TAPHONOMY OF AMMONITES FROM THE SANTONIAN–LOWER CAMPANIAN SANTA MARTA FORMATION, ANTARCTICA: SEDIMENTOLOGICAL CONTROLS ON VERTICALLY EMBEDDED AMMONITES

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ABSTRACT

Different morphotypes of vertically embedded ammonoid shells are abundant in the 1-km-thick deposits of the Santa Marta Formation, Antarctica, that record the evolution of a deep-water delta system. Vertical shells deposited in water depths well below the theoretical limit imposed by hydrodynamic and hydrostatic analyses are preserved as isolated specimens, dense concentrations associated with abundant wood fragments (pod preservation), or as dense concentrations inside and around large ammonites (sheltered preservation). Taphonomic analysis indicates that (1) vertical shell orientation is primary; (2) postburial reworking was minimum or absent, as indicated by consistent shell orientation parallel to regional paleocurrents and complete preservation of fragile shells with phragmocones filled with drusy calcite; and (3) vertical orientation is not biased towards a preferred morphotype. Rapid sedimentation, including deposition from high- and low-density currents, tempestites, and weak bottom currents carrying a dense suspension of ammonoid shells and wood fragments, was one of the main factors controlling the vertical preservation below the limits imposed by theoretical hydrostatic analyses. Another important factor was the plugging of the siphuncular tube with clay particles during transportation. The clay plug was stiff enough to resist the ambient hydrostatic pressure, avoiding or delaying the waterlogging of the phragmocone.

INTRODUCTION

The main objectives of this study are to describe and interpret the different types of ammonite preservation in the Santonian–lower Campanian Santa Marta Formation on James Ross Island, Antarctica (Figs. 1–2) and to discuss the role of sedimentary processes on the vertical preservation of ammonite shells. Emphasis is placed on the deviating effect with respect to ideal hydrodynamic or hydrostatic calculations produced by the plugging of the siphuncular tube with silt and clay particles during transport of ammonoid shells within a turbid cloud of sediment. Different ammonoid morphotypes are found in vertical positions, including heteromorphic genera—*Baculites*, *Scaphites*, *Yezoites*, *Ryugasella*, *Ainoceras*, *Eubostrychoceras*—and planispiral genera—*Neophylloceras*, *Gaudryceras*, *Anagaudryceras*, *Natalites*, *Anapachydiscus*, *Eupachydiscus*. In addition, vertical ammonoid shells are preserved as isolated specimens or concentrated inside the body chamber of large pachydiscid ammonites (sheltered preservation; Maeda, 1991).

Ammonoid landing marks, which represent the ventral imprint made by intact shells sinking in a vertical position (Lehmann, 1981; Maeda and Seilacher, 1996), and vertically embedded shells (e.g., Reyment, 1970; Crick, 1983) are well documented. Ammonoid shells, however, are often preserved with their plane of symmetry lying parallel to bedding and represent the normal type of ammonoid preservation. These contrasting modes of preservation have been explained traditionally by paleobathymetric, hydrodynamic, and hydrostatic controls.

As with *Nautilus*, living ammonoids probably floated with neutral buoyancy in the water column (Kennedy and Cobban, 1976; Westermann, 1996). In the *Nautilus* model, after death, the soft tissues (which have higher densities than seawater) rapidly decompose, and the shell gains buoyancy as the soft parts are replaced by seawater, thereby causing the intact shell to rise to the surface. Hydrodynamic analysis, however, has demonstrated that the surfacing of an empty shell with intact gas-filled chambers depends on the water pressure and, thus, on the depth at which the animal died (Chamberlain et al., 1981). In an intact shell, pressure-induced waterlogging of the gas chambers via the siphuncular tube could compensate for the initial gain in buoyancy, with the shell becoming denser than seawater and sinking to the bottom. Only a relatively small amount of water—about 15% of the total cameral volume—entering the intact phragmocone is needed to make an empty shell heavier than seawater. The critical depth at which this is accomplished divides the postmortem fate of ammonoid shells into surfacing and never-surfacing categories (Maeda and Seilacher, 1996).

Depending on such factors as size, filling rate, and permeability of the siphuncle, the critical surfacing depth for an empty *Nautilus* shell has been estimated to be between 100 m and 300 m (Chamberlain et al., 1981; Wani et al., 2005). Intact ammonoid shells are thought to represent never-surfacing shells, especially when the buccal mass is preserved in situ (Seilacher and LaBarbera, 1995; Maeda and Seilacher, 1996). With a low rate of waterlogging, a never-surfacing, intact ammonoid shell may touch the sea bottom in a vertical position, producing a landing mark. It will remain vertical until stability is lost when ~50% of the cameral volume is filled with water. It will then lean on one side, resting with the plane of symmetry in a horizontal position. Landing marks adjacent to horizontally preserved ammonites in the Upper Jurassic Solnhofen limestones represent outstanding examples of this taphonomic pathway (Lehmann, 1981; Maeda and Seilacher, 1996).

Hydrostatic analysis suggests that permanent vertical stability of *Nautilus* and ammonoid shells resting on the sea floor is only possible at very shallow depth. Raup (1973) found that the hydrostatic pressure at 10 m depth would cause a reduction of ~50% in the volume of the cameral gas based on experiments with *Nautilus*. Except for extreme cadicone shells, these results could be applied to ammonoids. Raup (1973) concluded that most vertically oriented ammonoid shells could only be preserved if they were deposited in water depths less than about 10 m (see also Weaver and Chamberlain, 1976; Crick, 1983).

MATERIAL AND METHODS

The database for this study consists of 2,350 ammonites observed or collected during the Antarctic summer field seasons of 1975, 1986, and 1988–1990. The interpretation of sedimentary facies and paleoenvironments is based on Pirrie (1989), Scasso et al. (1991), Olivero et al. (2004), and unpublished data. The biostratigraphy and ammonoid systematics are based on Olivero (1984, 1988, 1992) and Olivero and Medina (2000).

The composition, orientation, and type of preservation of ammonite
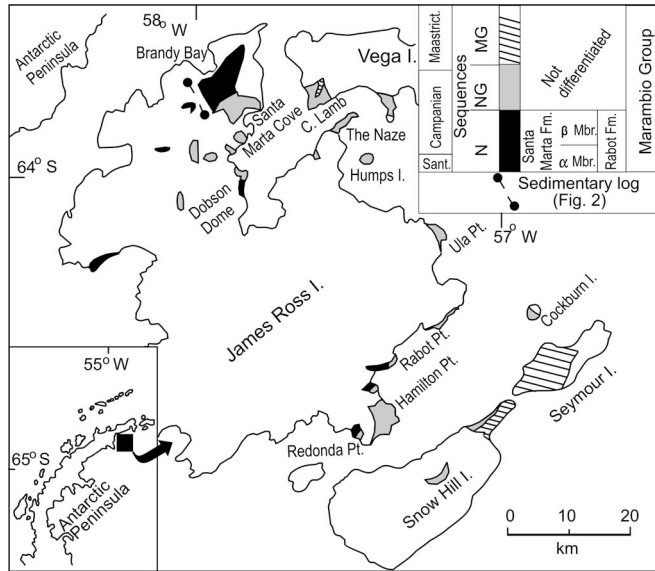
FIGURE 1—Location of study area, geology, and generalized stratigraphy of the Marambio Group.
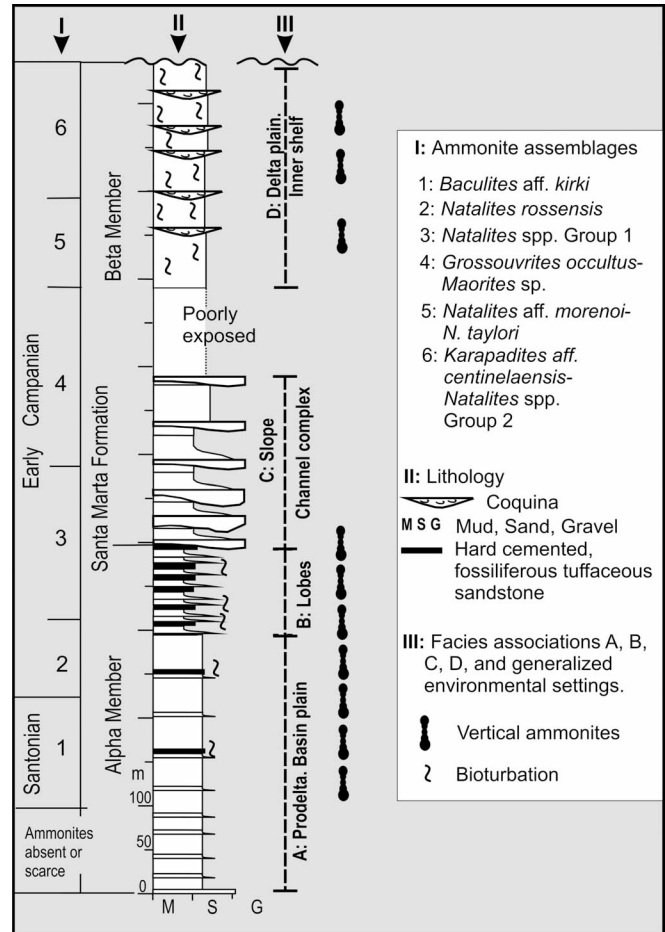

FIGURE 2—Sedimentary log of the Santa Marta Formation showing the stratigraphy, lithology, facies associations, generalized paleoenvironmental settings, and distribution of vertically preserved ammonites. Paleoenvironmental settings adapted from Scasso et al. (1991). Biostratigraphy adapted from Olivero and Medina (2000).

shells contained within large pachydiscid ammonites were noted in the field by level-by-level dissection of the body chambers, and selected samples were taken from several levels. The location and orientation of large shelter shells, as well as the orientation of the ammonites grouped outside the shelter, were mapped. Orientation data were measured only in fossil material located outside the shelter. Isolated, vertically preserved ammonoid shells were also collected. Twenty-five specimens were cut along the siphuncular plane and polished to inspect for the type of filling, integrity of the phragmocone, and preservation of the jaw apparatus. Results were compared to the rest of the samples by visual inspection with a binocular microscope. Rock slabs with vertically preserved ammonoids were also cut along the vertical plane and polished to look for associated sedimentary structures, textures, and mineralogical composition. Oiled polished sections were photographed with a digital camera, and detailed drawings were prepared by tracing the digital pictures on a computer screen. The orientation of vertical ammonoids was recorded by measuring the azimuth of the plane of symmetry of the shell; thus, it is treated as bidirectional data. The orientation of cylindrical vegetal fragments was treated as bidirectional data. Unidirectional data were only recorded for gastropods, where the measured azimuth points to the shell apex. Results of fossil orientation were compared with the regional paleocurrent vectors obtained from physical sedimentary structures (Pirrie, 1989; Martinioni, 1992; Olivero and Mussel, 1993).

