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Insights on the Behavior of Late Paleozoic Aquatic Crustaceans (Pygocephalomorpha?): Compound Trace Fossils from Western Argentina

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We describe intergradations between the arthropod repichnial trace fossils *Diplichnites gouldi* (Gevers et al., 1971), *Dendroidichnites* Demathieu et al., 1992, and *Monomorphichnus* Crimes, 1970 with two distinct cubichnial traces, *Gluckstadtella cooperi* Savage, 1971 and *Huilmuichnus santracruzensis* new ichnogenus and ichnospecies. These compound ichnofossils are part of high ichnodiversity arthropod-dominated trace fossil associations from the Late Carboniferous Agua Escondida Formation of the San Rafael Basin (Argentina). The complex ichnotaxonomy of *Diplichnites* and the ichnospecies *D. gouldi* are discussed and some possible working solutions are proposed. The most likely producer of the compound trace fossils are the Pygocephalomorpha, a group of Late Paleozoic crustaceans that are recorded in nearby basins from Uruguay and Brazil. The compound trace fossils are used to infer a number of complex behaviors of pygocephalomorphs in a subaqueous setting, including caridoid (tail flip) or more primitive escape reactions, landing followed by resting and transient resting during normal walking. In addition, different gaits can be inferred from well-preserved *D. gouldi*, which can be correlated with contrasting trackway morphology.

Keywords   Compound trace fossils, Pygocephalomorpha, Crustacea, *Diplichnites*, *Huilmuichnus santacruzensis* new igen. and isp., Caridoid escape reaction

INTRODUCTION

Arthropod trace fossils, including trackways, trails, and resting traces, provide direct information on the locomotory habits of fossil arthropods. Some Late Paleozoic postglacial sequences of Gondwana contain abundant arthropod-produced trace fossils, including those from the Karoo Basin of South Africa (which are considered relatives to the Pygocephalomorpha by Anderson, 1981; Savage, 1971), the Paraná Basin of Brazil (Balistieri et al., 2002; Gandini et al., 2007; Netto et al., 2009) and the San Rafael Basin of Argentina (Melchor et al. 1993, in prep.; Pazos et al., 2007). The Late Carboniferous Agua Escondida Formation of the San Rafael Basin has yielded several trace fossil associations of high ichnodiversity, where arthropod-produced trace fossils are commonly a dominant component (Melchor et al., 1993; in prep.). In this contribution, we will describe intergradations between the arthropod repichnial trace fossils *Diplichnites gouldi* (Gevers et al., 1971); *Dendroidichnites* Demathieu et al., 1992; and *Monomorphichnus* Crimes, 1970 with two distinct resting traces *Gluckstadtella cooperi* Savage, 1971 and *Huilmuichnus santracruzensis* new ichnogenus and ichnospecies. These compound trace fossils are employed to infer some locomotory traits of a common producer, an aquatic crustacean, probably the extinct group of the Pygocephalomorpha. A proper analysis of these compound trace fossils should be supported by a detailed ichnotaxonomic assignment of component ichnotaxa. As a consequence, a revision on the usage of *Diplichnites,* specially the species *D. gouldi,* and a proposal for the ichnotaxonomy of this commonly reported arthropod trackway is also offered.

This ichnological information would be the first direct evidence on the behavior of the Pygocephalomorpha. In addition, if this assignment is correct, these trace fossils would suggest the presence of pygocephalomorphs in Argentina, which are not yet recorded as body fossils. The fossil record of Late Paleozoic arthropods from Argentina is scarce and limited to two basins. The most prolific is the Paganzo Basin that yielded insects (Gutierrez et al., 2000 and references therein), conchostracans (Leguizamón, 1975), arachnids (Pinto and Hünicken, 1980), and a giant eurypterid (Selden et al., 2005). The Tepuel-Genoa Basin produced essentially insect remains

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(Pinto, 1972, 1992, 1994; Schneider, 1983), in addition to ostracods (Díaz Saravia and Jones, 1999) and a single species of trilobite (Amos et al., 1960).

GEOLOGICAL SETTING

The San Rafael Basin is a Middle Carboniferous to Early Permian retroarc foreland basin developed along the paleo-Pacific margin of Gondwana (Fig. 1A). The basin filling is composed of the El Imperial Formation in the San Rafael Block (Mendoza province) and the Agua Escondida Formation in southeastern Mendoza and northwestern La Pampa provinces. The succession of the Agua Escondida Formation is laterally equivalent and probably partially coeval with the El Imperial Formation although its age is not well-constrained (e.g., Melchor, 1996; Polanski, 1970). A Late Carboniferous or Early Permian age for the unit has been proposed on the basis of fossil plant remains (González Díaz and García, 1968). The Agua Escondida Formation in its homonymous area is characterized by cross-bedded quartz arenites

alternating with dark laminated mudstones. The broad environmental setting interpreted for the succession is an estuarine or fjord-like environment with marked tidal influence (Melchor et al., in prep.). The studied compound trace fossils have been recovered from the laminated mudstone (rhythmite) facies of the unit at the Mina Santa Cruz (MSC) locality (Fig. 1B). At this locality, three trace fossil-bearing sections were logged, which are referred as to MSC1, MSC2, and MSC3 (Fig. 2). Additional material of *D. gouldi* has been collected at other localities (Fig. 1): Puesto Yantén 1 and 2 (PY1, PY2) and Lomas Piedra de Afilar (LPA).

The resting and locomotion trace fossils described herein were mainly recovered from grey mudstone with horizontal millimeter-thick lamination and occasional wrinkle marks. They were also found in black shale with papery lamination, olive grey to light brown mudstone with millimeter-thick laminae and wave-generated structures (flat-topped symmetrical ripples, undulated lamination or wave cross-lamination), and mudstone and siltstone with lenticular bedding. These mudstone facies commonly have a rhythmitic lamination. The
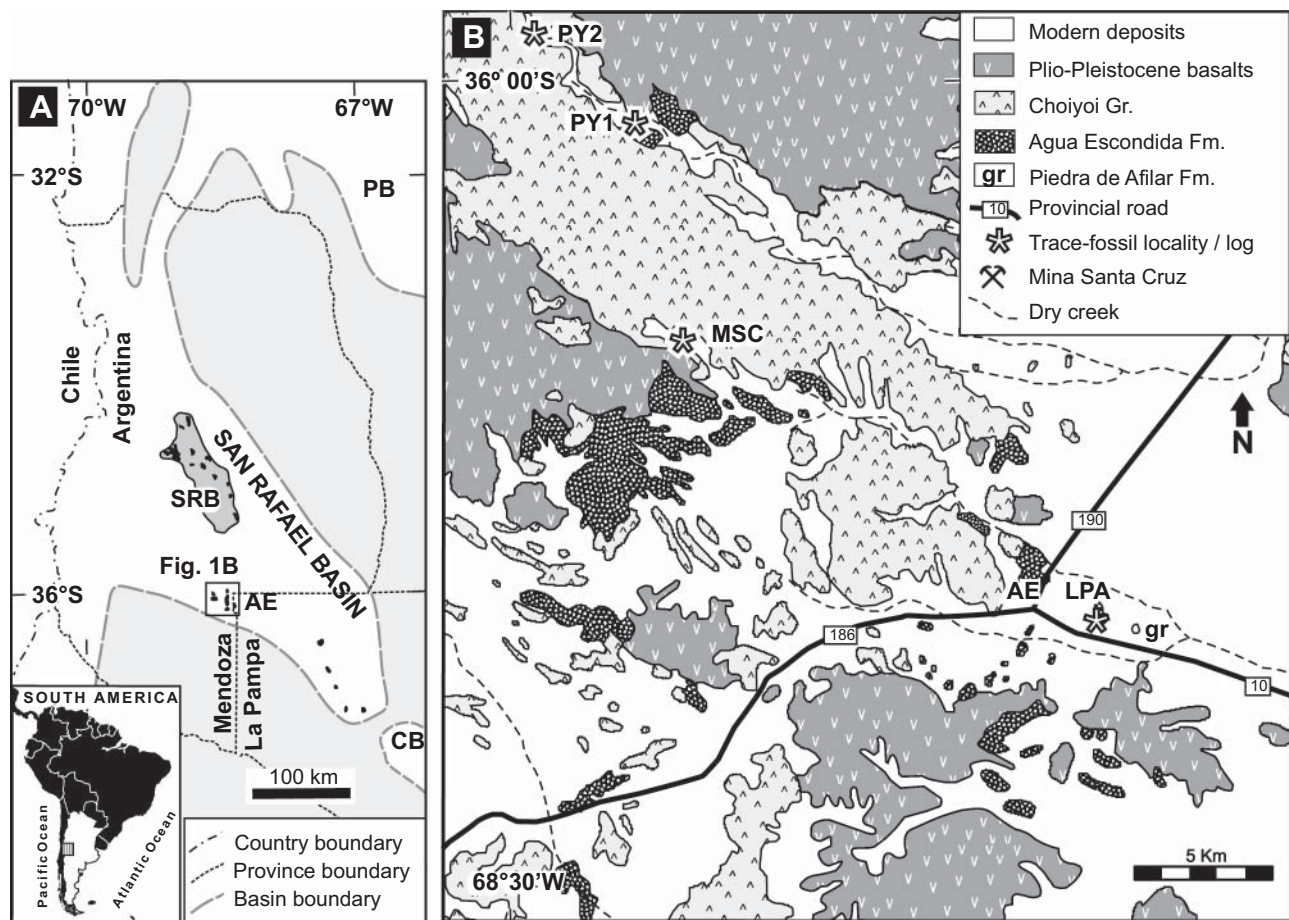
FIG. 1. Location map. **A.** paleogeographic map of the San Rafael Basin and adjacent Late Paleozoic basins. Outcrops are shown in black. AE: Agua Escondida, PB: Paganzo Basin, CB: Carapacha Basin, SRB: San Rafael Block. **B.** Detailed geologic map of the study area and trace fossil-bearing localities. MSC: Mina Santa Cruz, PY1 and PY2: Puesto Yantén 1 and 2, LPA: Lomas Piedras de Afilar, AE: Agua Escondida. Modified from Melchor (1996), Archangelsky (1996) and Narciso et al. (2007).
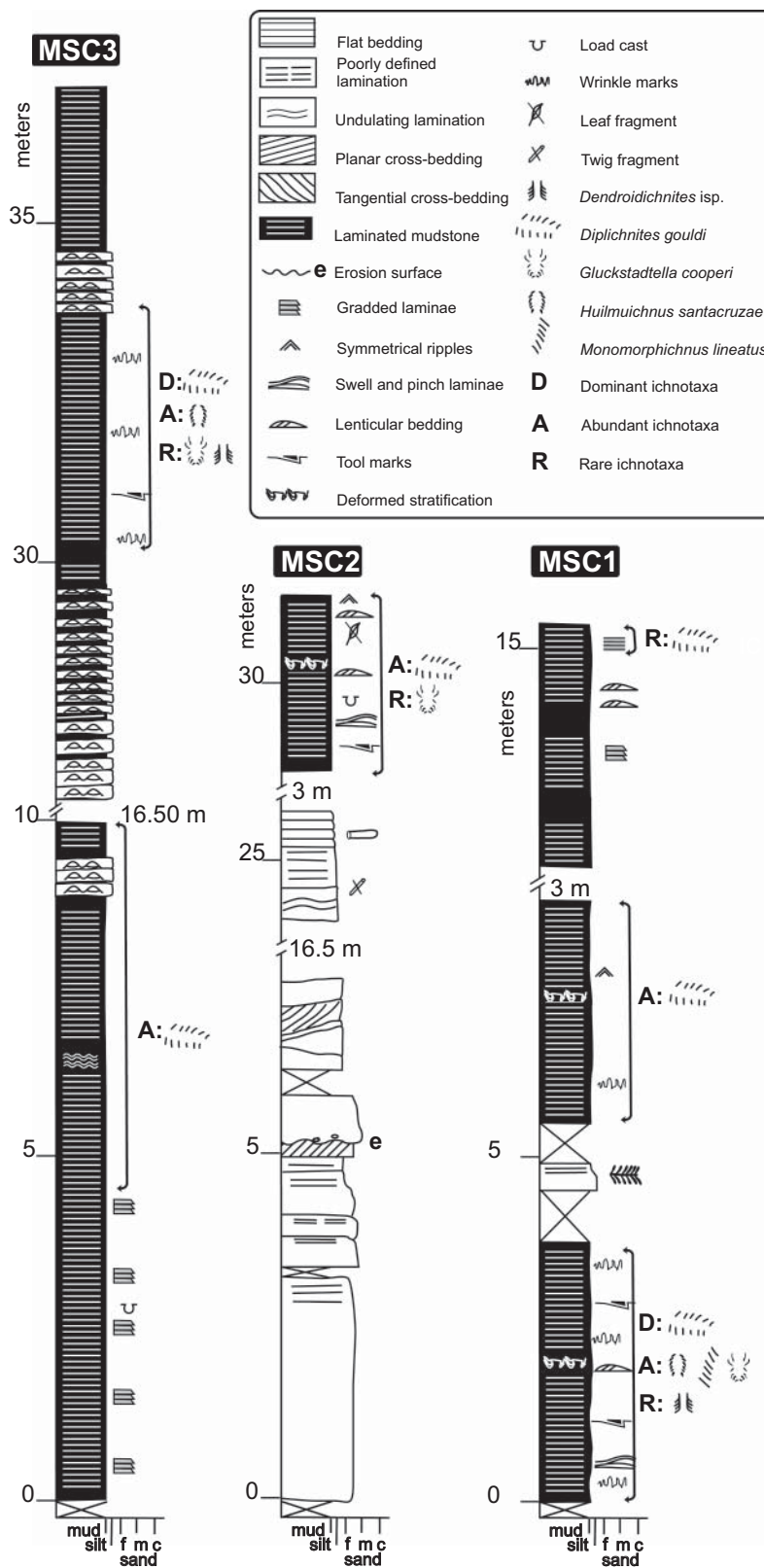
FIG. 2.   Sedimentary logs of the Agua Escondida Formation at Mina Santa Cruz locality (MSC) showing the provenance of the described trace fossils.

