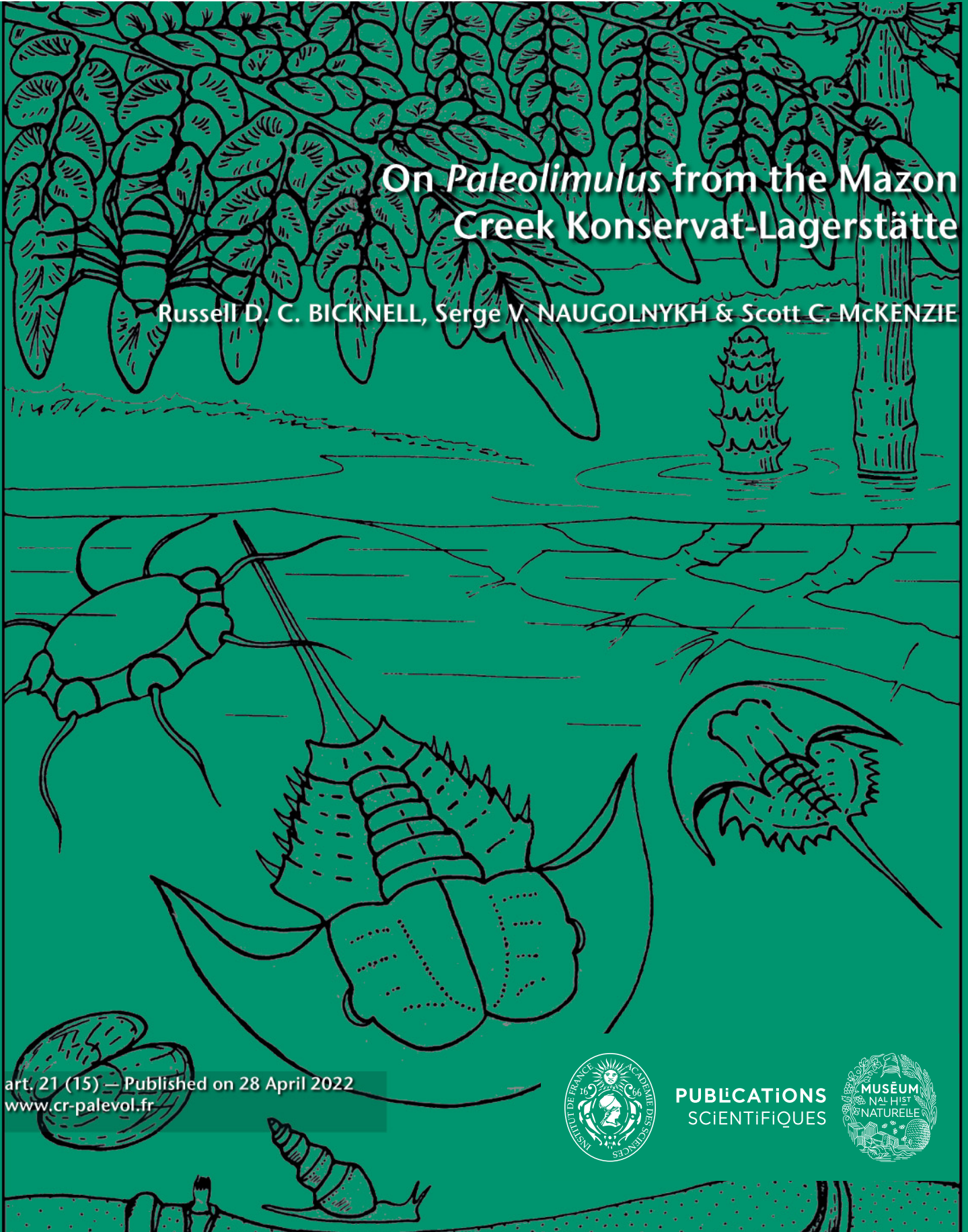


On *Paleolimulus* from the Mazon Creek Konservat-Lagerstätte

Russell D. C. BICKNELL, Serge V. NAUGOLNYKH & Scott C. MCKENZIE



art. 21 (15) — Published on 28 April 2022
www.cr-palevol.fr



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ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

On *Paleolimulus* from the Mazon Creek Konservat-Lagerstätte

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Submitted on 27 October 2020 | Accepted on 11 January 2021 | Published on 28 April 2022

urn:lsid:zoobank.org:pub:0AE53C84-0402-4B86-9E63-FCD44BA8BB94

Bicknell R. D. C., Naugolnykh S. V. & McKenzie S. C. 2022. — On *Paleolimulus* from the Mazon Creek Konservat-Lagerstätte. *Comptes Rendus Palevol* 21 (15): 303–322. <https://doi.org/10.5852/cr-palevol2022v21a15>

ABSTRACT

Horseshoe crabs are extant chelicerates with a fossil record extending back to the Ordovician. Despite the documentation of their long evolutionary history, xiphosurids are rarely preserved within fossil assemblages due to their unmineralized cuticular exoskeleton. However, in exceptional circumstances, an abundance of fossil xiphosurid specimens have been documented. The Moscovian-aged Mazon Creek Konservat-Lagerstätte represents one such fossil deposit with a high abundance and diversity of xiphosurids. Although fairly well known, the *Paleolimulus* specimens from the Mazon Creek have not yet been subject to a thorough taxonomic examination. In the light of recent efforts to organise *Paleolimulus*, we revisit this undescribed material, erect *Paleolimulus mazonensis* n. sp., and present a phylogenetic analysis that places *P. mazonensis* n. sp. as a sister taxon to *P. signata* (Beecher, 1904). The palaeoecology and possible ontogeny of *P. mazonensis* n. sp. are presented, as well as a statement on the future directions for understanding this xiphosurid genus.

