Insights from functional morphology and neoichnology for determining tracemakers: A case study of the reconstruction of an ancient glacial arthropod-dominated fauna

Short title: Tracemakers of an ancient glacial arthropod-dominated fauna

JOÃO H. D. LIMA, NICHOLAS J. MINTER AND RENATA G. NETTO

Apportioning trace fossils to producers is significant for palaeoecological and palaeoenvironmental studies. A tracemaker is usually attributed through the comparison of the morphology of the trace to the body plans of modern and extinct animals. However, hypotheses of tracemaker identifications may be tested with the use of further methods. This contribution aims to evaluate the potential tracemakers of a trackway-dominated ichnofauna preserved in the siltstone-claystone rhythmites of the Pennsylvanian Rio do Sul Formation in the southern Brazil. These deposits are typical of the deglaciation phase of the Late Paleozoic Ice Age of Gondwana in the Paraná Basin. Thus, the parameters applied in this work are: (1) functional analyses of the traces to infer the biomechanics of the locomotion of the producer and (2) neoichnology, whereby modern traces whose producers are known are compared to those of the ichnofauna in question. The conclusions obtained with these methods strongly support millipedes as the producers of *Diplichnites gouldi* and *Diplopodichnus biformis*. The malacostracan crustacean-related ichnogenera are *Umfolozia sinuosa* and *Gluckstadtella elongata*, produced by syncarids or peracarids, while isopods are suggested as the tracemakers of *Glaciichnium* isp. and *Protovirgularia dichotoma*. In terms of branchiopod crustaceans, *Cruziana problematica* is attributed to notostracans. *Helminthoidichnites tenuis*, *Mermia carickensis* and *Treptichnus pollardi* are considered
traces produced by insect larvae. The palaeobiology of the tracemakers that produced the ichnofauna preserved in the rhythmites of the Rio do Sul Formation permits inferences that terrestrial (millipedes) and aquatic (crustaceans and insect larvae) animals colonized the sediments. This conclusion points to a dynamic depositional environment, with changing physical and chemical parameters conditioning the biota.

Key words: Tracemakers, arthropod trackways, biomechanic, glacial, Carboniferous.

João H. D. Lima [jhdl_bio@hotmail.com] and Renata G. Netto [nettorg@unisinos.br], Geology Graduate Program, UNISINOS University, Av. Unisinos, 950, 93022-750, São Leopoldo, Rio Grande do Sul, Brazil; Nicholas J. Minter [nic.minter@port.ac.uk], School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK.
Two of the best known ichnological principles are that similar trace fossils may be produced by different animals and that individual animals can produce different trace fossils (e.g. Bromley 1996). Because of this, the study of the majority of trace fossils is usually not concerned with reliable determination of tracemakers. Arthropod trackways are often an exception because their morphology reflects producer-related morphological details to a large extent (Minter et al. 2007a). Locomotory trackways and isolated tracks and resting traces usually comprise appendage and body impressions that record the anatomy of the producer, and to a lesser extent the behaviour of the producer and the substrate conditions (Minter et al. 2007a).

The accuracy of tracemaker determination can be enhanced by examining large amounts of material, taking behavioral (functional morphological) information and by doing simulation (neoichnological) experiments with modern animals (e.g. Braddy 2001a; Davis et al. 2007). Arthropod trackway-dominated ichnofaunas recorded in Carboniferous and Permian glacial deposits from Gondwanaland are an excellent case study for tracemaker determination. Such ichnofaunas are well-known in the Itararé Group (Paraná Basin, southern Brazil) and Dwyka Group (Karoo Basin, South Africa), being composed of circa 20 ichnogenera, half of them representing arthropod trackways and trails (e.g. Netto et al. 2012). Arthropod trackways and trails represent the majority of specimens in these assemblages, forming dense accumulations of exceptionally well preserved trace fossils on bedding surfaces. This favors detailed morphological analyses and facilitates behavioral evaluation. There is also a growing body of neoichnological research on epistratal traces (e.g. Uchman & Pervesler 2006; Davis et al. 2007) that permits comparison of the traces from the Rio do Sul Formation with those of modern analogues.
Many studies have been made in order to better characterize and understand the structure of the Itararé Group ichnofauna (e.g. Nogueira & Netto 2001a; Gandini et al. 2007; Netto et al. 2009; Lima et al. 2015) but with few exceptions, all potential tracemakers were inferred following previous interpretations available in the ichnological literature. Detailed analyses of the functional morphological and biomechanical potential involved in the preserved trackways and trails and in the estimated behavior expressed by the shallow burrows are still lacking. Thus, more accurate studies are necessary to determine the tracemakers and propose the likely producers of the trace fossils found in the Itararé Group. Furthermore, this proposition will help to resolve questions such as if colonization occurred in subaquatic or subaerial substrates; as well as what was the estimated water depth and salinity of subaquatic substrates; and under what hydrodynamic conditions these substrates were formed. To shed some light on this discussion, this paper aims to discuss the potential tracemakers of some of the most celebrated ichnotaxa present in the Itararé Group ichnofauna, in order to determine their producers and to contribute to solve some of the mentioned questions, based on a palaeobiological and palaeoecological approach.

**Material and methods**

The database of this study is composed of hundreds of specimens exposed in three quarries located in Trombudo Central, Santa Catarina State (southern Brazil) (Fig. 1). Slabs of thin-bedded varve-like siltstone-claystone rhythmites are extracted in these quarries to be used chiefly as paving stone. The thickness of each slab is controlled by the thickness of the siltstone layers and the extraction is made level-by-level, exposing large surfaces with
dense accumulation of trace fossils. The ichnotaxonomy of the analyzed specimens was discussed in detail by Lima et al. (2015). The collected samples are housed in the trace fossils collection of the Laboratório de História da Vida e da Terra (LaViGea) at UNISINOS University, under the numbers UMVT-10707 to UMVT-10721 and ULVG-11550 to ULVG-11577.

