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Ichnology of shallow marine deposits in the Miocene Chenque Formation of Patagonia: complex ecologic structure and niche partitioning in Neogene ecosystems

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Abstract. Exposures of the Lower Miocene Chenque Formation in central Patagonia contain superbly preserved ichnofaunas that allow detailed examination of cross-cutting relationships and tiering structure. This study is focused on lower shoreface deposits of the Borja sequence, exposed in coastal cliffs, in two localities near the city of Comodoro Rivadavia: Punta Delgada (south of Chubut Province) and Playa Las Cuevas-Punta Peligro (north of Santa Cruz Province). The ichnofauna is preserved in fine-grained silty sandstone, which intercalate with thin lenticular shell beds. The intervals analyzed are intensely bioturbated with discrete traces superimposed on an undifferentiated background mottling. The ichnofauna is dominated by feeding traces of infaunal deposit feeders, such as *Phycosiphon, Teichichnus, Helicodromites, Asterosoma, Schaubcylindrichnus,* and *Taenidium,* but grazing trails of deposit feeders (e.g. *Planolites, Scolicia*), feeding traces of chemosymbionts (*Chondrites*), and dwelling traces of suspension feeders (e.g. *Ophiomorpha, Palaeophycus*) and deposit feeders (e.g. *Rosselia*) are present also. Associated body fossils include bivalves, echinoderms, bryozoans, serpulids, gastropods and sponges. Associated body fossils are bioeroded (*Entobia, Rogerella, Gastrochaenolites*). High degree of bioturbation together with high ichnodiversity, the lithofacies assemblage and variety of body fossils indicate slow or discontinuous sedimentation in well oxygenated open marine settings under normal salinity conditions. Low energy deposition was disrupted by minor storm events that produced thin coquinas and flat erosive bounding surfaces. Ichnofabric analysis indicates a complex tiering structure, suggestive of finely tuned, climax communities displaying vertical niche partitioning and a remarkable use of the infaunal ecospace. These Miocene communities are comparable in complexity to Cretaceous chalk communities and modern communities.

Resumen. Icnología de depósitos marinos someros en la Formación Chenque, Mioceno de Patagonia: Estructura ecológica compleja y partición del nicho en ecosistemas neógenos. Los afloramientos de la Formación Chenque, Mioceno Inferior de la Patagonia central, contienen icnofaunas muy bien preservadas que posibilitan analizar en detalle las relaciones de corte y la estructura de escalonamiento. Este estudio se focalizó en depósitos de *shoreface* inferior de la secuencia Borja aflorante en acantilados costeros de dos localidades cercanas a la ciudad de Comodoro Rivadavia: Punta Delgada (sur de la provincia de Chubut) y Playa Las Cuevas-Punta Peligro (norte de la provincia de Santa Cruz). Esta icnofauna está preservada en areniscas muy finas limosas, que se intercalan con delgados bancos lenticulares de conchillas. Los intervalos analizados están intensamente bioturbados con trazas fósiles discretas sobreimpuestas a un moteado de bioturbación indiferenciado. La icnofauna está dominada por estructuras de alimentación de depositívoros infaunales, tales como *Phycosiphon, Teichichnus, Helicodromites, Asterosoma, Schaubcylindrichnus* y *Taenidium,* si bien las pistas de pastoreo de depositívoros (e.g. *Planolites, Scolicia*), las estructuras de alimentación de quimiosimbiontes (*Chondrites*) y las estructuras de habitación de suspensívoros (*e.g. Ophiomorpha, Palaeophycus*) y depositívoros (*e.g. Rosselia*) también están presentes. Los cuerpos fósiles asociados están bioerosionados (*Entobia, Rogerella* y *Gastrochaenolites*). El alto grado de bioturbación junto a la alta icnodiversidad, el conjunto de litofacies y la variedad de cuerpos fósiles indica sedimentación lenta o discontinua en ambientes marinos abiertos bien oxigenados y de salinidad normal, más especificamente un *shoreface* de baja energía y débilmente afectado por tormentas. Las condiciones de baja energía fueron interrumpidas por eventos de tormenta menores que generaron las coquinas y las superficies erosivas. El análisis de icnofábricas indica un patrón de escalonamiento complejo, que sugiere comunidades de climax muy adaptadas con partición vertical del nicho endobentónico y una notable utilización del ecoespacio infaunal en ambientes siliciclásticos, cuya complejidad es comparable a la que poseen las comunidades de cretas mesozoicas y las comunidades actuales.

Keywords. Ichnology. Trace fossils. Ichnofabric. Tiering. Miocene. Patagonia. Argentina.

Palabras clave. Icnología. Trazas fósiles. Icnofábrica. Escalonamiento. Mioceno. Patagonia. Argentina.

