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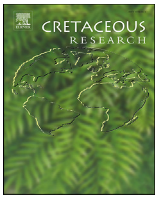

# Onshore–offshore trends in Campanian ammonite facies from the Marambio Group, Antarctica: Implications for ammonite habitats

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## ABSTRACT

Recent biostratigraphic and sedimentologic studies in the lower–mid Campanian ammonite-rich shelf deposits of the James Ross Basin, Antarctica made possible a precise reconstruction of facies tracts along an onshore–offshore transect about 70 km in length. In proximal, inner-shelf settings the Santa Marta Formation include trigoniid-rich coquinas and cross-bedded and massive sandstones. In distal, mid- to outer-shelf settings the age-equivalent Rabot Formation consists of bioturbated mudstones and interbedded inoceramid- and brachiopod-rich tempestites. Each of these sedimentary facies is characterized by a very distinctive ammonite facies, whose characterization along a neritic-oceanic gradient offer clues to ammonite habitats. Ammonite facies of proximal settings are dominated by relatively large and ornate kossmaticeratids, with subordinated heteromorphs, desmoceratids, gaudryceratids and tetragonitids. Taphonomy, size–frequency distribution, and non-lethal injuries attributed to arthropods consistently suggest a shallow habitat and a nektobenthic (demersal) mode of life for the kossmaticeratids. Conversely, in distal settings the ammonite facies is dominated by gaudryceratids, including large *Anagaudryceras* sp., and tetragonitids, with subordinated small kossmaticeratids and large pachydiscids. Restriction to offshore oceanic-influenced facies suggests that these gaudryceratids have a mesopelagic, planktic mode of life. The hamitocone heteromorphs are equally distributed in shallow and deep facies with a high degree of shell fragmentation, particularly in shallow settings. This pattern suggests that hamitocones were exposed to extensive post-mortem drift.

## 1. Introduction

The interpretation of possible causative relationships between assemblages of ammonite morphotypes and their host sedimentary facies has been controversial. As summarized in Kennedy and Cobban (1976), Westermann (1996) and Lukeneder (2015), two extreme interpretations exist: 1) the host sedimentary facies can be considered as an indicator of the habitat of the living animal or 2) the host sediment is not a reliable indicator of the living organism habitat due to extensive post-mortem transport. The first interpretation is the traditional view of European researchers, which concluded that relatively smooth morphotypes (leiostracans) and relatively ornate morphotypes (trachyostracans) were mostly restricted to deep and shallow marine facies, respectively (See Tanabe, 1979; Marcinowski and Wiedmann, 1985; Westermann, 1996, and the bibliography therein). The second interpretation has some supporting evidence from the known fact that actual *Nautilus* shells can drift hundreds or even thousands of kilometers after death of the organism (Reyment, 1973, 2008).

As with modern cephalopods ammonites are also interpreted as living in the water column, either with a planktic, nektic or nektobenthic mode of life (cf. Westermann, 1996). Accordingly, the ammonite shells can never be preserved *in situ* and there always be some degree of post-mortem transport. Thus the main problem revolves around how to assert whether post-mortem transportation displaced the ammonite shells outside the limits of their original habitat or not. One important line of evidence against the idea of a universal post-mortem superficial drift is based on the concept of a water depth that function as a threshold between surfacing and never surfacing dead shells (Chamberlain et al., 1981; Maeda and

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Seilacher, 1996). Hydrostatic pressure below this boundary will rapidly flood the phragmocone chambers causing the shell to sink. Small shells and those with large siphuncle diameter will flood the phragmocone chambers quickly and so they will sink at lower water depths than larger shells (see Wani and Gupta, 2015, and the bibliography therein). Nonetheless, dead cephalopod shells sinking below the never surfacing threshold depth can still be transported by bottom currents (Maeda, 1991; Maeda and Seilacher, 1996; Olivero, 2007; Wani and Gupta, 2015), which can move them outside their original habitat complicating paleoecological interpretations.

Relative changes of water depth in sedimentary basins can be detected using sedimentologic criteria. When these changes are analyzed in connection to quantitative data on ammonite faunal spectra from proximal to distal sedimentary facies, the join analysis can offer important independent evidence to evaluate if a given faunal spectrum represents original ammonite habitats or post mortem dispersal. Extensive post-mortem drift of ammonite shells will result in lack of coherence between sedimentary and ammonite facies, whereas close relationships between sedimentary facies and ammonite groups will reflect minimal post-mortem dispersal of ammonite shells (Kennedy and Cobban, 1976; Westermann, 1996; Lukeneder, 2015). In this study, we present an analysis of ammonite spectra, including the distribution of morphotypes and shell sizes, in the lower to mid Campanian of the Marambio Group, James Ross Basin, Antarctica. We restrict the analysis to a relatively short time spanning the Ammonite Association 6 (Olivero, 2012a, 2012b), with the finding that the ammonite assemblages of the shallower northwestern deposits of the upper Beta Member of the Santa Marta Formation are significantly different, both in terms of relative frequency of ammonite morphotypes and individual shell size, from that of the deeper, contemporaneous southeastern deposits of the Rabot Formation. Interestingly, the distribution patterns of Campanian ammonites facies from the Marambio Group shares many features in common with the Turonian ammonite facies of the Yezo Group in Japan (cf. Tanabe, 1979; Wani, 2007). Thus, the main objectives of this paper are to document onshore–offshore trends in ammonite facies from the Campanian of the Marambio Group, Antarctica; to discuss the implications of the segregation of particular ammonite assemblages to sedimentary facies; and to make some generalizations on the habitat of certain Antarctic ammonite groups, particularly kossmaticeratid and gaudryceratid groups.

## 2. Stratigraphic and paleoenvironmental settings

The James Ross Basin is a back arc basin located to the east of the Antarctic Peninsula (Fig. 1A). The basin fill includes two major Cretaceous stratigraphic units: the deep-water Aptian–Coniacian Gustav Group (Ineson, 1989) and the shelfal Santonian–Danian Marambio Group (Rinaldi et al., 1978). The Marambio Group is highly fossiliferous throughout its 3-km-thick clastic succession of mainly fine-grained sandstone and mudstone, with subordinate conglomerate and coquina (Crame et al., 1996, 2004; Pirrie et al., 1997; Olivero and Medina, 2000; Olivero et al., 2008; Olivero, 2012a).

During deposition of the Marambio Group, clastic provenance was located along the Antarctic Peninsula towards the west; clastic particles were transported to the east–southeast and east–northeast; and the shelf prograded for more than 100 km into the proto-Weddell Sea. The expansion of the shelf was punctuated by three major sedimentary cycles (Olivero and Medina, 2000; Olivero, 2012a): the N (Santonian–early Campanian); NG (late Campanian–early Maastrichtian); and MG (early Maastrichtian–Danian) sequences (Fig. 1B). The N Sequence includes the Santa Marta and Rabot formations; the NG Sequence includes the Snow Hill Island Formation and Haslum Crag Sandstone and the MG Sequence consists of the López de Bertodano Formation. These formations were correlated across the basin by means of 15 Santonian–Maastrichtian ammonite assemblages (see Olivero and Medina, 2000; Olivero et al., 2008; Olivero, 2012a, 2012b; and the bibliography therein).

The studied sections (Fig. 1) comprise the upper Beta Member (Scasso et al., 1991) of the Santa Marta Formation exposed in the Brandy Bay area, NW James Ross Island (Brandy Bay Section, Fig. 2) and the Rabot Formation (Lirio et al., 1989; Marenssi et al., 1992) exposed in Hamilton Norte and Redonda points, in SE James Ross Island (Hamilton and Redonda Points Sections, Fig. 2). In the Brandy Bay Section, six successive ammonite assemblages (Figs. 1B, 2) are recognized in the Alpha and Beta members of the Santa Marta Formation. The lowest, Santonian Ammonite Assemblage 1 (*Baculites* cf. *kirki*) lacks kossmaticeratids (Olivero, 1992), but the bases of the following early Campanian ammonite assemblages 2–6 were defined at the first occurrence of a particular kossmaticeratid genus and/or species. The stratigraphic interval that contains the Ammonite Assemblage 6 in Brandy Bay can be continued in a down-dip direction across the basin to the south east of James Ross Island (Fig. 2, Olivero, 1992; 2012a, 2012b; Raffi and Olivero, 2016).

