

## GYROLITHES AS A MULTIPURPOSE BURROW: AN ETHOLOGIC APPROACH

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**ABSTRACT** – Spiral burrows perpendicular to the bedding plane are well known in the fossil record and are usually referred to the ichnogenus *Gyrolithes*. Common in Mesozoic and Cenozoic marginal-marine, brackish-water deposits, the only records of *Gyrolithes* in Paleozoic rocks are from the Cambrian. In Permian rocks of the Paraná Basin (Rio do Sul and Rio Bonito formations), south Brazil, some short, irregularly spiraled burrows similar to *Gyrolithes* occur in marginal-marine, brackish-water siltstone and mudstone, closely associated with *Thalassinoides*, forming a *Glossifungites* suite. These burrows seem to play the same ethologic role of the corkscrew-shaped burrows that grade into modern *Thalassinoides* burrow systems. The corkscrew shape of *Gyrolithes* is assumed to represent a widespread architectural adaptation to deal with extreme salinity fluctuations in Mesozoic and Cenozoic brackish-water environments. However, spirals produced by thalassinidean shrimps in brackish water connected to modern *Thalassinoides* burrow systems are related to feeding activities. Instead of behavior to avoid extreme salinity fluctuations, the decapod spiral burrows may represent a feeding strategy to exploit organic-rich zones of the substrate in calm and protected environments. The discovery of spiral burrows in Permian marginal-marine stiffgrounds to firmgrounds indicates that this strategy was already adopted by some group of infaunal crustaceans in brackish-water ecosystems during the late Paleozoic.

**Key words:** *Gyrolithes*, corkscrew-shaped burrows, Paleozoic, brackish-water, ethology, evolutionary paleoecology.

**RESUMO** – Escavações espirais perpendiculares ao plano de acamamento são bem conhecidas no registro fóssil e normalmente referidas ao icnogênero *Gyrolithes*. Apesar de comuns em depósitos salobros marginais marinhos do Mesozóico e do Cenozóico, o único registro de *Gyrolithes* em rochas paleozóicas data do Cambriano. Escavações curtas semelhantes a *Gyrolithes*, mas formando espirais irregulares, são registradas em siltitos e argilitos permianos da bacia do Paraná (formações Rio do Sul e Rio Bonito), no sul do Brasil, representativas de depósitos salobros marginais marinhos. Tais escavações ocorrem normalmente associadas a *Thalassinoides*, compondo uma suíte *Glossifungites*, e, aparentemente, desempenham a mesma função ecológica que os túneis espirais modernos associados a galerias de decápodes talassinídeos (tipo *Thalassinoides*). A forma espiral de *Gyrolithes* é assumida, tanto para as ocorrências cenozóicas como as mesozóicas, como uma adaptação arquitetural bem sucedida para suportar flutuações extremas na taxa de salinidade em ambientes salobros. Contudo, túneis espirais produzidos por talassinídeos modernos em águas salobras e conectados a galerias do tipo *Thalassinoides* parecem estar relacionados à atividade de alimentação. Assim, mais do que uma estratégia para suportar flutuações extremas de salinidade, as escavações espirais de decápodes podem representar uma estratégia de exploração de zonas ricas em conteúdo orgânico, em ambientes calmos e protegidos. A descoberta de escavações espiraladas em rochas permianas representativas de substratos marginais marinhos compactados e/ou firmes sugere que tal estratégia já era adotada por alguns grupos de crustáceos infaunais em ecossistemas salobros desde o final do Paleozóico.

**Palavras-chave:** *Gyrolithes*, escavações em espiral, Paleozóico, água salobra, etologia, paleoecologia evolutiva.

### INTRODUCTION

Centimetric-scale, vertical to inclined corkscrew-shaped burrows in the fossil record are generally assigned to the ichnogenus *Gyrolithes*, which is common in Mesozoic and Cenozoic marginal-marine deposits (e.g., Keij, 1965; Gernant, 1972; Ranger & Pemberton, 1988, 1992; Mayoral & Muñiz, 1993, 1995, 1998). *Gyrolithes* is inferred to be produced by

decapod crustaceans due to its common interconnection with *Ophiomorpha* and *Thalassinoides* or by the presence of scratch marks in the burrow inner wall (Gernant, 1972; Bromley & Frey, 1974). Aside from a possible Carboniferous example (Devera, 1989), the only evidence of corkscrew burrows in Paleozoic rocks until now was the diminutive Cambrian *Gyrolithes polonicus*, attributed to worm-like animals (Fedonkin, 1980; Hein *et al.*, 1991; Jensen, 1977; Mayoral &

Muñiz, 1998). Powell (1977) showed that the modern capitellid polychaete *Notomastus lobatus* constructs descending helical burrows and concluded that *Gyrolithes* actually represents capitellid burrows instead of crustaceans. However, the observation of spiral components in burrow systems produced by modern thalassinidean shrimps (Dworschak & Rodrigues, 1997) reinforces the prevalent idea among ichnologists of a crustacean trace-maker for *Gyrolithes*.

There is general agreement (e.g., Wightman *et al.*, 1987; Beynon *et al.*, 1988; Pemberton & Wightman, 1992; Buatois *et al.*, 2005a) that *Gyrolithes* represents a permanent dwelling burrow produced chiefly in marginal-marine settings, as originally suggested by Gernant (1972). Considering that a deep infaunal habitat protects the organism against rapid and extreme salinity variations in brackish-water settings (e.g., Sanders *et al.*, 1965; Knox, 1986; Pemberton & Wightman, 1992), the helical morphology of *Gyrolithes* has been interpreted to be an adaptation to seek refuge from extreme salinity fluctuations (e.g., Beynon & Pemberton, 1992; Buatois *et al.*, 2005a). However, there seems to be a link between coiled burrows of modern decapods and organic-rich layers into the substrate (Dworschak & Rodrigues, 1997), which suggests that corkscrew burrows may represent feeding strategies in addition to a refuge against salinity fluctuations, or even be a multipurpose burrow.