described ichnofossils were found in three trace fossil associations of high ichnodiversity (range from 15 to 19 ichnotaxa). Associated ichnotaxa include: *Archaeonassa fossulata*, *Cruziana problematica*, *Helminthoidichnites tenuis*, *Helminthopsis abeli*, *H. tenuis*, *Lockeia* isp., *Palaeophycus tubularis*, *Planolites montanus*, *Protovirgularia dichotoma*, *Ptychoplasma vagans*, *Rusophycus carbonarius*, *R.* cf. *furcosus*, *R. versans*, *Treptichnus bifurcus*, *T. pollardi*, *Umfolozia sinuosa*, *Undichna bina*, *U. britannica*, *U. insolentia*, *U. unisulca*, brush-like trace fossils, and biloled traces with crescentic ridges.

METHODS

For the description of arthropod locomotion traces, we mostly follow the terminology proposed by Trewin (1994), Braddy (2001) and Minter et al. (2007a), although some changes were introduced (see also Fig. 3). Track is reserved for appendage marks and imprint is used for those marks that do not correspond to appendages. A series is a group of tracks that is repeated along each track row; the tracks in a series are conventionally designated with numbers. A complete set includes two series from opposite sides of a trackway. An imaginary line dividing the set in two halves is here referred to set midline, which is commonly oblique to the trackway midline. The series length was estimated as the line joining the first and last track of the series, parallel to the set midline. The series width is the maximum separation between the external part of equivalent tracks of opposite series. The stride was estimated as the distance along the trackway midline between equivalent tracks of successive series on the same track row. The overlap between successive series on each track row (series overlap) was estimated as the distance between the first track of a series and the last track of the next series, measured parallel to the trackway midline. This distance is positive if series overlap and negative if no overlap is observed. The pace was measured as the distance along the set midline between the positions of the last tracks of opposite series. The series angle is the angle formed between the trackway midline and a line joining the first and last track of each series. This angle is considered positive if the vertex points backward and negative if the vertex points forward. The direction of movement of the producer of a trackway is inferred from the angle formed by the series of a complete set. A complete set usually forms a "V" that is open toward the direction of movement for trilobites (Osgood, 1970; Seilacher, 1955). The same rule can be applied to *Diplichnites gouldi*, as inferred from push back mounds in some specimens.

Most of the described specimens are stored in the paleontological collection at the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, from Santa Rosa city, La Pampa, Argentina (acronym GHUNLPam). Additional material is housed at the collection of the del Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano,"
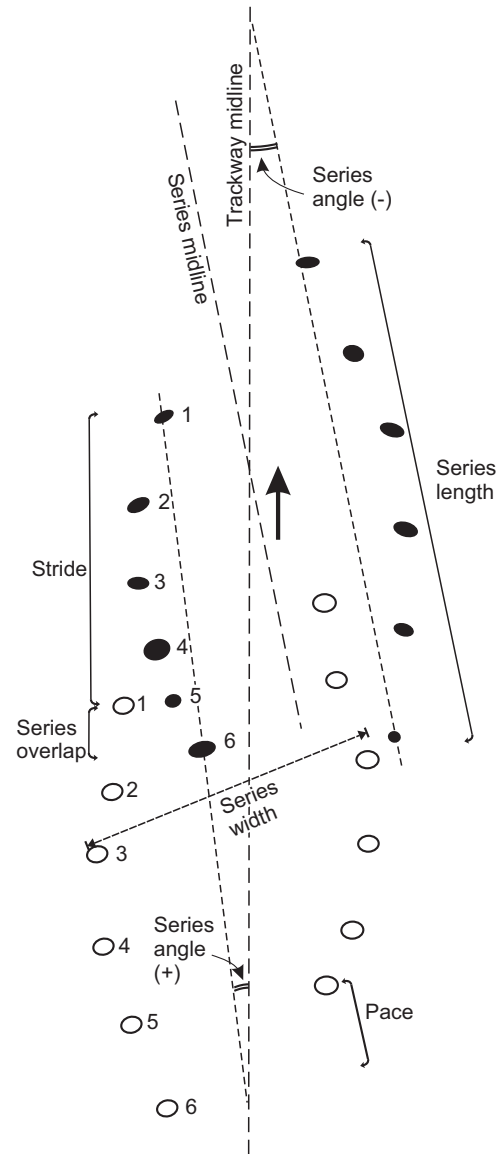
FIG. 3. Measurements on arthropod trackways. The diagram shows two consecutive complete sets (groups of black and white tracks, respectively). 1–6: tracks in a series. See text for details. The arrow indicates the inferred displacement direction.

from Mendoza City, Argentina (acronym MCNAM PI). The program ImageJ v. 1.45 (http://rsbweb.nih.gov/ij/) was employed for detailed measurements on orthogonal photographs of the specimens.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Dendroidichnites* Demathieu, Gand and Toutin-Morin, 1992
Dendroidichnites isp.
Figures 4A, 4B, 5A, 5C, 6D, and 6F

Material: GHUNLPam 12090 from MSC3, and GHUNLPam 12152 and 12238 from MSC1.
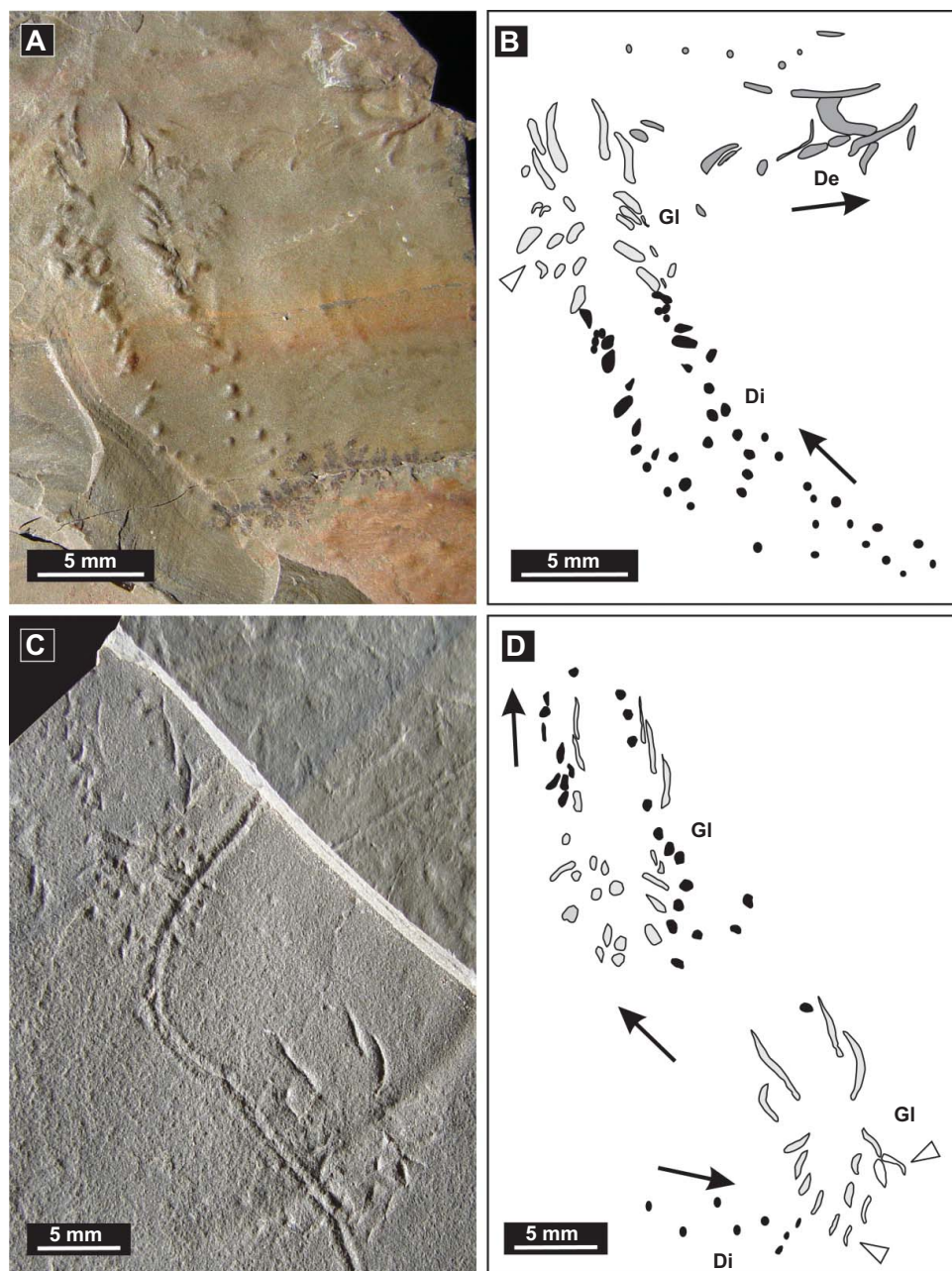
FIG. 4. Photographs and interpretative drawings of compound trace fossils involving *Diplichnites gouldi* (Di, black), *Gluckstadtella* cooperi (Gl, light gray) and *Dendroidichnites* isp. (De, dark gray). The black arrows indicate the inferred direction of displacement. See description in the text. **A., B.** GHUNLPam 12152. The white arrow indicates the repetition of tracks. **C., D.** GHUNLPam 12237. Note repetition of the right posterior tracks in the lower *G. cooperi* specimen (white arrows). (See Color Plate I.)

Description: Short (up to 27 mm long), straight trackways composed of two parallel track rows with oblique elongate tracks that overlap toward the midline or describe a chevron-like pattern. Track rows are symmetrical (GHUNLPam 12090) or asymmetrical (GHUNLPam 12152, 12238). No definite series was identified. External trackway width is 4.0−6.6 mm and internal trackway width is 1.0−2.7 mm.

Individual tracks form a 23−35 degrees angle with the midline.

Remarks: The ichnotaxonomy of the ichnogenus and its distinction from sole marks have been discussed by Buatois et al. (1998a) and Minter and Braddy (2009). The specimens described in this study are considered of organic origin as they are connected to resting trace fossils.
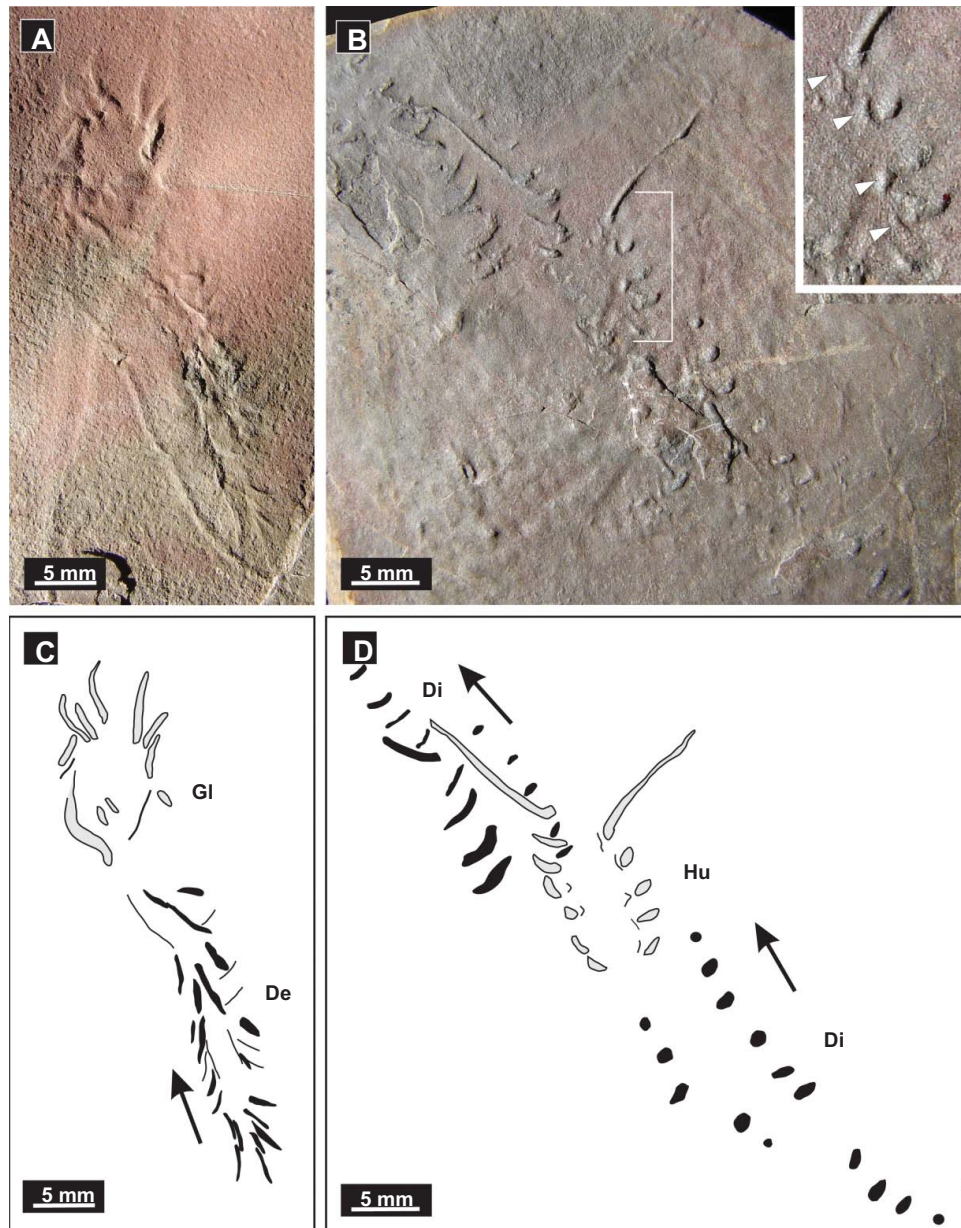
FIG. 5. Photographs and interpretative drawings of compound trace fossils. Black arrows indicate the inferred direction of movement. **A., C.** GHUNLPam 12090. *Dendroidichnites* isp. (De, black) ending in *Gluckstadtella cooperi* (Gl, light gray). **B., D.** GHUNLPam 12116. *Diplichnites gouldi* (Di, black) leading to *Huilmuichnus santacruzensis* (Hu, light gray) with long anterior tracks and followed by a partial *D. gouldi*. The inset in B is an enlargement of the area indicated by a bracket. The white arrows in the inset point to crescentic marks near the medial end of the tracks. (See Color Plate II.)

Ichnogenus *Diplichnites* Dawson, 1873

***Emended diagnosis*:** Trackway composed of two roughly parallel rows of well-defined simple tracks, individual tracks typically elongated and arranged transversaly or obliquely to trackway midline, tracks regularly and closely spaced. Trackway symmetrical or asymmetrical, track series may or may not occur within trackway, medial impressions or imprints absent (modified from Briggs et al., 1979, and Fillion and Pickerill, 1990).

Remarks: Arthropod trackways frequently display morphological intergradations resulting from behavioral, substrate, and taphonomical factors (e.g., Minter et al., 2007a). The taxonomy of *Diplichnites* has a long and complicated history (e.g., Keighley and Pickerill, 1998), in part related with these morphological intergradations and description of small number of specimens. The taxonomy of the ichnogenus has been partially revised by Fillion and Pickerill (1990), Trewin and McNamara (1995), and Smith et al. (2003). The diagnosis of
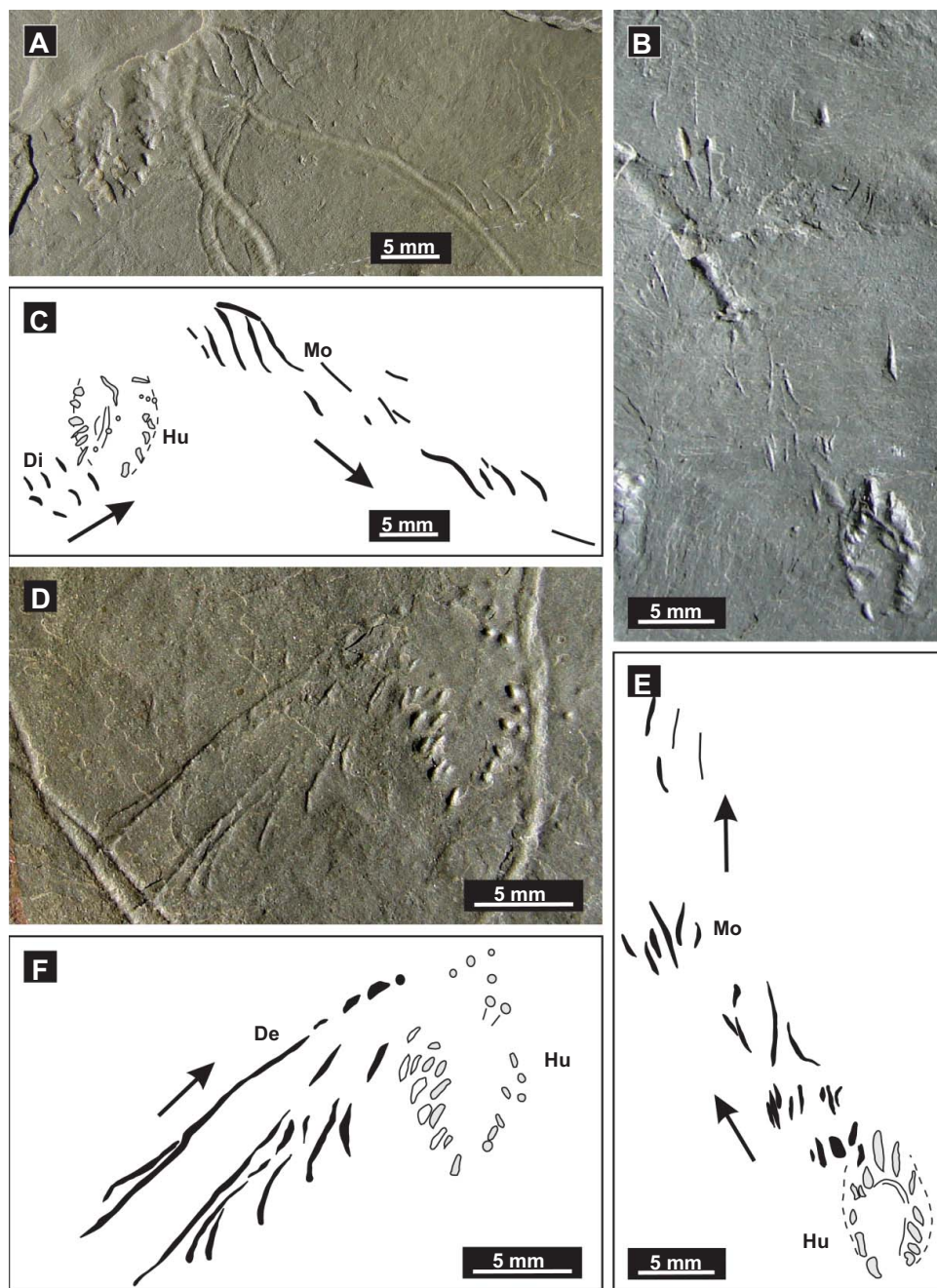
FIG. 6. Photographs and interpretative drawings of compound trace fossils including *Huilmuichnus* (Hu, light gray), *Monomorphichnus* (Mo, black), *Dendroidichnites* (De, black), and *Diplichnites* (Di, black). Black arrows indicate the inferred direction of displacement. **A., C.** GHUNLPam 12252, short *Diplichnites* isp. leading to *H. santacruzensis* and then to *Monomorphichnus lineatus*. **B., E.** GHUNLPam 3431, holotype of *H. santacruzensis* igen. and isp. nov. and *Monomorphichnus* isp. **D., F.** GHUNLPam 12238, *Dendroidichnites* isp. leading to *H. santacruzensis*. The white marks are interpreted as a group of tracks that are repeated on the right side of the trace fossil. (See Color Plate III.)

the ichnogenus proposed by Briggs et al. (1979) and the emendations by Briggs et al. (1984) and Ryan (1986), includes several size features (commonly considered an invalid ichnotaxobase for invertebrate trace fossils) and described the ichnogenus as a trail, a term currently reserved for continuous traces (e.g., Frey, 1973). Fillion and Pickerill (1990) and

Keighley and Pickerill (1998) proposed an alternative redaction for the diagnosis of *Diplichnites* that included forms with varied track morphology, although *Diplichnites* is typified by simple tracks with no definite track series. The track morphology, as described in the literature, may be ellipsoidal, elongate, comma-shaped, tapered and scratch-shaped (terminology after

Trewin, 1994). Intergradations of these morphologies to circular tracks are common as result of the undertrack fallout phenomenon (Goldring and Seilacher, 1971). Continuous or discontinuous medial traces are not characteristic of *Diplichnites*, although they may occasionally appear (e.g., Minter et al., 2007b; Trewin and McNamara, 1995). Bradshaw (2010) suggested that *Diplichnites* should be used for trackways that rarely display a definite track series, although this author proposed an emended diagnosis suggesting common superposition of individual tracks and occasional presence of series of eight or more tracks. The presence of track superposition may be the result of preservational variants and should not be considered a diagnostic feature. These comments highlight the lack of agreement on a hierarchy of criteria for use in arthropod trackway taxonomy in general and for *Diplichnites* in particular. Therefore, we advocate a broad characterization for *Diplichnites*, including simple track morphology with or without definite track series and the absence of medial traces. The trackways may be symmetrical or asymmetrical.

There are several ichnogenera that exhibit a morphology similar to *Diplichnites*, including *Petalichnus* Miller, 1880; *Acripes* Matthew, 1910; *Tasmanadia* Chapman, 1929; and *Mirandaichnium* Aceñolaza, 1978. As shown below, they can be considered junior synonyms of *Diplichnites*; however, they are occasionally recognized in recent literature and new ichnospecies have been erected lately (e.g., Braddy and Almond, 1999; Buatois et al., 1998a; Gand et al., 2008; Schlirf, 2005). *Petalichnus* was proposed for a trackway with transverse, elongate tracks arranged in three to five indistinct rows. One of the distinguishing features of *Petalichnus* is the large morphological variability, as remarked by Rindsberg (1994). The type specimen of *Petalichnus*, along with other trackways described by Miller (1880) under additional names, can be accommodated under *Diplichnites* (Osgood and Drennen, 1975). Rindsberg (1994) suggested to keep *Diplichnites* for large forms with parallel rows and to assign most forms described in the literature under *Diplichnites* to *Petalichnus*. This suggestion, followed by Erdoğan et al. (2004), is not supported here because *Petalichnus* is a broadly defined ichnogenus and *Diplichnites* is a better defined and widely used ichnotaxon. Schlirf (2005), quoting Rindsberg (1994), suggested that most forms described in the literature under *Diplichnites* be considered under *Tasmanadia*. According to the description and illustration by Glaessner (1957), the unique difference between *Tasmanadia* and *Diplichnites* is the sporadic occurrence of bifid tracks. This is not considered a distinctive feature because occasional bifid tracks are the result of overprinting (as described herein for *Diplichnites gouldi*) instead of reflecting the morphology of the producer. *Acripes* Matthew, 1910 was synonymized under *Diplichnites* by Häntzschel (1975), and the original specimens fit under the emended diagnosis of *Diplichnites* above. Some authors (e.g., Demathieu et al., 1992; Gand et al., 2008) followed the

proposal of Walter (1983) for retaining *Acripes* as a separate ichnogenus. In a more recent publication, Gand et al. (2008) described under a new ichnospecies of *Acripes* a bewildering variety of arthropod trackways that, in many cases, are best described as compound trace fossils. Part of the material of *Mirandaichnium* was compared with *Umfolozia* (Savage, 1971) by Aceñolaza and Buatois (1993), who proposed that the former ichnogenus be restricted to arthropod trackways with eight tracks in a series (see also Buatois et al., 1998a). Anderson (1981) concluded that *Umfolozia* is characterized by five crescentic tracks per series, accompanied by two sinuous rows of dots in the inner margin of the track rows.

Kim et al. (2005) suggested that the ichnogenus *Octopodichnus* Gilmore, 1927 can be considered a junior synonym of *Diplichnites* Dawson, 1873. We do not agree with this proposal as *Octopodichnus* has a characteristic morphology that consists of sets of four tracks with alternate symmetry, which strongly contrasts with the typical morphology of *Diplichnites*.

Diplichnites gouldi (Gevers et al., 1971)
Figures 4A, 4B, 5B, 5D, 7A–J, 8A, and 8B

Emended diagnosis: *Diplichnites* with 6 to 20 tracks per series. Track series may describe a low angle with the midline, form a "V" or an *en echelon* arrangement.

Remarks: At least 15 *Diplichnites* ichnospecies have been named, including *D. aenigma* Dawson, 1873, *D. triassicus* (Linck, 1943); *D. cuithensis* (Briggs et al., 1979); *D. gouldi* (Gevers in Gevers et al., 1971); *D. govenderi* Savage, 1971; *D. incertipes* (Matthew, 1910); *D. minor* (Matthew, 1910); *D. leavitti* (Matthew, 1910); *D. giganteum* (Gevers and Twomey, 1982); *D. binatus* Webby, 1983; *D. minimus* Walter and Gaitzsch, 1988; *D. logananus* (Marsh, 1869); *D. midlinearis* Wang, 2007; *D. minimum* Wang, 2007; and *D. arboreus* Gibb et al., 2009. *Diplichnites aenigma* is the type ichnospecies and apparently has not been recognized since its proposal. *Diplichnites govenderi* was synonymized under *Umfolozia sinuosa* by Anderson (1981) on the basis of the examination of a large collection of arthropod trackways from Dwyka and Ecca Series of South Africa. *Diplichnites arboreus* is probably an undertrack of a rusophyciform. Similarly, *D. binatus* (known from a single specimen and characterized by paired tracks) and *D. midlinearis* (with a medial trace) do not agree with the distinguishing features of the ichnogenus. *Diplichnites minimus* was distinguished by the small size of the track rows; however, it is characterized by highly variable, composite, and poorly defined tracks. Therefore, its inclusion under *Diplichnites* is dubious.

The ichnospecies most commonly described in the literature are *D. cuithensis*, *D. gouldi* and *D. triassicus*. They can be compared with other proposed *Diplichnites* ichnospecies using a few prospective taxobases adopted by most recent workers, including external trackway width, number of tracks in a series and series overlap (Table 1). Most of these features were used by Osgood and Drennen (1975) to distinguish "groups"
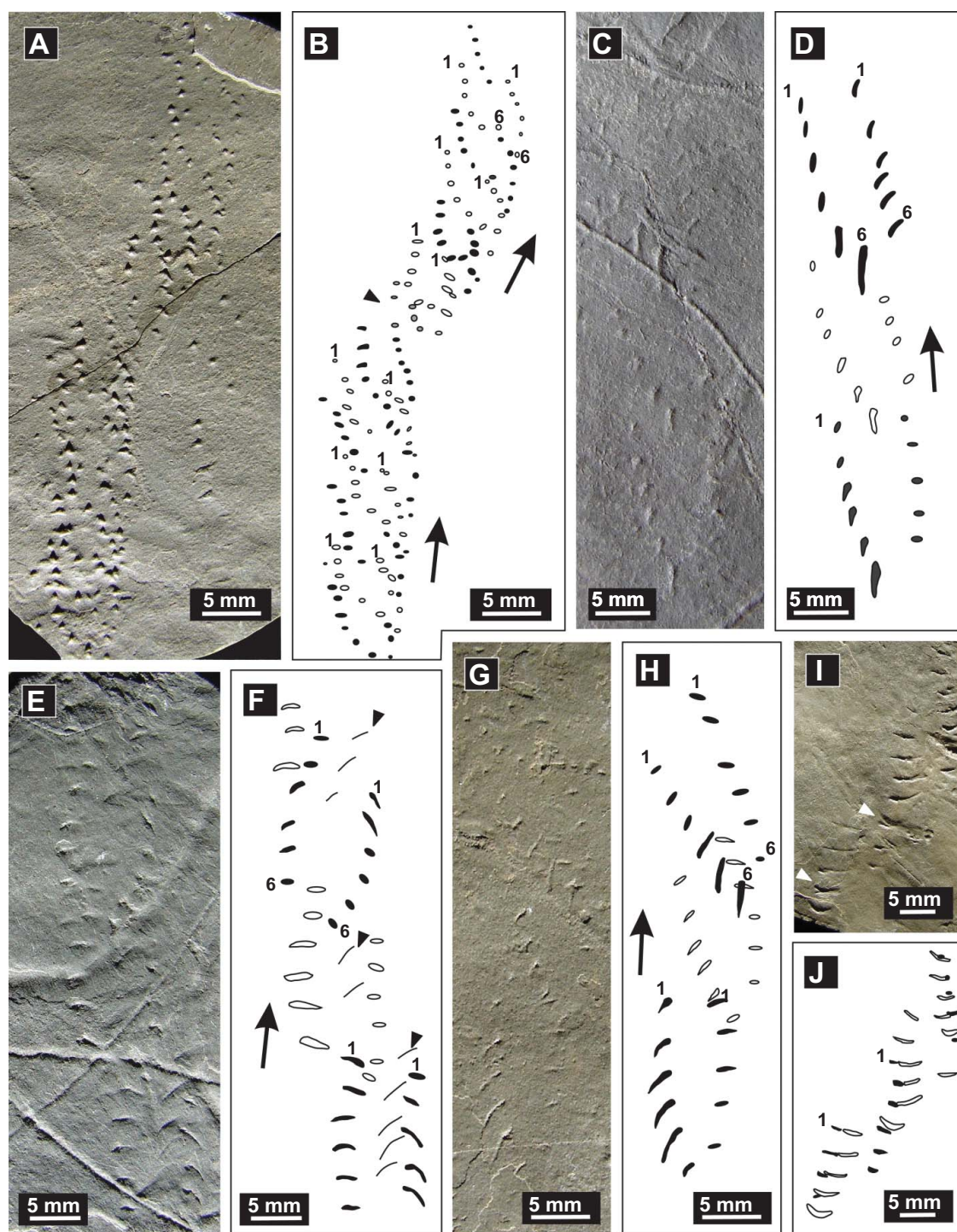
FIG. 7. Photographs and interpretative drawings of selected specimens of *Diplichnites gouldi* showing its morphologic variability. Successive complete sets are distinguished by alternate black and white color. 1 and 6 refer to the first and sixth track in a series. **A., B.** GHUNLPam 3427, trackway with a marked series overlap. The small arrow indicates a change in trackway direction and slight change in gait. In this area, series are incomplete (gray tracks). **C., D.** MCNAM PI 24268, trackway with a reduced series overlap. **E., F.** MCNAM PI 24269, trackway with a zero to negative series overlap. The arrows point to a shallowly imprinted and odd group of tracks that are located along the midline. **G., H.** GHUNLPam 12175, trackway with variable set overlap. **I., J.** GHUNLPam 12156, note overlap between tracks of successive series producing some tracks that appear Y-shaped or bifid (arrows). Trails in C and E are assigned to *Protovirgularia* isp. The large arrows indicate the inferred displacement direction. (See Color Plate IV.)
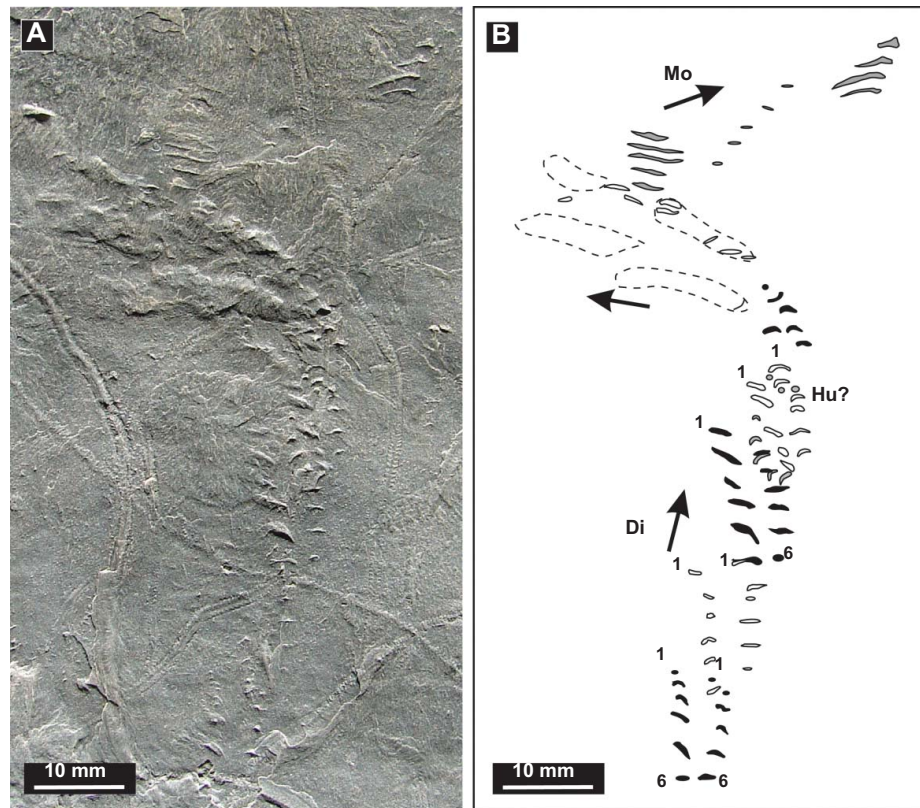
FIG. 8. Compound trace fossil (GHUNLPam 12162) including *Diplichnites gouldi* (Di), possible *Huilmuichnus* or a complete set of *D. gouldi* with opposite symmetry (Hu?, white), shallow paired mounds (dashed lines) and *Monomorphichnus lineatus* (Mo, dark gray). **A.** Photograph. **B.** Interpretative drawing. Successive complete sets in *D. gouldi* are distinguished by alternate black and white color. 1 and 6 refer to the first and sixth track in a series. Black arrows indicate the inferred direction of displacement. (See Color Plate V.)

within *Diplichnites*, and more recently by several authors to recognize morphotypes within *D. gouldi* (e.g., Buatois et al., 1998b; Minter et al., 2007b; Smith et al., 2003; Trewin and McNamara, 1995). *Diplichnites cuithensis* includes the widest trackways (up to 502 mm) with series of up to 23 tracks and a high series overlap. In this ichnospecies a large internal trackway width may also be considered a key feature. *Diplichnites gouldi* was originally proposed for small forms (22–43 mm wide, after Gevers et al., 1971, see Table 1 herein) but was latter extended to forms reaching up to 300 mm in external trackway width (Bradshaw, 1981; Gevers and Twomey, 1982; Trewin and McNamara, 1995), which leads Buatois et al. (1998b) to consider *D. giganteum* a junior synonym of *D. gouldi*. Gevers et al. (1971) did not recognize track series in *D. gouldi*, though they can be inferred from the illustrations. *Diplichnites gouldi* has been commonly used for trackways with a track series ranging from 6 to 11 tracks (rarely five tracks, see Table 1) or from 11 to 20 tracks (11 to 16 tracks are more common). The series overlap is variable between zero and 70% in both groups. The first group, typified by 6–11 tracks per series, includes the specimens described by Bradshaw (1981), Form B of Trewin and McNamara (1995), Form B of Draganits et al. (2001), Type A of Smith et al. (2003),

Types A and B of Minter et al. (2007b), Type A of Morrissey and Braddy (2004), and the specimens described by Retallack (2009) and Morrissey et al. (2011). A similar track series is also found in Group A of *Diplichnites* isp. of Osgood and Drennen (1975) (Table 1). The second group has a track series ranging from 11 to 20 tracks and is composed of Form C of Trewin and McNamara (1995), Type B of Buatois et al. (1998b), Type B of Smith et al. (2003), Type B of Morrissey and Braddy (2004), and the specimens from the Buckley Formation described by Briggs et al. (2010). *Diplichnites* isp. group B of Osgood and Drennen (1975) can be accommodated in this group. Only *D. gouldi* Type A of Buatois et al. (1998b), which is transitional to *Diplopodichnus*, and *D. gouldi* Form A of Draganits et al. (2001) were described as lacking recognizable track series.

Following the position of most authors that have worked on the taxonomy of *D. gouldi*, it is herein proposed that this ichnospecies be restricted to *Diplichnites* having between 6 and 20 tracks in a series. *Diplichnites triassicus* has been applied to relatively small trackways (external trackway width between 7 and 19 mm, Table 1), having 6 or 7 to 9 track per series, which are commonly arranged *en echelon* (Goldring et al., 2005; Pollard et al., 2008; Pollard, 1985). It is worth

TABLE 1
Compilation of distinguishing features of proposed *Diplichnites* ichnospecies

Ichnospecies	References	Morphotype	Track per series	External trackway width (mm)	Series overlap	Age	Comments
Diplichnites isp.	Osgood and Drennen (1975)	Group A	6–11	13–15	12–62%	Silurian	"V" pattern in series
	Osgood and Drennen (1975)	Group B	10–16	35–40	50–60%	Silurian	"V" pattern in series
	Osgood and Drennen (1975)	Group C	No			Silurian	Discontinuous, simple to pentadactyl tracks
D. cuithensis	Briggs et al. (1979, 1984) Ryan (1986)		23	108–502	about 50%	Carboniferous	High internal trackway width
	Martino and Greb (2009)		5–6	200–420		Carboniferous	
D. gouldi	Gevers et al. (1971)		Yes [*]	22–43	high	Devonian	Transitional to *Diplopodichnus*
	Bradshaw (1981)	Form A	8–10	20–220	40–50%	Devonian	Transitional to *Diplopodichnus*
	Trewin and McNamara (1995)	Form A	5	10–40	no	Ordovician	
	Trewin and McNamara (1995)	Form B	10–11	50–200	60–70%	Ordovician	
	Trewin and McNamara (1995)	Form C	16	200–300	50%	Ordovician	
	Buatois et al. (1998b)	Type A	No	5–8		Carboniferous	
	Buatois et al. (1998b)	Type B	11 a 16	4–9.6		Carboniferous	
	Draganits et al. (2001)	Form A	No	18–140		Devonian	
	Draganits et al. (2001)	Form B	≥ 8	51–107		Devonian	
	Smith et al. (2003)	Type A	6–9	10–28	40%	Devonian	
	Smith et al. (2003)	Type B	16–20	38–102	40–60%	Devonian	
	Morrisey and Braddy (2004)	Type A	6–9	8–52	10–50%	Silurian–Devonian	
	Morrisey and Braddy (2004)	Type B	≤ 14	25–160	up to 50%	Silurian–Devonian	
	Minter et al. (2007b)	Type A	(5) 6–11	2.7–11	30–66%	Permian	"V" pattern in series
	Minter et al. (2007b)	Type B	8	15.9–21.9		Permian	
	Retallack (2009)		8–11	15.8 (average)		Cambrian–Ordovician	
	Briggs et al. (2010)		8	10	up to 45%	Triassic	One specimen from Fremouw Fm.
	Briggs et al. (2010)		13	21–25	25%	Permian	Specimens from Buckley Fm.

Species	Reference				Age	Remarks
D. incertipes	Bradshaw (2010)	8	114	high	Devonian	One specimen
	Morrissey et al. (2011)	6–8	10–60		Devonian	
	This work	6	3.1–9.3	0–40%	Carboniferous	
	Matthew (1910)	6–8	8–10	About 30%	Silurian	
D. minor	Matthew (1910)	6	15		Silurian	plate I, figs. 4, 5
D. leavitti	Matthew (1910)	6	8			
D. giganteum	Gevers and Twomey (1982)	Yes *	95–200	high	Silurian–Devonian	
D. minimus	Walter and Gaitzsch (1988)	No	28–40		Carboniferous–Permian	High variability. Transitional to *Diplopodichnus*
D. minimum	Wang (2007)	8–9			Cambrian	
D. triassicus	Pollard (1985)	7–9	up to 15		Triassic	Complete series forms *en echelon* arrangements
	Malchaski and Malchaska (1994)	5–8	7–11		Triassic	
	Pollard et al. (2008)	7–9	15–19		Carboniferous	
	Goldring et al. (2005)	6–9	12		Cretaceous	
	Lucas et al. (2006)	No	7–10		Jurassic	The authors doubt about assignation to *D. triassicus* or *D. gouldi*

*Observed in the illustrations but not indicated by the authors.

nothing that these features are identical to those proposed in the emended diagnosis of *Acripes* by Walter (1983). Both the range of track series and external width of *D. triassicus* fall within the known range of *D. gouldi* (compare track series and external width in Table 1). *Diplichnites triassicus* has been typically applied to Mesozoic forms (except for Pollard et al., 2008), whereas *D. gouldi* was used for Paleozoic trackways (except for a single Triassic specimen described by Briggs et al., 2010). *Diplichnites triassicus* (Linck, 1943) may have priority over *D. gouldi*, although the latter is widely used and accepted, and it is thus suggested that it be retained.

Similarly, the ichnospecies *D. incertipes*, *D. minor*, and *D. leavitti* were considered as belonging to *D. gouldi* by Falcon-Lang and Miller (2007). These ichnospecies are indistinguishable from *D. gouldi* considering overall morphology, number of tracks in a series, and trackway width, as is the case for *D. minimum* (Table 1). In consequence, these ichnospecies can be synonymised under *D. gouldi*, although definite assignments can be made only after revision of type material.

Material: GHUNLPam 3420 from LPA; GHUNLPam 3404, 3413, 3422, 3427, 3429, 3432, 3433, 3436, 3444, 3446, 3453, 3458, 3461, 3463, 3464, 3467, 3470, 3471, 3473, 3485, 12146, 12148, 12152, 12154, 12156, 12162, 12163, 12175, 12211, 12220, 12224, 12243, 12249, 12251, and 12252 from MSC1; GHUNLPam 3406, 3408, 3415, 3452, and 12182 from MSC2; GHUNLPam 12089, 12091, 12098, 12113, 12116, 12129, 12232, and MCNAM PI 24279 from MSC3; MCNAM PI 24268, PI 24269, and PI 24279 and PY1; GHUNLPam 3486, 3487, and 3494 from PY2.

Description: Two rows of elongate, comma-external, crescentic or nearly circular tracks, arranged oblique to perpendicular to the midline. Intergradations between two of these track morphologies have been observed in a single trackway. Arcuate series of opposite (rare) or staggered symmetry, composed of 6 tracks. Adjacent series may form *en echelon* or V-shaped arrangements, and are commonly asymmetrical with respect to the midline. The series angle ranges from 2 to 26 degrees (Table 2). In some specimens (e.g., GHUNLPam 3427) one of the series angle is negative (from −6 to − 20 degrees) and the remaining is positive. This is a result of a typical arrangement of complete series with the longitudinal axis forming an oblique angle with the midline (Figs. 7A−H). Series length average 10.4 mm (range 5.8−15.6 mm, n = 16) and usually the series of a set are of similar length although a difference of up to 20% was observed. Mean external trackway width is 5.9 mm (range 3.1−9.3 mm, n = 17). The average stride length is 9.1 mm (range 4.4–14.2 mm, n = 12) and the average pace length is 2.6 mm (range 0.6–7.0 mm, n = 15). The series overlap ranges between 0 to 40% and in many specimens the overlap is different in both series (right and left) of a complete set. In a single specimen (MCNAM PI 24269), the complete series does not show overlap (Figs. 7E and F). In some examples, overlap between series results in tracks from different series overprinting to form composite V- or Y-shaped tracks (Figs. 7I

and J). The trackways are straight or slightly curved and are preserved in positive hyporelief or negative epirelief.

Discussion: The large number of examined specimens (more than 55) suggests a significant morphological variability and intergradations between trackways ascribed to this ichnospecies. In terms of the ichnotaxobases considered for *D. gouldi* (Table 1), the specimens from the Agua Escondida Formation are close to *D. gouldi* Type A of Minter et al. (2007b). The asymmetrical nature of most trackways is in agreement with a subaqueous origin inferred for the succession from the sedimentary facies and has been suggested as an indicator of current dragging the producer during displacement (Osgood, 1970; Seilacher, 1955). Intergradations of track morphology in single trackways suggest that these morphological differences are due to taphonomical or behavioral factors.

Ichnogenus *Gluckstadtella* Savage, 1971

Remarks: Keighley and Pickerril (1998) proposed a modified diagnosis of the ichnogenus, suggesting that *Rotterodichnium* Walter, 1983 should be considered a junior synonym of *Gluckstadtella*. However, *Rotterodichnium* has been recently recognized as a distinct ichnogenus (Braddy and Briggs, 2002; O'Brien et al., 2009). *Gluckstadtella* is distinguished by six pairs of appendage marks, two of them longest, located at one extreme and directed parallel or at low angle with the longitudinal axis; and four pairs directed at a higher angle and in opposite direction (Savage, 1971); whereas *Rotterodichnium* includes three to four pairs of tracks which are shorter at one extreme and increases in length toward the other (Braddy and Briggs, 2002; Walter, 1983).

Gluckstadtella cooperi Savage, 1971
Figures 4A−D, 5A, 5C, 9A−C, and 9E

Material: GHUNLPam 3429, 3456, 3478, 12152, 12175, 12237 from MSC1, GHUNLPam 12182 from MSC2, and GHUNLPam 12090 from MSC3.

Description: Group of six pairs of elongate tracks, two longest and anteriorly directed and four posteriorly directed. The longest appendage marks (range 2.9–5.3 mm) are about two times the length of the remaining imprints (1.7–2.3 mm). Track morphology is slightly crescentic or segmented and curved inward for the longest marks, and elongate for the remaining ones. Tracks are commonly oblique to the midline, except for the longest ones that may display a quasi-parallel orientation. Average overall length is 11.1 mm (range 7.6−14.4 mm, n = 8) and average external width is 7.2 mm (range 4.9−10.0 mm, n = 8), and the length/width ratio is in the range 1.3 to 1.8. Several *G. cooperi* specimens are located at one end of a *D. gouldi* trackway, both having a similar. Preserved both in negative epirelief and positive hyporelief.

Discussion: In addition to the original description from the Upper Carboniferous-Lower Permian Dwyka Group of South

TABLE 2
Detailed measurements on selected *D. gouldi* specimens from the Agua Escondida Formation. See text for explanation of parameters

Specimen number (*)	Series length		Series overlap		Pace	Left stride	Right stride	Series angle (°)		Tracks per series	Series width
	left	right	left	right				left	right		
3408	nd	nd	nd	nd	nd	nd	nd	nd	nd	6	4.5
3413	7.8	nd	2.2	nd	nd	nd	nd	18	13	6	5.9
3415	6.1	6	−0.9	1.1	2.2	6.5	5.4	4.8	2.9	6	3.6
3427	6.1	7.5	2.8	2.6	2	5.2	3.8	−20	26	6	4.5
3427	6.9	6.9	2.4	2.6	1.8	4.2	4.6	−19	25	6	4.8
3427	8.0	9.5	2.6	2.6	4.2	6.7	5.2	26	−16	6	4.6
3444	11.4	10.2	2	2.3	0.8	10	8.9	2.6	4.3	6	6.8
12154	11.6	13	nd	nd	1.3	nd	nd	5.5	1.8	6	6.7
12156	15.6	15.6	2.4	1.4	7	13.6	14	−6	4	6	7.3
12162	13.6	13.5	−0.4	1.4	2.2	15	12.4	3.4	4.1	6	6.0
12163	9.3	9.6	nd	nd	6.9	nd	nd	nd	nd	6	6.5
12175	13.9	14.7	3.2	1.6	1.1	9.9	13.2	4.1	2.8	6	7.7
12249	5.8	5.8	nd	nd	0.6	5.8	7.5	3.1	4.1	6	3.1
12251	12	10.6	−1.5	5.8	1.6	8.8	5.3	2.9	10.3	6	6.8
MCNAM PI 24268	11.2	10.8	2.2	0.5	2	9.4	11.3	5.3	8	6	5.3
MCNAM PI 24269	14.6	12.9	−0.4	−1.5	4	14.6	13.7	−6.1	6.5	6	9.3

*Unless otherwise stated, the acronym of specimens is GHUNLPam and measurements are in millimeters.

Africa (Savage, 1971), the ichnospecies has been identified in several locations of the Upper Carboniferous-Lower Permian Itararé Group of southern Brazil (Balistieri et al., 2002; Gandini et al., 2007; Lermen, 2006; Nogueira and Netto, 2001), and from the Upper Carboniferous Mabou Group of eastern Canada (Keighley and Pickerill, 1998). The single specimen described from Canada displays a medial groove in addition to the six pairs of tracks, for this reason its inclusion under the ichnospecies is doubtful. All previous examples are from freshwater deposits, the South African and Brazilian examples come from glaciolacustrine deposits, and the Canadian example from floodplain ponds. The size range of the specimens from the Agua Escondida Formation is similar to the South African examples and slightly smaller than the Brazilian examples.

Ichnogenus *Huilmuichnus* igen. nov.

Type ichnospecies: Huilmuichnus santacruzensis isp. nov.

Holotype: GHUNLPam 3431 from MSC1.

Paratypes: GHUNLPam 12182 from MSC2, GHUNLPam 12116 from MSC3.

Additional material: Six specimens (GHUNLPam 3404, 3437, 3446, 12162, 12238, 12252) from MSC1 section and a single specimen (GHUNLPam 12091) from MSC3 section.

Derivation of name: From the Mapuche language of central and southern Argentina, *Huilmu* meaning oval (Erize, 1960), and from the Greek *Ikhnos* for trace.

Diagnosis: Isolated group of four to six pairs of tracks forming an elongate subelliptical to horseshoe-shaped, bilaterally symmetrical trace with an open end. Individual comma-shaped, elongated or crescentic tracks are oblique to subparallel to the long axis and always oriented in the same direction. Closed end is more deeply imprinted and may exhibit a pair of elongate imprints, either twice or up to five times the length of the remaining tracks, arranged at a low or 45 degrees angle with the long axis of the trace fossil. Preserved both in negative epirelief and positive hyporelief.

Remarks: Huilmuichnus is morphologically different from other known arthropod resting traces that are also characterized by having an elliptical or horseshoe-shaped outline. The ichnogenera that are more akin to *Huilmuichnus* are *Arborichnus* Romano and Meléndez, 1985; *Gluckstadtella* Savage, 1971; *Kingella* Savage, 1971; and *Selenichnites* (Romano and Whyte, 1987). *Arborichnus* is typified by sets of five pairs of marks that are shorter and oblique anteriorly and pass gradually backwards to long and transverse. In addition, the only known ichnospecies, *A. repetitus*, was defined as a trackway (Romano and Meléndez, 1985). *Huilmuichnus* differs from *Arborichnus* in being typically an isolated group of six pairs of short tracks arranged oblique to the trace fossil midline, plus longer anterior imprints (absent in *Arborichnus*). *Gluckstadtella* and *Huilmuichnus* have six pairs of imprints, but the former is distinguished by the presence of two pairs of longer tracks directed forward, whereas *Huilmuichnus* has six pairs

directed obliquely backward. In addition, the presence of an additional longer anterior pair of imprints in *Huilmuichnus* is a further distinction from *Gluckstadtella*. *Solusichnium* O'Brien et al., 2009 shares with *Huilmuichnus* the two anterior long imprints, but its tripartite structure is clearly different from the oval shape of *Huilmuichnus*. *Kingella* shares with *Huilmuichnus* an oval outline and two anterior long imprints, but differs in having a larger size, being more deeply impressed, and clearly bilobed. *Selenichnites* is a suboval trace, slightly wider than long, with strongly convex lunate or paired crescent-shaped lobes directed antero-laterally, with or without appendage marks. *Hulmuichnus* differs from *Selenichnites* in being longer than wide, lacking a crescentic shape and lobes, and always possesses appendage marks, which may be absent in *Selenichnites*.

In some cases, it may be difficult to distinguish a complete set of *D. gouldi* from *Huilmuichnus*, a clear example is shown in Figure 8. In a compound trace fossil, *Huilmuichnus* is usually shorter than an associated complete set of *D. gouldi* and tend to display an opposite symmetry, instead of the typical staggered symmetry of the discussed examples of *D. gouldi*.

Huilmuichnus santacruzensis isp. nov.
Figures 5B, 5D, 6A–F, 9D and 9E

Diagnosis: Same as for the ichnogenus, only known ichnospecies.

Derivation of name: santacruzensis is derived from the Santa Cruz Mine, where all specimens were found.

Description: Average length of the group of up to six pairs of tracks is 9.8 mm (range 5.5–12.5 mm, n = 9) and average external width is 6.1 mm (range 4.9–9.2 mm, n = 9), and the mean length/width ratio is 1.6 (range 1.1–2.1, n = 9, Table 3). Two preservational variants can be distinguished: the most common is composed of five or six pairs of tracks arranged oblique to the midline depicting an elongate subelliptical trace, more deeply imprinted in the closed (anterior?) end (Figs. 6A–F). Tracks are commonly comma-shaped and up to 2 mm long. The closed end may exhibit another pair of tracks that is longer that the remaining ones (up to 4.4 mm long) and directed parallel to the

midline (GHUNLPam 3404, 3431; Figs. 6B and E). In GHULPam 12116 the closed end exhibits another pair of tracks that may reach 12.6 mm and be arranged parallel or transverse to the midline (Figs. 5B and D). Commonly, one half of the trace (left or right with respect to the midline) is more deeply imprinted. Part of the tracks from one side of the trace fossil can be duplicated (Figs. 6D and F). The tracks are bounded externally by an oval depression (Figs. 6C and E) and ventral features of the producer are evident in some specimens. These ventral features include shallow curved grooves that may lie parallel to the outline of the trace fossil (GHUNLPam 3431, 12252; Fig. 6E) and possible proximal marks of the limbs (Fig. 5B, insert). The second preservational variant is represented by three to four pairs of shallow crescentic tracks that are arranged with the longest axis describing the elliptical trace with an open (posterior?) end (GHUNLPam 3437, 12182; Fig. 9E). In the specimen GHUNLPam 3446 it is possible to recognise *Huilmuichnus* (although the individual appendage marks are poorly defined) located within *D. gouldi*.

Ichnogenus *Monomorphichnus* Crimes, 1970
Monomorphichnus lineatus Crimes et al., 1977
Figures 6A–C, 8A, 8B, and 8E

Material: GHUNLPam 3431, 12162, 12175, 12252 from MSC1

Description: Groups of four to five parallel, slighty curved to straigth, in some cases comma-shaped striae, arranged roughly parallel to the long axis of the trace fossil. Striae within each group are almost parallel, 5–7 mm long and the lateral separation between rows ranges from 4 to 10 mm. Spacing between striae in a row is fairly uniform and averages 2.6 mm (n = 6). Maximum length of individual striae is also uniform and averages 5 mm (n = 6).

COMPOUND TRACE FOSSILS

The intergradations between the resting traces *Gluckstadtella* and *Huilmuichnus* with the locomotion traces *Diplichnites*, *Dendroidichnites* and *Monomorphichnus* are considered

TABLE 3
Summary of length, width and length/width ratios of *Diplichnites*, *Gluckstadtella* and *Huilmuichnus* with similar parameters from their potential producer, the Pygocephalomorpha

	Diplichnites	*Gluckstadtella*	*Huilmuichnus*	Pygocephalomorpha[1]
W	5.9 mm (3.1–9.3 mm)	7.2 mm (4.9–10.0 mm)	6.2 mm (4.9–9.2 mm)	6.3 mm (2.3–15.0 mm)
L	10.4 mm (5.8–15.6 mm)	11.1 mm (7.6–14.4 mm)	9.8 mm (5.5–12.5 mm)	10.2 mm (4.0–20.0 mm)
L/W	1.8 (1.4–2.3)	1.5 (1.3–1.8)	1.6 (1.1–2.1)	1.7 (1.3–2.3)
n	16	8	9	9

[1]Source of data: Kensley (1975), Pinto and Adami-Rodrigues (1996), and Piñeiro et al. (2012a, 2012b).
W: Width of *Gluckstadtella* and *Huilmuichnus*, complete series width in *Diplichnites*, width of insertion of pereopods in Pygocephalomorph remains. L: Length of *Gluckstadtella* and *Huilmuichnus,* average series length for *Diplichnites*, and length of insertion of pereopods for Pygocephalomorphs. L/W: Length/width ratio; n = number of specimens.
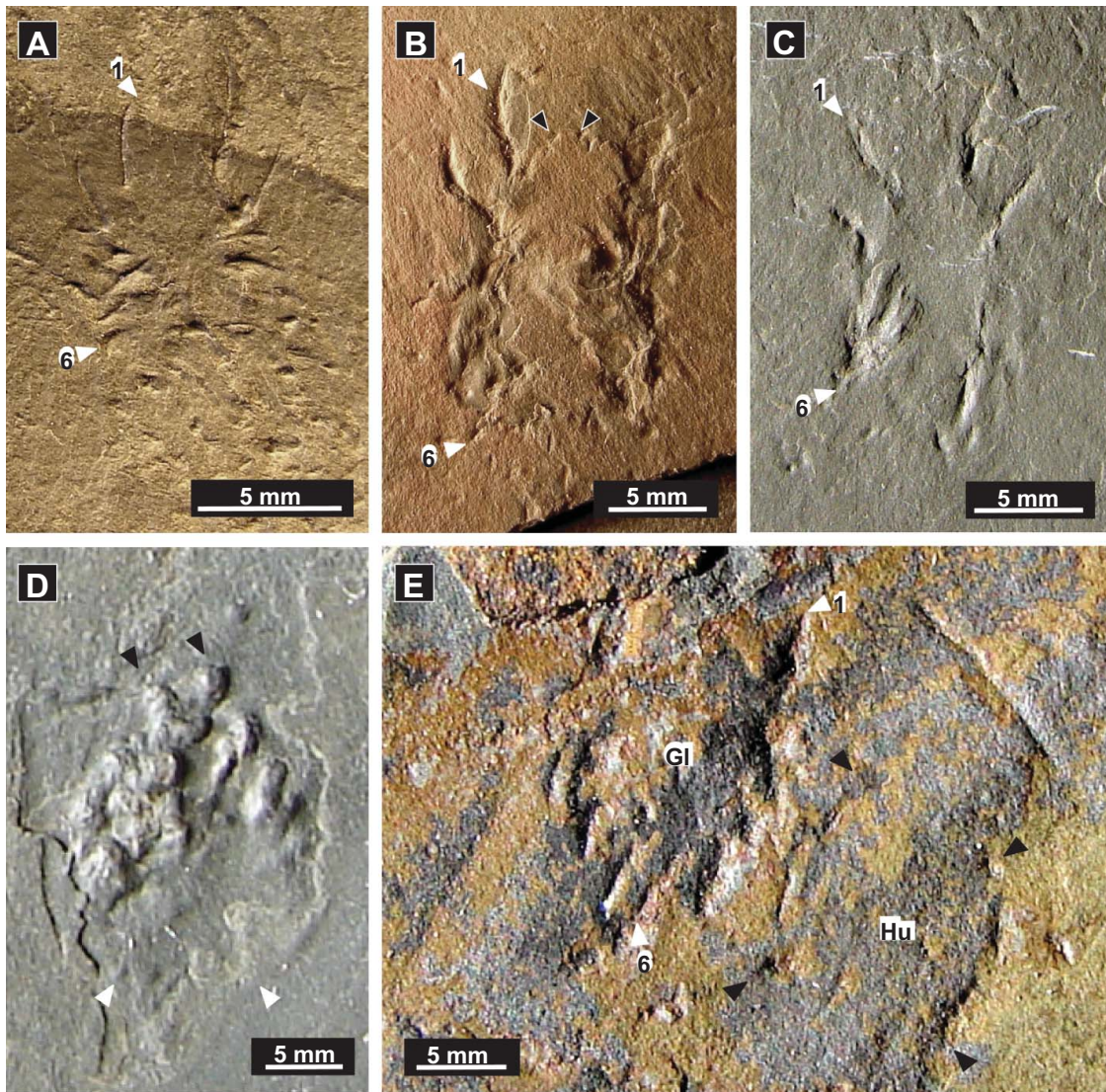
FIG. 9. Arthropod resting traces. **A–C., E.** *Gluckstadtella cooperi*. The white arrows point to the first and sixth tracks (1 and 6). Note that the first two pairs of appendage marks are larger and clearly imprinted, whereas the remaining four are shorter and less clearly imprinted. **D., E.** *Huilmuichnus santacruzensis* igen. and isp. nov. A, GHUNLPam 3429. B, GHUNLPam 3478. Note the presence of additional marks between the anterior pair of tracks (black arrows). C, GHUNLPam 12175. D, GHUNLPam 3404, undertrack of *H. santacruzensis* (outline indicated by arrows). The black arrows point to the pair of anterior marks, the white arrows to the posterior part. E, GHUNLPam 12182, *G. cooperi* (Gl) adjacent to *H. santacruzensis* (Hu). The arrows in *H. santacruzensis* indicate the outline of the trace fossil. (See Color Plate VI.)

compound trace fossils (Minter et al., 2007a; Pickerill, 1994; Pickerill and Narbonne, 1995). These compound specimens are described below according to the resting and associated locomotion trace fossils.

Gluckstadtella and *Diplichnites* (*Dendroidichnites*)

In these specimens, usually *Gluckstadtella* co-occurs with *Diplichnites* and occasionally with *Dendroidichnites*. The most complex specimen, GHUNLPam 12152 (Figs. 4A and B), is composed of a transition from a curved *D. gouldi*

showing series of six tracks and displaying the characteristic "V" asymmetric arrangement of this ichnospecies (black in Fig. 4B), then there is a complete set with a transitional arrangement, and a clear *G. cooperi* (light grey in Fig. 4B) with two larger appendage marks directed forward and four appendage marks directed obliquely backward. Some of the later impressions are repeated, especially on the left side of the figure. The anteriorly directed marks exhibit at least two segments, and a pointed end. The compound trace fossil ends with chevron-like trace broadly comparable with *Dendroidichnites* (dark grey in Fig. 4B). The turn angle between the midline of *G. cooperi* and *Dendroidichnites* is 102 degrees.

Most of the specimens in this category are composed of a short *Diplichnites* that ends in (GHUNLPam 3429, 3478, 12237) or arise from (GHUNLPam 12175) *G. cooperi*. A particular case is found in specimen GHUNLPam 12237 (Figs. 4C and D), where two successive *G. cooperi* are linked by a trackway comparable with *Diplichnites*. The mentioned compound trace fossil starts with a short portion of a curved *Diplichnites* connected to the first *G. cooperi*, which display a repetition of the four posterior tracks on the right (external) side of the trace fossil (white arrows in Fig. 4D). The distance to the next *G. cooperi* is approximately equal to the length of the resting trace, this space have sparse tracks with no definite arrangement. The second *G. cooperi* is oriented at a low angle with the previous one and have a number of associated dot-like tracks roughly comparable with *Diplichnites* that follows the resting trace. These tracks seem to be duplicated in both sides of the posterior part of *G. cooperi*. This is one of the few specimens of *G. cooperi* where the position of all tracks can be clearly discerned. The two anterior pairs are longer, segmented and always clearly impressed, the third pair is directed laterally and the three last pairs are almost parallel to the midline.

Gluckstadtella or *Huilmuichnus* Associated with *Dendroidichnites*

Specimen GHUNLPam 12090 (Figs. 5A and C) is composed of a moderately long (25 mm) trace with a chevron-like appearance that is compared with *Dendroidichnites* isp., which ends in a poorly preserved *Gluckstadtella* that is essentially recognized by the forward pointing tracks. The transition between *Dendroidichnites* and *Gluckstadtella* is blurred.

GHUNLPam 12238 (Figs. 6D and F) includes an asymmetrical chevron-like trackway (*Dendroidichnites* isp.) that ends up in a group of elongate to dot-like tracks with an oval arrangement (*H. santacruzensis*). In the later, a repetition of tracks on the right side of the trace fossil was observed. The angle between the midline of both trace fossils is 42 degrees.

Huilmuichnus and *Diplichnites*

Huilmuichnus santacruzensis is found within *D. gouldi* trackways in four specimens (GHUNLPam 3446, 12116, 12152, and 12249). *H. santacruzensis* is distinguished because of its opposite symmetry instead of the staggered symmetry characteristic of a typical set of tracks of *D. gouldi* (Figs. 5B and D). Specimen GHUNLPam 12116 is remarkable because of the presence of a pair of long anterior tracks in *H. santacruzensis*. These marks are slender (0.5 mm wide at the base and decreasing in width toward the distal end), subequal in length (11.4 mm long), forming a right angle, and symmetric with the midline. This anterior track and the remaining ones on the right side of the picture of *H. santacruzensis*, exhibit an additional crescentic imprint that is located medially (Fig. 5B,

inset). In GHUNLPam 12116, *D. gouldi* tracks are circular to ellipsoidal before *H. santracruzae* and become elongated after it.

Huilmuichnus and *Monomorphichnus* (*Diplichnites*)

The compound specimens GHUNLPam 3431, 12162, and 12252 display an association between *Huilmuichnus* and *Monomorphichnus*. *Diplichnites* is also recognized in the last two specimens. GHUNLPam 3431 includes a resting trace assigned to *H. santacruzensis* (Figs. 6B and E) which exhibits a discontinuous oval ridge surrounding the tracks and internal ridges that are parallel to the boundary of the trace fossil (positive hypichnia). At least four sets of four to six subparallel linear ridges are recognized starting from the anterior end of *H. santacruzensis*, which are compared with *Monomorphichnus* isp. The angle between the midline of *H. santacruzensis* and the line defined by equivalent points of the successive sets of ridges in *Monomorphichnus* is 33 degrees.

GHUNLPam 12252 (Figs. 6A and C) includes a short curved *Diplichnites* isp., associated with *H. santacruzensis*, composed of six pairs of tracks associated with a shallow oval depression. Some tracks on the right side of *H. santacruzensis* are repeated. The later are followed by two sets of four or five parallel grooves with sigmoidal outline assigned to *Monomorphichnus lineatus*. The grooves are up to 5.8 mm long and successive sets are 25 mm apart. The angle between the midline of *H. santacruzensis* and equivalent points between successive sets of ridges in *M. lineatus* is 118 degrees.

GHUNLPam 12162 (Figs. 8A and B) is roughly similar to the previously described specimen. It includes a straight and moderately long *D. gouldi* (at least three complete sets are represented) that ends in an oval group of tracks that is akin with *Huilmuichnus* (although the identification of this ichnogenus is dubious in this specimen). The latter is followed by two pairs of elongate parallel mounds (each pair up to 14 mm long by 9.4 mm wide) and finally three sets of four to five subparallel ridges (*M. lineatus*). The turn angle between the midline of mounds and *M. lineatus* (equivalent points in successive sets of ridges) is 139 degrees.

DISCUSSION

Probable Trackmaker

The transitions between two or three discrete ichnotaxa observed in the compound specimens suggest that the trace fossils described herein were produced by a single group of arthropods. The candidate arthropod trackmaker must have had at least six pairs of locomotor appendages and a benthic mode of life. Further constraints are provided by the width and length/width ratio of the resting trace fossils (*Gluckstadtella* and *Huilmuichnus*) and the width and length/width ratio of the complete sets in *Diplichnites* (see summary in Table 3). A

comparison between these measurements suggests a marked overlap in the range of observed values and similar average measurements. The widths of these trace fossils fall in the range 3.1–10.0 mm. Similarly, the length/width ratio is in the range of 1.1–2.3. These values suggest a small animal with a reduced elongation of the pereon and possible absence of an extended pleon, as no traces of this part of the body has been recorded. In addition, it is considered unlikely that all these faint traces are undertracks and those of the pereon were lost due to the undertrack fallout phenomenon. The producer could be either a marine or freshwater arthropod, as the associated trace fossils and lithofacies suggest an estuarine or fjord-like environment. An examination of the Late Paleozoic record of arthropods from western Gondwana, mainly from Argentina, Brazil, and southern Africa, suggest as possible candidates that meet the above mentioned morphological features to syncarid, isopods, and pygocephalomorph crustaceans. Savage (1971) inferred a syncarid or peracarid crustacean origin for *G. cooperi* and associated traces from the lacustrine rhythmites of the Dwyka Group. However, the number of appendages inferred from the trace fossils allows discarding the syncarid crustaceans, which have eight pairs of appendages in the pereon (Brooks et al., 1969).

Isopods use seven pairs of pereopods for locomotion, that exhibits a particular arrangement: first to third pair directed forward, fourth laterally, and fifth to seventh directed backward (Brooks et al., 1969). Neither the number of appendages nor the arrangement of limbs in isopods match the morphology of the trace fossils described herein. The oldest isopod remains are known from the Late Carboniferous estuarine Essex fauna of Mazon Creek, near Chicago, Illinois, USA (Baird et al., 1986; Schram, 1974). The Late Carboniferous specimens belong to the Phreatoicidea, which are characterized by a laterally compressed body, with an elongated pereon (length/width ratio in excess of three). Isopods have been recorded from the Early Permian shallow marine facies of the Parana Basin, Brazil (Holz et al., 2010; Martins Neto, 2001; Mezzalira and Martins Neto, 1992). The isopods from the Permian of Brazil are preserved in dorsal view and lack appendages. The width of the pereon of these species is in the range of 3.8–7.7 mm and the length/width ratio of pereon is an average 1.1 (Martins Neto, 2001; Mezzalira and Martins Neto, 1992). Although Late Paleozoic isopod remains are scarce, they seem to be smaller and/or with a different length/width ratio than the purported producer of the analyzed trace fossils.

The Pygocephalomorpha is a group of Mississippian to Permian Malacostraca that were preferentially recorded from coastal lagoons, estuaries, and swamps. These crustaceans had eight pereonites, each bearing a pair of pereopods, including one or two anterior pairs of appendages modified for feeding (Fig. 10). A common distinctive feature of pygocephalomorph appendages is the presence of a single segment in the protopod (Brooks, 1969). Pygocephalomorphs were adapted to a dominantly benthic mode of life, which is reflected by a reduction
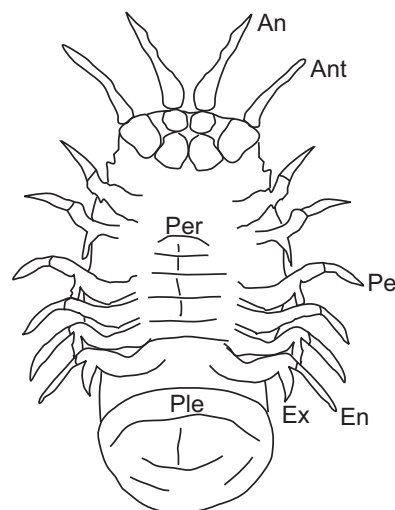

FIG 10. Schematic diagram of the pygocephalomorph *Notocaris tapscotti* from South Africa. An: antennules, Ant: antenna, Per: pereon, Ple: pleon, Pe: pereopod, En: endopod, Ex: exopod. Modified after the figures 4E and 4J by Kensley (1975). About 20 mm long.

of the relative size of the pleon, widening of the pereon, and modification of the two anterior pereopods into maxillipeds. In some Permian pygocephalomorhs the abdomen was reduced and flexed under the pereon (Brooks, 1969). Although little is known about the feeding mode of pygocephalomorphs, some fossils contain sediments in the intestine suggesting ingestion of the bottom organic-rich detritus and a likely scavenging to low-grade carnivorous mode of life (Brooks, 1969; Schram, 1981). Among Late Paleozoic crustacean communities, pygocephalomorphs compose a distinctive association with syncarids in fresh to brackish water assemblages, including the example from the Permian Iratí Formation of the Parana Basin, Brazil (Pinto and Adami-Rodrigues, 1996; Schram, 1981). Pygocephalomorphs are also known from the Early Permian of Uruguay (Piñeiro et al., 2012a; 2012b). A comparison between the width of a complete set of tracks in *D. gouldi*, the width of *G. cooperi* and *H. santacruzensis*, with the width of insertion of pereopods in pygocephalomorphs from South Africa, Brazil and Uruguay (Table 3), indicates a strong overlap between these values. The values for *Gluckstadtella* are slightly larger as expected for an arthropod in resting position (tip of appendages) compared with the width of insertion of appendages in pygocephalomorphs. Similarly the length/width ratio is very close in the analysed trace fossils and pygocephalomorphs. In addition, *Notocaris tapscotti* from South Africa illustrated by Kensley (1975, figs. 4e and f) possesses six pairs of appendages with an arrangement similar to *G. cooperi* (compare Figs. 4C and D with Fig. 10) and antennules or antenna with similar arrangement to those seen in some specimens of *H. santacruzensis* (compare Figs. 5B and D with Fig. 10).

There have been a few trace fossils assigned to pygocephalomorphs in the literature. Trace fossils described as trackways

of "Oliveirania santa catharinae" from the Parana Basin of Brazil by Beurlen (1952) were tentatively considered to be produced by pygocephalomorphs (see also Fernandes et al., 2002, pp. 131–132), as these crustaceans are very abundant in the same unit. The morphology of these trackways is roughly comparable with *Dendroidichnites*.

A further trackway from the Early Permian of Uruguay (Mangrullo Formation) identified as *Diplichnites* isp. was tentatively considered as produced by pygocephalomorphs by Piñeiro (2006). This 15 mm wide trackway differs from those described herein under *D. gouldi* in lacking a definite track series and having opposite symmetry. The Mangrullo Formation also contain abundant remains of pygocephalomorphs (Piñeiro, 2006; Piñeiro et al., 2012a, 2012b), providing a direct linkage between some of the trace fossils discussed in this work (*Diplichnites*) and its presumed producer.