KEY WORDS
Xiphosurida,
horseshoe crabs,
exceptional preservation,
Paleozoic,
Carboniferous,
Paleolimulidae,
new species.

RÉSUMÉ

Sur Paleolimulus de la Konservat-Lagerstätte de Mazon Creek.

Les xiphosuridés, aussi appelés limules, incluent des chélicérates actuels dont le registre fossile remonte à l'Ordovicien. Malgré les traces de leur longue histoire évolutive, les xiphosuridés sont rarement préservés dans les assemblages fossiles en raison de leur exosquelette cuticulaire non minéralisé. Cependant, dans des circonstances exceptionnelles, une abondance de spécimens de xiphosuridés fossiles a été documentée. Le Konservat-Lagerstätte de Mazon Creek, d'âge Moscovien, représente

MOTS CLÉS

Xiphosurida,
les limules,
préservation
exceptionnelle,
Paléozoïque,
Carbonifère,
Paleolimulidae,
espèce nouvelle.

un tel dépôt de fossiles qui présente une grande abondance et diversité de xiphosuridés. Bien que relativement bien connus, les spécimens de *Paleolimulus* de Mazon Creek n'ont pas encore fait l'objet d'un examen taxonomique approfondi. A la lumière des efforts récents pour organiser *Paleolimulus*, nous revisitons ce matériel non décrit, érigeons *Paleolimulus mazonensis* n. sp., et présentons une analyse phylogénétique qui place *P. mazonensis* n. sp. comme un taxon frère de *P. signata* (Beecher, 1904). La paléoécologie et l'ontogenèse possible de *P. mazonensis* n. sp. sont présentées, ainsi que des perspectives de recherches futures pour mieux comprendre ce genre xiphosuride fossile emblématique.

INTRODUCTION

Gould, in paraphrasing Darwin, summarised the fossil record as “a book preserving just a few pages, of these pages few lines, of the lines few words, and of those words few letters” (Gould 1989: 60). This statement reflects most fossil deposits. However, under rare circumstances, an unexpected wealth of palaeontological information is preserved. Such deposits are called exceptional preservation deposits – Konservat-Lagerstätten – and are well documented within Paleozoic-aged rocks (Martin *et al.* 2016). One Konservat-Lagerstätte that has been thoroughly studied is the late Carboniferous (Pennsylvanian, Moscovian) Mazon Creek Konservat-Lagerstätte, within the Francis Creek Shale Member of the Carbondale Formation, Illinois, United States (Briggs & Gall 1990; Feldman *et al.* 1993; Shabica & Hay 1997; Clements *et al.* 2019). At least 465 documented species, across at least 103 orders, are known from the deposit (Clements *et al.* 2019). One particularly abundant order is Xiphosurida, the so-called horseshoe crabs, with at least three taxa: *Euproops danae* (Meek & Worthen, 1865), *Liomesaspis laevis* (Raymond, 1944), and *Paleolimulus* sp. (Raymond 1944; Fisher 1977, 1979; Babcock & Merriam 2000; Racheboeuf *et al.* 2002; Haug & Rötzer 2018 [Fig. 1]). Of these three, the *Paleolimulus* material has received the least examination (Fisher 1979; Babcock & Merriam 2000; McKenzie 2012). Here we present the largest collation of Mazon Creek *Paleolimulus* specimens to-date and rectify this dearth of information. This examination aligns with recent research motivated to uncover the true *Paleolimulus* diversity (Tashman 2014; Lerner *et al.* 2016; Naugolnykh 2017; Bicknell 2019; Bicknell & Pates 2020; Bicknell *et al.* 2020; Lamsdell 2020) and highlights taxonomic differences between the Mazon Creek species and other morphologically comparable paleolimulids (*sensu* Bicknell & Pates 2020). We also illustrate the phylogenetic placement of this material within Paleolimulidae and a possible record of ontogeny. Together, this evidence prompted the erection of *Paleolimulus mazonensis* n. sp. – the oldest species within *Paleolimulus*.

INSTITUTIONAL ABBREVIATIONS

CM	Carnegie Museum of Natural History, Pittsburgh, PA;
FMNH	Field Museum of Natural History, Chicago, IL;
GIN	Geological Institute of the Russian Academy of Sciences, Moscow;
INHS	Illinois Natural History Survey in Champaign, IL;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA;

NSM
USNM
YPM IP

Nova Scotia Museum, Halifax, NS;
United States National Museum, Washington, DC;
Division of Invertebrate Paleontology in the Yale Peabody Museum, New Haven, CT.

METHODS

Specimens of the Mazon Creek *Paleolimulus* and other morphologically comparable paleolimulids (*sensu* Bicknell & Pates 2020) were photographed by either the authors or requested from collection staff and other researchers. Photographs of the Mazon Creek *Paleolimulus* were taken with SLR cameras under different lighting directions to highlight features. Select specimens were photographed after coating with ammonium chloride sublimate. We follow the systematic taxonomy of Lerner *et al.* (2016), Naugolnykh (2017), and Bicknell *et al.* (2020) and anatomical terminology of Bicknell *et al.* (2018, 2019, 2020), Bicknell & Pates (2019, 2020), and Bicknell (2019).