The studied material is housed at the Centro Austral de Investigaciones Científicas (CADIC), Ushuaia, Argentina, under the numbers CADIC PI 59 to CADIC PI 78.

GEOLOGICAL AND PALEOENVIRONMENTAL SETTINGS

The James Ross Basin is a back arc basin developed to the east of an active magmatic arc located along the Antarctic Peninsula (Fig. 1). Cretaceous strata are well exposed in the James Ross archipelago and include two major stratigraphic units. The basal coarse-grained Gustav Group (Aptian–Coniacian) is ~2.1 km thick and consists of deep-water conglomerates and sandstones, representing base-of-the-slope and slope-depositional settings. Overlying these deposits are shelf and fan-delta deposits that originated during the partial tectonic inversion of the basin (Ineson, 1989). The overlying finer-grained, 3-km-thick Marambio Group is dominated by mid-outer-to-inner-shelf, highly fossiliferous fine-grained sandstones, and mudstones. There is no overall agreement on the stratigraphic subdivision of the Marambio Group, although three main sedi-

mentary successions are recognized: Late Coniacian?–Santonian–Early Campanian, Late Campanian–Early Maastrichtian, and Maastrichtian–Danian (differentiated in Fig. 1 as the N, NG, and MG Sequences, respectively; Olivero and Medina, 2000; Crame et al., 2004, and references therein).

In Brandy Bay, northwestern James Ross Island, at the basal part of the N Sequence, the 1-km-thick Santa Marta Formation constitutes a gently dipping homoclinal succession that includes the Alpha and Beta Members. The stratigraphic distribution of the ammonite fauna defines six successive Santonian–Early Campanian ammonite assemblages (Fig. 2; Olivero, 1992; Olivero and Medina, 2000). In southeastern James Ross Island, the Rabot Formation is a lateral equivalent of the upper Beta Member (Fig. 1). At Brandy Bay, the Alpha and Beta Members consist of four vertically stacked intergrading facies associations (Fig. 2) that define a regressive sequence (Scasso et al., 1991).

Facies Association A is dominated by friable, massive, or laminated muddy tuffaceous, very fine-grained sandstone with minor intercalation of hard, tuffaceous, graded coarse-to-fine-grained sandstone capped by bioturbated siltstone. Small fragments of carbonaceous plant material as well as large tree trunks are abundant locally. Articulated inoceramid bivalves are dominant in the friable muddy sandstones. The accompanying ammonite fauna is dominated by heteromorphs, and several graded sandstone beds contain abundant specimens of *Baculites* aff. *kirki* Matsumoto preserved commonly in vertical position.

Facies Association B consists of a regular alternation of coarsening and thickening upward, friable, graded tuffaceous sandy turbidites capped
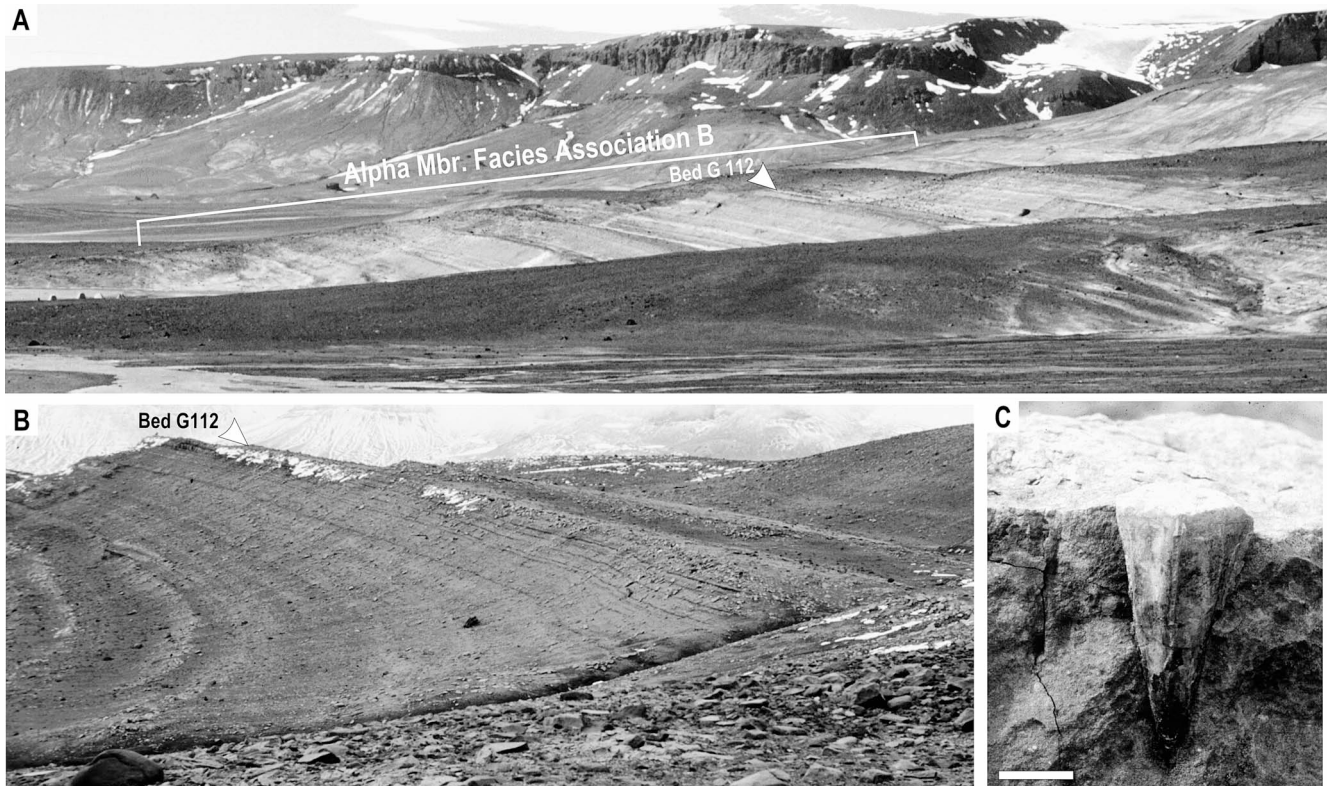
FIGURE 3—General outcrop features of the Santa Marta Formation. A) Panoramic view of Facies Association B, Alpha Member, showing regular alternations of friable, tuffaceous turbidites (recessive slopes) and hard-cemented, fossiliferous tuffaceous sandstones (resistant beds). B) Detailed view of Bed G112. C) *Pinna* sp. preserved in life position. Alpha Member, Facies Association B, Bed G112. Scale bar = 2 cm. Mbr. = Member.
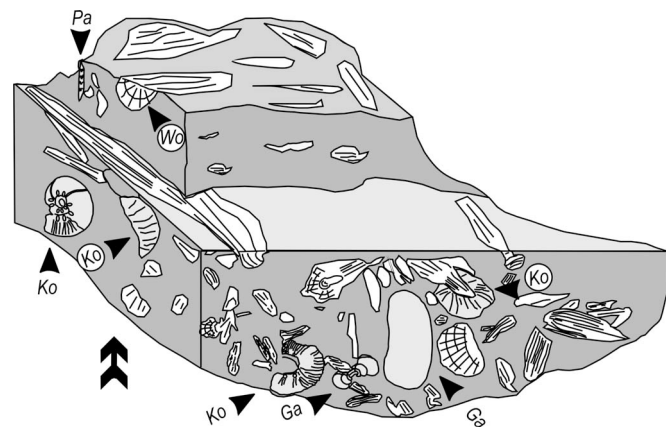
by laminated, carbonized plant fragments. At regular intervals of ∼4–6 m, highly bioturbated and fossiliferous, well-cemented beds of tuffaceous turbidites are intercalated within the succession (Figs. 3A–B). The later beds preserve an abundant and diverse ammonite fauna, with many specimens in a vertical position, either dispersed in the bed or concentrated within and around the body chamber of large pachydiscids. The topmost part of these beds preserves abundant specimens of the serpulid *Rotularia* sp. and the gastropod *Cerithium* sp.; less abundant is the bivalve *Pinna* sp. in life position (Fig. 3C), solitary corals, crinoids, and brachiopods. These fossiliferous beds are located at the top of the coarsening and thickening-upward turbidites.

Facies Association C is characterized by a coarser lithology, including regular bedded packages composed of thick-graded tuffaceous, pebbly or coarse-grained sandy turbidites cut erosively by resedimented, channeled conglomerates and debris flows. Resedimented fossils, including ammonites, belemnites, and bivalves, are abundant locally.

Facies Association D consists of an alternation of thick, bioturbated packages of fine-grained, well-sorted, micaceous sandstone, silty very fine-grained sandstone, and mudstone, with abundant plant fragments, leaves, and large tree trunks. Small ammonites are associated generally with wood fragments. Bivalves, dominated by *Pterotrigonia* sp. and *Cu-*


FIGURE 4—Proximal tempestites of Facies Association D, Beta Member, showing a basal coquina conglomerate with current aligned scaphopods and belemnites capped by cross-bedded sandstones.

