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# The Early Devonian eurypterid *Leiopterella tetliei* from Arctic Canada

Simon J. Braddy, Jason A. Dunlop and Joseph A. Bonsor

Simon J. Braddy. Manorbier, United Kingdom.

**Jason A. Dunlop.** Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, D-10115 Berlin, Germany.

**Joseph A. Bonsor.** Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom and Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath, BA2 7AY, United Kingdom.

Corresponding author: Jason A. Dunlop (email: jason.dunlop@mfn.berlin).

**Abstract**: The stylonurid eurypterid *Leiopterella tetliei* Lamsdell et al., 2010 (Chelicerata: Eurypterida: Rhenopteridae) from the Early Devonian (Lochkovian) of Nunavut in Arctic Canada is redescribed. Restudy of the holotype under polarized light revealed a labrum, epistomal sutures, prosomal appendage III and deltoid plates anterior to the genital appendage. An additional new specimen preserves the distal podomeres of appendage VI and gradually tapering opisthosomal tergites. The characters resolved here support the hypothesis that *L. tetliei* was relatively basal within the wider Stylonurina clade, its tapering postabdomen supporting a more basal position within Rhenopteridae than previously suggested.

Résumé: [insert here]

Key words: Eurypterida. Stylonurina. Morphology. Appendages.

# Introduction

The eurypterids (Chelicerata: Eurypterida) are a group of extinct predatory arthropods known from around 250 species. Some lineages, notably the pterygotids, attained very large size (ca. 2.5 m long) probably due to ecological competition (Lamsdell and Braddy 2010). Eurypterids as a group have a global distribution, but are rare as fossils due to their thin, unmineralised chitinous cuticle, although sometimes they are locally abundant in Palaeozoic Konservat-Lagerstätte, especially in eastern North America and Europe. The earliest eurypterid is Pentecopterus decorahensis Lamsdell et al. 2015, from the Middle Ordovician (Darriwilian) of lowa; the number of podomeres, lack of cercal blades, and opisthosomal differentiation, actually indicates that it is intermediate between the megalograptids and the other Eurypterina. Lamsdell et al. (2015) resolved the megalograptids in a more derived position than is generally suggested (e.g., Tetlie 2007) dragging down the ghost range of all eurypterid lineages into the Early Ordovician, but the number and morphology of their podomeres, primitive prosomal doublure, metastoma, operculum, opisthosomal differentiation and cercal blades all denote the "fundamental distinction" of megalograptids (Caster and Kjellesvig-Waering 1964, p. 303). The eurypterid fossil record more generally refutes the phylogenetic hypothesis of Lamsdell et al. (2015); there should be some evidence of these missing eurypterid lineages, if it were correct.

Eurypterids recorded from Canada tend to be nekto-benthic forms in the Suborder Eurypterina. In this group the posterior prosomal appendage (limb VI) was modified into a paddle, implying an active swimming lifestyle. Canadian Eurypterina are known from the Late

Ordovician (Stott et al. 2005) and the Silurian (Copeland and Bolton 1960, 1985; Rudkin et al. 1998) of Ontario and Quebec and the Silurian and Devonian of Arctic Canada (Braddy and Dunlop 2000; Stott et al. 2005 and references therein), including several records assigned to the genera *Megalograptus*, *Orcanopterus*, *Onychopterella*, *Erettopterus*, *Carcinosoma*, *Rhinocarcinosoma*, *Eurypterus* and *Erieopterus*.

The other eurypterid suborder is the Stylonurina, in which the posterior prosomal appendage is leg-like and was presumably used, along with the other limbs, primarily for walking on the substrate. Compared to Eurypterina, Canadian Stylonurina are very rare. Published records include a kokomopterid from the Early Wenlock of Ontario (Rudkin et al. 1998), an unidentified specimen from the Middle Devonian of Quebec (Jeram 1996), *Pagea plotnicki* Lamsdell et al., 2010a from the Early Devonian of Cornwallis Island, Nunavat (Plotnick and Elliott 1995), *Drepanopterus odontospathus* Lamsdell, 2012 from the Early Devonian of the Northwest Territories (Braddy and Dunlop 2000; Lamsdell 2012), and two species from the Early Devonian of Prince of Wales Island, Nunavat: *Pagea plotnicki* and *Leiopterella tetliei* Lamsdell et al., 2010a. Any new material has the potential to yield valuable information on the morphology and distribution of Canadian stylonurid eurypterids. Here we redescribe *Leiopterella tetliei* based on a reinterpretation of the holotype, together with a second specimen originally misinterpreted as an arachnid (cf. Lamsdell et al. 2010a, p. 1406).

