonation of Macellari (1986), including: (12) *Pachydiscus ootacodensis*; (13) *P. riccardii*; and (14) *P. ultimus* (Figure 2). The top of the last zone is the conformable Cretaceous–Tertiary boundary (Macellari, 1986; 1988a, Zinsmeister & Feldmann, 1996) and this defines a latest Maastrichtian age for the *P. ultimus* Zone; the lower two zones are assigned to the Maastrichtian.

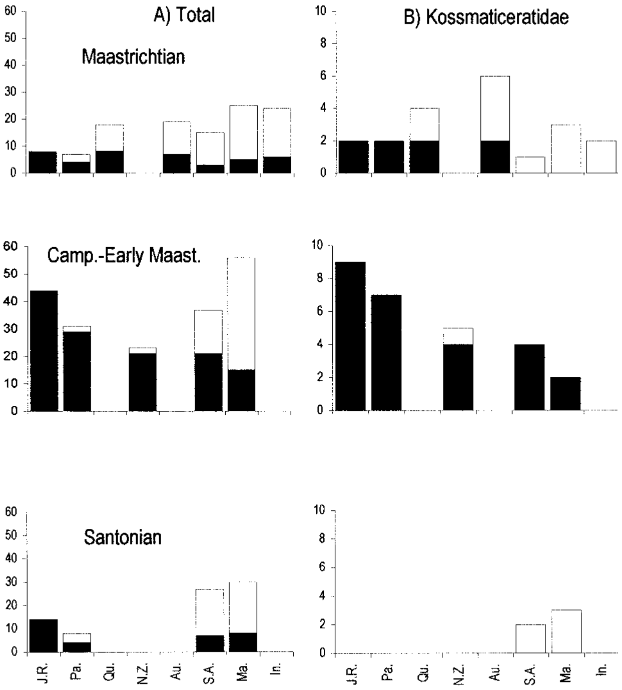

Figure 3. Total ammonite (A) and Kossmaticeratidae (B) generic/subgeneric diversity for the Santonian, Campanian–early Maastrichtian, and Maastrichtian of: James Ross Basin (J.R.); southern Patagonia (Pa.); Quiriquina (Qu.); New Zealand (N.Z.); Australia (Au.); eastern South Africa (S.A.); Madagascar (Ma.); and southern India (In.). Number of ammonite genera common to (black), or absent from (white), the James Ross Basin.

3. Weddellian and eastern Gondwana Late Cretaceous ammonites

Figure 3 depicts the total ammonite (3A) and kossmaticeratid (3B) generic/subgeneric diversity for Santonian–Maastrichtian localities around southern Gondwana. The analysis includes the ammonite fauna from James Ross Basin; Patagonia and Tierra del Fuego; Quiriquina, Chile; New Zealand; South Africa; Madagascar; Australia; and India. The source of data is the same as used by Macellari (1987) with new studies from India (Kennedy & Henderson, 1992a, b); Australia (Henderson *et al.*, 1992); South Africa (Kennedy & Klinger, 1985); Quiriquina (Stinnesbeck, 1986); Patagonia (Macellari, 1988b;