The presence of simple, irregularly coiled burrows in organic-rich Upper Carboniferous-Lower Permian marginal-marine mudstone of the Rio do Sul and Rio Bonito formations (Paraná Basin, southern Brazil) supports this idea. The burrows are invariably associated with *Thalassinoides* and show similar diameters, supporting a crustacean trace-maker. The aim of this paper is threefold: (i) to document the presence of *Gyrolithes*-like burrows in Paleozoic brackish-water stiffgrounds to firmgrounds, (ii) to discuss the burrow architecture and the trace-maker behavior, and (iii) to address the paleoecologic significance of Permian coiled burrows within an evolutionary framework.

## SEQUENCE-STRATIGRAPHIC AND DEPOSITIONAL SETTING

Both the Upper Carboniferous-Lower Permian Rio do Sul Formation (Itararé Group) and the Lower Permian Rio Bonito Formation (Guatá Group) represent part of the fill of the Paraná Basin in southern Brazil (Rocha-Campos, 1967; Schneider *et al.*, 1974; Lavina *et al.*, 1985; Aboarrage & Lopes, 1986; Lavina & Lopes, 1987; Zálan *et al.*, 1990; Milani *et al.*, 1994; Santos *et al.*, 1996). Six second-order sequences have been recognized in the Paraná Basin (Milani, 1997); the Carboniferous-Lower Triassic sequence contains the deposits analyzed in this paper.

### The Rio do Sul Formation

The glacial deposits of the Rio do Sul Formation are widespread in the Santa Catarina State, both in outcrops and in the subsurface (Schneider *et al.*, 1974; Figure 1). However, correlations between surface and subsurface deposits are

not straightforward, especially because of the diachronic character and lenticular geometry of the sandstone and diamictite (França & Potter, 1988, 1991). Marine deposits are dominant, suggesting the existence of an embayment, where alternating transgressive and regressive episodes were controlled by glaciation-deglaciation cycles.

The Gondwanan glacial-postglacial sedimentary succession of the Itararé Group consists of thinly-laminated rhythmite and mudstone, dark gray to black shale, massive siltic-argillaceous matrix diamictite, heterolithic siltstone and sandstone, and fine- to medium-grained sandstone with trough cross-stratification, parallel to subparallel stratification, climbing ripple cross-lamination and wave ripples. Intraclasts and mud drapes are common in the sandy deposits (Balistieri, 2003). Milimetric to metric-scale dropstones are abundant. The Lontras Shale and associated siltstone beds mark the base of the Rio do Sul Formation in the studied area. The facies stacking pattern, the stratigraphic framework, and trace fossil content are summarized in Figure 2.

The *Gyrolithes*-like specimens from the Itararé Group occur in a 2 m-thick massive siltstone interval near the base of the Rio do Sul Formation in Mafra (northern Santa Catarina State, Figure 1), and are part of a brackish-water trace fossil assemblage together with *Thalassinoides* isp. (dominant), *Diplocraterion* isp., *Palaeophycus tubularis*, *P. striatus*, and *?Rhizocorallium* isp. (Balistieri & Netto, 2002; Figure 2), representing a *Glossifungites* suite. The spreite is tiny in *Diplocraterion* and has not been observed in *?Rhizocorallium*. *Gyrolithes*-like specimens are invariably associated with *Thalassinoides*. The sharpness of burrow boundaries in all ichnotaxa, the scratches in the burrow walls of *P. striatus*, the limited development of spreiten in *Diplocraterion*, the absence of spreiten in *?Rhizocorallium*, and the passive burrow infill with material from the overlying bed are diagnostic of burrowing activity in firmgrounds. The occurrence of the *Glossifungites* suite in the basal siltstone interval of Rio do Sul Formation has been linked to a co-planar surface of lowstand erosion and transgressive erosion by Balistieri (2003) (SB/FS of Van Wagoner *et al.*, 1990). The co-planar surface represents the top of the first sedimentation cycle in the Itararé Group in Mafra region. The overlying Lontras Shale marks the beginning of the second sedimentation cycle and represents a major transgressive event.

### The Rio Bonito Formation

Integrated analysis of cores, outcrops, and logs from the northern of Mina do Iruí coal field in Cachoeira do Sul (Rio Grande do Sul State, Figure 1) indicates a depositional evolution from a narrow fluvio-estuarine valley to regionally extensive open-marine environments (Netto, 1998; Buatois *et al.*, 2001a,b, 2005b). The successions representative of the Rio Bonito Formation in the northeast area of the Iruí coal field mostly records sedimentation in fluvial to tide-dominated estuarine environments, and it is present as stacked, unconformity-bounded valley-fill sequences (Figure 3). Lowstand fluvial deposits are non-bioturbated. Estuarine deposits of the transgressive systems tracts comprise tidal



CHRONO-STRAT.	LITHOSTRATIGRAPHY				
	SANTA CATARINA			RIO GRANDE DO SUL	
LOWER PERMIAN	GUATÁ GROUP	PALERMO FORMATION		PALERMO FM.	
		RIO BONITO FORMATION	SIDERÓPOLIS MB.		RIO BONITO FORMATION
			PARAGUAÇÚ MB.		
			TRIUNFO MB.		
CARBONIF.	ITARARÉ GROUP	RIO DO SUL FORMATION		RIO DO SUL FM.	
		MAFRA FORMATION			
		CAMPO DO TENENTE FM.			
DEVON.	PARANÁ GROUP	PONTA GROSSA FM.			
		FURNAS FM.			
PROTEROZOIC BASEMENT					