Measurement and description of arthropod trackways follows the terminology of Trewin (1994) and Minter et al. (2007a). Stratinomic classification of trace fossils follows Seilacher (1964). Criteria adopted here to develop hypotheses for producers of trackways, isolated impressions, trails and burrows from the Rio do Sul Formation were adapted from those proposed by Minter et al. (2012). When possible, the correlation of trackway features with the anatomy of modern animals and of coeval body fossils groups (with emphasis on the Carboniferous record) was made. Further emphasis was given to comparison with body fossils from similar palaeobiogeographic regions and environments represented by the Rio do Sul Formation rhythmites. Trackway measurements were then used to make functional morphological inferences and to compare fossil to modern trackways in order to test hypotheses for potential producers.

**Geological setting**

The rhythmites of the Rio do Sul Formation represent part of the deglaciation deposits that characterize the end of the Gondwana Ice House in the Paraná Basin (southern Brazil). The Rio do Sul Formation is thickest in the area surrounding Trombudo Central (circa 300 m-thick), and the rhythmite succession, exposed in three quarries (UTM 620026/6981727, UTM 619637/6981821 and UTM 619813/6981938) reaches up to 40 m in thickness. Black
shales, thin-bedded laminated rhythmites, lenticular sandstones and siltic-argillaceous matrix diamictites are the main sedimentary facies observed in the Rio do Sul Formation sedimentary succession. Granule- to boulder-size faceted dropstones are widespread throughout the succession. These rhythmite deposits were originally assumed as varvites by Rocha-Campos (1981) due to the tabular geometry and regular recurrence of thin-bedded rhythmites. However, the presence of marine fossils in the black shales and acritarchs in the rhythmites led to inferences of sedimentation in tide-influenced shallow marine and coastal environments (e.g. Schneider et al. 1974; Rocha-Campos & Sundaram 1981; Santos et al. 1996; Nogueira & Netto 2001a). Studies involving the rhythmite beds of the top of the Itararé Group in the last two decades interpret them as distal turbiditic deposits in shallow fjords (e.g. Puigdomenech et al. 2014; Aquino et al. 2016) or shallow freshwater lakes formed in the supratidal settings related with these fjords (e.g. Netto et al. 2009, 2012; Buatois et al. 2010). The best trace fossil exposures are found in the quarries around Trombudo Central (Fig. 1). These exhibit an arthropod-dominated trace fossil assemblage preserved preferentially in the centimeter-scale siltstone-claystone beds. Microbially induced sedimentary structures (MISS) are abundant and occur in all exposed beds (Fig. 2).

Lima et al. (2015) integrated the geological and the ichnological data of the Rio do Sul Formation in the Trombudo Central region, interpreting the rhythmites as resulting from sediment input in outwash plains during deglaciation events, which then accumulated in marginal-marine shallow ponds. Recent radiometric data point to a Late Pennsylvanian age for the Rio do Sul Formation deposits (see discussion in Lima et al. 2015), being coincident with the final deglaciation phase of the Gondwana glaciers in the Paraná Basin.

Trace fossil assemblage
The ichnofauna of the Rio do Sul Formation preserved in the rhythmites exposed in Trombudo Central quarries is composed of two main groups of biogenic structures: 1) trackways and isolated impressions, and 2) furrows, trails and burrows. The ichnotaxonomy of this ichnofauna was extensively discussed by Lima et al. (2015). *Diplichnites gouldi*, *Umfolozia sinuosa* and *Glaciichnium* isp. are representative of trackways while *Gluckstadtella elongata* is the sole resting impression. Furrows are represented by *Cruziana problematica*, trails by *Diplopodichnus biformis*, *Protovirgularia dichotoma*, *Helminthoidichnites tenuis* and *Mermia carickensis* and burrows by *Treptichnus pollardi*.

**Trackways and isolated impressions**

*Diplichnites gouldi* Gevers et al. (1971) is recorded as two parallel rows of closely and regularly spaced tracks (Fig. 3A). The constant spacing of about 2 mm indicates that the trackways were produced by animals with numerous, oppositely paired, very small walking limbs (Gevers et al. 1971). The tracks are circular-, scratch- or elongate-shaped (*sensu* Trewin 1994), but variation in track shape observed between different specimens can be attributed to changes in the substrate moistness or in the animal behavior (Trewin 1994). There is no morphological variation between the tracks along the same sample, indicating that the producer was homopodous. Undertrack fallout (*sensu* Goldring & Seilacher 1971) cannot be ruled out, given the finely laminated nature of the sediment. Moreover, none of the hundreds of studied specimens has recognizable track series (Fig. 3B) and so symmetry may not be properly determined. The lack of series also implies a multi-legged arthropod as
tracemaker whose leg lengths do not vary along the body. Furthermore, this means that number of legs cannot be determined. Trackway trajectory is generally straight, suggesting locomotion behavior. Some specimens are strongly curved. Overlapping of *D. gouldi* specimens is commonly observed. Asymmetry and abrupt stops are absent.

*Umfolozia sinuosa* is formed of two parallel rows of crescentic- or comma-shaped tracks, with clearly recognizable series of five tracks (Fig. 4A). There is no morphological variation between the tracks along a simple track row. Where series overlap, compound track rows consist of groups of two or three imprints of different shape. These two types of track rows are observed in trackways that are asymmetrical. Most of the *U. sinuosa* specimens are slightly curved and have opposite symmetry (Fig. 4B), while alternate symmetry is not present. A few specimens are preserved as convex hyporelief casts with tracks up to 1 mm deep. Some specimens preserved in concave epirelief have internal, discontinuous, dot-shaped or straight imprints. At the same time, many specimens with this type of preservation lack several details, suggesting undertrack washout. Series overlap is uncommon and the pace and stride within a trackway are constant. The internal width is usually less in the first and the fifth pairs than in the three middle pairs of each series.