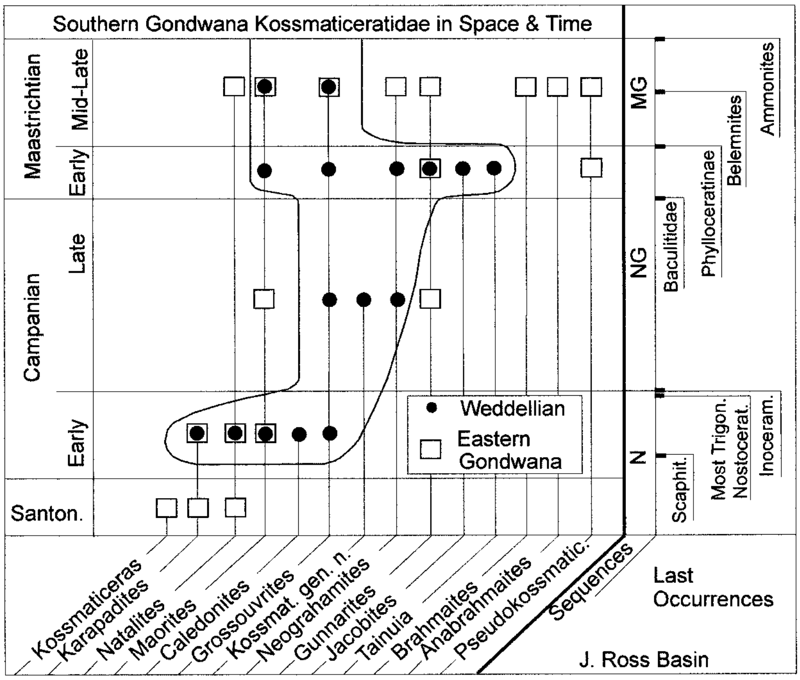

Figure 4. Weddellian and eastern Gondwana Santonian–Maastrichtian Kossmaticeratidae in space and time. Weddellian genera/subgenera within outlined area; the stratigraphic position of the Antarctic sequences (N, NG, and MG) and last occurrences of selected non-kossmaticeratid taxa are shown on the right.

Riccardi & Aguirre Urreta, 1988); and James Ross Basin (Olivero; 1992; Medina & Buatois, 1992; and references therein). Owing to uncertainties in correlation and the incomplete record of Late Cretaceous deposits in these areas we use only three general intervals: Santonian, Campanian (including part of the early Maastrichtian), and Maastrichtian. The localities are approximately arranged with increasing palaeogeographic distances from James Ross Basin (left to right in Figure 3) as estimated from maps by Lawver *et al.* (1992). The results in Figure 3 are comparable with those of Macellari (1987). The composition of the ammonite faunas reveals two broadly distinct areas: the Weddellian Province (Antarctica-New Zealand-Patagonia) (Zinsmeister, 1982) and eastern Gondwana. Two factors are important for the distinction of the Weddellian Province: the geographic dominance of the kossmaticeratids at high latitudes, specially in the late Campanian–early Maastrichtian (Macellari, 1987), and the absence of typical lower latitude ammonites, forming sometimes the dominant groups in eastern Gondwana (e.g., South Africa and Madagascar; Figures 3, 4).

In the Santonian, distinction between Weddellian and eastern Gondwana areas is due to the absence of lower-latitude ammonites in Antarctica, including *Pseudoschloenbachia* and all the texanitids (Figure 3). Santonian kossmaticeratids from South Africa or Madagascar (Kennedy & Klinger, 1985; Collignon, 1955) are not recorded in the basal NS in James Ross Island (Figures 2–4). *Peroniceras* was mentioned from the Coniacian of the James Ross Basin (Thomson, 1984) and one of us (FAM) recorded a possible kossmaticeratid fragment in the underlying beds of the NS. The possible presence of these taxa does not change substantially the fact that texanitids and kossmaticeratids were mostly restricted to eastern Gondwana in the Santonian. Mention of possible *Kossmaticeras* in Patagonia (Macellari, 1988b) and New Zealand (Henderson, 1970) are based on scarce and poorly dated material, so they are not included here. Most Santonian Antarctic ammonites have a wide distribution in the Indopacific realm (cf. Henderson, 1970), including among others *Anagaudryceras*, *Anapachydiscus*, *Baculites*, *Eubostrychoceras*, *Gaudryceras*, *Madagascarites*, *Polyptychoceras*, *Scaphites*, *Tetragonites*, *Yezoites* (Olivero, 1992). In Patagonia, Santonian ammonites are not well known but recorded scaphitids, baculitids, and *Anapachydiscus* (Paulcke, 1906; Riccardi & Aguirre Urreta, 1988) are similar to the Antarctic material.

During the Campanian–early Maastrichtian a clear differentiation of the Weddellian Province from the rest of southern Gondwana was evident (Figure 3). Likewise, there was a maximum diversification of kossmaticeratids with the number of genera decreasing away from the Weddellian Province (cf. Macellari, 1987). As discussed below, much of the diversity component shown in Figure 3 was attained during the early Campanian and endemism, especially in the kossmaticeratids, was at a maximum in the late Campanian–early Maastrichtian.