To explore the phylogenetic position of *Paleolimulus mazonensis* n. sp., the species was coded into the Bicknell (2019) matrix; modified from Lamsdell (2016). This matrix represents a broad sampling of euchelicerates, especially horseshoe crabs (Appendix 1). Analysis was performed under equally weighted parsimony in TNT 1.5 (Goloboff & Catalano 2016) using the 100 replicates of the “New Technology” tree search strategy using random and constrained sectorial searches, 100 iterations of the parsimony ratchet, 50 cycles of drifting, and five rounds of tree fusing. All multistate characters were considered unordered following the original analysis. *Fuxianhuia protensa* Hou, 1987 was the designated outgroup taxon, following Lamsdell (2013). Additionally, character codings for *P. signata* (Beecher, 1904) were reviewed and adjusted based on our re-examination of material used for taxonomic comparisons.

Length and width measurements of the prosoma and thorax sections of examined specimens were collated to explore any ontogenetic patterns within the sampled material (Appendix 2). These data were imported into R (R Core Team 2020), log-normalised, and plotted. The points were colour coded for the two main exoskeletal sections.

STRATIGRAPHIC DETAILS

The Mazon Creek area in north-eastern Illinois is underlain by the extensively mined Colchester Number 2 coal. This coal is overlain by the Francis Creek Shale Member of the Carbondale Formation. Herein, sideritic nodules are preserved in the



FIG. 1. — Examples of *Euproops danae* (Meek & Worthen, 1865) and *Liomesaspis laevis* (Raymond, 1944) from the Mazon Creek Konservat-Lagerstätte. **A–F**, *Euproops danae* specimens: **A**, NHS X341, holotype; **B**, YPM IP 25153; **C**, YPM IP 28514; **D**, YPM IP 50514; **E**, YPM IP 50644; **F**, YPM IP 50687. **G–I**, *Liomesaspis laevis* specimens: **G**, YMPIP 16913, paratype; **H**, YPM IP 168041; **I**, YPM IP 168053. Image credits: A, Jessica Tashman; B–I, Russell Bicknell. Scale bars: A–F, 10 mm; G–I, 3 mm.

lower portions. The Francis Creek Shale is broadly divided into two faunas: the Essex and Braidwood faunas. The marine to brackish Essex Fauna is typified by extensive sideritic nodules found at the Pit 11 site (now Illinois Department of Natural Resources Mazonia South Unit) in Essex and Kankakee Counties. The Essex Fauna has a diverse fauna and animals outnumber plant fossils. Conversely, the Braidwood Fauna represents fresh to brackish water conditions and is typified by a plant-dominated biota with occasional animals including

insects, bivalves, millipedes, arachnids, and crustaceans. The Braidwood Fauna is commonly separated from the adjacent Essex Fauna, with few examples of grading between the two. *Paleolimulus mazonensis* n. sp. and *Euproops danae* are known from the marine Essex Fauna. *Euproops danae* is uncommon and mostly represented by isolated or multiple disarticulated prosomal and thoracetrone sections, indicating an allochthonous presence. *Paleolimulus mazonensis* n. sp. specimens are also uncommon but are usually found as complete, presumptively

autochthonous individuals. Conversely, *E. danae* and *Liomesaspis laevis* are known from the Braidwood Fauna, where *E. danae* is common compared to *L. laevis*. Both genera are usually found mostly complete, although the telsons are frequently missing, or buried in the nodule. As *Paleolimulus* is seldom observed in Braidwood-type faunas, it was likely a marine taxon.

SYSTEMATIC PALAEOONTOLOGY

Subphylum CHELICERATA Heymons, 1901
Class XIPHOSURA Latreille, 1802
Order XIPHOSURIDA Latreille, 1802
Superfamily PALEOLIMULOIDEA Raymond, 1944
Family PALEOLIMULIDAE Raymond, 1944
Genus *Paleolimulus* Dunbar, 1923

Paleolimulus mazonensis n. sp.
(Figs 2-10)

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Paleolimulid – Fisher 1979: 396.

Paleolimulus sp. – Robison 1987: fig. 13.46, A. — Eldredge 1991: 90. — Mikulic 1997: 138, figs 10.6, 10.7. — Anderson & Shuster 2003: 217. — Lerner & Lucas 2015: 150.

Paleolimulus signatus – Babcock & Merriam 2000: 76. — Lerner *et al.* 2016: 200.

Paleolimulus avitus – Shuster & Anderson 2003: 175.

“*Paleolimulus*” – McKenzie 2012: fig. 2.

HOLOTYPE. — FMNH PE 81596.

PARATYPES. — FMNH PE 38980, FMNH PE 56851, FMNH PE 84071, FMNH PE 84078, FMNH PE 84081, FMNH PE 84087, CM 53793, CM 53794, CM 53795, CM 53796, CM 53797, CM 53798, CM 53799.

ETYMOLOGY. — The species name is attributed to the Mazon Creek Konservat-Lagerstätte.

REFERRED MATERIAL. — Private Specimen 1, S. McKenzie teaching collection, Erie, Pennsylvania.

TYPE LOCALITY, FORMATION, AGE. — Mazon Creek Konservat-Lagerstätte, Francis Creek Shale Member, Carbondale Formation, Illinois, United States, Pennsylvanian (Moscovian).

DISTRIBUTION. — Essex Fauna of the Mazon Creek Konservat-Lagerstätte.

DIAGNOSIS. — *Paleolimulus* with pronounced cardiac lobe ridge, occipital bands that extend from posterior margins of ophthalmic ridges to genal spine terminus, a thoracetrone without articulations, and six nodes along a pronounced medial thoracetrone ridge.

