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NEW TRACE FOSSIL EVIDENCE FOR EURYPTERID SWIMMING BEHAVIOUR

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Abstract: We describe a recently discovered trace fossil from a eurypterid Konservat-Lagerstätte in the upper Silurian Tonoloway Formation of Pennsylvania, and formally describe contemporaneous traces from the Williamsville Formation Lagerstätte of Ontario. The traces from both localities are assigned here to *Arcuites bertiensis* igen. et isp. nov. Based on comparisons with previously described eurypterid trackways, neoichnological experiments, and the co-occurrence with eurypterid remains, *Arcuites* is interpreted as having been made by the swimming leg (sixth prosomal appendage) of swimming juvenile to adult eurypteroid eurypterids, and represents the first unambiguous trace fossil evidence for eurypterid swimming behaviour. The morphology of *Arcuites* indicates that eurypteroid eurypterids swam using drag-based rowing, whereby the animal propelled itself forward by moving its oar blade-like swimming paddles in an in-phase backstroke. *Arcuites* morphology also indicates that the eurypteroid swimming appendage had a greater degree of movement than was previously suggested, and a revised rowing model is proposed. Differences in the abundance of *A. bertiensis* in the Tonoloway and Williamsville formations suggest a bathymetric control on eurypterid swimming behaviour and trace production. The association of *Arcuites* with eurypterid body fossils in both units indicates that these Lagerstätten were autochthonous assemblages and provides additional evidence for eurypterid inhabitation of shallow subtidal marine environments in the late Silurian.

Key words: eurypterine eurypterid, swimming biomechanics, trace fossils, Konservat-Lagerstätte, Silurian, Appalachian Basin.

EURYPTERIDS (Arthropoda, Chelicerata) were diverse and widespread aquatic Palaeozoic predators (Tetlie 2007). Their predatory ability has been inferred due to a combination of size (Lamsdell & Braddy 2010), visual acuity (Anderson *et al.* 2014; McCoy *et al.* 2015) and swimming aptitude (Selden 1981; Plotnick 1985). Unlike the first two traits, which have been assessed reliably from fossils, eurypterid swimming behaviour remains unresolved. Following early interpretations based on gross morphology (e.g. Størmer 1934; for a review see Plotnick 1985) eurypterid swimming behaviour has been more accurately inferred by modelling involving biomechanics, detailed comparisons to modern analogues, and computer simulations (Selden 1981, 1984; Plotnick 1985; Plotnick & Baumiller 1988; Knight 1997). Two competing hypotheses on swimming style were advanced for eurypterine (swimming) eurypterids from these modelling studies: swimming paddles were employed as either an oar blade (e.g. Selden 1981) or a hydrofoil (e.g. Plotnick 1985). However, there has been no firm consensus on the more likely locomotory technique.

Trace fossil analysis represents a method to further validate these behavioural hypotheses, but whereas ichnological evidence for eurypterid walking or crawling behaviour has been well documented (e.g. Richter 1954; Hanken & Størmer 1975; Briggs & Rolfe 1983), unambiguous eurypterid swimming traces were previously unknown. *Palmichnium macdonaldi* has been interpreted as either imprints made by a hopping subaqueous eurypterid or swimming-stroke tracks made while the eurypterid was walking on a subaerially exposed substrate (Braddy 1995). *P. capensis* was similarly interpreted as the result of short subaqueous hops on the substrate by a eurypterid employing a swimming-stroke-like motion (Braddy & Almond 1999). Braddy & Milner (1998) ascribed *P. antarcticum* to a eurypterid transitioning from a walking to swimming mode of locomotion on the substrate, but actual swimming behaviour can only be loosely inferred because walking appendage tracks comprise most of the trackway. Ciurca (2002) documented unusual curved, non-serial traces from the upper Silurian Williamsville Formation Konservat-Lagerstätte in south-western Ontario and implied that eurypterid swimming legs could have produced these impressions. Ciurca was not confident of the producer identity, however, because

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halite structures in the unit suggested extreme hypersalinity at the time of deposition, and an environment unlikely to support eurypterid inhabitation.

Subsequent palaeoenvironmental analysis of upper Silurian units in the northern Appalachian Basin now indicates that the Williamsville Formation was deposited under nearly normal marine, rather than hypersaline, conditions (Vrazo *et al.* 2016). This study, together with a later stratigraphical and palaeoecological analysis of this region (Vrazo *et al.* 2017), support eurypterid inhabitation of the Williamsville Formation, and consequently remove Ciurca's (2002) environmental constraint on a eurypterid tracemaker in this unit. New trace fossil evidence from a contemporaneous upper Silurian eurypterid Lagerstätte in the Tonoloway Formation of Pennsylvania (Vrazo *et al.* 2014) also supports Ciurca's (2002) eurypterid tracemaker interpretation. Among abundant trace fossils ascribed to eurypterid makers that include walking appendage and swimming leg impressions, the Pennsylvania site has recently yielded a new trace form that closely resembles the traces described by Ciurca (2002).

In this paper we formally describe the new trace specimen from the Tonoloway Formation, and the Williamsville Formation traces previously documented by Ciurca (2002). A new ichnogenus and ichnospecies, *Arcuites bertiensis*, are erected to encompass the traces from both localities, which are interpreted as those made by swimming eurypterids. *Arcuites* tracemaker behaviour is discussed within the context of previously proposed eurypterid swimming models, and we consider the implications for *Arcuites* on the relative palaeodepths of the Tonoloway and Williamsville formations, and the palaeoecology of the eurypterids therein.

GEOLOGICAL SETTING

The Tonoloway Formation (upper Ludlow–Pridoli) of central Pennsylvania and Williamsville Formation (Pridoli) of western New York and south-western Ontario were deposited respectively on the eastern and northern margins of the Appalachian Basin during the late Silurian (Fig. 1A). The upper Tonoloway Formation beds of interest may be considered to be slightly older than the Williamsville Formation based on zonation of the brachiopod *Eccentricosta jerseyensis* (Swartz 1929; Berdan 1963; Ciurca 1982). Nevertheless, both units represent similar shallow nearshore marine environments, deposited under arid conditions along a very gently dipping carbonate ramp that was similar to the modern Persian Gulf (Belak 1980; Bell & Smosna 1999).

The Tonoloway Formation of central Pennsylvania is a thick, carbonate-dominated unit that consists of numerous metre-scale, shallowing-up cycles deposited in a lagoonal–intertidal–sabkha environment (Cotter & Inners 1986; Bell & Smosna 1999). These cycles typically contain thin to medium bedded micrites at the base, commonly interbedded with mounded microbial structures (thrombolites), and thin, laminated, calcareous shales toward the top that contain evaporitic features (vugs, gypsum/anhydrite moulds, breccias) and evidence of subaerial exposure (desiccation cracks). This formation overlies the more siliciclastic Wills Creek Formation and underlies the more fossiliferous, nodular limestones of the Keyser Formation (Laughrey 1999). Eurypterids have been noted from several localities in the Tonoloway Formation of the central and southern Appalachian Basin, but only occur in abundance in the Turbotville Member of the uppermost Tonoloway Formation of central Pennsylvania, approximately 9 m below the contact with the overlying Keyser Formation (Inners 1997; Vrazo *et al.* 2014). At Winfield Quarry (40.898621° N, 76.890593° W; Fig. 1B) eurypterid body fossils and a limited euryhaline fauna are found on the upper horizons of two adjacent, thinly laminated calcareous shale packages, near the thrombolitic base of a minor deepening succession. One of the two shale packages also contains trace fossils ascribed to a chelicerate tracemaker, probably a eurypterine eurypterid (e.g. *Eurypterus*) (Vrazo *et al.* 2014, fig. 8). These traces include apparent resting traces made by a pair of swimming paddles (appendage VI) (Fig. 2), walking appendage traces (Vrazo *et al.* 2014, fig. 8C–D), and *Arcuites bertiensis* igen. et isp. nov. The single shale slab containing *Arcuites* was found in float but lithologically matches the trace fossil bed and is presumed to be from the same horizon. Linear branching or 'bird's foot' triple junction synaeresis cracks (or 'subaqueous sedimentary cracks'; see McMahon *et al.* 2017) that bear a passing resemblance to the trace fossils have been documented at Winfield Quarry (Vrazo *et al.* 2014, fig. 4B). However, these cracks are only found on a horizon subjacent to the eurypterid and trace fossil-bearing packages, and their distinct morphology and distribution allows them to be easily distinguished from *Arcuites* and other previously described traces.

The Williamsville Formation of south-western Ontario and western New York consists of medium to thick bedded fine-grained, argillaceous dolomite ('waterlime') and dolomitic mudstone. This unit overlies the shaly and dolomitic Scajaquada Formation and underlies the reefal, mottled and dolomitized Akron Formation (Belak 1980). At Ridgemount Quarry, Ontario (42.921166° N, 79.009769° W), the Williamsville Formation is about 1.5 m thick, and is divided into three lettered members (A–C) (Ciurca 1990; Fig. 1B). Elsewhere, a transitional and shaly D Member may also be present. Eurypterids are only found in abundance in the A Member where they occur with a relatively diverse marine fauna that includes soft-bodied taxa (Ciurca 1982; Tollerton 1997). This member is also the only unit that contains *Arcuites*, which is found on a single horizon