In the early Campanian, ammonite diversity reached a maximum peak in Antarctica as well as in Madagascar (Collignon, 1969). In Antarctica, the NS records representatives of the Phylloceratidae, Tetragonitidae, Gaudryceratidae, Scaphitidae, Baculitidae, Nostoceratidae, Diplomoceratidae, Desmoceratidae, Kossmaticeratidae, Pachydiscidae, and Placenticeratidae comprising a minimum of 50 ammonite species distributed in 30 genera (Olivero, 1992). Most of the early Campanian Antarctic fauna comprises Indopacific and cosmopolitan taxa. The heteromorphs, e.g., *Ainoceras*, *Baculites bailyi* (Woods), *B.* aff. *kirki* Matsumoto, *B. rectus* Marshall, *Eubostrychoceras*, *Polyptychoceras* and *Ryugasella*, have close specific affinities with forms from Japan, South Africa, New Zealand, Patagonia, and the Pacific Coast of North America (cf. Olivero, 1992). *Karapadites*, *Maorites*, and *Natalites* (Figures 2, 4) are also recorded from deposits of early Campanian age in Madagascar, India, South Africa, and Patagonia (Collignon, 1955; Kennedy & Klinger, 1985; Riccardi, 1983). *Caledonites* is only shared with New Caledonia (Collignon, 1977) and *Grossouvrites occultus* Olivero & Medina (1989) – the oldest known record of the genus – is only known from Antarctica. On this basis the early Campanian fauna of the NS can be characterized as relatively diverse and of low endemism. As in the Santonian, typical lower latitude groups, dominant in Madagascar and South Africa, such as texanitids and varied subgenera of *Pseudoschloenbachia* in Madagascar (Collignon, 1969; Klinger & Kennedy, 1980), were not present during the early Campanian in Antarctica.

In the upper Campanian–early Maastrichtian of the James Ross Basin (NG, Figure 2) six kossmaticeratid genera are recorded: Kossmaticeratidae n. gen., *Grossouvrites*, *Gunnarites*, *Maorites*, *Neograhamites*, *Jacobites*. However, diversity at any given horizon is very low, with only one or two prolific genera represented by hundreds or thousands of specimens, especially in the upper part of the sequence (Figure 2). The accompanying ammonite fauna is less abundant, except for some horizons with *Anagaudryceras*, *Phyllopachyceras* and the heteromorph *Astreptoceras* (Strelin *et al.*, 1992). Dominance of kossmaticeratid genera is very characteristic of the NG Sequence and this feature has no obvious similarities with any other late Campanian–early Maastrichtian fauna, except in southernmost Patagonia, Tierra del Fuego (Macellari, 1988b), New Caledonia (Collignon, 1977) and New Zealand (Henderson, 1970) (Figure 4). *Jacobites*, not previously mentioned from Patagonia, was identified by one of the authors (E.B.O.) while examining the ENAP collection at the Instituto de la Patagonia, Punta Arenas, Chile. With the addition of *Jacobites (Tainuia)* from New Zealand (Henderson, 1970), a total of 7 kossmaticeratid genera and subgenera are present in (and mostly restricted to) the Weddellian Province (Figure 4).

In the Maastrichtian, ammonite generic diversity around southern Gondwana was considerably lower than in the Campanian (Figure 3). In the James Ross Basin, the highly fossiliferous mid-upper part of the MGS, about 500 m thick (Figure 2), contains only 8 ammonite genera (Macellari, 1986; Zinsmeister & Feldmann, 1996). These include species of *Anagaudryceras*, *Diplomoceras*, *Grossouvrites*, *Kitchinites*, *Maorites*, *Pachydiscus*, *Pseudophyllites* and *Zelandites*. With the exception of the kossmaticeratids, these genera are either widely distributed in the Indopacific region (e.g., *Kitchinites*) or cosmopolitan (e.g., *Diplomoceras*, *Pseudophyllites*). Important Maastrichtian genera not present in Antarctica but well represented elsewhere including partly India, South Africa, Madagascar, Australia and Quiriquina are *Baculites*, *Eubaculites*, *Hoploscaphites*, *Nostoceras*, and some phylloceratids. Except for *Grossouvrites* and *Maorites*, the diverse kossmaticeratid genera from Australia (Henderson & McNamara, 1985) are all absent from mid-upper Maastrichtian deposits in Antarctica.

