Nature and Origin of Spectacular Marine Miocene Shell Beds of Northeastern Patagonia (Argentina): Paleoecological and Bathymetric Significance

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Biofacies and taphonomic analysis has allowed for the reconstruction of the paleoenvironmental history of accumulation of a series of spectacular mollusk-dominated shell-concentrations from the Puerto Madryn Formation and the benthic assemblages that inhabited the Miocene sea in northern Patagonia, Argentina. An upward-shallowing from open mid-shelf to more restricted shoreface-foreshore environments has been recognized. Transgressive, Maximum Highstand and Regressive phases are recognized based on the integrated approach of assemblages and lithofacies arrangement. Eleven mollusk-dominated fossil assemblages were defined and grouped into Associations A, B, and C. Transgressive and Maximum Highstand phases preserve three main shell beds that record an upwards change from dynamic to complete bypassing conditions. These were deposited in tidal current-dominated mid- and inner-shelf environments and belong within Association A. The top bedding surface records the maximum depth attained by the sea. The Regressive Phase is characterized by three upward-deepening cycles comprised of foreshore-shoreface sandbar deposits containing Association C. Sandbars are capped by environmentally condensed shell-beds of Association B and record deposition from the shoreface (wave-breaking zone) to mid-shelf environments, all above storm-wave base.

Based on these fossil assemblages, seven benthic life associations can be identified. The deepest ones inhabited the mid-to-inner shelf and were represented by suspension-feeders from gravel-substrata swept by strong tidal currents and by suspension-feeders from lower energy firm bottoms. Lower shoreface sandy bottoms, close to fairweather wave base and affected by weak tidal currents, were inhabited by epifaunal suspension-feeders, whereas sandy bottoms close to the fairweather wave-breaking zone were characterized by semi-infaunal deposit feeders and suspension feeders. The shallowest living assemblages inhabited intertidal and foreshore settings and were represented by soft-bottom infaunal suspension feeders, as well as by firm bottom, vagile carnivorous and suspension-feeding epifauna.

INTRODUCTION

One of the most conspicuous features of the marine Miocene deposits of northeastern Patagonia are the thick beds composed of accumulations of exceptionally well-preserved molluskan shells. These shell beds comprise 55% of the total thickness of the sequence reported herein, and their detailed paleoecologic and taphonomic analyses provide new insights on Miocene sea-level dynamics (T-R cycle), and environmental conditions.

The species composition of each assemblage is described, along with taphonomic insights and their paleoecological significance. Additionally, a refined set of paleoenvironmental interpretations is provided, based on cluster analysis of the faunal data and the spatial distribution of assemblages. Exceptionally well-preserved and varied faunas have allowed for extensive autoecological investigation. Bathymetric interpretations from comparison of Miocene taxa with their congeneric Recent taxa are consistent with the environmental conditions derived from classical facies analysis and from comparison with well studied, modern sedimentary environments (e.g., German Bight). Finally, consideration of discontinuities, internal stratigraphy, and context of the major shell beds provided the opportunity to reconstruct sedimentary history in the context of relative sea-level changes.

STRATIGRAPHY AND PALEOGEOGRAPHY

A large area of Argentina was flooded during Miocene times by a shallow sea known in the literature as the "Entrerriense" or "Paranense" sea (see del Río and Martínez, 1998a; del Río, 2000 and bibliography herein; Fig.1A). A southern branch of this "Entrerriense" sea occupied península Valdés and the area surrounding the city of Puerto Madryn (Chubut Province) in northeastern Patagonia (Fig.1B). In this region, the "Entrerriense" deposits are part of the Puerto Madryn Formation (Haller, 1978), which overlies the Late Oligocene—Early Miocene? "Patagoniense" horizons and comprises 150 m of heterolithic and cross-bedded sandstones, muddy sandstones, and sandy mudstones interbedded with white tuffs and distinctive shell beds (Fig. 2).

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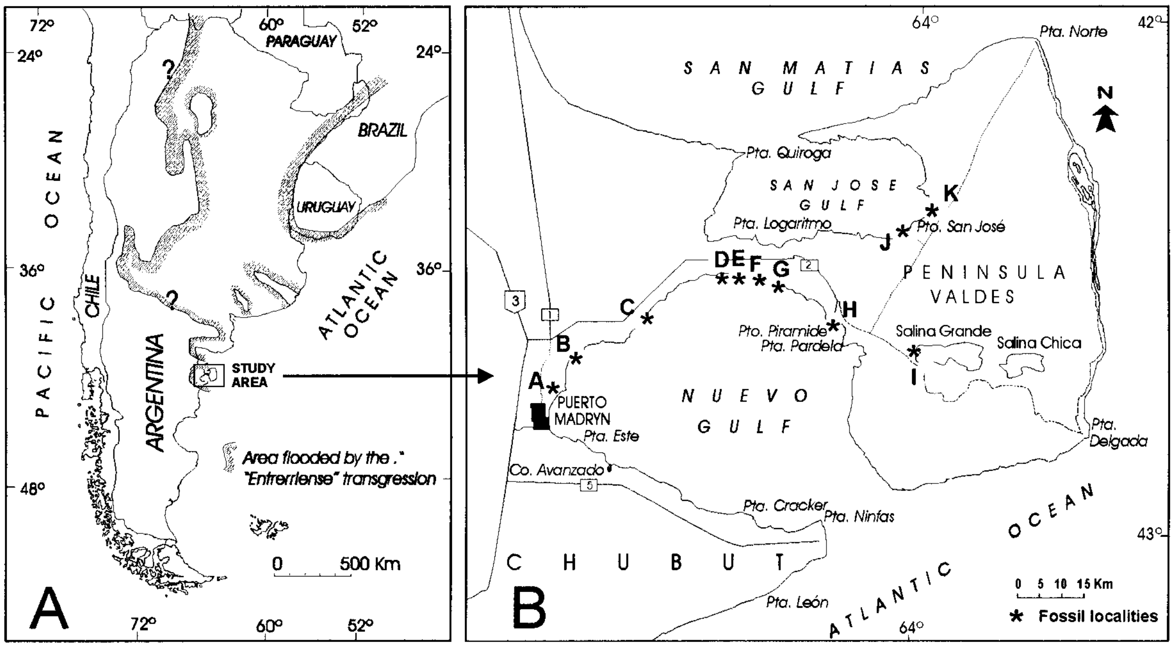

FIGURE 1—Argentina and area of the present investigation. (A) Paleogeography of Argentina during the Miocene. (B) Location of fossiliferous sections of Miocene coastal outcrops. A—Bajo de Madryn, B—El Doradillo, C—Cerro Prismático, D—Las Charas, E—Eje tentativo W, F—Eje Tentativo Ob, G—Eje Tentativo E, H—Puerto Pirámide's area, I—Salina Grande, J—San José, and K—Lote 39.

The age of "Entrerriense" deposits in Argentina has been discussed largely since the last century. On the basis of molluskan faunas, these deposits have been assigned to the late Middle Miocene (del Río, 1988, 1989, 1992, see discusion of age herein) and to the early Late Miocene based on ^{87}Sr/^{86}Sr evidence (Scasso et al. 1999a).

Reconstruction of "Entrerriense" paleogeography (Scasso and del Río, 1987) indicates that deposition of the "Entrerriense" beds took place in a gulf or a wide bay that extended west from the main oceanic water body. As with most marine Tertiary deposits of Patagonia, the distribution of the "Entrerriense" indicates the westward penetration of a sea that was open to the east, to the Atlantic Ocean. The sea did not extend beyond a N-S line 25 km west the city of Puerto Madryn. To the north, the paleocoast can be traced along the Sierra Grande highs and their eastern extension (currently below sea level). The south coast can be traced along the río Chubut area, where no "Entrerriense" deposits are recorded, and its continuation to the east on the present shelf. The existence of a paleohigh in the south is inferred; the Middle-Late Miocene of the río Chubut area is characterized by continental deposits with many internal discontinuities, and facies and paleocurrent patterns within the "Entrerriense" basin point to provenance and sediment dispersion from the south and southwest.

Based on the vertical recurrence of faunal assemblages (this paper) and lithofacies arrangement (Scasso and del Río,1987), the lowermost fossiliferous 75 meters of the Puerto Madryn Formation can be subdivided into a Transgressive Phase, a Maximum Highstand Phase, and a Regressive Phase (Figs. 2–3). The Maximum Highstand Phase refers to deposits that accumulated when the sea level was at its maximum, before the regression took place. Thus, this term is not equivalent to highstand system tract as it is normally used in sequence stratigraphy, (i.e., for maximum highstand and regressive phases).

The combined Transgressive and Maximum Highstand Phases are 30 meters thick, and are well exposed along the northern coastline of the Golfo Nuevo in the Eje Tentativo area (Fig.3) The overlying Regressive Phase of the sequence is 45 meters thick, and the best exposures extend from the Puerto Pirámide area eastwards to Península Valdés. Westwards from Cerro Prismático, where the shallowest deposition is recorded (Fig.4), it is not possible to subdivide the "Entrerriense" deposits, but the lowermost transgressive horizons are recognizable at El Doradillo and Cerro Prismático. The Regressive Phase represents the gradual regression of the "Entrerriense" sea, a product of relatively high sedimentation rates of volcaniclastic materials sourced from basic and mesosilicic volcanic eruptions in the extra-Andean and in the Cordillera de los Andes, respectively (Scasso and del Río, 1987). As a result of sediment aggradation, the entire system prograded and depocenters shifted to the east and northeast during deposition. The Peninsula Valdes region probably became emergent about 9 Ma ago (Scasso et al., 1999a).

DESCRIPTION OF FOSSIL ASSEMBLAGES

The "Entrerriense" fauna consists mostly of mollusks, which were studied by del Río (1992, 1994), del Río and Martínez (1998b) and Martínez et al. (1998), who described 29 gastropods and 42 bivalves species. These are accompanied by subsidiary bryozoans, brachiopods, barnacles, crabs, and one species of irregular echinoid. Vertebrate fossils also are fairly common and consist of marine and terrestrial mammal, bird, and fish remains, recovered from the lowermost and uppermost horizons of the sequence (Cione, 1978, 1988; Cione and Tonni, 1981; Coz-

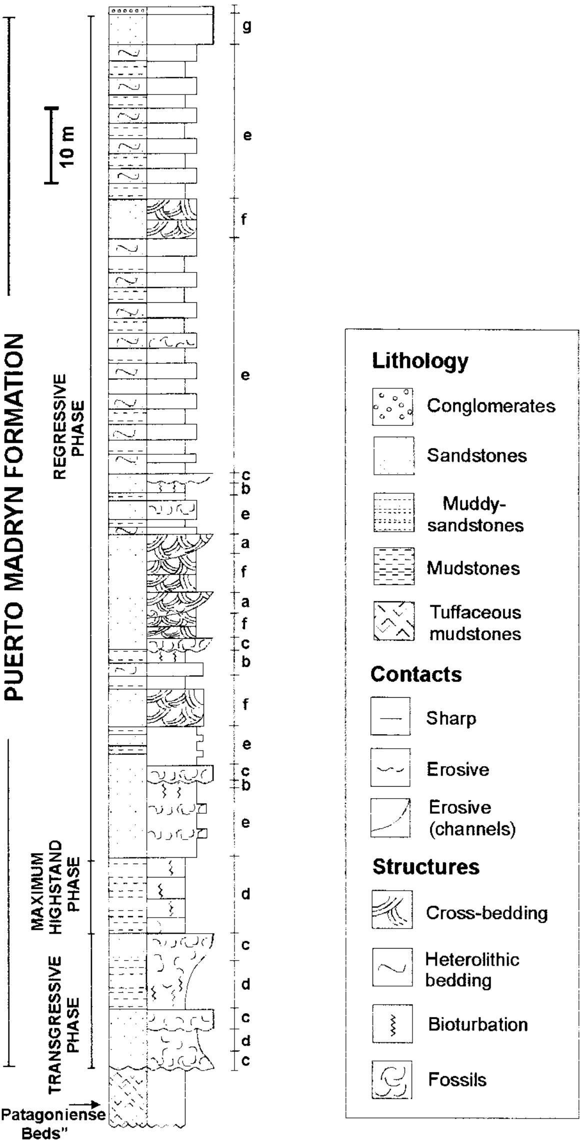

FIGURE 2—Composite stratigraphic column of the Puerto Madryn Formation: Lithofacies coded as in Scasso and del Río (1987): (a) reworked shell beds and conglomeratic sandstones with cross bedding (tidal channels); (b) Fossiliferous shoreface sandbars; (c) Fossiliferous storm-beds from lower shoreface to inner-shelf settings; (d) massive or laminated mudstones (inner mid-shelf); (e) heterolithic beds (shoreface sand tongues and tidal flat) (f) cross-bedded sandstones from megaripples and sand waves (tidal channels and subtidal shoreface bars); (g) paleosols and mudstones (terrestrial and saline marsh environments).

zuol et al., 1993; Riva Rossi, 1996; Dozo et al., 1999). Bivalves are the most diverse and abundantly represented group, with oysters and pectinids the prevalent taxa. Although not abundant, veneroids constitute a diverse group.

Regarding trophic structure (Table 1), the largest group corresponds to suspension feeders, largely dominated by sessile as well as by free-lying epifauna that inhabit firm bottoms, and by semi–infaunal dwellers from gravel substrata. Shallow and deep burrowing infauna typical of soft bottoms are less frequent. Deposit feeders are represented by the lunulate echinoid *Monophoraster darwini* that usually makes up monospecific assemblages. In specific horizons vagile carnivorous epifauna, mostly characteristic of firm bottoms, also are common.

Both simple and complex shell beds are recognized, following the classification proposed by Kidwell (1986, 1991). Simple beds are single-event concentrations, typically a few centimeters thick, that pinch-out over short distances and may "float" in almost barren intervals with no defined lower and upper contacts. They typically capture census or time-averaged fossil assemblages. Complex shell beds, in contrast, are amalgamated, multi-event concentrations up to 10 m thick; these are commonly lenticular bodies of large lateral extent, with sharp lower and/or upper contacts, and contain time-averaged, within-habitat, or environmentally condensed fossil assemblages.

Eleven fossil assemblages were recognized from Q-mode cluster analysis based on the relative abundances of species from 166 samples of 50 to 200 specimens each. Samples were recovered from different events that make up 107 shell beds from 15 sections. Appendix 1 summarizes the relative abundance of species and the resulting assemblages that were subsequently assigned to each sample. Cluster analyses (Fig. 5) were done using three similarity indexes (Manhattan, Eucliddean, and Squared distances; Appendix 1). Complete, simple, and UPGMA linkage methods were performed. The resulting dendrograms show minor differences with a large number of closely similar shell beds clustering into 11 clearly defined groups. However, a few samples remain separate from the defined groups. These include B21, D7, F4, F5,G4, G7, H11, I3, I7, and K13, all of which are pavements made up by *Glycymerita magna* and, hence, were included in Assemblage GROT. Samples A4, A6, A11, J3, I19, J8, H4c, and F16, also do not cluster with any defined groups and, because all are constituted by different species of veneroids, they were considered as belonging in the V Assemblage. Group D2-D4 links with samples belonging in Assemblage GROT, but field data (see Appendix I) reveals that their composition is closer to Assemblage OCAT.

Assemblages are of low to moderately low diversity and mostly record indigenous, within-habitat concentrations of hardparts. Their stratigraphic distribution is illustrated in Figure 3, and taxonomic composition, taphonomic features of each assemblage, as well as ecological and environmental requirements are summarized in Tables 1, and 2 and Appendix 1.

Oyster (Os) Assemblage

This is the most common assemblage and is recovered throughout the Puerto Madryn Formation. The dominant taxa are the suspension feeders *Ostrea patagonica* and *Ostrea alvarezi*, the former often making up monospecific assemblages. According to autoecological comparison with Recent relatives, oysters may live in different substrates due to a high phenotypic plasticity. They can adopt a cemented type of life and constitute biostromes or bioherms on firm bottoms, or be "secondary soft-bottom dwellers" with different morphologic adaptations to environments with high net sedimentation rates (Seilacher, 1984; Chinzei, 1995; Sprechmann et al., 1998). In the study area, two ecophenotypes of "secondary soft-bottom dwellers"

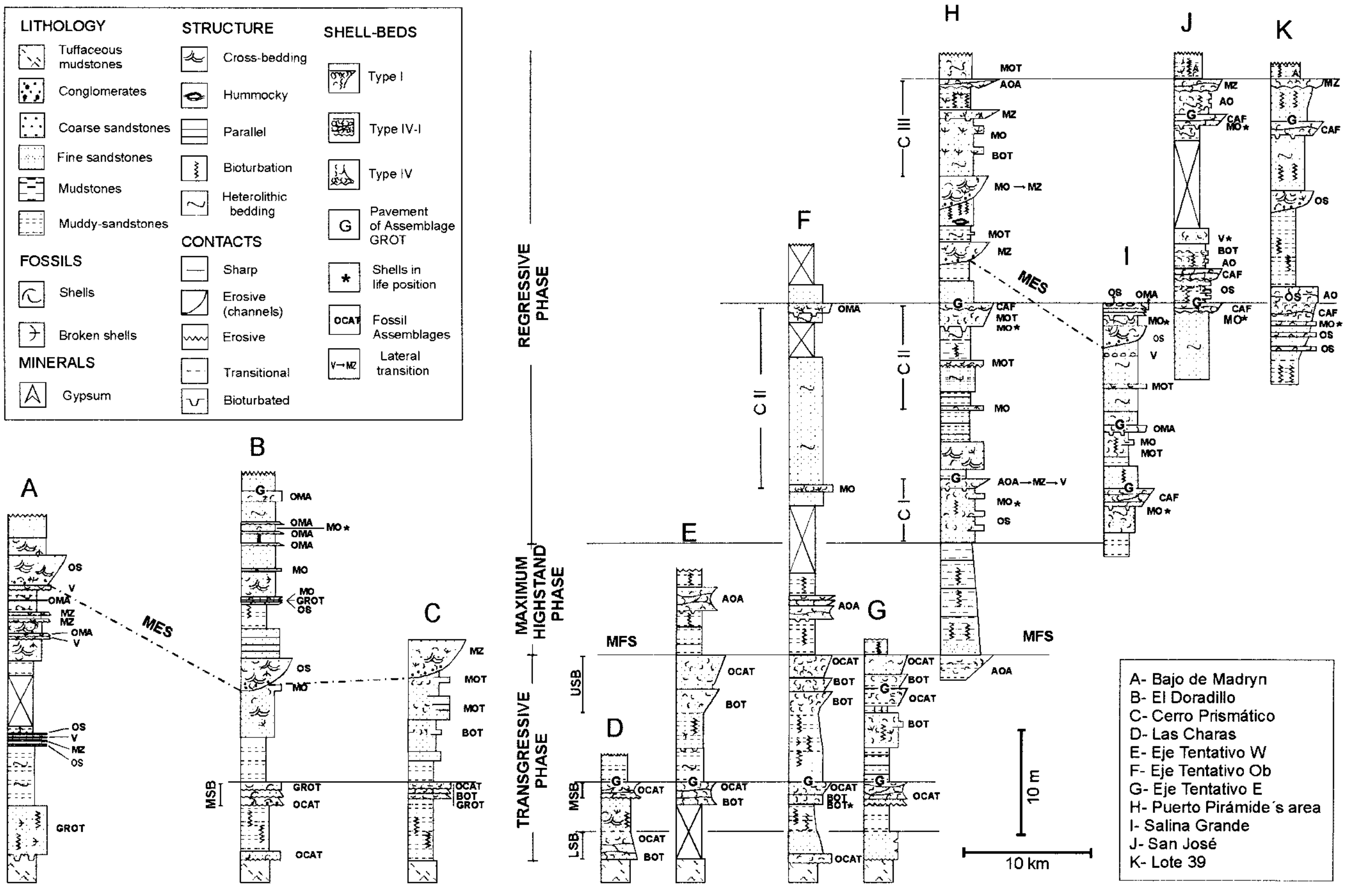

FIGURE 3—Correlation of stratigraphic sections of the Puerto Madryn Formation with occurrences of Assemblages. LSB (Lower shell bed), MSB (Middle shell bed), USB (Upper shell bed); C = sedimentary cycles; MFS = maximum flooding surface; MES = major erosional surfaces from incised valleys to the west, and large channels to the east.

are recognized: bunched forms (*O. alvarezi* and *O. patagonica*) and recliner boulder–shaped forms (*O. patagonica*), both being free lying types that inhabit soft muddy or sandy bottoms. The former consists of nearly vertical bunches of at least three valves cemented to each other, while the latter one has shells that lie on the left convex valve. On the basis of the mentioned antecedents, higher sedimentation rates are inferred for bunched oysters than for free-lying ones.

Three taphofacies are recognized (Table 2): (1) census assemblages that may be "floating" in otherwise barren intervals or constitute pavements at the top of other coquinas; (2) thin, single-event and time-averaged accumulations, often lying on erosive bed contacts; and (3) thick, time-averaged multi-event accumulations that constitute channel infillings and, wherein some cases, oysters are accompanied by pectinid, veneroid, gastropod, and echinoid remains.

FIGURE 4—The shallowest deposits of the Puerto Madryn Formation (dark strata) overlying the "Patagonian beds" (whitish strata) at Bajo de Madryn.

Glycymerita magna (GROT) Assemblage

This assemblage is recovered almost exclusively from thick multi-event accumulations in the Transgressive Phase of the sequence and also from thin single-event pavements that cap shell beds throughout the unit (Fig. 6).

The closest Recent relative of the dominant taxon of this assemblage (*Glycymerita magna*) is *Glycymeris glycymeris,* from the English Channel. It is an opportunistic reophile species (Levinton, 1970) that inhabits shell–gravel substrates strongly swept by tidal currents, at depths ranging from 40 to 100 m. It tolerates high turbulence levels and is a member of the low-diversity "Boreal Offshore Gravel Association" of Holmes (1966). A living counterpart of *Retrotapes ninfasienses* is the widespread *R. exalbida*, a species that also prefers shell-gravel substrates where dense populations are recorded. According to Thomas

TABLE 1—Relative abundances of taxa within each Fossil Assemblage. D = Dominant (>50%); A = abundant (25%–50%); C = common (25%–5%); R = rare (<5%); AT = attached; VAG = vagile; F = free; EPI = epifauna; INF = infauna; SINF = semi-infaunal.

	Assemblages														
SPECIES	GROT	OCAT	BOT	OS	AO	AOA	CAF	MO	OMA	V	MOT	MZ	LIFE HABITAT	TROPHIC GROUP	DEPTH RANGE
Bryozoans	R	R	D									C	AT-EPI	Suspension	INNER-MID-SHELF
“*Turritella*” sp.	C	C	A						R		R	C	VAG-SINF	Omnivorous	SHOREF-MID-SHELF
Retrotapes ninfasiensis	A												SINF	Suspension	INNER-SHELF
Glycymerita magna	D												SINF	Suspension	INNER SHELF
Ostrea alvarezi	C	C	C	A			C				D	C	AT-EPI	Suspension	UBIQUITOUS
Ostrea patagonica	C	C	R	D	D	C	C	D	C			C	AT/F-EPI	Suspension	UBIQUITOUS
Chlamys actinodes		D					C						AT-EPI	Suspension	INNER MID-SHELF
Aequipecten paranensis		A				A	A		A		R	C	AT-EPI	Suspension	SHOREF-INNER-SHELF
Amusium paris					D	D	A						F-SINF	Suspension	SHOREF.
Flabellipecten piramidesensis							C						F-SINF	Suspension	SHOREF.
Chesapecten crassus							C						AT-EPI	Suspension	SHOREF
Monophoraster darwini								D	A		R	C	VAG-SINF	Deposit	U-SHOREFACE
Ameghinomya argentina		R								C		C	SINF	Suspension	SHOREF-INER-SHELF
Ameghinomya meriodionalis										C			SINF	Suspension	SHOREF-INNER-SHELF
Pachymagas piramidesia		C				C	R					C	AT-EPI	Suspension	SHOREF-INNER-SHELF
Panopea regularis	R	R					R						INF	Suspension	FORE-SHOREF.
Pteromyrtea danieli							R		R				INF	Suspension	FORE-SHOREF.
Purpurocardia leonensis	C	R					R						SINF	Suspension	FORE-SHOREF.
Dosinia meridionalis	R	R								C		C	INF	Suspension	FORE-SHOREF.
Dosinia elsai										C			INF	Suspension	FORE-SHOREF.
Pitaria ninfasiensis										C		C	INF	Suspension	FORE-SHOREF.
Pitaria trigonus										C		C	INF	Suspension	FORE-SHOREF.
Anomalocardia entrerriana										C		C	INF	Suspension	FORE-SHOREF.
Chionopsis australis										C		C	INF	Suspension	FORE-SHOREF.
Mactra sp.										C		C	INF	Suspension	FORE-SHOREF.
Dinocardium novus										C			SINF	Suspension	FORE-SHOREF.
Cyrtopleura lanceolata										C			SINF	Suspension	FORE-SHOREF.
Anadara lirata										R		R	SINF	Suspension	FORE-SHOREF.
Trophon laciniatus		R							R		A	C	VAG-EPI	Carnivorous	FORE-SHOREF.
Mytilus trigonus							R				C	R	AT-EPI	Suspension	FORE-SHOREF.
Eiptonium borcherti											C		VAG-EPI	Carnivorous	FORE-SHOREF.
Calliostoma spp.											C		VAG-EPI	Carnivorous	FORE-SHOREF.

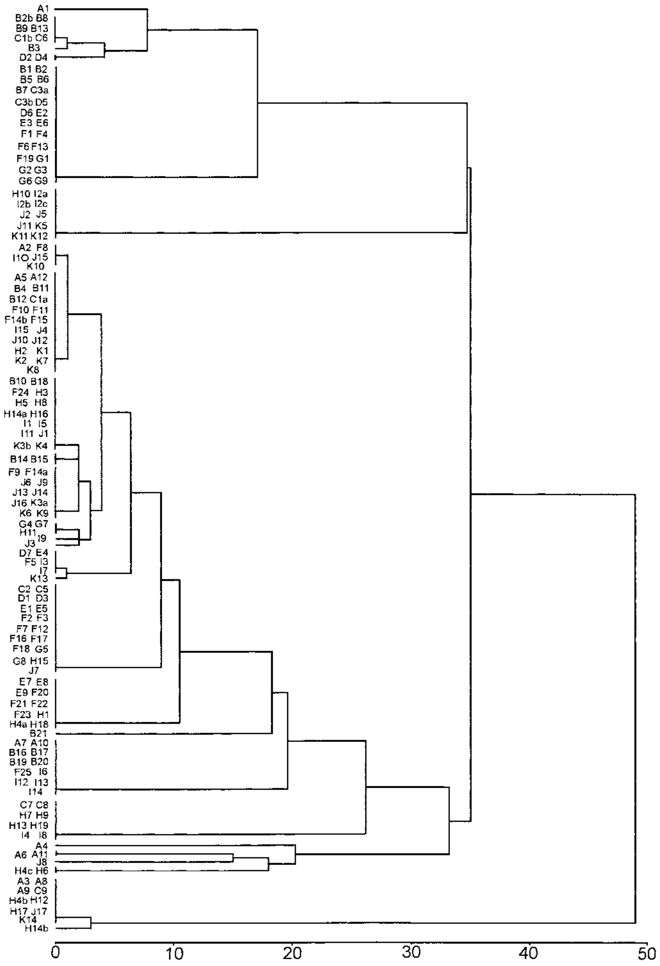

FIGURE 5—Cluster analysis from the data matrix shown in Appendix 1. Manhattan Distance, UPGMA.

(1975), ecological requirements of glycymerids remained stable from Cretaceous to Recent times. Thus, based on taphonomic features of these deposits, Assemblage GROT probably represents accumulations of indigenous benthic fauna on shell-gravel substrates in inner-to-mid-shelf environments swept by strong currents.

Oysters, *Chlamys actinodes*, *Aequipecten paranensis* and *"Turritella* sp." (OCAT) Assemblage

Taphonomic features of species that make up this assemblage are highly variable. Pectinid valves are mostly entire, and interior and exterior valve surfaces show variable degrees of infestation by clionid sponges, naticids (boreholes), and encrusting epibionts (serpulids, solitary corals, barnacles). Oysters are mostly articulated and do not show signs of encrusting or bioerosion. Bryozoan colonies are highly fragmented. In the lower coquinid at Eje Tentativo (Fig. 3) the Assemblage OCAT varies laterally from patches of *C. actinodes* and *O. patagonica,* in life position, to articulated but randomly oriented shells of these taxa, and finally to a highly disarticulated encrusted skeletal accumulation that reveals long residence time on the seafloor before final burial. Soft-bottom infauna include articulated shells as well as disarticulated valves of veneroids.

Modern counterparts of *Chlamys actinodes* and *Aequipecten paranensis* are the pectinids *C. patagonica* and *A. tehuelcha,* taxa widely distributed in the San José and Nuevo Gulfs adjacent to península Valdés (Fig.1), as well as in more open marine environments. In the latter setting, there is no overlap of bathymetric ranges of these taxa: *C. patagonica* occurs in depths ranging from 70 to 185 m, while *A. tehuelcha* lives at depths from 30 to 60 m (Zaixo, 1996). In the more restricted environments of San José Gulf, both species inhabit shell-gravel or firm sandy bottoms in shallower waters than in the open Atlantic, and their bathymetric distribution ranges slightly overlap each other. *Chlamys patagonica* lives at depths from 30 to 90 m and *Aequipecten tehuelcha* from 2 to 60 m. According to Zaixo's data (1996), although *Aequipecten tehuelcha* tolerates low-to-moderate turbidity levels and may inhabit substrates affected by waves of the upper-shoreface zone, the densest populations are found in deeper settings like those of the inner-shelf, where they co-occur with the shallowest settlements of *Chlamys patagonica.* The latter species does not tolerate wave disturbance but prefers the strong currents of tide swept areas, like those at the gulf mouth, where the highest settlements of *Chlamys patagonica* are in patches oriented parallel to the tidal current flow. Taphonomic features of fossil *Aequipecten paranensis* and *Chlamys actinodes,* along with the autoecology of their Recent congeneric species, suggest that this assemblage was indigenous to shell-gravel or firm sandy bottoms swept by tidal currents in shallow inner-to-mid-shelf settings, below fairweather wave base.

Bryozoans, Oysters and "*Turritella*" sp. (BOT) Assemblage

The dominant taxa in this assemblage are encrusting bilaminar cheilostome bryozoans (*Aspidostoma* sp., *Cellepora* sp., and *Sertella* sp. reteporid type). Most of the shell beds are composed of small-to-moderate sized broken bryozoan colonies, sometimes including basal fixation surfaces. Oyster shells are disarticulated but unbroken, and turritelloids are represented by randomly-oriented internal molds.

The Recent bryozoan taxa that inhabit the Argentinian Shelf are probably the same species as the Miocene ones. Their ecological requirements are well known and similar to those of *Chlamys patagonica*; they inhabit firm substrates, fixed to small gravel or dead shells at depths ranging from 15 to 100 m, in offshore areas swept by strong currents but devoid of turbidity and far below fairweather wave base (Lopez Gappa, pers. comm., 1999). Erect colonies have deeper life habitats today on the Burwood Bank (Southern Atlantic Ocean) at 100 to 200 m in areas strongly swept by currents. According to Lopez Gappa (pers. comm., 1999), although bryozoans have not yet been found living in the San José and Nuevo Gulfs of the study area, their ecological requirements are the same as those of the *Chlamys patagonica* community, and they should be associated in the same areas at the gulf mouth where the densest populations of *C. patagonica* are recorded. Thus, autoecological data point to a current-swept inner-to-midshelf environment as the probable setting for Assemblage BOT.

Amusium paris and *Ostrea patagonica* (AO) Assemblage

Three taphofacies are recognized within this assemblage (Table 2): (1) Multi-event, time-averaged accumulations with erosive lower contacts; (2) single-event, time-averaged concentrations; and (3) census assemblages. Single-event and census accumulations form concentrations with no defined lower contacts and consist of the recliner ecophenotype of *O. patagonica* in life position, changing laterally to concentrations of articulated *Amusium paris.* There is no evidence of exhumation; instead, a sudden entombing event is inferred, proceeded by a low-energy hydraulic event that removed *Amusium* from life position but did not affect the heavier oyster shells. Concentrations of this type are fairly common in the San José and Lote 39 sections. At these sites, 3 m of muddy, highly bioturbated strata contain dispersed and randomly oriented articulated shells of *Amusium*, with no exhumation features. The accumulations are inferred to have been originally census assemblages that were later bioturbated. Thin intercalations of Assemblage AO and OS also are common and indicate a lateral transition between the assemblages.

Autoecological references of congeneric Recent species and the paleoecological significance of this assemblage are discussed in the following section (Assemblage AOA and CAF).

Pectinid and Oyster (CAF and AOA) Assemblages

Assemblages AOA and CAF are usually found in vertical succession, but lateral transitions between them also are recorded frequently. Both assemblages have erosive lower contacts, are capped by a pavement of Assemblage OS or GROT, and lie on thin census accumulations of Assemblage MO.

As it is shown in Table 2, Assemblage AOA occurs as two taphofacies: multi-event concentrations (Fig.7) and census accumulations (Fig. 8). The latter accumulations are not common, but a good example occurs to the east of the Lote 39 section. This consists of a thin, muddy, matrix-supported accumulation of *Ostrea patagonica* (bunched ecophenotype) and clumps of *Aequipecten paranensis* and *Pachymagas piramidesia* in life position. This is the only record of *Aequipecten paranensis* clumps with shells in upright-living position, inclined on the right (byssated) valve. Most specimens of *Amusium paris* are articulated and recline on their right valves, but a moderate percentage of shells have been overturned and some are oriented vertically. The muddy matrix is densely penetrated by large-diameter burrows, and bioturbators are considered to have been responsible for overturning the *Amusium* valves.

According to autoecological data of congeneric Recent species, it is inferred that the various pectinid taxa probably differed in ecological requirements. Based on the ecological requirements of Recent *Amusium balloti* and *Amusium japonicum* (Heald and Caputi, 1981; Joll, 1988, 1989), the Miocene *A. paris* probably occupied lower-shoreface-to-inner-shelf sandy bottoms, above or below fairweather wave base, swept only by low or moderately low tidal currents. Recent *Flabellipecten* species are adapted to variable energy, substrata, and depth conditions. Consequently, no paleoecologic inferences can be made with confidence for the fossil taxa. Paleoecologic inferences made by Bernasconi and Robba (1993) on a similar Miocene assemblage from Italy, where *Flabellipecten burdigalensis, Amusium cristatum,* and *Pecten fuchsi* dominate the fossil community, placed this assemblage in a shallow, low-energy, slightly offshore shoal environment, swept by currents and/or influenced by wave action, at approximately 10–12 m water depth (Bernasconi and Robba, 1993, p. 281, 283). This environment is similar to that of modern *Amusium* and is consistent with sedimentologic features of the sequence. The *Amusium paris–Flabellipecten piramidesensis* assemblage also is considered to have inhabited sandy bottoms in shallower environments than *Chlamys actinodes*, either above or just below fairweather wave base, where currents are low to moderate and wave motion is slight, in the lower shoreface-to- inner-shelf zones. According to paleoecological data inferred in this paper (see Assemblage OCAT), *Aequipecten paranensis* was associated with both *Amusium paris* and *Flabellipecten piramidesensis* in shallower waters as well as with *Chlamys actinodes* in deeper ones. Taking into account its stratigraphic succession with Assemblage MO (discussed below), and based on the presence of indigenous material from different substrates, as well as from variable depths and energy conditions, amalgamated deposits of the Assemblage CAF, AOA, and MO are considered as environmentally condensed shell beds whose origins will be fully discussed in the following section.

Monophoraster and Oysters (MO) Assemblage

The MO Assemblage is very common in the Regressive Phase and *Monophoraster darwini* and the recliner ecophenotype *Ostrea patagonica,* occur both separately and intermixed with each other.

Census accumulations consist of hardparts that “float” either in an ochreous, massive, medium-to-fine sandy matrix or in the sandy portions of gray heterolithic beds. They are overlain by a strongly bioturbated *Skolithos* and *Ophiomorpha* Ichnofacies that constitutes the base of the overlying Assemblage CAF-AOA. The echinoid assemblage commonly grades laterally into oyster accumulations in life position. Single-event concentrations can intergrade laterally with the V, AO, and MZ Assemblages. Multi-event concentrations of disarticulated and entire oyster valves and fragmented *M. darwini* infill large erosive tidal channels.

The closest living relatives of *M. darwini* are the mellitid sand dollars (Mooi et al., 2000), which range along the western Atlantic Ocean south to the Río de la Plata (Argentina). Mellitids can be found in dense populations in clean, sandy bottoms in high-energy coastal environments. Species of *Mellita,* in particular, usually occur as densely populated bands approximately 100 m seaward from the wave-breaking zone, in the shoreface zone at depths of up to 10 m (Mooi, pers. com., 1999). Because of their occurrence in a high-energy environment, tests of dead individuals are reworked and usually immediately broken after death, except when rapidly buried by sediment associated with storm events that can rearrange beach topography. The Miocene *Monophoraster* seems to have inhabited environments, and very likely exhibited behaviors, that were similar to those of modern mellitids.

TABLE 2—Taphonomic features of Fossil Assemblages. Stratigraphic distribution: T = Transgressive Phase; MH = Maximum Highstand Phase; R = Regressive Phase; Taphonomic features—ms = matrix-supported; ss = shell-supported; L = low, M = medium; H = high.

				Taphonomic features	
Assemblages	Stratigraphic distribution	Association w/other assemblages	Type of shell—concentrations	Close packing	Fragmentation
OS	T-MH-R	GROT-OCAT-AO-MO-CAF-OMA-MOT-AOA	1—0.1 m census (highly frequent) 2—0.1 m autochthonous single-event, time-averaged 3—0.8 m allochthonous multi-event, time-averaged	1—ms 2—ss 3—ss	1—none 2—L 3—H
GROT	1—T 2—MH-R	OCAT-BOT OS-CAF AOA	1—3 m autochthonous multi-event, time-averaged 2—0.1 m autochthonous single-event, time-averaged (pavements)	1—ss 2—ms	1—none 2—none
OCAT	T-MH	GROT-BOT OS	0.3–0.5 m autochthonous within-habitat, single-event	ss	variable (see text)
BOT	T-MH	OCAT-GROT OS	up to 0.4 m parautochthonous multi-event	ss	see text
AO	T-R	AOA-CAF OS-MO	1—0.1 m census (unfrequent); 2—0.4 m autochthonous single event, within-habitat, time averaged; 3—0.2 multi-event, time-averaged	1—ms 2—ms 3—ms	1—none 2—L 3—L
CAF	R	AO-OS MO-AOA	0.6 m autochthonous multi-event environmentally condensed	ss	none–L
AOA	R	CAF-OS AO-MO	1—3 m autochthonous time-averaged multi-event 2—0,2 m census (unfrequent)	1—ss 2—ms	none
MO	R	1—CAF-OS 2—AO-AOA 3—V-MZ-AOA	1—up to 0.04 m census (highly frequent) 2—0.3 m autochthonous single-event, time-averaged 3—0.3–0.5 m allochthonous multi-event	ms	1—none 2—M 3—H
OMA	R	MO-OS-V	0.3 m allochthonous single-event	ms	variable (see text)
V	R	AO-MO	1—0.2 m census (unfrequent) 2—up to 0.3 m autochthonous single-event	1—ms 2—ss	none–L
MOT	R	OMA-OS-V	0.1 m allochthonous time-averaged	ss	M–H
MZ	R	CAF-V	0.4 m autochthonous multi-event, time-averaged	ss	M–H

Therefore, for *M. darwini,* a shallow and very high-energy environment with strong wave action over clean sandy bottoms is inferred. As this species was only a shallow burrower that feeds on (or just below), the sediment surface, rapid and deep burial of the population by storm sediments would prevent the echinoids from re-attaining the surface. Both extant sand dollars and *M. darwini* almost always occur as monospecific assemblages. The lack of mixing with other species and the preservation in life position, with the oral surface directed downwards, support the idea that populations of *M. darwini* were catastrophically buried. *Monophoraster* co-occurs with oysters only in tidal channel deposits, where both have been reworked post-mortem. The reclining oyster *O. patagonica* apparently lived on sands exposed to less direct wave action and lateral to echinoid habitats.

Oyster, *Monophoraster darwini,* and *Aequipecten paranensis* (OMA) Assemblage

This assemblage constitutes shell beds with erosive lower contacts. Oysters are unbroken but have a high proportion of disarticulated valves; tests of *Monophoraster* are highly fragmented; and pectinid shells are strongly size- and right-left valve sorted, may be entire or fragmented, have eroded margins, and moderate to poorly preserved ornamentation, and are highly bored and infested. This assemblage commonly overlies thin, time-averaged or census assemblages of Assemblage MO and is capped by census concentration of Assemblage OS. According to the life habitats for these taxa (discussed above), Assemblage OMA records accumulations in high-energy shoreface environments where *M. darwini* was probably the only taxon adapted to local conditions. Ecologically disparate forms and different sources of shells, in addition to the large extent of boring, rounding, and fragmentation of shells from different environments and substrata, indicate that these shells largely accumulated out of their habitat after having suffered transport and prolonged exposure on the seafloor.

Veneroid (V) Assemblage

Taxonomic composition and taphonomic features of each shell bed of this assemblage is usually variable (see Table 2 and Appendix 1). This assemblage occurs infrequently in the Regressive Phase at Bajo de Madryn and in those sections east of Puerto Pirámide.The San José section records low-diversity census assemblages "floating" in a gray, very fine sandstone and is composed of clumps of unsorted articulated *P. rostrata mutabile, Mactra* sp., and *P. regularis* in life position. Assemblage V is represented at the Bajo de Madryn section by thin, single-event shell beds with erosive lower contacts that are intercalated with

TABLE 2—Continued

Assemblages	Taphonomic features					
	Abrasion	Disarticulation	Encrusting	Bioerosion	Orientation	Size Sorting
OS	1—none 2—L 3—H	1—art. 2—art./dis. 3—dis.	1—none 2—L 3—H	1—none 2—L 3—H	1—bunched or recliner shells in life position; 2—convex up & down; 3—chatoic	1—L 2—M–H 3—H
GROT	1—none 2—none	1—art./dis. 2—art./dis.	1—none 2—none	1—none 2—none	1—chaotic 2—concordant	L
OCAT	L	art./dis. pectinids; art. oysters & veneroids	see text	see text	pectinids & oyster stacked or chaotic	M
BOT	see text	see text	none	none	chaotic	
AO	none	1—art. 2—dis. 3—dis.	1—none 2—none 3—M	none	1—life position 2–3 stacked *Amusium* & concordant oysters	L
CAF	M	dis. pectinids & osyters; art. veneroids	H	H	stacked pectinids; convex up & down oysters; chaotic brachiopods & veneroids	H
AOA	none–L	1—dis./art. 2—art.	none–L	none–L	1—chaotic or stacked 2—life position	L–M
MO	1—none 2—M 3—H	3—dis. oysters	none	none	1—life position w/aboral side up 2—chaotic 3—chaotic	1—L 2—M–H 3—H
OMA	see text	see text	see text	see text	chaotic	H
V	none–L	1—art 2—dis	none	none	1—clumps in life position 2—chaotic or imbricated	1—L 2—H
MOT	M	dis	M–H	M–H	chaotic	H
MZ	M–H	dis	M	M	chaotic	M–H

time–averaged, highly fragmented accumulations of Assemblage MO. These concentrations exhibit a well-ordered, oblique fabric of sorted, entire, and disarticulated right valves of *P. rostrata mutabile and D. meridionalis* (Fig.9). Other types of shell beds are constituted by a highly diverse assemblages where almost all veneroids and arcoids species are present (Puerto Piramide's section).

According to ecological data obtained from congeneric species living in the area (*P. rostrata, Amiantis purpuratus*) and closest relatives (*Chionopsis, Dosinia, Panopea)*, this fossil assemblage is inferred to have inhabited soft substrates in intertidal to shoreface settings (Villaverde et al., 1974; Zaixo, 1975; Escofet et al., 1978; Abbott and Dance, 1986).

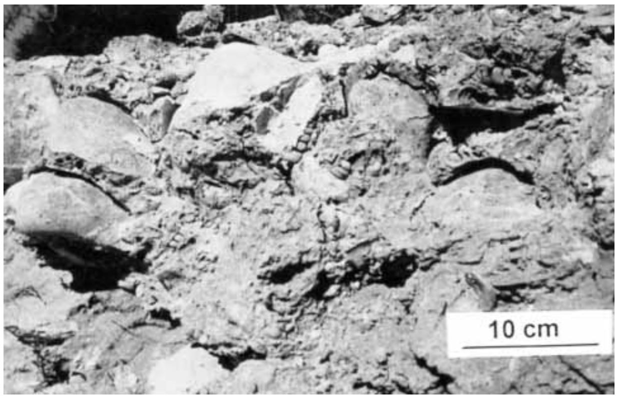

FIGURE 6—Assemblage GROT at El Doradillo, dominated by disarticulated valves of *Glycymerita magna* and *Ostrea patagonica* and turritelloid molds.

Trophon laciniatus, Mytilus trigonus and Oysters (MOT) Assemblage

The Recent closest relatives from the study area, *Epitonium orbigny, Mytilus edulis,* and *Trophon geversianus,* inhabit hard–bottom settings ranging from intertidal to shoreface zones, but are most abundant in intertidal environments (Olivier et al., 1966; Zaixo, 1975).

Mixed (MZ) Assemblage

Mixed assemblages are those characterized by representatives from more than one of the assemblage defined above. Taphonomic features of these accumulations indicate that fossils were transported from different substrates and depths, and later accumulated out of their original life habitat resulting in the admixtures of different ecological forms. These concentrations commonly infill large erosive tidal channels and also make up the complex

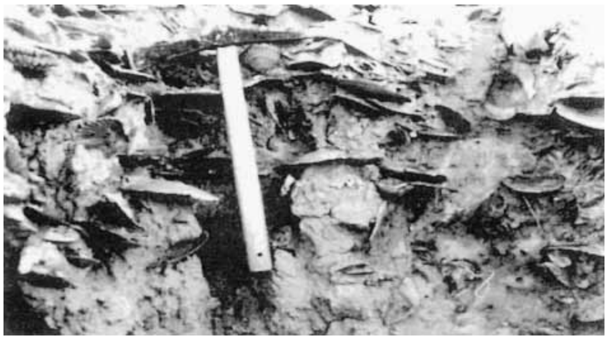

FIGURE 7—Time-averaged accumulation of Assemblage AOA, showing entire, and disarticulated valves of *Amusium paris, Aequipecten paranenis,* and *Ostrea patagonica* at Eje Tentativo Ob.

shell beds at top of the study sequence (sections San José, Lote 39, Puerto Pirámide).

ASSEMBLAGE ASSOCIATIONS AND GENERAL SEDIMENTARY ENVIRONMENTS

Q-Mode Cluster analysis (Manhattan distance, UPGMA figured, but with minor differences applying Euclidean, Squared Euclidean distances indexes, and complete, simple and WPGMA linkages) (Fig.10), based on relative frequencies of species, defines three main groups of assemblages: (1) OCAT and GROT; (2) V and MZ; and (3) BOT, OS, AO, MO, OMA, AOA, and MOT. In this latter group, assemblages OS, AO, and MO are closely tied together and are more related to BOT than the remaining assemblages. This group reflects the large influence of oysters, which strongly influence the clustering of Assemblage AO, OS, and MO. A distinctive lateral and vertical transition between assemblages MO and OS also occurs in several sections (Fig. 3). Assemblage CAF, with a low similarity value, clusters with the first two groups defined above, probably due to the presence of the same pectinid species that constitute CAF and the remaining assemblages.

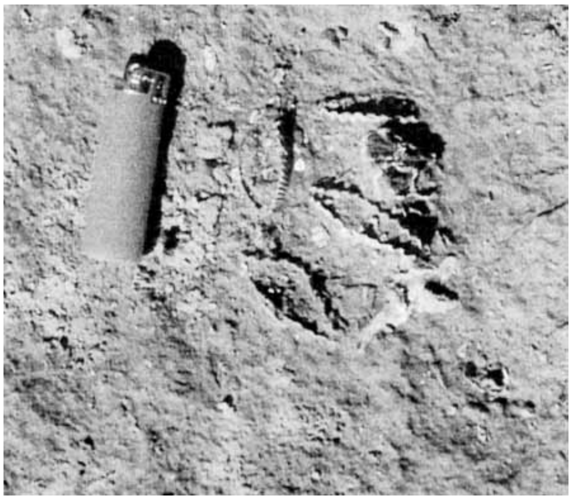

FIGURE 8—Cluster of vertically-oriented, articulated *Aequipecten paranensis* in life-position, representing accumulation of Assemblage AOA at the Regressive Phase, near Lote 39.

FIGURE 9—Single-event, time-averaged accumulation of hydraulically-oriented, disarticulated valves of *Pitaria mutabile* of Assemblage V at Bajo de Madryn.

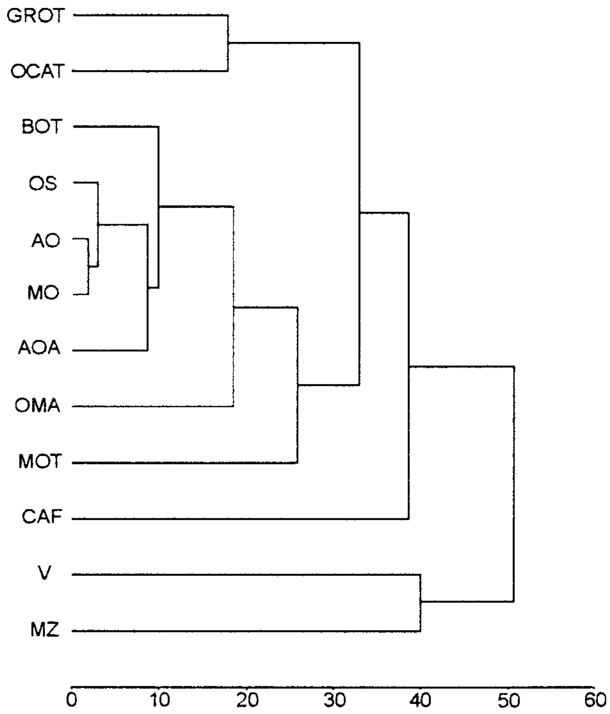

FIGURE 10—Dendogram illustrating association of assemblages based on cluster analysis (UPGMA) using Manhattan Distance indexes (data matrix in Table 1).

The results from cluster analysis, along with the vertical and lateral relations observed among assemblages in outcrops (Fig. 3), are used to define three assemblage associations. Association A is composed exclusively of GROT, OCAT, BOT, and OS Assemblages. It is restricted to the lowermost 30 m of the sequence (Fig. 3) and is present in the Transgressive Phase of most analyzed sections (although it is not clearly identified in the Bajo de Madryn section where only thin accumulations of Assemblage GROT were recognized). Association A is composed of amalgamated, indigenous fossiliferous accumulations with a distinct, complex internal stratigraphy of successive assemblages.

Association B is only recorded in sections east of El Doradillo and is characterized by vertical succession of recurrent census concentrations of: (1) Assemblages MO and OS; overlain by (2) autochthonous-parautochthonous, environmentally condensed accumulations of Assemblages AOA, CAF, AO, and OS; and capped by (3) a thin pavement of Assemblage GROT.

Association C is made up by the cluster of OMA, MOT, V, and MZ, with a minor participation of Assemblages OS and MO. These assemblages occur individually in thin, concentrations that "float" in barren intervals, or in thin single-event shell beds with erosive lower contacts, or constitute large tidal-channel infillings where shells are pervasively broken. An exception to this is the appearance of the MZ Assemblage at the top of the complex shell beds that tops Cycle III of the Regressive Phase (see below). With the exception of a census accumulation of Assemblage V at the San José section, shells in Association C show evidence of transport out of the original life habitat and long exposure times on seafloor before burial. Association C constitutes the only fossil assemblages recovered from exposures west of El Doradillo, where the study sequence consists of the shallowest marine lithofacies recorded in the basin.

RECONSTRUCTION OF THE MIOCENE LIVING ASSEMBLAGES

Base on (1) the dominance of exceptionally well preserved, time-averaged, within-habitat accumulations (indigenous material), (2) the accurate paleoecologic data provide by autoecological comparison with Recent relatives, many of which inhabit the modern Patagonian littoral zone, and (3) the integration of sedimentologic and paleoecological inferences, the shelly benthic communities that inhabited the study area during Miocene times can be reconstructed with high confidence (Fig. 11).

Shell-gravel substrates from inner-to-mid-shelf settings, placed below the fairweather wave base but swept by strong tidal currents, would have been the proper environments for the settlement of the suspension-feeders *Chlamys actinodes, Glycymerita magna, Aequipecten paranensis, Retrotapes ninfasiensis,* and bunched oysters. These species were probably the dominant shell-producing epifaunal and semi-infaunal dwellers. In similar water depths but in a lower-energy environment, settlement of erect bryozoan colonies took place. The taxonomic composition of these living assemblages is partially coincident with that of the fossil assemblages BOT, OCAT, and GROT and, in this way, Association A undoubtedly represents an inner- to mid-shelf assemblage characteristic of relatively high energy and clear water conditions.

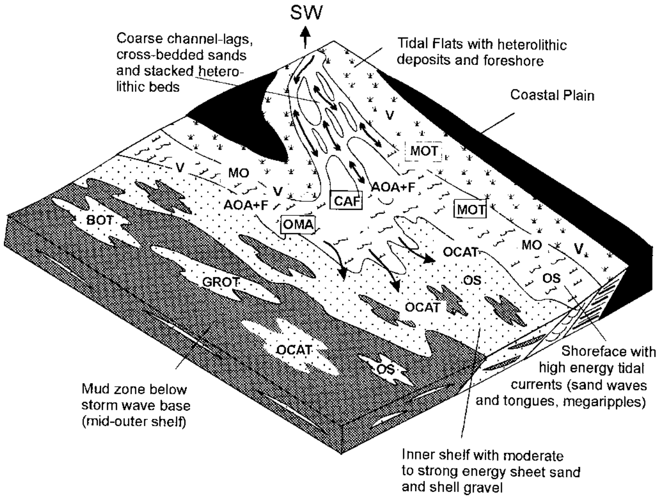

FIGURE 11—Reconstruction of spatial distribution of benthic assemblages in the Miocene Puerto Madryn Formation. Fossil assemblages BOT, GROT, OCAT, MO, AOA, and V are coincident with living communities and are bathymetrically placed where they actually lived. Assemblages CAF, MOT and OMA do not represent living assemblages and are plotted in settings where they accumulated; CAF is an environmental assemblage that involved taxa from mid-inner shelf settings (*Chlamys actinodes*), and *Flabellipecten piramidesensis* from shoreface environments (see text); OMA and MOT are allochthonous assemblages; AOA + F = living *Flabellipecten piramidesensis* associated with *Amusium paris, Ostrea patagonica,* and *Aequipecten paranensis* and forming part of a same living community. Enviromental diagram modified from Levell (1980), and Johnson and Baldwin (1996).

In shallower environments of the shoreface and inner-shelf close to fairweather wave base, the suspension-feeders *Ostrea patagonica, Aequipecten paranensis, Amusium paris,* and *Flabellipecten piramidesensis* dominated benthic communities in soft sandy or muddy bottoms affected only by weak tidal currents and wave motion. Species of *Ostrea, Amusium,* and *Aequipecten* constituted a living association similar to that of the fossil AOA and AO Assemblages. *Flabellipecten* is recovered from the condensed CAF Assemblage that does not represent any single living community. Instead, taxa from very different bathymetric settings co-occur.

Clean sandy soft bottoms from upper-shoreface settings, situated just seaward of the breaking wave zone, were inhabited by a low-diversity assemblage dominated by the vagile deposit feeder *Monophoraster darwini* and the reclining suspension feeder *Ostrea patagonica.* This coincides with the fossil MO Assemblage.

Foreshore and upper-shoreface settings were inhabited by shallow and deep infaunal suspension feeders (veneroids) in soft sandy seafloors, while vagile carnivorous gastropods (*Epitonium borcherti, Trophon laciniatus)* and sessile suspension feeders (*Mytilus trigonus)* settled down on locally firm substrates. The veneroids living association is represented by the fossil Assemblage V. The remaining taxa are recovered from the fossil allochthonous assemblages MOT, OMA, and MZ.

Aequipecten paranensis and the various oysters, which are the most common taxa in the Puerto Madryn fauna,

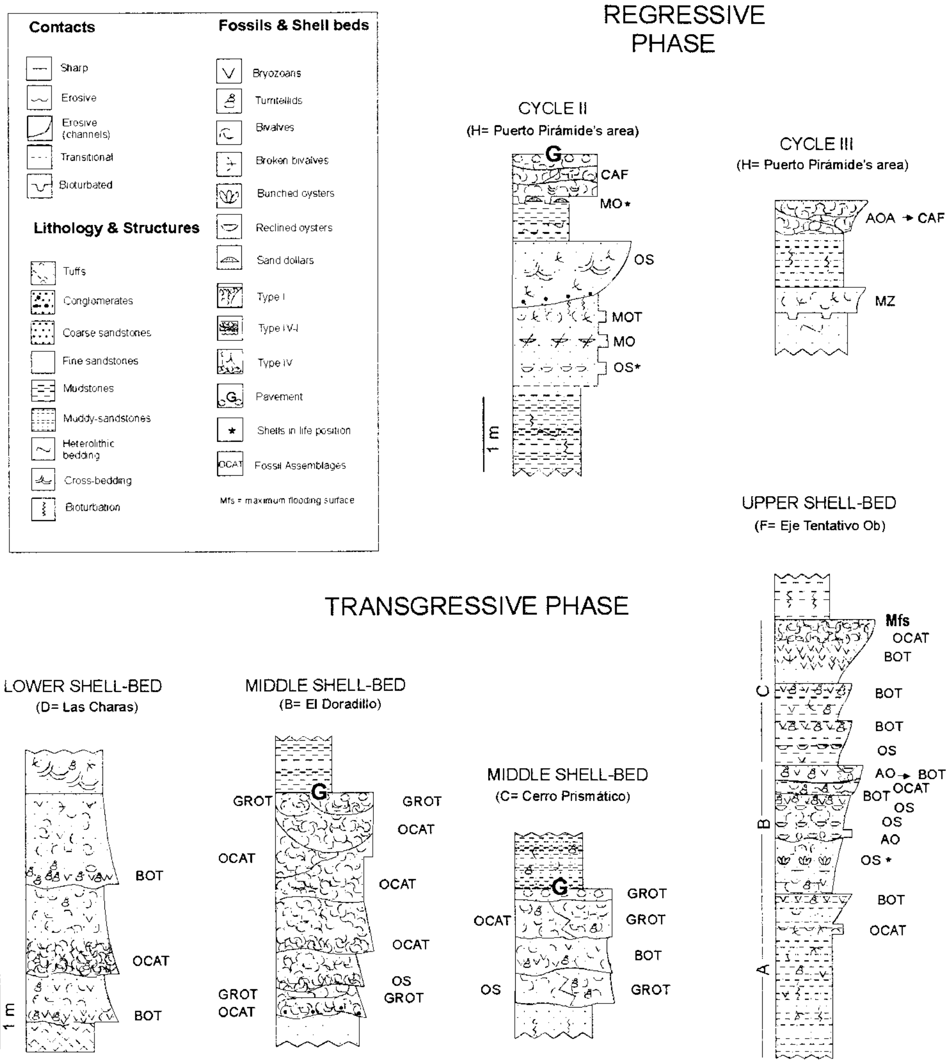

FIGURE 12—Schematic stratigraphic columns showing detailed taphonomic aspects and vertical distribution of assemblages in the Lower shell bed, Middle shell bed, and Upper shell bed of the Transgressive Phase and cycles of the Regressive Phase.

are present in almost all assemblages. Taking into account the ecology of their closest living relatives, these Miocene taxa were probably associated with fossil accumulations deposited in a wide depth range and energy conditions within the shoreface and inner shelf (i.e., they were eurytopes).

TAPHONOMY AND STRATIGRAPHY OF SHELL BEDS

According to Kidwell's terminology (1986), and reflecting changes in net sedimentation/shell input rate, complex shell beds in the Puerto Madryn Formation are of three types: (1) Type I shell beds, which display an upwards increase in shell-packing density and terminate in an omission (non-erosional) bedding surface; (2) Type IV shell beds, which have a sharp erosive lower contact and grade upwards from shell-supported to matrix-supported fabric; and (3) composite Type IV-I shell beds with both lower and upper sharp contacts and with internal discontinuities usually well developed.

Transgressive and Maximum Highstand Phases

The Transgressive Phase comprises three main complex shell beds: these are labeled the lower [LSB], middle [MSB], and upper [USB] shell beds in Figure 3. Each records a vertical recurrence of assemblages BOT, OCAT, OS, and GROT (Association A), with a slight upsection increase in the importance of Assemblage AO and a gradual disappearance of Assemblage GROT. Detailed internal discontinuities and fossil assemblage distribution are illustrated in Figure 12.

The Lower shell bed [LSB] directly overlies the "Patagonian beds." The top of the "Patagonian beds" is oxidized, enriched in phosphates, and bears the *Glossifungites* ichnoassemblage. The thickness of the LSB varies from a 3 m thick, slightly amalgamated, multi-event Type IV shell bed at Las Charas (Fig. 13) to a 0.3- m- thick, strongly amalgamated, composite Type IV-I shell bed at Eje Tentativo Ob and El Doradillo. At these two localities, the LSB also bears phosphatic concretions, marine mammal remains, shark teeth, regular echinoids spines, intraclasts

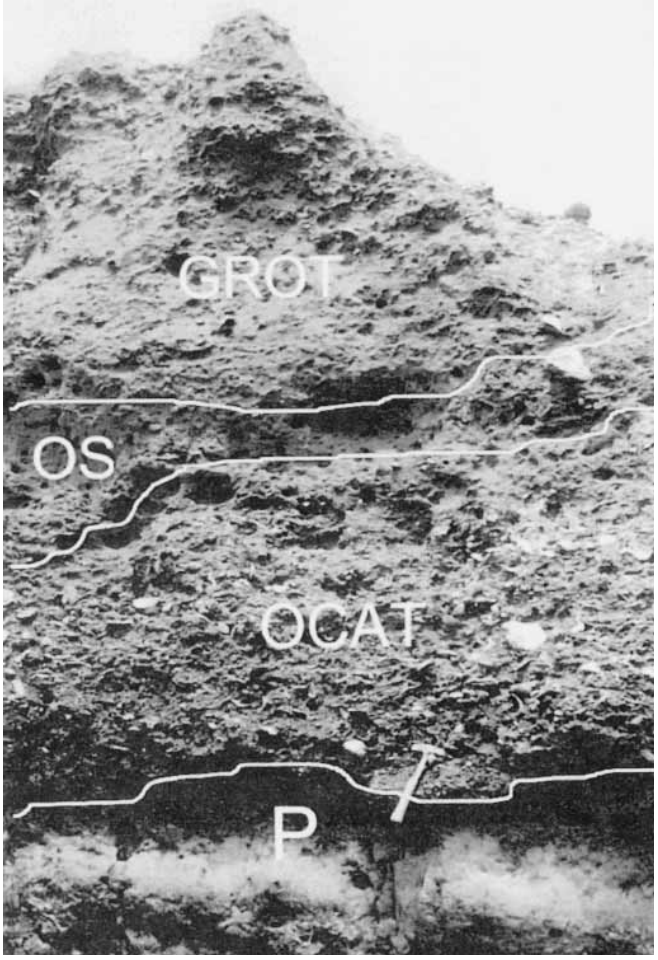

FIGURE 13—Lower complex shell bed of the Transgressive Phase at Las Charas, showing two Type IV shell beds with erosive lower and transitional upper contacts, yielding time-averaged, within-habitat and shell-supported accumulations of assemblage OCAT, GROT, and OS. The shell beds are underlain by the ''Patagonian beds.''

FIGURE 14—Lower Type IV shell bed (LSB) and Middle composite Type IV-I shell bed (MSB). P = ''Patagonian'' beds.

and terrigenous gravels. The LSB is overlain by 5 m of unfossiliferous ochreous, cross-bedded sandstones, or massive highly bioturbated silty sandstones from shoreface to inner-shelf settings.

The Middle shell bed [MSB] (Figs. 12, 14) is a 3-m-thick, highly-amalgamated composite Type IV-I fossiliferous unit that can be correlated over 30 km, and terminates in a pavement of Assemblage GROT. The LSB and MSB are both multi-event, time-averaged, shell-supported accumulations and their taphonomic features are those described for Assemblage OCAT, GROT, and BOT, indicating long time exposure on the seafloor with negligible transport of shells out of habitat.

The Upper shell bed [USB] is a major Type I shell bed. It is 12 meters thick and made up of at least three subsidary Type I shell beds (A, B and C in Figs. 12, 15). It also includes many interbedded simple shell beds. The base of the USB is gradational and rests on heterolithic, highly bioturbated muddy sandstones, massive sandy mudstones, and laminated mudstones from inner-shelf environments, with isolated and fragmented valves that gradually increase upwards. The USB exhibits an overall up-section increase in the stratigraphic close-spacing of simple shell-beds (increase in their degree of amalgamation, shell-packing, and the thickness of densely fossiliferous component intervals). The upper contact of the USB has been correlated over 35 km and is overlain by 13 m of laminated and highly bioturbated mudstone rich in radiolaria and diatoms and exhibiting the *Cruziana* Ichnofacies. These capping mudstones are especially well exposed in the Puerto Pirámide and Eje Tentativo areas (Fig.16), and record the maximum depth attained by the sea in the study area.

Each subsidary Type I shell bed within the USB grades upwards from a bioturbated muddy sandstone or sandy mudstone wherein shells are matrix-supported, to a less muddy shell-supported interval. Shells within matrix-supported intervals may be evenly dispersed or concentrated in thin single-event or multi-event shell beds. The single-event shell beds commonly represent census assemblages of Assemblages OS and AO, whereas the multi-event ones are constituted by Assemblage AO with erosive lower contacts and no internal discontinuities. Stratigraphy and taphonomic features of assemblages of the shell-supported and matrix-supported intervals of subsidary Type I shell beds are illustrated in Figure 12 and summarized in Table 2.

FIGURE 15—Major Type I, Upper shell beds at Eje Tentativo Ob, showing subsidary ''A,'' ''B,'' and ''C'' Type I shell beds. Overlying the maximum flooding surface (mfs) there are bioturbated and laminated mudstones recording the deepest depth attained by the Miocene sea. The mfs extends for 35 km and is recorded at the base of the section illustrated in Figure 16.

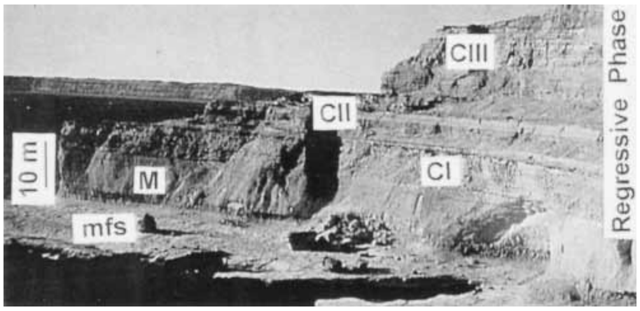

FIGURE 16—Regressive Phase of the Puerto Madryn Formation in Puerto Pirámide's area. mfs = maximum flooding surface. Overlying mudstones (M) correspond to the deepest deposits recorded. C = upward-deepening sedimentary cycles represented by sandbars deposits. Prominent layers at the top of each cycle represent environmentally condensed shell beds that cap the sandbars.

Regressive Phase

The Regressive Phase consists of a 45-m-thick interval of intercalated gray and bluish massive or cross-stratified sandstones, whitish massive pyroclastic horizons, sandy or muddy heterolithic beds, and densely fossiliferous accumulations. One of the most conspicuous features of this phase is the development of large channels infilled with thin, single-event hardpart accumulations, and the presence of three sedimentary cycles (CI, CII, and CIII in Figs. 3, 16).

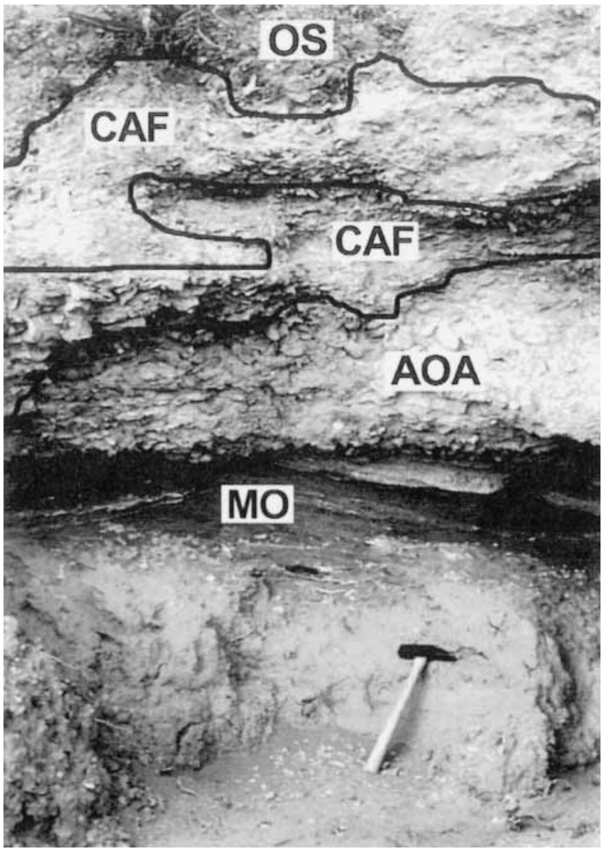

FIGURE 17—Environmentally condensed Type IV-I shell bed deposited in upper shoreface (MO: census assemblage of *Monophoraster darwini* and *Ostrea patagonica*), lower shoreface (Assemblage AOA), to inner-shelf environments (Assemblage CAF) capping upward-deepening Cycle I in Salina Grande. Shoreface sandbar deposits underlying the shell bed.

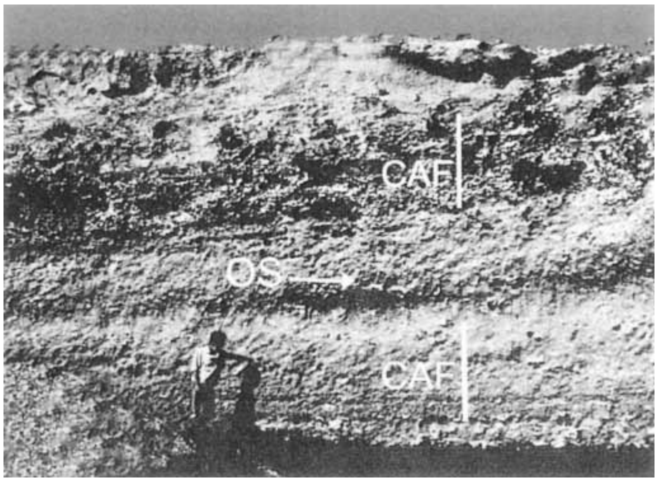

FIGURE 18—Exceptionally thick example of multi-event shell bed at the top of Cycle II at San José section.

Lenticular sandstones, shell beds, and conglomerate bodies up to 6 m thick, persist laterally for hundreds of meters in outcrops and have strongly erosive lower and planar upper contacts. Sandy shell beds are cross-stratified and contain allochthonous, multi-event, shell-supported accumulations. They represent large tidal-channel deposits and yield Assemblage OMA, OS, and MZ. Accumulations mainly consist of shell hash or highly fragmented and abraded valves of pectinids, oysters, veneroids, gastropods, bryozoan colonies, and tests of *Monophoraster*, but accumulations composed exclusively of entire and disarticulated valves of oysters are also common.

Each of the three sedimentary cycles is composed of up to 15 m of heterolithic deposits or massive bioturbated muddy or sandy strata (Fig. 12). Thin, time-averaged accumulations of Assemblage MO, AO, and MOT, as well as census concentrations of *Cyrtopleura lanceolata* in life position, are recorded from these heterolithic strata, which are otherwise barren. The upper part of each cycle is bioturbated and the top is a strongly bioturbated surface dominated by *Skolithos* and *Ophiomorpha* that can be correlated over 30 km. Beneath each of these surfaces, in CI and CII, and sometimes disrupted by bioturbators, is a thin census assemblage of *Monophoraster darwini* in life position (Assemblage MO). Each bioturbated surface is overlain by a 0.3-to-0.8-m-thick, multi-event, strongly amalgamated and shell-supported (30% sedimentary matrix) Type IV-I shell bed (Fig.17). These have lower erosive and upper planar contacts and yield Assemblage AOA and CAF, and less frequently Assemblage OMA. Each of these shell-beds is capped by a pavement of Assemblage GROT, although pavements of *Dosinia meridionalis* or *Monophoraster darwini* are frequent in the Punta Pirámide and San José sections. An exceptionally thick, multi-event and slightly amalgamated shell bed caps the Cycle II at the San José section (Fig. 18).

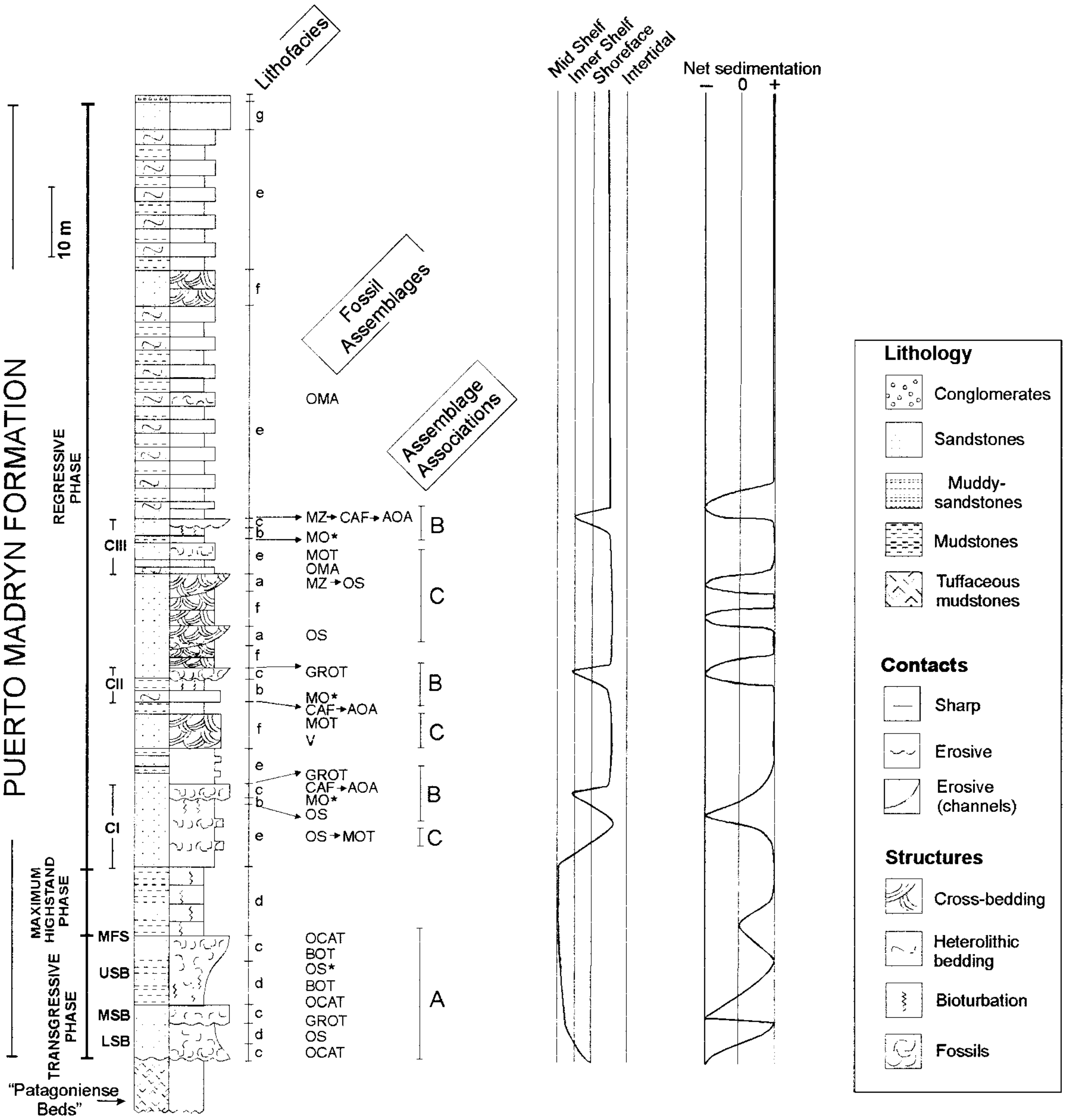

FIGURE 19—Record of water depth deposition and changes in net sedimentation of the Miocene sequence related to lithofacies and fossil assemblages. Lithofacies code as in Figure 2; Association A recovered from storm shell beds, deposited in mid-and inner- shelf environments (*autochthonous time-averaged assemblages*); Association B recovered from the top of shoreface sandbars; records deepening in water-depth from upper shoreface settings to lower shoreface and inner shelf environments (census assemblages and environmentally condensed shell-beds); Association C recovered from upper shoreface tidal channels (census and allochthonous assemblages).

History of Dynamic Accumulation

The contact of the Lower shell bed with the "Patagoniense" beds is considered a coplanar transgressive-ravinement and subaerial unconformity surface (Scasso et al., 1999b). In measured sections, to the west and southwest, the characteristics of the Lower shell-bed match that of a lag-concentration coquina of Banerjee and Kidwell (1991), showing laterally discrete lens geometry and evidence of exhumation and shoreface erosion. Dense hardpart concentrations that characterize the Lower and Middle shell beds mostly correspond to within-habitat, time-averaged assemblages accumulated under omission conditions. Taphonomic features, including the internal stratigraphy of the shell beds, indicate omission was caused by conditions of dynamic bypass with alternating periods of deposition and erosional events, promoted by frequent storm-wave reworking and strong tidal currents. The presence of minor internal discontinuities, relative abundance of shell-gravel taxa, considerable high post-mortem damage of valves by encruster and borer epibionts, disarticulation of shells, lack of size, and right/left valve sorting, and low degree of fragmentation all point to a concentration of indigenous taxa of successive assemblages that might have been exposed on the seafloor during ecologically prolonged periods of non-deposition. Omission conditions were probably interrupted by short aggradational intervals that entombed shell-gravel taxa and allowed colonization by soft-bottom shallow and deep burrowers (*Dosinia meridionalis* and *Panopea regularis* among others). Erosional deep reworking events and winnowing of sedimentary matrix amalgamated a mosaic of different assemblages indigenous to the area, leading to a vertical admixture of shell-gravel and soft-bottom dwellers and to densely packed shell beds with internal discontinuities. Owing to the high percentage of articulated shells of *Glycymerita magna* and *Eurhomalea ninfasiensis*, depositional events might have been rapid, causing an immediate burial of shells. Otherwise, those taxa should have disarticulated rapidly in these areas strongly swept by tidal currents.

The Upper shell bed, situated immediately below Maximum Highstand deposits, reflects lower-energy conditions characterized by alternating aggradation and omission (Pathway 2 of Kidwell and Jablonski, 1983). The highly bioturbated muddy sandstone intervals accumulated during dominant depositional intervals, which were interrupted by brief omissional intervals during which thin census and thicker multi-event Assemblages AO and OS accumulated. Taphonomic features of census assemblages reflect no evidence of post-mortem infestation and suggest only brief periods of post-mortem residence on the seafloor and rapid burial that isolated the assemblage from subsequent bioturbation or hydraulic reworking. Multi-event accumulations suggest alternation of brief periods of deposition and longer intervals of non-deposition that allowed repeated colonization of the soft-bottom reclining *Ostrea* sp. and *Amusium paris* assemblage. Weak hydraulic events winnowed the matrix but accomplished little movement or disarticulation of *Amusium*.

Based upon data, a gradual upwards change from aggradation to predominantly non-deposition is believed to be the responsible for the generation of the densely packed parautochthonous-autochthonous multi-event accumulations at the top of each subsidary Type I shell bed within the Upper shell-bed. Omission intervals are more frequent and more prolonged towards the top of the main complex shell bed. It is suggested that omission was caused by complete bypassing and sediment starvation, based on the absence of internal discontinuity surfaces, low degree and local absence of amalgamation, lack of vertical admixture of successive assemblages, dominance of shell-gravel taxa, complete absence of soft-bottom burrowers, well-preserved ornamentation but total disarticulation of shells, and the high degree of post-mortem infestation by borers and especially by encrusting bryozoan colonies (*Membranipora* sp. on turritellids).

During accumulation of the Transgressive and Maximum Highstand phases, the paleogeography of the area probably was open to the Atlantic Ocean. Although these deposits represents the greatest water depths for the entire formation (mudstones below storm-wave base), depositional environments largely remained in an inner-shelf affected by strong tides, as well as by fairweather and storm waves. Recorded assemblages inhabited firm gravel or sandy substrata in areas swept by strong currents, probably situated laterally or distally to the mouth of large tidal channels, in inner-to-mid-shelf environments, above the storm-wave base. Sand ridges and shoals reworked during a transgression by tidal currents or waves (Rine et al., 1986; Penland et al., 1986) can be modern environmental analogues for the accumulation of this part of the section.

Agraddational intervals represented by scarcely disturbed hardparts or simple census shell- beds, as well as sedimentary matrix of fossil accumulations at the top of each subsidary Type I sell.beds, record deposition in lower energy and deeper enviroments towards the top of this lowest section. High rates of transgression with rapid deepening and/or reworking of shelf deposits into sand ridges reflect an accomodation/supply ratio > 1 (e.g., Swift et al., 1991).

Deposition of the Regressive Phase was strongly influenced by tidal regimes and it reflects a more closed environment. According to paleocurrent data (Scasso and del Río, 1987), sediment transport was mainly along a large embayment oriented NE-SW. The fauna indicates normal marine conditions, and no definitive evidence of brackish or fresh water (fluvial) deposits have been found in the Península Valdés area, although important channel incision is evident to the southwest. Cross-bedded sandstones, together with gravel and broken-shell coquina lags, are frequent there and were interpreted as the deposits of large tidal channels (Scasso and del Río, 1987). At the SW part of the embayment they are associated with stacked sets of inclined heterolithic stratification, which are typical of estuarine incised channels (e.g., Eberth, 1996).

To the NE, the heterolithic deposits of the Regressive Phase are intercalated with mud-draped cross-bedded sands and shell beds and constitute Cycles I, II, and III. These deposits are interpreted to be tidal bars and “sand tongues” (fan-shaped sandbars that run parallel to tidal channels and normal to the coast similar to those described in Nordergründe area, southward of the Elbe estuary—see Reineck and Singh, 1980) deposited in environments alternately dominated by tidal currents or waves. Wave action is evident in the form of wave-ripple bedding within heterolithic beds, and bioturbation is low (compare with Davis and Flemming, 1995). These sand bodies are often capped by shell-rich beds (cf. Hertweck, 1998). During formation of sandbars, short omission events are inferred due to the presence of census Assemblages MO, or by single-event, time-averaged concentrations of Assemblage AO, after which of deposition suddenly resumed. The top of sandbars record a definite change from positive values of net sedimentation towards dominant omission conditions. Bar tops are defined by the last accumulation of *Monophoraster darwini* in life position in highly turbulent environment, placed very close to the breaker zone. A short and catastophic depositional event, probably promoted by storms, accumulated a thick sedimentary increment leading to sudden entombment of the echinoids. Following the burial of this community, omission conditions are indicated by the activity of soft bottom-dwellers that bioturbated the entombing sediment resulting in *Skolithos* and *Ophiomorpha* ichnofabrics. Subsequent deepening and prolonged omission are recorded. Once appropriate depths were attained, *Amusium paris*, *Flabelllipecten piramidesensis*, and *Aequipecten paranensis* colonized shoreface soft-sandy bottoms, situated close to fairweather wave base and often swept by weak currents or waves. Continuous deepening allowed the settlement of *C. actinodes* in lower inner shelf gravel-substrata swept by strong tidal currents, situated well below wave base. Omissional phases often were interrupted by deposition of thick increments of sediments that allowed deep and shallow infaunal soft-bottom dwellers to colonize the seafloor. Occasionally, strong erosional storm events promoted amalgamation and vertical admixture of successive soft and gravel-substrata assemblages, as well as the winnowing of matrix leading to strongly amalgamated shell beds. However, this reworking apparently was limited in effect, because most of the deep burrowers are preserved articulated.

Each of the cycles records an upwards deepening from restricted upper shoreface (sandbars) to inner-shelf environments. The complex Type IV-I shell beds that cap each cycle appear to be environmentally condensed accumulations that represent flooding surfaces and prolongedphases of non-deposition. Whether these water-depth fluctuations were caused by autocyclic (channel and sand tongue lateral shifting) or allocyclic (sea-level fluctuations) mechanisms remains uncertain, but the general style of accumulation is regressive-progradational, probably with expanded offlapping parasequences (sensu Embry, 1995) reflecting accomodation/supply ratio $<<<1$.

Figure 19 summarizes the history of the accumulation of the sequence, the environmental variation during deposition, and the resulting changes in living benthic faunas represented by the fossil assemblages.

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APPENDIX 1

Relative abundance of species composition of the study shell-beds of the Miocene Puerto Madryn Formation. D = Dominant (> 50%); A = abundant (25%–50%); C = common (25–5%); R = rare (<5%). (A1,C3b = stratigraphic beds in sections as illustrated in Figure 3)

	RELATIVE ABUNDANCE OF SPECIES																		
SHELL-BEDS	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	B1	B2a	B2b	B3	B4	B5	B6
FOSSIL ASSEMBLAGES	GROT	OS	MZ	V	OS	V	OMA	MZ	MZ	OMA	V	OS	OCAT	OCAT	GROT	GROT	OS	OCAT	OCAT
Bryozoans	R		C					C	C				R	R	R	R		R	R
"*Turritella*" sp.	R		C				R	C	C	R			C	C	C	C		C	C
Retrotapes ninfasiensis	A														A	A			
Glycymerita magna	D														D	D			
Ostrea alvarezi	C	A	C		C			C	C			C	C	C	C	C	C	C	C
Ostrea patagonica	C	D	C		D		C	C	C	C		D	C	C	C	C	D	C	C
Chlamys actinodes													D	D				D	D
Aequipecten paranensis			C				A	C	C	A			A	A				A	A
Amusium paris																			
Flabellipecten piramidesensis																			
Chesapecten crassus																			
Monophoraster darwini			C				A	C	C	A									
Ameghinomya argentina			C					C	C				R	R				R	R
Ameghinomya meriodionalis				C		C					C								
Pachymagas piramidesia			C					C	C				C	C				C	C
Panopea regularis	C												R	R	R	C		R	R
Pteromyrtea danieli							R			R									
Purpurocardia leonensis													R	R	R	R		R	R
Dosinia meridionalis	C		C	C		C		C	C		C		R	R	R	R		R	R
Dosinia elsai																			
Pitaria ninfasiensis			C			C		C	C		C								
Pitaria trigonus			C	C		C		C	C		C								
Anomalocardia entrerriana			C			C		C	C		C								
Chionopsis australis			C			C		C	C		C								
Mactra sp.			C	C				C	C										
Dinocardium novus																			
Cyrtopleura lanceolata																			
Anadara lirata			R					R	R										
Trophon laciniatus			C				R	C	C	R			R	R				R	R
Mytilus trigonus			R					R	R										
Epitonium borcherti																			
Calliostoma spp.																			

APPENDIX 1

Continued.

	RELATIVE ABUNDANCE OF SPECIES																		
SHELL-BEDS	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	B18	B19	B20	B21	C1a	C1b	C2	C3a
FOSSIL ASSEMBLAGES	OCAT	GROT	GROT	MO	OS	OS	GROT	MO	MO	OMA	OMA	MO	OMA	OMA	GROT	OS	GROT	BOT	OCAT
Bryozoans	R	R	R				R										R	D	R
"*Turritella*" sp.	C	C	C				C			R	R		R	R			C	A	C
Retrotapes ninfasiensis		A	A				A								R		A		
Glycymerita magna		D	D				D								D		D		
Ostrea alvarezi	C	C	C		C	C	C									C	C	C	C
Ostrea patagonica	C	C	C	D	D	D	C	D	D	C	C	D	C	C		D	C	R	C
Chlamys actinodes	D																		D
Aequipecten paranensis	A									A	A		A	A					A
Amusium paris																			
Flabellipecten piramidesensis																			
Chesapecten crassus								D	D										
Monophoraster darwini				D						A	A	D	A	A					
Ameghinomya argentina	R																		R
Ameghinomya meridionalis																			
Pachymagas piramidesia	C																		C
Panopea regularis	R	R	R				R								C		R		R
Pteromyrtea danieli										R	R		R	R					
Purpurocardia leonensis	R	R	R				R								C		R		R
Dosinia meriodionalis	R	R	R				R								C		R		R
Dosinia elsai																			
Pitaria ninfasiensis																			
Pitaria trigonus																			
Anomalocardia entrerriana																			
Chionopsis australis																			
Mactra sp.																			
Dinocardium novus																			
Cyrtopleura lanceolata																			
Anadara lirata																			
Trophon laciniatus	R									R	R		R	R					R
Mytilus trigonus																			
Epitonium borcherti																			
Calliostoma spp.																			

APPENDIX 1

Continued.

	RELATIVE ABUNDANCE OF SPECIES																		
SHELL-BEDS	C3b	C5	C6	C7	C8	C9	D1	D2	D3	D4	D5	D6	D7	E1	E2	E3	E4	E5	E6
FOSSIL ASSEMBLAGES	OCAT	BOT	GROT	MOT	MOT	MZ	BOT	OCAT	BOT	OCAT	OCAT	OCAT	OCAT	BOT	OCAT	OCAT	GROT	BOT	OCAT
Bryozoans	R	D	R			C	D	R	D	R	R	R	R	D	R	R		D	R
"*Turritella*" sp.	C	A	C	R	R	C	A	C	A	C	C	C	C	A	C	C		A	C
Retrotapes ninfasiensis			A														C		
Glycymerita magna			D														D		
Ostrea alvarezi	C	C	C	D	D	C	C	C	C	C	C	C	C	C	C	C		C	C
Ostrea patagonica	C	R	C			C	R	C	R	C	C	C	C	R	C	C		R	C
Chlamys actinodes	D							D		D	D	D	D		D	D			D
Aequipecten paranensis	A			R	R	C		A		A	A	A	A		A	A			A
Amusium paris																			
Flabellipecten piramidesensis																			
Chesapecten crassus																			
Monophoraster darwini				R	R	C													
Ameghinomya argentina	R					C		R		R	R	R	R		R	R			R
Ameghinomya meridionalis																			
Pachymagas piramidesia	C					C		C		C	C	C	C		C	C			C
Panopea regularis	R		R					R		R	R	R	R		R	R			R
Pteromyrtea danieli																			
Purpurocardia leonensis	R		R					R		R	R	R	R		R	R			R
Dosinia meriodionalis	R		R			C		R		R	R	R	R		R	R			R
Dosinia elsai																			
Pitaria ninfasiensis						C													
Pitaria trigonus						C													
Anomalocardia entrerriana						C													
Chionopsis australis						C													
Mactra sp.						C													
Dinocardium novus																			
Cyrtopleura lanceolata																			
Anadara lirata						R													
Trophon laciniatus	R			A	A	C		R		R	R	R	R		R	R			R
Mytilus trigonus				C	C	R													
Epitonium borcherti				C	C														
Calliostoma spp.				C	C														

APPENDIX 1

Continued.

	RELATIVE ABUNDANCE OF SPECIES																		
SHELL-BEDS	E7	E8	E9	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14a	F14b	F15
FOSSIL ASSEMBLAGES	AOA	AOA	AOA	OCAT	BOT	BOT	OCAT	GROT	OCAT	BOT	OS	AO	OS	OS	BOT	OCAT	AO	OS	OS
Bryozoans				R	D	D	R		R	D					D	R			
"*Turritella*" sp.				C	A	A	C		C	A					A	C			
Retrotapes ninfasiensis								C											
Glycymerita magna								D											
Ostrea alvarezi				C	C	C	C		C	C	A		C	C	C	C			C
Ostrea patagonica	C	C	C	C	R	R	C		C	R	D	D	D	D	R	C	D	D	D
Chlamys actinodes				D			D		D							D			
Aequipecten paranensis	A	A	A	A			A		A							A		D	
Amusium paris	D	D	D									D					D		
Flabellipecten piramidesensis																			
Chesapecten crassus																			
Monophoraster darwini																			
Ameghinomya argentina				R			R		R						R				
Ameghinomya meriodionalis																			
Pachymagas piramidesia	C	C	C	C			C		C						C				
Panopea regularis				R			R		R							R			
Pteromyrtea danieli																			
Purpurocardia leonensis				R			R		R							R			
Dosinia meridionalis				R			R		R							R			
Dosinia elsai																			
Pitaria ninfasiensis																			
Pitaria trigonus																			
Anomalocardia entrerriana																			
Chionopsis australis																			
Mactra sp.																			
Dinocardium novus																			
Cyrtopleura lanceolata																			
Anadara lirata																			
Trophon laciniatus				R			R		R							R			
Mytilus trigonus																			
Epitonium borcherti																			
Calliostoma spp.																			

APPENDIX 1

Continued.

	RELATIVE ABUNDANCE OF SPECIES																		
SHELL-BEDS	F16	F17	F18	F19	F20	F21	F22	F23	F24	F25	G1	G2	G3	G4	G5	G6	G7	G8	G9
FOSSIL ASSEMBLAGES	BOT	BOT	BOT	OCAT	AOA	AOA	AOA	AOA	MO	OMA	OCAT	OCAT	OCAT	GROT	BOT	OCAT	GROT	BOT	OCAT
Bryozoans	D	D	D	R							R	R	R		D	R		D	R
"*Turritella*" sp.	A	A	A	C						R	C	C	C		A	C		A	C
Retrotapes ninfasiensis																			
Glycymerita magna														D			D		
Ostrea alvarezi	C	C	C	C							C	C	C		C	C		C	C
Ostrea patagonica	R	R	R	C	C	C	C	C	D	C	C	C	C		R	C		R	C
Chlamys actinodes				D							D	D	D			D			D
Aequipecten paranensis				A	A	A	A	A		A	A	A	A			A			A
Amusium paris					D	D	D	D											
Flabellipecten piramidesensis																			
Chesapecten crassus																			
Monophoraster darwini									D	A									
Ameghinomya argentina				R							R	R	R			R			R
Ameghinomya meriodionalis																			
Pachymagas piramidesia				C	C	C	C	C			C	C	C			C			C
Panopea regularis				R							R	R	R			R			R
Pteromyrtea danieli										R									
Purpurocardia leonensis				R							R	R	R			R			R
Dosinia meridionalis				R							R	R	R			R			R
Dosinia elsai																			
Pitaria ninfasiensis																			
Pitaria trigonus																			
Anomalocardia entrerriana																			
Chionopsis australis																			
Mactra sp.																			
Dinocardium novus																			
Cyrtopleura lanceolata																			
Anadara lirata																			
Trophon laciniatus				R						R	R	R	R			R			R
Mytilus trigonus																			
Epitonium borcherti																			
Calliostoma spp.																			

APPENDIX 1

Continued.

	RELATIVE ABUNDANCE OF SPECIES																		
SHELL-BEDS	H1	H2	H3	H4a	H4b	H4c	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14a	H14b	H15	H16
FOSSIL ASSEMBLAGES	AOA	OS	MO	AOA	MZ	V	MO	V	NOT	MO	MOT	CAF	GROT	MZ	MOT	MO	MZ	BOT	MO
Bryozoans					C									C			C	D	
"*Turritella*" sp.					C				R		R			C	R		C	A	
Retrotapes ninfasiensis																			
Glycymerita magna													D						
Ostrea alvarezi		C			C				D		D	C		C	D		C	C	
Ostrea patagonica	C	D	D	C	C		D			D		C		C		D	C	R	D
Chlamys actinodes												C							
Aequipecten paranensis	A			A	C				R		R	A		C	R		C		
Amusium paris	D			D								A							
Flabellipecten piramidesensis												C							
Chesapecten crassus												C							
Monophoraster darwini			D		C		D		R	D	R			C	R	D	C		D
Ameghinomya argentina					C	C								C			C		
Ameghinomya meriodionalis						C		C											
Pachymagas piramidesia	C			C	C			C				R		C			C		
Panopea regularis												R							
Pteromyrtea danieli												R							
Purpurocardia leonensis												R							
Dosinia meridionalis					C	C		C						C			C		
Dosinia elsai						C		C											
Pitaria ninfasiensis					C	C		C						C			C		
Pitaria trigonus					C	C		C						C			C		
Anomalocardia entrerriana					C	C		C						C			C		
Chionopsis australis					C	C		C						C			C		
Mactra sp.					C	C		C						C			C		
Dinocardium novus						C		C									C		
Cyrtopleura lanceolata						C		C											
Anadara lirata					R	R		R						R			R		
Trophon laciniatus					C				A		A			C	A		C		
Mytilus trigonus					R				C		C			R	C		R		
Epitonium borcherti									C		C				C				
Calliostoma spp.									C		C				C				

APPENDIX 1

Continued.

SHELL-BEDS	H17	H18	H19	I1	I2a	I2b	I2c	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14
	RELATIVE ABUNDANCE OF SPECIES																		
FOSSIL ASSEMBLAGES	MZ	AOA	MOT	MO	CAF	CAF	CAF	GROT	MOT	MO	OMA	GROT	MOT	V	OS	MO	OMA	OMA	OMA
Bryozoans	C																		
"*Turritella*" sp.	C		R						R		R		R				R	R	R
Retrotapes ninfasiensis								C				C							
Glycymerita magna								D				D							
Ostrea alvarezi	C		D		C	C	C		D				D		A				
Ostrea patagonica	C	C		D	C	C	C			D	C				D	D	C	C	
Chlamys actinodes					C	C	C												
Aequipecten paranensis	C	A	R		A	A	A		R		A		R				A	A	A
Amusium paris		D			A	A	A												
Flabellipecten piramidesensis					C	C	C												
Chesapecten crassus					C	C	C												
Monophoraster darwini	C		R	D					R	D	A		R			D	A	A	A
Ameghinomya argentina	C																		
Ameghinomya meriodionalis																			
Pachymagas piramidesia	C	C			R	R	R												
Panopea regularis					R	R	R												
Pteromyrtea danieli					R	R	R				R						R	R	R
Purpurocardia leonensis					R	R	R												
Dosinia meridionalis	C																		
Dosinia elsai																			
Pitaria ninfasiensis																			
Pitaria trigonus	C																		
Anomalocardia entrerriana	C																		
Chionopsis australis	C																		
Mactra sp.	C																		
Dinocardium novus	C																		
Cyrtopleura lanceolata															D				
Anadara lirata	R																		
Trophon laciniatus	C		A						A		R			A			R	R	R
Mytilus trigonus	R		C						C					C					
Epitonium borcherti			C						C					C					
Calliostoma spp.			C						C					C					

APPENDIX 1

Continued.

SHELL-BEDS	I15	J1	J2	J3	J4	J5	J6	J7	J8	J9	J10	J11	J12	J13	J14	J15	J16	J17	K1
	RELATIVE ABUNDANCE OF SPECIES																		
FOSSIL ASSEMBLAGES	OS	MO	CAF	V	OS	CAF	AO	BOT	V	AO	OS	CAF	OS	AO	AO	OS	AO	MZ	OS
Bryozoans								D										C	
"*Turritella*" sp.								A										C	
Retrotapes ninfasiensis																			
Glycymerita magna																			
Ostrea alvarezi	C		C		C	C		C			C	C	C			A		C	C
Ostrea patagonica	D	D	C		D	C	D	R		D	D	C	D	D	D	D	D	C	D
Chlamys actinodes			C			C						C							
Aequipecten paranensis			A			A						A						C	
Amusium paris			A			A	D			D		A		D	D				
Flabellipecten piramidesensis			C			C						C					D		
Chesapecten crassus			C			C						C							
Monophoraster darwini		D																C	
Ameghinomya argentina																		C	
Ameghinomya meriodionalis																			
Pachymagas piramidesia			R			R						R						C	
Panopea regularis			R			R			C			R							
Pteromyrtea danieli			R			R						R							
Purpurocardia leonensis			R			R						R							
Dosinia meridionalis				D					C									C	
Dosinia elsai									C										
Pitaria ninfasiensis									C									C	
Pitaria trigonus									C									C	
Anomalocardia entrerriana									C									C	
Chionopsis australis									C									C	
Mactra sp.									C									C	
Dinocardium novus																			
Cyrtopleura lanceolata																			
Anadara lirata									C									R	
Trophon laciniatus																		C	
Mytilus trigonus																		R	
Epitonium borcherti																			
Calliostoma spp.																			

APPENDIX 1

Continued.

	RELATIVE ABUNDANCE OF SPECIES													
SHELL-BEDS	K2	K3a	K3b	K4	K5	K6	K7	K8	K9	K10	K11	K12	K13	K14
FOSSIL ASSEMBLAGES	OS	AO	MO	MO	CAF	AO	OS	OS	AO	OS	CAF	CAF	GROT	MZ
Bryozoans														C
"*Turritella*" sp.														C
Retrotapes ninfasiensis													A	
Glycymerita magna													D	
Ostrea alvarezi	C				C		C	C		A	C	C		C
Ostrea patagonica	D	D	D	D	C	D	D	D	D	D	C	C		C
Chlamys actinodes					C						C	C		
Aequipecten paranensis					A						A	A		C
Amusium paris		D			A	D			D		A	A		
Flabellipecten piramidesensis					C						C	C		
Chesapecten crassus					C						C	C		
Monophoraster darwini			D	D										C
Ameghinomya argentina														C
Ameghinomya meriodionalis														
Pachymagas piramidesia					R						R	R		C
Panopea regularis					R						R	R		
Pteromyrtea danieli					R						R	R		
Purpurocardia leonensis					R						R	R		
Dosinia meridionalis														C
Dosinia elsai														
Pitaria ninfasiensis														C
Pitaria trigonus														C
Anomalocardia entrerriana														C
Chionopsis australis														C
Mactra sp.														C
Dinocardium novus														
Cyrtopleura lanceolata														R
Anadara lirata														C
Trophon laciniatus														R
Mytilus trigonus														
Epitonium borcherti														
Calliostoma spp.														