*Leiopterella tetliei* is placed in the family Rhenopteridae. Together with Stylonuridae, they are among the most poorly understood stylonurid families making any new discoveries important. Rhenopterids were small eurypterids, characterized by appendages II–IV being quite short and only having fixed (i.e., not movable) spines, a rounded posterior margin of the metastoma, and a short telson. Rhenopterids often resolve as the most basal clade among the stylonurids (Lamsdell et al. 2010b), making them significant for reconstructing the ground pattern morphology of Stylonurida in general.

# Materials and methods

The specimens described here were collected in 1973 as part of a joint expedition by the University of Bristol and the University of Ottawa, led by David Dineley and Brian Jones. The fossils originate from the Peel Sound Formation, 29 kilometres SW of Bellot Cliff on the north coast of Prince of Wales Island, Nunavut, in the Canadian Arctic (Fig. 1; Dineley 1994, fig. 1, locality F). The locality has been dated as Early Devonian (Lochkovian) based on agnathans and gnathostomes (Elliott 1984). The environmental setting was probably a non-marine, alluvial fan system (Broad et al. 1968), whereby the marine Douro Formation grades into the Peel Sound Formation (Dineley 1965; Miall et al. 1978). The fossils were found in a calcareous sandstone in a poorly laminated pale brown marl unit. The sequence yields abundant large pteraspids, *Ctenaspis*, arthrodires (Arctolepida), acanthodian spines, possible antiarchs, vascular plants, ostracodes and both stylonurid and pterygotid eurypterids (see also Lamsdell et al. 2010a).

The two specimens now assigned to *Leiopterella tetliei* are deposited in the collections of the Canadian Museum of Nature, Ottawa, Canada under the repository numbers CMN 3573 (holotype) and CMN 3574 (new specimen). They were photographed for this study using a Nikon D40 with 60 mm micro Nikkor lens, with polarized light revealing additional details described for the holotype herein. Morphological terminology follows Tollerton (1989) and higher systematics follows Lamsdell et al. (2010b). All measurements are in mm.

# Systematic Palaeontology

Order Eurypterida Burmeister, 1843

Suborder Stylonurina Diener, 1924

Superfamily Rhenopteroidea Størmer, 1951 (nom. trans. Lamsdell et al. 2010b)

Family Rhenopteridae Størmer, 1951

Remarks. This family is equivalent to Brachyopterellidae Tollerton, 1989 and Alkenopteridae Poschmann and Tetlie, 2004. Lamsdell et al. (2010b) assigned *Alkenopterus* and *Rhenopterus* to the subfamily Rhenopterinae, diagnosed on a non-spiniferous appendage IV and a caudal postabdomen. More recently, *Alkenopterus* was reassigned to the family Onychopterellidae (Poschmann 2014) within the Eurypterina, effectively rendering the subfamily Rhenopterinae redundant.

Genus Leiopterella Lamsdell et al., 2010a

Diagnosis. Rhenopterid eurypterid with turbinate carapace; non-spiniferous prosomal appendages II–V; VI-7 trapezoidal (lacking podomere 7a) with large VI-8; type-B genital appendage short with bilobed termination. Tergites gradually tapering (emended from Lamsdell et al., 2010a).

Leiopterella tetliei Lamsdell et al. 2010a

(Figs. 2–5)

Leiopterella tetliei Lamsdell et al. 2010a, pp. 1408–1410, figs 3a–b.

"Arachnid", Lamsdell et al. 2010a, p. 1406 (misidentification).

Material. CMN 3573 (holotype) and CMN 3574.