The data shown in Figure 3 are consistent with previous interpretations of the kossmaticeratids as distinctive elements of the Weddellian Province during the late Campanian–early Maastrichtian (Macellari, 1987). However, for most of Santonian–Maastrichtian time the Weddellian ammonite faunas were distinguished by the remarkable absence of lower latitude groups and the successive earlier exclusion of several taxa that ranged into the Maastrichtian elsewhere in the world. This phenomenon of earlier disappearance of taxa in Antarctica was previously noted for the inoceramids and belemnites (Zinsmeister & Feldmann, 1996; Crame *et al.*, 1996). The detailed biostratigraphy presented here confirms and expands this phenomenon to several taxa. Thus, our data (Figures 2, 4) show that the last occurrences of the families Scaphitidae and Nostoceratidae in Antarctica are within the lower Campanian NS. The top of the NS also records the last occurrences of most of the Inoceramidae and also the Trigoniidae, including the genera *Austrotrigonia*, *Nipponitrigonia*, *Pacitrigonia* and *Pterotrigonia* (Figure 2; Medina, 1980). The NGS late Campanian records the last occurrence of the Inoceramidae near its base and the last occurrence of the Baculitidae near its top (Figure 2). These earlier exclusions are followed in the Maastrichtian MGS by the last occurrences of the Phylloceratina, the belemnites, and finally by the ammonites at the K/T boundary (Figure 2; Macellari, 1986; Zinsmeister & Feldmann, 1996).

4. Biogeography of southern Gondwana kossmaticeratids

Though not generally accepted (cf. Wright, 1996), three subfamilies are included herein the Kossmaticeratidae: Marshallitinae Matsumoto (Albian–Turonian); Kossmaticeratinae Spath (late Turonian–Maastrichtian); and Brahmaitinae Collignon (latest Campanian–Maastrichtian). The Marshallitinae attained a peak diversity with 12 genera in the Albian–Cenomanian of the North Pacific area (Matsumoto, 1991). The first record of the Kossmaticeratinae is in the Turonian with *Kossmaticeras* and *Yokoyamaoceras*. Of these, only the first genus is well represented in the Turonian–Coniacian of the southern Indopacific region (Collignon, 1955).

Based on published data, and using for New Zealand and Patagonia the same stratigraphic succession as for Antarctica, Figure 4 depicts the spatial and temporal distribution of the Kossmaticeratidae in southern Gondwana. The evidence indicates that diversification of the Kossmaticeratinae and Brahmaitinae took place in several phases, occurring in different places at different times in southern Gondwana (Figures 3, 4). Early diversification of the Kossmaticeratinae occured during the Santonian–early Campanian and this is followed by two major diversification phases in the late Campanian–early Maastrichtian, and Maastrichtian. In total, the Santonian–Maastrichtian Kossmaticeratinae and Brahmaitinae of southern Gondwana include 14 genera. As explained below, the resulting pattern is very interesting in that it suggests a connection between the evolving biogeography of the family and the phenomenon of earlier exclusion of taxa from Antarctica.

The Santonian early diversification phase in eastern Gondwana is typified by species of *Karapadites*, *Kossmaticeras* and *Natalites*. These genera are present locally in Madagascar, South Africa and India but, with the possible exception of *Kossmaticeras*, they are not known in the Santonian of the Weddellian Province. By the early Campanian *Karapadites*, *Maorites* and *Natalites* were present in both the Weddellian Province and eastern Gondwana, with *Caledonites* and *Grossouvrites* restricted to the former. After the unconformity at the boundary between the NS and NGS, there was a major reorganization of the ammonite fauna and the late Campanian–early Maastrichtian diversification records a total of seven kossmaticeratid genera endemic to the Weddellian Province. Of these, only *Gunnarites* and *Maorites* have been reported, albeit poorly represented, from eastern Gondwana (Kennedy & Klinger, 1985). Prior to this second major diversification phase and high latitudinal restriction of the kossmaticeratids, the NS witnessed in Antarctica the last occurrences of the Scaphitidae and Nostoceratidae, as well as of most of the inoceramids and trigoniids (Figures 2, 4).