In SE James Ross Island, the Ammonite Assemblage 6 in the Rabot Formation (Fig. 2, Olivero and Medina, 2000; Olivero, 2012a, 2012b) is characterized by abundant *Natalites* cf. *hauthali* associated with *Parasolenoceras* sp., *Antarcticeramus rabotensis* and abundant *Gaudryceras rabotense* Raffi and Olivero and two relatively large species of *Anagaudryceras* (Olivero, 2012b; Raffi and Olivero, 2016). The succeeding mudstones and intercalated fine-grained sandstones of the Ammonite Assemblage 7 bear abundant specimens of *Neokossmaticeras redondensis*, *Polyptychoceras* sp., *Gaudryceras rabotense*, *Anagaudryceras* spp., *Tetragonites* spp. and *A. rabotensis*, with rare records of *Metaplacenticeras subtilistriatum* and *Hoplitoplacenticeras* sp. (Olivero, 2012b; Raffi and Olivero, 2016).

The top of the Santa Marta and Rabot formations is defined by an unconformity, which defines a notable, marked change in the Antarctic kossmaticeratid fauna. Below the unconformity, the N (for *Natalites*) Sequence records a relatively diverse fauna dominated by species of *Natalites*. Above the unconformity, the *Natalites* fauna is replaced in the NG (for *Neograhamites* and *Gunnarites*) Sequence by a low-diversity fauna dominated by abundant specimens of these two kossmaticeratid genera (Olivero and Medina, 2000). Erosion associated with this unconformity eliminated most of the stratigraphic interval encompassing Ammonite Assemblage 7 (*Neokossmaticeras redondensis*) and part of Ammonite Assemblage 8–1 (*Neograhamites primus*) in the basin (Fig. 1B).

At Brandy Bay, the Alpha and Beta Members of the Santa Marta Formation consist of four vertically stacked intergrading facies associations interpreted as prodelta-basin plain; base of slope depositional lobes; delta slope channel complexes; and delta plain–inner shelf depositional settings, respectively (Fig. 2A–C) that represent a regressive, deep-water delta sequence (Scasso et al., 1991; Olivero, 2007). The uppermost facies association (subaqueous delta plain–inner shelf), dominated by coquinas with abundant shells of *Pterotrigonia*, *Cuccullaea* and *Aporrhais* (Fig. 2C), will be fully described in section 4. Nonetheless, we note here that in this facies association ornate kossmaticeratid and compressed desmoceratid shells dominate the ammonite fauna, with a relative frequency of more than 60%. In SE James Ross Island, the Rabot Formation comprises more than 300 m of storm dominated deposits, with a characteristic inoceramid–bachiopod biofacies, interpreted as originated in mid-outer shelf settings (Fig. 2, Hamilton–Redonda Point sections; Martinioni, 1992; Olivero, 2012a).

## 3. Methodology

Quantitative data on relative abundance of different morphotypes and/or species of ammonite were obtained partly in the field

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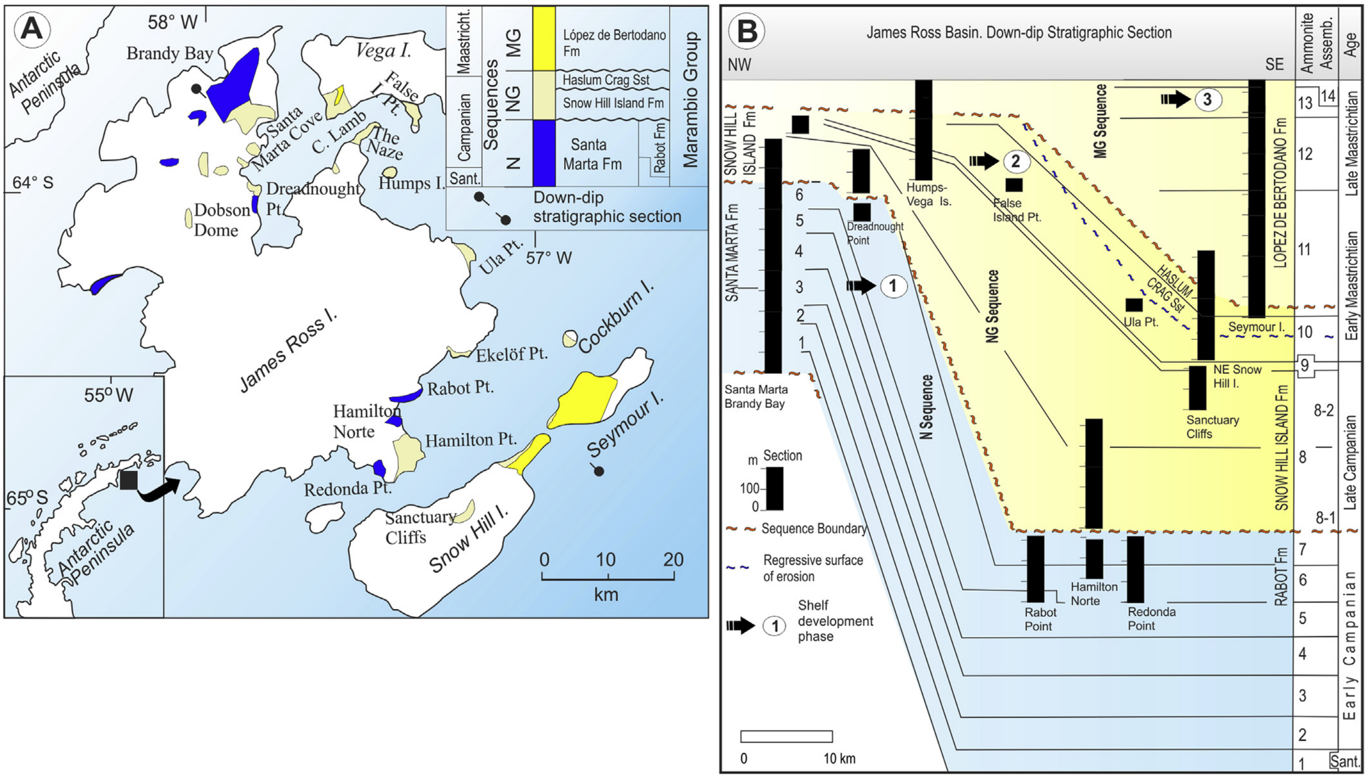

**Fig. 1.** A: Location and geological sketch map showing distribution of the Marambio Group in the James Ross Basin. B: Across-basin, down-dip stratigraphic section of the Marambio Group showing the stratigraphy, correlation of sections by means of 15 ammonite assemblages, and the three phases that punctuate the development of the shelf during the Santonian–Maastrichtian. Adapted from Olivero (2012a).

and partly from collections, noted or made by the senior author during the 1986–2010 field seasons and by both authors during the 2011–2014 Antarctic field seasons. Repositories of the ammonite collections are the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Avenida Ángel Gallardo 470, 1405 Buenos Aires, under the code MACN CIRGEO, and Centro Austral de Investigaciones Científicas (CADIC–CONICET), B. Houssay 200, 9410 Ushuaia, Tierra del Fuego, under the code CADIC PI.