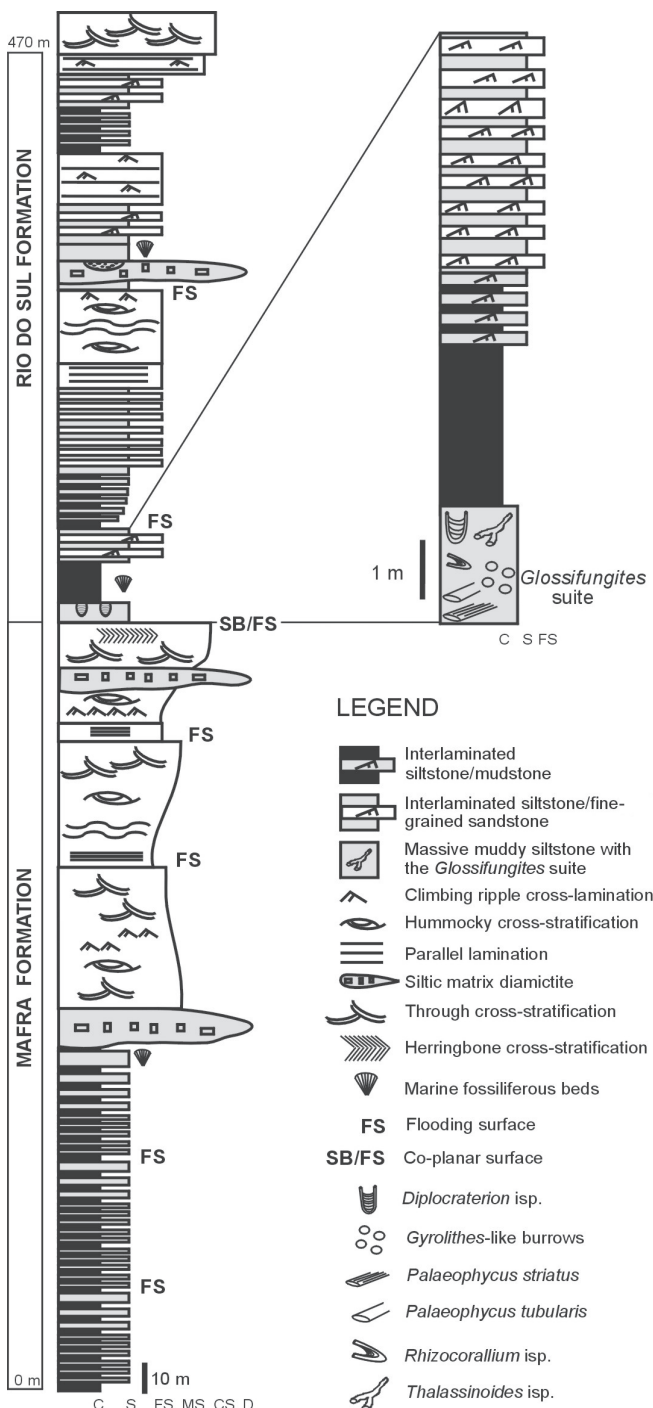
**Figure 1.** Location map of the Paraná Basin showing the study areas and lithostratigraphic chart the Carboniferous-Lower Permian deposits in Mafra (Santa Catarina State) and Cachoeira do Sul (Rio Grande do Sul State), according to Schneider *et al.* (1974).

channel and point bar, marsh, and estuary-mouth facies. The estuarine-valley ichnofauna includes *Ophiomorpha irregulaire*, *Skolithos*, *Planolites*, *Palaeophycus*, *Thalassinoides*, *Rhizocorallium*, *Lockeia* and root traces (Netto, 1994; Buatois *et al.*, 2001a,b, 2005b). The overlying Palermo Formation represents transgressive deposition in open-marine environments (Figure 3). Open-marine strata consist of stacked storm-dominated regional parasequences, and contain *Asterosoma*, *Bergaueria*, *Chondrites*, *Cylindrichnus*, *Diplocraterion*, *Helminthopsis*, *Monocraterion*, *Ophiomorpha*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Rhizocorallium*, *Rosselia*, *Teichichnus*, *Thalassinoides*, and escape trace fossils of cerianthid anemones and bivalves (Netto, 1994; Buatois *et al.*, 2001a,b, 2005b). Offshore-transition to upper- and lower-offshore deposits are commonly punctuated by transgressive surfaces of erosion demarcated by *Glossifungites* suites.

The uppermost interval of the Rio Bonito Formation displays features indicative of deposition in a restricted, brackish-water environment. These deposits exhibit an incised basal contact truncating storm-dominated, hummocky cross-stratified, lower/middle shoreface deposits that transgressively overlie valley sequences of the Rio Bonito Formation. Towards the south, however, the surface rests directly on estuarine tidal-flat deposits. This surface is locally mantled by a 2.5-3 cm-thick lag of well sorted medium- to very coarse-grained sand. The surface is interpreted as a co-planar surface of lowstand erosion and transgressive erosion (SB/FS of Van Wagoner *et al.*, 1990) (Figure 4). This uppermost interval of the Rio Bonito Formation locally contains poorly sorted, very

coarse-grained sandstone and pebbly sandstone, with abundant mudstone intraclasts and carbonaceous lenses, known to Brazilian geologists as *pedra-areia* (Gamermann & Coulon, 1975). These coarse-grained deposits laterally interfinger with, and ultimately pass into, parallel laminated siltstone with synaeresis cracks, interbedded with siderite bands and fine- to very fine-grained sandstone with starved wave ripples and microhummocky cross-stratification. In contrast to the typical fully-marine facies of the Palermo Formation, these basal deposits contain a depauperate ichnofauna suggestive of stressful, brackish-water conditions, which includes *Thalassinoides*, *Gyrolithes*-like burrows, *Diplocraterion*, *Teichichnus*, and *Planolites*. This ichnofauna is characterized by simple tiering structures, low degrees of bioturbation, low diversity, and dominance of simple burrows produced by trophic generalists, reflecting adaptations to brackish-water, stressed environments (Buatois *et al.*, 2005a). Fine-grained deposits are punctuated by ravinement surfaces demarcated by the *Glossifungites* ichnofacies. Specimens similar to *Gyrolithes* are associated with at least three such surfaces, where they occur together with *Thalassinoides* (Figure 4). *Gyrolithes*-like burrows are present in three core wells, namely IC-O7-RS, CA-62-RS and CA-78-RS. Coeval surfaces containing a suite of stiffground to firmground *Thalassinoides* were observed in several other wells (Figure 4). This lowermost interval of the Palermo Formation is bounded at the top by a 1- to 3-cm thick transgressive lag of moderately sorted, medium- to coarse-grained sand, demarcated by stiffground to firmground *Thalassinoides* of the *Glossifungites* suite. This transgressive lag represents a regionally extensive





**Figure 2.** Generalized stratigraphy and depositional setting of the Itararé group in the region of Mafra with a detailed graphic log of the Campo da Lança outcrop, where *Gyrolithes*-like burrows occur in the *Glossifungites* suite (modified from Balistieri & Netto, 2002). **Abbreviations:** C, clay; CS, coarse-grained sand; D, diamictite; FS, fine-grained sand; MS, medium-grained sand; S, silt.

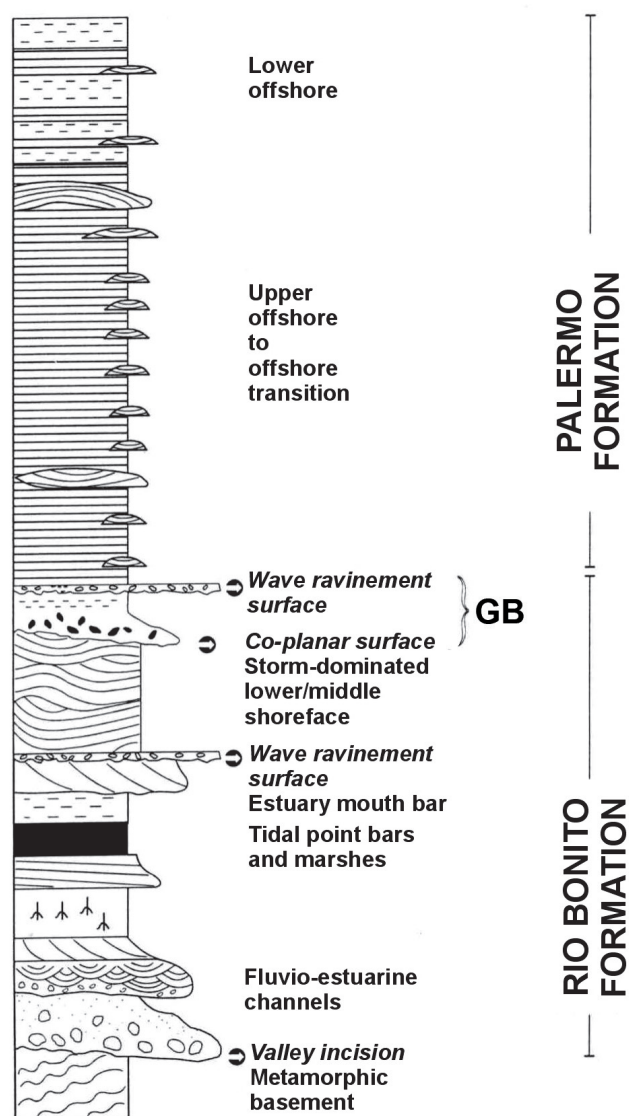
wave ravinement surface that separates the restricted, brackish-water deposits of Rio Bonito Formation from the open-marine strata that characterize the Palermo Formation. The uppermost interval of the Rio Bonito Formation is attributed to deposition within a brackish-water embayment, specifically a lagoonal complex such as that documented by MacEachern *et al.* (1998) from the Joffre Field in Alberta.

## THE PERMIAN SPIRAL BURROWS

**Description.** Short corkscrew-shaped spiral burrows oriented perpendicular to bedding and composed of few, irregularly curved coils (Figures 5A, 6F-G). Tunnel cross-section is subcircular to circular or oval. In core, their morphology is expressed either as offset subcircular to circular cross sections of burrow segments (Figures 5B, 6A-B,E) (cf. Pemberton & Wightman, 1992, fig. 20) or as a series of inclined to horizontal elongated ovals (Figures 5C, 6C-D) (cf. Ranger & Pemberton, 1988, fig. 4A-B; Beynon & Pemberton, 1992, fig. 6A-B). Shaft diameter is 9-13 mm; coil diameter is 24-33 mm; length is 32-59 mm (see basic terminology in Gernant, 1972). Burrows are unbranched, sharp-walled, but unlined, locally showing a diagenetic halo. Specimens are preserved as endichnia in organic-rich mudstone and siltstone and are passively filled by well sorted, fine-grained sandstone derived from overlying beds.

**Discussion.** The described specimens are similar to those recorded by Bromley & Frey (1974), who revised the original description of the ichnogenus *Gyrolithes* by Saporta (1884). In the analyzed deposits, *Gyrolithes* occurs together with sharp-walled, unlined *Thalassinoides* with equivalent shaft diameter. This close association allows linking both galleries to the same trace-maker. *Thalassinoides* is regarded as a decapod crustacean burrow, being produced by thalassinidean crustaceans in modern marine environments (Bromley, 1996). Some *Thalassinoides* show spiraled portions in the gallery, which led Bromley & Frey (1974) to interpret that *Gyrolithes*, *Ophiomorpha*, and *Thalassinoides* were different parts of the same burrow system.

Although the radiation of thalassinidean decapods took place during the Jurassic (Förster, 1985; Feldmann, 2003), *Thalassinoides* commonly occurs in Paleozoic rocks (Carmona *et al.*, 2004). Most of Paleozoic *Thalassinoides* are smaller (shaft diameter commonly 10-15 mm) and display a simpler architecture than their Mesozoic-Cenozoic counterparts. In particular, Late Paleozoic specimens may have been produced by other malacostracans, such as stomatopods, reflecting adaptive convergence (Carmona *et al.*, 2004). Like *Thalassinoides*, the *Gyrolithes* specimens described in Mesozoic and Cenozoic rocks comprise well-developed corkscrew-shaped burrows of several sizes, locally occurring in such abundance that there is almost no space between vertical corkscrews (e.g. specimens from the Pliocene-Pleistocene Cubagua and Tortuga formations in Venezuela, see Estevez *et al.*, 2002). Therefore, the more irregular morphology of Permian *Gyrolithes*-like burrows parallels the trend displayed by *Thalassinoides*. The *Gyrolithes*-like specimens in the Lower Permian deposits of Rio do Sul and Rio Bonito formations occur invariably as part of stiffground to firmground suites, representing the *Glossifungites* ichnofacies (Frey & Seilacher, 1980; Pemberton & Frey, 1985; MacEachern *et al.*, 1992; Balistieri & Netto, 2002; Gingras *et al.*, 2001; Carmona *et al.*, 2006). In siliciclastic deposits, recognition of substrate-controlled ichnofacies, particularly the *Glossifungites* ichnofacies, is useful to



**Figure 3.** Generalized stratigraphy and depositional setting of the Rio Bonito and Palermo formations in the region of Cachoeira do Sul. **GB**, *Gyrolithes*-like burrow-bearing interval.

identify allostratigraphic surfaces, such as ravinement surfaces (MacEachern *et al.* 1992, 1999; Pemberton *et al.*, 1992; Pemberton & MacEachern, 1995).

### ETHOLOGIC SIGNIFICANCE OF *GYROLITHES*

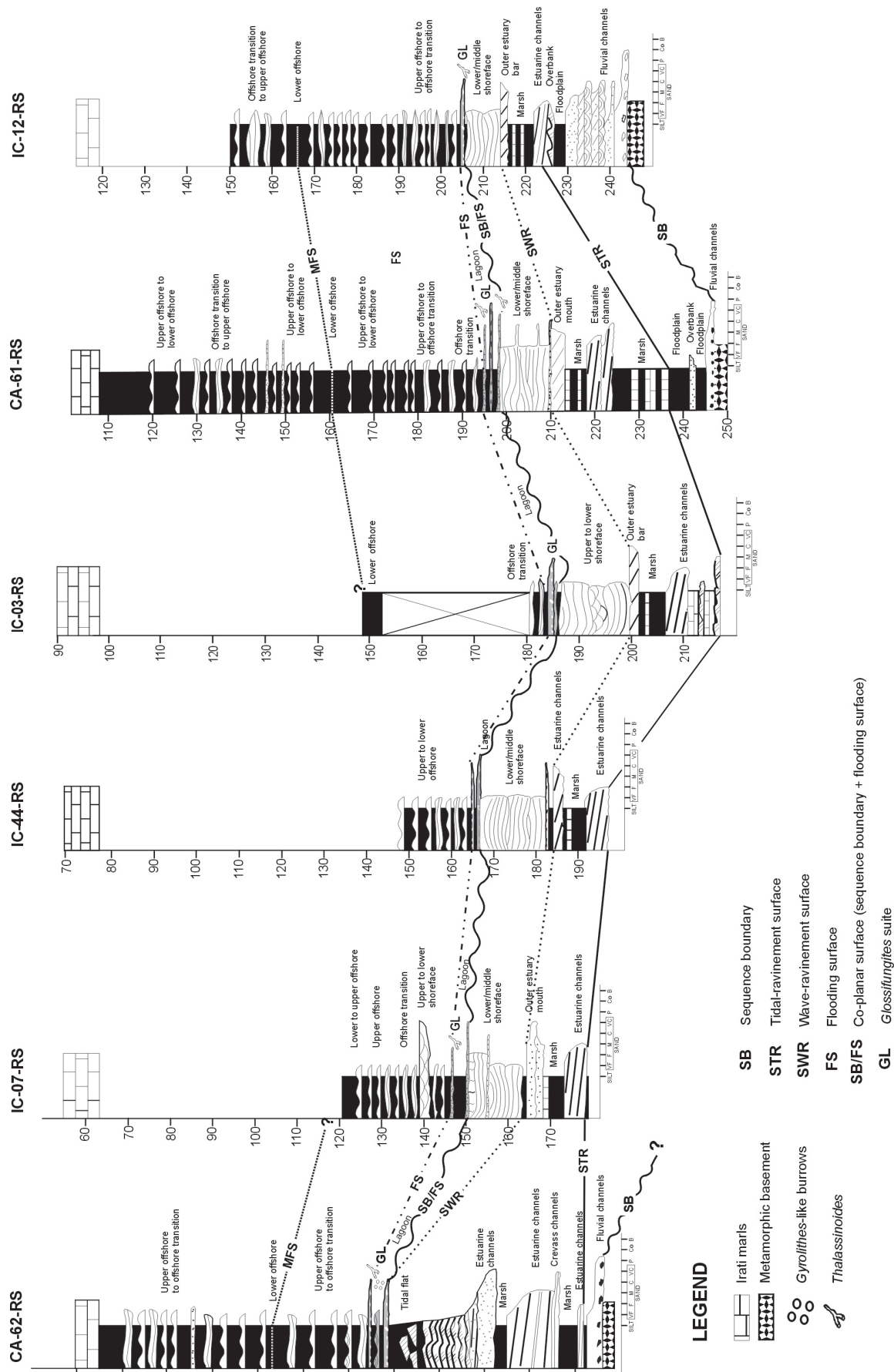
There is general agreement that *Gyrolithes* is a deep dwelling burrow common in marginal-marine settings and that its vertical helical morphology represents a specialized burrowing architecture to seek refuge from extreme salinity fluctuations in brackish-water environments (e.g., Beynon & Pemberton, 1992; Buatois *et al.*, 2005a). Infaunalization is a common survival strategy in harsh environments characterized by extreme salinity fluctuations: The deep infaunal habitat is a refuge from the stressful conditions at the sediment surface (Rhoads, 1975). Because fine sediment slows down the exchange of pore water, the effect of salinity fluctuations is diminished (Sanders *et al.*, 1965). Other spiral

ichnotaxa, however, may serve for different purposes and bear various paleoecologic and paleoenvironmental implications. For example, large spirals in continental environments, currently assigned to the ichnogenus *Daimonelix*, represent dwelling structures of rodents (Voorhies, 1975) or therapsids (Smith, 1987). Relatively small spirals, included in the ichnogenus *Helicodromites*, are predominantly horizontal and probably produced by polychaetes such as *Notomastus* (Powell, 1977; Rindsberg, 1992). *Helicodromites* is common in open-marine environments (Hill, 1985; Baldwin & McCave, 1999). Coiling in this ichnotaxon may be related to anchoring mechanisms and no adaptation to escape from salinity fluctuation is involved in this case.

The modern laomediid shrimp *Axianassa australis* sometimes produces spirals identical to *Gyrolithes* (Dworschak & Rodrigues, 1997; Felder, 2001). The spiral portion of the *A. australis* burrow is unlined and irregularly coiled. The distance between consecutive whorls is inconsistent, and alternation between dextral and sinistral coiling is common. Locally, turnover involving either a U-turn or a swollen “elbow” occurs. The shaft diameter of *A. australis* spirals is more or less constant, but the width and length are variable. This vertical corkscrew-shaped burrow component connects with horizontal dichotomically branching tunnels analogue to *Thalassinoides*.

Five of the six known species of *Axianassa* inhabit intertidal zones, near mangrove areas (mud flats and channels); only one species lives in deep-marine settings (Dworschak & Rodrigues, 1997). This environmental distribution of vertically oriented corkscrew-shaped burrows is consistent with the fossil record of *Gyrolithes*, commonly reported from brackish-water mudstone, siltstone and sandstone (see discussion below). In mud flats and mangrove areas, organic-rich sediment is commonly concentrated in fine-grained layers at high tide. These layers are capped by others in which the organic matter content is relatively low (Flemming & Bartoloma, 1995). Thus, it is expected that the amount of organic matter within the substrate inhabited by *A. australis* varies from level to level.

The deposit-feeder *A. australis* reworks fine-grained, organic-rich substrates in low-energy environments. It usually excavates in zones where compacted mud occurs at just a few centimeters below the surface (Dworschak & Rodrigues, 1997; Coelho & Rodrigues, 2001; Felder, 2001). Because it does not need to prevent the burrow from collapse, lining is unnecessary. Thus, its burrows are unlined, sharp-walled, and passively filled, as is the case of the Permian *Gyrolithes*-like burrows from the Rio do Sul and Rio Bonito formations. Dworschak & Rodrigues (1997) tentatively suggested that the spiraled portion of the *A. australis* burrow system is developed where the animal reaches an organic-rich layer. At this level, the animal stops excavating exploratory horizontal or gently inclined dichotomic-branching tunnels and starts to coil down. As with the majority of thalassinidean shrimps, *A. australis* rarely leaves the burrows, eating inside the galleries, excavating new branches and changing its



**Figure 4.** Stratigraphic cross-section of the Rio Bonito and Palermo formations in the Cachoeira do Sul region. The gray-colored interval corresponds to the brackish-water lagoon deposits that characterize the GB interval of Figure 3. **Abbreviations:** B, boulders; Co, conglomerate; C, coarse; F, fine; M, medium; P, pebbles; VC, very coarse; VF, very fine. Scale in meters.



feeding strategy according to food supply. Where the animal reaches substrate levels with unusually organic-rich content, it produces a corkscrew branch, most likely in order to maximize the exploited area, seizing the available food.

Large horizontal spiral burrows attributed to deposit-feeders or farmers are commonly observed in deep-sea environments (Bromley, 1996). This burrowing behavior seems to be a strategy to enhance the exploiting area in search for food. Farming has also been pointed as a specialized feeding strategy developed by some deposit-feeding thalassinids (e.g., Griffis & Suchanek, 1991; Coelho *et al.*, 2000; Felder, 2001), either by grass debris storage, which favored bacterial growing, or by gardening of the burrow walls to cultivate microorganisms for posterior consumption. *Axianassa australis* is a good candidate to develop farming behavior because its burrows are commonly associated with red mangrove (*Rhizophora mangle* L.) zones, “well below the densest concentration of living rootlets in strongly hypoxic and sulfidic muds” (Felder, 2001). Among the several hypotheses raised to explain the function of spiral portions of *A. australis* burrows, Felder (2001) listed the optimization of burrow wall surface area for microbial lining.

In modern sediments, these spirals are not always perfect corkscrews and may change their loops from right to left in the middle of the burrow course, or they may be composed of ‘loose’ loops. The coiling diameter is limited by the body size of the animal, and the distance between consecutive whorls is determined by the maximum antero-posterior angle curvature that the animal body can reach (S.A. Rodrigues, personal communication). Smaller angles correspond to closer consecutive whorls and more symmetrical corkscrew-shaped burrows. Although deposit-feeding strategies are uncommon in firmgrounds because highly compacted substrates commonly lack nutritious particles, trace fossils of deposit feeders may be present in low-energy suites of the *Glossifungites* ichnofacies (e.g. MacEachern & Burton, 2000).

The general occurrence of *Gyrolithes* in stiffgrounds and firmgrounds and the preference of the laomeddid shrimps for compacted muds in intertidal and supratidal zones have an additional environmental implication. The compacted nature of the substrate and the richness in organic matter reduce considerably the amount of oxygen into the substrate. In fact, the modern producers of corkscrew burrows similar to *Gyrolithes* seem to prefer poorly oxygenated substrates in protected environments (Dworschak & Rodrigues, 1997; Felder, 2001). Therefore, spiral burrows may be representative of dysaerobic substrates in marginal-marine settings.

Felder (2001) suggested that the corkscrew shape *Axianassa* burrows could be also a strategy against predation. This strategy was suggested by Basan & Frey (1977) to explain the irregular spirals found in some fiddler crab burrows (*Uca* spp.). Furthermore, males of some species of ghost crabs (e.g., *Ocypode jousseaumei*, *O. gaudichaudii*) construct spiral burrows for courtship (Schober & Christy, 1993; Clayton, 2005). Thus, corkscrew burrows seem to serve for several different functions, supporting the notion of *Gyrolithes* as a multipurpose burrow.

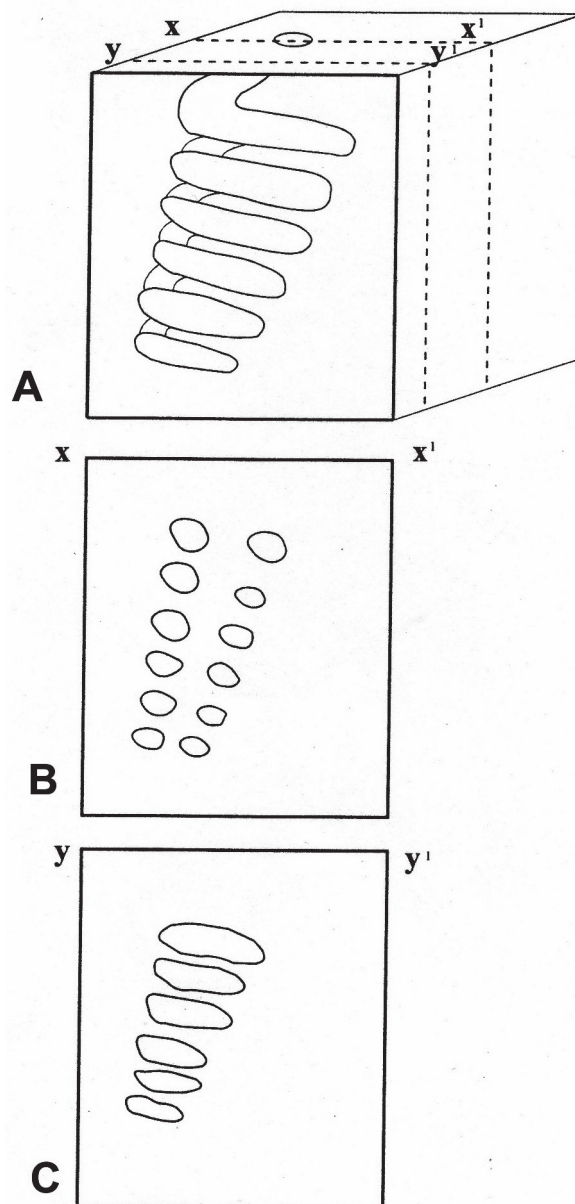
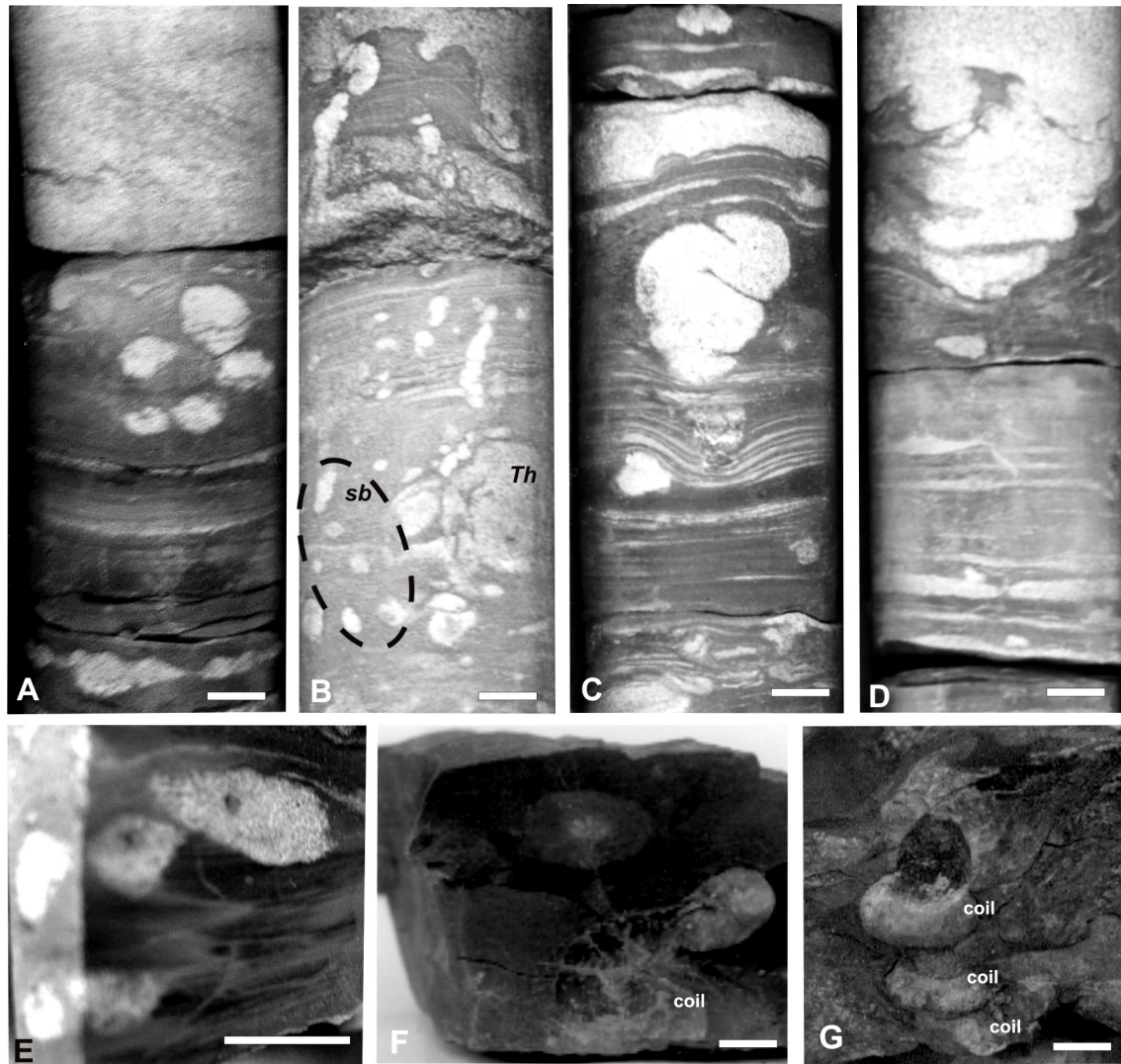


Figure 5. Morphology of the ichnogenus *Gyrolithes*. A. Reconstruction of general morphology. B-C. Core expression.

#### PALEOECOLOGIC SIGNIFICANCE OF PERMIAN *GYROLITHES*-LIKE BURROWS WITHIN AN EVOLUTIONARY FRAMEWORK

Paleozoic brackish-water ichnofaunas display some differences with respect to post-Paleozoic marginal-marine assemblages. Buatois *et al.* (2002, 2005a) compared estuarine ichnofaunas from the Pennsylvanian of Kansas and the Cretaceous of Canada, and noted that Pennsylvanian estuarine facies are characterized by lower ichnodiversity, lower degree of bioturbation, scarcity of crustacean burrows, an absence of firmground suites of the *Glossifungites* ichnofacies, and lack of specific architectural adaptations for coping with extreme salinity fluctuations at the sediment-water interface. Differences between Pennsylvanian and post-Paleozoic brackish-water ichnofaunas were tentatively linked



**Figure 6.** A-D, core expression of *Gyrolithes*-like burrows from the Lower Permian Rio Bonito Formation, preserved in the core wells CA-78-RS (A, C-D) and IC-07-RS (B). The morphology is expressed by offset subcircular to circular cross sections of burrow segments (A-B) or by inclined to horizontal elongated ovals (C-D) burrows generally showing sharp boundaries and only two or three spiral whorls; E, inclined view of the sample illustrated in C showing the cross sections of *Gyrolithes*-like burrow segments both in the polished inner core face and the curved external face; F-G, *Gyrolithes*-like burrows from the base of the Rio do Sul Formation (Upper Carboniferous-Lower Permian). Note the irregular pattern of the spiral whorls, varying from incipient, simple coils (E) to short corkscrew-shaped burrows (F). Scale bars = 10 mm.

to evolutionary innovations in Mesozoic estuarine ecosystems, most likely the crustacean radiation and colonization of brackish water soft to firm biotopes.

The ichnogenus *Gyrolithes* is a common component of brackish-water, estuarine deposits in Cretaceous to Tertiary strata. Occurrences of this ichnogenus in marginal-marine facies have been documented in detail in several basins, including the Cretaceous Western Canadian Sedimentary Basin (Ranger & Pemberton, 1988, 1992; Beynon & Pemberton, 1992) and the Miocene to Pliocene Guadalquivir Basin of Spain (Mayoral & Muñiz, 1993, 1995, 1998). The presence of *Gyrolithes*-like burrows in brackish-water, valley-fill deposits of the Paraná Basin suggests that a group of infaunal invertebrates developed a similar strategy to deal with the same ecological conditions during the Permian. The occurrence of spiral burrows in Permian and Cretaceous-

Tertiary estuarine valleys represents an example of behavioral convergence. The producer of the Permian burrows is, however, a matter of discussion.

A crustacean origin for *Gyrolithes* has been suggested by Gernant (1972) and Kennedy (1967), among others. The oldest representatives of Decapoda come from Upper Devonian (Schram *et al.*, 1978) and Lower Carboniferous (Schram & Mapes, 1984) strata, but are more common since the Permian-Triassic (Glaessner, 1969). In particular, thalassinoid decapods are known since the Jurassic, when crustaceans experienced an evolutionary radiation (Förster, 1985; Feldmann, 2003). However, burrow systems assigned to *Thalassinoides* are known from early (e.g., Sheehan & Schiefelbein, 1984; Myrow, 1995) and late (e.g., Archer, 1984) Paleozoic carbonates, while examples of *Ophiomorpha* have been reported from late Paleozoic siliciclastics (e.g., Driese &



Dott, 1984; Chamberlain & Baer, 1973) (see review by Carmona *et al.*, 2004). Glaessner (1969) noted that one of the oldest occurrences of Mesozoic fossil crustaceans comes from Lower Triassic brackish-water deposits. Brackish-water crustaceans are not known from the Jurassic, but are common in the Cretaceous and Tertiary. Decapod crustaceans are good candidates as producers of late Mesozoic and Cenozoic *Gyrolithes*, but a decapod origin for late Paleozoic corkscrew-shaped spirals is hard to reconcile with the poor Paleozoic record of decapods. However, shrimp-like crustaceans (eocarids) are common in upper Paleozoic marginal-marine, brackish-water deposits (Briggs & Clarkson, 1990). Burrowing behavior of eocarids is poorly understood, but their lack of chelae, specialized appendages, and calcified cuticles may have been disadvantageous for burrowing in cohesive substrates such as those exhumed during ravinement (Carmona *et al.*, 2004). Stomatopod crustaceans are known since the Carboniferous (Tasch, 1973), but their modern burrows resemble *Thalassinoides* rather than *Gyrolithes* (Howard & Frey, 1975).

Capitellid polychaetes have been documented to produce *Gyrolithes*-like structures (e.g., Howard & Frey, 1975; Powell, 1977; Frey & Wheatcroft, 1989; Buatois *et al.*, 2005a). In modern estuarine systems, spiral burrows are produced by some capitellid, maldanid, and nereid polychaetes, as well as enteropneusts (Gingras *et al.*, 1999), though these are smaller than typical crustacean spirals. Mobile polychaetes are known since the Cambrian (Howell, 1962). Thus, the possibility that late Paleozoic *Gyrolithes*-like burrows were produced by burrowing polychaetes cannot be disregarded, although the observed close interconnection between these *Gyrolithes*-like burrows and *Thalassinoides* points to a common crustacean producer.

Helical burrows are also very common in Cambrian strata (e.g., Fritz, 1980; Fedonkin, 1981, 1983; Liñán, 1984; Crimes & Anderson, 1985; Hein *et al.*, 1991; Jensen, 1997; Jensen & Grant, 1998; Stanley & Feldmann, 1998), generally referred to *G. polonicus*. Compared with younger ichnospecies, *G. polonicus* is characterized by its small size, and the absence of terminal expansion, scratch marks and carapace impressions (Jensen, 1997). Additionally, Cambrian *Gyrolithes* are considerably shallower than Mesozoic-Cenozoic representatives. Stanley & Feldmann (1998) documented annulation in specimens of *G. polonicus* as evidence of peristaltic movements, which suggests an annelid producer. Notably, all Cambrian specimens of *Gyrolithes* occur in open-marine facies suggestive of normal salinity conditions, which differ from the settings where younger *Gyrolithes* have commonly been reported, and from the preferential habitat of their modern crustacean analogues.

## CONCLUSIONS

The presence of corkscrew-shaped trace fossils similar to *Gyrolithes* in Permian marginal-marine deposits suggests that specific burrowing architectures to survive in brackish-water environments represent an adaptive threshold that had been attained during the late Paleozoic. Similar strategies have been

commonly recorded in Cretaceous to Tertiary marginal-marine environments, but were previously unknown in Paleozoic brackish-water ecosystems. Additionally, the dominance of crustacean burrows (e.g. *Thalassinoides*) and the occurrence of firmground suites of the *Glossifungites* ichnofacies in Lower Permian brackish-water deposits of the Paraná Basin render late Paleozoic and post-Paleozoic brackish-water ichnofaunas more similar. Spiral burrows may have been constructed for exploitation of organic-rich layers within a dysaerobic substrate. Late Mesozoic to Cenozoic *Gyrolithes* most likely records the evolutionary radiation of decapod crustaceans and their colonization of brackish-water niches, although some groups of polychaetes are also potential trace-makers. The fact that similar structures are present in Lower Permian estuarine deposits suggests the relevance of infaunalization in the colonization of marginal-marine ecosystems. Permian *Gyrolithes*-like burrows were probably produced by eocarid crustaceans. The occurrence of spiral burrows in Permian and Cretaceous-Tertiary brackish-water deposits represents an example of behavioral convergence. Notably, Permian marginal-marine ichnofaunas show more affinities with Cretaceous to Tertiary brackish-water ichnofaunas than with their Carboniferous counterparts. Comparative analysis of brackish-water ichnofaunas through geologic time provides valuable evidence for understanding the colonization of marginal-marine environments during the course of the Phanerozoic.

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