By the mid-late Maastrichtian the MG Sequence records in Antarctica another major faunal change, with only the relatively long ranging *Maorites* and *Grossouvrites* persisting until the final extinction of the ammonites at the K/T boundary. A similar situation is recorded in southern Patagonia where, after a major faunal break immediately above the *Hoplitoplacenticeras* beds (Malumián and Caramés, 1997), *Grossouvrites* and *Maorites* are the only known Maastrichtian kossmaticeratids (Hünicken, 1965). This striking diversity change in southern high latitudes is in marked contrast to the situation in the rest of southern Gondwana (or even the Northern Hemisphere), where eight kossmaticeratid genera are known in the Maastrichtian (Figures 3, 4). Most likely, the genera of the Brahmaitinae (*Anabrahmaites*, *Brahmaites* and *Pseudokossmaticeras*) were derived from *Neograhamites* (cf. Matsumoto, 1991) which probably originated in Antarctica, as the stratigraphic succession of morphologically related taxa indicates (Figure 2). In this third diversification phase, the Brahmaitinae – not known in Antarctica – apparently spread out to form important Maastrichtian groups in eastern Gondwana and the Northern Hemisphere (cf. Wiedmann & Kullmann, 1996).

The persistence of several Weddellian kossmaticeratids, found together with allied genera, into the late Maastrichtian of Australia (Henderson & McNamara, 1985; Henderson *et al.*, 1992) is of biogeographic interest. It is also interesting to note that the marked reduction in the generic diversity of the Antarctic kossmaticeratids was preceded by the exclusion of the baculitids in the early Maastrichtian, and was accompanied by the last occurrence of the Phylloceratina, recorded at the base of the MG

Sequence (Figures 2, 4). *Neophylloceras* and *Phyllopachyceras* are known to reach the topmost Maastrichtian in several parts of the world, including the complete sections of Spain and France (Wiedmann & Kullmann, 1996). Thus, the apparent earlier disappearance from Antarctica of the cosmopolitan phylloceratids is also of biogeographic interest.

The kossmaticeratids were probably a stenothermal group (Macellari, 1987). Accordingly, the detected pattern of three diversification phases, taking place in different areas at different times, could have a wider meaning for the understanding of climatic and oceanographic changes, and for the role they could have played in the biotic crisis at the end of the Cretaceous. Recent isotopic studies in macro- and microfossils from southern high latitudes indicate that a long-term cooling of surface waters began in the Late Cretaceous (Ditchfield *et al.*, 1994; Huber *et al.*, 1995). The calcareous plankton biogeography of the southern oceans was interpreted to reflect this long-term cooling (Huber & Watkins, 1992) and, significantly, the interpreted biogeographic pattern for the Santonian–Maastrichtian kossmaticeratids mirrors that of the calcareous plankton. In parallel with the plankton, the Santonian–early Campanian ammonite fauna of the NS has a relatively low degree of endemism. In upper Campanian–lower Maastrichtian deposits, above, the marked mid-Campanian unconformity, both the calcareous plankton in the southern oceans and the ammonites in the NGS display an endemic fauna that is restricted to southern high latitudes. During the mid-late Maastrichtian, the diversity of both groups was markedly reduced in southern high latitudes, with several elements migrating towards lower latitudes (cf. Huber & Watkins, 1992; Malumián & Náñez, 1996).

Zinsmeister & Feldmann (1996) and Crame *et al.* (1996) have suggested that the earlier extinction of some mollusc groups in Antarctica, and the consequent early decline in diversity in southern high latitudes, heralded the global biotic crisis at the end of the Cretaceous. The diachronous latitudinal disappearance of inoceramids and belemnites and the sharp decline of ammonite diversity were apparently related to global cooling of oceanic waters, starting first in southern latitudes (Zinsmeister & Feldmann, 1996). In this regard, it is interesting to note that while a decreasing evolutionary rate and diversity holds true for most of the Late Cretaceous ammonites (Wiedmann & Kullmann, 1996) the Kossmaticeratinae and Brahmaitinae display an opposite trend. The general trend depicted in Figure 4 suggests a diversity increase for these subfamilies, with three genera in the Santonian and eight genera in the Maastrichtian. The late Campanian–early Maastrichtian kossmaticeratid diversification was restricted to southern high latitudes and was preceded by the earlier disappearance of many mollusc taxa. However, in the final Maastrichtian diversification the kossmaticeratids spread out toward lower latitudes, strengthening the point that they were a stenothermal group of ammonites which migrated towards their preferred seawater temperature.