PRESERVATION. — Specimens are preserved within siderite nodules as partly domed exoskeletons as part and counterpart. Due to the mode of preservation, anatomical features are variably preserved. In particular, the prominence of medial lobes varies between specimens, the prosomal doublure is rarely observed, and only proximal sections of appendages are noted. Colour of specimens ranges between red and dark brown.

DESCRIPTION

FMNH PE 81596

An articulated prosoma (synonym of cephalothorax), thoracetrone (synonym of opisthosoma), and complete telson (Fig. 2). Specimen 51.6 mm long. Prosoma parabolic in outline, 15.3 mm long at midline, 26.7 mm wide at widest section. Prosomal rim 0.8 mm wide. Ophthalmic ridges 9.3 mm long. Ridges converge anteriorly into an M-shape. Lateral compound eyes *c.* 3.5 mm along ophthalmic ridges. Cardiac lobe 3.9 mm wide posteriorly, tapering anteriorly into a triangle, terminating at ophthalmic ridge joint. Lobe 11.5 mm long with prominent medial ridge. Both genal spines terminate within first third of thoracetrone. Left genal tip 12.1 mm from midline. Angle between left genal spine and left thoracetrone side 58.2°. Right genal spine broken distally. Distal section 12.0 mm from midline. Angle between right genal spine and right thoracetrone side 75.5°. Occipital bands inflated, extend from ophthalmic ridges to genal spine termini. Prosomal-thoracetrone hinge 12.0 mm wide, and 1.2 mm long.

Thoracetrone trapezoidal, 12.3 mm long, 13.2 mm wide anteriorly, tapering to 4.0 mm posteriorly. Reduced free lobe. Node on left side of free lobe. Medial thoracetrone lobe 11.6 mm long with defined medial thoracetrone ridge. Left pleural lobe 12.0 mm long, 6.6 mm wide, tapering posteriorly to terminal spine, with 0.4 mm wide rim. Three moveable spine notches observed on counterpart. Right lobe 12.0 mm long, 7.2 mm wide, tapering posteriorly to terminal spine. Telson 24.0 mm long with weak keel.

FMNH PE 38980

An articulated prosoma, thoracetrone, and complete telson (Fig. 3A, B). Specimen 42.3 mm long. Prosoma parabolic in outline, 13.9 mm long at midline, and 25.4 mm wide at widest section. Prosomal rim 0.7 mm wide. Both ophthalmic ridges straight, 10.2 mm long, converging anteriorly into an M-shape. Lateral compound eyes *c.* 4.2 mm along ophthalmic ridges. Cardiac lobe 9.4 mm long, has prominent medial ridge. Lobe tapers anteriorly into a triangular joint, terminating at ophthalmic ridge joint. Both genal spines terminate within first third of thoracetrone. Left genal tip 12.4 mm from midline. Angle between left genal spine and left thoracetrone side 61.2°. Right genal spine 13.0 mm from midline. Angle between right genal spine and right thoracetrone side 72.8°. Occipital bands inflated, extend from ophthalmic ridges to genal spine termini. Prosomal-thoracetrone hinge 14.8 mm wide, 0.5 mm long.

Thoracetrone trapezoidal, 12.7 mm long, 15.1 mm wide anteriorly, tapering to 3.7 mm posteriorly. Medial thoracetrone lobe 11.8 mm long. Left pleural lobe 12.0 mm long, 5.2 mm wide, tapering posteriorly. Right pleural lobe 11.1 mm long, 5.2 mm wide, tapering posteriorly. Telson 15.7 mm long with weak keel.

FMNH PE 56851

An articulated prosoma, thoracetrone, and partial telson (Fig. 3C-D). Specimen 27.9 mm long. Prosoma parabolic in outline, 10.9 mm long at midline, and 25.8 mm wide