Trackway Analysis

Accepting that pygocephalomorph crustaceans are likely producers of the studied trace fossils, some inferences on the mode of locomotion of the track makers can be drawn from the analysis of *D. gouldi*. The studies on arthropod locomotion summarized in Manton (1977) have been employed by several authors in the analysis of fossil arthropod trackways (e.g., Braddy, 2001; Briggs et al., 1979; Briggs et al., 1984; Minter and Braddy, 2006; Minter et al., 2012; Smith et al., 2003). In arthropods, one step cycle is divided into the protraction period (p, forward stroke), and the retraction period (r, backward stroke). Arthropods regulate the movement of their legs, in order to avoid interference between them and walking efficiently, according to three parameters: the gait or p: r ratio (expressed as a proportion of 10), the opposite phase difference (opp, the proportion of the step cycle that the right legs move after the left legs), and the successive phase difference (suc, the proportion of the step cycle that a leg moves in advance of the leg in front) (see Braddy, 2001; Manton, 1952). The walking techniques of Pygocephalomorph crustaceans may be assessed by calculating the gait parameters, based on trackway data in conjunction with anatomical information from the fossil record, according to the following formula (Braddy, 2001; Minter and Braddy, 2006; Minter et al., 2012):

$$r = (\text{backstroke/stride}) \times 10; p = 10 - r$$
$$\text{opp} = \text{pace/stride}$$
$$\text{suc} = (\text{stride} - \text{exsagittal distance}$$
$$- \text{distance between tracks})/\text{stride}$$

Pygocephalomorph remains from South Africa, Brazil, Uruguay, the United States, and England (see online supplement S1) were used to estimate an average ratio between pereonite length and leg length. This ratio is averaged at 3.1 (range 2.4–4.9, n = 8). It is assumed that the distance between tracks in *D. gouldi* series is directly related to the pereonite

length, in consequence, the approximate average leg length for every trackway can be estimated (distance between tracks x 3.1; see online supplement S2). In order to estimate the backward stroke distance (i.e., distance covered by the distal part of the leg during the propulsive stroke) it is necessary to estimate the angle of swing of the leg. According to Manton (1952) this angle is in the range of 16–27 degrees for the Arthropoda; therefore, an average angle of 21.5 degrees is adopted here. This estimation of the angle of swing allows calculating the backstroke by trigonometry. The average gait ratio inferred for the *D. gouldi* trackways is 7.3:2.3 (p:r), which is suggestive of a fairly high-geared gait (compare with table 2 of Manton, 1952). The range of estimated gaits has a correlation with the overall trackway morphology. The trackway with the highest-geared gait (GHUNLPam 12249; gait: 8.0:2.0, opp.: 0.09, suc: 0.6) has well-spaced sets of tracks with almost opposite symmetry, and individual tracks with marked elongation (Figs. 7C and D illustrate a similar arrangement). The low opposite phase difference is suggestive of a transition to a half–swimming mode of locomotion for that trackway, in agreement with subaqueous setting as indicated by sedimentologic evidence. The lowest-geared gait is 6.5:3.5, opp: 0.41, suc: 0.35; it was estimated in a trackway with staggered symmetry with nested sets of tracks, and predominantly dot-like tracks (Figs. 7A and B). For the high geared gaits the number of limbs in a metachronal wave is 3, and the wave appears to travel backwards (compare Smith et al., 2003).

Interpretation of Compound Trace Fossils

Gluckstadtella *and* Diplichnites (Dendroidichnites).

Specimen GHUNLPam 12152 (Figs. 4A and B) can be interpreted as reflecting normal walking with a curved path of a Pygocephalomorph crustacean (*D. gouldi*), which intermittently stopped, producing the resting trace (*G. cooperi*). When coming to rest or after stopping the animal produced an additional set of impressions on the right (external) side of the resting trace fossil probably reflecting slight adjustment to the new position (white arrow in Fig. 4B). The trace compared with *Dendroidichnites* ("De" in Fig. 4B) is tentatively interpreted as an escape reaction probably reflecting a half-swimming gait after launching.

In GHUNLPam 12237 (Figs. 4C and D), both specimens of *G. cooperi* are interpreted as produced by the same animal as they exhibit a similar orientation and size, but it is not clear if the scarcity of tracks in the space in between may suggest that the producer jumped. The repetition of the posterior tracks in *G. cooperi* seen in GHUNLPam 12237 and 12152 is related to its occurrence at the external side of a curved *Diplichnites* and probably represents the first set of appendages to touch the ground before a full stop. The two pairs of segmented anterior appendage marks in *G. cooperi* may correspond to antennae or antennule impressions.

Gl{uckstadtella *or* Huilmuichnus *and* Dendroidichnites

The compound trace fossil GHUNLPam 12090 (Figs. 5A and C) is composed of a locomotory trace (*Dendroidichnites*) reflecting the gradual approximation of the producer to the bottom sediment ("landing"), probably with a half-swimming gait. The compound specimen ends in a blurred *Gluckstadtella*, suggesting sediment with a fluid-like consistency. Similarly, specimen GHUNLPam 12238 (Figs. 6D and F) includes a short landing trace fossil (*Dendroidichnites*) followed by a resting trace (*H. santacruzensis*). *Dendroidichnites* has been commonly interpreted as reflecting interaction with a soft substrate that is dragged by the producer during its displacement (Buatois et al., 1998a; Davis et al., 2007; Minter and Braddy, 2009). A half-swimming mode of locomotion was proposed by Bandel (1967) for material later ascribed to this ichnogenus (Buatois et al., 1998a).

Huilmuichnus *and* Diplichnites

Most of the specimens reflect normal walking (*D. gouldi*) and a transient stop (*Huilmuichnus*) before returning to walk. The marked elongation of *Diplichnites* tracks after *Huilmuichnus* in specimen GHUNLPam 12116 is probably related to a faster displacement after the stop (Figs. 5B and D), as suggested by the comparison between D. gouldi trackway with slow and faster gaits (Figs. 7A and C).

Huilmuichnus *and* Monomorphichnus (Diplichnites)

The compound specimens GHUNLPam 3431, 12162, and 12252 can be interpreted as reflecting normal walking, followed by a rest and then an escape trace. *Monomorphichnus* is considered a swimming trace fossil with minimal interaction of the producer with the substrate. The alternance of longer and shorter group of traces in *Monomoprhichnus* (Figs. 6C and 8A) could be the result of alternate movement of the limbs from one side of the producer during swimming. Specimen GHUNLPam 12162 is distinctive because of the presence of shallow paired mounds between *Huilmuichnus* and *Monomorphichnus*. These may reflect furrowing in search for food or an attempt to hide before escaping.

Behavioral Implications

Although both *Gluckstadtella* and *Huilmuichnus* are considered pygocephalomorph resting traces, they exhibit morphological differences that can be explained by anatomical or behavioral features. *Gluckstadtella* displays a clear differentiation of the tracks of locomotory appendages (Figs. 4C and D): two longest anterior pair of tracks directed forward, the third pair directed laterally, and the three last pairs shorter and directed backward. These tracks are interpreted as due to the dactylus. In contrast, *Huilmuichnus* exhibit tracks of similar length and orientation, and a width smaller than *Gluckstadtella*. These differences can be due to minor anatomical

features in the producer of both resting traces or can be due to a different posture of the same producer. In particular, it is likely that *Huilmuichnus* corresponds to the marks of the proximal part of the limb (protopod) instead of the distal end (dactylus) as is the case with *Gluckstadtella*. The latter hypothesis is supported by the presence of ventral features in some *Huilmuichnus* specimens. For example GHUNLPam 12116 displays medial crescentic marks that may correspond to the articulation of the limb with the pereon (Fig. 5B, inset). In GHUNLPam 3431 there is an oval mark external to the tracks that may correspond to the outline of the pereon and an arcuate imprint in the center of the trace fossil (Figs. 6B and E).

Some compound trace fossils involving *Dendroidichnites* and ending in *Gluckstadtella* or *Huilmuichnus* (GHUNLPam 12090 and 12238; Figs. 5A, 5C, 6D, and 6F) are interpreted as landing traces of pygocephalomorph crustaceans. During approach the producer interacted with a soft mud and come to rest at an angle ranging from 28 to 42 degrees with the landing path.

Four compound trace fossil specimens (GHUNLPam 3431, 12152, 12162, 12252; Figs. 4A, 4B, 6A–C, 6E, 8A, and 8B) are interpreted as escape reaction of pygocephalomorph crustaceans starting from a resting position. They involve either *Gluckstadtella* and *Dendroidichnites* or *Huilmuichnus* and *Monomorphichnus*. There is no indication of the stimulus that produced this reaction and the observed turn angles range between 33 and 139 degrees. It is inferred that the pygocephalomorph escaped using a half-swimming or swimming gait, because both *Dendroidichnites* and *Monomorphichnus* are interpreted as reflecting these locomotion methods. These compound trace fossils may represent the caridoid or tail flip escape reaction, which is typical of shrimp-like crustaceans and is commonly related to a marine pelagic or transitional benthic mode of life (Dahl, 1983). This escape reaction usually drives the animal backward although lateral escape trajectories has been recorded for small decapods and mysids (Neil and Ansell, 1995), the latter are considered relatives to Pygocephalomorpha (Schram, 1986). The initial escape in extant *Crangron crangron* is directed in a range of 75 to 156 degrees in relation with the body axis (Arnott et al., 1999), which is partially coincident with the range of observed escape angles in the compound trace fossils. The presence of an elongated abdomen with massive abdominal musculature serving strong ventral flexion, and a tail fan are strongly related to the caridoid escape reaction (Hessler, 1983). Theoretical studies of escape swimming in the penaeid shrimp *Pandalus danae* by Daniel and Meyhöfer (1989), indicated that small abdomens (<50% body length) yield very small forces and a poor performance in tail flip swimming. There is no clear evidence as if the abdomen was extended or reflexed in Pygocephalomorpha, as nearly complete specimens exhibit both preservations in similar proportions (Piñeiro et al., 2012a). The abdomen in selected specimens of Pygocephalomorpha

from the literature accounts for 43–53% (average 47%, n = 7) of the body length (Kensley, 1975; Pinto and Adami-Rodrigues, 1996; Piñeiro et al., 2012a) suggesting that they were not well adapted for tail flip locomotion. A more primitive mechanism of escape reaction has been documented in *Squilla mantis*, which belongs to a crustacean group (hoplocarids) that diverged early in malacostracan evolution. *Squilla mantis* escape reaction is gradual and primarily mediated by a sudden forward flick of the limbs, while tail flexion may be added for a more powerful response. The compound trace fossils may reflect either caridoid escape response or a more primitive limb-mediated response. It is not certain if the protopodial tracks in *H. santacruzensis* are related to the limb mediated escape response.

CONCLUSIONS

It is proposed that the ichnogenus *Diplichnites* be restricted to symmetrical or asymmetrical trackways composed of two rows of simple tracks, with or without definite track series, and absence of medial traces. Similarly, the ichnospecies *D. gouldi* should be restricted to *Diplichnites* with 6–20 tracks per series.

Compound arthropod trace fossils from the rhythmite facies of the San Rafael Basin, western Argentina are composed of intergradations between the following ichnotaxa: *G. cooperi*, *H. santacruzensis* new igen. and isp., *D. gouldi*, *Dendroidichnites* isp., and *Monomorphichnus lineatus*.

These compound trace fossil are tentatively interpreted as produced by an extinct group of crustaceans, the Pygocephalomorpha. This group of crustaceans match the size and length/width ratio inferred from trace fossils, have six pairs of locomotor appendages and a benthic mode of life.

Gluckstadtella and *Huilmuichnus* are interpreted as resting traces of pygocephalomorph crustaceans. *Gluckstadtella* is produced when the hypothesized pygocephalomorph tracemaker touch the bottom sediment with the dactyli and *Huilmuichnus* when they come to rest on the protopods (and other ventral parts).

Diplichnites gouldi displays a range of gaits. The fastest gait has well-spaced sets of tracks with opposite symmetry, and markedly elongated tracks suggesting transitions to a half–swimming mode of locomotion. The lowest gait is from a trackway with staggered symmetry with nested sets of tracks with dominantly dot-like morphology. *Dendroidichnites* isp. reflects a half-swimming locomotion with interaction of the producer with a fluid-like sediment during landing or take-off.

Monomorphicnus lineatus is produced during swimming with minimal interaction of a crustacean with the bottom sediment. The compound trace fossils reflect complex behaviors including transient resting during normal walking, landing and possible caridoid or tail flip escape reaction of hypothesized pygocephalomorph crustaceans tracemaker.

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