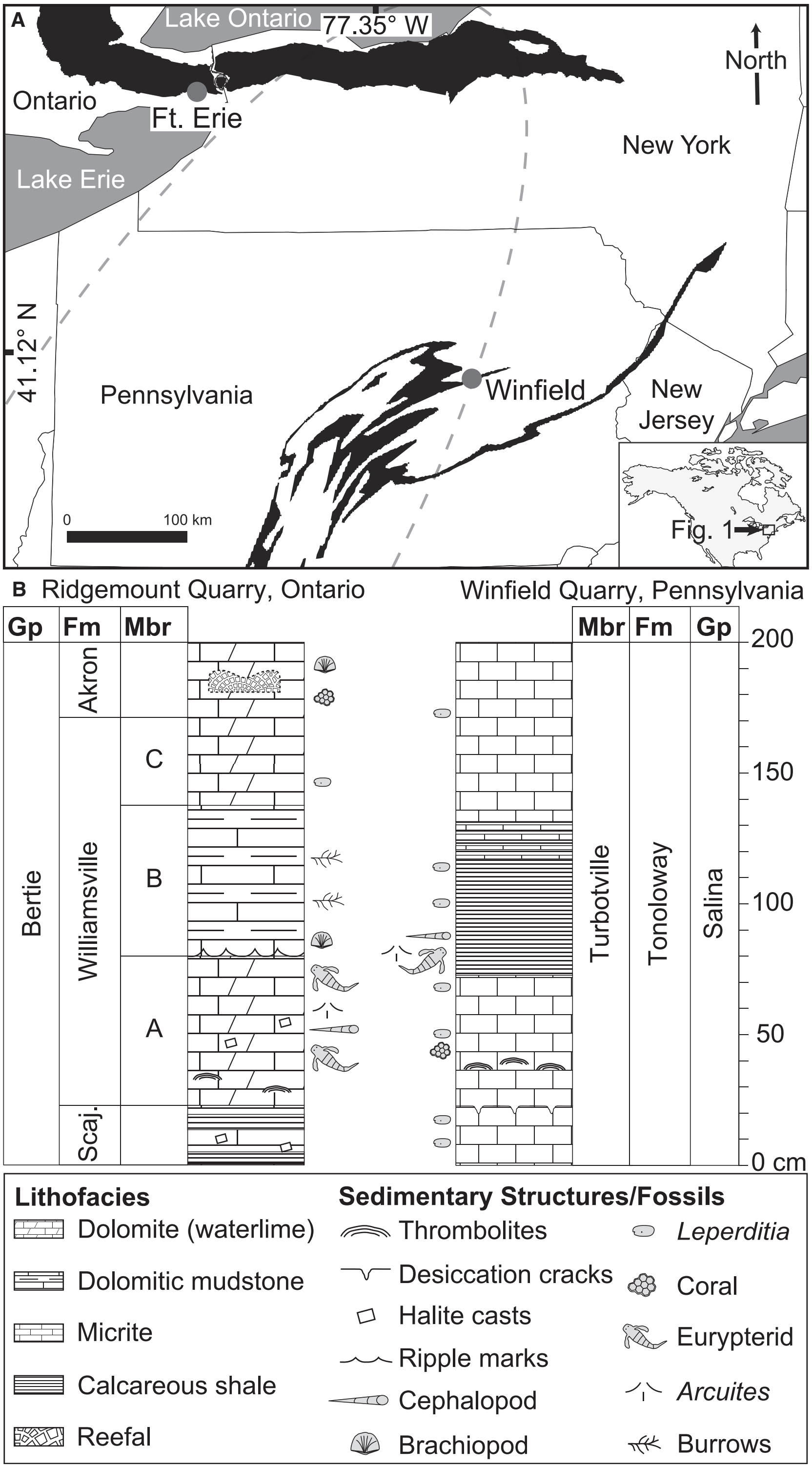


FIG. 1. Regional map of study area and stratigraphical columns of key localities. A, Silurian bedrock exposures in the central and northern Appalachian basin (in black); approximate margins of the Appalachian basin indicated by dashed line; localities: Fort Erie, Ridgemount Quarry, Ontario; Winfield, Winfield Quarry, Pennsylvania. B, stratigraphy of the Williamsville and Tonoloway formations; Scaj., Scajaquada Formation; stratigraphical horizons bearing eurypterid and *Arcuites* igen. nov. are probably not correlative and sub-formation units are not considered to be time-equivalent.

in the middle of the unit, approximately 12 cm from the top, often on the opposite side of thin (2–3 cm) beds that contain eurypterid remains (Ciurca 2002) (Fig. 3). Sedimentary features in the A Member include fine laminae, dark (microbial?) blotches, local thrombolites, and rare halite pseudomorphs that locally disrupt organismal remains. Organismal remains in the A Member are also frequently found in accumulations termed 'windrows' (e.g.

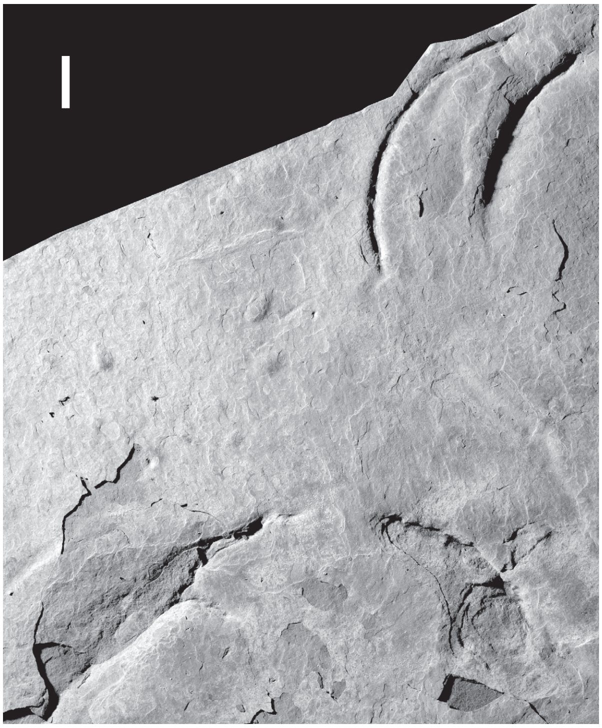


FIG. 2. Traces ascribed to the swimming paddle of a eurypterid tracemaker, from the Turbotville Member, Tonoloway Formation, Winfield Quarry, Pennsylvania (YPM.560639). Scale bar represents 1 cm. Reproduced from Vrazo *et al.* (2014).

Ciurca 2010) whose semi-linear arrangements are suggestive of current-driven orientation. Scours and ripple marks are common on the A–B member contact surface and Ciurca (2010, 2013) suggested that these structures are further indicators of currents, possibly storm-generated, that truncated parts of the uppermost A Member. The B Member contains abundant *Eccentricosta* and tubular burrows, and rare high-spired gastropods, and the C Member is largely unfossiliferous, with only very rare *Leperditia*? observed.

Owing to its status as one of the most productive sites for eurypterid remains in the world, the Williamsville Formation, and its depositional environment, have received considerable attention. Palaeoenvironmental interpretations vary widely, however, and include deposition in: a deltaic marine environment (O'Connell 1916); a lagoon into which stenohaline organisms were occasionally transported (Chadwick 1930; Monahan 1931); and the shallow subtidal or intertidal zone within a nearshore setting (Treesh 1972; Belak 1980; Hamell 1982; Hamell & Ciurca 1986; Ciurca & Hamell 1994). The stratigraphic lumping of the relatively diverse Williamsville Lagerstätte fauna with other barren evaporite-bearing units has probably complicated past interpretation of its environment and salinity (see Vrazo *et al.* 2016); however, indicators of hypersalinity are present in the A Member. At Ridgemount Quarry Ciurca (2002) observed reticulate patterns suggestive of halite structures on the same bedding plane as *Arcuites,* in addition to halite pseudomorphs. Halite crystals have historically been thought to form within brines (i.e. 350 ppt and higher; Scruton 1953) which led Ciurca (2002) to question whether eurypterids could be the potential makers of *Arcuites* as this would require that they (and by extension, the associated fauna) could tolerate extremely hypersaline conditions.

Vrazo *et al.* (2016) recently showed that the co-occurrence of eurypterids and other fauna with isolated halite pseudomorphs, including disruptive forms, reflects post-burial, early-stage diagenetic overprinting, rather than life habitat conditions. These authors also argued that the relatively diverse faunas in subtidally deposited dolomite units, such as the Williamsville Formation A Member, were evidence against primary dolomite precipitation under hypersaline conditions. No other sedimentary indicators of subaerial exposure or non-halite evaporites have been observed in the Williamsville Formation at Ridgemount Quarry (Ciurca 1990, 2013), further limiting the likelihood of deposition under hypersaline conditions (Vrazo *et al.* 2016).

Biogenic features in the Williamsville Formation also indicate that salinity was not elevated at the time of eurypterid inhabitation. Eurypterids have been observed with or above thrombolites and other microbialites in the A Member and in a number of other upper Silurian units, including the Tonoloway Formation, in the central and northern Appalachian Basin (Ciurca 2013; Vrazo *et al.* 2014, 2017). These microbialites are typically interpreted as lying on, or just above, the flooding surfaces of small-scale shallowing-up cycles (Vrazo *et al.* 2017). This close eurypterid–microbialite association, in conjunction with a significant increase in faunal diversity in the eurypterid-bearing beds, has been taken as evidence that eurypterids and other fauna preferentially occupied the shallow subtidal zones of the Williamsville Formation and other Bertie Group units during minor transgressive freshening events (i.e. when salinity levels were nearly euhaline; Vrazo *et al.* 2017). Although O'Connell's (1916) early deltaic interpretation has since been widely contested, the presence of terrestrial plants (*Cooksonia*; Edwards *et al.* 2004) and early fish (Burrow & Rudkin 2014) in the Williamsville Formation A Member may be indication of a nearby fluviatile source and thus further evidence for reduced salinity levels.

MATERIAL AND METHOD

All specimens described in this study were collected by the authors during field excursions in Ontario and

Pennsylvania. Several specimens may represent part and counterpart pairs; however, this information is not recorded in specimen accession data and no trace-bearing slabs could be physically matched, hence all specimens are treated as individuals herein. Figured specimens were photographed with a Nikon 5100 digital camera at the University of Cincinnati or Hasselblad H4D-200MS digital camera in the Yale Peabody Museum Digitization Lab. RTI images (available directly from the authors) were compiled using Meshlab software (Cignoni *et al.* 2008).

Terminology used for trace fossil descriptions and metrics follow Braddy & Anderson (1996). Trace fossils comprise a pair of primary grooves and, if present, secondary grooves or impressions and a medial groove. Ancillary scratches or traces associated with some specimens are not considered to be diagnostic. Figure 4 shows the position of the measurements referred to in the diagnosis and results (Table 1). All specimen measurements were made in ImageJ (Rasband 2011). Measurement error ranges (length: ±1 mm; angle: ±1°) are conservatively large because of a frequent lack of definition between groove edges and the substrate. The length of primary grooves was measured at the furthest distance between the anterior and posterior ends of the groove. Primary groove depth is defined as the deepest point along the impression curve relative to the anteroposterior line; measurements were taken at a right angle from the length line to the inner concave edge of the groove impression (Fig. 4). The primary groove arc angle was taken at the point of maximum depth to the distal anteroposterior end. Angle from midline measurements were taken from the best approximation of a medial axis when the anterior bases of the groove pairs are aligned along a 180° axis (taking into account that not all grooves are symmetrical). The internal and external trace widths were taken from the most anterior and most posterior points, respectively, on the left and right primary grooves, at a 90° angle to the relative medial axis (i.e. not from point to point).

Institutional abbreviations. All type and figured specimens described in this study are housed in the Ciurca Collection at the Yale Peabody Museum (YPM).

SYSTEMATIC ICHNOLOGY

Ichnogenus ARCUITES nov.

LSID. urn:lsid:zoobank.org:act:2CF6BC71-F3C2-4812-818E-882991DAEF0F

Derivation of name. Latin *arcus* (arch) with reference to the distinct curvature of the trace fossil; *-ites*, denotes antiquity.

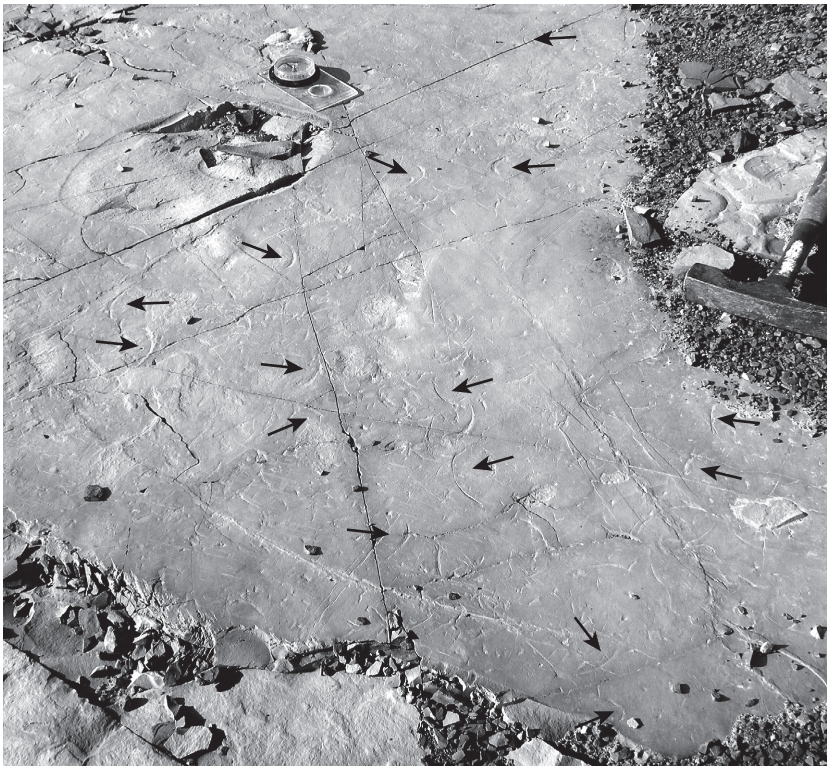


FIG. 3. Trace fossil horizon in the A Member, Williamsville Formation, Ridgemount Quarry, Ontario. Hammer and compass for scale. Arrows point to the concave side of some of the numerous *Arcuites bertiensis* igen. et isp. nov. present on the bedding plane.

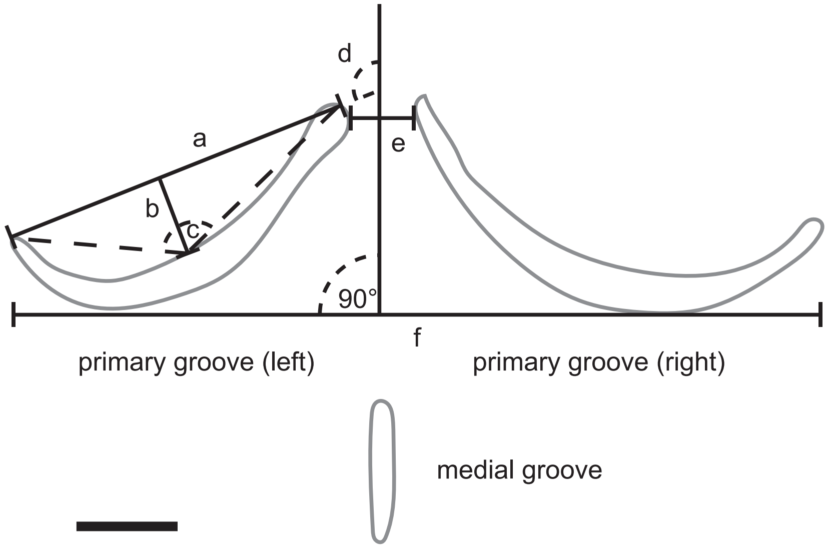


FIG. 4. Outline sketch of *Arcuites bertiensis* igen. et isp. nov. (YPM.534280) showing the trace metrics used in this study (see Material and Method for metric description). *Metrics*: a, primary groove length; b, primary groove depth; c, primary groove arc angle; d, angle of primary groove from medial axis; e, internal trace width; f, external trace width. Scale bar represents 1 cm.

Type ichnospecies. Arcuites bertiensis isp. nov. by monotypy. Upper Silurian, A Member, Williamsville Formation (Bertie Group), Ridgemount Quarry, Fort Erie, Ontario.

Diagnosis. Small (*c.* 47 mm wide) to medium-sized (*c.* 122 mm wide) traces, with paired, bilaterally symmetrical, lunate to obliquely curvilinear grooves that are concave outward. A second pair of small, lunate to semi-elliptical grooves or impressions is rarely present anterior to the primary grooves and at an oblique angle. A thin medial groove may also be present posterior to the primary grooves.

Age. Late Silurian (late Ludlow–Pridoli).

Stratigraphical range. Arcuites occurs in the middle A Member of the Williamsville Formation (Bertie Group) at Ridgemount Quarry, near Fort Erie, Ontario (Ciurca 2002; Fig 1), and in the upper Turbotville Member of the upper Tonoloway Formation (Salina Group), approximately 9 m beneath the Tonoloway–Keyser Formation contact at Eastern Industries Quarry, near Winfield, Pennsylvania (Vrazo *et al.* 2014; Fig. 1).

Remarks. Ichnogenera with suggested eurypterid makers share a number of morphological similarities with *Arcuites* igen. nov. The primary grooves of *Arcuites* are similar to the curved fourth track in *Palmichnium palmatum* (Richter 1954), ascribed to a walking eurypterid. However, *Arcuites* cannot be generically related to *Palmichnium* because it does not display the diagnostic *en echelon* track series. The primary grooves of *Arcuites* also bear some resemblance to the large ‘A’ tracks that form part of a trackway described by Hanken & Størmer (1975). These crescentic tracks were inferred to have been made by the swimming paddle (appendage VI) of a eurypterid (*Mixopterus*?) while walking in wet sediment. However, the latter impressions curve concave inward, toward the center of the trackway, and are in series, suggesting a different ethological category to *Arcuites*, and ultimately separate ichnotaxonomic status (see Bertling *et al.* 2006).

In comparison to other non-eurypterid arthropod traces, *Arcuites* is very similar to the xiphosuran resting trace *Arborichnus* (Romano & Meléndez 1985; Lucas & Lerner 2005). Caster (1938) originally noted the association of *Arborichnus*-like trace sets with the Upper Devonian xiphosuran walking trace *Kouphichnium* (= *Paramphibius*) and traces made by modern resting xiphosurans. Several factors preclude *Arcuites* from being included within *Arborichnus*, however. Individual *Arborichnus* traces comprise one symmetrical impression (Caster 1938, p. 7, suggested these resembled ‘inverted printers’ braces’), whereas *Arcuites* comprises two bilaterally symmetrical grooves separated at the median. In addition, no examples of *Arcuites* are found in *Arborichnus*-like trace sets (cf. Caster 1938, pl. 9, fig. 3–4; Lucas & Lerner 2005, fig. 2F), suggesting different trace-maker behaviour to *Arborichnus*. *Arcuites* can also be excluded from inclusion within *Kouphichnium* because it lacks the serially-paired bifid scratches and continuous medial drag that characterize the latter (see Caster 1938, for examples). Moreover, no ancillary scratches or tracks that can be definitely assigned to *Kouphichnium* have been found in the Williamsville or Tonoloway formations (Ciurca 2002; Vrazo *et al.* 2014). *Arcuites* morphology is similar to another arcuate arthropod walking trace, *Lunulipes* (= *Lunula*) *obscura* from the Early Jurassic (Hitchcock 1865; Getty 2017), but a relationship to this ichnotaxon can be disregarded because *Arcuites* lacks the seriality of the latter and contains medial and secondary grooves that are absent in *Lunulipes*.

TABLE 1. Length and angle measurements for all specimens of *Arcuites bertiensis* igen. et isp. nov. examined in this study.

YPM #	Left side of trace				Right side of trace					
	Length (mm)	Depth (mm)	Arc angle (°)	Angle from midline (°)	Length (mm)	Depth (mm)	Arc angle (°)	Angle from midline (°)	Internal width (mm)	External width (mm)
534278	40	10	125	118	NA	NA	NA	NA	15	NA
534279	31	5	141	116	32	9	115	98	14	74
534280	32	8	125	117	39	9	130	98	8	76
534281	35	8	127	102	33	7	131	107	11	77
534282	22	3	139	80	17	3	150	92	11	50
534525	36	9	127	102	33	8	124	107	12	79
534526	51	17	113	108	48	6	153	108	28	122
534527	37	6	143	105	41	7	140	105	40	116
534528	32	3	149	126	31	6	150	141	15	64
534530	46	14	116	NA	NA	NA	NA	NA	NA	NA
534531	NA	NA	NA	NA	31	9	121	90	13	NA
534532	47	9	139	NA	NA	NA	NA	NA	NA	NA
534533	23	3	147	NA	29	2	163	NA	39	47
534534	27	4	145	97	30	6	138	103	37	93
534535	31	2	160	NA	29	5	143	NA	30	87
534536	45	12	124	108	NA	NA	NA	NA	17	NA
534537	28	6	132	91	31	5	147	105	16	74
534538	27	6	128	NA	NA	NA	NA	NA	NA	NA
534539	35	3	159	130	40	8	134	116	12	75
534540	31	7	133	NA	NA	NA	NA	NA	NA	74
604238	40	10	127	101	39	9	129	105	20	97
604239	NA	NA	NA	NA	57	15	122	122	14	NA
604240	NA	NA	NA	NA	26	3	154	NA	18	NA
604241	37	6	139	116	36	5	149	120	11	76
604242	31	4	144	145	29	8	121	142	20	60
604243	37	4	154	116	NA	4	NA	111	25	88
604250	35	8	129	106	33	6	138	121	16	78

All specimens are housed in the Yale Peabody Museum. See Fig. 4 for illustration of measurements. YPM.534282 is from the Tonoloway Formation, Winfield Quarry, Pennsylvania; all other specimens are from the Williamsville Formation, Ridgemount Quarry, Ontario. NA, partial, incomplete, or missing trace.

Arcuites resembles several ichnogenera that have been ascribed to swimming vertebrates. The bilaterally symmetrical arcuate traces and linear medial groove of *Arcuites* bear a strong similarity to the fish swimming ichnogenus *Broomichnium* (Benner *et al.* 2008). However, *Broomichnium* contains a diagnostic inner pair of prints that *Arcuites* lacks, and *Broomichnium* lacks the secondary grooves of *Arcuites*. It is conceivable that *Arcuites* represents undertracks of *Broomichnium*, in which case the inner trace pair may not be preserved. That being said, the generally oblique groove boundaries in *Arcuites*, as well as its association with fine, minute appendage traces at both source localities suggests that *Arcuites* is a true surface trace, or perhaps only a shallow undertrack from which little or no morphology is likely to have been lost. Thus, we consider these ichnogenera to be unrelated.

The paired traces and medial groove of *Arcuites* somewhat resemble another fish ichnogenus, *Undichna* (Anderson 1976), and in particular the ichnospecies *U. trisulcata* (Morrissey *et al.* 2004); however, a number of key differences separate these ichnogenera. *Arcuites* lacks both the continuity and characteristically sinusoidal shape of the medial groove and, if present, paired traces of *Undichna*. The linear paired traces of *U. trisulcata* are also morphologically distinct from the arcuate primary traces of *Arcuites*, and *U. trisulcata* lacks the secondary grooves present in some examples of *Arcuites*. *U. trisulcata* is also an intermittent, semi-continuous trace, unlike *Arcuites*.

Finally, within known tetrapod traces, *Arcuites* is comparable to the swimming amphibian trackway *Lunichnium*, and specifically, *L. rotterodium*, which comprises paired arcuate imprints or impressions that curve concave outward (Minter & Braddy 2006). *Lunichnium* is distinct from *Arcuites*, however, as it exhibits alternating symmetry and seriality that are absent in the latter. In light of the differences between the presented material and the existing trace fossil taxa described above, the erection of a new ichnogenus is warranted.

Interpretation. Arthropods and fish represent the most likely candidates for an *Arcuites* producer based on known fauna from the upper Silurian of the Appalachian basin. In comparing traces from these two groups, several lines of evidence further indicate to us that *Arcuites* was produced by a swimming arthropod rather than a vertebrate. Firstly, *Arcuites* and associated traces lack the continuity and sinuous morphology that characterize fish traces (e.g. *Undichna*; see Minter & Braddy 2006, fig. 2). Although not all traces ascribed to fish are continuous (e.g. *Broomichnium* types A–D, Benner *et al.* 2008) the absence of any *Undichna*-like traces in the Williamsville and Tonoloway formations largely negates a fish identity for the maker of *Arcuites*. Secondly, the bi- or trifurcated nature of the secondary grooves of *Arcuites* and associated scratches (Ciurca 2002; Vrazo *et al.* 2014; this study) indicate that *Arcuites* was made by an aquatic arthropod with spinose or ramose appendages. This limits potential candidate taxa in the late Silurian to chelicerates (such as xiphosurans, scorpions and eurypterids) and phyllocarid crustaceans.

Comparisons of *Arcuites* to the impressions made by the swimming paddle in previously interpreted eurypterid trackways (e.g. Hanken & Størmer 1975; Braddy 1995) and modern insects (Loeb & Getty 2015) strongly suggest that the primary grooves in *Arcuites* were made by a dedicated swimming appendage. There is no evidence for such an appendage in scorpions or phyllocarids and thus they can be ruled out as possible tracemakers. The gross similarity of *Arcuites* to the individual impressions within trace sets of *Arborichnus* (e.g. Caster 1938, pl. 9, figs 3–4; Lucas & Lerner 2005, fig. 2F) could evoke a xiphosuran identity for the tracemaker. However, we consider xiphosurans and xiphosuran-like synziphosurines to be unlikely tracemakers for several reasons. Aside from the morphological differences noted above, and the fact that *Arborichnus* was probably made by the doublure of a xiphosuran prosoma rather than a swimming appendage (Caster 1938), associated traces that can be confidently assigned to a xiphosuran or xiphosuran-like tracemaker (e.g. *Koupichnium*) are absent in the Williamsville and Tonoloway formations. Moreover, synziphosurine arthropods collected from these units (e.g. pseudoniscines) are small (*c.* 2 cm long; Ciurca 2002; Vrazo *et al.* 2014) and could not have produced the widest *Arcuites*. This constrains the potential tracemaker to a eurypterid, and specifically the swim paddle-bearing Eurypterina. Within this interpretation, the secondary semicircular grooves present in some *Arcuites* (e.g. Figs 5, 6C) represent impressions made by the fifth prosomal appendage, and the medial grooves on the medial axis (e.g. Figs 5, 7D) represent traces or drags from a eurypterine styliform telson.

Several eurypterine genera are known from the Williamsville and Tonoloway formations (Ciurca 1982; Tollerton 1997; Vrazo *et al.* 2014). The common eurypteroid *Eurypterus*, which dominates the fossil assemblages at both localities, has broad oar-like paddles and is a likely producer of *Arcuites*. The Dolichopteridae is another eurypteroid family that is present at both localities; dolichopterids are of similar size to *Eurypterus*, bear similar-shaped paddles, and are thus potential tracemakers. *Eurypterus* and dolichopterids both have similar styliform telsons that could produce the narrow medial grooves present in some examples of *Arcuites*. Acutiramids are also somewhat common eurypterine eurypterids that are found at both localities. However, acutiramids have a wide, paddle-shaped telson and a more flipper-shaped swimming paddle, making them a less likely candidate for tracemaker.

Arcuites bertiensis isp. nov.

Figures 5; 6A–D; 7; 9

LSID. urn:lsid:zoobank.org:act:AB058586-B63A-4FD3-A0F6-6BFB09DF8377

Derivation of name. The ichnospecific name refers to the Bertie Group of Ontario, in which the type specimen was found.

Holotype. YPM.604241 (Fig. 5).

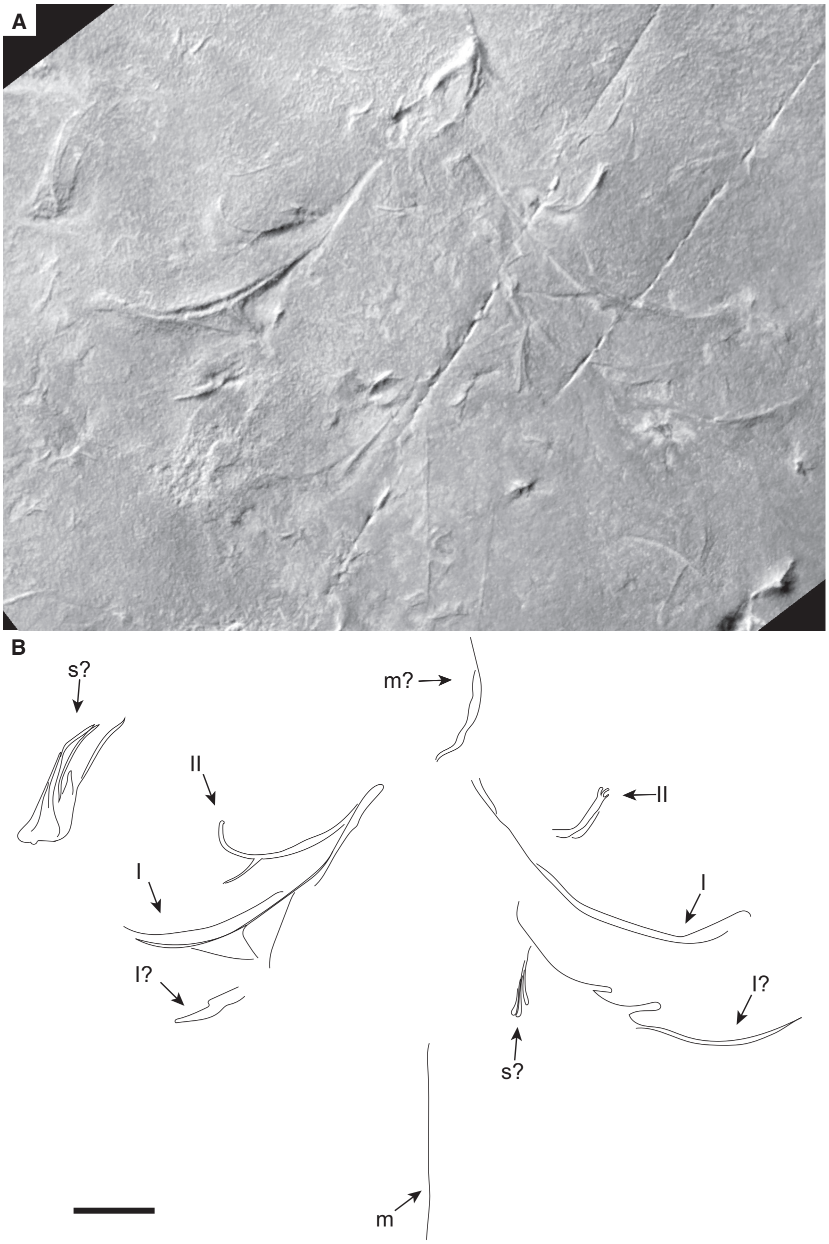
Type horizon. Upper Silurian, middle A Member, Williamsville Formation (Bertie Group), Ridgemount Quarry, Fort Erie, Ontario, Canada.

Paratypes. YPM.534278; YPM.534279–534280 (Fig. 6B, C); YPM.534281; YPM.534282 (Fig. 6A); YPM.534525–534528; YPM.534530–534533 (Fig. 9); YPM.534534–534536; YPM.534537 (Fig. 7D); YPM.534538; YPM.534539 (Fig. 7A); YPM.534540; YPM.604238–604239; YPM.604240 (Fig. 7B); YPM.604242 (Fig. 7C); YPM.604243; YPM.604250 (Fig. 9).

Diagnosis. As for ichnogenus.

Description. Traces are preserved in concave epichnial or convex hypichnial relief, with adjacent sediment mounding displaying reverse relief, if present. Primary grooves are symmetrical or slightly asymmetrical. Individual primary grooves vary widely in length (*c.* 17–57 mm) and depth (*c.* 2–17 mm) (see Table 1 for all measurements). The curvature of individual primary grooves ranges from nearly symmetrical to highly asymmetrical and the angle of the groove arc is variable (*c.* 113–163°). Individual primary groove thickness may be homogenous or may vary along the impression, with the posterior end of the groove thicker than the anterior. The posterior end of individual primary grooves may display one of several termination types: (1) wide and rounded, ending abruptly; (2) wide and grading into

FIG. 5. *Arcuites bertiensis* igen. et isp. nov., holotype, Williamsville Formation, Ridgemount Quarry, Ontario. A, YPM.604241. B, outline sketch. *Abbreviations*: I, primary groove; II, secondary groove; m, medial groove; s, ancillary striae. Scale bar represents 1 cm.



substrate; (3) narrowing to a point; or (4) bifurcated (e.g. Fig. 7A). The anterior end of individual primary grooves may terminate in a thin impression or a rounded point, with small substrate depressions or mounding commonly present around the distal end of the track anterior. Internal and external trace widths range widely (*c.* 8–40 mm, *c.* 47–122 mm, respectively). The angle of the individual primary grooves from the medial axis is extremely variable (*c.* 80–145°) and may or may not be similar for both sides.

Small, secondary semicircular grooves or impressions are present in some trackways (e.g. Figs 5, 6C). These grooves occur at an oblique angle to the primary grooves and stem from the distal end of the anterior of the primary groove, or are isolated. The distal end of the secondary grooves may be bi- or trifurcated, or rounded. A short medial groove or impression of homogenous thickness along its length may be present posterior to the primary grooves (e.g. Figs 5, 7D). The anterior and posterior of this groove or impression end in either a rounded or tapered termination.

Remarks. As for ichnogenus.

DISCUSSION

The close association of a trace fossil with its suggested maker is rare in the fossil record. The co-occurrence of

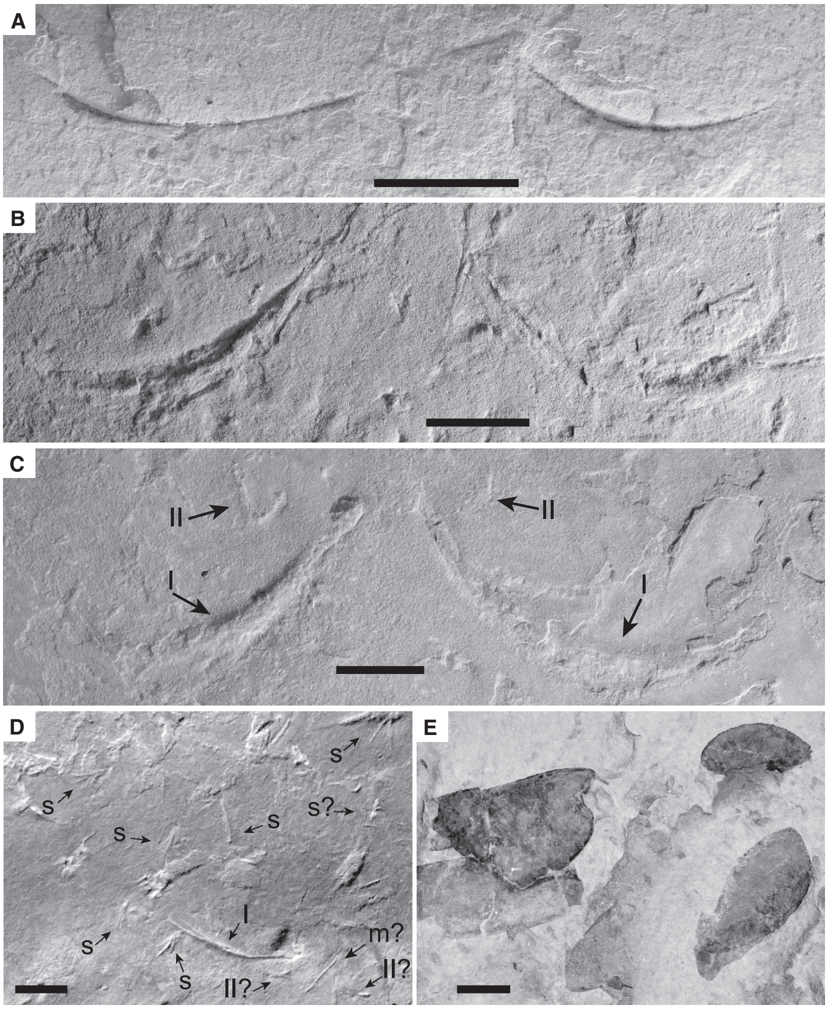


FIG. 6. *Arcuites bertiensis* igen. et isp. nov., associated traces, and eurypterids from the upper Silurian of the Appalachian basin. A, YPM.534282, Tonoloway Formation, Winfield, Pennsylvania. B, YPM.534279, Williamsville Formation, Fort Erie, Ontario. C, YPM.534280 (underside), Williamsville Formation, Fort Erie, Ontario. D, scratch assemblage on YPM.604242, Williamsville Formation, Fort Erie; Ontario. E, isolated *Eurypterus* swimming leg podomeres, YPM.534280 (topside), Williamsville Formation, Fort Erie, Ontario. *Abbreviations*: I, primary groove; II, secondary groove; m, medial groove; s, striae. All scale bars represent 1 cm.

Arcuites and eurypterid remains on the same horizon or on opposite sides of thin beds therefore yields unique insights into not only eurypterid behaviour and functional morphology, but also their preferred life habitat. These aspects will be discussed below.

Eurypterid swimming behaviour

Following our interpretation above, *Arcuites* represents the most direct evidence for eurypterid swimming behaviour currently known. Although *Arcuites* only preserves one phase of the swimming cycle, a number of inferences about eurypterid propulsion-style, paddle motion and speed can be made through analysis of *Arcuites* morphology and metrics, comparison to previously proposed models for eurypterid swimming mechanics and behaviour, and neoichnological experimental results. We will first describe interpreted *Arcuites* tracemaker behaviour, and then review previously proposed models before considering the implications of *Arcuites* within the context of these studies.

Arcuites tracemaker behaviour. A concave-anterior orientation for the primary grooves in *Arcuites*, and thus the direction of travel for the eurypterid tracemaker, is indicated by comparisons to the lunate traces of modern swimming water boatmen (Loeb & Getty 2015). The bilateral symmetry of *Arcuites* indicates that the eurypterid tracemaker employed an in-phase swimming stroke. We suggest that the eurypterid swimming appendages began the stroke cycle perpendicular to the body, before undergoing a propulsive backstroke that drew the paddles posteriorly toward the midline of the animal. It is during the middle–later phase of the backstroke that the ventral edge of the swimming paddle made first contact with the substrate (Fig. 8A). The eurypterid paddle–sediment contact was apparently greatest after the initial disturbance of the substrate with the broad edge of the paddle based on the wider incision observed in the middle of the primary

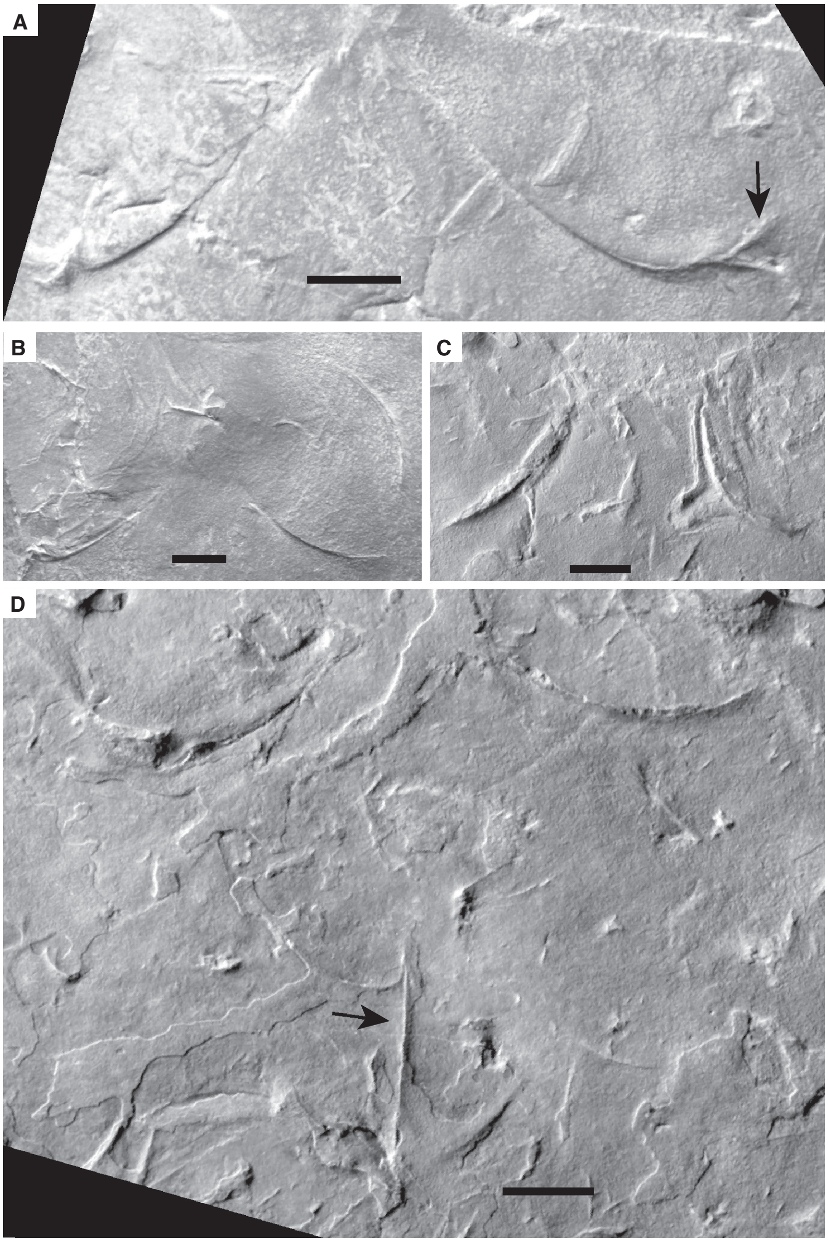


FIG. 7. *Arcuites bertiensis* igen. et isp. nov., Williamsville Formation, Fort Erie, Ontario. A, YPM.534539, arrow indicates bifurcation. B, YPM.604240. C, YPM.604242. D, YPM.534537, arrow indicates medial groove. All scale bars represent 1 cm.

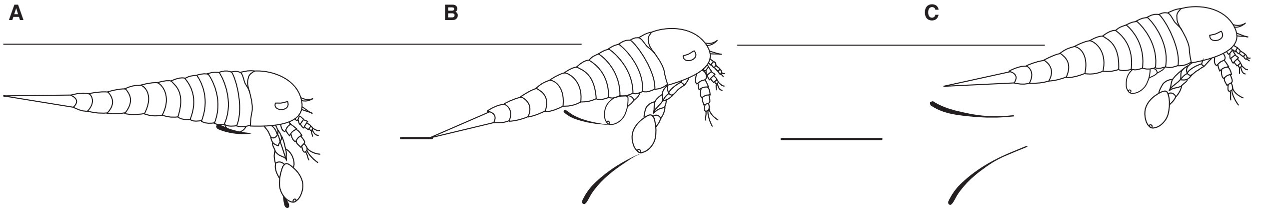


FIG. 8. Cartoon series of interpreted eurypteroid eurypterid swimming behaviour and *Arcuites bertiensis* igen. et isp. nov. production. See text for details.

grooves in *Arcuites* (e.g. Figs 6B–C, 7C). As the appendage was retracted closer to the body during the later phase of the backstroke, the paddle became increasingly dorsoventrally aligned with the direction of travel (Fig. 8B), before being removed from the substrate prior to the recovery stroke (Fig. 8C).

The curvature of the secondary grooves made by appendage V (e.g. Figs 5, 6C) indicates that this

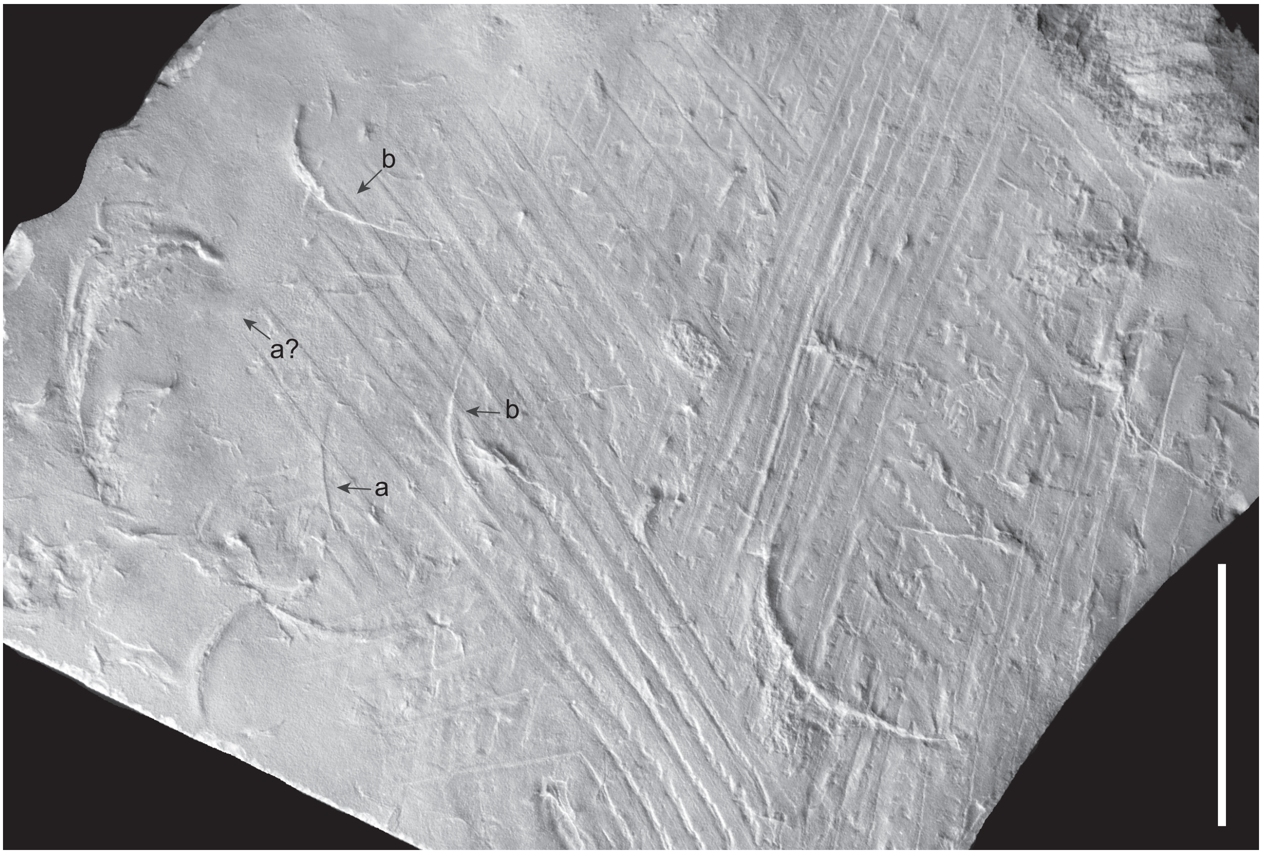


FIG. 9. Slab (YPM.536963) containing multiple *Arcuites bertiensis* igen. et isp. nov. specimens from the Williamsville Formation, A Member (running counterclockwise, from left corner: YPM.534530–534533, 604250). *Abbreviations*: a, first *Arcuites* series pair; b, second *Arcuites* series pair. Note the cross-cutting, wavy striation on the bedding surface. Scale bar represents 5 cm.

appendage moved in concert with appendage VI, perhaps for steering (see Selden 1981). The discontinuous nature of the inferred telson traces suggests that if the telson functioned as a type of rudder (e.g. Størmer 1934; Størmer 1936; Plotnick & Baumiller 1988) it did not remain in contact with the substrate for a period longer than the backstroke phase. Selden (1981) suggested that the telson may have been used to balance the animal on the substrate when unstable, but did not consider the caudal region of eurypterine eurypterids with styliform telsons (such as *Eurypterus*) to be capable of providing thrust. The inconsistent preservation of telson drag traces among *Arcuites* specimens does not provide sufficient evidence to support or refute its role as either a rudder or stabilizer, but does suggest that the telson and postabdomen were angled ventrally during the swim stroke, perhaps providing minor additional lift.

Previous eurypterid swimming models. The biomechanical properties of the eurypterine swimming appendage were previously considered by three studies that each proposed a different predictive swimming model (Selden 1981; Plotnick 1985; Knight 1997; see Plotnick (1985) for a review of earlier swimming hypotheses). Selden (1981) performed the first in-depth analysis of eurypterid swimming locomotion based on an exhaustive morphological examination of *Eurypterus* (= *Baltoeurypterus*; Tetlie 2006). Selden (1981) proposed that swimming eurypteroids (i.e. *Eurypterus*) used the paddle on their swimming leg in a manner similar to an oar blade and employed a drag-based rowing-style of propulsion. Selden interpreted the morphology of appendage VI as allowing for primarily anteroposterior pivoting and rotation of the swimming blade as the animal swam, with limited dorsoventral mobility. Following the propulsive backstroke, during which the paddle blade was held vertically, the pivot joint between podomeres 6 and 7 permitted the distal end of the appendage, including the blade, to be folded backward or collapsed horizontally during the recovery stroke. Selden's model is similar to rowing behaviour observed in some small aquatic insects, such as water boatmen (Corixidae; Ngo & McHenry 2014).

Plotnick (1985) then carried out an experimental analysis of eurypterid swimming using the blue crab

(*Callinectes sapidus*) as a modern analogue. Plotnick was generally in agreement with Selden's (1981) in-phase swimming model, whereby a propulsive backstroke is responsible for most of the forward thrust. However, Plotnick (1985) suggested that swim paddle motion during the forestroke was responsible for not only minor thrust, but also significant buoyant lift. Thus, instead of rowing, alteration of the paddle angle during the stroke would allow it to be used as a hydrofoil, to perform what Plotnick described as 'subaqueous flying'. Plotnick stated that eurypterids probably used this lift-based model of propulsion as there was otherwise no force to counteract body weight and drag. This type of paddle motion could also be modified to allow for hovering, as is common among some modern insects and birds.

In considering Plotnick's (then unpublished) model, Selden (1984) acknowledged that the underwater flying model may have been more efficient than rowing depending on the swimming speed achieved, relative size of the animal and type of paddle morphology. Using the Reynolds calculation, which determines whether viscosity or velocity is more dominant based on length, and comparisons to modern aquatic animals (e.g. water beetles) Selden (1984) calculated that even smaller eurypterids (*c.* 10 cm) may have been too large to utilize a rowing motion without excessive drag. Nevertheless, Selden suggested that eurypteroids probably still swam using a rowing motion, albeit at slower speeds, due to their oar-like swimming paddle, while other non-eurypteroid eurypterine taxa (e.g. hughmilleroids and large pterygotids, some of which grew up to *c.* 2.5 m long; Braddy *et al.* 2008) may have used the faster subaqueous flying method due to their flipper-like paddles and streamlined body shapes.

Later, Knight (1997) carried out biomechanical modelling experiments on reconstructions of the swimming appendage of several eurypterine taxa including *Eurypterus* (= *Baltoeurypterus*), during which the most efficient stroke motion and angle was calculated. Using this quantitative approach, Knight found that an ideal swimming motion involved an entirely lift-based stroke whereby the paddle was swept forward and down on the forestroke, and backward and up on the backstroke, with the paddle angled at 45°. This method of propulsion is similar to that of modern sea lions (English 1976) and is hydrodynamically more similar to the hydrofoil model suggested by Plotnick (1985) than Selden's (1981) rowing model. However, Knight (1997) also determined that a drag-based swimming mechanism (i.e. rowing) would be more efficient for smaller eurypterids (e.g. < 1 cm long).

A revised eurypterid swimming model. With respect to the eurypterid swimming models proposed hitherto (Selden 1981; Plotnick 1985; Knight 1997) *Arcuites* supports the in-phase, propulsive-style of swimming locomotion predicted by all three authors. In terms of paddle motion, the inferred tracemaker behaviour of *Arcuites* aligns most closely with the rowing model proposed by Selden (1981), in which the paddle is used like an oar blade. However, *Arcuites* and associated trace morphology also reveal new behaviour within the rowing paradigm. The close proximity of the anterior ends of the primary grooves in some specimens (e.g. Figs 6C, 7A), interpreted as impressions from paddles at the end of the backstroke phase, and the presence of parallel grooves most likely made by eurypteroid swim paddles dragging through the substrate in tandem (akin to skis; Fig. 2, upper right corner) are taken to suggest that the swimming appendage was capable of being drawn directly underneath the animal's body. Such positioning would appear to require a greater range of dorsoventral mobility for appendage VI than was implied by Selden's (1981) model. Conversely, in Plotnick's (1985) and Knight's (1997) models there is a greater degree of dorsoventral mobility implied for appendage VI in the regular forward swimming motion and the figure-of-eight pattern required for hovering, but these models do not incorporate the range of anteroposterior mobility needed to produce the steep angles of the primary groove to the medial axis in *Arcuites*. Thus, *Arcuites* extends the possible range of movement for appendage VI in both the dorsoventral and anteroposterior planes when employed within a rowing-style swim stroke. Drag-based rowing is considered to be a less efficient and slower method of propulsion than, for example, underwater flying (Plotnick 1985), but *Arcuites* morphology metrics nonetheless yield evidence for variation in swimming speed within this locomotory style. The wide range in the angle of the primary grooves to the medial axis most likely reflects stroke exertion, and thus the speed of the animal. Angles closer to 90° probably reflect slower movement, perhaps from a near-standstill, whereas larger angles (up to 145°) probably reflect a faster stroke while in motion.

Although *Arcuites* provides general support for a rowing-style of propulsion for eurypteroid eurypterids, the possibility that these traces only represent the behaviour of certain eurypterid instars should be considered. To test this hypothesis, we would ideally determine the size of the eurypterid tracemakers using an *Arcuites* metric (e.g. trace width). There is a non-significant correlation between the internal and external trace widths (Pearson's, $n = 18$, $r^2 = 0.15$, $p > 0.05$); this indicates that the distance between the respective left and right grooves from the medial axis in *Arcuites* is decoupled, and hence total width may not be an accurate reference for the animal's size. Nevertheless, if the external *Arcuites* width is used as an approximate indicator of the distance between the tips of the ninth podomere on the left and right eurypteroid swimming paddle, this measurement can still provide a crude estimate of total body length.

When all *Arcuites* external widths are scaled conservatively to a typical diagrammatic depiction of *Eurypterus* in which appendage VI is displayed somewhat outstretched (e.g. Clarke & Ruedemann 1912, fig. 2), this translates to body lengths of 65–168 mm (mean = 109 mm, SD = 5.96). This body size range falls within the juvenile to adult size ranges identified by Vrazo & Braddy (2011) in a size survey of *Eurypterus* from the Williamsville Formation of western New York and south-western Ontario. Thus, *Arcuites* appears to indicate that rowing was characteristic of most eurypteroid eurypterid growth stages, even though smaller traces that could be attributed to the larval size class are absent.

In considering our inference of a rowing motion for the production *Arcuites*, it should be noted that this conclusion does not necessarily refute the alternative lift-based hypotheses because we cannot predict the exact paddle motion following the backstroke, or swimming behaviour of non-eurypteroid taxa. We also cannot discount the close proximity of the eurypterid to the substrate (perhaps because of shallow water depth, see Palaeoenvironmental Interpretation, below) which may have caused the animal to swim in a way that differs to when it is higher in the water column. That being said, all available trace fossil evidence supports our conclusion that *Arcuites* was produced by true swimming behaviour, rather than an immobile organism–sediment interaction (i.e. resting), walking or some other mode of subaqueous surface locomotion (e.g. hopping). Firstly, distinct paddle impressions in the Tonoloway Formation (Fig. 2) provide a good example of a likely eurypterid resting trace and thus preclude a similar interpretation for *Arcuites*. Secondly, the absence of definitive walking traces (e.g. *Palmichnium*) and the erratic nature of walking appendage impressions or scratches in the Tonoloway and Williamsville formations (e.g. Vrazo *et al.* 2014, fig. 8A, C; Fig. 5D) suggest that the tracemakers were buoyant and only made occasional contact with the substrate. Moreover, the absence of walking trackways associated with *Arcuites* precludes it from being a transitional walking to swimming push-off trace (e.g. Braddy & Milner 1998). An alternative mode of subaqueous locomotion in which eurypterid tracemakers hopped across the substrate using a swimming stroke-like motion (Braddy 1995; Braddy & Almond 1999; Seilacher 2007) can also be disregarded because there are no consecutive and unidirectional examples of *Arcuites* (see Figs 3, 9). Thirdly, several specimens contain a second single or pair of primary groove impressions (e.g. YPM.604241, Fig. 5; YPM.604250, Fig. 9), which we interpret as the rare preservation of two consecutive stroke periods. Preservation of repeated stroke impressions without associated walking appendage or paddle traces seems unlikely if the animal was not already progressing through the water column. Fourthly, the wide range of primary groove to medial axis angles observed in *Arcuites* suggests variable swimming speeds for animals already in motion, as opposed to animals beginning movement from complete standstill. Finally, the preservation of short telson drags in *Arcuites* suggests behaviour by an animal that only briefly grazed the sediment while progressing through the water column, rather than one at standstill or walking (cf. the continuous telson drag in the eurypterid walking trackway *P. antarcticum*; Braddy & Milner 1998). In sum, these observations support the interpretation that *Arcuites* was the result of true swimming locomotion. Furthermore, the abundance and size range of *Arcuites* implies that the behaviour that produced this trace was part of the regular swimming repertoire for eurypteroid eurypterids.

Palaeoenvironmental interpretation

The single occurrence of *Arcuites bertiensis* at the thoroughly examined Winfield Quarry is interesting when compared to the abundance of specimens at Ridgemount Quarry. The isolation of the former is particularly notable when considering that the frequency of ancillary striae and other appendage traces is similar at both localities, as is the abundance and size of eurypteroid body fossils. Undertracks are more common than surface traces for arthropods in subaqueous environments (Seilacher 2007) and if *Arcuites* represented undertracks, respective trace abundance might be explained by sedimentological differences between the sites. Although trace fossil depth is comparable at both localities, the sharp and well-defined nature of some traces at Winfield Quarry could be suggestive of undertracks (e.g. Vrazo *et al.* 2014, fig. 8C; Fig. 2). On the other hand, the small size of *A. bertiensis* in the Turbotville Member and its association with minute traces on the same horizon indicate that they are probably surface traces or perhaps very shallow undertracks; a small animal would be less likely to create a deeply impressed trace that might only be retained as a deep undertrack. Likewise, it is unlikely that associated fine and delicate traces would be preserved as deep undertracks at either locality. Therefore, if there is no undertrack bias at either site, sedimentological controls on *Arcuites* abundance are unlikely.

Seilacher (2008) argued that the presence of microbial mats on the substrate increased the preservational potential of arthropod trackways. Both Tonoloway and Williamsville formations contain evidence for microbial structures and matting either adjacent to or on the eurypterid-bearing horizons (Ciurca 2013; Vrazo *et al.* 2014) and thus it is possible that microbial activity on the sediment surface promoted trace preservation in either unit. Moreover, we note that a striate, wavy structure that occurs on a slab from the same horizon as *Arcuites* in the Williamsville Formation A Member (Fig. 9) resembles the pattern on a slab figured by Caster (1938, pl. 11, fig. 5). Caster noted that this pattern occurs on the *Koupichnium* (= *Paramphibius*) track-bearing horizon of the Upper Devonian Wellsburg Formation, but could not explain its occurrence. It is difficult to discern whether the patterns in Caster's example or in the present study are biogenic (e.g. microbial) or abiotic (e.g. microripples). The observation of this pattern in the present study only on trace-bearing horizons that lack obvious ripples would appear to support a microbial origin; however, we cannot be certain that the structure is not an abiotic feature such as a tool mark, which is suggested by the pattern's linear nature. In either case, trace preservation due to the presence of microbial matgrounds at either site appears possible.

If the potential for trace preservation in the substrate was similar at both localities, differences in *Arcuites* abundance may be the result of some other environmental parameter, such as water depth. In this scenario, trace-making behaviour by modern analogues is informative. Loeb & Getty (2015) performed a series of controlled, neoichnological experiments using aquatic insects. In these experiments, water boatmen created traces very similar to *Arcuites* when restricted to shallow water. Although these traces were created under experimental conditions, P.R. Getty (pers. comm. 2015) has noted similar traces in the field (from an unobserved maker), suggesting that such trace production represents normal behaviour. Applying the results of the water boatman experiments to the present study, *Arcuites* abundance appears to reflect differences in relative palaeodepth in the trace fossil-bearing beds of the Tonoloway Formation Turbotville Member and Williamsville Formation A Member. The water column at either locality was evidently deep enough that animals did not resort to walking behaviour (i.e. *Palmichnium*), but shallow enough that they could contact the substrate with their swimming appendages and walking appendage spines while swimming. However, the abundance of *Arcuites* in the A Member ultimately appears to indicate that swimming animals there were closer to the substrate, and more restricted in movement as a consequence of a shallower water depth, than in the Tonoloway Formation. A similar water depth control on fish swimming behaviour and *Undichna* production was interpreted for very shallow tidal settings in the Pennsylvanian of Alabama (Martin & Pyenson 2005).

Regardless of relative water depth, the very close association of well-preserved eurypterids and trace fossils ascribed to them in the Tonoloway and Williamsville formations is the best evidence to date that eurypterids were occasional inhabitants of both settings and that their remains were not simply transported from elsewhere. This evidence for inhabitation, along with the associated euryhaline or stenohaline fauna, supports recent interpretations of the eurypterid-bearing intervals of the Tonoloway and Williamsville formations as having nearly normal marine salinity (i.e. hypo- to slightly hypersaline) (Vrazo *et al.* 2014, 2016, 2017). In both formations exoskeletons (rather than carcasses) of *Eurypterus*, one of the presumed eurypteroid tracemakers, are much more abundant than all other eurypterid taxa, occur in a wide range of sizes, and are sometimes found in aggregated moult ensembles (Tetlie *et al.* 2008; Vrazo & Braddy 2011; Vrazo *et al.* 2014). These assemblages of shed exuviae from juvenile to adult eurypteroid instars and traces made by individuals of similar-sizes may reflect a tendency toward moulting, or mating or spawning, *en masse* in shallow subtidal settings in the late Silurian (Braddy 2001; Vrazo & Braddy 2011; Vrazo *et al.* 2014).

CONCLUSION

Morphologically similar trace fossils from the upper Silurian Williamsville Formation of Ontario and Tonoloway Formation of Pennsylvania are diagnosed as a new ichnogenus and ichnospecies, *Arcuites bertiensis*. These traces are interpreted as a swimming trace made by a eurypteroid eurypterid, that employed its oar-blade-like paddle in a rowing-style backstroke near the substrate. *Arcuites* generally supports the in-phase, drag-based rowing model for eurypteroid swimming behaviour proposed by Selden (1981), but also extends the potential anteroposterior and dorsoventral range of motion for appendage VI beyond previous predictions. The combination of well-preserved eurypterid remains and *Arcuites* in both formations confirms that eurypterids were occasional inhabitants of these nearshore shallow subtidal settings, while the difference in *Arcuites* abundance between the two localities suggests minor variation in palaeodepth. Inasmuch as *Arcuites* appears to reflect typical behaviour by a common eurypteroid taxon (e.g. *Eurypterus*) future models of eurypterid swimming should take into consideration the range of motion implied by this trace fossil.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/515683FE-4AA8-4B21-BD3D-3E4DFC2C2B6B

Editor. Duncan McIlroy

REFERENCES

ANDERSON, A. 1976. Fish trail from the Early Permian of South Africa. *Palaeontology*, **19**, 397–409.

ANDERSON, R. P., McCOY, V. E., McNAMARA, M. E. and BRIGGS, D. E. G. 2014. What big eyes you have: the ecological role of giant pterygotid eurypterids. *Biology Letters*, **10**, 20140412.

BELAK, R. 1980. The Cobleskill and Akron members of the Rondout Formation: late Silurian carbonate shelf sedimentation in the Appalachian basin, New York State. *Journal of Sedimentary Research*, **50**, 1187–1204.

BELL, S. C. and SMOSNA, R. 1999. Regional facies analysis and carbonate ramp development in the Tonoloway Limestone (upper Silurian; central Appalachians). *Southeastern Geology*, **38**, 259–278.

BENNER, J. S., RIDGE, J. C. and TAFT, N. K. 2008. Late Pleistocene freshwater fish (Cottidae) trackways from New England (USA) glacial lakes and a reinterpretation of the ichnogenus *Broomichnium* Kuhn. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **260**, 375–388.

BERDAN, J. M. 1963. *Eccentricosta*, a new upper Silurian brachiopod genus. *Journal of Paleontology*, **37**, 254–256.

BERTLING, M., BRADDY, S. J., BROMLEY, R. G., DEMATHIEU, G. R., GENISE, J., MIKULÁŠ, R., NIELSEN, J. K., NIELSEN, K. S. S., RINDSBERG, A. K., SCHLIRF, M. and UCHMAN, A. 2006. Names for trace fossils: a uniform approach. *Lethaia*, **39**, 265–286.

BRADDY, S. J. 1995. A new arthropod trackway and associated invertebrate ichnofauna from the Lower Permian Hueco Formation of the Robledo Mountains, southern New Mexico. 101–106. *In* LUCAS, S. G. and HECKERT, A. B. (eds). *Early Permian footprints and facies*. New Mexico Museum of Natural History & Science Bulletin, **6**.

—— 2001. Eurypterid palaeoecology: palaeobiological, ichnological and comparative evidence for a ‘mass-moult-mate’ hypothesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **172**, 115–132.

—— and ALMOND, J. E. 1999. Eurypterid trackways from the Table Mountain Group (Ordovician) of South Africa. *Journal of African Earth Sciences*, **29**, 165–177.

—— and ANDERSON, L. I. 1996. An Upper Carboniferous eurypterid trackway from Mostyn, Wales. *Proceedings of the Geologists’ Association*, **107**, 51–56.

—— and MILNER, A. R. C. 1998. A large arthropod trackway from the Gaspe Sandstone Group (Middle Devonian) of eastern Canada. *Canadian Journal of Earth Sciences*, **35**, 1116–1122.

—— POSCHMANN, M. and TETLIE, O. E. 2008. Giant claw reveals the largest ever arthropod. *Biology Letters*, **4**, 106–109.

BRIGGS, D. E. G. and ROLFE, W. D. I. 1983. A giant arthropod trackway from the Lower Mississippian of Pennsylvania. *Journal of Paleontology*, **57**, 377–390.

BURROW, C. J. and RUDKIN, D. 2014. Oldest near-complete acanthodian: the first vertebrate from the Silurian Bertie Formation Konservat-Lagerstätte, Ontario. *PLoS One*, **9**, 1–9.

CASTER, K. E. 1938. A restudy of the tracks of *Paramphibius*. *Journal of Paleontology*, **12**, 3–60.

CHADWICK, G. H. 1930. Studies in the New York Siluric. *Geological Society of America Bulletin*, **41**, 80.

CIGNONI, P., CALLIERI, M., CORSINI, M., DELLEPIANE, M., GANOVELLI, F. and RANZUGLIA, G. 2008. MeshLab: an open-source mesh processing tool. 129–136. *In* SCARANO, V., DE CHIARA, R. and ERRA, U. (eds). *Eurographics Italian Chapter Conference 2008: Salreno, Italy*. The Eurographics Association.

CIURCA, S. J. Jr 1982. Eurypterids, stratigraphy, late Silurian-Early Devonian of western New York State and Ontario, Canada. 99–120. *In* BUEHLER, E. J. and CALKIN, P. E. (eds). *Geology of the Northern Appalachian Basin western New York*. New York State Geological Association Guidebooks, Field Trips, 54th Annual Meeting.

—— 1990. Eurypterid biofacies of the Silurian-Devonian evaporite sequence: Niagara Penninsula, Ontario, Canada and New York State. D1–D23. *In* LASH, G. G. (ed.) , New York State Geological Association Guidebooks, Field Trips, 62nd Annual Meeting.

—— 2002. A new trace fossil horizon within the late Silurian, eurypterid-bearing Bertie Group in Ontario, Canada. *MAPS Digest*, **25** (EXPO XXIV edition), 52–56.

—— 2010. *Eurypterids illustrated: the search for Prehistoric Sea Scorpions*. PaleoResearch, Rochester, NY, 30 pp.

—— 2013. Microbialites within the eurypterid-bearing Bertie Group of western New York and Ontario, Canada. 154–179. *In* DEAKIN, A. K. and LASH, G. G. (eds). *Lake Erie heritage grape belt*. New York State Geological Association Guidebooks, Field Trips, 85th Annual Meeting.

—— and HAMELL, R. D. 1994. Late Silurian sedimentation, sedimentary structures and paleoenvironmental settings within an eurypterid-bearing sequence (Salina and Bertie groups), western New York State and southwestern Ontario, Canada. 457–488. *In* BRETT, C. E. and SCATTERDAY, J. (eds). New York State Geological Association Guidebook, Field Trips, 66th Annual Meeting.

CLARKE, J. M. and RUEDEMANN, R. 1912. The Eurypterida of New York. *New York State Museum Memoir*, **14**, 1–439.

COTTER, E. C. and INNERS, J. D. 1986. Stop 1.5; Allenport. 27–39. *In* SEVON, W. D. (ed.) *Selected geology of Bedford and Huntington Counties: guidebook for the 51st Annual Field Conference of Pennsylvania Geologists*. Field Conference of Pennsylvania Geologists, Juniata University, Huntington, PA.

EDWARDS, D., BANKS, H. P., CIURCA, S. J. Jr and LAUB, R. S. 2004. New Silurian cooksonias from dolostones of north-eastern North America. *Botanical Journal of the Linnean Society*, **146**, 399–413.

ENGLISH, A. W. 1976. Limb movements and locomotor function in the California sea lion (*Zalophus californianus*). *Journal of Zoology*, **178**, 341–364.

GETTY, P. R. 2017. *Lunulipes*, a replacement name for the trace fossil *Lunula* Hitchcock, 1865, preoccupied. *Journal of Paleontology*, **91**, 577.

HAMELL, R. D. 1982. Stratigraphy, petrology and paleoenvironemntal interpretation of the Bertie Group (late Cayugan) in New York. *Empire State Geogram*, **18**, 37–38.

—— CIURCA, S. J. Jr 1986. Paleoenvironmental analysis of the Fiddlers Green Formation (late Silurian) in New York state. 199–218. *In* CISNE, J. L. (ed.) New York State Geological Association Guidebooks, Field Trips, 58th Annual Meeting.

HANKEN, N.-M. and STØRMER, L. 1975. The trail of a large Silurian eurypterid. *Fossils & Strata*, **4**, 255–270.

HITCHCOCK, E. 1865. *Supplement to the ichnology of New England: a report to the Government of Massachusetts*. Wright & Potter, Boston, MA, 96 pp.

INNERS, J. D. 1997. *Geology and mineral resources of the Allenwood and Milton quadrangles, Union and Northumberland Counties, Pennsylvania*. Pennsylvania Geological Survey, 4th ser., Atlas 144cd, Harrisburg, PA 135 pp.

KNIGHT, G. J. 1997. A reconstruction of eurypterid swimming. Unpublished PhD thesis, University of Manchester, UK, 271 pp.

LAMSDELL, J. C. and BRADDY, S. J. 2010. Cope's Rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biology Letters*, **6**, 265–269.

LAUGHREY, C. D. 1999. Silurian and transition to Devonian. *In* SHULTZ, C. H. (ed.) *The geology of Pennsylvania*. Pennsylvania Geological Survey, Harrisburg & Pittsburgh Geological Society, Pittsburgh, PA, 90–107.

LOEB, S. B. and GETTY, P. R. 2015. The neoichnology of aquatic insects and a possible fossil analog. *Geological Society of America Abstracts with Programs*, **47** (7), 341.

LUCAS, S. G. and LERNER, A. J. 2005. Lower Pennsylvanian invertebrate ichnofossils from the Union Chapel Mine, Alabama: a preliminary assessment. 147–152. *In* BUTA, R. J., RINDSBERG, A. K. and KOPASKA-MERKEL, D. C. (eds). *Pennsylvanian footprints in the Black Warrior Basin of Alabama*. Alabama Paleontological Society Monograph, **1**.

MARTIN, A. J. and PYENSON, N. D. 2005. Behavioral significance of vertebrate trace fossils from the Union Chapel site. 59–112. *In* BUTA, R. J., RINDSBERG, A. K. and KOPASKA-MERKEL, D. C. (eds). *Pennsylvanian footprints in the Black Warrior Basin of Alabama*. Alabama Paleontological Society Monograph, **1**.

McCOY, V. E., LAMSDELL, J. C., POSCHMANN, M., ANDERSON, R. P. and BRIGGS, D. E. G. 2015. All the better to see you with: eyes and claws reveal the evolution of divergent ecological roles in giant pterygotid eurypterids. *Biology Letters*, **11**, 20150564.

McMAHON, S., VAN SMEERDIJK HOOD, A. and McILROY, D. 2017. The origin and occurrence of subaqueous sedimentary cracks. *Geological Society London, Special Publications*, **448**, 285–309.

MINTER, N. J. and BRADDY, S. J. 2006. The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA. *Palaeontology*, **49**, 1123–1142.

MONAHAN, J. W. 1931. Studies of the fauna of the Bertie Formation. *American Midland Naturalist*, **12**, 377–400.

MORRISSEY, L. B., BRADDY, S. J., BENNETT, J. P., MARRIOTT, S. B. and TARRANT, P. R. 2004. Fish trails from the Lower Old Red Sandstone of Tredomen Quarry, Powys, southeast Wales. *Geological Journal*, **39**, 337–358.

NGO, V. and McHENRY, M. J. 2014. The hydrodynamics of swimming at intermediate Reynolds numbers in the water boatman (Corixidae). *Journal of Experimental Biology*, **217**, 2740–2751.

O'CONNELL, M. 1916. The habitat of the Eurypterida. *Bulletin of the Buffalo Society of Natural Sciences*, **11**, 1–227.

PLOTNICK, R. E. 1985. Lift-based mechanisms for swimming in eurypterids and portunid crabs. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **76**, 325–337.

—— and BAUMILLER, T. K. 1988. The pterygotid telson as a biological rudder. *Lethaia*, **21**, 13–27.

RASBAND, W. 2011. *ImageJ. Version 1.45s*. National Institutes of Health. https://imagej.nih.gov/

RICHTER, R. 1954. Fährte eines "Riesenkrebses" im Rheinischen Schiefergebirge. *Natur und Volk*, **84**, 253–284.

ROMANO, M. and MELÉNDEZ, B. 1985. An arthropod (merostome) ichnocoenosis from the Carboniferous of northwest Spain. *Proceedings of the 9th International Carboniferous Congress, Urbana, USA*, **5**, 317–325.

SCRUTON, P. C. 1953. Deposition of evaporites. *AAPG Bulletin*, **37**, 2498–2512.

SEILACHER, A. 2007. *Trace fossil analysis*. Springer, 226 pp.

—— 2008. Biomats, biofilms, and bioglue as preservational agents for arthropod trackways. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270**, 252–257.

SELDEN, P. A. 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **72**, 9–48.

—— 1984. Autecology of Silurian eurypterids. 39–54. *In* BASSETT, M. G. and LAWSON, J. D. (eds). *Autecology of Silurian organisms*. Special Papers in Palaeontology, **32**, The Palaeontological Association.

STØRMER, L. 1934. Merostomata from the Downtonian Sandstone of Ringerike, Norway. *Matematisk-Naturvidenskapelig Klasse*, **10**, 1–125.

—— 1936. Eurypteriden aus dem Rheinischen Unterdevon. *Abhandlungen der Preugischen Geologischen Landesanstalt*, **175**, 1–74.

SWARTZ, F. M. 1929. The Helderberg group from central Pennsylvania to southwestern Virginia. *Proceedings of the Pennsylvania Academy of Science*, **3**, 75–88.

TETLIE, O. E. 2006. Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus. *Journal of Systematic Palaeontology*, **4**, 397–412.

—— 2007. Distribution and dispersal history of Eurypterida (Chelicerata). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**, 557–574.

—— BRANDT, D. S. and BRIGGS, D. E. G. 2008. Ecdysis in sea scorpions (Chelicerata: Eurypterida). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **265**, 182–194.

TOLLERTON, V. P. Jr 1997. Eurypterids and associated fauna at Litchfield, a classic locality. 253–264. *In* RAYNE, T. W., BAILEY, D. G. and TEWKSBURY, B. J. (eds). New York State Geological Association Guidebooks, Field Trips, 69th Annual Meeting.

TREESH, M. 1972. Sedimentology and stratigraphy of the Salina Group (upper Silurian) in east-central New York. B1–B22. *In* McLELLAND, G. G. (ed.) New York State Geological Association Guidebooks, Field Trips, 44th Annual Meeting.

VRAZO, M. B. and BRADDY, S. J. 2011. Testing the 'mass-moult-mate' hypothesis of eurypterid palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **311**, 63–73.

—— TROP, J. M. and BRETT, C. E. 2014. A new eurypterid Lagerstätte from the upper Silurian of Pennsylvania. *Palaios*, **29**, 431–448.

—— BRETT, C. E. and CIURCA, S. J. Jr 2016. Buried or brined? Eurypterids and evaporites in the Silurian Appalachian basin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **444**, 48–59.

—— —— —— 2017. Paleoecological and stratigraphic controls on eurypterid Lagerstätten: a model for preservation in the mid-Paleozoic. *Paleobiology* **43**, 383–406.