*Gluckstadtella elongata* is characterized by eight pairs of tracks, with two pairs parallel or sub parallel to the mid line at one end of the trace and the other six pairs nearly perpendicular to the mid line. The posterior half of the holotype of *G. elongata* (Fig. 5A) comprises two composed track rows after the sixth pair of parallel tracks. The specimens occur randomly-oriented on the substrate surface.

*Glaciichnium* isp. is composed of paired curved tracks, forming V-shaped series arranged with a very high degree of overlap (Fig. 5C). The trackway is ornamented on both sides with continuous, single or double dot-shaped tracks (Fig. 5D).
Furrows, trails and burrows

The only sample ascribed as *Protovirgularia dichotoma* in this study is preserved as a curved axial ridge (Fig. 5E) composed of paired wedge-shaped imprints arranged in a closely spaced chevron pattern (Fig. 5F).

One of the most common and widespread trace fossils in the studied succession is *Cruziana problematica*. It is preserved mainly as narrow, bilobate ridges ornamented by closely spaced scratch marks, which are arranged obliquely to the median groove (Fig. 6A). The oblique striations are well preserved and reach the furrow boundary (Fig. 6B). Furrows are overprinted by *U. sinuosa*. Specimens of *C. problematica* preserved in convex hyporelief are usually cast by clay.

*Didopodichnus biformis* is preserved as two curved, continuous, parallel, up to 1 mm wide ridges separated by an over 3 mm-wide median groove (Fig. 6C). The overall shape of the trace represents a surface trail preserved in convex hyporelief. The functional morphology of *D. biformis* denotes walking by pacing of an arthropod in a substrate that was not firm enough to allow the preservation of tracks. The resultant trace is a double trail with no ornamentation (Fig. 6D). In the studied assemblage, *D. biformis* is recorded in association but not in transition with *D. gouldi* (Nogueira & Netto 2001a; Lima et al. 2015).

*Helminthoidichnites tenuis* is characterized by a meandering trajectory (Fig. 7A) that includes rare random loops (Fig. 7B). This is by far the most common trail in the study area. It is up to 2.5 mm wide and is observed in a dense monospecific assemblage in some surfaces (Lima et al. 2015). *Mermia carickensis* are densely looped (Fig. 7D), including a
slightly circular trajectory (Fig. 7E). In a few samples the infill is slightly lighter in colour than the host rock. The width varies among different specimens from 1.81 mm to 1.98 mm.

*Treptichnus pollardi* is characterized by horizontal burrow segments with small pits as junction points (Fig. 7G). Each segment that forms this trace is straight and the width is constant, 1.1 mm (Fig. 7H).

**Tracemaker determination and palaeoecology**

Neoichnology is a useful tool to evaluate potential producers of trace fossils and the role of the substrate conditions in resulting morphological variations of trace fossils (e.g. Davis *et al.* 2007). Moreover, from neoichnological observations is possible to infer broad animal behavioral responses to environmental conditions, like survival, feeding or procreation (Dashtgard & Gingras 2012). Neoichnological studies have been carried out in both the laboratory and field, concerning the main invertebrate tracemakers, with terrestrial (e.g. Brady 1947; Johnson *et al.* 1994; Davis *et al.* 2007; Corrêa *et al.* 2014), freshwater (e.g. Gibbard & Stuart 1974; Chamberlain 1975; Uchman 2005; Martin 2009) and shallow marine organisms (e.g. Uchman & Pervesler 2006; Dashtgard 2011; Baucon & Felletti 2013). Studies to determine a tracemaker that belongs to an extinct animal group, however, can be conducted only through comparison of body fossil anatomy and trace fossil morphology, and the investigation of functional morphology. The absence of body fossils at the study area is a limitation to this approach, although records from different localities with similar ages can be used.

Trackways are useful for functional studies and biomechanical modelling (Briggs *et al.* 1979, 1984; Braddy 2001a; Smith *et al.* 2003). The deepness of the tracks, the irregular
shape of some trackways and the absence of details can be considered to suggest the destructive action of erosion (Goldring & Seilacher 1971), the modelling action of currents (Braddy 2001a; Smith et al. 2003), or sediment desiccation (Johnson et al. 1994). Based on these criteria, it is possible to reveal the shape and the number of locomotory appendages of the tracemaker, its flexibility and even if the walking techniques are typical of terrestrial or aquatic arthropods (e.g. Briggs et al. 1979, 1984; Johnson et al. 1994; Braddy 2001a; Seilacher 2008).

*Diplichnites gouldi* occurs in all exposed beds. The absence of series in the trackway is a key feature in these specimens, reinforcing the current idea of a multi-legged tracemaker with equivalent walking legs. The occurrence of strongly curved specimens in the studied assemblage suggests capability for high lateral flexibility. Some multi-segmented crustaceans show high lateral flexibility but have few walking limbs (Johnson et al. 1994). According to Braddy (2001a) and Smith et al. (2003), aquatic arthropods tend to walk in-phase, forming trackways with opposite symmetry while terrestrial arthropods usually walk out-of-phase, resulting in trackways with alternate symmetry. However, the lack of series means that it is not possible to properly determine symmetry and the multi-segmented and multi-legged body plan reduces this biomechanical restriction.

Asymmetry and abrupt stops are absent in the analyzed specimens, suggesting that there were no currents lifting and carrying away the tracemakers during the production of the traces. There is also no evidence of current action (unidirectional ripples) on the surface of the slabs with *D. gouldi* in the studied area. The specimens preserved as convex hyporelief penetrate up to 3 mm down in the substrate. The formation of deep tracks is possible in soft subaqueous substrates but unlikely, since in underwater conditions the buoyancy would reduce the weight of the animal resulting in shallower tracks (Draganits et
The close association of *D. gouldi* with photoautotrophic cyanobacteria-rich microbial mats preserved as MISS at almost all trace fossil bearing surfaces in the study area (Netto *et al.* 2009) points to shallow subaqueous (in the photic zone) context for the deposition of these beds. Johnson *et al.* (1994) reported *D. gouldi* that were made subaerially in Ordovician rocks of England, based on the close association of the trackways with desiccation cracks. Desiccation cracks are lacking in the studied beds of the Rio do Sul Formation. Then same is true for occurrences of *D. gouldi* from the Lower Devonian Muth Formation of India (Draganits *et al.* 2001). Evidence of microbial mats are present in both deposits and these mats might be providing the maintenance of moist conditions during potential subaerial exposure of the substrates, allowing colonization by terrestrial organisms.

The presence of internal, discontinuous tracks in the trackways assigned to *D. gouldi* can be the result of a lateral probing behavior employed when the arthropod changed direction, which is observed in modern millipedes (Briggs *et al.* 1984). Moreover, neoichnological studies strongly support millipedes as producers of *Diplichnites* that lack series (Brady 1947; Johnson *et al.* 1994; Davis *et al.* 2007; Corrêa *et al.* 2014; Fig. 3C); whereas *Diplichnites* with series are considered to be of potential aquatic crustacean origin (e.g. Gevers *et al.* 1971; Buatois *et al.* 1998b; Minter *et al.* 2007b). Myriapods with spiracles (= tracheal breathing) are preserved in terrestrial settings since the Late Silurian (Garwood & Edgecombe 2011). Despite the lack of desiccation cracks, the combined biological and sedimentary features (MISS) reinforce the hypothesis that the studied specimens of *Diplichnites* were produced by myriapods (Fig. 3D, Table 1) on very shallow subaqueous to temporarily subaerially exposed substrates.
In comparison to the *Diplichnites* material described here, asymmetry is a prominent feature in *Umfolozia sinuosa*, reflecting trackways produced under current action (Smith *et al.* 2003). Opposite symmetry in *U. sinuosa* allows recognition of an in-phase walking technique (Braddy 2001a) and buoyancy is a likely reason for the dominance of shallow tracks (Draganits *et al.* 2001). Moreover, *U. sinuosa* suggests frequent repositioning of the animal and indicates that some swimming action was present, as suggested by Anderson (1981). Thus, *U. sinuosa* is considered to be produced in subaqueous conditions, but not deep enough to preclude the development of the associated microbial mats. Series overlap is uncommon in *U. sinuosa* at the study area, but even in the absence of this feature the preservation of these trackways is good enough to exclude the occurrence of overprinting of tracks. The pace and stride within a trackway are constant, suggesting that locomotion behavior did not change during production of each trackway. The smaller internal width in the first and the fifth pairs of each series suggests that the tracemaker was an animal with at least five pairs of walking appendages and with variation in limb length.

Among aquatic arthropods, only merostomes (Eurypterida and Xiphosura) and branchiopod (Notostraca and Anostraca) and malacostracan (Syncarida and Peracarida) crustaceans show at least five pairs of walking limbs. Body fossils of all these groups date from the Carboniferous or older rocks (Glaessner 1957; Braddy & Almond 1999; Dunlop 2010; Edgecombe & Legg 2014). Living xiphosurids are most common in marine environments, but some species of this group were recorded in estuarine, tidal flat and lacustrine settings (e.g. Goldring & Seilacher 1971; Babcock *et al.* 2000). However, limulids are unlikely producers of *U. sinuosa* because for locomotion they use four chelate pairs of legs which tend to generate V-shaped series of tracks (Seilacher 2007, p. 20) or a
chevron pattern, as in *Maculichna varia* (Anderson 1975). Moreover, their telson usually leaves a continuous medial impression, as in the ichnogenus *Kouphichnium* (Braddy 2001a). Gandini *et al.* (2007) considered eurypterids among the possible tracemakers of *U. sinuosa* specimens recorded in glaciogenic trace fossil assemblages from the Itararé Group, taking into account the presence of *Hastimima* body fossils in Carboniferous–Permian rocks of the Paraná Basin. Eurypterids had a wide environmental range, including brackish and freshwater bodies and non-aquatic settings (e.g. Braddy, 2001b). These animals had six pairs of ventral appendages but probably used just three or four pairs of paddle-shaped legs to walk (Gevers *et al.* 1971; Seilacher 2007, p. 22), generating trackways composed of series of less than five pairs of tracks like the ichnogenus *Palmichnium* (e.g. Braddy 2001a; Braddy & Almond 1999).

*U. sinuosa* was clearly produced by a combination of swimming and pacing, the latter being a locomotion style in which the body is suspended above the substrate, not touching it, while the animal is repositioning (Craig 1972, p. 218). Among branchiopod crustaceans, only notostracans can walk by pacing, but these would generate series with more than five tracks as they have from 20 to 80 pairs of trunk limbs (Rogers 2009), so they are not candidates to produce *U. sinuosa*. Among malacostracan crustaceans, however, all adults have a thorax with eight somites (Watling 1981) and are the best candidates as tracemakers of *U. sinuosa*. Within the Syncarida, just Palaeocaridacea were present in the Carboniferous (Brooks 1969, p. R353). They had a pair of biramous legs in each thoracic segment and the first five abdominal segments possessed pleopods (Brooks 1969, p. R347; Schram & Schram 1974). Schram & Schram (1979) noted variation in limb length in a palaeocaridacean from the Carboniferous of USA, which fits with the morphology of *U. sinuosa*. Peracarida, especially Amphipoda and Isopoda, are also good candidates as *U.*
*sinuosa* tracemakers. Crawling or leaping is the normal method of locomotion in amphipods, both in normal position or lying on one side (Glaessner 1957). Indeed, extant Gammaridae walk quickly on the mud, leaning to one side (Ruppert & Barnes 1996, p. 715). This mode of walking could generate the asymmetry observed in some of the studied *U. sinuosa* specimens. According to Bousfield (1982), Gammaridae amphipods might be present in the Carboniferous. The fossil record of isopods also extends to the Carboniferous (Schram 1970). Isopods are better adapted to swim and dig into the substrate, but they can also walk or run with their thoracic limbs (Glaessner 1957; Craig 1972, p. 253; Ruppert & Barnes 1996, p. 722).

Considering that Syncarida and Peracarida (Amphipoda and Isopoda) crustaceans have abdominal limbs able to produce series of five pairs of tracks, thoracic limbs that can create marks (internal imprints) in the sediment and a fan-shaped telson that may not touch the ground, these animals are the most likely producers of *U. sinuosa* (Table 1) from the Trombudo Central region. Syncarid and peracarid crustaceans were proposed as *U. sinuosa* tracemakers by Savage (1971), based on the glaciolacustrine context inferred for the Dwyka Group rhythmites from where the holotype comes and the presence of these groups in the body fossil assemblage of the Karoo Basin. Syncarid and peracarid crustaceans also occur as body fossils in the Paraná Basin, but only in the mid-Permian Irati Formation (Adami-Rodrigues & Pinto 2000). Despite the occurrence of acritarchs in several beds of the ichnofossiliferous rhythmite succession from the Trombudo Central area (Nogueira & Netto 2001a), suggesting marine-influenced settings, the huge freshwater input from melting glaciers allowed the establishment of a dominant freshwater assemblage in these areas (Buatois *et al.* 2010; Lima *et al.* 2015).
Gluckstadtella elongata is the only resting trace preserved in the Trombudo Central area. However, G. cooperi has been recorded in glacial trace fossil assemblages of the Karoo (Savage 1971) and Paraná basins, as well as other resting traces, like Rusophycus cf. carbonarius and Tonganoxichnus isp. (Balistieri et al. 2002; Gandini et al. 2007; Netto et al. 2009, 2012). The presence of podial imprints denotes an arthropod tracemaker. The random orientation of the specimens on the same surface indicates absence of currents during their production (Craig 1972, p. 383). Keighley & Pickerill (1998) questioned the assumption of the two first pairs of imprints in the type ichnospecies G. cooperi as “anterior” appendage marks by Savage (1971), since these structures could represent the other end of the producer. However, Keighley & Pickerill (1998) considered the parallel pairs of imprints as the hindmost tracks because in their specimens the parallel imprints are the termination of a median groove. The samples from Trombudo Central have no median impression. All extinct and extant crustaceans have two pairs of antennae, but they are positioned in the dorsum of the head, and they are likely to only locally make contact with the substrate. Thus, the two pairs of tracks parallel to the mid line in G. elongata are here considered two pairs of imprints made by modified anterior appendages. Accordingly, the producer had two pairs of maxillipeds, at least six pairs of thoracic appendages and some pairs of abdominal limbs able to generate compound track rows. These morphological features are not found in terrestrial animals, but are common in crustaceans.

The co-occurrence of G. elongata and U. sinuosa on the same surfaces is observed in the study area, but the absence of transitional forms suggests that the G. elongata producer used swimming instead of walking locomotion. G. elongata is composed of more pairs of tracks than U. sinuosa, but a common producer cannot be ruled out, since it is expected that a change in behavior of a given animal is manifested by a change in trace
morphology. On the left side of the *G. elongata* holotype (Fig. 5B), the second pair of imprints is branched. This feature is coincident with the shape of the anterior appendages of malacostracans, but does not fit with the morphology of branchiopods (Glaessner 1957; Rogers 2009). Several peracarids have seven thoracopods with the first one modified as maxillipeds (Hessler 1969). Thus, these animals are proposed herein as *G. elongata* tracemakers (Table 1).

*Glaciichnium* is assumed as a locomotion trace of an aquatic arthropod (Walter 1985). Similar structures made by the isopod *Asellus* sp. were observed by Gibbard & Stuart (1974) in proglacial lake sediments. Davis *et al.* (2007, fig. 14) carried out a neoichnological experiment with the terrestrial *Oniscus asellus* and obtained a central furrow morphology of this modern trace that fits with that of *Glaciichnium* isp. Uchman & Pervesler (2006, fig. 4B) also observed isopods and amphipods in soft substrates of a tidal flat emplaced in a delta plain producing furrows that have the chevron pattern of *G. isp.*. Thus, neoichnological evidence strongly supports Peracarida as tracemakers for this ichnospecies (Table 1).

*Protovirgularia* was considered by Seilacher & Seilacher (1994) as a locomotion trace of cleft-foot, protobranch bivalve. Seilacher & Seilacher (1994) assumed that *P. dichotoma* was an endogenic structure, possibly produced by scaphopods. Mángano *et al.* (2002) recognized that *P. dichotoma* is “somewhat reminiscent” of an arthropod trackway and that substrate conditions play a major role in the morphology of *Protovirgularia*. As in the case of *G. isp.*, some of the V-shaped furrows with chevrons and levees observed by Uchman & Pervesler (2006, fig. 4D) being produced by isopods and amphipods have a similar morphology of *P. dichotoma*. Thus, peracarids are assumed as tracemakers of *P. dichotoma* from Trombudo Central (Table 1).
Cruziana problematica is the most abundant ichnotaxon in the Trombudo Central region. U. sinuosa always cross-cuts C. problematica in the studied trace fossil assemblage, indicating that furrows were produced before the trackways in soft mud, in potentially subaqueous conditions and then the trackways produced later when the sediment was more firm. Cruziana is generally interpreted as a result of arthropod locomotion into the substrate, chiefly by trilobites. The unique ichnospecies not attributed to trilobites is C. problematica due to its occurrence in non-marine and post-Paleozoic strata (see discussion in Lima & Netto 2012). However, the presence of faint scratch marks and the similar behaviour with other Cruziana ichnospecies led many authors to assume the tracemaker to be an arthropod that behaved like a trilobite (e.g. Bromley & Asgaard 1979; Nogueira & Netto 2001b; Kighley & Pickerill 2006).

According to Chamberlain (1975), ploughing the substrate with numerous paired legs would produce a striated, bilobate furrow. Minter et al. (2007b) argued that anostracans and lipostracans scrape the substrate rather than ploughing it, producing scratch traces but not furrows. Gammaridae amphipods may be epifaunal herbivores, but they swim or walk instead of ploughing the sediment (Hessler 1969, p. R388). Chamberlain (1975) observed that resting, walking and ploughing traces made by notostracans are similar to those made by trilobites. Notostracans are known since the Late Devonian (Lagebro et al. 2015). Modern notostracans are usually found at or next to the bottom of temporary pools or playa lakes (Rogers 2009). They can be detritus-feeders, digging the appendages and telson into the mud or even adopting a scavenging habit in turbid waters (Garrouste et al. 2009). Thus, as assumed by Minter et al. (2007b) for Permian samples from the USA, notostracans are the most likely producers of C. problematica specimens from the Itararé Group (Table 1).
Despite being common in the Itararé Group trace fossil assemblages, *Diplopodichnus biformis* occurs as an accessory ichnotaxon in Trombudo Central area. Due to the common association with *D. gouldi* forming compound structures elsewhere, these two ichnospecies have been typically interpreted as locomotion traces of myriapods. The difference in morphology between the two ichnotaxa is related to substrate consistency (e.g. Keighley & Pickerill 1996; Buatois *et al.* 1998a; Draganits *et al.* 2001). Neoichnological studies conducted both in the laboratory and the field resulted in trails similar to *D. biformis* produced by myriapods (Brady 1947; Johnson *et al.* 1994; Davis *et al.* 2007; Corrêa *et al.* 2014). Taking into account that substrate conditions play a major role in the origin of *D. biformis*, the simple requirements of the producer anatomy are a consistent body width and closely spaced pairs of walking legs. Adult wingless insects tend to avoid softgrounds. In turn, small benthonic crustaceans that are able to make incursions onto land can produce trails similar to *Diplopodichnus*, as evidenced by the isopod traces observed by Uchman *et al.* (2011) in modern temporary puddles. However, the external width of the *D. biformis* from the Rio do Sul Formation is twice the size than that of the specimens studied by Uchman *et al.* (2011). Based on the external width – equivalent to the average width of *D. gouldi* – and on the depth of the ridges (over 1 mm), myriapods must be considered the most likely tracemakers of *D. biformis* from Trombudo Central (Table 1).

Animals burrow for many purposes including protection, respiration, feeding and reproduction (Bromley 1996). Burrowing animals can be infaunal for their whole life, as polychaetes and some nematodes, or spend a developmental phase within the sediment, as crustaceans and insects. The burrows (*Treptichnus pollardi*) preserved in the rhythmites of the Rio do Sul Formation at Trombudo Central were made in the most superficial tier of the substrate and possess unlined walls and constant width. These burrows are horizontal,
unbranched and filled with the same sediment as the host rock (Lima et al. 2015). These features and the close association between the burrows and MISS point to mat grazing behaviour, observed in vermiform animals, small crustaceans and insect larvae.

Nematodes and oligochaetes were assumed as producers of modern *Helminthoidichnites*-like traces in freshwater settings (Martin 2009). However, nematodes are unlikely producers in this case, because of their simple musculature of elongate muscles that results in their typical regular sinusoidal movement. Amphipods and isopods were presented as tracemakers in muddy-sandstone tidal flats (Uchman & Pervesler 2006). Baucon & Felletti (2013) observed traces similar to *Helminthoidichnites* being produced by dipteran larvae in a barrier-island system. Insect larvae were also observed producing shallow burrows comparable to *Helminthoidichnites* in moist silty substrates of a quarry at Trombudo Central (Fig. 7C). The oldest insect body fossils date from the Devonian (Grimaldi & Engel 2005, p. 66), but in the Carboniferous insects underwent significant diversification. The wide range of burrowing insects in Carboniferous makes it difficult to assign a specific producer to *H. tenuis* from the Rio do Sul Formation, but the evidences suggest that insect larvae might be considered as potential tracemakers (Lima et al. 2015; Table 1).

The known record of *Mermia carickensis* is restricted to freshwater settings (Lima et al. 2015). In freshwater settings, however, simple grazing trails and burrows can be made by a wide range of invertebrates. Modern coleopteran (Carabeidae) larva were observed making grazing trails that mimic the morphology of *M. carickensis* in subaerial silty softgrounds (Corrêa et al. 2014; Fig. 7F). Insect larvae have been considered by Buatois & Mángano (1993) as a potential tracemaker of *M. carickensis* preserved in the Carboniferous glacial beds of the Paganzo Basin. Insect body impression (*Tonganoxichnus* isp.) and body
fossils (Blattodea and Gryloblattodea) occur in the rhythmites and shales of the Rio do Sul Formation (Pinto 1990; Netto et al. 2012). Blattoidea are hemimetabolous insects, not possessing a larval developmental stage. Grylloblattoidea, contrastingly, are holometabolous insects and their adult form have an elongate body with small thoracic legs that is similar to those of some coleopteran larvae (Wipfler et al. 2014). Known as ice-crawlers, extant grylloblattoideans are wingless and inhabits glacially-influenced environments of the Northern Hemisphere. Extinct specimens, however, occurred in Gondwanaland since the Late Carboniferous (Cui et al. 2011). The presence of grylloblattoidean insects in the body fossil assemblage of the Rio do Sul Formation (Pinto 1990) and its life habit suggests that these insects may be potential tracemakers for the *M. carickensis* recorded in the Trombudo Central area (Table 1).

As for *M. carickensis*, *Treptichnus pollardi* is more common in non-marine settings (see discussion in Lima et al. 2015). According to Rindsberg & Kopaska-Merkel (2005), the morphology of *Treptichnus* represents deposit-feeding behavior in a serial pattern, with each burrow segment abandoned by the animal to be filled by collapse. *T. pollardi* has not been attributed to a particular producer to date and the tracemaker of the similar modern traces observed in a quarry of Trombudo Central (Fig. 7I, 7J) is unknown. However, traces with diagnostic features of *Treptichnus* were observed being produced in subaerial softgrounds for dipteran larvae of the families Tabanidae (Buatois et al. 1998b), Tipulidae and Chironomidae (Uchman 2005). Martin (2009) also suggested dipteran larvae as producers of modern, wide *Treptichnus* in an Arctic fluvial setting and assumed the ovoid forms adjacent to the burrows as pupation structures. Thus, insect larvae – likely dipteran – are here assumed as *T. pollardi* producers.
CONCLUSIONS

The ten ichnospecies recorded in the Pennsylvanian Rio do Sul Formation at Trombudo Central region, Brazil, consist of trackways, isolated impressions, furrows, trails and burrows that were produced by both aquatic and terrestrial arthropods. Most of the ichnotaxa are here attributed to crustaceans, including some of the dominant forms, such as *Cruziana problematica* (notostracans) and *Umfolozia sinuosa* (syncarids or peracarids). On the other hand, the widespread occurrence of *Diplichnites gouldi* results from activity of millipedes, while the abundant *Helminthoidichnites tenuis* were produced during the burrowing stage of insect larvae. Millipedes were also producers of *Diplopodichnus biformis*, by pacing in soft sediments. Isopods (Malacostraca) are the likely tracemakers of *Glaciichnium* isp. and *Protovirgularia dichotoma*. Given the strong morphological similarity between the trace and the modern producer, *Gluckstadtella elongata* is attributed to peracarids. As for *H. tenuis*, the sedimentary features of the studied succession suggest a palaeoecological setting were insect larvae are the most likely producers of *Treptichnus pollardi* and *Mermia carickensis*, while this last ichnospecies could also be produced by adult Grylloblattoidea.

Acknowledgements

The authors thank to CNPq by the research grants 401826/2010-4 and 311473/2013-0 that supported this work. JHDL thanks to UNISINOS for the Pe. Milton Valente graduation grant and CAPES for the scholarship BEX 8693/14-5. The owners of the quarries are thanked for allowing the access to the study areas. The authors are grateful to M. G.
Mángano, who helped to improve the original manuscript with a critical review. We are grateful to A. Uchman for a thoughtful review, which, though differing in opinion and interpretation, led to substantial improvements.

References


Cui, Y., Béthoux, O. & Ren, D. 2011: Intraindividual variability in Sinonomuropteridae forewing venation (Grylloblattida; Late Carboniferous): taxonomic and nomenclatural implications. *Systematic Entomology* 36, 44-56.


Figure legends

**Fig. 1.** Location map of the study area. **A**, Study area within Santa Catarina State. **B**, Map of Brazil with the Santa Catarina State in black. **C**, Location of the quarries at the outcropping area of the Rio do Sul Formation deposits.

**Fig. 2.** Compound sedimentary log of the deposits exposed in Trombudo Central region. **A**, Sandstone/claystone rhythmtes. **B**, Siltstone/claystone rhythmtes with pebble-size dropstones. **C**, Wrinkle structures (MISS). **D**, Siltstone/claystone rhythmtes with granule-size dropstones. Scale bars: 100 mm.

**Fig. 3.** Tracemaker determination. **A**, *Diplichnites gouldi* (ULVG-11561). **B**, Line drawing of the trackway shown in (A) detailing the constant distance between the pairs of tracks. **C**, Modern *D. gouldi* produced for a millipede. **D**, Modern millipede *Rhinocricus padbergi* used in the experiment shown in (C). Scale bars: 10 mm.

**Fig. 4.** Tracemaker determination. **A**, *Umfolozia sinuosa* (UMVT-10714). **B**, Line drawing of the trackway shown in (A) detailing the series of five pairs of tracks. Scale bars: 10 mm.

**Fig. 5.** Tracemaker determination. **A**, *Gluckstadtella elongata* (ULVG-11562D, holotype). **B**, Line drawing of the isolated impression shown in (A) detailing the imprints made for modified appendages. **C**, *Glaciichnium* isp. (ULVG-11577). **D**, Line drawing of the trackway shown in (C) detailing the dot-shaped tracks on both sides. **E**, *Protovirgularia dichotoma* (UMVT-10716). **F**, Line drawing of the trail shown in (E) detailing the chevron pattern of the tracks. Scale bars: 10 mm.

**Fig. 6.** Tracemaker determination. **A**, *Cruziana problematica* (ULVG-11574). **B**, Line drawing of the furrow shown in (A) detailing the transverse striations. **C**, *Diplopodichnus*
biformis (ULVG-11569). D, Line drawing of the trail shown in (C) detailing the parallel ridges. Scale bars: 10 mm.

