A large arthropod trackway from the Gaspé Sandstone Group (Middle Devonian) of eastern Canada

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Abstract: A large arthropod trackway from the Cap-aux-Os Member of the Battery Point Formation (Gaspé Sandstone Group, Middle Devonian), from the Baie de Gaspé, eastern Canada, is described and assigned to the ichnotaxon *Palmichnium* (= *Paleohelcura*) *antarcticum* (Gevers et al., 1971). A large stylonurid eurypterid or scorpion is considered the most likely producer. A shallow-water marginal fluvial environment is inferred as the setting, the animal making a transition from walking to swimming along the course of the trackway.

Résumé : La trace d'une piste d'un grand arthropode dans le Membre de Cap-aux-Os, de la Formation de Battery Point (Groupe Grès de Gaspé, Dévonien moyen), dans la Baie de Gaspé, dans l'Est du Canada, est décrite et assignée à l'ichnotaxon *Palmichnium* (= *Paleohelcura*) *antarcticum* (Gevers et al., 1971). Il semble que la trace ait été produite par un grand euryptéride stylonuride ou un scorpion. On présume que c'est dans un environnement fluviatile marginal, sous une mince tranche d'eau, que l'animal a creusé cette empreinte en marchant vers un lieu de nage.

[Traduit par la Rédaction]

Introduction

A large arthropod trackway was discovered in 1988 (Milner 1992) along the northern shore of the Baie de Gaspé (grid reference: 20U LK 993112), approximately 5 km east of the town of Gaspé, near the village of Cap-aux-Os, on the Forillon Peninsula in the Province of Quebec, eastern Canada (Fig. 1). The locality is within the Cap-aux-Os Member of the Battery Point Formation (Gaspé Sandstone Group), approximately 750 m above the base of the formation in the lower part of unit 4 (Lawrence and Rust 1988, Fig. 7). The Battery Point Formation comprises a coarsening-upwards clastic sequence, ranging in age from early Emsian to early Eifelian (Middle Devonian), based on abundant spores occurring throughout the formation (McGregor 1977). The Cap-aux-Os Member, approximately 640 m thick, consists mainly of interbedded sandstones and mudstones, which were deposited in a meandering fluvial system. The prevailing palaeocurrent direction varied from the north-northwest to the west-northwest (Lawrence and Rust 1988). Sand was deposited in the river channels and finer grained silts and muds on the extensive vegetated floodplain (Lawrence 1986; Lawrence and Rust 1988).

The Cap-aux-Os Member has produced a number of classic fossil localities that yield a diverse flora and fauna, including abundant remains of early land plants (e.g., Gensel and Andrews 1984), fish (osteostracans, acanthodians, and placoderms; e.g., Pageau and Prichonnet 1976; Belles-Iles 1989), eurypterids, and other invertebrates. Brachiopods (*Lingula*, *Orthis*, and *Dalmanella*) and small bivalves (?*Lunilicardium*) were also noted by Lawrence (1986). The Battery Point Formation has also produced cuticular fragments of early terrestrial arthropods such as millipedes, eoarthropleurids, and scorpions (Shear et al. 1996). The eurypterids known from this unit include a very large and articulated *Pterygotus gaspesiensis* (Russell 1954), and an unidentified stylonurid (Jeram 1996). Apart from *Gyrichnites gaspensis* (Whiteaves 1883), trace fossils are largely unknown from this sequence. We report here on the discovery of a large arthropod (eurypterid/scorpion) trackway and discuss ichnotaxonomic revisions required for this trackway.