Introduction

Trace fossils are particularly abundant and diverse in Cenozoic shallow-marine deposits of Patagonia (*e.g.* Lech *et al.*, 2000). However, the potential of these Cenozoic ichnofaunas for reconstructing paleoecosystems and ancient depositional environments has not yet been explored. Cliff exposures of the Lower Miocene Chenque Formation in central Patagonia contain superbly preserved ichnofaunas, which can be studied during low tides. It should be noted that visibility of the ichnofabrics is optimal only under precise conditions of humidity and light.

The ichnofaunas studied are preserved in lower shoreface deposits. Ichnologic aspects of shoreface deposits have been discussed in a series of papers (*e.g.*, McCarthy, 1979; Frey and Howard, 1985, 1990; MacEachern and Pemberton, 1992; Buatois *et al.*, 1999, 2002), but still little is known about the tiering structure of shoreface ichnofabrics. Degree of bioturbation in the shoreface deposits of the Chenque Formation is so intense that virtually no primary sedimentary structures are preserved. Accordingly, biogenic structures are essential to establish environ-

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mental zonations in these thoroughly bioturbated deposits (*cf.* Martin and Pollard, 1996).

The aim of this study is: (1) to document the ichnofauna preserved in lower shoreface deposits of the Chenque Formation, (2) to evaluate its paleoecological and paleoenvironmental significance, and (3) to discuss its importance in evolutionary paleoecology, emphasizing its complex tiering structure.

Stratigraphic and depositional setting

The Lower Miocene Chenque Formation (Aquitanian-Burdigalian) records the Leonian and Superpatagonian transgressions in the San Jorge Basin, central Patagonia (Bellosi, 1990a, 1995). This formation unconformably overlies Upper Cretaceous (Bajo Barreal Formation) to Upper Oligocene (Puesto Almendra Member of Sarmiento Formation) units and conformably overlies the Lower Miocene Colhue-Huapi Member (Sarmiento Formation) in different positions of the basin (Bellosi, 1995). The Chenque Formation conformably passes upward into the estuarine to fluvial and eolian, Lower to Middle Miocene Santa Cruz Formation. The Chenque Formation records a wide variety of depositional settings from open marine, shallow water deposits in the lower interval to restricted, tide-dominated estuarine to lagoonal deposits in the upper interval (Bellosi, 1986, 1987, 1988, 1995, 2000; Bellosi and Barreda, 1993; Bellosi and Jalfin, 1996).

The age of this formation was based on the sequence stratigraphic framework (Bellosi, 1990a; Bellosi and Barreda, 1993), dinoflagellates (Palamarczuk and Barreda, 1998; Barreda and Palamarczuk, 2000a, 2000b), pollen and spores (Barreda, 1993, 1996; Barreda and Palamarczuk, 2000a, 2000b), foraminiferans (Bertels and Ganduglia, 1977), vertebrates (Caviglia, 1978; Cione, 1978), and isotope dating (Riggi, 1979; Bellosi, 1990b). Although previous studies suggest that the formation may range into the uppermost Eocene and Oligocene, recent analysis of its continental and marine palynomorphs suggests an Early Miocene age for the Chenque Formation (Bellosi and Barreda, 1993; Bellosi, 1995; Barreda and Palamarczuk, 2000b).

The Chenque Formation is approximately 500 m thick and is divided into five depositional sequences (Bellosi, 1990a, 1995). This study is focused on lower shoreface deposits that occur in the lower sequence (Borja sequence of Bellosi, 1987) exposed in two localities near the city of Comodoro Rivadavia: Punta Delgada (south of Chubut Province) and Playa Las

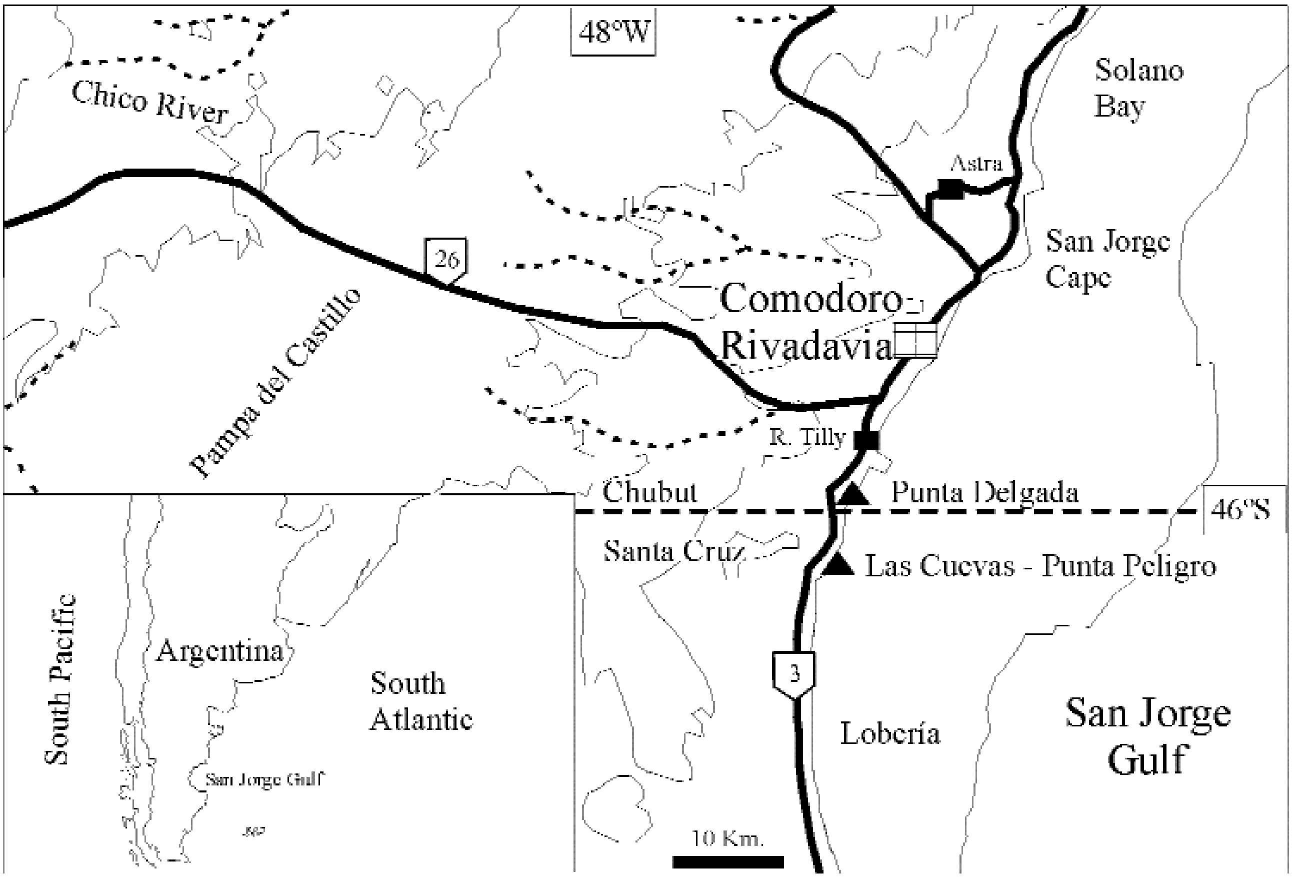

Figure 1. Location map of the study localities near Comodoro Rivadavia / *Mapa de ubicación de las localidades estudiadas en los alrededores de Comodoro Rivadavia.*

Figure 2. Stratigraphic section at Punta Delgada. The studied interval comprises a coarsening upward parasequence at the base of sequence 1. Note intense bioturbation in the proximal lower shoreface deposits. *Ophiomorpha* is present throughout the whole shoreface interval. / *Sección estratigráfica en Punta Delgada. El intervalo estudiado comprende una parasecuencia granocreciente en la base de la secuencia 1. Nótese intensa bioturbación en los depósitos de* shoreface *inferior proximal.* Ophiomorpha *está presente en la totalidad del intervalo de* shoreface.

Figure 3. Stratigraphic section at Playa Las Cuevas-Punta Peligro. The studied interval comprises distal lower shoreface deposits at the lowermost part of the section. Note intense bioturbation in the distal lower shoreface deposits. *In situ* oysters are restricted to the base of the package. Several *Pinna* (bivalve) horizons occur throughout the distal lower shoreface deposits. Thin storm beds are present at the middle zone of the distal lower shoreface deposits. An omission surface delineated by firmground *Thalassinoides* occurs at the RSME (regressive surface of marine erosion). / *Sección estratigráfica en Playa Las Cuevas-Punta Peligro. El intervalo estudiado comprende depósitos de* shoreface *inferior distal en el sector basal de la sección. Nótese intensa bioturbación en los depósitos de* shoreface *inferior distal. Las ostras* in situ *están restringidas a la base del intervalo. Varios horizontes de* Pinna *(bivalvo) se distribuyen a lo largo de todo el intervalo de* shoreface *inferior distal. Delgadas tempestitas se concentran en la zona media del intervalo de* shoreface *inferior distal. Una superficie de omisión delineada por* Thalassinoides *se presenta en RSME (superficie regresiva de erosión marina).*

Cuevas-Punta Peligro (north of Santa Cruz Province) (figure 1). Correlation and assessment of both successions to sequence 1 of the Chenque Formation was checked by dinocysts and spore-pollen assemblages (Barreda, 1996). The age of this sequence is Early Miocene (Aquitanian) based on palynomorphs (Bellosi and Barreda, 1993; Barreda, 1996).

At Punta Delgada, lower shoreface deposits are 3.5 m thick and consist of intensely bioturbated, upper very fine-grained silty sandstone (figure 2). The sandstone is glauconitc and greenish grey (5GY5/1) in color. A lower shoreface interpretation is suggested by the intensity of bioturbation and the presence of the *Cruziana* ichnofacies. The sandy nature of the deposits also suggests a shoreface environment, rather than an offshore setting. These deposits occur at the lower portion of a coarsening upward parasequence and pass by means of an erosive planar contact into a 2.4 m thick lower fine-grained sandstone that records deposition in the middle shoreface. The slight increase in grain size and the dominance of elements of the *Skolithos* ichnofacies suggest progressive shallowing, supporting deposition in a middle shoreface. The parasequence culminates in a 2.6 m thick upper fine-grained massive sandstone with a planar, erosive base covered by shell debris, which probably accumulated in the upper shoreface. The increase in grain size with respect to the underlying deposit and the stratigraphic position immediately above the middle shoreface unit suggest an upper shoreface environment. With unusually low tide at the outcrop, the lowermost interval of the parasequence becomes exposed.

At Playa Las Cuevas-Punta Peligro, lower shoreface deposits are 5 m thick and consist of very fine-grained silty sandstone (figure 3). As in the case of the Punta Delgada basal unit, lower shoreface deposition is indicated by the intensity of bioturbation, the presence of the *Cruziana* ichnofacies and the very fine-grained sandstone lithology. This deposit is punctuated by distinct horizons containing shells of *Pinna* (bivalve) in life position. These horizons, together with thin lenticular shell beds and with minor variations in ichnofauna composition, reveal the presence of cycles within this package. The upper contact of this deposit is marked by an omission surface delineated by firmground *Thalassinoides* that are as much as 1.28 m deep. Several such omission surfaces occur above the lower shoreface deposits, and they probably record rapid shallowing during a forced regression. A fine-grained sandstone unit occurs above the stacked omission surfaces. Coarse-grained skeletal deposits within this interval are represented by erosive based *Turritella* (gastropod) coquinas with undulated tops (1.0 m; A = 0.2 m), occurring towards the base of the unit, and other storm shell beds concentrated at the middle part of the unit. Fine-grained sandstone and associated high energy shell beds possibly accumulated in the middle shoreface. Sequence 1 culminates in through cross-bedded fine-grained sandstone that record migration of 3-D dunes in the upper shoreface.

A diverse body fossil fauna, commonly forming discontinuous shell beds and shell pockets, occurs at both localities. The fauna includes bivalves, echinoderms, bryozoans, serpulids, gastropods and sponges. Transported oysters are fairly common in these deposits, while *in situ* specimens seem to be restricted to the lowermost part of the section at Playa Las Cuevas-Punta Peligro.

Composition and characteristics of the ichnofauna

Punta Delgada

The Punta Delgada ichnofauna is dominated by *Ophiomorpha* isp. and *Asterosoma* isp. Detailed descriptions of *Ophiomorpha* are provided by Carmona (2000) and Carmona and Buatois (this volume).

Figure 4. *Asterosoma* isp. in plan view. Specimens of *Asterosoma* isp. (A) form large, lobed structures, and they display relatively poor preservation. *Asterosoma* is cut by *Phycosiphon incertum* (P) and *Ophiomorpha* (O). Punta Delgada. Lens cap 5 cm. / Asterosoma *isp. en planta. Los especimenes de* Asterosoma *isp. (A) forman estructuras lobadas grandes, de preservación relativamente pobre.* Asterosoma *es cortada por* Phycosiphon incertum *(P) y* Ophiomorpha *(O). Punta Delgada. Protector de lente de 5 cm.*

Ophiomorpha systems typically have a passive laminated infill, and in some places they terminate downward into *Gyrolithes*-like spirals. *Asterosoma* forms large laminated, lobed structures, up to 38 cm wide (figure 4). *Thalassinoides suevicus* Rieth 1932 and *Phycosiphon incertum* Fischer-Ooster 1858 are abundant also. *Phycosiphon* displays a very well defined pale mantle surrounding a dark core, and they may reach up to 0.6 cm in diameter (figure 5.A). Secondary components (*sensu* MacEachern and Pemberton, 1994) include *Schaubcylindrichnus freyi* Miller 1995, *Chondrites* isp., *Scolicia* isp., and *Rosselia* isp. *Palaeophycus heberti* (Saporta 1873), *Palaeophycus tubularis* Hall 1847, *Planolites montanus* Richter 1937, and *Teichichnus rectus* Seilacher 1955 are accessory components. These ichnotaxa are superimposed on an undifferentiated background mottling. The trace fossils are uniformly distributed along the outcrop, both laterally and vertically within the lower shoreface strata. The *Asterosoma*-*Ophiomorpha* ichnofabric of the lower shoreface is replaced vertically by an *Ophiomorpha* ichnofabric that marks the transition into the middle shoreface.

Playa Las Cuevas-Punta Peligro

The ichnofauna at Playa Las Cuevas-Punta Peligro includes a wide variety of ichnotaxa, and dominant elements are not apparent. Discrete trace fossils are superimposed on an undifferentiated background mottling. *Chondrites* (large and small), *Phycosiphon incertum* (large and small), and *Thalassinoides suevicus* are abundant through the whole interval. *Teichichnus zigzag* Frey and Bromley 1985, *Teichichnus rectus*, *Helicodromites mobilis* Berger 1957, *Palaeophycus heberti*, and *Scolicia* (large and small) are abundant at certain horizons. *Teichichnus zigzag* differs from typical representatives of this ichnospecies in its tendency to develop a horizontal sweep in its vertical spreite. The causative burrow is filled with pale sand in contrast to the dark muddy spreite (figure 5.B). *Helicodromites mobilis* is very well preserved forming horizontal spirals up to 65 cm long, filled with pale colored very fine sand that contrasts with the darker silty surrounding sediment (figure 5.D). *Planolites montanus*, *Schaubcylindrichnus coronus* Frey and Howard 1981, *S. freyi*, *Taenidium* isp. (figure 5.C), *Asterosoma* isp., *Rosselia* isp., and *Teichichnus* isp. are less common.

Associated body fossils are bioeroded, displaying *Entobia* isp., *Rogerella* isp. and *Gastrochaenolites* isp. The bioerosion of the body fossils, in particular the large oyster *Ostrea maxima*, tells a different story. Occurrence of abundant *Gastrochaenolites* in lower shoreface environments is unexpected. Bivalve borers tend to be restricted to shallower environments. Their abundance in the sediments under study suggests that these oysters were bioeroded in shallower water and subsequently were transported into lower shoreface regions.

Lateral distribution of the ichnotaxa is generally uniform. However, the trace fossil content is vertically variable within the lower shoreface interval. Vertical variations in ichnocoenosis within lower shoreface deposits record subtle environmental fluctuations probably associated with minor storms.

Comparison and environmental implications

Both localities contain intensely bioturbated lower shoreface deposits hosting abundant and well preserved trace fossil assemblages. The ichnofauna is dominated by feeding traces of infaunal deposit feeders, such as *Phycosiphon*, *Teichichnus*, *Asterosoma*, *Schaubcylindrichnus* and *Taenidium*, but grazing trails of deposit feeders (*e.g.*, *Planolites* and *Scolicia*), feeding traces of chemosymbionts (*Chondrites*), and dwelling traces of suspension feeders (*e.g.*, *Ophiomorpha* and *Palaeophycus*) and deposit feeders (*e.g.*, *Rosselia*) are present also. Most ichnotaxa (*Phycosiphon*, *Teichichnus*, *Asterosoma*, *Schaubcylindrichnus*, *Planolites*, *Scolicia*, *Chondrites*, *Thalassinoides*, *Palaeophycus* and *Rosselia*) are common to both localities. The similarity of the ichnofaunas at both localities suggests similar paleoenvironmental conditions.

However, comparison between lower shoreface deposits from the two localities allows refinement of environmental zonation. Ichnodiversity is markedly higher in Playa Las Cuevas-Punta Peligro than in Punta Delgada, suggesting more stable paleoenvironmental conditions at the former (*i.e.*, lower disturbance due to physical processes). Additionally, the diversity and abundance of deposit feeder trace fossils is higher in Playa Las Cuevas-Punta Peligro. Conversely, *Ophiomorpha*, which is very abundant in middle and lower shoreface deposits of Punta Delgada, is absent at Playa Las Cuevas-Punta Peligro. Tiering structure is more complex in Playa Las Cuevas-Punta Peligro than in Punta Delgada. Overall higher ichnodiversity, higher proportion of deposit feeder trace fossils with respect to suspension feeder trace fossils, and more complex tiering structure in Playa Las Cuevas-Punta Peligro suggest that the Punta Delgada deposits were emplaced in a proximal lower shoreface, while those of Playa Las Cuevas-Punta Peligro represent deposition in a distal lower shoreface.

The lower shoreface ichnofauna is composed of fairweather trace fossil suites that record the activity of the resident benthic fauna. High degree of bioturbation coupled with high ichnodiversity and variety

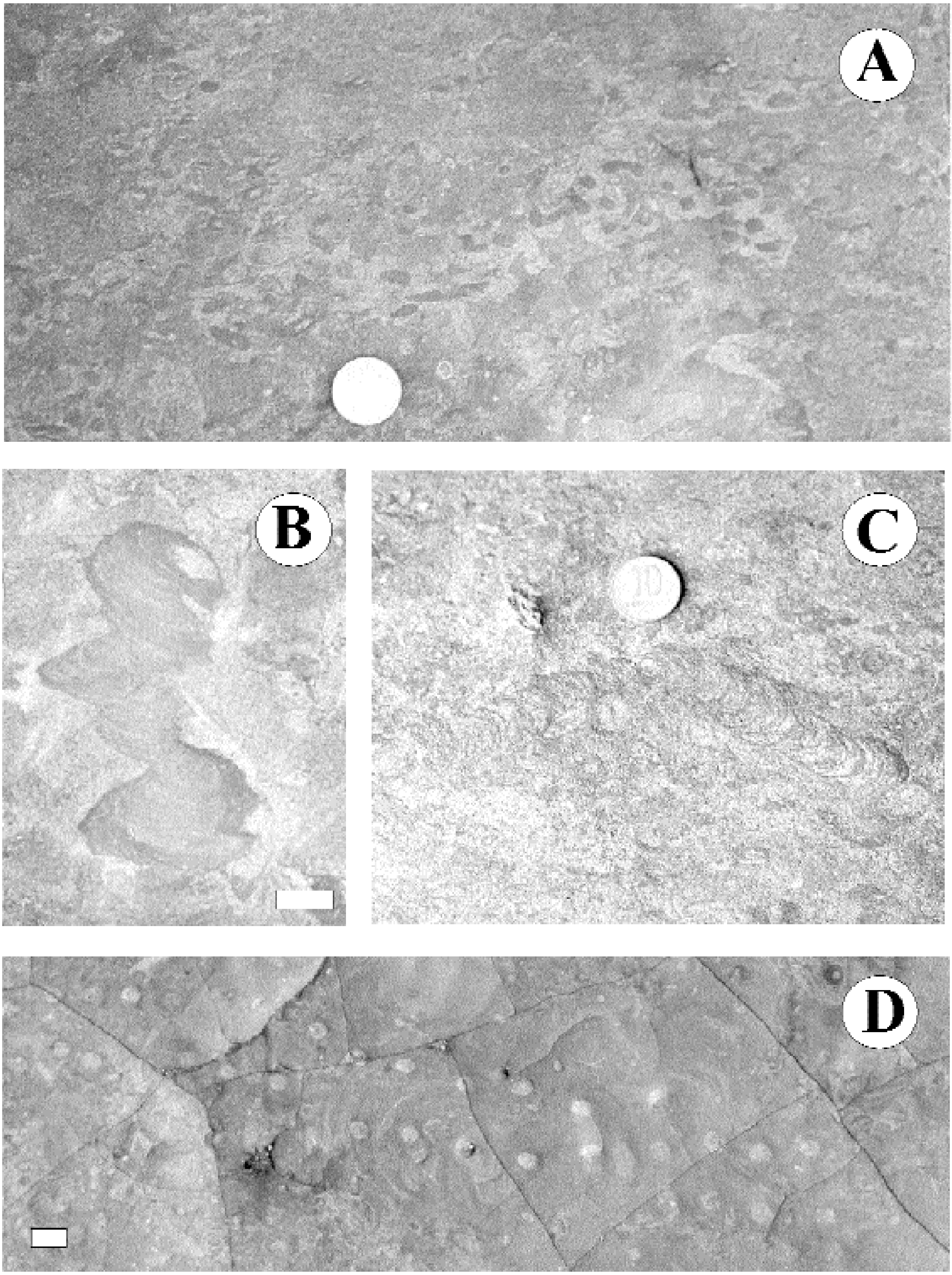
A
B
C
D

Figure 6. Dense occurrence of trace fossils in plan view. Specimens of *Scolicia* isp (S) cut by *Chondrites* isp. (C), *Teichichnus rectus* (Tr) and *Phycosiphon incertum* (P). A specimen of *Taenidium* isp. (Ti) is cut by *Scolicia*. Playa Las Cuevas-Punta Peligro. Lens cap 5 cm. / *Densa asociación de trazas fósiles en planta. Los especimenes de* Scolicia *isp (S) están cortados por* Chondrites *isp. (C),* Teichichnus rectus *(Tr) y* Phycosiphon incertum *(P). Un especimen de* Taenidium *isp. (Ts) es cortado por* Scolicia*. Playa Las Cuevas-Punta Peligro. Protector de lente de 5 cm.*

of body fossils indicate slow or discontinuous sedimentation in well oxygenated open marine settings under normal salinity conditions. In such stable setting, with few environmental fluctuations, the large bivalve *Pinna* also grew to form laterally continuous nests. Low energy deposition was disrupted by very minor storms that produced thin coquinas with planar erosive bounding surfaces. Other storm deposits, if formed at all, were thoroughly obliterated by bioturbation. These deposits are classified as low energy, weakly storm-affected shorefaces (*sensu* MacEachern and Pemberton, 1992). More energetic shoreface deposits, displaying alternating fairweather and colonization trace fossil suites associated with hummocky cross-stratified facies, were documented in the coeval Gaimán Formation of northeastern Patagonia (Scasso and Castro, 1999; see also Lech *et al.*, 2000).

Different paleontological evidence, including planktonic foraminifera (*Martinottiella-Spirosigmoilinella* association, Náñez, 1988; Malumián and Náñez, 1991), ostracodes (Echeverría, 1991), cetacean and penguin remains suggest cold-temperate sea water due to polar currents reaching Central Patagonia (Bellosi, 1994, 1995). During Late Oligocene-Early Miocene time, the dynamics of marine currents probably favored coastal upwelling and high pro-

Figure 5. Common ichnofossils in the Chenque Formation. **A.** *Phycosiphon incertum* in oblique section displaying a very well defined pale mantle surrounding a dark core and superimposed on a background ichnofabric consisting of *Planolites montanus* and *Schaubcylindrichnus freyi*. Punta Delgada. Coin is 1.8 cm in diameter. **B.** *Teichichnus zigzag* in oblique section with dark muddy spreite and causative burrow filled with pale sand. Playa Las Cuevas-Punta Peligro. Bar = 1 cm. **C.** *Taenidium* in plan view showing its characteristic meniscate infill. Playa Las Cuevas-Punta Peligro. Coin is 1.8 cm in diameter. **D.** *Helicodromites mobilis* in plan view forming well defined, long, horizontal spirals, filled with pale colored very fine sand and overprinted on a background ichnofabric consisting of *Scolicia* isp. Playa Las Cuevas-Punta Peligro. Bar = 1 cm. / *Icnofósiles característicos de la Formación Chenque.* ***A.*** Phycosiphon incertum *en sección oblicua mostrando un manto pálido muy bien definido rodeando un núcleo oscuro y sobreimpuesto a una icnofábrica de fondo integrada por* Planolites montanus *y* Schaubcylindrichnus freyi*. Punta Delgada. Moneda de 1.8 cm.* ***B.*** Teichichnus zigzag *en sección oblicua, con un spreite fangoso oscuro y un tubo causativo rellenado por arena clara. Playa Las Cuevas-Punta Peligro. Barra = 1 cm.* ***C.*** Taenidium *en planta mostrando su característico relleno meniscado. Playa Las Cuevas-Punta Peligro. Moneda de 1.8 cm.* ***D.*** Helicodromites mobilis *en planta formando espirales horizontales bien definidos, rellenos con arena muy fina clara y sobreimpuestos a una icnofábrica de fondo integrada por* Scolicia *isp. Playa Las Cuevas-Punta Peligro. Barra = 1.*

ductivity (Bellosi, 1995; Barreda and Palamarczuk, 2000a; Palamarczuk and Barreda, 2000), which promoted high ichnodiversity.

Discussion: ichnofabrics and tiering structure

Ichnofabric analysis reveals a complex tiering structure in the lower shoreface deposits of the Chenque Formation. Cross-cutting relationships and degree of preservation of the different ichnotaxa suggest the existence of approximately ten tiers. With the exception of post-omission crustacean systems recording subsequent burrowing events, the other elements reflect simultaneous activity of the infaunal community. Undifferentiated mottling is overprinted by discrete structures, forming a background ichnofabric that most likely records the activity of the mixed layer infauna (Berger *et al.*, 1979; Ekdale *et al.*, 1984).

Simple trace fossils of deposit feeders, assigned to *Planolites montanus*, are poorly defined and are crosscut by almost all the discrete trace fossils, suggesting very shallow emplacement close to or at the boundary between the mixed and transition layers. *Asterosoma*, one of the dominant forms in Punta Delgada, is cut by all the discrete ichnotaxa with the exception of *Planolites montanus* (figure 4). This fact, together with its relatively poor preservation, indicates that *Asterosoma* records the activity of a shallow deposit feeder within the transition layer. Cross-cutting relationships of *Schaubcylindrichnus* are difficult to evaluate, because this ichnotaxon is not very abundant. However, it has been observed to be cut by *Chondrites* and *Ophiomorpha. Scolicia* exhibits moderate preservation and is cut by *Chondrites*, *Phycosiphon*, *Helicodromites*, *Ophiomorpha*, *Teichichnus zigzag*, *Teichichnus rectus*, and *Taenidium* (figure 6). In turn, spreite lamellae of *Teichichnus rectus* locally are reworked by *Chondrites*. *Chondrites* even cuts the fill of *in situ Pinna* shells (figure 7).

Two different generations of *Ophiomorpha* occur in Punta Delgada. The first generation is part of the lower shoreface community and is cut by *Phycosiphon*, *Scolicia* and *Chondrites*, suggesting emplacement at moderate depths below the sediment-water interface (figure 8). *Gyrolithes*-like spiral terminations of *Ophiomorpha* systems are cut by *Chondrites* and *Phycosiphon*. The second generation of *Ophiomorpha*

Figure 7. Plan view of a *Pinna* (bivalve) horizon. Note *Chondrites* isp. (C) inside the fill of several *Pinna*. Playa Las Cuevas-Punta Peligro. Coin is 1.8 cm in diameter. / *Vista en planta de un horizonte de* Pinna *(bivalvo). Nótese presencia de* Chondrites *isp. (C) dentro del relleno de varias* Pinna. *Playa Las Cuevas-Punta Peligro. Moneda de 1.8 cm.*

extends from the middle, and possibly upper, shoreface deposits downward into lower shoreface strata, cutting across all the other trace fossils, including *Ophiomorpha* burrows of the first generation. *Ophiomorpha* burrow systems of the second generation are as much as 2.5 m deep and commonly are filled with cleaner sand and shells from the overlying more proximal deposits.

Three different generations of *Thalassinoides* occur at Playa Las Cuevas-Punta Peligro. The first generation consists of sand-filled burrows that only locally are crosscut by other traces. However, *Thalassinoides* was observed to be crosscut only by *Chondrites*, *Phycosiphon* and even *Asterosoma*, suggesting that rarity of cross-cutting relations reflects avoidance by other organisms of sand-filled burrow fills rather than indicating the deep emplacement of *Thalassinoides*. A second generation of this ichnogenus is represented by *Thalassinoides* burrows cutting across *Scolicia*, *Phycosiphon* and *Helicodromites*, reflecting a deeper tier position. A third generation is recorded by the postomission *Thalassinoides* penetrating into the upper interval of the lower shoreface deposits from the overlying regressive surface of marine erosion, which represents the activity of a different endobenthic community.

To summarize, upper tiers are occupied by background mottling, *Planolites*, shallow *Thalassinoides*, *Asterosoma* and *Schaubcylindrichnus*. Intermediate tiers include relatively shallow *Ophiomorpha*, *Scolicia*, *Phycosiphon* and *Palaeophycus*. Lower tiers are occupied by deep *Ophiomorpha* and *Thalassinoides*, *Teichichnus*, *Helicodromites* and *Chondrites.* Postomission *Thalassinoides* from the overlying surface cut across all traces and record a subsequent burrowing event.

The complex tiering structure suggests finely tuned, climax communities displaying vertical niche partitioning. These Miocene communities are comparable in complexity to Cretaceous chalk communities. Studies in the Cretaceous chalk of northern Europe documented nine tiers, with *Thalassinoides* and *Planolites* occupying shallow tiers, *Phycosiphon* at moderate depths, and *Zoophycos* and *Chondrites* deep into the substrate (Bromley and Ekdale, 1984; Ekdale

Figure 8. *Ophiomorpha* isp. (O) in plan view cutting across one specimen of *Scolicia* isp. (S, right), but the same *Ophiomorpha* is cut by another *Scolicia* specimen (S, upper center). Note the concentration of *Chondrites* isp. (C) reworking part of the *Ophiomorpha* gallery and the widely distributed *Schaubcylindrichnus freyi* (Sf). A poorly preserved specimen of *Asterosoma* isp (A) is present also. Punta Delgada. Coin is 1.8 cm in diameter. / Ophiomorpha *isp. (O) en planta cortantando a través de un especimen de* Scolicia *isp. (S, derecha), pero el mismo ejemplar de* Ophiomorpha *es cortado por otro especimen de* Scolicia *(S, centro superior). Nótese la concentración de* Chondrites *isp. (C) retrabajando parte de la galería de* Ophiomorpha *y* Schaubcylindrichnus freyi *(Sf) ampliamente distribuidos. Un especimen pobremente preservado de* Asterosoma *isp (A) está presente también. Punta Delgada. Moneda de 1.8 cm.*

and Bromley, 1984, 1991). Comparable tiering patterns were detected in Cretaceous chalks of southeastern United States (Frey and Bromley, 1985).

In comparison with Paleozoic and Mesozoic siliciclastic ichnofabrics, Chenque ichnofabrics reveal a more complex tiering structure, reflecting evolutionary innovations that were conducive to more sophisticated biotic interactions of the infauna during the Cenozoic. Ichnofabric analysis from shallow marine deposits of the Chenque Formation indicates that a remarkable use of the infaunal ecospace was attained in siliciclastic environments by the early Neogene, reaching similar levels of complexity than that observed in modern, shallow-marine, siliciclastic environments.

Conclusions

Lower shoreface deposits of the Miocene Chenque Formation are intensely bioturbated. They contain a very diverse ichnofauna that includes feeding traces of infaunal deposit feeders (*e.g.*, *Phycosiphon*, *Teichichnus*, *Helicodromites*, *Asterosoma*, *Schaubcylindrichnus* and *Taenidium*), grazing trails of deposit feeders (*e.g.*, *Planolites* and *Scolicia*), feeding traces of chemosymbionts (*Chondrites*), and dwelling traces of suspension feeders (*e.g.*, *Ophiomorpha* and *Palaeophycus*) and deposit feeders (*e.g.*, *Rosselia*).

High degree of bioturbation coupled with high ichnodiversity and variety of *in situ* body fossils indicate slow or discontinuous sedimentation in well oxygenated open marine settings under normal marine salinity conditions, typifying low energy, weakly storm-affected shoreface environments.

Ichnofabric analysis reveals a complex tiering structure, suggestive of finely tuned, climax communities that display a sophisticated pattern of vertical niche partitioning. These Miocene communities are comparable in complexity to Cretaceous chalk communities, and they indicate a remarkable use of the infaunal ecospace in siliciclastic environments by the early Neogene.

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