Fig. 7. Tracemaker determination. A, Helminthoidichnites tenuis (UMVT-10708). B, Line drawing of the trail shown in (A) detailing the randomic trajectory. C, Modern trace similar to H. tenuis. D, Mermia carickensis (UMVT-10712). E, Line drawing of the trail shown in (D) detailing the successive loops. F, Modern trace similar to M. carickensis, being produced for a coleopteran larvae (black arrow). G, Treptichnus pollardi (ULVG-11567). H, Line drawing of the shallow burrow shown in (G) detailing the small rounded pits. I, J, Modern traces similar to T. pollardi. Scale bars: 10 mm.
Table 1: Comparison of the morphology of the trackways, isolated impressions and trails from the Rio do Sul Formation with the expected anatomy, ecology and behaviour of the proposed tracemakers. 1 – Key features of the ichnotaxa from this work and Lima et al. (2015). Key features of Notostraca from Rogers (2009). Key features of other tracemakers from Ruppert & Barnes (1996).

<table>
<thead>
<tr>
<th>Ichnotaxon</th>
<th>Key features¹</th>
<th>Tracemaker</th>
<th>Key features¹</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Diplichnites gouldi</strong></td>
<td>Maximum external width (MEW) of 12.90 mm; tens of paired, homogeneous tracks; no series; pace of 2 mm.</td>
<td>Millipede (Diplopoda, Myriapoda)</td>
<td>Up to 10 mm wide and 90 regularly spaced pairs of uniramous legs; homopodous</td>
</tr>
<tr>
<td></td>
<td>Subaerial, firmground sediment</td>
<td></td>
<td>Moist soils in several terrestrial habitats</td>
</tr>
<tr>
<td></td>
<td>Walking or grazing</td>
<td></td>
<td>Herbivores and grazers</td>
</tr>
<tr>
<td><strong>Umfolozia sinuosa</strong></td>
<td>MEW of 17.59 mm; series of 5 heterogeneous tracks; strongly curved trajectory</td>
<td>Syncarida or Peracarida (Malacostraca, Crustacea)</td>
<td>Up to 25 mm wide; at least 5 walking legs; heteropodous</td>
</tr>
<tr>
<td></td>
<td>Shallow, subaqueous setting</td>
<td></td>
<td>Marine, freshwater, brackish water, a few terrestrial</td>
</tr>
<tr>
<td></td>
<td>Combined swimming and pacing</td>
<td></td>
<td>Walking, crawling or leaping</td>
</tr>
<tr>
<td><strong>Gluckstadtella elongata</strong></td>
<td>MEW of 24 mm; average length of 43 mm; 2 anterior pairs of imprints (one of them branched); 6 lateral, paired homogeneous tracks</td>
<td>Peracarida (Malacostraca, Crustacea)</td>
<td>Typically 15 mm wide and 42 mm in length; 1 maxilliped; up to 6 pairs of thoracopod</td>
</tr>
<tr>
<td></td>
<td>Low energy, subaqueous sediment</td>
<td></td>
<td>Marine and freshwater, a few terrestrial</td>
</tr>
<tr>
<td></td>
<td>Resting</td>
<td></td>
<td>Swimming, walking, crawling or leaping</td>
</tr>
<tr>
<td><strong>Glaciichnium isp.</strong></td>
<td>MEW of 7.44 mm; tens of lateral, paired, homogeneous tracks; no series; central, overlapping V-shaped imprints</td>
<td>Isopoda (Peracarida, Malacostraca)</td>
<td>Typically 10 mm wide; 7 pairs of uniramous legs; heteropodous</td>
</tr>
<tr>
<td></td>
<td>Subaqueous, softground to firmground sediment</td>
<td></td>
<td>Marine and freshwater, a few terrestrial</td>
</tr>
<tr>
<td></td>
<td>Walking</td>
<td></td>
<td>Swimming, digging or walking</td>
</tr>
<tr>
<td><strong>Protovirgularia dichotoma</strong></td>
<td>MEW of 2.32 mm; tens of paired, homogeneous tracks; chevron-shaped central ridge</td>
<td>Isopoda or Amphipod (Peracarida, Malacostraca)</td>
<td>Typically 10 mm wide; 7 pairs of uniramous legs; heteropodous</td>
</tr>
<tr>
<td></td>
<td>Subaqueous, softground to firmground sediment</td>
<td></td>
<td>Marine and freshwater, a few terrestrial</td>
</tr>
<tr>
<td></td>
<td>Walking</td>
<td>Swimming, digging or walking</td>
<td></td>
</tr>
<tr>
<td>----------------</td>
<td>---------</td>
<td>-----------------------------</td>
<td></td>
</tr>
<tr>
<td><em>Cruziana</em> <em>problematica</em></td>
<td>MEW of 1,87 mm; 2 parallel ridges ornamented for oblique scratch marks; central median groove</td>
<td><em>Notostraca</em> <em>(Branchiopoda, Crustacea)</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subaqueous, softground to firmground sediment</td>
<td>From 10 mm to 100 mm in width; up to 80 pairs of legs; simple telson; homopodous</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Walking or ploughing</td>
<td>Ephemeral, stagnant, freshwater bodies</td>
<td></td>
</tr>
<tr>
<td><em>Diplopodichnus</em> <em>biformis</em></td>
<td>MEW of 5,74 mm; 2 parallel, 1 mm wide ridges; no ornamentation; slightly curved trajectory</td>
<td><em>Millipede</em> <em>(Diplopoda, Myriapoda)</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subaerial, softground sediment</td>
<td>Up to 10 mm wide and 90 regularly spaced pairs of uniramous legs; homopodous</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Walking</td>
<td>Moist soils in several terrestrial habitats</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Herbivores and grazers</td>
<td></td>
</tr>
</tbody>
</table>