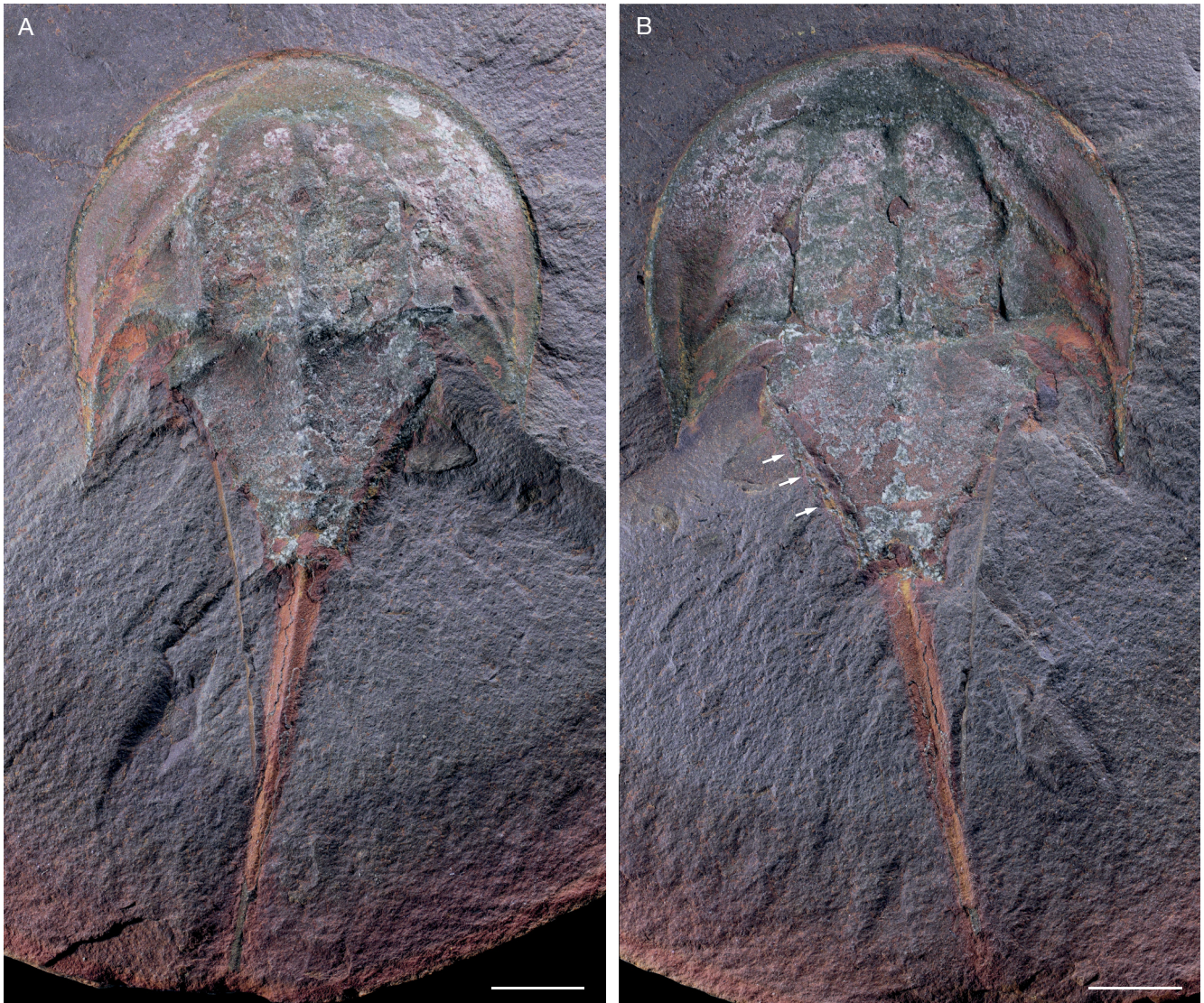


FIG. 2. — Holotype of *Paleolimulus mazonensis* n. sp.: **A**, FMNH PE 81596a, part; **B**, FMNH PE 81596b, counterpart, showing moveable spine notches (white arrows). Scale bars: 5 mm.

at widest section. Prosomal rim 0.3 mm wide. Both genal spines terminate within first third of thoracetrone. Left genal spine broken distally. Most distal section 11.6 mm from midline. Angle between left genal spine and left thoracetrone side 63.5°. Right genal spine broken distally. Most distal section 12.9 mm from midline. Angle between right genal spine and right thoracetrone side 73.2°. Occipital band of left genal spine extends from thoracetrone margin to genal spine terminus.

Thoracetrone trapezoidal, 11.7 mm long, 11.8 mm wide anteriorly, tapering to 3.1 mm posteriorly. Medial thoracetrone lobe rectangular, 10.8 mm long. Potential cololite along medial section. Left pleural lobe 12.1 mm long, 5.0 mm wide, tapering posteriorly to terminal spine. Right pleural lobe 12.4 mm long, 3.9 mm wide, tapering posteriorly to terminal spine. Four longitudinal thoracetrone ridges on right lobe that are between 2.4 and 3.3 mm wide. Telson section 5.3 mm long with weak keel.

FMNH PE 84071

An articulated prosoma, thoracetrone, and partial telson (Fig. 4A, B). Specimen 38.9 mm long. Prosoma parabolic in outline, 15.9 mm long at midline, and 28.3 mm wide at widest section. Prosomal rim 0.5 mm wide. Prosomal doublure prominent in counterpart (Fig. 4B). Both ophthalmic ridges have slight lateral curvature, *c.* 11 mm long and converge anteriorly into an M-shape. Lateral compound eye 5.5 mm along left ophthalmic ridge. Cardiac lobe 5.6 mm wide posteriorly, tapering anteriorly into a triangle, terminating at ophthalmic ridge joint. Lobe 11.9 mm long, has prominent medial ridge. Both genal spines broken distally. Most distal section of left genal spine 12.5 mm from midline. Most distal section of right genal spine 13.8 mm from midline. Angle between right genal spine and right thoracetrone side 74.5°. Occipital band on right genal spine extends from posterior margin of ophthalmic ridge to genal spine terminus. Prosomal-thoracetrone hinge 13.4 mm wide, 1.0 mm long.

TABLE 1. — Exceptional preservation deposits containing at least two xiphosurid genera. Known taxa from these deposits are present. Data derived from Bicknell & Pates (2020).