Terminology

The terminology applied to the description of this specimen follows that of Osgood (1970), Hanken and Størmer (1975), Briggs and Rolfe (1983), Trewin (1994), and Braddy (1996). A track is defined as a single mark attributable to a walking leg, as opposed to an imprint (if discrete) or impression (if more continuous), which can be formed by any part of the animal (e.g., body or telson drag). A trackway is defined as a repeated succession of tracks (Anderson 1975). The outer tracks are denoted by the letter "A," with successive inner tracks denoted by the letters "B" and "C." A series defines a discrete grouping of tracks that occur on one side of the midline of the trackway. A set is a pair of series, either side of the midline. Successive series may be numbered in the presumed direction of motion. The external width denotes the distance between the outer point of the outer tracks (A) on either side of the trackway. The internal width defines the distance between the innner point of the inner tracks (C). The stride is the distance between succes-

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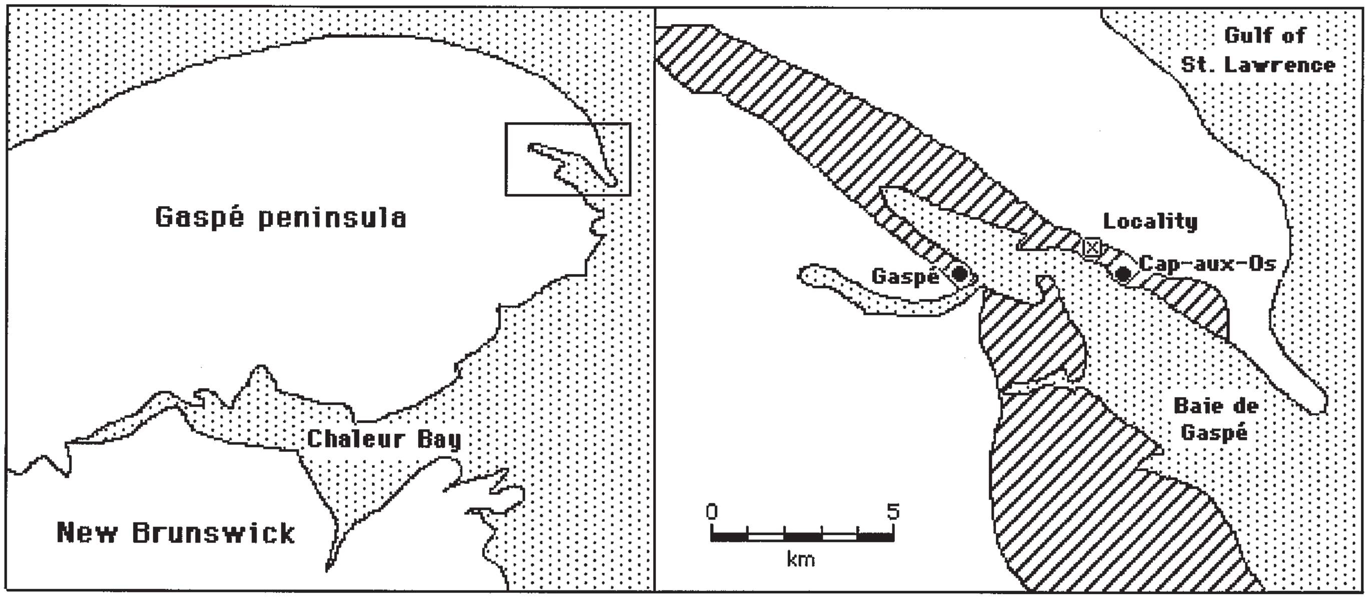
Fig. 1. Map of the Gaspé peninsula in Quebec, eastern Canada, showing the trackway locality (northern shore of the Baie de Gaspé, near Cap-aux-Os). Diagonal shading denotes outcrop of the Battery Point Formation.



sive footfalls of the same appendage, along the length of the trackway.

Systematic ichnology

Ichnogenus *Palmichnium* Richter, 1954

Diagnosis

Large trackways, usually with symmetrically opposed rows of three (occasionally four) tracks disposed en echelon, each track ranging from subcircular to adaxially concave, within the same trackway, the series at a high angle to the axis of the trackway. Median groove or ridge usually present (Briggs and Rolfe 1983).