Acknowledgements

We thank the Instituto Antártico Argentino and Fuerza Aérea Argentina for all the logistic and personal support during the field seasons. D. A. Martinioni, F. A. Mussel, and G. Robles, actively collaborated in the fieldwork. EBO thanks M. E. López C. for helping with the ammonite distribution database and T. Hromic and E. L. Cárdenas for all their help at Instituto de la Patagonia. Critical review and comments by P. Bengtson and H. C. Klinger greatly improved the original text. Field research in Antarctica was partially financed by PID 3-148100 (CONICET).

References

Askin, R. A., Elliot, D. H., Stilwell, J. D. & Zinsmeister, W. J. 1991. Stratigraphy and paleontology of Campanian and Eocene sediments, Cockburn Island, Antarctic Peninsula *Journal of South American Earth Sciences* **4,** 99–117.

Collignon, M. 1955. Ammonites Nèocrètacèes du Menabe (Madagascar). III. Les Kossmaticeratidae. *Annales Gèologiques du Service des Mines, Madagascar* **22,** 7–52, 12 pls.

Collignon, M. 1969. Atlas des fossiles caractèristiques de Madagascar. (Ammonites). (Campanien Inferieur). *Service Gèologique Tananarive* **15,** 2–83.

Collignon, M., 1977. Ammonites Nèocrètacèes de la Nouvelle Caledonie. *Bureau des Recherches Gèologiques et Minières, Bulletin, Section 2* **14,** 7–36.

Crame, J. A., Lomas, S. A., Pirrie, D. & Luther, A. 1996. Late Cretaceous extinction patterns in Antarctica. *Journal of the Geological Society, London* **153,** 503–506.

Ditchfield, P. W., Marshall, J. D. & Pirrie, D. 1994. High latitude paleotemperature variation: new data from the Tithonian to Eocene of James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **107,** 79–101.

Henderson, R. A. 1970. Ammonoidea from the Mata Series (Santonian–Maastrichtian) of New Zealand. *Special Papers in Palaeontology* **6,** 1–82.

Henderson, R. A. & McNamara, K. J. 1985. Maastrichtian non-heteromorph ammonites from the Miria Formation, Western Australia. *Palaeontology* **28,** 35–88.

Henderson, R. A., Kennedy, W. J. & McNamara, K. J. 1992. Maastrichtian heteromorph ammonites from the Carnarvon Basin, Western Australia. *Alcheringa* **16,** 133–170.

Huber, B. T. & Watkins, D. K. 1992. Biogeography of Campanian–Maastrichtian calcareous plankton in the region of the Southern Ocean: paleogeographic and paleoclimatic implications. In *The Antarctic paleoenvironment: a perspective on global change* (eds Kennett, J. P. & Warnke, D. A.), *Antarctic Research Series* **56,** 31–60 (AGU for American Geophysical Union).

Huber, B. T., Hodell, D. A. & Hamilton, C. P. 1995. Middle-Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients. *Geological Society of America, Bulletin* **107,** 1164–1191.

Hünicken, M. 1965. Algunos cefalópodos supracretácicos de Río Turbio (Santa Cruz). *Revista Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba* **26,** 49–99.

Kauffman, E. G. 1973. Cretaceous Bivalvia. In *Atlas of palaeobiogeography* (ed. Hallam A.), pp. 351–383 (Elsevier, Amsterdam).

Kennedy, W. J. & Henderson, R. A. 1992a. Heteromorph ammonites from the Upper Maastrichtian of Pondicherry, South India. *Palaeontology* **35,** 693–731.

Kennedy, W. J. & Henderson, R. A. 1992b. Non-heteromorph ammonites from the Upper Maastrichtian of Pondicherry, South India. *Palaeontology* **35,** 381–442.

Kennedy, W. J. & Klinger, H. C. 1985. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family, Kossmaticeratidae Spath, 1922. *Annals of the South African Museum* **95,** 165–231.

Klinger, H. C. & Kennedy W. J. 1980. The Umzamba Formation at its type section, Umzamba Estuary (Pondoland, Transkei), the ammonite content and paleogeographical distribution. *Annals of the South African Museum* **81,** 207–222.

Kilian, W. & Reboul, P. 1909. Les Cèphalopodes Nèocrètacèes des Îles Seymour et Snow Hill. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903* **3,** 1–75 (Stockholm).

Lawver, L. A., Gahagan, L. M. & Coffin, M. F. 1992. The development of paleoseaways around Antarctica. In *The Antarctic paleoenvironment: a perspective on global change* (eds Kennett, J. P. & Warnke, D. A.), *Antarctic Research Series* **56,** 7–30 (AGU for *American Geophysical Union*).