Deposit	Locality	Age	Species	Groups present
Bear Gulch Limestone	Montana, United States	Mississippian (Serpukhovian)	<i>Anderella parva</i> Moore, McKenzie & Lieberman, 2007 <i>Boeotiaspis longispinus</i> (Schram, 1979) <i>Euproops</i> sp.	Synziphosurine Belinuridae Austrolimulidae
Mazon Creek Konservat-Lagerstätte, Carbondale Formation	Illinois, United States	Pennsylvanian (Moscovian)	<i>Euproops danae</i> <i>Liomesaspis laevis</i> <i>Paleolimulus mazonensis</i>	Belinuridae Paleolimulidae
Almaznaya Formation	Ukraine	Pennsylvanian (Bashkirian)	<i>Belinurus iswariensis</i> (Tschernyshev, 1928) <i>Belinurus stepanowi</i> Tschernyshev, 1928 <i>Euproops danae</i>	Belinuridae
South Wales Lower Coal Measures Formation	Wales, United Kingdom	Pennsylvanian (Bashkirian)	<i>Belinurus arcuatus</i> Baily, 1863 <i>Belinurus bellulus</i> Pictet, 1846 <i>Belinurus carwayensis</i> Dix & Pringle, 1929 <i>Belinurus concinnus</i> Dix & Pringle, 1929 <i>Belinurus koenigianus</i> Woodward, 1872 <i>Belinurus morgani</i> Dix & Pringle, 1930 <i>Belinurus pustulosus</i> Dix & Pringle, 1929 <i>Belinurus reginae</i> Baily, 1863 <i>Belinurus truemani</i> Dix & Pringle, 1929 <i>Euproops cambrensis</i> Dix & Pringle, 1929	Belinuridae
British Middle Coal Measures	England, United Kingdom	Pennsylvanian (Moscovian)	<i>Belinurus arcuatus</i> <i>Belinurus bellulus</i> <i>Belinurus koenigianus</i> <i>Belinurus lunatus</i> (Martin, 1809) <i>Euproops rotundatus</i> Prestwich, 1840	Belinuridae
Wellington Formation	Oklahoma, United States	Cisuralian (Wolfcampian)	<i>Anacontium carpenteri</i> Raymond, 1944 <i>Anacontium brevis</i> Raymond, 1944 <i>Paleolimulus signata</i> <i>Liomesaspis leonardensis</i> (Tasch, 1961)	Belinuridae Paleolimulidae
Alcover Limestone Formation	Spain	Middle Triassic (Ladinian)	<i>Heterolimulus gadeai</i> Vía & De Villalta, 1966 <i>Mesolimulus crespelli</i> Vía Boada, 1987 <i>Tarracolimulus rieki</i> Romero & Vía Boada, 1977	Limulidae

Impressions of proximal sections of prosomal appendage sections about midline.

Thoracetrone trapezoidal, 12.7 mm long, 11.8 mm wide anteriorly, tapering to 3.9 mm posteriorly. Medial thoracetrone lobe rectangular, 12.5 mm long, with five medial thoracetrone nodes. Both pleural lobes broken, tapering to terminal thoracetrone spines. Telson section 10.3 mm long with weak keel.

FMNH PE 84081

An articulated prosoma, thoracetrone, and complete telson (Fig. 4C, D). Specimen 44.0 mm long. Prosoma parabolic in outline, 15.4 mm long at midline, and 27.8 mm wide at widest section. Prosomal rim 0.4 mm wide. Left ophthalmic ridge slightly curved, *c.* 10.8 mm long. Right ophthalmic ridge straight, 8.2 mm long. Lateral compound eyes *c.* 4.8 mm along ophthalmic ridges. Cardiac lobe 11.5 mm long, with prominent medial ridge. Both genal spines broken distally. Distal section of left genal spine 13.5 mm from midline. Angle between left genal spine and left thoracetrone side 73.3°. Distal section of right genal spine 13.9 mm from midline. Angle between right genal spine and right thoracetrone side 77.7°.

Thoracetrone trapezoidal, 12.6 mm long, 14.8 mm wide anteriorly, tapering to 3.7 mm posteriorly. Medial thoracetrone lobe rectangular, 12.3 mm long, 3.6 mm wide, with three nodes along medial ridge. Left pleural lobe 12.0 mm long, 4.5 mm wide, tapering posteriorly. Right pleural lobe 12.0 mm long, 5.0 mm wide, tapering posteriorly. Telson 16.0 mm long with weak keel.

FMNH PE 84078

An articulated prosoma, thoracetrone, and partial telson (Fig. 5). Specimen 34.6 mm long. Prosoma parabolic in outline, 15.3 mm long at midline, 29.7 mm wide at widest section. Prosomal rim 0.4 mm wide. Ophthalmic ridges fragmentary. Ridges converge anteriorly into an M-shape. Lateral compound eyes observed in counterpart (Fig. 5B). Cardiac lobe 13.7 mm long, with prominent medial ridge. Left genal spine broken distally. Most distal point 13.8 mm from midline. Angle between left genal spine and left thoracetrone side 74.3°. Right genal spine point 14.7 mm from midline and terminates within first third of thoracetrone. Occipital bands extend from ophthalmic ridges to genal spine termini. Prosomal-thoracetrone hinge not pronounced, 13.7 mm wide, and 0.8 mm long.