Locality. Peel Sound Formation, 29 kilometres SW of Bellot Cliff, north coast of Prince of Wales Island, Nunavut, Canadian Arctic. Early Devonian (Lochkovian).

Description. The holotype (CMN 3573) consists of the prosoma and anterior mesosoma, preserving small chelicera, appendage III, proximal podomeres of appendages IV–VI, the

metastoma, genital operculum and genital appendage and three paired Blattfüsse (opercula) (Figs. 2, 4a). Some redescription is possible compared to the Lamsdell et al. (2010a), based on re-examination under polarized light. The carapace is turbinate, 36.3 long, 34.8 wide at its base (reconstructed as corners lacking), with a lateral angle of 82°. A narrow marginal rim/doublure is 1.9 wide. Possible paired epistomal sutures are faintly preserved; 1.1 separating them, 6.7 long; with a median suture (*Eurypterus*-type doublure) also faintly visible. A possible labrum is displaced to the left of the chelicera, drawn out into paired posterior processes, each 4.8 long and 4.4 wide. Two slightly curved short flat spines, 3.7 long, 1.9 wide at base, are overlying and to left of the left process; these are probably posterior lateral extensions of the labrum. The left chelicera, basis square, 1 long and wide, fixed finger 7.4 long, 1.5 at base, tapers to a point, the free finger, 4.1 long, 1.1 at base, articulating mid-way along the length of the fixed finger, also tapering to a point.

The left coxae all well preserved with thickened margins, showing gnathobasic teeth, displaced to the edge of the prosoma on the right side. II-1 (coxa) length 3.1, widening to 4.1; II-2 to II-7 small and lacking spines, disarticulated anteriorly, but relative positions uncertain. III-1 (coxa) length 10.4, width 1.9 widening to 5.9. III-2 to III-8 tiny and lacking spines, but articulated to left of coxa: III-2 length 2.5, width 2.25; III-3 to 5 length 1.25, width 2; III-6 length 1.5, width 2.25 narrowing to 1.75; III-7 length 1, width 1.75 narrowing to 1; III-8 a small triangular podomere length 1. Appendages II and III would not have extended much beyond the carapace, in life. IV-1 (coxa) length 12.2, proximal width 2.2 widening to 6.3, with attached IV-2, 3.3 long, 4.8 wide. It is possible that IV-3 to IV-6 are poorly preserved to the right of the prosoma, each podomere widening into blunt fixed spines: IV-3 3.7 long, 2.6 wide; IV-4 5.2 long; IV-5 6.7 long; IV-6 is better preserved 5.9 long, 1.9 wide. Distal podomeres missing. V-1 (coxa) length 15.2, width 4.1 widening to 10.7, with attached V-2, 8.1 long, 7 wide. V-3 to V-5 preserved to right of appendage VI, on right side: V-3 is squarish 7.4 long and wide; V-4 elongate, 12.2 long, 3 wide; V-5 is 5.8 long, 2.6 wide. VI-1 (coxa) large, extending over anterior opercular plate, length 23.7 mm, width 7.4 widening to 13. The coxal gnathobases are preserved as dark stains. VI-2 to VI-5 are best preserved on the right side: VI-2 is 5.9 long and 5.6 to 7 wide, with a proximal notch; VI-3 is 6.7 long, narrowing from 7 to 4.4 wide; VI-4 is elongate, 12.6 long, 3.7 wide; VI-5 preserved length 8.9 long, 3 wide.

The metastoma, length unknown, width 8.3, is faintly preserved between coxae VI, its anterior margin clearly visible, with an anterior notch, its sides faintly preserved, but their curvature indicating the metastoma is smaller than that interpreted by Lamsdell et al. (2010a). The posterior margin is barely distinguishable. The genital operculum is 14.3 long (mid-way along its width), each opercular lobe 15.9 wide, preserving large anterior (5.5 long), median (3.3 long) and posterior (5.5 long) plates. Possible deltoid plates, each 3.7 long and wide at their base, are anterior to the (?type B) genital appendage length 9.3, divided into a short proximal diamond-shaped segment, 3.7 long, 2.2 wide, and an elongate (5.2 long) segment, with a bilobed termination (?furca). Superimposed dorsal (more angular laterally, apparently anteriorly curved) tergites and ventral (more rounded laterally) opercula; former projecting slightly beyond latter. The maximum width (31.1) is at the second tergite. Three paired Blattfüsse preserved; first 5.2 long with each lobe 15.6 wide, second 4.4 long, each lobe 14.1 wide. No ornamentation or cuticular sculpture is evident.

CMN 3574 reveals a small corner of the carapace, three disarticulated podomeres of appendage ?IV or V and most of appendage VI, all the tergites, 2–4 with tubercles along their posterior margin, and a proximal portion of the telson (Fig. 3). The carapace width is 21.4, reconstructed by doubling the distance to the mid-line. It expands anteriorly with a lateral angle of 71°. Isolated, disarticulated podomeres, probably of appendage IV or V are scattered to the left of the body: One podomere is 7.1 long, 2.6 wide, the next is 6.4 long, 1.6 wide, and the next is 6.4 long and widens from 1.9 to 3.1. Appendage VI has five podomeres preserved. VI-4 is 10.2 long, 3.1 wide; VI-5 is 8.3 long, widening from 2.4 to 3.3 wide; VI-6 is 7.9 long, 3.1 wide. VI-7 is best preserved on the right side, trapezoidal in shape, the outer edge 9.8 long, the inner 4 long, widening from 2.4 to 3.6, with a thickened distal edge; VI-8 is large, 2.6 long, 3.3 wide. Podomere 9 not visible, presumably very small.

Opisthosomal tergites are widest at tergite 2, gently tapering, 9–12 narrowing considerably: Tergite 1, length 5.7, width 24.8; tergite 2, length 6.2, width 25; tergite 3, length 5.7, width 24; tergite 4, length 5.7, width 23.6. tergite 5, length 5, width 23.6; tergite 6, length 5, width 21.4; tergite 7, length 4.5, width 19.5; tergite 8, length 5.5, width 17.6; tergite 9, length 6.2, width 15.7 narrowing to 12.9; tergite 10, length 4.8, width 12.9 narrowing to 10; tergite 11, length 4, width 9.3 narrowing to 7.1, posterior margin anteriorly curved; tergite 12, length 2.9 mm, width 6 narrowing to 3.6, posterior margin poorly preserved but possibly anteriorly curved. Tubercles are present on posterior margin of tergites 2-4, 0.5 wide. Tergites 5-7 have well developed lateral epimera. A small part of the telson is preserved, length 4.3, width at base 2.6. Based on its rate of taper the telson can be reconstructed as short and styliform, ca. 15.5 long in life.

Remarks. CMN 3574 is interpreted as conspecific with the holotype, as both have an anteriorly expanding prosoma (lateral angles differ slightly, but in both cases are estimates), procurved anterior tergites, and the proportions of podomere VI-4 match closely when ontogenetic changes are taken into consideration. Based on tergite width, the holotype is 1.2 times larger than CMN 3574. The morphology of CMN 3574 is somewhat confused by a faint bilobed trail, plant material and two tiny, probably juvenile, eurypterids preserved overlying the specimen (Fig. 4b). The first juvenile (Fig. 4b) consists of a small carapace, 6.7 mm long, 8.7 mm wide (ratio 0.74), preserved over the posterior left corner of the carapace of CMN 3574. Two very small appendages preserved to the left of the anterior three tergites are probably associated with this juvenile. The second juvenile (Fig. 4c) is represented by an even smaller carapace, 3.9 mm long, 5.5 mm wide (ratio 0.71), with several faint body segments and a thin telson, preserved over tergites 5 and 6 of CMN 3574. This juvenile is only about 17 mm long. These two juveniles have very different carapace proportions (see above) to the holotype (1.27), thus it is questionable whether they belong to the same species and we prefer to leave them unassigned taxonomically.

Plant material associated with CMN 3574 is represented by faint silvery stems scattered around the specimen, and a cluster of five small rugby ball-shaped (ovoid with pointed apices) structures, ranging from 3.5 mm long and 1.1 mm wide to 5.3 mm long and 2.1 mm wide, preserved over the right side of tergite 9, to the left of podomere VI-7. These may represent the

sporangia of *Oocampsa catheta* Andrews et al., 2011, known from the Early-Mid Devonian of New Brunswick.

## Discussion

Restudy of the holotype under polarized light has revealed new features (Fig. 4a) not detected by Lamsdell et al. (2010a), notably a labrum (a rare feature in any eurypterid) and epistomal sutures, a small prosomal appendage III and deltoid plates anterior to the genital appendage. Additionally, the metastoma is interpreted as smaller than Lamsdell et al. (2010a) suggest. The second specimen (CMN 3574) reveals for the first time the morphology of the distal podomeres of appendage VI and the gradually tapering nature of the opisthosomal tergites, with tubercles on at least tergites 2 to 4, enabling a more complete picture of the overall anatomy and a reconstruction of its probable appearance in life (Fig. 5). These fossils are not simply juveniles of the stylonurid genus Pagea, which is known from notably larger fossils from the same locality (Lamsdell et al. 2010a), due to lack of spinosity of the anterior appendages of *L. tetliei*, the unique form of appendage VI and the much smaller pretelson. Instead, the relatively simple, unspecialized and non-spiniferous prosomal appendages II–V suggest that *L. tetliei* is a basal stylonurid belonging to the family Rhenopteridae. The limb podomeres of *L. tetliei* resemble stacked cones, i.e., they widen distally with thickened margins. This is a trait seen in other basal stylonurids such as *Brachyopterella* and was also observed in a large undescribed specimen of a basal eurypterine, Onychopterella augusti from the late

Ordovician Soom Shale of South Africa (SJB, unpublished obs.). Appendage VI of *L. tetliei* has a unique morphology in the trapezoidal shape of podomere 7; see also the Diagnosis above.

*Leiopterella tetliei* and *Brachyopterella* share an anterior widening of the carapace, and (also shared with *Brachyopterus*) a narrow marginal rim of the carapace. The eyes of *L. tetliei* are not preserved, but were probably large and converged anteriorly, as in *Brachyopterella* and *Kiaeropterus*, with the ocelli situated within an ocellar area. *Leiopterella tetliei*, *Brachyopterella*, *Brachyopterus* and *Kiaeropterus* share the condition of the widest point of the mesosoma being at around the second segment. *Brachyopterus* and *Kiaeropterus* share a lack of cuticular sculpture, but *L. tetliei* has tubercles on at least tergites 2 to 4. *L. tetliei* also differs from *Brachyopterus* in lacking ridges on its podomeres, and from *Brachyopterella* in the overall shape of the carapace.

### Relationships within Rhenopteridae

Rhenopteridae occur most commonly in the Devonian of Germany, but *Leiopterella tetliei* from the Devonian of Canada confirms that the group was geographically more widespread at this time. *Leiopterella tetliei* appears to have been part of a Devonian radiation, possibly stemming from the European early rhenopterids. The other putatively basal rhenopterids are known from the Ordovician and Silurian and appear to have become extinct by the Devonian with only the North American genus (*Leiopterella*) and the Rheno-Hercynian terrane genus (*Rhenopterus*) surviving.

Lamsdell et al. (2010a) suggested that *L. tetliei* was sister group to *Rhenopterus*, with the Silurian genera *Brachyopterella* and *Kiaeropterus* forming a clade, and the Ordovician *Brachyopterus* sister group to both, i.e. (*Brachyopterus* ((*Brachyopterella* + *Kiaeropterus*) (*Leiopterella* + *Rhenopterus*))). The gently tapering (i.e., not caudal) postabdomen of *L. tetliei* supports an even more basal position within Rhenopteridae. Generally, we note an apparent progression throughout rhenopterid evolution from broad carapaces narrowest at their base (*Brachyopterus*, *Brachyopterella*, *Leiopterella*) to narrower carapaces narrow at the front (*Rhenopterus*).