FIGURE 5—Pod preservation in Facies Association D. Three-dimensional drawing, based on the photos in Figure 6, showing dense concentration of small, vertical ammonites and wood fragments. Black double-headed arrows point to the upward direction in the vertical plane. Pa = vertical fragment of a small *Parasolenoceras* phragmocone; Ko = complete, small kossmaticeratid ammonites; Ga = Gaudryceratid ammonites; Wo = wood fragments.
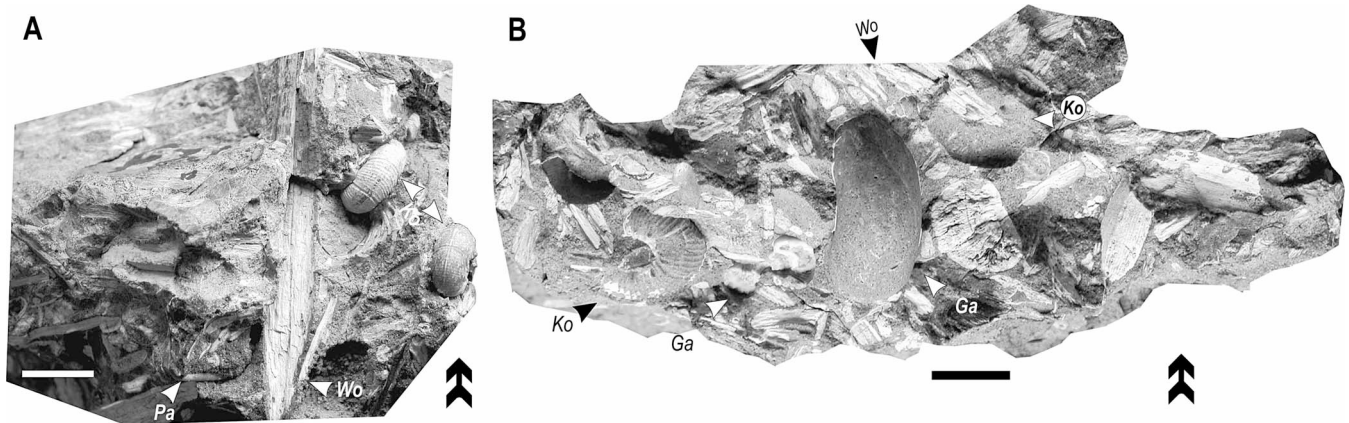
FIGURE 6—Pod preservation showing dense concentration of vertical ammonites and wood fragments in Facies Association D. A) Upper left view of cartoon in Figure 5. B) Lateral, front view of cartoon in Figure 5. CADIC PI 59. See Figure 5 for abbreviations. Scale bar = 1 cm.
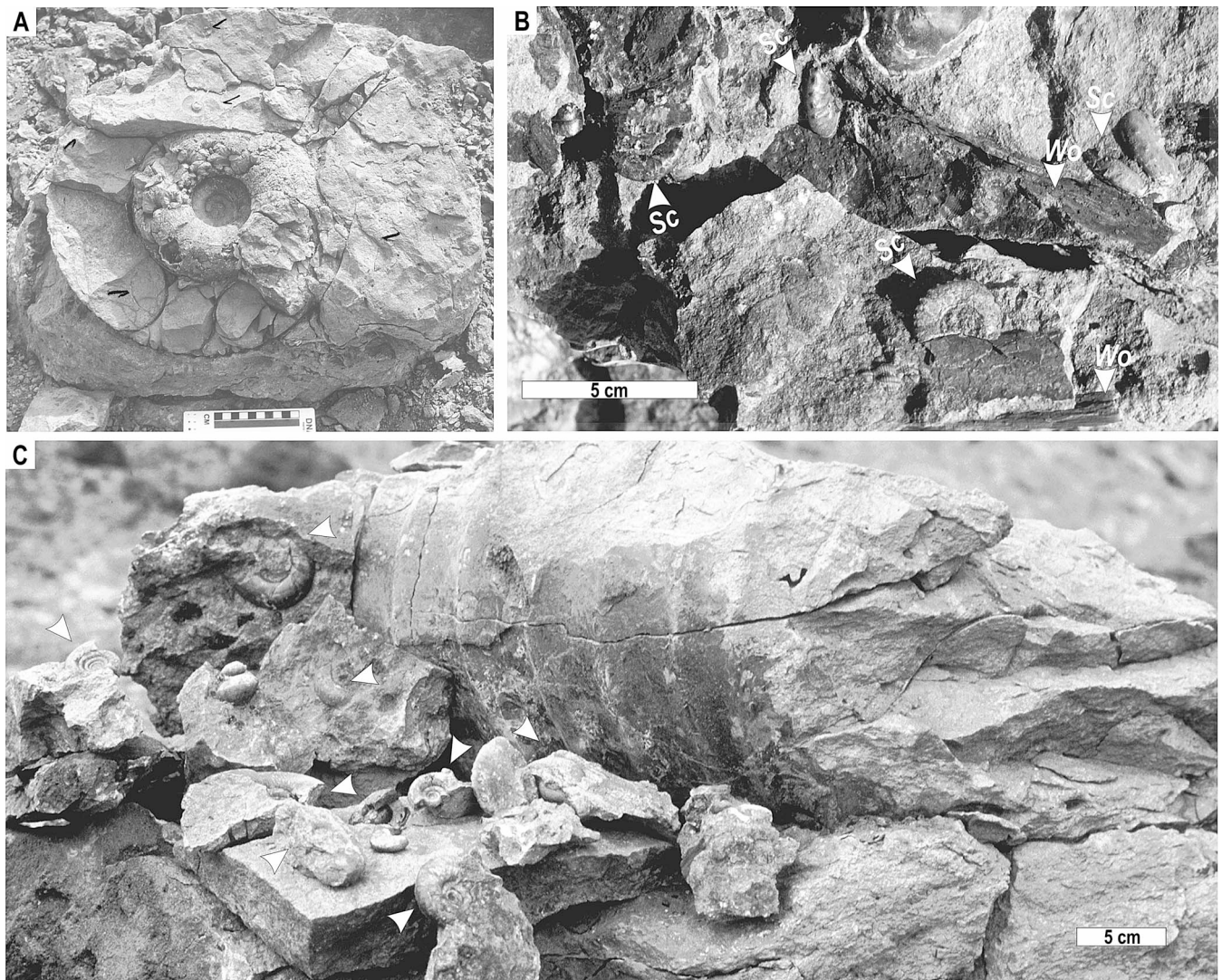
FIGURE 7—Pachydiscid shelters and their fossil content, Alpha Member Facies Association B. Bedding plane view. A) Large *Eupachydiscus* shell on top of a hard-cemented bed showing partial shell dissolution and body chamber and camerae filled with sediment. B) Sandstone slab from inside the body chamber of the same specimen with dense concentration of current aligned small scaphitid ammonites and wood fragments. C) Lateral view of the same *Eupachydiscus* shelter, with many complete ammonites (arrows) recovered within its body chamber. Sc = scaphitid ammonites; Wo = wood fragments.
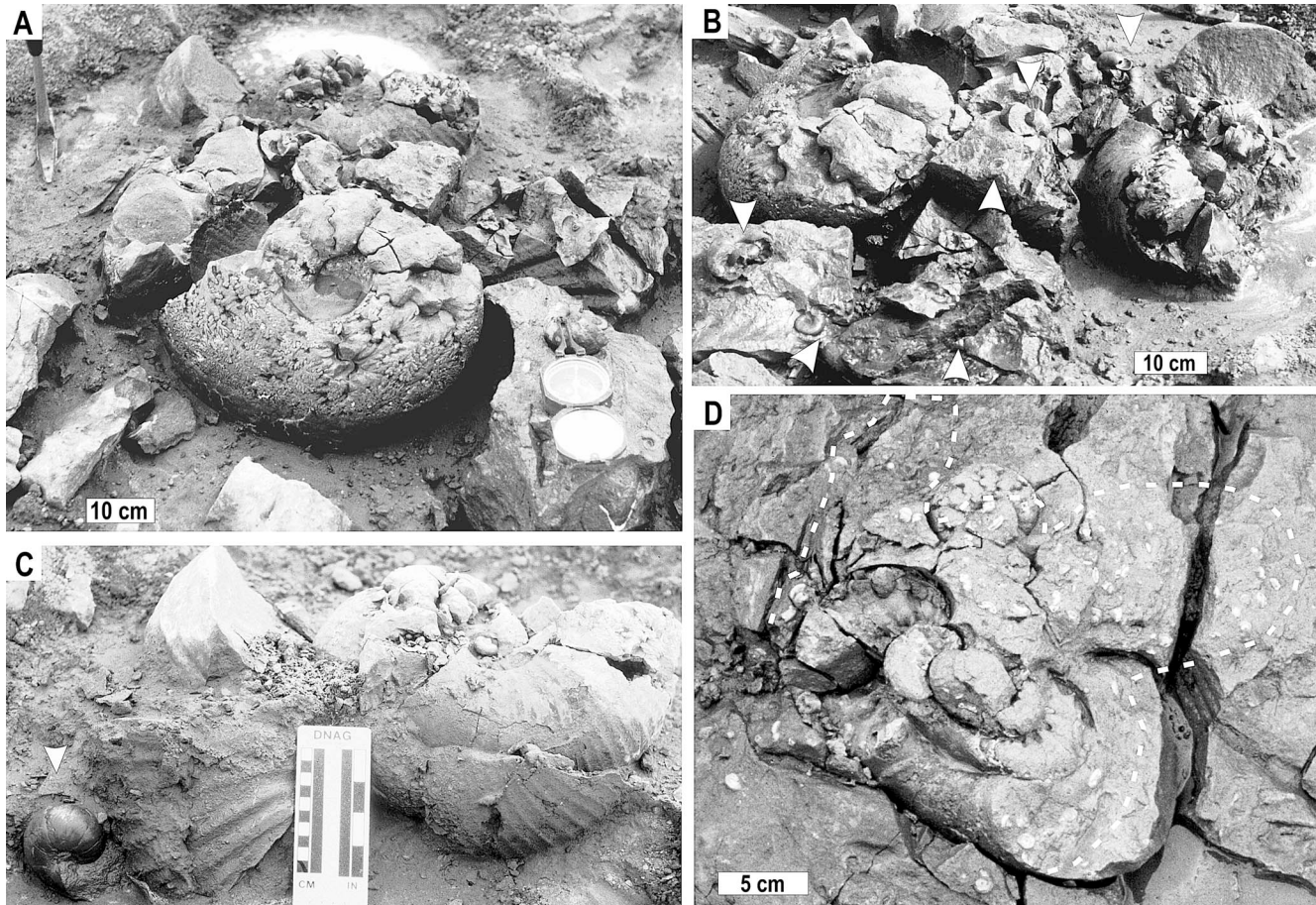
FIGURE 8—Pachydiscid shelters and their fossil content, Alpha Member, Facies Association B, Bed G112. Bedding plane view. A–C) Two large, imbricate shells of *Anapachydiscus constrictus* (specimen 1 of Fig. 9). A) North-northeast directed view. B) West directed view, arrows indicate ammonite specimens concentrated outside and on the lee side of the shelter. C) Vertically oriented nautiloid (*Eutrephoceras* sp.) preserved at the contact between the two imbricate shelters. D) Vertical, medium-sized *Eupachydiscus paucituberculatus* with the upper part of its phragmocone partially dissolved. After partial dissolution, a thin layer with many individuals of *Rotularia* sp. (*Rotularia* fan, white dashed line) covered the upper part of the phragmocone.

cullaea sp., are preserved commonly with both valves articulated in their presumed life position. Aporrhaid gastropods are also abundant. Bioturbated beds are cut erosively by lenticular packages (e.g., channels) that consist of basal, clast-supported conglomerate and coquina, overlain by parallel-laminated or cross-bedded sandstone (Fig. 4). Coquinas bear the same macrofauna as in other units, as well as relatively abundant belemnite rostra and scaphopods. Vertical ammonites are preserved occasionally within parallel-laminated sandstone.

Petrographic analysis reveals abundant volcaniclastic components, mainly glass shards, pumice lapilli, and lithic (andesitic) components produced by the coeval volcanic activity in the magmatic arc. The matrix of tuffaceous turbidites consists of a mixture of clay particles and micrite (Pirrie, 1989). The ordered, intergradational vertical stacking of these four facies associations indicates the evolution of a progradational deep-water delta system (Scasso et al., 1991), which includes the following subenvironments arranged in a distal-to-proximal position (Fig. 2): prodelta-basin plain (Facies Association A); base-of-slope depositional lobes (Facies Association B); slope-channel complex (Facies Association C); and inner-shelf-delta plain (Facies Association D). Pirrie (1989) reached a similar paleoenvironmental interpretation for the Santa Marta Formation.

TAPHONOMY OF VERTICAL AMMONOIDS

The following descriptors are useful for the taphonomic interpretation of vertically embedded ammonoids in the Santa Marta Formation: (1) type of concentration: isolated vertical specimens versus dense, confined concentrations; (2) primary or secondary character of the vertical preservation; (3) integrity of the shell: complete or fragmented shells, type of filling of body chamber and phragmocone, and presence or absence of in situ jaw apparatus; and (4) proportion of vertical ammonoid morphotypes within a given facies association or ammonoid assemblage.

Type of Concentration of Vertical Ammonoids

The ammonoids, either horizontally or vertically oriented, are preserved as isolated specimens or as dense concentrations usually including more than 10 closely associated individuals. Isolated, vertically embedded specimens are ubiquitous in all facies associations. Dense concentrations of vertically embedded shells are restricted to Facies Association B and D. Two types of preservation of dense concentrations are recognized: pod preservation, restricted to Facies Association D; and sheltered preservation (Maeda, 1991), restricted to Facies Association B.

Pod Preservation.—This type of preservation includes dense concentrations of wood particles and ammonoid shells filling small pods, defined as elongate, scoop-shaped depressions ~30 cm long and 10 cm wide. Pods are filled mainly with abundant wood fragments and small, vertically oriented ammonite shells, dominated by kossmaticeratids and gaudryceratids, and have a patchy distribution in otherwise homogeneous, very fine-grained sandstone (Figs. 5–6).

Sheltered Preservation.—Sheltered preservation includes the combination of large pachydiscid shelters—*Anapachydiscus constrictus* Olivero and *Eupachydiscus paucituberculatus* Olivero—whose body chambers or
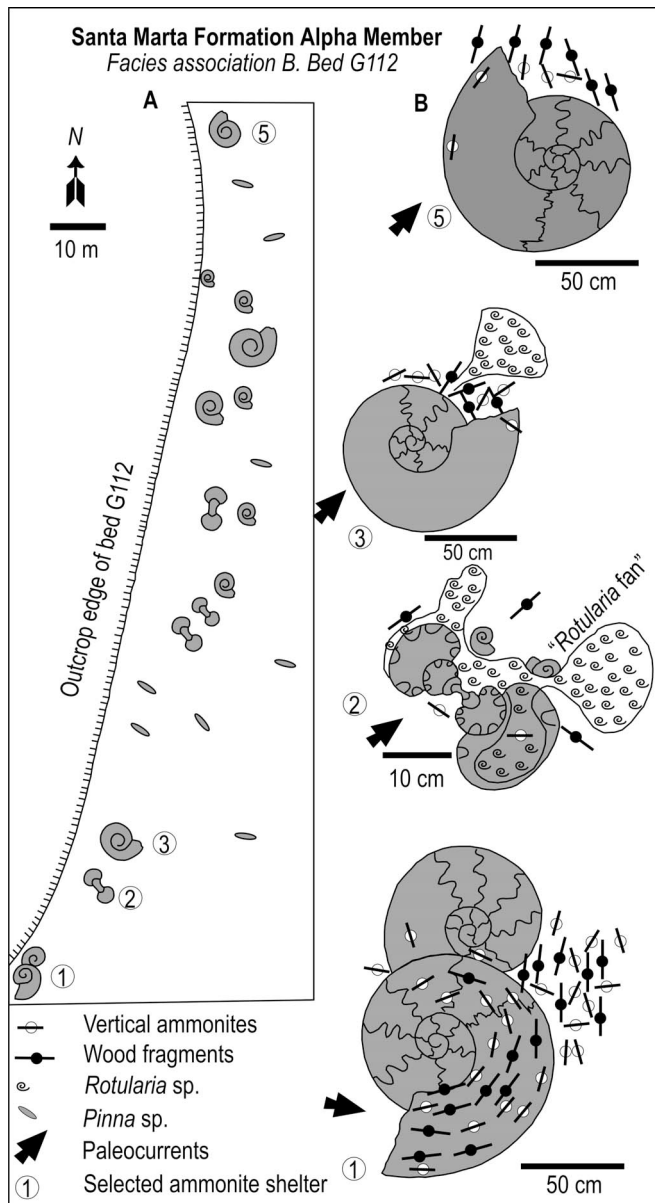
FIGURE 9—Map of dense fossil concentration (sheltered preservation) in bed G112, Facies Association B, Santa Marta Formation (plan view). A) Relative location of large pachydiscid shelters and specimens of *Pinna* sp. in life position. B) Preservation features of ammonite shelters 1, 2, 3, and 5. Note the large concentration of ammonites and wood fragments inside the body chamber of shelter 1 and outside the shell of shelters 3 and 5. Axis of symbols for vertical ammonites and wood fragments indicate the measured orientation.

broken camerae are filled with small ammonites, dominated by gaudry-ceratids, tetragonitids, scaphitids, and juvenile pachydiscids.

A pachydiscid shelter consists of large shells up to 100 cm in diameter, lying with their plane of symmetry parallel to bedding near the top of the hard-cemented, fossiliferous tuffaceous turbidite sandstone of Facies Association B. In addition to ammonites, these beds also preserve gastropods (mainly *Cerithium* sp.), *Pinna* sp.—found commonly in its presumed life position (Fig. 3C)—*Rotularia* sp., solitary corals, irregular echinoids, and crinoids. The pachydiscid shelters consist mainly of isolated shells (Figs. 7A–C). An exceptional case includes two imbricate shelters (Figs. 8A–C). Most of these large shelters show evidence of partial shell dissolution. Clear evidence of partial shell dissolution is indicated by a medium-sized, vertically oriented *Eupachydiscus* specimen,

in which only the lower half of the shell is preserved and covered by a fanlike layer of numerous individuals of *Rotularia* sp. (Fig. 8D).

Inside the body chamber of the shelters are dense concentrations of small ammonites (Figs. 7, 8A–C), <75 individuals. Outside the body chamber of the large shelter shells, dense concentrations of small ammonites are also found, grouped preferentially on only one side of the shelters. Smaller ammonites found either inside or outside the body chamber of the shelters are associated with abundant, elongate wood fragments, occasional fragments of irregular echinoids, and rare bivalve fragments (Fig. 7). Interestingly, the plane of symmetry of vertical ammonoid shells is oriented parallel to elongated wood fragments (Fig. 9).

All the results of orientation data from elongate wood fragments, conical gastropods (*Cerithium* sp.), and vertical ammonoids show preferred orientations consistent with the known regional paleocurrent pattern (Fig. 10). Elongate wood fragments show a dominant orientation trending WNW–ESE and a secondary orientation trending NNE–SSW. A similar pattern results from the orientation data of vertically preserved ammonoid shells and from conical gastropods. This interpretation is consistent with previous research on orientation of elongate wood particles (MacDonald and Jefferson, 1985) and conical fossil particles (Seilacher, 1972). For the ammonites, the interpretation is consistent with the previous field data of Seilacher (1972) but contradicts the interpretation of Crick (1983), who indicated that the plane of symmetry of vertically embedded ammonites should be oriented at right angles to the direction of flow (see also Reyment, 1973). Present data indicate that only a few vertical ammonites were oriented at right angles to the inferred direction of the current (Figs. 9–10). This orientation could have resulted from flow around an obstacle because freely moving ammonite shells are oriented mostly with the plane of symmetry parallel to flow direction.

Alignment of wood fragments and vertical ammonites accumulated on one side of the shelter provides additional evidence that the plane of symmetry of the ammonites is oriented parallel to the flow. Figure 9 shows that this accumulation was concentrated preferentially on the lee side of the shelters. Moreover, it also shows a differential concentration of individuals depending on the orientation of the aperture of the shelters with respect to the direction of the flow. Shelter shells oriented with the aperture pointing WNW (i.e., upcurrent) were filled with large numbers of ammonoids, whereas apertures oriented downcurrent contain almost no ammonoids inside the body chamber.

Vertical Orientation of the Ammonoid Shells

Evidence indicates that ammonoids are preserved primarily in a vertical orientation (Figs. 11–12). In all specimens, geopetal structures in the phragmocone—camerae that are partially filled with sediment, or fossil spirit levels (Lehmann, 1981)—have their tops always parallel to bedding. An outstanding example is the *Natalites* sp. of Figure 11A, which preserves three criteria of primary vertical orientation: (1) the shell is itself oriented vertically; (2) one of the camerae in the upper part of the phragmocone was punctured and partially filled with sediment, and the top surface of the resulting geopetal structure is parallel to bedding; and (3) the body chamber preserves a second small *Natalites* sp. near the aperture, also oriented vertically. This type of vertical preservation is seen occasionally in nonbioturbated, massive, or parallel-laminated sandstone (e.g., *Maorites* sp., Figs. 11B–C) capping lenticular coquinas or conglomerates in tempestite beds of Facies Association D.

In all sedimentary facies most of vertically oriented ammonoids are preserved with the heaviest body chamber down, with the centers of buoyancy and mass near the inferred correct position (Figs. 11A–D, F–J) as if the ammonite shells would have been deposited more or less in the presumed life orientation (cf. Klug and Korn, 2004). In addition, there are a few cases in which this orientation is consistent with the orientation of associated burrowing bivalves, for example, the vertical *Baculites* aff. *kirki* Matsumoto specimen associated with a vertical *Panopea* sp. (Fig. 11I). There are, however, some specimens of vertical *Baculites* aff. *kirki*,
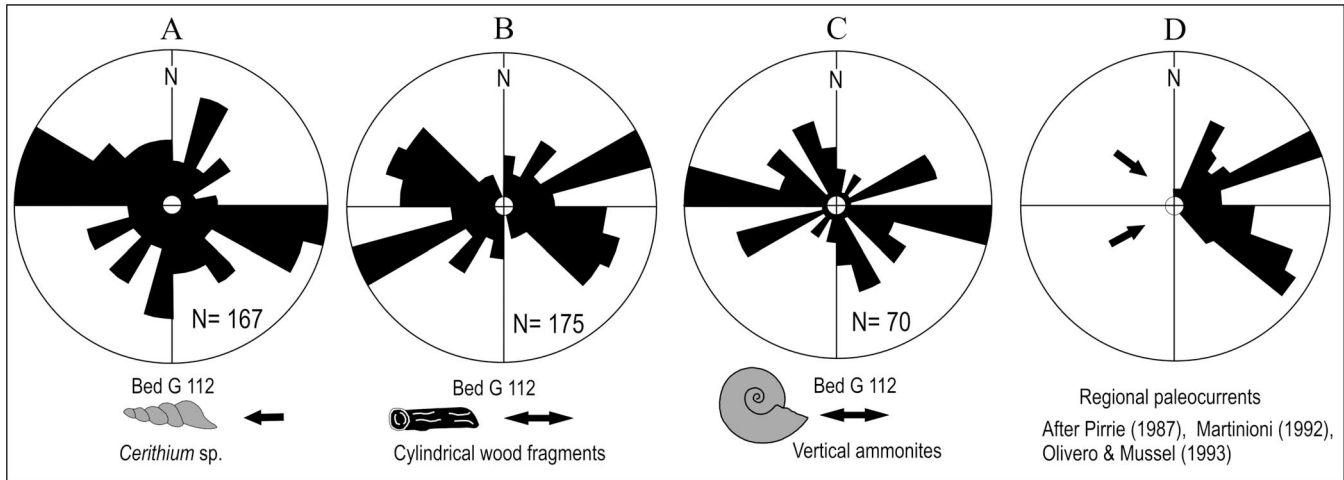
FIGURE 10—Local and regional paleocurrent patterns for the Santa Marta Formation. A) Unidirectional data from elongated gastropods (*Cerithium* sp.). B–C) Bidirectional data from cylindrical wood fragments and vertical ammonites. D) Regional data measured from physical sedimentary structures.

Ryugasella antarctica Olivero, and *Yezoites* sp. oriented upside down—that is, with the phragmocone pointing toward the base of the bed (Figs. 11E; 12F–I). Polished slabs indicate that these oddly preserved shells are included in pumicite-rich and wood-rich layers with internal erosion surfaces, within a high-density turbidite bed (Figs. 12H–I). Moreover, the orientation of trace fossils inside the body chamber of *Baculites* aff. *kirki* (Fig. 12G) indicates that the trace makers entered the body chamber through the aperture after the vertical position was acquired. This inverted vertical orientation, thus, appears to be primary as well.

Other polished specimens show that the concentration of coarser grains within the sediment-filled body chamber is always consistent with a vertical position—they were concentrated by gravity at the lowest part of the vertical body chamber (Fig. 12B). The shells of many vertically embedded ammonoids are stretched typically along a horizontal plane (Fig. 11D, H, J). Obviously, this deformation originated by loading of the sedimentary column deposited on top of the vertically oriented ammonoid shell, and thus, it is also a valid criterion of primary vertical orientation (cf. Müller, 1979; Maeda et al., 2003).

Integrity and Type of Filling of the Ammonoid Shells

Most of the horizontally or vertically embedded ammonoid shells in Facies Association A and B preserve the complete shell with body chambers filled with sediment and phragmocones filled with sparry calcite. These occurrences imply minimum reworking as demonstrated by common and complete preservation of delicate and fragile shells of *Ainoceras* (*Stelloceras*) *zinsmeisteri* Olivero and *Eubostrychoceras medinai* Olivero (Figs. 11–12). Baculitids, scaphitids, gaudryceratids, tetragonitids, and kossmaticeratids also preserve the complete shell as shown by polished or natural sections cut along the siphuncular plane (Fig. 12).

In contrast, the large shelter pachydiscids recorded in Facies Association B show evidence of partial shell dissolution, and both the body chamber and phragmocone are filled with sediments. Most body chambers of phylloceratids are not preserved and apparently were lost before burial (Fig. 13); they are always recorded in low frequencies. A similar preservation was found in the phylloceratids of the Cretaceous Yezo Group in Japan, suggesting postmortem drift and reworking (Maeda and Seilacher, 1996).

The dominant kossmaticeratid species (*Natalites* spp. Group 2, *Karapadites* aff. *centinelaensis* Riccardi, *Maorites* spp., and *Grossouvrites occultus* Olivero and Medina) as well as compressed desmoceratids (*Oiophyllites decipiens* Spath) in Facies Association D preserve the complete shell generally (Fig. 11). Small complete or broken shells represent the gaudryceratids, whereas the most abundant heteromorph—*Parasolenoceras*—is fragmented commonly; sometimes fragments of the phragmocone filled with sparry calcite are oddly preserved in a vertical position (Figs. 5–6).

No polished median sections of intact Santa Marta ammonoid shells preserve the jaw apparatus within the body chamber; apparently the soft body was lost prior to burial. In one vertically oriented specimen of *Ainoceras zinsmeisteri*, however, only the distal part of the body chamber is filled with sediment and most of the larger part of the body chamber is filled with sparry calcite (Figs. 12D–E). This type of preservation suggests that the animal soft body, or a portion of it, was still trapped in the adapical part of the body chamber at the time of burial. No jaw apparatus was found inside the body chamber, however. As delicate, calcified siphuncular necks with the connecting rings and septa are preserved normally within the phragmocone (Figs. 12B–C), postburial dissolution of the calcitic parts of the jaw apparatus offers no satisfactory explanation. It seems that in this case, the distal part of the soft body containing the jaw apparatus of *A. zinsmeisteri* was lost before burial, while the rest of the soft tissues still adhered to the proximal part of the body chamber. Calcitic cement-filled spaces inside the body chambers can alternatively be explained by incomplete sediment filling of the body chambers.

The composition of the filling of the siphuncular tube is of particular interest. In general, the ammonoid body chambers are filled with fine sand and silt grains, composed mostly of fresh pyroclastic material, floating in a dark-colored matrix of clay particles and micrite. The camerae in the phragmocone, in contrast, are filled with clean, light-colored sparry calcite. The intervening siphuncular tube, especially in its adoral portion, is always filled with a mixture of clay particles and micrite, similar to the material observed in the body chamber (Fig. 12C). This indicates that during transportation, or soon after deposition of the shell, the wall of the siphuncular tube acted as a barrier to the incorporation of the mixture of clay particles into the phragmocone.

Faunal Spectra and Composition of Vertical Ammonoids

For each ammonite assemblage or facies association, the most common vertically oriented ammonite species is also the dominant component species of the associated faunal spectrum. In Facies Association A, the heteromorph *Baculites* aff. *kirki*, thus, is the dominant species that constitutes ~50% of the total fauna (Fig. 13) and is the most frequent species found in a vertical position. The same pattern is found in Facies Association B and D, where vertically oriented ammonites are more or less represented equally by gaudryceratids-tetragonitids, heteromorphs, and kossmaticeratids-pachydiscids in Facies Association B and by kossmaticeratids in Facies Association D (Figs. 2, 13). Quantitative data on the faunal composition of vertical ammonites and the whole faunal spectrum are only available for three localities containing the sheltered type of preservation; these data support the qualitative estimations given here (Fig. 13).
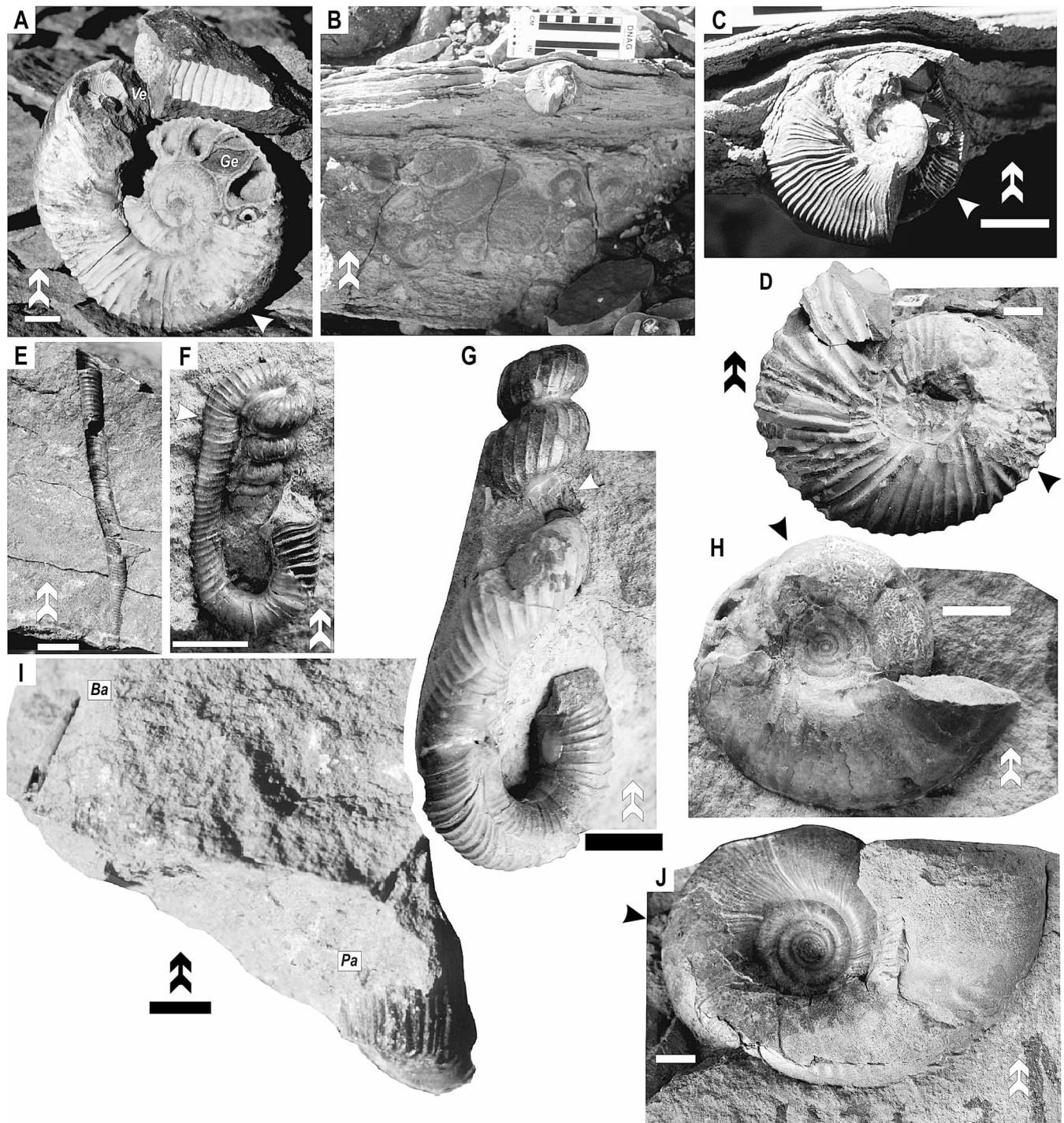
FIGURE 11—Primary vertical orientation in ammonoids from the Santa Marta Formation. A–D) Facies Association D. A) triple geopetal criteria in *Natalites* sp., CADIC PI 61. Ge = sedimentary filled chamber; Ve = small, vertical *Natalites* sp. B) *Maorites* sp. preserved in the parallel laminated division of a coarse-grained tempestite bed, CADIC PI 62. C) Closeup of the same specimen. D) Stretched *Natalites taylori* (Spath) deformed by sedimentary loading, CADIC PI 63. E–H) Facies Association B. E) *Ryugasella antarctica* Olivero in inverted vertical position, that is, with the body chamber pointing upward, field photograph. F) *Ainoceras* (*Stelloceras*) *zinsmeisteri* Olivero, CADIC PI 64. G) *Eubostrychoceras medinai* Olivero, CADIC PI 65. H) *Anagaudryceras* sp., CADIC PI 66. I–J) Facies Association A. I) *Baculites* aff. *kirki* Matsumoto (Ba) associated with the bivalve *Panopea* sp. (Pa) preserved in life position, field photograph. J) Stretched *Gaudryceras* sp. deformed by sedimentary loading, CADIC PI 67. Black or white single arrowheads indicate position of the last preserved septum. Black or white doubleheaded arrows point to the upward direction in the vertical plane. Scale bars = 1 cm. See text for further explanation.

DISCUSSION

The biostratinomic history of cephalopod shells commonly involves a complex series of sedimentological processes prior to final burial due to their peculiar hydrostatic and hydrodynamic properties. Vertically embedded cephalopod shells are relatively common in shallow-water settings, and they have been recognized in several previous taphonomic studies (Seilacher, 1968, 1971; Reyment, 1970; Crick, 1983; Maeda et al., 2003; and references therein). Yet extensive reworking and resedimentation processes typical of shallow, energetic settings have
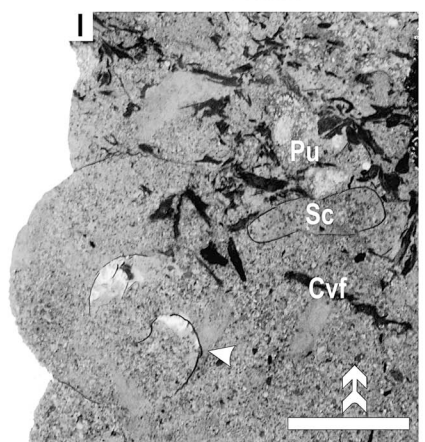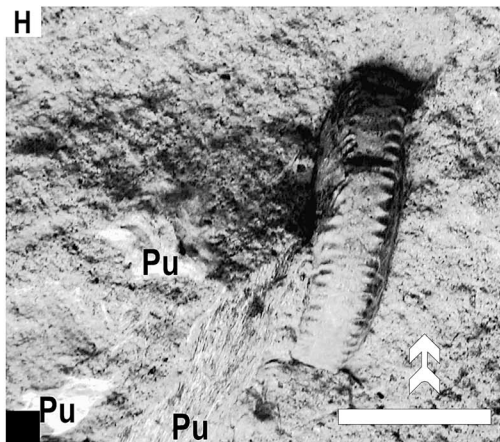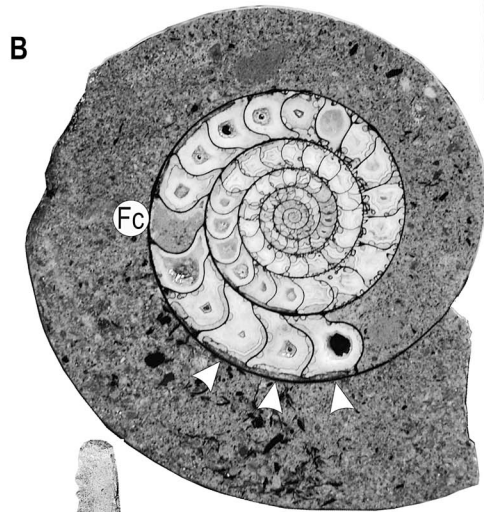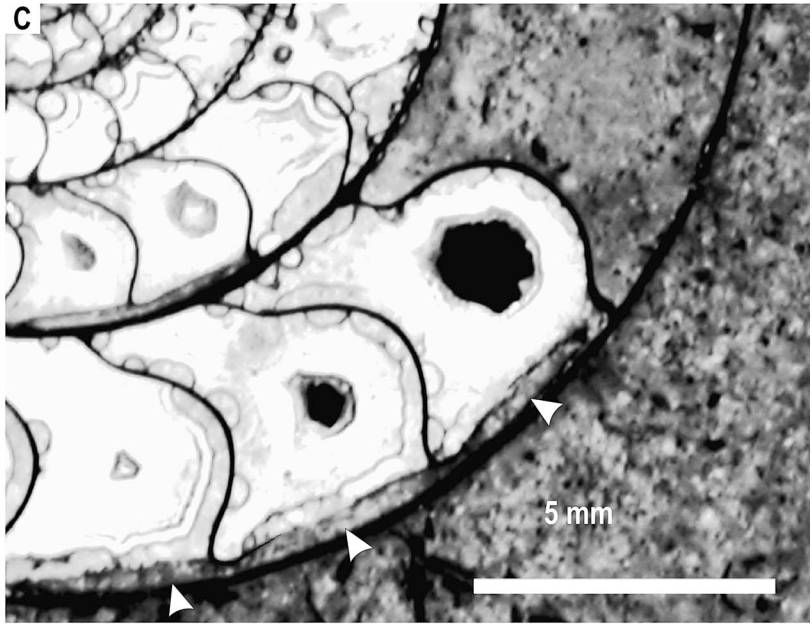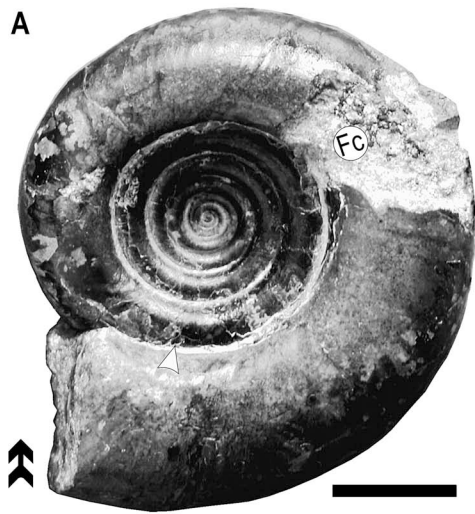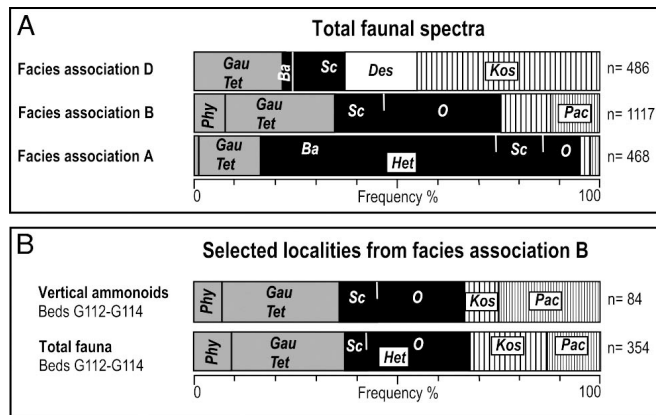
FIGURE 13—Frequency distribution of main ammonite morphotypes of the Santa Marta Formation. A) Total faunal spectra for Facies Associations A, B, and D. Heteromorphs dominate the deepest Facies Association A and ornate kossmaticeratids the shallowest Facies Association D. B) Relative frequency distribution of vertical ammonites respect to the total faunal spectra for selected localities of Facies Association B, Alpha Member. Frequency of vertically preserved morphotypes is similar to that of the total faunal spectra. Phy = Phylloceratidae; Gau-Tet = Gaudryceratidae and Tetragonitidae; Het = heteromorphs, including Ba = Baculitidae, Sc = Scaphitidae, and O = other heteromorphs; Des = Desmoceratidae; Kos = Kossmaticeratidae; Pac = Pachydiscidae; n = number of specimens.

subsequently reoriented the shells. For example, most of the mid-Triassic ceratites from the Muschelkalk of Germany are embedded horizontally in the strata; however, studies of their sedimentary fill confirm that most of them were resting in a vertical position at the sea bottom originally before reworking and final burial (Seilacher, 1971). As many of these shells were vertically embedded in their first sedimentation phase, they do not seem to violate the theoretical paradigm that vertical stability can only be possible at very shallow depths (Raup, 1973).