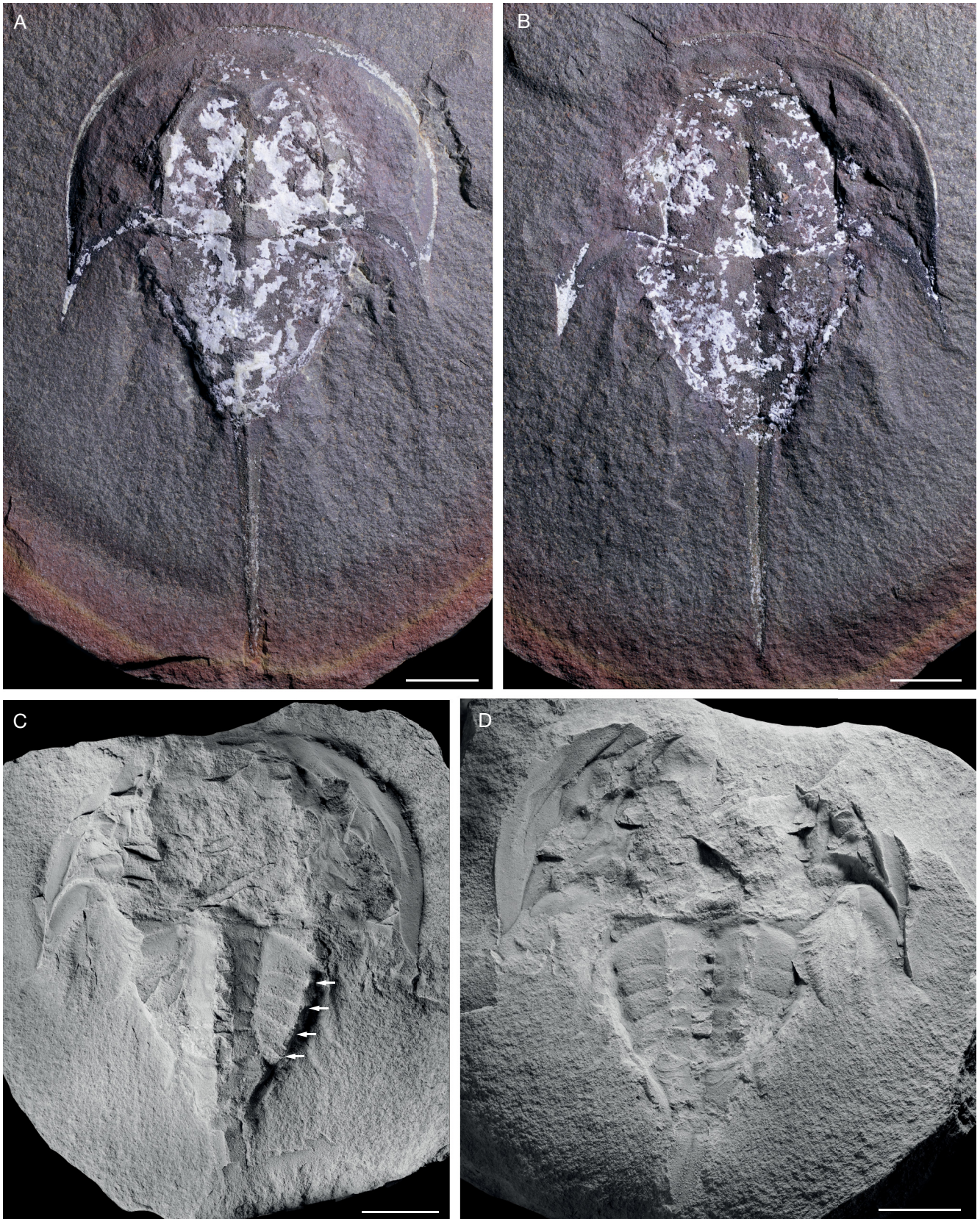


FIG. 3. — Exceptionally preserved *Paleolimulus mazonensis* n. sp.: **A**, FMNH PE 38980a, part; **B**, FMNH PE 38980b, counterpart; **C**, FMNH PE 56851a, part, showing longitudinal thoracetrionic ridges (**white arrows**); **D**, FMNH PE 56851b, counterpart; **C**, **D**, coated in ammonium chloride sublimate and images converted to greyscale. Image credits: Russell Bicknell. Scale bars: 5 mm.



FIG. 4. — Exceptionally preserved *Paleolimulus mazonensis* n. sp.: **A**, FMNH PE 84071a, part; **B**, FMNH PE 84071b, counterpart; **C**, FMNH PE 84081a, part, showing longitudinal thoracetrionic ridges; **D**, FMNH PE 84081b, counterpart. Specimens coated in ammonium chloride sublimate and images converted to greyscale. Image credits: Russell Bicknell. Scale bars: 5 mm.