Type ichnospecies

Palmichnium palmatum Richter, 1954.

Palmichnium antarcticum (Gevers et al., 1971) (Fig. 2)

1863 Crustacean tracks; Gordon and Joass, pp. 507, 509
1864 Crustacean tracks; Harkness, pp. 440–441
1971 *Arthropodichnus antarcticum* Gevers; Gevers et al., p. 87, Pl. 20, figs. 1–3
1972 *Arthropodichnus chelopodous* Greiner, p. 1776, Figs. 11–13
1973 *Beaconichnus antarcticum* (Gevers); Gevers, p. 1002
1975 *Beaconichnus antarcticum* (Gevers); Häntzschel, p. W45, Fig. 27, 1*a*
1976 Unnamed trackways; Friend et al., pp. 63–67, Fig. 35, Pl. 28
1979 *Paleohelcura antarcticum* (Gevers); Briggs et al., p. 278
1980 *Paleohelcura antarcticum* (Gevers); Rolfe, p. 131
1981 *Paleohelcura antarcticum* (Gevers); Bradshaw, p. 645, Fig. 50
1984 *Paleohelcura antarcticum* (Gevers); Selden, p. 43
1987 Unnamed tetrapod and arthropod trackways; Rogers, pp. 153–156, 229–235, Figs. A2.2, 6.1–6.3, Pls. 6.1*a*–6.1*d*
1990 Giant arthropod trackways (*Paleohelcura*); Bradshaw et al., p. 37, Fig. 6
1990 Unnamed tetrapod and arthropod trackways; Rogers, p. 747, Fig. 1
1995 ?*Paleohelcura antarcticum* (Gevers); Trewin and McNamara, p. 199, Fig. 28
1996 *Palmichnium antarcticum* (Gevers); Braddy, p. 367, Figs. 101*b*, 101*e*, p. 374, Figs. 102*c*–102*e*, p. 384, Figs. 104*c*–104e
1998 *Palmichnium antarcticum* (Gevers); Draganits et al. 1998, Figs. 4*a*, 4*b*, 6
In press *Palmichnium antarcticum* (Gevers); Buatois et al.

Material

The specimen is housed in the palaeontological collections of the Royal Ontario Museum, Toronto, Ontario, Canada (ROM 49881).

Horizon and locality

The Cap-aux-Os Member, Battery Point Formation, Gaspé Sandstone Group (upper Emsian to lower Eifelian, Middle Devonian). Collected from the northern shore of the Baie de Gaspé (grid reference: 20U LK 993112), approximately 5 km east of the town of Gaspé, near the village of Cap-aux-Os, on the Forillon Peninsula, Quebec, eastern Canada.

Emended diagnosis

Large trackways, consisting of opposite (or slightly asymmetrical) en echelon series of three, occasionally four, oval or bifid tracks, diverging in regular (sometimes irregular) short series from a continuous medial impression (occasionally absent). Rarely, series are arranged parallel to the midline, appearing as two single rows of tracks (emended after Gevers et al. 1971).

Fig. 2. *Palmichnium antarcticum*. ROM 49881. Royal Ontario Museum, Palaeontological Collections. Gaspé, Canada. Preserved as a negative epichnion. (A) Photograph of specimen. Note presence of adhesion ripples. Scale ×0.098. (B) Interpretive drawing. Numbers denote series. i, discrete imprint within medial impression; l, linear scratches; m, medial impression. Scale ×0.098.

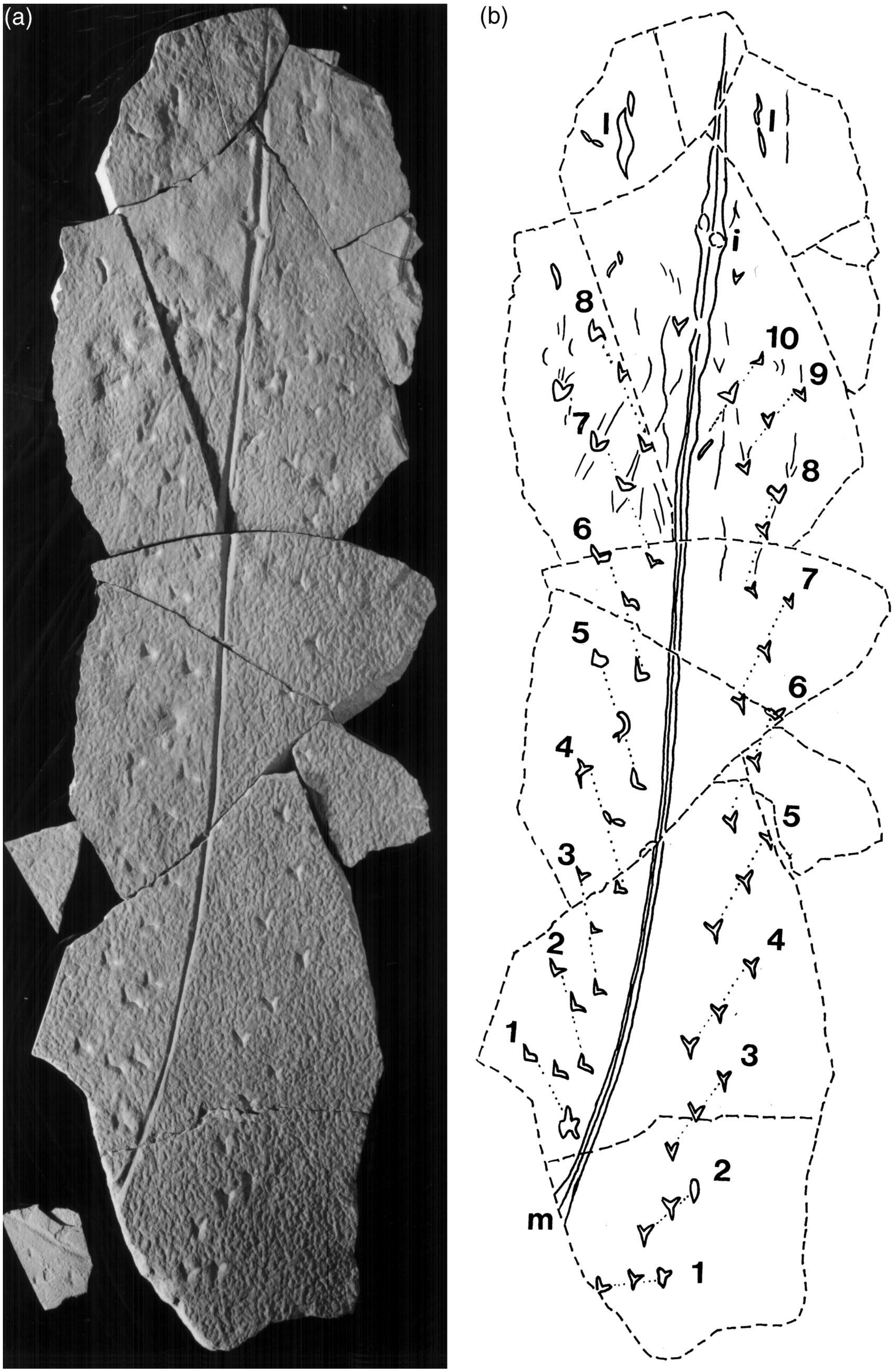


Table 1. Proportions of the trackway.

	Left side of trackway				Right side of trackway					
	Stride (mm)				Stride (mm)					
Series	A	B	C	Angle (°)	C	B	A	Angle (°)	External width (mm)	Internal width (mm)
1	—	—	—	—	—	—	—	63	480[a]	227[a]
2	—	—	—	48	122	157	189	28	423	168
3	179	138	118	29	176	189	214	21	392	174
4	195	161	157	19	201	201	227	23	384	166
5	214	225	205	24	235	262	253	20	397	166
6	229	185	220	20	214	227	239	13	365	164
7	210	262	233	21	235	220	210	23	375	153
8	220	222	212	27	214	225	195	16	375	155
9	203	214	225	30	231	205	179	32	380	155
10	—	—	—	—	135	90	111	53	388[a]	78[a]
Average	207.1	201	195.7	27	195.9	197.3	201.9	29	395.9	160.6

Notes: Stride denotes distance to preceding series. All measurements in millimetres.
[a]Estimated value (calculated by doubling distance to midline), value not included in determination of average.

Description

The trackway is preserved in negative epirelief on the upper surface of a well-sorted, medium-grained (0.25–0.5 mm) sandstone slab that is 264 cm long (Fig. 2). There are 71 imprints on the surface of the slab, of which 59 are definite tracks, the remainder comprising linear scratches and irregular markings. We interpret the bedding plane upon which this trackway is preserved as an undertracked surface (see Goldring and Seilacher 1971) as the tracks are sharp and well defined. This surface is covered almost entirely by adhesion ripples. The trackway fades towards the top of the slab, along with the adhesion ripples. At the locality where this trackway was discovered, there is no evidence that the trackway or adhesion ripples continue along the bedding surface beyond the extent of the collected slab.

The trackway consists of successive series of three (occasionally four) Y-shaped tracks arranged in linear groupings, diverging in the presumed direction of motion (Fig. 2). Ten complete series occur on the right side and eight occur on the left side. The angle to the midline of the series is highly variable, ranging from 13 to 63°, with an average value of 27° on the left side and 29° on the right side (Table 1). The series are disposed slightly asymmetrically, at regular intervals either side of a continuous medial impression. The overall course of the trackway is straight. The proportions of the trackway are shown in Table 1. The average external width is 39.6 cm. The internal width averages 16.1 cm. These proportions remain relatively constant along the length of the trackway. The average stride is slightly greater on the left side of the trackway than on the right.

The individual tracks are Y-shaped, opening forwards. The average width of the tracks on the left side is 27 mm, those on the right side 30 mm. Each track is of similar size and shape and is deepest on its anterior side, shallowing gradually backwards (i.e., the two anterior projections are deepest). Sediment back-push mounds are evident behind the tracks towards the posterior end of the trackway. Each of the tracks is inclined slightly towards the midline, those on the left side of the trackway slightly more than those on the right.

The medial impression is not situated exactly along the midline but is displaced slightly towards the left side of the trackway. A slight sinuosity in the course of the medial impression is also apparent. The medial impression has a total length of 229 cm, a maximum width of 34 mm, and a minimum width of 14 mm. The average depth of the medial impression is approximately 6 mm.

Towards the posterior end of the trackway, the series becomes irregular, the trackway less well defined, and the tracks grade into linear scratches. These scratches reach 4.5 cm in length and 1 cm in depth. The majority of the scratches are approximately parallel to the medial impression. The medial impression displays depth variation towards the posterior end of the trackway. Approximately 35 cm from the top of the slab the medial impression is interrupted by a discrete mark. Above the mark the medial impression is immediately deeper by approximately 3 mm and then shallows gradually towards the top of the slab until it almost entirely fades away.

Remarks

Arthropodichnus antarcticum (Gevers et al. 1971) was transferred to *Beaconichnus* by Gevers (1973) and then to *Paleohelcura* by Bradshaw (1981). This transferral was adopted by various subsequent authors but is here considered unsatisfactory. These trackways display a much larger external width and size of the tracks than is evident in *Paleohelcura*. More importantly, the main feature separating *Palmichnium* from *Paleohelcura*, as noted by Trewin and McNamara (1995), is the symmetry of the series: generally opposite or staggered in *Palmichnium* and alternate in *Paleohelcura*. Häntzschel (1975) noted that *P. antarcticum* bears a much closer resemblance to *Palmichnium* than *Paleohelcura* but suggested that it differed in the angle made by the series to the midline and complete isolation of the tracks from the median impression. These differences, however, are based only on comparisons with *P. palmatum* and not the other ichnospecies of *Palmichnium*. The size of the individual tracks, relative to the external width, is far greater in these trackways than is known in *Paleohelcura*, which displays much smaller tracks. *Protichnites* Owen 1852, is a poorly defined ichnogenus in need of revision (Trewin and McNamara 1995) and comprises “trackways of two rows of bifid or trifid imprints and a commonly narrow, intermittent double tail drag in the middle” (Häntzschel 1975, p. W97). As these trackways are characterized by only one medial impression, they do not qualify for inclusion in *Protichnites*. This ichnotaxon is therefore referred to a discrete ichnospecies within *Palmichnium*. Several ichnospecies are recognized within this ichnogenus (see Braddy 1996 for a review). Of these, *Palmichnium antarcticum* resembles *Palmichnium kosinskiorum* most closely, yet is distinguished from it by being somewhat smaller, having a considerably narrower median impression and the morphology of the tracks, which may be oval to bifid.

Interpretation

The size of this trackway and the distribution of the tracks suggests that the tracemaker was a large heteropodous arthropod (with its shortest legs located anteriorly), utilizing a hexapodous gait. Known Devonian crustaceans and xiphosurans are too small to have produced this trackway, besides the fact that their trackways are known and most unlike that described herein.

Gigantic scorpions, approximately 1 m in length (e.g., *Praearcturus* and *Brontoscorpio*), are known from the Lower Devonian (Kjellesvig-Waering 1972) and so must be considered as candidates for producing this trackway. Neoichnological investigations by Brady (1947) and Sadler (1993) dealt with subaerial scorpion trackways, but trackways formed subaqueously were not considered. Diverging track series are apparent in the scorpion trackway *Paleohelcura tridactyla* (Brady 1947; Sadler 1993). Converging track series, however, have generally been interpreted for eurypterid trackways (e.g., Hanken and Størmer 1975; Briggs and Rolfe 1983; Braddy 1995; Braddy and Anderson 1996), although computer modelling of eurypterid walking techniques (Braddy 1996) indicates that their trackways may consist of series that either converge or diverge in the direction of motion, depending on the morphology of the producer and the walking technique being used, particularly the successive phase difference. Such modelling procedures indicate that stylonurid trackways would also have diverged in the direction of travel (Braddy 1996).

It is likely, therefore, that this trackway was produced by a large eurypterid. The only eurypterid body fossils known from the succession are *Pterygotus gaspesiensis* (Russell 1954) and an unidentified stylonurid (Jeram 1996). It is unlikely that a pterygotid was responsible for this trackway because there is no evidence that any of the tracks were formed by a swimming paddle (appendage VI), and the anterior walking limbs of pterygotids (appendages III–V) lack distal spinosity, which would have been necessary to form the arrow-shaped tracks present in this trackway. The trackways of pterygotids are here considered to resemble *Protichnites gallowayi*, described by Sharpe (1932), and referred to *Sharpichnium* by Walter (1984) and *Palmichnium* by Braddy (1996). It is therefore considered that a stylonurid eurypterid was responsible for this trackway, many Devonian forms (see Waterston 1979) reaching sufficient size to have produced this trackway.