Ammonite spectra for the Beta Member of the Santa Marta Formation were constructed using the relative proportions of the following morphotypes: lytoceratids, phylloceratids, heteromorphs, desmoceratids, kossmaticeratids, and pachydiscids, e.g. Fig. 2. For the beds containing the Ammonite Assemblage 6, Santa Marta and Rabot formations, and Ammonite Assemblage 7, Rabot Formation, both specific and morphotype frequency were computed (Fig. 3). In these cases, the size distribution of the dominant ammonite fauna conformed by kossmaticeratids and lytoceratids, which together constitutes more than 75% of the total ammonite fauna, was also computed. In the resulting size–distribution plots (Figs. 5 and 6) data are binned in 10 mm bins. The data include only complete or almost complete ammonite shells, i.e. with phragmocone and body chamber (see Figs. 4–7) that were available for measurements.

## 4. Sedimentary and ammonite facies

As described in section 2, recent biostratigraphic and sedimentologic studies in the lower to mid Campanian ammonite-rich shelf deposits of the James Ross Basin, Antarctica made possible a precise reconstruction of facies tracts along an onshore–offshore transect, about 70 km in length that includes the stratigraphic interval spanning the Ammonite Assemblage 6 and, partially, Ammonite Assemblage 7. The precise correlation of shallow depositional systems of the upper part of the Beta Member, Santa Marta Formation with relatively deeper depositional systems of the Rabot Formation (Fig. 2) allows the characterization of proximal vs. distal trends in ammonite facies of age-equivalent successions.

### *4.1. Santa Marta Formation, Ammonite Assemblage 6*

### *4.1.1. Sedimentary facies*

Strata of the Ammonite Assemblage 6 consist of an alternation of thick, bioturbated, well-sorted, fine-grained sandstone, silty very fine-grained sandstone and mudstone (Fig. 4A) with abundant plant fragments, leaves, seeds, and large tree trunks (Scasso et al., 1991; Olivero, 2007; Iglesias, 2016). Within the bioturbated fine-grained sandstones, the bivalves *Pterotrigonia* and *Cucullaea* are commonly preserved with both valves articulated and in their presumed life position. Several horizons with fossiliferous calcareous concretions occur within the fine-grained sandstone beds. The concretion bears very well preserved ammonite shells, many of them still with the pristine iridescent nacreous material (Fig. 4C–D; Olivero, 1992, 2007; 2012a), and lobsters (Feldmann and Tshudy, 1989). Lenticular packages with erosive basal contact, composed of clast-supported conglomerate and coquina, overlain by parallel-laminated or cross-bedded sandstone are common (Fig. 2). Coquinas bear abundant fragmented shells of bivalves, gastropods, scaphopods, ammonites and belemnites (Fig. 4B).

### *4.1.2. Note on ammonite taphonomy*

Within this interval the ammonite fauna is generally well preserved. The dominant groups, including kossmaticeratids, lytoceratids, and desmoceratids (Fig. 3B) preserve the complete shell, with calcite-filled phragmocones and sediment-filled body chambers,

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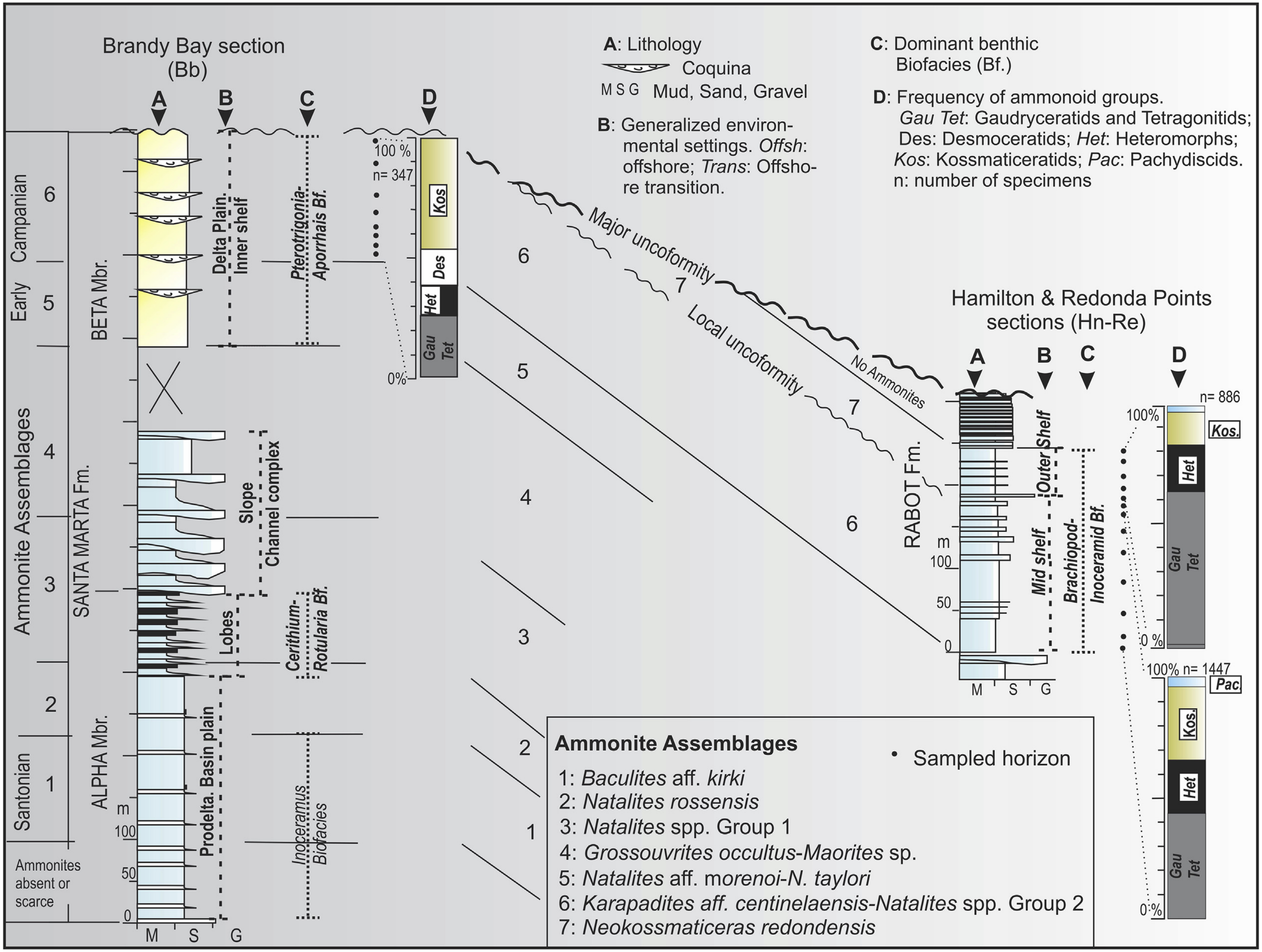

**Fig. 2.** Stratigraphy and correlation of the studied sections of the Santa Marta Formation at Brandy Bay and the Rabot Formation at Hamilton and Redonda points sections. Note that only the stratigraphic interval containing the Ammonite Assemblage 6 is continuous across the basin, albeit with marked facies changes between the shallower Santa Marta and the deeper Rabot formations. The generalized lithologies (A), environmental settings (B), benthic biofacies (C) and frequency of ammonite morphotypes are also shown. Adapted from Olivero (2007; 2012b).

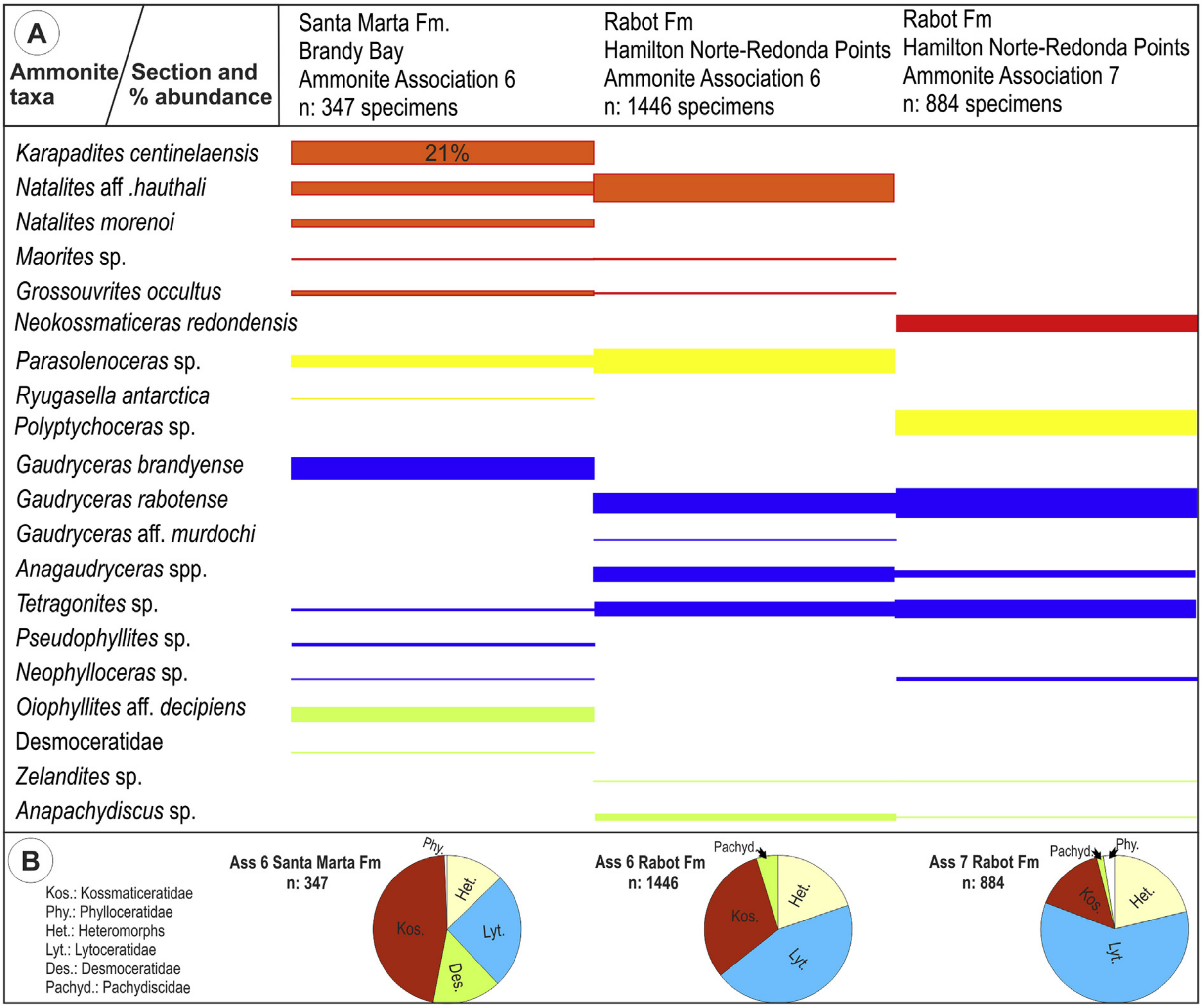

**Fig. 3.** Ammonite spectra (A) and dominant morphotype groups (B) for the Ammonite Assemblage 6 of the Santa Marta Formation at the Brandy Bay section; the Rabot Formation at the Hamilton Norte–Redonda points section; and Ammonite Assemblage 7 for the Rabot Formation. In A, the width of the bars indicates the percent abundance of taxa, e.g. the bar for *K. centinelaensis* represents 21% of abundance.

commonly still preserving iridescent aragonitic material (Fig. 4C–E). On the contrary, the shell of the heteromorphs, constituted almost exclusively by *Parasolenoceras* sp., is fragmented and only parts of the phragmocone or body chamber are recorded (Olivero, 2007).

Isolated complete planispiral ammonite shells are recorded either with the plane of symmetry in a horizontal position within calcareous concretions in fine-grained sandstones (Fig. 4C–E) or vertically embedded in the upper parallel-laminated interval of proximal tempestite beds (Fig. 4F). Several specimens of kossmaticeratids preserving non-lethal injuries, expressed by backwards V-shaped rib inflexions (Fig. 4G), were recovered from calcareous concretions in the same level preserving abundant fossil lobsters (Feldmann and Tshudy, 1989). Dense concentrations of well-preserved shells, both horizontally and vertically embedded, are commonly associated with abundant plant material (Olivero, 2007, figs. 5–6). These dense concentrations of wood particle and ammonoid shells, referred to as pod preservation (Olivero, 2007), are filling small scoop-shaped depressions c. 30 in length and 10 cm wide patchily distributed in very fine-grained sandstones, the origin of which was interpreted as formed by erosive bottom currents. The following weak current tail with dense concentrations of waterlogged wood fragments and ammonite shells was subsequently deposited into these depressions (Olivero, 2007).

### 4.1.3. Ammonite facies

The ammonite faunal spectrum in Ammonite Assemblage 6 is dominated by the kossmaticeratids *Karapadites centinelaensis* Riccardi (21%) and *Natalites* cf. *hauthali* (Paulcke) (12%). Less represented are *Natalites morenoi* (Riccardi); *Grossouvrites occultus* Olivero and Medina and *Maorites* spp. (Fig. 3A). The ornate kossmaticeratid morphotype (trachyostraca) represents c. 47% (Fig. 3B) of the total ammonite specimens (n: 347) observed in Ammonite Assemblage 6.

The feebly ornamented or smooth morphotype (leiostraca) is dominated by a single species of *Gaudryceras* (*G. brandyense* Raffi and Olivero), which represents 20% of the spectrum, and by the compressed desmoceratid *Oiophyllites decipiens* Spath (14%) (Fig. 3A). There is only a single specimen of large *Anagaudryceras* sp. and one *Tetragonites* sp. The leiostracan morphotype, which includes phylloceratid, lytoceratid, and desmoceratid ammonites, represents c. 41% of the total fauna (Fig. 3A–B).

The heteromorphs are represented almost exclusively by *Parasolenoceras* sp. (c. 11%), accompanied by few specimens of *Ryugasella antarctica* Olivero (c. 1%; Fig. 3).

For the most abundant morphotype groups, i.e. kossmaticeratids and gaudryceratids, we have computed (Fig. 5, Table 1) the distribution of the relative size frequency of all available specimens

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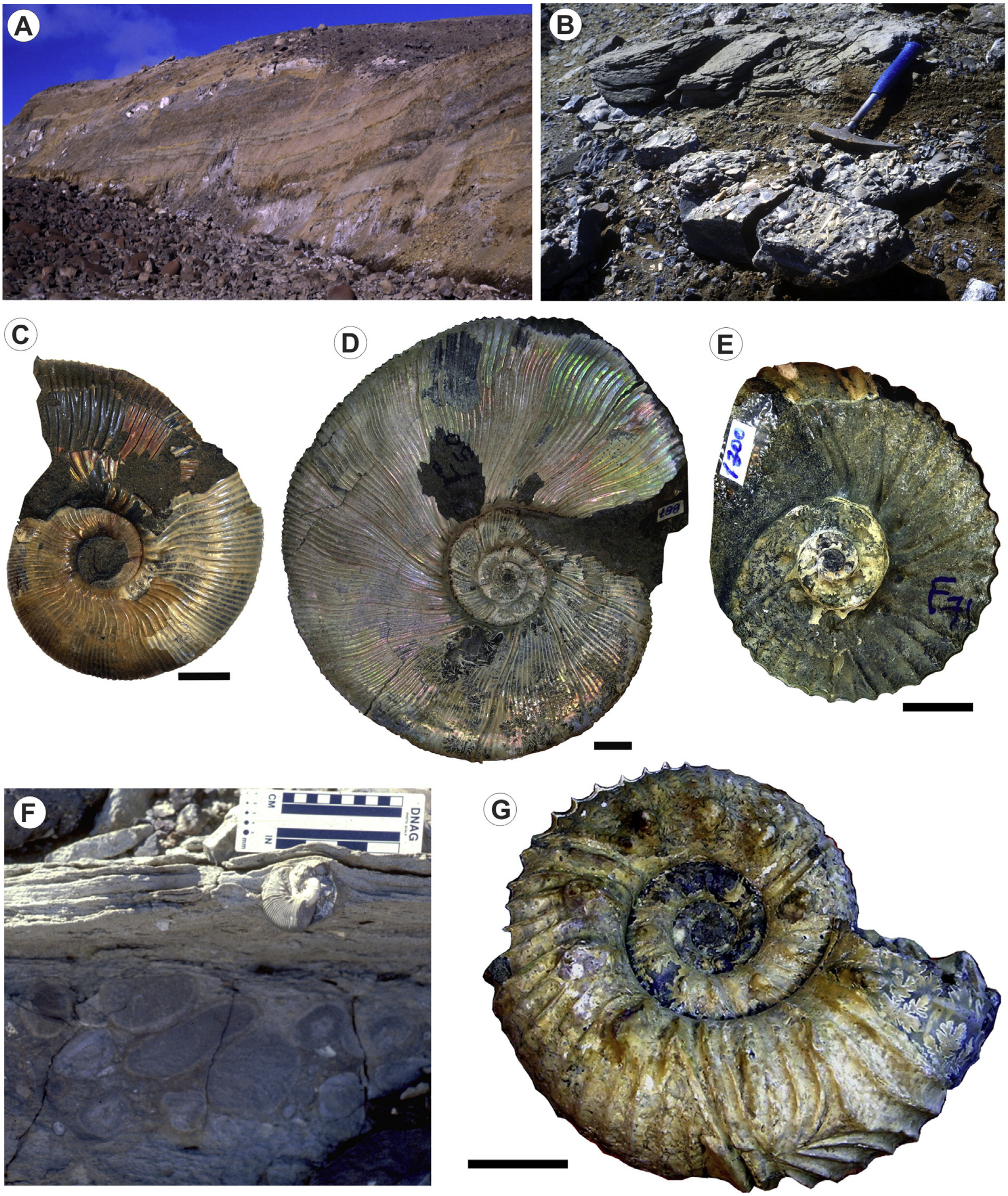

**Fig. 4.** Santa Marta Formation, Ammonite Assemblage 6. A: Aspects of the fine-grained sandstones with concretionary levels of the upper Beta Member. Height of cliff is about 15 m. B: Lenticular coquina with oriented shells of bivalves, scaphopods, gastropods and belemnites, capped by cross-bedded sandstones. C–D: Typical excellent preservation of shells with pristine nacre in Ammonite Assemblage 6. C, *Grossouvrites occultus* (CADIC PI 165). D, *Maorites* sp. (MACN CIRGEO 887). E: *Natalites* cf. *hauthali*, complete internal mold preserving patches of the shell material (MACN CIRGEO 1300). F: *Maorites* sp., vertically embedded in the plane parallel division of a tempestite (CADIC PI 62). G: Phragmocone of *Natalites morenoi* showing a non-lethal injury (ribs with apical V-shaped inflexions, (MACN CIRGEO 925). Scale bars: 1 cm.

preserving the phragmocone and body chamber (n: 111). The size of the lytoceratid specimens, represented almost exclusively by *Gaudryceras brandyense* Raffi and Olivero is relatively small, with a bin-mode size of 20–29.0 mm and dominant shell diameters ranging between 12 and 58.2 mm, with a single specimen reaching 96.5 mm. On the contrary, the more diverse kossmaticeratid, including four genera, are represented by larger specimens, with a bin-mode size of 70–79.9 mm and a range of sizes between 39 and 140 mm.

## 4.2. Rabot Formation, Ammonite Assemblages 6–7

### 4.2.1. Sedimentary facies

In Redonda and Hamilton points the Rabot Formation conforms a well-stratified succession that consists dominantly of fine-grained sandstone, mudstone and tuff (Fig. 7A). Near the base of the succession are intercalations of fine-conglomerate beds. At Rabot Point the formation includes near its base, thick,

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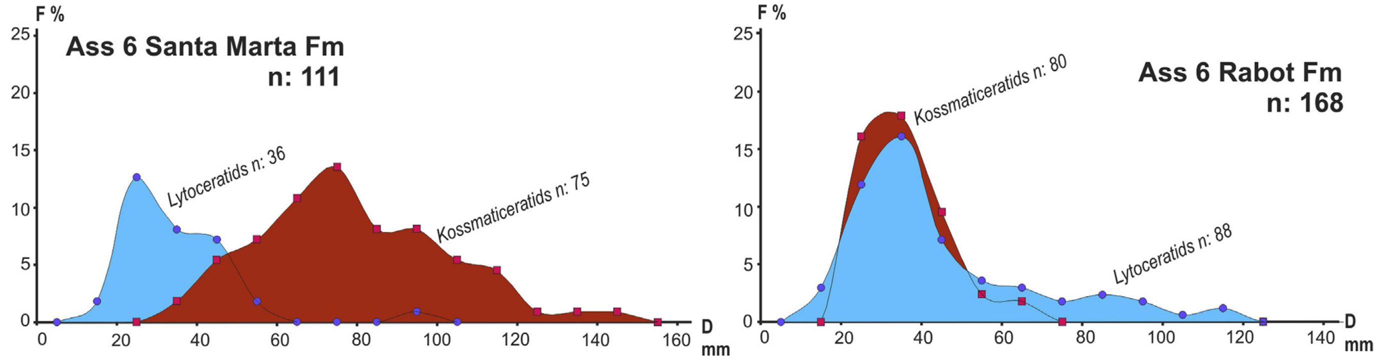

**Fig. 5.** Size–frequency distribution of complete specimens of the most abundant ammonite morphotypes (gaudryceratids and kossmaticeratids), Ammonite Assemblage 6, Santa Marta and Rabot formations.

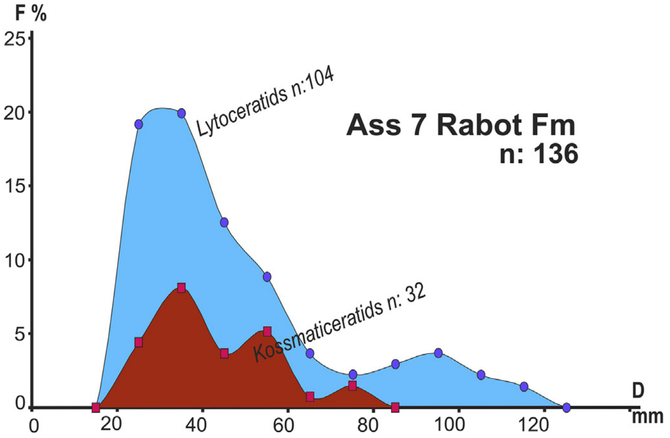

**Fig. 6.** Size frequency distribution of complete specimens of the most abundant ammonite morphotypes (gaudryceratids and kossmaticeratids), Ammonite Assemblage 7, Rabot formations.

disorganized, coarse resedimented conglomerate beds (Marenssi et al., 1992; Martinioni, 1992; Olivero et al., 2011). For most of the stratigraphic interval containing the Ammonite Association 6, dominant sedimentary facies consists of graded fine-grained sandstone with erosive, fluted bases followed by massive, hummocky cross-stratified, and finally wave-rippled intervals (Fig. 7B). Flute casts indicate paleocurrents directed to the ESE (Martinioni, 1992; Olivero and Mussel, 1993). Graded sandstone beds are intercalated with massive or laminated, highly bioturbated sandy and silty mudstones (Olivero and López Cabrera, 2013). The mudstone beds bear abundant valves of the large *Antarcticeramus rabotensis* Crame and Luther (Crame et al., 1996), which are associated with abundant articulated terebratulid and rhynchonellid brachiopods and ammonites (Fig. 2C, Olivero and Mussel, 1993).

The base of the stratigraphic interval containing the Ammonite Assemblage 7 is erosive and marked by a very thick (up to 2 m), characteristic greenish sandstone bed containing green mud-chips and volcaniclastic fragments. The lithology of the rest of the following succession is similar to that described for the previous interval, except that the upper, sandier part lacks body fossils and some beds bear graphoglyptid trace fossils at the base of sandy turbidites (Olivero, 2012a).

### 4.2.2. *Note on ammonite taphonomy*

Similar taphonomic attributes characterize the kossmaticeratid, lytoceratid, and heteromorph ammonites morphotypes recovered from the stratigraphic intervals of Ammonite Assemblages 6–7. Most of the ammonite fauna is preserved as dense concentrations around (Fig. 7C) or inside (Fig. 7D–E) the large bivalve *Antarcticeramus rabotensis*. The ammonite specimens are preserved as internal molds, with rare patches of the original shell material. Nonetheless, most of them are complete specimens, with the phragmocone, filled with sparry calcite, still attached to the sediment-filled body chamber (Fig. 7F–K). The ammonite shells concentrated around or inside the inoceramid valves are oriented with the plane of symmetry lying in a horizontal position. However, geopetal structures in phragmocone chambers or even in small ammonites preserved inside the body chamber of larger specimens, usually indicate a former vertical position during initial burial of the shell (Fig. 7I–J).

In addition to the above described shell concentrations, there are rare isolate complete specimens embedded in a vertical or horizontal position. The heteromorph shells of *Parasolenoceras* sp., in Ammonite Assemblage 6, and *Polyptychoceras* sp., in Ammonite Assemblage 7, are commonly recorded as fragments, preserving part of the phragmocone or body chamber, although complete specimens are not uncommon. Particularly, many complete specimens of *Polyptychoceras* sp. were recorded in Ammonite Assemblage 7 (Fig. 8).

### 4.2.3. *Ammonite facies*

The ammonite faunal spectrum computed from the large number of specimens (n: 1446) in Ammonite Assemblage 6 is dominated by lytoceratids, which are composed mainly by *G. rabotense* (17%); *Anagaudryceras* spp. (13%) and *Tetragonites* sp. (12%). Less represented are *Gaudryceras* aff. *murdochi* (1%) and *Zelandites* sp. (1%, Fig. 3A). In total, the smooth or feebly ornate leiostracan morphotype constitutes more than c. 44% of the fauna (Fig. 3B). The ornate morphotype (trachyostraca) is dominated by the kossmaticeratid species *Natalites* aff. *hauthali* (27%, Fig. 3A), whereas *Maorites* sp. (2%) and *G. occultus* (2%) are relatively less represented. *Anapachydiscus* sp. is another less represented ornate morphotype (5%). The heteromorphs are exclusively represented by a large number of *Parasolenoceras* sp. (21%, Fig. 3A). The relative frequencies of different morphotype groups represented in Ammonite Assemblage 6 are: leiostracan lytoceratids, c. 44%; trachyostracan kossmaticeratids and pachydiscids, c. 35%; and heteromorphs c. 21% (Fig. 3B).

The number of specimens with complete phragmocone and attached body chamber is relatively high (n: 168) for the most abundant lytoceratid and kossmaticeratid morphotypes in Ammonite Assemblage 6. The computed relative size frequency for these groups indicates a small size for the kossmaticeratids, with a bin-mode size of 30–39.9 mm and a total shell diameter ranging

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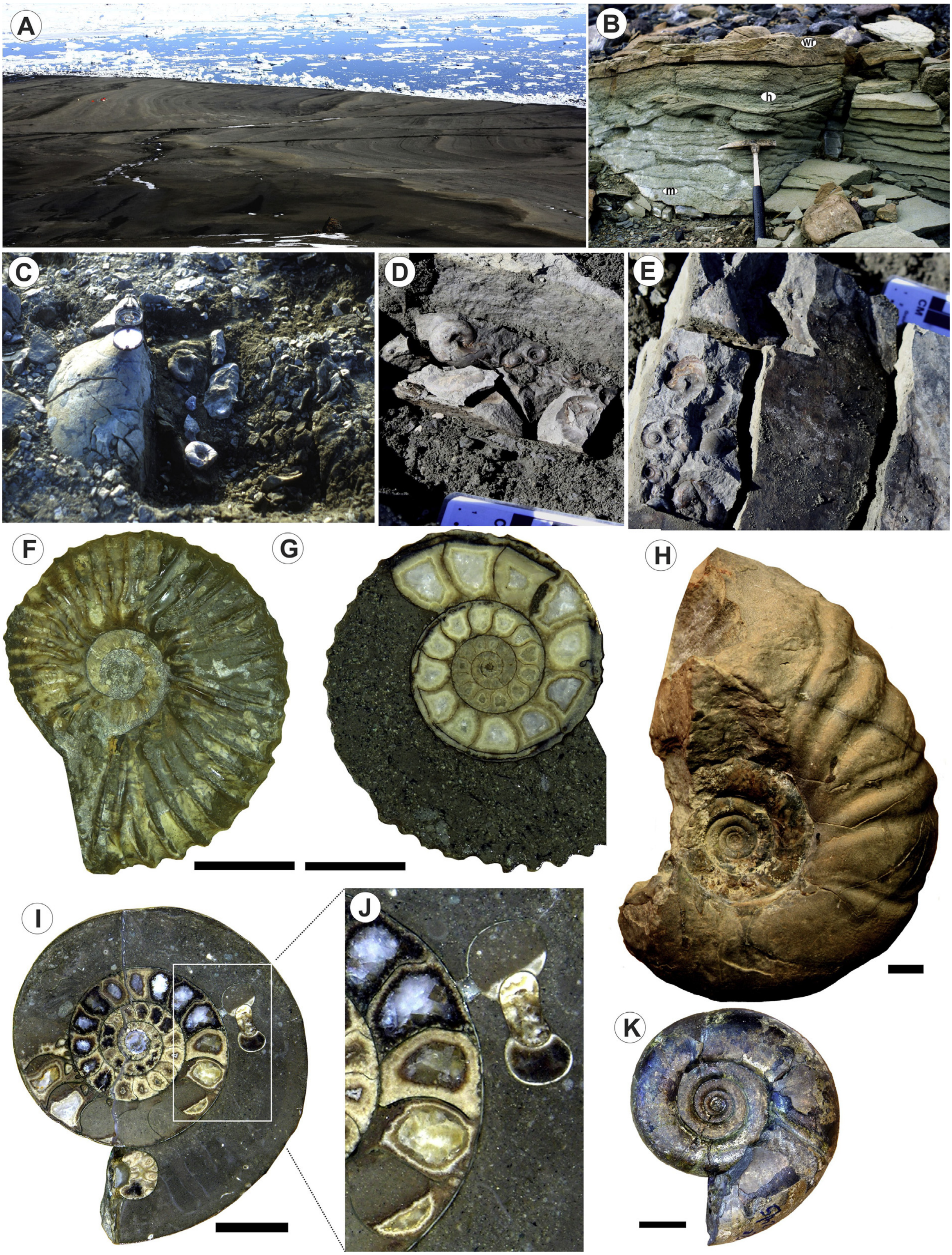

**Fig. 7.** A. Rabot Formation, Ammonite Assemblages 6–7, general aspect of outcrops at Redonda Point. B: Thick bedded, wave-modified turbidite, Hamilton Point section (m: massive; h: hummocky cross stratification; wr: wave-rippled lamination). C–E: shelter preservation, with characteristic dense concentrations of well-preserved ammonite shells outside (C) and inside (D–E) large valves of *Antarcticeramus rabotensis*, Redonda Point section. F–K: well-preserved ammonite shells, Redonda Point section. F–G, *Natalites* cf. *hauthali*, lateral view (F), CADIC PI 412; and polished median section (G) showing calcite-filled phragmocone, CADIC PI 414. Note the clay plug in the apertural part of the siphuncle. Ammonite Assemblage 6. H–K: *Anagaudryceras* spp., Ammonite Assemblage 7, Redonda Point section; including a large, adult specimen (H), CADIC PI 411 and a juvenile, complete specimen of another species, lateral view (K) and polished median section (I–J), rectangle in I indicates location of close-up (J), CADIC PI 413. Note the geopetal structures in the partially calcite-filled phragmocone of the large specimen as well as in the smaller specimen within its body chamber; the orientation of geopetal structures is coherent with an initial vertical orientation. Scale bars: 1 cm.

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**Table 1**
Descriptive statistical measures of complete (phragmocone and body chamber) ammonite shells studied. N: number of specimens; Lyt.: Lytoceratids; Koss.: Kossmaticeratids.

| Descriptive measures | Ammonite Assemblage 6 | | | | Ammonite Assemblage 7 | |
|---|---|---|---|---|---|---|
| | Santa Marta Formation | | Rabot Formation | | Rabot Formation | |
| | Lyt. | Koss. | Lyt. | Koss. | Lyt. | Koss. |
| N | 36 | 75 | 88 | 80 | 104 | 32 |
| Maximum Value | 96.5 | 140 | 110.7 | 66.7 | 114.6 | 79.4 |
| Minimum Value | 12 | 39 | 10 | 20 | 20,1 | 20 |
| Mean | 36.34 | 77.33 | 44.11 | 35.25 | 47.4 | 41.76 |
| Median | 35.35 | 75 | 36.5 | 32 | 39 | 38.4 |
| Mode | 20–29.9 | 70–79.9 | 30–39.9 | 30–39.9 | 30–39.9 | 30–39.9 |
| Variance | 212.0 | 559.62 | 514.81 | 90.05 | 541.83 | 192.89 |
| Standard deviation | 14.80 | 23.66 | 22.69 | 9.49 | 23.28 | 13.89 |
| Skewness | 1.81 | 0.48 | 1.20 | 1.3 | 1.26 | 0.72 |
| Kurtosis | 5.43 | −0.30 | 0.81 | 1.76 | 0.63 | 0.04 |

between 20 and 66.7 mm (Fig. 5, Table 1). The bin-mode size for the lytoceratids is approximately the same (30–39.9 mm), but the frequency curve shows a long tail, with several size modes reaching up to 110.7 mm (Fig. 5B, Table 1). These relatively large shells correspond to specimens of *Anagaudryceras*, which includes two species characterized by an adult body chamber with coarse ribs or band-like ribs (e.g. Fig. 7K, 7H), respectively.

In comparison with Ammonite Assemblage 6, the ammonite spectrum of Ammonite Assemblage 7 (Figs. 3 and 6) has an increment in the leiostracan morphotype (c. 60%); a reduction in the ornate morphotype (16%) and a similar proportion of heteromorph morphotype (c. 24%; Fig. 3B), with *Parasolenoceras* sp. replaced by *Polyptychoceras* sp. (Fig. 3A). The kossmaticeratids are represented by the single species *Neokossmaticeras redondensis*.

## 5. Discussion

The thick succession of bioturbated silty fine-grained sandstone and mudstone of the upper Beta Member of the Santa Marta Formation (Ammonite Assemblage 6) is interpreted as relatively shallow water inner shelf deposits, originated between the shoreface and the transition zone. The lenticular coquina and conglomerate beds probably represent proximal, channelized tempestites. The recurrence of fine-grained bioturbated deposits containing a benthic fauna characterized by articulated *in situ* bivalves and complete gastropods and scaphopods, the *Pterotrigonia–Aporrhais* biofacies (Fig. 2) and fragmented mollusk bioclasts in the coquinas is consistent with an alternation of energy levels in an inner shelf, normal marine environment, periodically influenced by storm events (Scasso et al., 1991; Olivero, 2007).

The graded sandstones of the Rabot Formation have been interpreted as tempestites (Martinioni, 1992) or wave-modified turbidites (Olivero, 2012a). These storm beds are intercalated with thick packages of highly bioturbated sandy and silty mudstones that bear an abundant benthic fauna characterized by large inoceramid bivalves and brachiopods (Fig. 2). The sedimentary

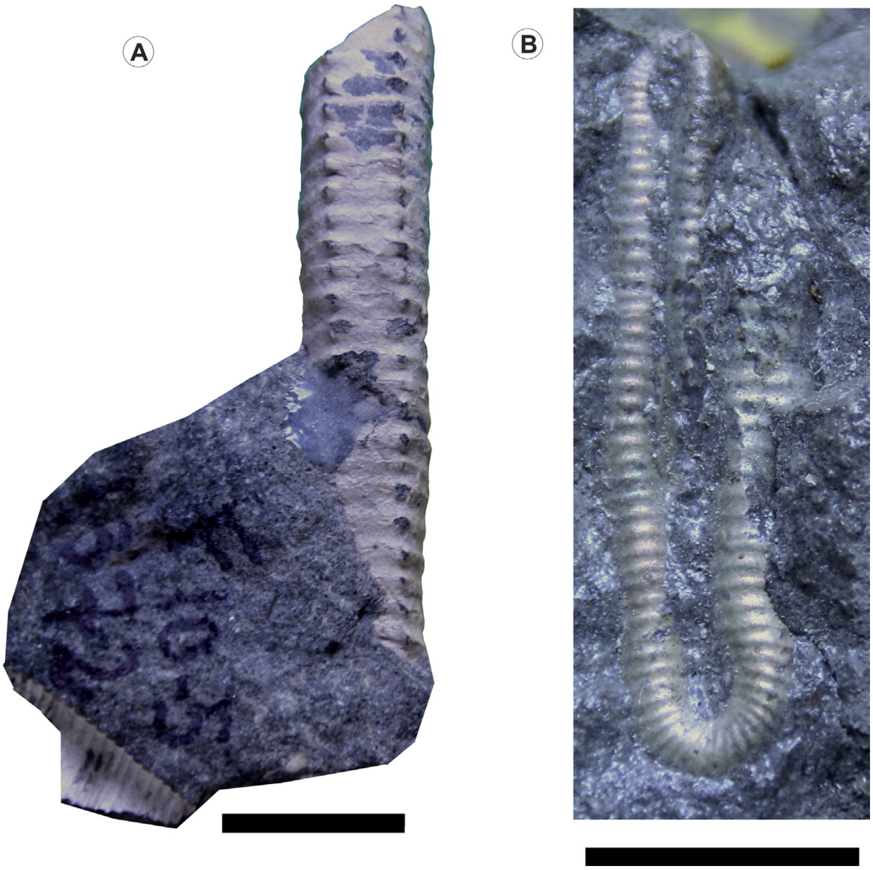

**Fig. 8.** A. Santa Marta Formation, Ammonite Assemblage 6, ventral and side views of fragments of broken body chamber of *Parasolenoceras* sp. (MACN CIRGEO 1372) B. Rabot Formation, Ammonite Assemblage 7, complete shell of *Polyptychoceras* sp. (CADIC PI 603) Scale bars: 1 cm.

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facies, biofacies, and trace fossils recorded in the Rabot Formation during the Ammonite Assemblage 6 are all consistent with storm-influenced deposition in mid shelf settings. The succeeding interval deposited during the Ammonite Assemblage 7 was also characterized by storm deposition, but originated in deeper, mid-outer shelf settings, probably very close to the shelf edge as evidenced by their graphoglyptid trace fossils (Olivero, 2012a; Olivero and López Cabrera, 2013).

Accordingly, along a basinal down-dip transect of about 70 km in length the stratigraphic interval of Ammonite Assemblage 6 displays a facies tract of shallow, inner shelf deposits to the northwest (Brandy Bay section, Fig. 2), linked to relatively deeper mid to outer shelf deposits to the southeast (Hamilton and Redonda Points sections, Fig. 2). Based on this stratigraphic framework, it seems clear that different ammonite spectra and morphotypes, particularly for the ornate kossmaticeratids and smooth lytoceratids, are characteristic of shallower and deeper facies. The kossmaticeratids are dominant in the shallower facies of the Brandy Bay section and the lytoceratids are dominant in the deeper facies of Redonda and Hamilton points sections (Fig. 3). Hence, the distribution pattern of these two groups mimics the classical interpretation for the distribution of trachyostracan (ornate kossmaticeratids) and leiostracan (smooth lytoceratids) (See Westermann, 1996; Lukeneder, 2015).

Different patterns in size distribution of the most common kossmaticeratid and gaudryceratid morphotypes for shallower —Brandy Bay section, and deeper —Redonda and Hamilton points sections facies (Fig. 5) strongly suggests also a paleoecological control. In the shallow facies of Brandy Bay, a relatively great number of kossmaticeratids consists of large, complete shells preserving the iridescent nacre (Fig. 4). The absolute lack of encrusting organism suggests that the shells did not drift on the sea surface (See Wani and Gupta, 2015). On the contrary, the record of non-lethal injuries probably made by arthropods (see Hoffmann and Keupp, 2015) on the shell of some kossmaticeratids (Fig. 4G) strongly suggests a life habitat close to the sea bottom (demersal or nektobenthic) for these ammonoids (cf. Lukeneder, 2015, and the bibliography therein).

Conversely, in the deeper facies of the Rabot Formation kossmaticeratids are dominated by small complete specimens (Fig. 4F–G) while lytoceratids also records a relatively high number of large, complete specimens (Figs. 5, 6, 7C, H). A similar pattern is observed for the deepest facies of Ammonite Assemblage 7 (Compare Figs. 5 and 6). In the case of the kossmaticeratids recorded in deeper facies, they are dominated by non-encrusted, complete shells of small *Natalites* cf. *hauthali* in Ammonite Assemblage 6 and by similarly preserved *Neokossmaticeras redondensis* in Ammonite Assemblage 7 (Figs. 3, 5, 6). The small shell of *N.* cf. *hauthali* (Fig. 7G) with characteristic wide siphuncle diameter, probably favored rapid water filling of the phragmocone after the organism death (Chamberlain et al., 1981; Maeda and Seilacher, 1996; Wani and Gupta, 2015), suggesting a life habitat below the never-surfacing bathymetric threshold. The large gaudryceratids of Ammonite Assemblage 6 and 7 correspond probably to two new species of *Anagaudryceras*, which are characterized by relatively smooth juvenile whorls and coarser band-like ribs on the adult body chamber, e.g. *Anagaudryceras* sp. (Fig. 7H). The latter, is clearly related to the group of *A. sacya* (Forbes) (= A. *buddha*)–*A. limatum* (Yabe) (cf. Kennedy and Klinger, 1979; Matsumoto, 1995). It is interesting to note that *A. limatum* has been interpreted to be dominant in offshore facies in the Turonian of the Yezo Group, Hokkaido while it is rarely found in contemporaneous shallower environments (Wani, 2007). This is the same pattern found for *Anagaudryceras* sp. in the Ammonite Assemblage 6 (Fig. 5) and it is also probably true for the Ammonite Assemblage 7 (Fig. 6), but here we do not have contemporaneous shallow facies to corroborate the pattern.

The disjoint distribution of the two species of *Gaudryceras*; with *G. brandyense* restricted to shallow facies and *G. rabotense* to deeper facies of the Ammonite Assemblage 6 and 7 (Fig. 3) is striking. Marked differences in the ornamentation on the neanoconch, among several other characters, suggest that they should be treated as different species (Raffi and Olivero, 2016). Hence, the disjoint distribution probably reflects true different habitats of these two related species, resulting from adaptations to different properties of the water masses along a neritic-oceanic gradient. A similar distribution pattern is known for recent squids, which along a neritic-oceanic gradient are either dominated by loliginids and ommastrephids species, respectively (Nesis, 2003). Nonetheless more detailed studies, e.g. oxygen stable isotopes, are needed to further assess this interpretation.

Contrary to the lytoceratids and kossmaticeratids, hamitocones are characterized by a more uniform distribution and higher degree of shell fragmentation, particularly in the shallower settings. Taphonomic attributes of the dominant morphotype (*Parasolenoceras* and *Polyptychoceras*) show a high degree of shell fragmentation in the shallow facies of the Santa Marta Formation (Fig. 8A, Olivero, 2007) and less fragmentation, with common preservation of complete shells (Fig. 8B), in the deeper Rabot Formation. These attributes suggest a life habitat restricted to the mid-outer shelf area and subsequent extensive post-mortem drift. During storm events, some of the shells could have been washed ashore, with subsequent reworking and fragmentation of the delicate hamitocone shells by bottom currents. Conversely, the shells that were capable of sinking to the bottom near their life habitat will be less fragmented or complete.

## 6. Conclusions

The distribution of ammonoid facies and its implications for the relative importance of post-mortem drift vs. ecological fidelity were evaluated using independent evidence on relative changes in water depth along a neritic-oceanic gradient in the Santa Marta and Rabot formations, James Ross Basin, Antarctica. The evaluation of the faunal spectra of three common morphotypes, ornate kossmaticeratids, relatively smooth lytoceratids, and hamitocones heteromorphs, together with their relative abundance, frequency of size distribution in complete specimens, and taphonomic attributes for shallow and deep sedimentary facies, resulted in the following conclusions.

The ornate, large, and complete shells of kossmaticeratids, commonly preserving pristine nacre, greatly outnumber lytoceratids and heteromophs in the shallow facies the Santa Marta Formation. Many of them, which are associated with fossil crustacean decapods in the same horizon, show typical non-lethal injuries interpreted as produced by arthropods. Consequently a shallow habitat and a nektobenthic (demersal) mode of life are interpreted. Conversely, complete shells of small kossmaticeratids characterized by wide siphuncles, are relatively common in deeper facies of the Rabot Formation. These features would have favored rapid sinking of the shell after death of the organism below a critical never-surfacing bathymetric threshold. In this case, also a nektobenthic mode of life is interpreted, but probably with a deeper habitat than the kossmaticeratids of the Santa Marta Formation. In both, shallow and deep dominant kossmaticeratids it seems that the shells were deposited within or close to their original habitats.

Conversely, relatively smooth lytoceratids are dominant in deeper facies of the Rabot Formation. Large, complete shells of *Anagaudryceras* sp. are restricted to offshore facies, probably with oceanic influence. The living organism probably has a mesopelagic,

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planktic mode of life and an offshore habitat, similar to that of *Anagaudryceras limatum* from the Turonian of Hokkaido. Small gaudrycertid shells display a more complex pattern, with two closely related species living simultaneously in shallow or deep settings. This pattern is tentatively interpreted as adaptations different to different water mass conditions along a neritic-oceanic gradient.

The hamitocone heteromorphs are more or less equally distributed in shallow and deep facies but with a high degree of shell fragmentation, particularly for shallow settings. This pattern suggests that hamitocones had a life habitat restricted to the mid-outer shelf, but were exposed to extensive post-mortem drift.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2017.03.001.

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