Macellari, C. E. 1986. Late Campanian–Maastrichtian ammonite fauna from Seymour Island (Antarctic Peninsula). *Paleontological Society Memoir* **18,** 1–55.

Macellari, C. E. 1987. Progressive endemism in the Late Cretaceous ammonite family Kosmaticeratidae and the breakup of Gondwanaland. In *Gondwana Six: stratigraphy, sedimentology and paleontology* (ed. McKenzie, G. D.), *Geophysical Monograph* **41,** 85–92 (AGU for American Geophysical Union).

Macellari, C. E. 1988a. Stratigraphy, sedimentology and paleoecology of Upper Cretaceous/Paleocene shelf-deltaic sediments of Seymour Island (Antarctic Peninsula). In *Geology and paleontology of Seymour Island, Antarctic Peninsula* (eds Feldmann, R. M. & Woodburne, M. O.), *Geological Society of America, Memoir* **169,** 25–53.

Macellari, C. E. 1988b. Late Cretaceous Kossmaticeratidae (Ammonoidea) from the Magallanes Basin (Chile). *Journal of Paleontology* **62,** 889–905.

Malumián, N. & Caramés, A. 1997. Upper Campanian–Paleogene from the Río Turbio coal measures in southern Argentina: micropaleontology and the Paleocene/Eocene boundary. *Journal of South American Earth Sciences* **10,** 189–201.

Malumián, N. & Náñez, C. 1996. Microfósiles calcáreos y nanofósiles calcáreos de la plataforma continental. In *Geología y recursos naturales de la Plataforma Continental Argentina* (eds Ramos, V. A. & Turic, M. A.), *XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, Relatorio* **5,** 73–93.

Marenssi, S. A., Lirio, J. M., Santillana, S. N., Martinioni, D. R. & Palamarczuk, S. 1992. The Upper Cretaceous of southern James Ross Island, Antarctica. In *Geología de la Isla James Ross* (ed. Rinaldi, C. A.), pp. 89–99. (Instituto Antártico Argentino, Buenos Aires).

Matsumoto, T. 1991. The Mid-Cretaceous ammonites of the family Kossmaticeratidae from Japan. *Palaeontological Society of Japan, Special Papers* **33,** 1–143.

Medina, F. A. & Buatois, L. A. 1992. Bioestratigrafía del Aptiano–Campaniano (Cretácico superior) en la Isla James Ross. In *Geología de la Isla James Ross* (ed. Rinaldi, C. A.), pp. 7–36. (Instituto Antártico Argentino, Buenos Aires).

Medina, F. A., Buatois, L. A., Strelin, J. & Martino, E. 1992. La fauna del Cabo Polanski, Isla James Ross. In *Geología de la Isla James Ross* (ed. Rinaldi, C. A.), pp. 193–199. (Instituto Antártico Argentino, Buenos Aires).

Olivero, E. B. 1992. Asociaciones de ammonites de la Formación Santa Marta (Cretácico tardío), isla James Ross, Antártida. In *Geología de la Isla James Ross* (ed. Rinaldi, C. A.), pp. 47–76. (Instituto Antártico Argentino, Buenos Aires).

Olivero, E. B. & Medina, F. A. 1989. Dimorfismo en *Grossouvrites gemmatus* (Huppé) (Ammonoidea) del Cretácico superior de Antártida. *IV Congreso Argentino de Paleontología y Bioestratigrafía,* (Mendoza, 1986) *Actas* **4,** pp. 65–74.

Olivero, E. B. & Scasso, R. A. 1992. Ciclos transgresivos-regresivos en el Cretácico superior de Antártida y su relación con cambios globales en el nivel del mar. *Cuarta Reunión Argentina de Sedimentología (:a Plata), Actas* **1,** pp. 9–16.

Olivero, E. B., Martinioni, D. R. & Mussel, F. J. 1992. Upper Cretaceous sedimentology and biostratigraphy of Western Cape Lamb (Vega Island, Antarctica). Implications on sedimentary cycles and evolution of the basin. In *Geología de la Isla James Ross* (ed. Rinaldi, C. A.), pp. 147–166 (Instituto Antártico Argentino, Buenos Aires).