The shape and size of the tracks indicate that the animal used three walking legs, each possessing some distal spinosity. There is no evidence that any of the appendages were broad and flat (i.e., paddle-shaped). The opposing series are staggered (i.e., nearly opposite), indicating that opposing legs were moved nearly in-phase during the step cycle. The opposite phase difference between the opposing legs of the animal may be calculated by the distribution of tracks as approximately 0.3, following Braddy and Anderson (1996). This value remains relatively constant along the course of the trackway, although towards the posterior end of the trackway the tracks are more in-phase. The successive phase difference between adjacent legs on the same side of the body cannot be calculated from the trackway (as it is dependent on the body morphology and stance of the animal responsible) but computer modelling of stylonurid walking techniques by Braddy (1996) indicates that these animals could walk in-phase if their successive phase difference was low (in the order of 0.2). It is clear that as the animal walked it dragged its telson. If the animal had lifted its body and telson clear of the substrate it would have reduced friction, resulting in a more efficient walking technique and allowing the telson to act as a hydrodynamic structure to steer and stabilize the animal (Waterston 1979). This may suggest that the animal was not constrained to a stable gait pattern, so the successive phase difference may have been somewhat higher.

The fact that the medial impression is situated slightly closer to the left side of the trackway may indicate that the walking legs on the left side of the animal were held nearer to the body, perhaps as a current forced the animal to adopt an asymmetic stance. Alternatively, it may indicate that the telson was not dragged directly behind the animal but slightly to one side. The slight sinuosity in the course of the medial impression indicates that the posterior part of the opisthosoma swayed slightly from side to side as the animal walked. The stride length of the tracks varies throughout the course of the trackway (Table 1). The average stride length is comparable for the inner (C) tracks but is greater in the middle (B) and outer (A) tracks of the left side, indicating that the animal took longer steps on the left side of its body.

The presence of the irregular adhesion ripples suggest that this surface was at some time subaerially exposed. Adhesion ripples are formed when dry sand is blown across a wet surface and adheres to it. The wind was apparently blowing from the bottom left to the top right of the slab. However, as the tracks are apparently undertracks, the adhesion ripples do not prove this trackway was produced subaerially. The fact that the animal appears to have launched itself off the substrate (see below) infers the presence of water when the trackway was produced. Therefore, shortly after the formation of the adhesion ripples, shallow water must have covered the surface prior to the production of the trackway. Thus, we interpret this trackway as having been produced in shallow water, possibly on the margins of a river channel, given that the Cap-aux-Os Member has been interpreted as having been deposited in a fluvial setting.

The direction of movement of the animal may be deduced from the morphology of the tracks, comparisons with other trackways, and computer modelling procedures (see Braddy 1996). The animal responsible is considered to have walked in the direction of divergence of the track series (i.e., from the bottom to the top of Fig. 2), based on the orientation and depth variation of the tracks. The Y-shaped tracks are interpreted as being formed by anteriorly projecting distal spines on the walking legs. Slight sediment back-push mounds are also preserved, particularly towards the posterior end of the trackway, this feature supporting the presumed direction of motion.

We interpret that the deep, random linear scratches at the posterior end of the trackway (Fig. 2) were made by the animal's appendages forcefully scraping the substrate, perhaps as part of a swimming stroke, as it launched itself into the water and swam away. Thus, this trackway is interpreted as representing the transition from a walking to a swimming mode of locomotion. We interpret the discrete mark within the medial impression (Fig. 2) as representing the point where the animal inclined its body away from the substrate, the telson being more forcefully thrust into the substrate at this point. As the animal swam away the telson dragged behind it, until at the top of the slab, the animal was sufficiently clear of the substrate to leave only a slight medial impression.

Previous studies of the functional morphology of stylonurid walking techniques by Waterston (1979) suggested that these animals moved their opposite legs out of phase in order to maximize body stability. Most eurypterid trackways, including that described herein, display an opposite or staggered arrangement of tracks, indicating that these animals moved their opposing appendages in-phase or only slightly out of phase. The eurypterid responsible for this trackway most probably used a relatively low gear gait, perhaps in the order of 2:8 (see Selden 1981). An animal using such a low gait and short strides would have been relatively stable, enabling the eurypterid to make irregular footfalls, as are observed in this trackway.

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