Reworking is minimal or absent for the vertically embedded ammonite shells of the Santa Marta Formation (Figs. 11–12). Particularly, Facies Associations A and B represent deposition in marine environments well below wave base and are characterized by sporadic turbidite currents in basinal and base-of-the-slope settings of a deep-water deltaic system (see Fig. 2). As bottom currents oriented ammonite shells at the time of burial (see Figs. 9–10), reorientation by such postburial processes as bioturbation (cf. Maeda, 1987) or enhanced buoyancy of intact shells lying horizontally in soupy sediments (see the zombie model of Okamoto and Asami, 2002) seems unlikely. Consequently, the vertically embedded ammonite shells in these facies associations were deposited in water depths well below the theoretical limit imposed by hydrostatic analysis. Vertical embedding of ammonite shells in the Santa Marta Formation was likely controlled by a combination of sedimentary processes.

In some beds of Facies Associations A and B (Figs. 2, 11I, 12F–I), specimens of baculitids and scaphitids are embedded vertically in thick, graded, pumicite-rich beds with abundant plant fragments. In addition, some ammonites are preserved in an inverted position, with their body chamber pointing upright. Waterlogged pumice, wood, and ammonite shells are all slightly denser than seawater and behave hydraulically in a similar way during transportation (Maeda, 1987; Maeda and Seilacher, 1996). These ammonoids thus are interpreted as being transported within

a dense cloud of pumice and wood fragments of similar densities and deposited together by collapse of the dense cloud in a high-density turbidite bed. In these cases, the vertical orientation of ammonite shells was possible because they were frozen in place by a rapid sedimentation event, before full waterlogging of the phragmocone caused the shell to rest in a horizontal position.

Rapid sedimentation events also explain the vertical preservation of kossmaticeratid shells showing isolated preservation in Facies Association D but, in this case, during deposition of the parallel laminated division of tempestite beds (Figs. 11A–D). In all these kossmaticeratids, the body chamber angular length is about 180°, and, theoretically, the aperture should be oriented obliquely upward, forming an angle of about 60° while floating (cf. the brevidome apertural orientation of Westermann, 1996). The apertures of the kossmaticeratids from Facies Association D are much more raised, however, forming an angle of about 130°–140° (Figs. 11A–D). In contrast, floating lightweight ammonite shells are not expected to be concentrated together with medium sand grains during high-energetic bottom conditions necessary for the formation of parallel lamination. These hydrostatic and hydraulic abnormalities are best explained if, during near-bed transportation, sand grains differentially filled the adapical part of the body chamber. The general lack of wood and pumice fragments in these parallel laminated sandstones seems to support this interpretation.

The dense concentration of vertically embedded ammonite shells and wood fragments in the pod preservation of Facies Association D (Figs. 5–6) indicates a different sedimentary regime. Erosive bottom currents originally formed shallow depressions in homogeneous, fine-grained sandy bottoms. After this initial erosive phase, the following weak current tail with a dense concentration of waterlogged wood fragments and ammonite shells was subsequently deposited into these depressions. As depressions became crowded with wood and shells, mutual interference fixed the fossil particles in their final burial position.

The most striking case of vertically embedded ammonite shells is in the lobe deposits of Facies Association B. These deposits consist of regular alternations of nonfossiliferous, tuffaceous sandy turbidites and carbonaceous mudstone, capped by hard-cemented, highly fossiliferous, tuffaceous turbidites (Figs. 2, 3A–B). The latter include combinations of different guilds of benthic organisms—*Pinna* sp. in life position, as well as parautochthonous *Rotularia* sp. and *Cerithium* sp. (Figs. 3C, 8D)—and allochthonous reworked fossils—partially dissolved, large pachydiscid shells; sheltered preservation; and current-oriented wood fragments and vertically embedded ammonite shells (Figs. 7–10). The preservation history of this seemingly complex combination of different guilds is explained by cyclic sedimentary regimes associated with active progradation and shifting of depositional lobes (Fig. 14).

Active lobe progradation is reflected by the coarsening- and thickening-upward intervals of tuffaceous turbidites and carbonaceous mudstone (Fig. 14A). Environmental conditions at the site of lobe deposition were unfavorable either for benthic or planktic organisms, as suggested by the general lack of megafossils or trace fossils. The situation changed after the shift of depositional lobes to a different area. The shifting of the active depositional area was associated with low-sedimentation rates, promoting colonization of the seafloor. The uppermost bed of the previous lobe deposits was colonized by, among other organisms, *Pinna* sp., *Rotularia* sp., *Cerithium* sp., and the trace makers of different burrows, including

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FIGURE 12—Polished median sections of vertically embedded ammonoids. Facies Association B, Santa Marta Formation. A–C) *Anagaudryceras* sp., CADIC PI 68. A) Lateral view. B) Polished median section. C) Closeup of adoral part of the phragmocone preserving the siphuncular tube (white arrows) filled with a matrix similar to that of the body chamber. Some septa preserve the prochoanitic septal neck. Phragmocone filled with sparry calcite; Fc = punctured chamber. D–E) *Ainoceras* (*S.*) *zinsmeisteri*, lateral view and polished section of the same side. Only the adoral part of the body chamber is sediment filled, the rest of the body chamber was partially broken during specimen recovery, CADIC PI 69. F–G) *Baculites* aff. *kirki*, lateral view and polished section. The light gray, branched structure inside the body chamber is a trace fossil, CADIC PI 70. H–I) *Yezoites* sp., CADIC PI 71 ventral view and oblique polished median section of the same specimen; Pu = pumice fragments; Cvf = carbonized plant fragments; Sc = scaphitid shell. References as in Figure 11. Scale bar = 1 cm except for Figure 12C.
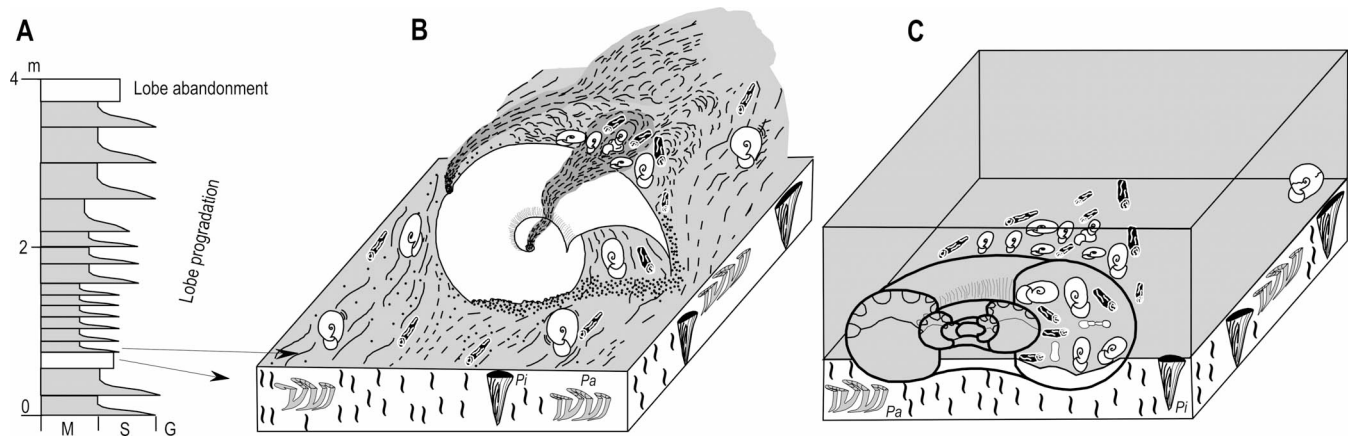
FIGURE 14—Sedimentary controls on the preservation of vertically embedded ammonites in lobe deposits of the Alpha Member, Santa Marta Formation. A) Typical sedimentary log showing prograding lobe deposits (gray shadowing) and intervening phases of lobe abandonment (white beds). B) After shifting of depositional lobes to a new area, low-sedimentation rates promote colonization of the uppermost layer of sediments (white bed) by *Pinna* sp., the trace makers of *Paradictyodora* and other unidentified burrows. Buried shells of large pachydiscid ammonites were partially dissolved. Renewal of active lobe deposition starts with dilute turbidite currents (gray area) that deposited dense fossil concentrations showing the sheltered mode of preservation. Pi = *Pinna* sp.; Pa = *Paradictyodora*. (C) Rapid sedimentation during the same depositional event bed covered the fossil concentration (dark gray bed), favoring the vertical preservation of the ammonite shells.

Paradictyodora antarctica (Olivero et al., 2004). During this abandonment phase, the shell of partially buried large pachydiscids started to dissolve in contact with the seawater (Fig. 14B). A shift of the depositional lobes back into this area restored deposition of turbidite beds. During the earliest phases of renewed sedimentation, the most distal part of the depositional lobe was reached only by fine-grained, dilute turbidite currents transporting a dense concentration of vertical ammonites and wood fragments that were deposited inside and around the large pachydiscid shelters (Fig. 14C).

In all cases discussed earlier, it is evident that during near-bed transportation the vertically floating cephalopod shells were frozen in position by rapid sedimentation events. It also seems evident that after death and subsequent decomposition of soft tissues, the shells remained oriented vertically in the water column for a period of time, as indicated by the general lack of aptychi within their body chambers. Less evident in this scenario is the mechanism that allowed for the vertical stability of the shells during that time, at depths well below the limit imposed by the hydrostatic analysis of Raup (1973).

After the soft body is removed from the shell, flooding of the phragmocone is a relatively rapid process. Recent *Nautilus* experimental data and theory on filling rates suggest that the critical reduction of 50% of the phragmocone gas volume would be reached in a few hours in most situations, above which vertical stability is not longer possible (Weaver and Chamberlain, 1976; Chamberlain et al., 1981). In addition, Wani et al. (2005) found that *Nautilus* shells filled rapidly if they are smaller than ~200 mm and concluded that the same size limit can be applied to ammonites. Is not possible to calculate the residence time of vertically floating ammonoid shells in the water column for the Santa Marta ammonites. The time needed to accomplish the sequence of events involved in the animal's death, removal of soft tissues, transportation, and final embedding seems, however, to be much longer than that required for waterlogging of the phragmocone in most situations, as deduced from experiment and theory.

All polished sections of vertically embedded ammonite shells show siphuncular tubes filled with a matrix of micrite and clay particles. The sedimentary material filling the body chambers also has a matrix of similar composition, but such material never entered into the phragmocone (cf. Seilacher, 1968), which is always filled with clear, drusy calcite (Figs. 12B–C). It is interpreted that the vertically floating shells were transported within a turbid cloud of suspended fine-grained sediments. The clay particles that entered into the siphuncular tube adhered to its walls forming a plug layer stiff enough to resist the ambient hydrostatic pres-

sure. This plug layer apparently acted as an effective barrier that avoided the free entrance of seawater into the phragmocone. In this way, the ambient hydrostatic pressure would not be in equilibrium with the internal pressure in the phragmocone at a given water depth. Hence, the ammonite shells could remain in a vertical position for an extended period of time and well below the water depths, indicated by hydrodynamic and hydrostatic calculations in clear water.

CONCLUSIONS

The taphonomic analysis of the vertically embedded ammonite shells of the Santa Marta Formation indicates that (1) vertical orientation dominates different types of ammonite preservation, including isolated specimens in Facies Associations A–D, pod preservation in Facies Association D, and sheltered preservation in Facies Association B; (2) vertical orientation is a primary feature; (3) postburial reworking is minimum or absent; and (4) the relative proportion of different ammonite morphotypes of vertically embedded shells is the same in the accompanying faunal spectrum, suggesting that the vertical orientation was not biased toward a preferred morphotype.

In Facies Association B, the primary character of the vertically embedded shells is also consistent with paleocurrent data. The orientation of the plane of symmetry of vertically embedded ammonites, wood fragments, and conical gastropod shells is consistent with the regional ESE- and ENE-directed paleocurrents inferred from physical sedimentary structures. Consequently, the filling of large pachydiscid shelters with ammonite shells and wood fragments was more effective when the aperture of the shelters faced upcurrent. When the aperture of the shelter faced downcurrent, the concentration of individuals was greatest on the outside of the shelters.

The vertically embedded ammonite shells of the Santa Marta Formation were deposited primarily in water depths well below the theoretical limit imposed by hydrostatic analysis. The analysis of particular cases indicates that rapid sedimentation associated with different depositional regimes—including high- and low-density turbidite currents, tempestites, and weak bottom currents—was one of the main factors controlling the preservation of vertically embedded ammonite shells. Another important factor was the plugging of the siphuncular tube with clay particles during transportation of ammonite shells within a dense, turbid cloud of suspended mud. The mud particles that adhered to the siphuncular tube were stiff enough to resist the hydrostatic pressure and acted as an effective

barrier avoiding or considerably delaying the waterlogging of the phragmocone.

REFERENCES

CHAMBERLAIN, J.A., JR., WARD, P.D., and WEAVER, J.S., 1981, Postmortem ascent of *Nautilus* shells: Implications for cephalopod paleobiogeography: Paleobiology, v. 7, p. 494–509.

CRAME, J.A., FRANCIS, J.E, CANTRILL, D.J., and PIRRIE, D., 2004, Maastrichtian stratigraphy of Antarctica: Cretaceous Research, v. 25, p. 411–423.

CRICK, R.E., 1983, The practicality of vertical cephalopod shells as paleobathymetric markers: Bulletin of the Geological Society of America, v. 94, p. 1,109–1,116.

INESON, J.R., 1989, Coarse-grained submarine fan and slope apron deposits in a Cretaceous back-arc basin, Antarctica: Sedimentology, v. 36, p. 793–819.

KENNEDY, W.J., and COBBAN, W.A., 1976, Aspects of ammonoid biology, biogeography and biostratigraphy: Special Papers in Palaeontology, v. 17, p. 1–94.

KLUG, C., and KORN, D., 2004, The origin of ammonoid locomotion: Acta Palaeontologica Polonica, v. 49, p. 235–242.

LEHMANN, U., 1981, The Ammonites: Their Life and Their World: Cambridge University Press, Cambridge, 246 p.

MACDONALD, D.I.M., and JEFFERSON, T.H., 1985, Orientation studies of waterlogged wood: A paleocurrent indicator?: Journal of Sedimentary Petrology, v. 55, p. 235–239.

MAEDA, H., 1987, Taphonomy of ammonites from the Cretaceous Yezo Group in the Tapu area, northwestern Hokkaido, Japan: Transactions and Proceedings of the Palaeontological Society of Japan, n.s., v. 148, p. 285–305.

MAEDA, H., 1991, Sheltered preservation: A peculiar mode of ammonite occurrence in the Cretaceous Yezo Group, Hokkaido, north Japan: Lethaia, v. 24, p. 69–82.

MAEDA, H., MAPES, R.H., and MAPES, G., 2003, Taphonomic features of a Lower Permian beached cephalopod assemblage from central Texas: PALAIOS, v. 18, p. 421–434.

MAEDA, H., and SEILACHER, A., 1996, Ammonoid taphonomy, *in* Landman, N.H., Tanabe, K., and Davies, R.A., eds., Ammonoid Paleobiology: Topics in Geobiology: vol. 13, Plenum Press, New York, p. 543–578.

MARTINIONI, D.R., 1992, La Formación Rabot (Cretácico superior, isla James Ross, Antártida): Un ciclo transgresivo-regresivo de plataforma con dominio de procesos de tormenta, *in* Rinaldi, C.A., ed., Geología de la isla James Ross, Antártida: Instituto Antártico Argentino, Buenos Aires, p. 101–123.

MÜLLER, A.H., 1979, Fossilization (Taphonomy), *in* Robinson, R.A., and Teichert, C., eds., Treatise on Invertebrate Paleontology, pt. A, Introduction: Geological Society of America, Boulder, Colorado, and University Press of Kansas, Lawrence, p. A2–A78.

OKAMOTO, T., and ASAMI, K., 2002, Peculiar mode of occurrence and its preservational history of *Polyptychoceras*, a Cretaceous heteromorph ammonite: Palaeontological Society of Japan, v. 71, p. 1–18 (in Japanese with English abstract).

OLIVERO, E.B., 1984, Nuevos amonites campanianos de la isla James Ross, Antártida: Ameghiniana: Revista de la Asociación Paleontológica Argentina, v. 21, p. 53–84.

OLIVERO, E. B., 1988, Early Campanian heteromorph ammonites from James Ross Island, Antarctica: National Geographic Research, v. 4, p. 259–271.

OLIVERO, E.B., 1992, Asociaciones de amonites de la Formación Santa Marta (Cretácico tardío), isla James Ross, Antártica, *in* Rinaldi, C.A., ed., Geología de la isla James Ross, Antártida: Instituto Antártico Argentino, Buenos Aires, p. 47–76.

OLIVERO, E.B., BUATOIS, L.A., and SCASSO, R.B., 2004, *Paradictyodora antarctica*: A new complex vertical spreite trace fossil from the Upper Cretaceous–Paleogene of Antarctica and Tierra del Fuego: Journal of Paleontology, v. 78, p. 783–789.

OLIVERO, E.B., and MEDINA, F.A., 2000, Patterns of Late Cretaceous ammonite biogeography in southern high latitudes: The Family Kossmaticeratidae in Antarctica: Cretaceous Research, v. 21, p. 269–279.

OLIVERO, E.B., and MUSSEL, F.A., 1993, Biofacies de *Inoceramus* (Bivalvia) en ambientes marinos proximales del Cretácico superior de Antártida: 2das jornadas sobre investigaciones antárticas: Instituto Antártico Argentino-INGEIS, Buenos Aires, p. 189–190.

PIRRIE, D., 1989, Shallow marine sedimentation within an active margin basin, James Ross Island, Antarctica: Sedimentary Geology, v. 63, p. 61–82.

RAUP, D.M., 1973, Depth inferences from vertically imbedded cephalopods: Lethaia, v. 6, p. 217–226.

REYMENT, R.A., 1970, Vertically inbedded cephalopod shells: Factors in the distribution of fossil cephalopods, pt. 2: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 7, p. 103–111.

REYMENT, R.A., 1973, Factors in the distribution of fossil cephalopods, pt. 3: Experiments with exact models of certain shell types: Bulletin of the Geological Institute of the University of Uppsala, n.s., v. 4, p. 7–41.

SCASSO, R.A., OLIVERO, E.B., and BUATOIS, L.A., 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, v. 4, p. 239–260.

SEILACHER, A., 1968, Sedimentationsprozesse in Ammonitengehäusen: Akademie der Wissenschaften und der Literatur: Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, v. 9, p. 191–203.

SEILACHER, A., 1971, Preservational history of ceratite shells: Palaeontology, v. 14, p. 16–21.

SEILACHER, A., 1972, Biostratinomy: The sedimentology of biologically standardized particles, *in* Ginsburg, R.N., ed., Evolving Concepts in Sedimentology: Johns Hopkins University Press, Baltimore and London, p. 159–177.

SEILACHER, A., and LABARBERA, M., 1995, Ammonites as Cartesian divers: PALAIOS, v. 10, p. 493–506.

WANI, R., KASE, T., SHIGETA, Y., and OCAMPO, R. DE, 2005, New look at ammonoid taphonomy, based on field experiments with modern chambered nautilus: Geology, v. 33, p. 849–852.

WEAVER, J.S., and CHAMBERLAIN, J.A., JR., 1976, Equations of motion for post-mortem sinking of cephalopods shells and the sinking of *Nautilus*: Paleobiology, v. 2, p. 8–18.

WESTERMANN, G.E.G., 1996, Ammonoid life and habit, *in* Landman, N.H., Tanabe, K., and Davies, R.A., eds., Ammonoid Paleobiology: Topics in Geobiology: vol. 13, Plenum Press, New York, p. 607–707.