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Tollerton, V.P., Jr. 1989. Morphology, taxonomy, and classification of the order Eurypterida Burmeister, 1843. Journal of Paleontology. **63**: 642–657. Fig. 1. Map of Prince of Wales Island showing the outcrop area of Precambrian (dark shading), Lower Palaeozoic (white), and the Peel Sound Formation (light shading), and the fossil locality. Base map after Dineley (1994). Map data after Broad et al. (1968). Locality NAD83 coordinates: 73°46'44.1"N 98°20'19.7"W

Fig. 2. *Leiopterella tetliei* Lamsdell et al., 2010a, Prince of Wales Island, Canada. (*a*) CMN 3573.
Scale bar equals 1 cm. (*b*) Interpretive drawing. Scale bar equals 1 cm. Abbreviations; ch = chelicera, g = gnathobases, l = labrum, m = metastoma, mr = marginal rim/doublure, aop = anterior opercular plate, mop = median opercular plate, pop = posterior opercular plate, ga = genital appendage, B = Blattfüsse.

Fig. 3. *Leiopterella tetliei* Lamsdell et al., 2010a, Prince of Wales Island, Canada. (*a*) CMN 3574.
(*b*) Interpretive drawing. Scale bar equals 1 cm. Abbreviations; c = carapace, j = juvenile eurypterids (1 and 2), o = possible sporangia of *Oocampsa catheta* Andrews et al., 2011, t = telson, tu = tubercles.

Fig. 4. *Leiopterella tetliei* Lamsdell et al., 2010a, Prince of Wales Island, Canada. (*a*) CMN 3573. Magnification of anterior prosoma showing marginal rim/doublure, epistomal sutures, chelicera (top right), displaced labrum with disarticulated posterior lateral extensions, disarticulated appendage II and articulated appendage III (bottom left). Scale bar equals 1 cm. (*b*) CMN 3574. Magnification of juvenile 1, carapace and two small appendages. Scale bar equals 1 cm. (*c*) CMN 3574. Magnification of juvenile 2, carapace, several body segments and telson. Scale bar equals 1 cm.

Fig. 5. Reconstruction of the probable appearance of *Leiopterella tetliei* Lamsdell et al., 2010 in life. (*a*) Dorsal view. (*b*) Ventral view.



Fig. 1. Map of Prince of Wales Island showing the outcrop area of Precambrian (dark shading), Lower Palaeozoic (white), and the Peel Sound Formation (light shading), and the fossil locality. Base map after Dineley (1994). Map data after Broad et al. (1968). Locality NAD83 coordinates: 73°46'44.1"N 98°20'19.7"W

84x138mm (300 x 300 DPI)



Fig. 2. Leiopterella tetliei Lamsdell et al., 2010a, Prince of Wales Island, Canada. (a) CMN 3573. Scale bar equals 1 cm. (b) Interpretive drawing. Scale bar equals 1 cm. Abbreviations; ch = chelicera, g = gnathobases, I = labrum, m = metastoma, mr = marginal rim/doublure, aop = anterior opercular plate, mop = median opercular plate, pop = posterior opercular plate, ga = genital appendage, B = Blattfüsse.

181x121mm (300 x 300 DPI)



Fig. 3. Leiopterella tetliei Lamsdell et al., 2010a, Prince of Wales Island, Canada. (a) CMN 3574. (b) Interpretive drawing. Scale bar equals 1 cm. Abbreviations; c = carapace, j = juvenile eurypterids (1 and 2), o = possible sporangia of Oocampsa catheta Andrews et al., 2011, t = telson, tu = tubercles.



Fig. 4. Leiopterella tetliei Lamsdell et al., 2010a, Prince of Wales Island, Canada. (a) CMN 3573. Magnification of anterior prosoma showing marginal rim/doublure, epistomal sutures, chelicera (top right), displaced labrum with disarticulated posterior lateral extensions, disarticulated appendage II and articulated appendage III (bottom left). Scale bar equals 1 cm. (b) CMN 3574. Magnification of juvenile 1, carapace and two small appendages. Scale bar equals 1 cm. (c) CMN 3574. Magnification of juvenile 2, carapace, several body segments and telson. Scale bar equals 1 cm.

144x199mm (300 x 300 DPI)



Fig. 5. Reconstruction of the probable appearance of Leiopterella tetliei Lamsdell et al., 2010 in life. (a) Dorsal view. (b) Ventral view.

182x131mm (300 x 300 DPI)