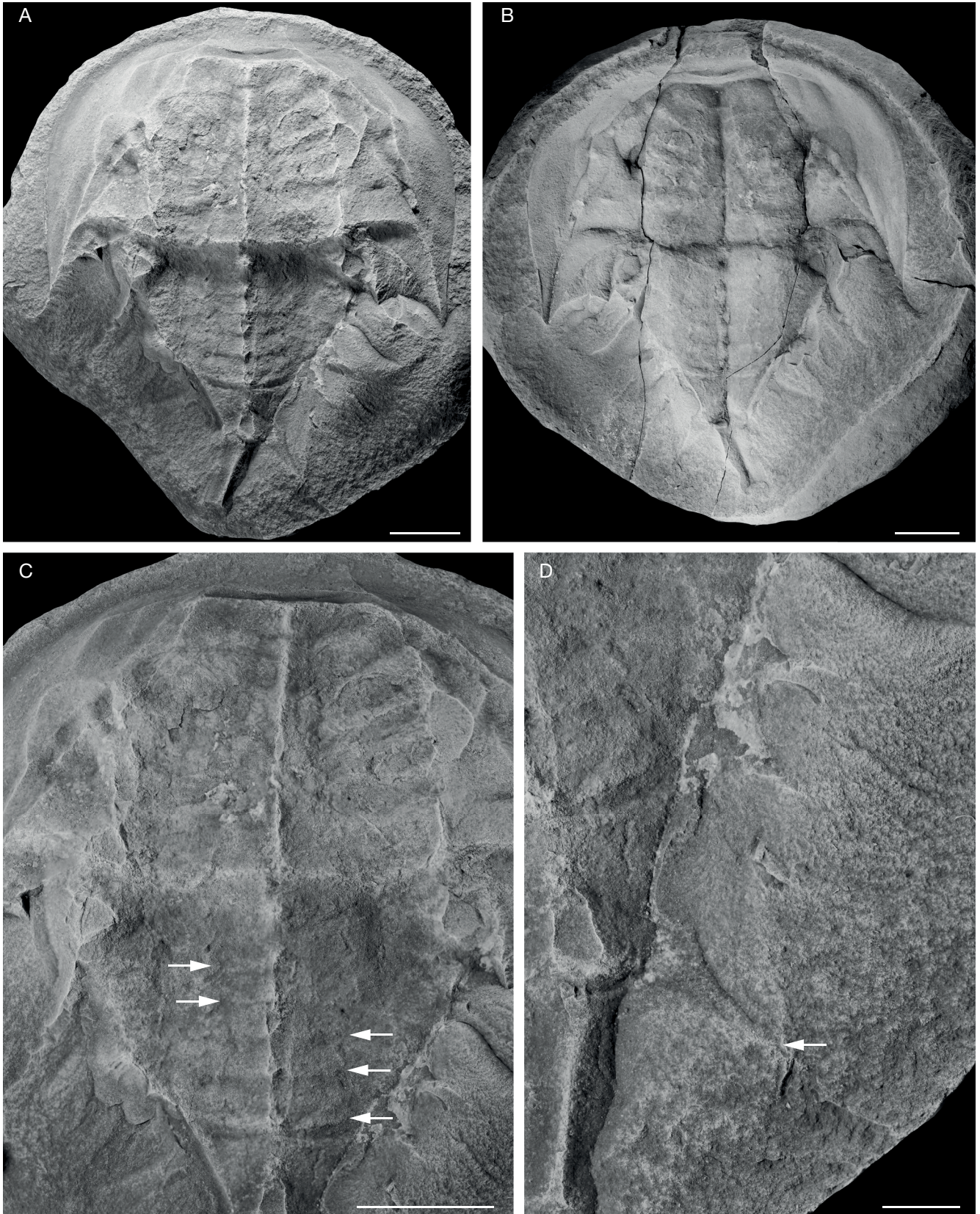


FIG. 5. — *Paleolimulus mazonensis* n. sp. showing possible posterolaterally deflected terminal spine: **A–D**, FMNH PE 84078. **A**, **C**, **D**, FMNH PE 84078a, part: **A**, complete specimen; **C**, close up of prosoma and thoracetrone showing longitudinal thoracetrone ridges (**white arrows**); **D**, close up of right pleural lobe showing possible posterolaterally deflected terminal spine (**white arrow**). **B**, FMNH PE 84078b, counterpart. All specimens coated in ammonium chloride sublimate and images converted to greyscale. Image credits: Russell Bicknell. Scale bars: A–C, 5 mm; D, 2 mm.



FIG. 6. — *Paleolimulus mazonensis* n. sp. preserved laterally within nodule: **A**, FMNH PE 84078a, part; **B**, FMNH PE 84078b, counterpart. Specimens coated in ammonium chloride sublimate and images converted to greyscale. Image credits: Russell Bicknell. Scale bars: 5 mm.

Thoracetrone trapezoidal, 13.9 mm long, 15.0 mm wide anteriorly, tapering to 3.4 mm posteriorly. Medial thoracetrone lobe 12.9 mm long, with five longitudinal thoracetrone ridges (Fig. 5C) and one medial node. Medial ridge broken revealing cololite. Left pleural lobe 12.1 mm long, 5.3 mm wide anteriorly, tapering posteriorly. Right pleural lobe 12.7 mm long, 6.5 mm wide anteriorly, tapering to posterolaterally deflected terminal spine (Fig. 5D). Telson 5.4 mm long with prominent keel, terminates at rock edge.

FMNH PE 84087

An articulated prosoma, thoracetrone, and partial telson (Fig. 6). Specimen 21.0 mm long. Centre and right side of prosoma present, 10.8 mm long at midline, and 20.1 mm wide at widest section. Prosomal rim 0.5 mm wide. Right ophthalmic ridge 8.9 mm long. Lateral compound eye 4.9 mm along ophthalmic ridge. Cardiac lobe 4.8 mm wide posteriorly, 9.8 mm long, tapering into a triangle anteriorly, with prominent medial ridge. Distal section of right genal spine 12.9 mm from midline. Angle between right genal spine and right thoracetrone side 71.2°. Right occipital band inflated, extends from ophthalmic ridge to genal spine terminus.

Thoracetrone trapezoidal, 10.2 mm long, 11.2 mm wide anteriorly, tapering to 3.8 mm posteriorly. Medial thoracetrone lobe 9.8 mm long. Right pleural lobe 10.7 mm long, 4.1 mm wide, tapering to posterior terminal spine. Telson fragmentary.

CM 53793

An articulated prosoma, thoracetrone, and partial telson (Fig. 7A). Specimen 45.1 mm long. Prosoma parabolic in outline, 20.7 mm long at midline, and 36.5 mm wide at widest section. Prosomal rim 0.8 mm wide. Both genal spines terminate within first quarter of thoracetrone. Left genal tip 16.4 mm from midline. Angle between left genal spine and left thoracetrone side 56.2°. Right genal spine 18.1 mm from midline. Angle between right genal spine and right thoracetrone side 55.7°. