Cenozoic trace fossils of the *Cruziana*, *Zoophycos* and *Nereites* ichnofacies from the Fuegian Andes, Argentina

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Abstract. The systematics, paleoenvironmental implications, and diversity of Cenozoic trace fossils from the Fuegian Andes are studied. The relatively complete Paleocene-Miocene stratigraphic column includes ichnoassemblages of the *Cruziana* (Leticia Formation, late Middle Eocene), *Zoophycos* and *Nereites* (Early Eocene-Early Miocene turbidite systems) ichnofacies. The last two ichnoassemblages contain the only known deep marine Cenozoic trace fossils in Argentina. The late Middle Eocene Leticia Formation represents a transgressive-regressive cycle and bears the ichnogenera *Curvolithus*, *Diplocraterion*, *Gyrochorte*, *Rosselia*, *Patagonichnus*, *Asterosoma*, *Palaeophycus*, *Paradictyodora*, *Planolites*, *Rhizocorallium*, *Schaubcylindrichnus*, *Taenidium*, and *Teichichnus*. Ichnogenera of the Early Eocene-Early Miocene turbidite systems include *Scolicia*, *Chondrites*, *Gyrophyllites*, *Nereites*, *Phycodes*, *Phycosiphon*, *Phymatoderma*, *Stelloglyphus*, *Zoophycos*, *Ophiomorpha* and graphoglyptids. Graphoglyptids are dominated by *Paleodictyon*, *Helicolithus*, *Helminthorhaphe*, *Desmograpton* and *Megagrapton*. They are recorded in thin-bedded turbidites and mudstones (lobe deposits) and assigned to the *Paleodictyon* ichnosubfacies (*Nereites* ichnofacies). *Ophiomorpha rudis* and *O. annulata* are common at the contact between thick-bedded turbidites and mudstones, with abundant plant fragments. In sand-rich, proximal channel-lobe deposits, they characterize the *Ophiomorpha rudis* ichnosubfacies (*Nereites* ichnofacies). *Scolicia prisca* and *Nereites* isp. are common in rippled fine-grained sandstones interbedded with thin mudstones. *Zoophycos* ispp. are dominant in slope mudstones with synsedimentary slumping. The maximum ichnodiversity is recorded in the late Middle-Late Eocene; which is concomitant with a marked cooling trend. The basal Oligocene displays an abrupt drop in diversity, whereas the Early Miocene shows a moderate diversity. These data do not support the alleged control of increased Eocene ichnodiversity by global warming during the Cenozoic thermal maximum. Specialized food competition, particularly for the graphoglyptid organisms, and generalized oligotrophy seem to offer a better explanation.

Resumen. Trazas fósiles de la ichnofacies de *Cruziana*, *Zoophycos* y *Nereites* del Cenozoico de Los Andes Fueguinos. Se dan a conocer resultados de estudios sistemáticos, implicancias paleoambientales y diversidad de trazas fósiles del Paleoceno-Mioceno de los Andes Fueguinos. Se reconocen las icnofacies de *Cruziana* (Formación Leticia, Eoceno Medio alto), y de *Zoophycos* y *Nereites* (sistemas de turbiditas del Eoceno-Mioceno temprano). Las dos últimas icnofacies constituyen las únicas icnoasociaciones marinas profundas del Cenozoico conocidas en la Argentina. La Formación Leticia representa un ciclo transgresivo-regresivo e incluye a *Curvolithus*, *Diplocraterion*, *Gyrochorte*, *Rosselia*, *Patagonichnus*, *Asterosoma*, *Palaeophycus*, *Paradictyodora*, *Planolites*, *Rhizocorallium*, *Schaubcylindrichnus*, *Taenidium*, y *Teichichnus*. Los sistemas de turbiditas del Eoceno temprano-Mioceno temprano incluyen a *Scolicia*, *Chondrites*, *Gyrophyllites*, *Nereites*, *Phycodes*, *Phycosiphon*, *Phymatoderma*, *Stelloglyphus*, *Zoophycos*, *Ophiomorpha*, y grafoglíptidos. *Paleodictyon*, *Helicolithus*, *Helminthorhaphe*, *Desmograpton* y *Megagrapton* son típicos grafoglíptidos de la icnosubfacies de *Paleodictyon* (icnofacies de *Nereites*). *Ophiomorpha rudis* y *O. annulata* caracterizan la icnofacies de *O. rudis* (icnofacies de *Nereites*), en turbiditas medias a gruesas, con abundante materia vegetal (depósitos arenosos proximales de canales y lóbulos). *Scolicia prisca* y *Nereites* isp. son comunes en areniscas finas con ondulitas e intercaladas con pelitas. *Zoophycos* ispp. domina en fangolitas de talud con deslizamientos sinsedimentarios. Concordantemente con una marcada tendencia de enfriamiento, el Eoceno Medio superior-Eoceno Superior registra la máxima icnodiversidad, el Oligoceno basal una caída abrupta en la diversidad y el Mioceno temprano una moderada recuperación de la diversidad. Estos datos no concuerdan con la teoría de aumento de icnodiversidad debido al calentamiento global durante el máximo termal (Paleoceno/Eoceno) del Cenozoico. La especialización trófica desarrollada por los organismos productores de grafoglíptidos y una oligotrofía generalizada ofrecen una mejor explicación para estas tendencias.

Key words. Fuegian Andes. Cenozoic. Ichnology. Graphoglyptids. Turbidites.

Palabras clave. Andes Fueguinos. Cenozoico. Icnología. Grafoglíptidos. Turbiditas.

Introduction

The Fuegian Andes region has a relatively complete, about 4 km thick stratigraphic column of Paleocene to Miocene sedimentary rocks, which includes the only known record of deep-marine Cenozoic deposits in Argentina. These circumstances make the Fuegian Andes as one of the most important areas of southern South America for the study of Cenozoic rocks (Olivero and Malumián, 1999, 2002; Olivero *et al.*, 2002, 2003; Malumián and Olivero, 2005, 2006).

Except for few taxonomic mentions and brief localized studies (*e.g.* Olivero and López C., 2001; Olivero *et al.*, 2005; Carmona *et al.*, 2006; López C. *et al.*, 2006, and Ponce *et al.*, 2007) the ichnology of this

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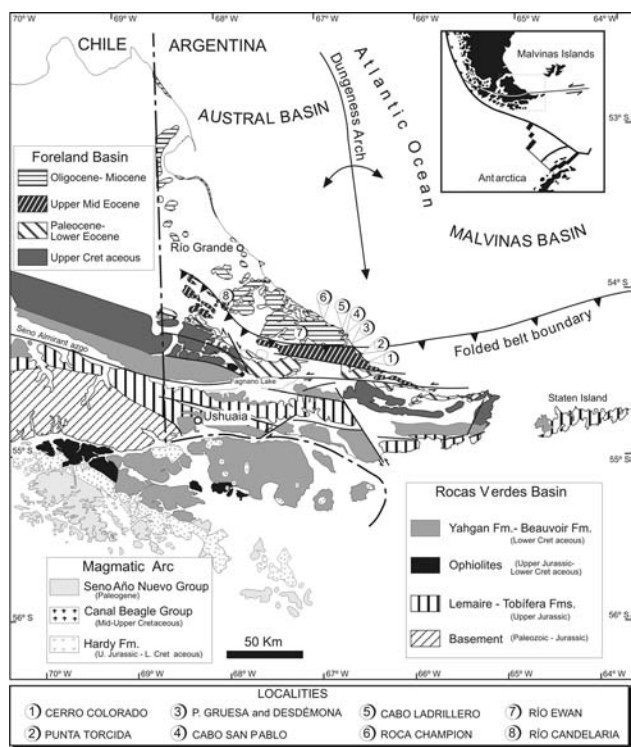
Figure 1. Geological sketch map of Tierra del Fuego, Argentina with location of studied sections / *bosquejo geológico de Tierra del Fuego, Argentina con la situación de las secciones estudiadas.*

important area is almost unknown. In this paper we attempt to present a general ichnological study of the Cenozoic of the Fuegian Andes. The study covers basinal and/or slope turbidite systems and marginal marine and shelf settings. Turbidite systems include the *Zoophycos* and *Nereites* ichnofacies of the Lower Eocene Punta Torcida Formation; upper Middle to Upper Eocene Cerro Colorado Formation; Lower Oligocene Estancia María Cristina beds; uppermost Oligocene-Lower Miocene Desdémona Formation; and Lower Miocene Cabo Ladrillero and Cabo San Pablo beds. Marginal marine and shelf settings include the *Cruziana* ichnofacies of the late Middle Eocene Leticia Formation.

The objectives of this study are to document partly the ichnological record of the Cenozoic of the Fuegian Andes and to discuss its implications for general characterization of paleoenvironmental conditions and contribution to global ichnodiversity trends, in particular to the known increase in deep-marine trace fossil diversity during the Eocene. The systematic description covers mainly the ichnology of the turbidite systems, which includes several ichnospecies distributed in 16 ichnogenera that were mostly unknown in the Cenozoic of Argentina. The systematics of the bulk of trace fossils from the

Leticia Formation (*Cruziana* ichnofacies) is the subject of an ongoing study by the authors. Thus, most of them will only be mentioned here except for some well preserved ichnotaxa, such as *Curvolithus* and *Gyrochorte*, which are barely known in the Cenozoic.

Late Cretaceous-Cenozoic stratigraphic framework

In southeastern Tierra del Fuego (figure 1), the Late Cretaceous-Cenozoic stratigraphy of the fore-land Austral Basin consists of four major synorogenic clastic wedges, which are mainly characterized by thick, deep marine siliciclastic deposits (Olivero and Malumián, 2002). Within the fold and thrust belt, the deposits of the older clastic wedges include a Maas-trichtian-Danian succession, the Late Paleocene-Early Eocene Río Claro Group, and the late Middle to Late Eocene La Despedida Group. These deposits are highly deformed and reach an aggregate thickness in excess of 3.500 m (Olivero *et al.*, 2002; 2003). The youngest, Oligocene-Miocene clastic wedge is principally exposed outside the folded belt and consists mainly of subhorizontal strata, the *c.* 1 km thick Cabo Domingo Group (Malumián and Olivero, 2006).

At the Cabo Campo del Medio-Punta Torcida anticline (figure 1), a very thick (*c.* 1.600 m) Eocene sedimentary succession comprises the Punta Torcida Formation, Early Eocene; the Leticia Formation, late Middle Eocene; and the Cerro Colorado Formation, late Middle to Late Eocene (figure 2).

The Punta Torcida Formation of the Río Claro Group is dominated by dark gray mudstones deposited under dysaerobic conditions, with sparse intercalation of thin-bedded turbidite sandstones (*c.* 220 m thick). At the northern limb of the anticline, the upper part of the Punta Torcida Formation includes an additional, unnamed sedimentary package (*c.* 225 m thick) consisting of thick-bedded turbidite sandstones, tuffs, and distorted mudstones. Trace fossils, including graphoglyptids, are common in some horizons of the unnamed, upper package. These deposits conform a turbidite system that includes the following elements: basin (basal, thin bedded turbidites); base of slope (mid, thick-bedded turbidites); and slope (upper, distorted mudstones). Planktonic foraminifers indicate a middle Early Eocene age equivalent to the *G. wilcoxensis* Zone from New Zealand, or the tropical equivalent Zone P7 to P8, or Zone AP6 from Antarctica (Olivero and Malumián, 1999).

La Despedida Group rests over the Río Claro Group on a deeply incised unconformity. The basal Leticia Formation is composed of three main sandstone-dominated intervals, which have a complex ar-

chitecture and display variable thickness along the northern and southern limbs of the anticline, *c.* 200 m and 500 m, respectively. The lower and upper intervals consist of thick, cross-bedded and parallel-laminated, channelized sandstone bodies, with minor, highly bioturbated heterolithic beds, which represent deltaic and estuarine settings (Olivero and López C., 2001). The scarcity of foraminifers and the absence of planktonic foraminifers suggest marginal, shallow, and restricted marine conditions for the lower and upper intervals of the Leticia Formation (Olivero and Malumián, 1999). The middle interval consists of glauconitic, fossiliferous, and highly bioturbated fine-grained sandstones, representing shelf settings. Minor horizons bear planktonic foraminifers and nannoplankton indicative of the *G. index* Zone to *G. inconspicua* Zone of New Zealand, or the equivalent to the interval upper Zone P12 to lower Zone P14 of tropical areas, *i.e.*, late Middle Eocene (Olivero and Malumián, 1999).

The overlying Cerro Colorado Formation (*c.* 855 m thick) consists of a vertical stacking of four coarsening and thickening upwards successions, included in the CCa, CCb, CCc, and CCd members, respectively. Each member is composed of dark gray mudstones at the base, regular intercalation of mudstones and turbidites at the mid part, and thick sandstones and pebbly sandstones at the top. The uppermost CCd member bears abundant radiolarians and planktonic foraminifera typical of an oxygen minimum habitat, indicative of a Late Eocene age (upper Zone P15 to upper Zone P16). The microfauna and stratigraphic position of the lower three members are consistent with a latest Middle Eocene age (mid Zone P14 to lower Zone P15, Olivero and Malumián, 1999). Foraminifers of the three lower members of the Cerro Colorado Formation represent neritic settings, whereas those in the uppermost CCd member record a marked deepening (Olivero and Malumián, 1999; Malumián and Olivero, 2006). The CCa, CCc, and CCd members have several horizons with abundant graphoglyptids.

The Cabo Domingo Group (Malumián and Olivero, 2006) started in the latest Eocene with a major deepening phase represented in the basin depocenter by the uppermost part of the Cerro Colorado Formation, which records the last appearance datum (LAD) of *Globigerinatheka index* and the
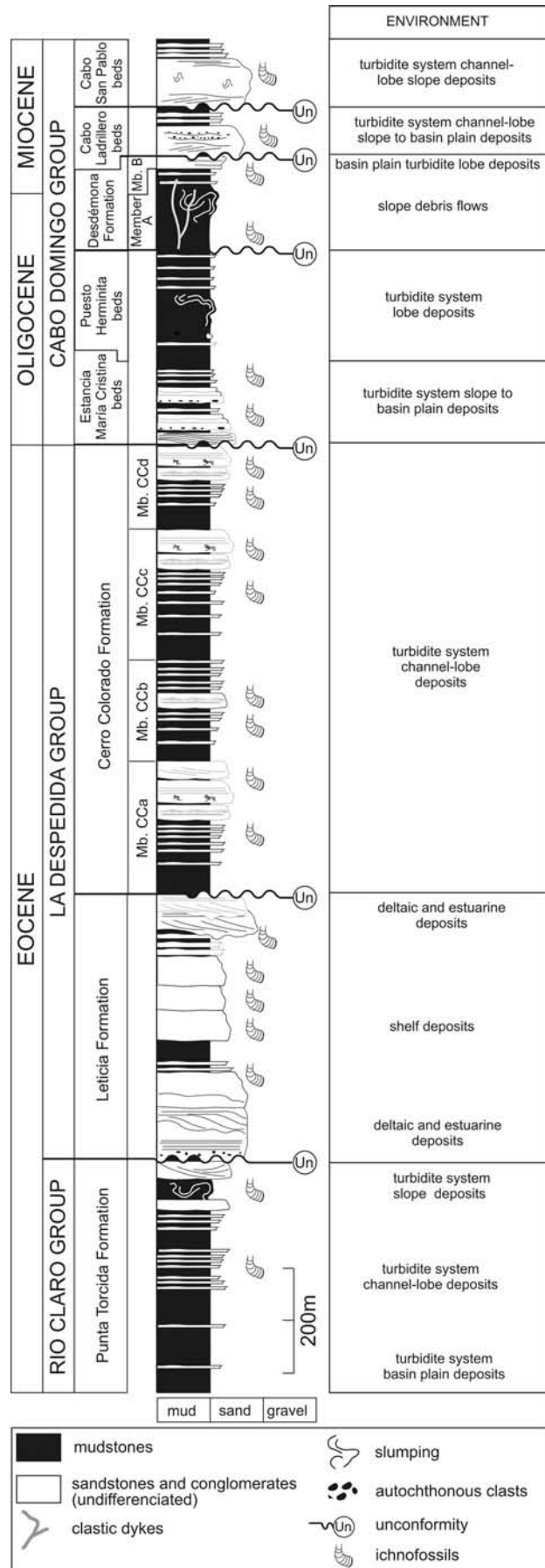

Figure 2. Schematic Early Eocene-Early Miocene stratigraphic column with location of main trace fossil bearing horizons and generalized paleoenvironmental conditions / *columna estratigráfica esquemática del Eoceno Temprano-Mioceno Temprano con la situación de los principales horizontes con trazas fósiles y paleoambientes generalizados.*

first appearance datum (FAD) of *Praetenuitella insolita* and *Isthmolithus recurvus*. The following Estancia María Cristina beds (claystones and sandstones, earliest Oligocene) and Puesto Herminita beds (claystones, Oligocene), with residual agglutinated foraminifera, were deposited below the calcite compensation depth during the maximum deepening of the basin that allowed for the entrance of corrosive Antarctic waters. The Desdémona Formation (tuffaceous, bioturbated mudstones deposited at or near the lisocline, with large slumped blocks), the Cabo Ladrillero beds (glauconitic sandstones and mudstones with outer neritic foraminifers, and carbonaceous mudstones, fine-grained sandstones and claystones with residual assemblages of *Spirosigmoilinella-Martinottiella*), and the Cabo San Pablo beds (sandstones and claystones) represents the latest Oligocene-early Miocene high sea level conditions. An extended unconformity and generalized regression is represented at *c.* 21 Ma. The overlying Cabo Viamonte beds (coarse breccias, conglomerates, sandstones and mudstones) represent the Neogene high sea level and climatic optimum (Malumián and Olivero, 2006), but are not the subject of this paper.

Ichnotaxonomy

Trace fossils are ordered alphabetically and descriptions are restricted to selected taxa, which were chosen by their paleoenvironmental significance or rarity of distribution in the Cenozoic of southern South America. Most of the material was studied in the field; the repository of collected material is the Laboratorio de Geología Andina, Centro Austral de Investigaciones Científicas, and it is identified with the labels CADIC PI 20, and CADIC PI 46 to 58.

Ichnogenus *Cardioichnus* Smith and Crimes, 1983

Cardioichnus isp.
Figure 3.1

Material. Many field specimens and one collected slab (CADIC PI 46) with one specimen.

Description. Resting trace, ovoid to subquadrate in outline, continuous with slightly sinuous burrow, preserved as positive hyporelief.
Remarks. Poor preservation of central V-shaped area and the lack of spine impressions avoid ichnospecific assignment. *Cardioichnus* ranges from Lower Cretaceous (Monaco *et al.*, 2005) to early Pliocene (Gibert and Martinell, 1994).
Occurrence. Cerro Colorado Formation, CCc member, late Middle Eocene and Cabo San Pablo beds, Early Miocene.

Ichnogenus *Cosmorhaphe* Fuchs, 1895

Cosmorhaphe isp.
Figure 3.2

Material. Field picture of one incomplete specimen.

Description. Hypichnial trace fossil with two orders of meanders. The strings are 2.7-2.8 mm in diameter.
Remarks. Incomplete preservation in a weathered surface avoids ichnospecific assignment. This graphoglyptid burrow is commonly found in the deep-marine *Nereites* ichnofacies. It ranges from Cambrian (Narbonne *et al.*, 1987) to Holocene (Ekdale, 1980).
Occurrence. Cerro Colorado Formation, CCa member, late Middle Eocene.

Ichnogenus *Curvolithus* Fritsch, 1908

Curvolithus simplex Buatois, Mángano, Mikuláš
and Maples, 1998
Figures 3.3-4

Material. Abundant specimens studied in the field and one polished slab (CADIC PI 47) with several specimens.

Description. Horizontal to oblique, straight to slightly curved endichnial burrows. Upper surface is trilobate, with a central lobe wider than the marginal ones. The central lobe is commonly divided by a furrow. Lower surface is bilobate. Burrows are about 10 mm in width.
Remarks. Buatois *et al.* (1998) distinguished two ich-

Figure 3. 1, *Cardioichnus* isp. Cabo San Pablo beds. CADIC PI 46. Positive hyporelief / *hiporelieve positivo*. **2,** *Cosmorhaphe* isp. Cerro Colorado Formation. Positive hyporelief / *hiporelieve positivo*. **3-4,** *Curvolithus simplex*. Leticia Formation. **3,** Full relief preservation / *preservación en relieve completo*. **4,** Lower bedding plane with bilobate, positive hyporelief and upper trilobate surface in negative hyporelief / *vista basal en hiporelieve positivo bilobado y superficie trilobada en hiporelieve negativo*. **5,** *Desmograpton ichthyforme.* Cerro Colorado Formation. Positive hyporelief / *hiporelieve positivo*. **6,** *Gyrophyllites rehsteineri*. Cabo Ladrillero beds. Full relief / *relieve completo*. **7,** *Gyrochorte comosa.* Leticia Formation. Basal view showing two bilobate furrows separated by a narrow crest (arrows) cross-cutting *Curvolithus simplex* (Cu) / *vista basal mostrando dos surcos separados por una cresta (flechas) cortando a* **Curvolithus simplex** *(Cu)*. **8,** *Helicolithus ramosus.* Cerro Colorado Formation. Positive hyporelief / *hiporelieve positivo*. **9,** *Helicolithus* isp. Punta Torcida Formation. Positive hyporelief / *hiporelieve positivo*. **10,** *Helicorhaphe* isp. Punta Torcida Formation. Positive hyporelief / *hiporelieve positivo*. Scale bar: 1 cm. Field phothographs except figure 3.1 / *Escala: 1 cm. Fotografías de campo, excepto figure 3.1.*
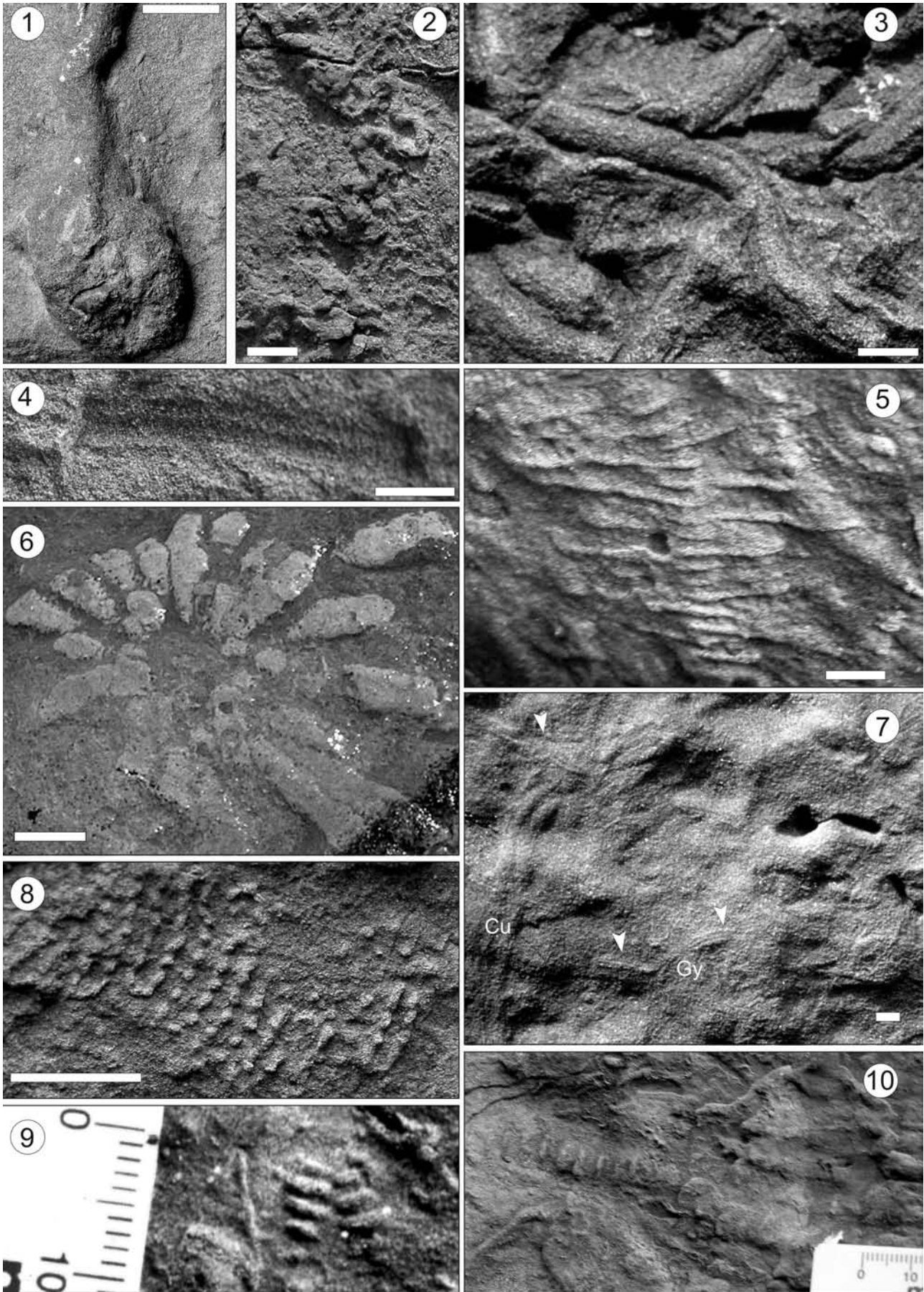
nospecies of *Curvolithus*: *C. multiplex* Fritsch 1908, with a convex quadralobate lower surface, and *C. simplex*, with a uni- to trilobate concave or convex lower surface. *Curvolithus* differs from similar trace fossils, such as *Psammichnites*, *Aulichnites* and *Gyrochorte*, by its trilobate upper surface. It occurs from Precambrian to Miocene (Buatois *et al.*, 1998).

Occurrence. Upper part of the Leticia Formation, late Middle Eocene.

Ichnogenus *Desmograpton* Fuchs, 1895

Desmograpton ichthyforme (Macsotay, 1967)
Figure 3.5

Material. Three specimens studied in the field.

Description. Hypichnial narrow parallel ridges corresponding to angular semi-meanders joined at the center in an alternate position, connecting bars are not preserved. The string is 1.5 to 2 mm in diameter.

Remarks. Seilacher (1977) includes *Desmograpton* in the graphoglyptid group of biramous meanders. It occurs from Silurian (McCann, 1989) to Miocene (Uchman, 1995).

Occurrence. Cerro Colorado Formation, CCa member, late Middle Eocene.

Ichnogenus *Gyrophyllites* Glocker, 1841

Gyrophyllites rehsteineri (Fischer-Ooster, 1858)
Figure 3.6

Material. Three field specimens.

Description. Radial trace fossil with horizontal and overlapping lobes that radiate from a vertical shaft. Lobes unbranched, drop-like in outline and with a rounded margin at the distal parts. In vertical section, lobes radiate at several levels. Total diameter is 50 mm. Endichnial preservation.

Remarks. The swollen, radial feeding galleries organized around a vertical axis, which do not branch or cut across each other, were considered as diagnostic features of *Gyrophyllites* (Fu, 1991). These features differentiate the present material from other ichnogenera with radial structure. *Gyrophyllites* is recorded from the Lower Paleozoic of Argentina (Mángano *et al.*, 2005) to the Miocene (this paper).

Occurrence. Cabo Ladrillero beds, Early Miocene.

Ichnogenus *Gyrochorte* Heer, 1865

Gyrochorte comosa Heer, 1865
Figure 3.7

Material. Abundant specimens studied in the field and one polished slab (CADIC PI 48) with several specimens.

Description. Hypichnial, curved burrows composed of two bilobate furrows separated by a narrow crest. Polished sections show that the burrow is vertically extended.

Remarks. All the specimens are only preserved in basal view. *Gyrochorte* has a discontinuous stratigraphic record (*cf.* Gibert, 2003), and the material from Tierra del Fuego is the only one recorded in the Paleogene.

Occurrence. Lower and upper parts of the Leticia Formation, late Middle Eocene.

Ichnogenus *Helicolithus* Azpeitia-Moros, 1933

Helicolithus ramosus (Vialov, 1971)
Figure 3.8

Material. Many specimens studied in the field and two slabs (CADIC PI 49-50) with two specimens.

Description. Hypichnial meandering rows of small dots corresponding to a meandering and helicoidal string.

Remarks. Uchman (2001) referred this type of preservation to washed-out parts of *Helicolithus* when only the apices of the turns are preserved. *Helicolithus* is a very common graphoglyptid in the Eocene flysch of Tierra del Fuego. This ichnogenus ranges from Late Cretaceous to Miocene (Uchman, 2003).

Occurrence. Cerro Colorado Formation, CCa and CCd members, late Middle Eocene and Late Eocene, respectively.

Helicolithus isp.
Figure 3.9

Material. One field specimen and a plaster cast (CADIC PI 51).

Description. Small segment of a horizontal winding trace fossil, with second order of helicoidal turns comprising two rows of four strings of small bars displaying an alternate and parallel pattern. Preserved at the sole of a sandstone bed.

Remarks. The alternate and parallel pattern of the two rows of bars suggests the "echelon" pattern (Seilacher, 1977) of *Helicolithus*. Incomplete preservation avoids ichnospecific assignment.

Occurrence. Punta Torcida Formation, Early Eocene.

Ichnogenus *Helicorhaphe* Ksiαzkiewicz, 1961

Helicorhaphe isp.
Figure 3.10

Material. One field specimen and a plaster cast (CADIC PI 52).

Description. Hypichnial, helicoidal string twisted along a horizontal axis. The trace is 60-70 mm long and the helicoidal ring is 1.5 mm in diameter.

Remarks. *Helicorhaphe* is a relatively rare graphoglyptid reported only from the Eocene of Poland and probably the Miocene of Iran (*cf.* Uchman, 1998).

Occurrence. Punta Torcida Formation, Early Eocene.

Ichnogenus *Helminthorhaphe* Seilacher, 1977

Helminthorhaphe isp.
Figure 4.1

Material. One specimen (CADIC PI 53).

Description. Horizontal, non-branching, meandering strings 2.2 to 2.8 mm in diameter, with high amplitude of irregular meanders, preserved as convex hyporelief on the soles of sandstone turbidites. Strings are filled with sand grains.

Remarks. Uchman (1995) discussed *Helminthoida* and *Helminthorhaphe* (Seilacher, 1977) and included *Helminthoida crassa* Schafhäutl within *Nereites irregularis* MacLeay.

He also proposed *Helminthorhaphe japonica* (Tanaka, 1970) as the type ichnospecies of *Helminthorhaphe*, and *Helminthorhaphe flexuosa* exclusively for convex hypichnial forms such as *Helminthoida crassa* Schafhäutl *sensu* Ksiazkiewicz (1970, 1977) and *Helminthorhaphe crassa* (Schafhäutl) *sensu* Seilacher (1977). The material of *Helminthorhaphe* isp. from Tierra del Fuego has an irregular meandering pattern similar to that of *Helminthorhaphe flexuosa* Uchman (1995) and apparently lacks the typical bulging turns of *Helminthorhaphe japonica* (Tanaka). String diameter is considerably bigger than those of specimens described in the literature (*e.g.* Uchman, 1995), but size is not a useful ichnotaxobase in this case. Only one incomplete specimen was recorded and does not allow ichnospecific assignment. *Helminthorhaphe* occurs from Early Cretaceous to Miocene (Uchman, 2003).

Occurrence. Cerro Colorado Formation, CCa member, late Middle Eocene.

Ichnogenus *Megagrapton* Ksiazkiewicz, 1968

Megagrapton submontanum (Azpeitia-Moros, 1933)
Figure 4.2

2001. *Protopaleodyction* isp. Olivero and López C.

Material. Many specimens studied in the field and one specimen cast (CADIC PI 54).

Description. Irregular nets of winding strings with short lateral appendages. Preserved as positive hyporelief. The string is 3-4 mm in diameter.

Remarks. Differences between *Protopaleodictyon* and *Megagrapton* were discussed by Uchman (1998). *M. submontanum* occurs in flysch deposits from Cenomanian to Eocene (Uchman, 1998).

Occurrence. Punta Torcida Formation, Early Eocene, and Cerro Colorado Formation, CCa member, late Middle Eocene.

Ichnogenus *Nereites* MacLeay, 1839

Nereites isp.
Figure 4.3

Material. Many specimens studied in the field.

Description. Horizontal, meandering burrows consisting of a meniscate backfilled median tunnel surrounded by a poorly developed, commonly not preserved, reworked zone. Meniscate area about 4.2-4.5 mm wide. Meanders irregular, but generally with partial overlapping turns.

Remarks. *Nereites* isp. is preserved at the top of fine-grained, organic rich sandstone beds interbedded with thin mudstone beds (Carmona *et al.*, 2006). *Nereites* isp. is similar to *N. irregularis* (Schafhäutl) but the holotype of the latter has more regular, guided meanders. *N. missuriensis* (Weller, 1899) contrasts by loose, winding meanders with a wide central backfilled area and enveloped zone of similar thickness (*cf.* Uchman, 1995). *Nereites* ranges from the late Precambrian to the Miocene (*cf.* Uchman, 1995). Modern forms, similar to *Nereites* are also known in the deep-sea bottoms (Wetzel, 2002).

Occurrence. Cerro Colorado Formation, CCc member, late Middle Eocene, and Cabo San Pablo beds, Early Miocene.

Ichnogenus *Ophiomorpha* Lundgren, 1891

Ophiomorpha annulata (Ksiazkiewicz, 1977)
Figure 4.4

Material. Several field specimens.

Description. Straight to winding, horizontal, cylindrical, lined and branched trace fossil. Y-shaped branching at acute angles and dead ends branches are common. Tubes are 5.5-6.8 mm in diameter. Pellets mostly elongate, transversal to burrow axis and not always well developed.

Remarks. Preserved on top of sandy turbidites and distributed along bedding surfaces rich in plant debris. Uchman (1995, 1998) considered *Ophiomorpha annulata* and *O. rudis* as normal components of the *Nereites* ichnofacies.
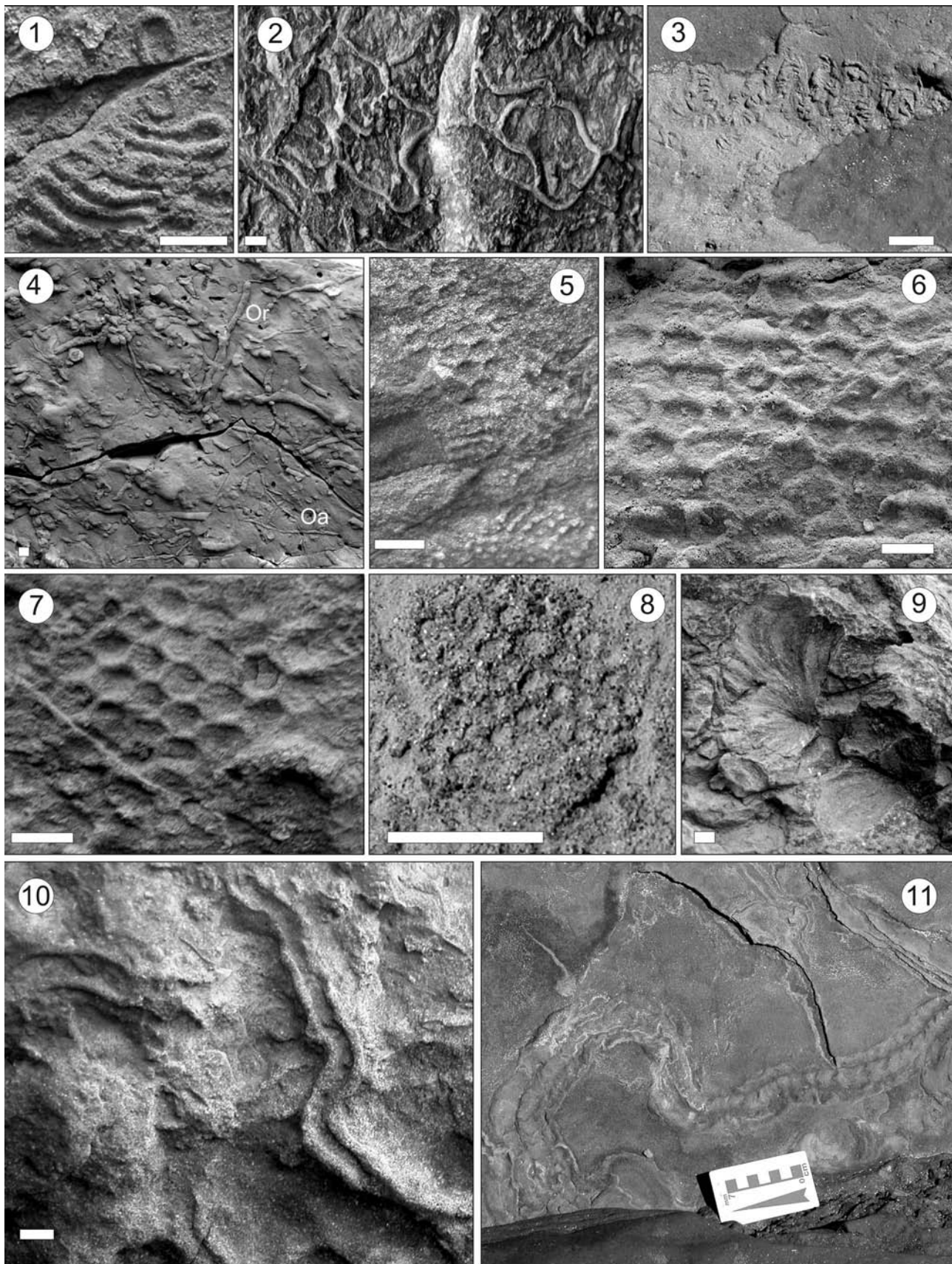
Figure 4. 1, *Helminthorhaphe* isp. Cerro Colorado Formation. Positive hyporelief / *hiporelieve positivo*. **2,** *Megagrapton submontanum.* Punta Torcida Formation. Positive hyporelief / *hiporelieve positivo*. **3,** *Nereites* isp. Cabo San Pablo beds. Positive epirelief / *epirelieve positivo*. **4,** *Ophiomorpha rudis* (Or) and *Ophiomorpha annulata* (Oa). Cerro Colorado Formation. Dense association at the sole of a sand-

Occurrence. Cerro Colorado Formation, CCa and CCb members, late Middle Eocene.

Ophiomorpha rudis (Ksiazkiewicz, 1977)
Figure 4.4

Material. Several burrow segments (CADIC PI 55) and many field specimens.

Description. Horizontal to oblique, cylindrical branched burrows, commonly with chevron-like backfill. Exterior surface partly covered with small pellets and bioglyphs. Single burrow segments with changes in diameter ranging from 5.7 to 20 mm. Some horizontal burrows segments as long as 200 mm. When present, branching is Y-shaped, with marked swellings at the point of bifurcation. Overcrossing and anastomosing are common.
Remarks. Preserved as full relief or as positive hyporelief at the base of fine-grained sandstone beds (López Cabrera *et al.*, 2006). Uchman (2004) typifies the *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies for medium- and thick-bedded flysch deposits, mainly of channels and proximal lobes.
Occurrence. Punta Torcida Formation, Early Eocene; Cerro Colorado Formation, CCa and CCb members, late Middle Eocene; and Desdémona Formation and Cabo Ladrillero beds, Early Miocene.

Ichnogenus *Paleodictyon* Meneghini in Savi and Meneghini, 1850

Remarks. Uchman (1995) reviewed *Paleodictyon* and his morphometric classification is followed here. Seilacher (1974) proposed the *Paleodictyon* ichnosubfacies within the deep-sea *Nereites* ichnofacies. *Paleodictyon* was recorded from Cambrian to recent. The latter record includes comparable traces recorded by several authors in the modern deep sea (Ekdale, 1980; Miller, 1991; Rona *et al.*, 2003). Seilacher (1977) and Roder (1971) interpreted *Paleodictyon* as a burrow system made to cultivate or trap microorganisms. Garlick and Miller (1993) suggest a small elongate crustacean as the tracemaker.

Paleodictyon strozzi Meneghini in Savi and Meneghini, 1850
Figure 4.5

Material. One specimen studied in the field.

Description. Small hexagonal net 0.81-0.88 mm in string diameter, mesh-size 4.9-4.8 mm; preserved as positive hyporelief.
Occurrence. Cerro Colorado Formation, CCa member, late Middle Eocene.

Paleodictyon maximum (Eichwald, 1868)
Figure 4.6

Material. One specimen studied in the field.

Description. Hypichnial horizontal net of medium size. String diameter 2.8 mm and total mesh size 11.8 mm.
Occurrence. Cerro Colorado Formation, CCa member late Middle Eocene.

Paleodictyon majus Meneghini in Peruzzi, 1880
Figure 4.7

Material. Several specimens studied in the field.

Description. Horizontal medium size hexagonal net, string diameter ranging from 1.2 to 1.7 mm; mesh-size ranging from 6.1 to 8.6 mm. Preserved as positive hyporelief.
Occurrence. Punta Torcida Formation, Early Eocene, Cerro Colorado Formation, CCa, CCc, and CCd members, the latter includes specimens partly covered by thin pyrite lamina, late Middle Eocene and Late Eocene.

Paleodictyon minimum Sacco, 1888
Figure 4.8

Material. Two specimens studied in the field.

Description. Very small, hypichnial horizontal net. String diameter 0.46-0.5 mm and total mesh size 2 mm.
Occurrence. Cabo San Pablo beds, Early Miocene.

Ichnogenus *Paradictyodora* Olivero, Buatois and Scasso, 2004

Paradictyodora antarctica Olivero, Buatois and Scasso, 2004
Figure 4.9

stone bed / *asociación densa en la base de un banco de arenisca.* **5,** *Paleodictyon strozzi.* Cerro Colorado Formation. Positive hyporelief / *hiporelieve positivo.* **6,** *Paleodictyon maximum.* Punta Torcida Formation. Positive hyporelief / Hiporelieve positivo. **7,** *Paleodictyon majus.* Cerro Colorado Formation. Positive hyporelief / *hiporelieve positivo.* **8,** *Paleodictyon minimum.* Cabo San Pablo beds. Positive hyporelief / *hiporelieve positivo.* **9,** *Paradictyodora antarctica.* Leticia Formation. Upper bedding plane view of a sandstone bed with two specimens / *vista en planta de la parte superior de un banco de arenisca con dos especímenes.* **10,** *Scolicia strozzi.* Cabo San Pablo beds. Positive hyporelief / *hiporelieve positivo.* **11,** *Scolicia prisca.* Cabo San Pablo beds. Negative epirelief / *epirelieve negativo.* Scale bar: 1cm. Field phothographs / *escala: 1 cm. Fotografías de campo.*

Material. Two collected specimens (CADIC PI 20) and several field specimens.

Description. Conical, upward enlarging vertical spreite structure with subvertical folded laminae produced by the migration of a J-shaped tube. Full relief preservation.

Remarks. The upward opening conical shape corresponds to one of the four morphotypes of *Paradictyodora antarctica* (Olivero *et al.*, 2004). *Paradictyodora* has been recorded from the Upper Cretaceous of Antarctica and the Eocene to Miocene of Tierra del Fuego.

Occurrence. Punta Torcida Formation, Early Eocene; Leticia and Cerro Colorado Formations, late Middle Eocene; Estancia María Cristina beds, Oligocene; and Cabo Ladrillero and Cabo San Pablo beds, Early Miocene.

Ichnogenus *Scolicia* de Quatrefages, 1849

Scolicia strozzi (Savi and Meneghini, 1850)
Figure 4.10

Material. Several specimens studied in the field and one collected slab (CADIC PI 56) with two specimens.

Description. Hypichnial, meandering to straight bilobate ridge separated by a median furrow, about 13 mm wide. Ridge width ranging from 2 to 8 mm.

Remarks. *S. strozzi* represents washed out and casts of *Scolicia* burrows. Straight to gently winding specimens are assigned to *S. strozzi* var. *vagans* (Ksiazkiewicz, 1977) and may correspond to locomotion activity of echinoids (Uchman, 1995).

Occurrence. Cabo Ladrillero and Cabo San Pablo beds, Early Miocene.

Scolicia prisca de Quatrefages, 1849
Figures 4.11

Material. Abundant specimens studied in the field. One collected slab (CADIC PI 57) with three specimens.

Description. Epichnial trilobate furrows, 40.3-50.2 mm wide, with concave, semicircular bottom and oblique slopes. Two parallel grooves occur along the edges of the bottom. Preserved at the top of sandstone beds with linguoid ripples, interbedded with thin mudstone laminae.

Remarks. Uchman (1995) reviewed this ichnogenus and included *Taphrhelminthopsis, Laminites, Subphyllochorda* and *Taphrhelminthoida* as toponomic variants of *Scolicia*. The producers are irregular echinoids of the *Spatangus* group, with two drainage tufts that produce the drain channels (*cf.* Smith and Crimes, 1983; Uchman, 1995).

Occurrence. Cabo San Pablo beds, Early Miocene.

Scolicia isp.

Material. Several specimens studied in the field.

Description. Horizontal, cylindrical, straight to sinuous trace fossil with backfill menisci. Full relief preservation.

Remarks. Incomplete preservation of these specimens precludes ichnospecific assignment.

Occurrence. Cerro Colorado Formation, CCd member, Late Eocene and Cabo Ladrillero beds, Early Miocene.

Ichnogenus *Stelloglyphus* Vialov, 1964

Stelloglyphus isp.
Figure 5.1

Material. Many specimens studied in the field.

Description. Rosette structure composed of several crowded lobes radiating at different levels from a central point. Lobes overlap and are generally curved at distal points. Internal fill with a well-defined meniscus-like structure. Rosette *c.* 92.5 mm in diameter. Endichnial preservation.

Remarks. Burrow morphology shows close similarity to *Gyrophyllites* Glocker but internal fill of *Gyrophyllites* lacks menisci (Uchman pers. comm.). Branched radial lobes, as diagnostic of *Cladichnus fischeri* (Heer, 1877), are absent in *Stelloglyphus* isp.

Occurrence. Cabo San Pablo beds, Early Miocene.

Ichnogenus *Urohelminthoida* Sacco, 1888

Urohelminthoida appendiculata Heer, 1877
Figure 5.2

Material. One collected specimen (CADIC PI 58) and several specimens studied in the field.

Description. Very small trace fossil consisting of hypichnial strings with tight meanders and lateral appendages protruding from the apical part of the meanders. Strings are 1.3 mm in diameter.

Remarks. Among graphoglyptids, *Urohelminthoida* was placed into the group of uniramous meanders, with a diagnostic lateral branch on the apex of each undulation (Seilacher, 1977). *U. dertonensis* Sacco, 1888 displays lateral appendages which pass straight into one arm of the meander but forms an angle with the second arm (Uchman, 1995). *Urohelminthoida* is recorded from the Jurassic to the Miocene (*cf.* Uchman, 1995). Modern traces similar to *Urohel-*
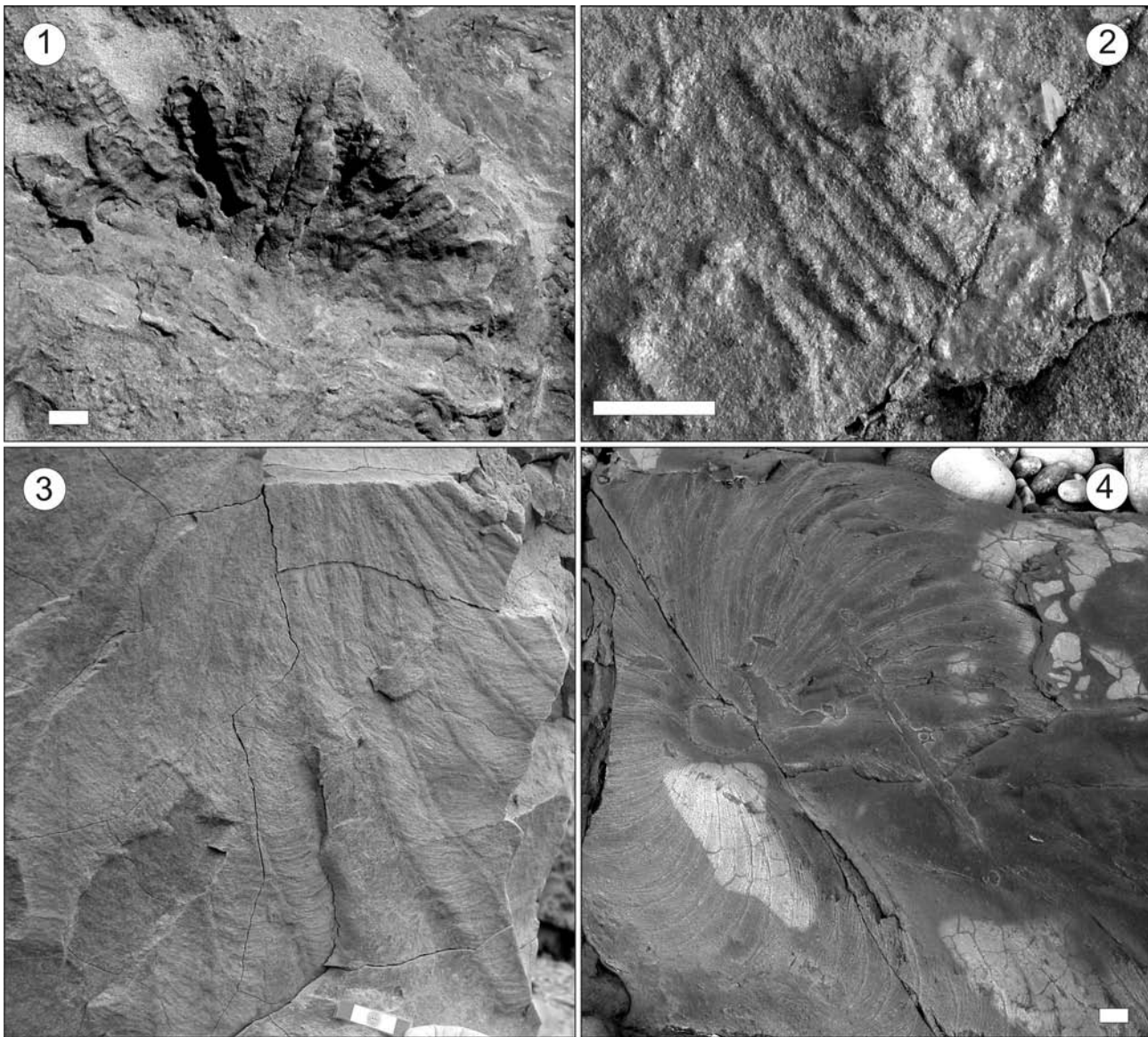
Figure 5. 1, *Stelloglyphus* isp. Cabo San Pablo beds. Incomplete specimen. Note lobes with well-defined meniscus in the filling of the rosette structure / espécimen incompleto. Note el relleno meniscado de los lóbulos en la estructura en roseta. **2,** *Urohelminthoida appendiculata*. Cerro Colorado Formation. Positive hyporelief / hiporelieve positivo. **3-4,** *Zoophycos* ispp. **3,** *Zoophycos* isp. Form B, Cerrro Colorado Formation. Note radial ribs across planar spreite / note las costillas radiales perpendiculares al spreite planar. **4,** *Zoophycos* isp Form C, Desdémona Formation. Note minor lamellae separated by mayor lamellae. Endichnial preservation / *note las láminas menores limitadas por láminas radiales mayores. Preservación endicnia.* Scale in centimeters. Field phothographs / *escala en centímetros. Fotografías de campo.*

minthoida were observed in the deep-sea floor (Gaillard, 1991).

Occurrence. Cerro Colorado Formation, CCd member, Late Eocene.

Ichnogenus ***Zoophycos*** Massalongo, 1855

Zoophycos ispp.
Figures 5.3-4

Material. Many field specimens.

Description. The material includes three main forms.

Form A, includes relatively simple, circular spreite structure. Form B (figure 5.3) consists of large planar spreite trace fossil with well developed radial ribs separating bundles of minor, sigmoidal or U-shaped spreite lamellae. Form C (figure 5.4), consists of large, planar, lobate spreite trace fossil with well developed bundles of minor sigmoidal lamellae limited by a major, radial, sub-parallel lamella. Spreite filled with large, ovoid to elongate pellets.

Remarks. Form B, characterized by radial ribs, is similar to the *Echinospira* group (*cf.* Uchman, 1995) and Form C, without radial ribs, to *Zoophycos rhodensis* Bromley and Hanken, 2003.

Occurrence. Form A was recorded from the Punta Torcida Formation, Early Eocene; Form B in the Cerro Colorado Formation, late Middle to Late Eocene and Cabo San Pablo beds, Early Miocene; and Form C in the Estancia María Cristina beds, Oligocene and Desdémona Formation, Early Miocene.

Discussion and conclusions

Two distinctive trace fossil assemblages are recognized in the studied Cenozoic deposits from Tierra del Fuego (figure 6). One is characterized by ichnogenera commonly found in the *Cruziana* ichnofacies and is restricted to the marginal marine and shelf deposits of the upper Middle Eocene Leticia Formation. The other one is characterized by ichnogenera common to the *Zoophycos* and *Nereites* ichnofacies, and is found in turbidite systems of the Eocene, Oligocene, and Miocene. Their paleoenvironmental significance and implication for the diversity trends of Cenozoic deep-sea trace fossils are briefly discussed below.

Trace fossils of the Leticia Formation

The following ichnogenera are restricted to the Leticia Formation: *Asterosoma*, *Rhizocorallium*, *Curvolithus*, *Gyrochorte*, *Palaeophycus*, *Patagonichnus*, *Rosselia*, *Schaubcylindrichnus*, *Taenidium* and *Teichichnus* (figure 6). They are not distributed uniformly and three distinctive packages located at the basal, middle, and upper parts of the formation are recognized. The lower and upper parts of the Leticia Formation are dominated by *Curvolithus*, *Diplocraterion*, *Gyrochorte*, *Rosselia*, *Patagonichnus* and *Tasselia*. The middle part is dominated by *Asterosoma*, *Palaeophycus*, *Paradictyodora*, *Planolites*, *Rhizocorallium*, *Schaubcylindrichnus*, *Taenidium* and *Teichichnus*. The ichnofabric features are also distinctive: whereas the lower and upper parts of the Leticia Formation includes a few centimeter thick bioturbated horizons, the middle part of the Formation includes meter thick, often several tens of meters thick, totally bioturbated packages. These two contrasting bioturbation patterns and ichnoassemblages of the Leticia Formation were interpreted as a symmetric, transgressive-regressive cycle, with the lower and upper parts representing shallow marine, and the middle part representing shelf settings (Olivero and López C., 2001).

Trace fossils from the turbidite systems

The trace fossil associations from the Early Eocene, Mid-Late Eocene, Oligocene and Miocene turbidite systems differ markedly from those of the Leticia Formation. The main characteristic components are *Scolicia*, *Chondrites*, *Gyrophyllites*, *Nereites*, *Phycodes*, *Phycosiphon*, *Phymatoderma*, *Stelloglyphus*, *Zoophycos*, *Ophiomorpha rudis*, *O. annulata* and several graphoglyptid ichnogenera (figure 6). These trace fossils, however, are not always found together, instead distinctive ichnoassemblages are recurrent in particular sedimentary facies.

Graphoglyptids are more common and diverse in fine grained, thin-bedded turbidites interbedded with thick mudstone beds, particularly in the basal unnamed strata of the Punta Torcida Formation (Early Eocene) and the CCa, CCc, and CCd members of the Cerro Colorado Formation (late Middle to Late Eocene). *Paleodictyon*, *Helicolithus*, *Helminthorhaphe*, *Desmograpton* and *Megagrapton*, particularly the two first ichnogenera, are relatively common, whereas *Cosmorhaphe*, *Helicorhaphe* and *Urohelminthoida* are rare. The thin-bedded turbidites and thick mudstone beds are interpreted as lobe deposits of turbidite systems and the trace fossil assemblage is assigned to the *Paleodictyon* ichnosubfacies (*cf.* Seilacher, 1974) within the *Nereites* ichnofacies. Graphoglyptids are considered diagnostic trace fossils of the *Nereites* ichnofacies, which is generally interpreted as indicative of deep-sea paleoenvironments, particularly in the Mesozoic and Cenozoic (*cf.* Seilacher, 1974, 1977; Uchman, 2004). In contrast to this interpretation, the foraminifers of the graphoglyptid-bearing deposits of the CCa and CCc members of the Cerro Colorado Formation suggest shallower, neritic settings (Olivero and Malumián, 1999; Malumián and Olivero, 2006). Some graphoglyptids, particularly *Paleodictyon* are recorded at the sole of event beds generated in shallower settings (see Fürsich *et al.*, 2007 and references therein). However, the graphoglyptids from Tierra del Fuego are not associated with typical elements of the *Cruziana* ichnofacies, as those described by Fürsich et al. (2007) for the Jurassic *Paleodictyon*-bearing storm and prodelta beds from Iran. The sedimentary facies and graphoglytid association from the Cerro Colorado Formation of Tierra del Fuego seems to be partially comparable to the Eocene Kusuri Formation in Turkey, where the occurrence of graphoglyptid elements in neritic deposits was interpreted as originated in a rapidly-shoaling, restricted basin (Uchman *et*

Figure 6. Eocene-Miocene stratigraphy, distribution of ichnogenera grouped by ethological categories, and total ichnogeneric diversity / *estratigrafía del Eoceno-Mioceno, distribución de icnogéneros agrupados por categorías etológicas y diversidad icnogenérica total.*

Ethological categories	EOCENE			OLIGOCENE			MIOCENE		STRATIGRAPHY / ICHNOGENERA DISTRIBUTION
	RIO CLARO GROUP	LA DESPEDIDA GROUP		CABO DOMINGO GROUP					
	Punta Torcida Formation	Leticia Formation	Cerro Colorado Formation	Estancia María Cristina Beds	Puesto Herminia Beds	Desdémona Formation	Cabo Ladrillero Beds	Cabo San Pablo Beds	
Cubichnia			X					X	Cardioichnus
Domichnia		X	X				X	X	Diplocraterion
	X	X	X			X	X		Ophiomorpha
		X							Schaubcylindrichnus
		X							Palaeophycus
		X							Rosselia
	X	X	X	X			X	X	Tasselia
		X			X	X		X	Thalassinoides
Repichnia		X							Curvolithus
		X							Gyrochorte
			X				X	X	Scolicia
								X	Protovirgularia
Fodinichnia		X						X	Asterosoma
	X		X	X			X	X	Chondrites
							X		Gyrophyllites
			X				X	X	Nereites
	X	X		X			X	X	Paradictyodora
	X	X							Planolites
		X							Patagonichnus
			X					X	Phycodes
			X					X	Phycosiphon
			X	X				X	Phymatoderma
		X							Rhizocorallium
								X	Stelloglyphus
		X							Taenidium
		X							Teichichnus
	X		X	X		X	X		Zoophycos
			X				X?		cf Rutichnus
Agrichnia			X						Cosmorhaphe
			X						Desmograpton
	X		X						Helicolithus
	X								Helicorhaphe
			X						Helminthorhaphe
	X		X						Megagrapton
	X		X	X				X	Paleodictyon
			X						Urohelminthoida
Total Igen.	10	16	19	6	1	3	10	15	36

al., 2004). Nevertheless, the analysis of this seemingly abnormal paleobathymetric record for the graphoglyptids of the Cerro Colorado Formation is out the scope of this paper and it requires a specific sedimentologic and paleoecologic study of the graphoglyptid-bearing strata.

Ophiomorpha rudis and *O. annulata* are associated commonly at the contact between thick-bedded turbidite sandstones and mudstones with high content of plant debris, where they could form dense mazes distributed preferentially along the bedding plane. These *Ophiomorpha* ichnospecies are relatively common in the sandstone-dominated intervals of the CCa and CCb members, Cerro Colorado Formation. Other thick-bedded sandstones, especially in the Cabo San Pablo beds, are characterized only by *Paleodictyon* and *Scolicia strozzi*. The occurrence of these trace fossils, and the sedimentary facies in which they are recorded, are consistent with the establishment of the ichnosubfacies of *Ophiomorpha rudis* for sand-rich, proximal channel-lobe deposits within the *Nereites* ichnofacies (*cf.* Uchman, 2001).

Scolicia prisca and *Nereites* isp. are commonly associated with thin, fine-grained sandstones with ripple lamination, rhythmically interbedded with thin mudstone beds rich in plant fragments (Carmona *et al.*, 2006). This ichnoassemblage is common in the Cerro Colorado Formation in distal, interbedded sandstone and mudstone, within the *Nereites* ichnofacies, and in the Cabo San Pablo beds in more proximal fine-grained beds.

Mudstone-dominated deformed beds involved in synsedimentary slumping are generally dominated by *Zoophycos* isp. This is the dominant trace fossil in the upper part of the unnamed strata of the Punta Torcida Formation and the lower part of the Desdémona Formation, both of which have been interpreted as representing slope deposits (*cf.* Olivero and López C., 2001; Malumián and Olivero, 2006), and thus they are included within the *Zoophycos* ichnofacies.

Diversity trends through Eocene to Miocene deep marine trace fossils

Uchman (2003, 2004) made a detailed analysis of Late Mesozoic-Cenozoic global trends in diversity of deep-sea trace fossils, mainly from sedimentary basins around the Tethys. After the Albian he found a rapid and continuous increase in diversity up to an optimum in the Eocene, then a marked drop at the Eocene-Oligocene boundary, and finally a reduced diversity in the Miocene. He also considered both the Eocene peak and the Oligocene drop in diversity as very distinctive.

In the Fuegian Andes, with the exception of the Maastrichtian Policarpo Formation, the Upper Cretaceous to Paleocene successions bear scarce trace fossils of low diversity (Olivero *et al.*, 2002, 2003) and ichnodiversity trends can only be studied for the Eocene-Miocene rocks. Within the turbidite successions (figure 6), the Early Eocene contains 10 ichnogenera (of which four are graphoglyptids); the late Middle Eocene-Upper Eocene 19 (of which seven are graphoglyptids); the Early Oligocene six (of which one is a graphoglyptid); the Oligocene one (without graphoglyptids); the uppermost Oligocene-basal Miocene three (without graphoglyptids); the basal Early Miocene nine (without graphoglyptids); and the late Early Miocene 15 ichnogenera (of which one is a graphoglyptid). Regarding the Eocene-Miocene trend in ichnodiversity, our data are partly in agreement with the findings of Uchman (2003, 2004), and they show a late Middle-Late Eocene optimum, an abrupt drop in the Oligocene, and a reduced ichnodiversity in the Early Miocene.

Uchman (2004) interpreted that these changes were controlled by competition and food supply, major paleoceanographic changes particularly bottom-water temperatures, and general tectonic conditions that favored an increased area of flysch deposits. Increased food supply, particularly phytodetritus, may have been favorable for graphoglyptids, which are mainly interpreted as specialized farmers that used phytodetritus for microbial cultivation. In an early study, Seilacher (1974) already noted that the increased graphoglyptid diversity in the Late Cretaceous might have been related to increased phytodetritus flux to the oceans associated with the terrestrial radiation of the angiosperms. Uchman (2004) related his ichnodiversity peak near the Paleocene-Eocene boundary to the advent of oligotrophic conditions associated to the Cenozoic thermal maximum and global warming of bottom waters. He also assigned the distinct Early Oligocene drop in ichnodiversity to the global crisis related to marked drop in seawater temperatures.

Whereas the ichnodiversity data from the Fuegian Andes seem to support Uchman's explanation for the Oligocene crisis in ichnodiversity, they are in contrast to his explanation for the Eocene optimum in diversity. Regarding the latter point, the distribution of trace fossils throughout the Early Eocene Punta Torcida Formation is not uniform. The lower and mid parts of the Formation are dominated by mudstones deposited in dysoxic to anoxic and warm bottom conditions (Olivero and Malumián, 1999). Trace fossils are very scarce and consist of *Planolites*, *Paradictyodora* and *Chondrites*. Trace fossils, including graphoglyptids, are more abundant in the upper, unnamed strata of the Punta Torcida Formation (figure

6). However, the Eocene peak in ichnodiversity in the Fuegian Andes, including the graphoglyptid peak in diversity, is found in the Cerro Colorado Formation of late Middle to Late Eocene age. This Formation bears different foraminiferal benthic assemblages that reflect cooling waters by replacement of the species known in the Leticia Formation by species of typical genera of temperate-cool water, such as *Ammoelphidiella*, *Antarcticella*, and *Buccella* (Malumián and Olivero, 2006). Thus, our data do not support the idea that increased Eocene ichnodiversity was controlled by global warming of bottom waters during the Cenozoic thermal maximum. On the contrary, ichnodiversity is higher in the upper Middle Eocene-Late Eocene of the Fuegian Andes, accompanying a cooling trend in the water masses (Malumián *et al.*, 2007).

A similar situation of increased diversity associated with a cooling trend of bottom waters is also found in the Maastrichtian of the Policarpo Formation, just above the inoceramid extinction level in the Fuegian Andes (Olivero *et al.*, 2003). The inoceramids were apparently adapted to warm and poorly oxygenated waters and their global extinction pulses, during the mid-Maastrichtian, were related to cooling and enhanced bottom ventilation, promoted by circulation of deep Antarctic waters. The strong contrast in the intensity of bioturbation between the upper Campanian-lower Maastrichtian Bahía Thetis Formation, almost devoid of trace fossils, and the highly bioturbated Maastrichtian-Danian Policarpo Formation reflects a change from dysoxic-anoxic to well ventilated bottom conditions, probably associated with the postulated paleoceanographic changes in the austral deep oceans (Olivero *et al.*, 2003).

Thus, in the Fuegian Andes the peak in ichnodiversity is not coincident with the Cenozoic thermal maximum and global warming of bottom waters. The relative lowered diversity of the Late Paleocene-Early Eocene in the Fuegian Andes is probably a local signal related to the generalized anoxic-dysoxic bottom conditions. Increased ichnodiversity is achieved during the late Middle Eocene to Late Eocene and the diversity maximum is accompanied by a cooling trend in the water masses as indicated by the occurrence of cold water foraminifers (Malumián *et al.*, 2007). Consequently, this increased diversity challenges the concept that maximum diversity is related to warm bottom conditions. The producers of the deep-sea trace fossils from the *Zoophycos* and *Nereites* ichnofacies, particularly the graphoglyptids, were apparently highly specialized for food competition in oceanic areas characterized by relatively low food supply (Seilacher, 1974; Uchman, 2004). Contrary to the temperature trend that is highly variable during the Eocene, the δ^{13}C

trend, a proxy for productivity, is remarkable constant except for the extreme negative excursion at the Paleocene-Eocene boundary (*cf.* Luterbacher *et al.*, 2004, and references cited therein). These trends suggest that the Eocene diversity optimum could be related to constancy of relative oligotrophy during the Eocene, a situation that favored the radiation of the graphoglyptid tracemakers.

Acknowledgments

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