Olivero, E. B., Scasso, R. A. & Rinaldi, C. A. 1986. Revision of the Marambio Group, James Ross Island, Antarctica. *Instituto Antártico Argentino, Contribución* **331,** 1–28.

Paulcke, W. 1906. Die Cephalopoden der oberen Kreide Sudpatagoniens. *Berichte der Naturforschenden Gesellschaft zu Freiburg* **15,** 1–82, pls 10–19.

Pirrie, D. 1989. Shallow marine sedimentation within an active margin basin, James Ross Island, Antarctica. *Sedimentary Geology* **63,** 61–82.

Pirrie, D., Crame, J. A., Lomas, S. A. & Riding, J. B. 1997. Late Cretaceous stratigraphy of the Admiralty Sound region, James Ross Basin, Antarctica. *Cretaceous Research* **18,** 109–137.

Riccardi, A. C. 1983. Kossmaticeratidae (Ammonitina), y nomenclatura estratigráfica del Cretácico tardío en el Lago Argentino, Santa Cruz, Argentina. *Ameghiniana* **20,** 317–345.

Riccardi, A. C. & Aguirre Urreta, M. B. 1988. Bioestratigrafía del Cenomaniano-Santoniano en la Patagonia Argentina. *V Congreso Geológico Chileno, Santiago* **2,** pp. 375–394.

Rinaldi, C. A., Massabie, A., Morelli, J., Rosenman, H. L. & Del Valle, R. A. 1978. Geología de la isla Vicecomodoro Marambio. *Instituto Antártico Argentino, Contribución* **217,** 1–44.

Robles Hurtado, G. M. & Concheyro, A. 1995. Sedimentología y bio-cronoestratigrafía (nanofósiles calcáreos) del nunatak Sanctuary Cliffs (Cretácico superior), Isla Cerro Nevado, Antártida. *VI Congreso Argentino de Paleontología y Bioestratigrafía* (Trelew), *Actas*, pp. 231–237.

Scasso, R. A., Olivero, E. B. & Buatois, L. 1991. Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine volcaniclastic fan-shelf depositional system (Upper Cretaceous-James Ross Island, Antarctica). *Journal of South American Earth Sciences* **4,** 239–260.

Spath, L. F. 1953. The Upper Cretaceous cephalopod fauna of Graham Land. *Falkland Island Dependencies Survey, Scientific Report* **3,** 1–60.

Stinnesbeck, W. 1986. Zu den faunistischen und palökologischen Verhältnissen in der Quiriquina Formation (Maastrichtium) zentral-Chiles. *Palaeontographica Abteilung A* **194,** 99–237.

Strelin, J., Scasso, R. A. & Olivero, E. B. 1992. New localities of the Santa Marta Formation (Late Cretaceous), James Ross island, Antarctica, stratigraphy and structural implications. In *Geología de la Isla James Ross* (ed. Rinaldi, C. A.), pp. 221–137 (Instituto Antártico Argentino, Buenos Aires).

Thomson, M. R. A. 1984. Cretaceous ammonite biostratigraphy of western James Ross Island, Antarctica. In *Memoria, III Congreso Latinoamericano de Paleontología* (Mexico) (ed. Perrilliat, M. de

C.), pp. 308–313 (Universidad Nacional Autonoma de México, Instituto de Geológia, Mexico).

Wiedmann, J. & Kullmann, J. 1996. Crises in ammonoid evolution. In *Ammonoid paleobiology* (eds Landman, N. H., Tanabe, K. & Davis, R. A.). *Topics in Geobiology* **13,** 795–811.

Wright, C. W. 1996. Cretaceous Ammonoidea. In *Treatise on invertebrate paleontology* (ed. Kaesler, R. L.), Part L, Mollusca 4, Revised, 362 pp. (The Geological Society of America, Boulder & The University of Kansas, Lawrence).

Zinsmeister, W. J. 1982. Late Cretaceous–Early Tertiary molluscan biogeography of the southern Circum-Pacific. *Journal of Paleontology* **56,** 84–102.

Zinsmeister, W. J. & Feldmann, R. M. 1996. Late Cretaceous faunal changes in the high southern latitudes: a harbinger of global biotic catastrophe? In *Cretaceous–Tertiary mass extinctions: biotic and environmental changes* (eds MacLeod, N. & Keller, G.), pp. 303–325 (W. W. Norton & Co., York, London).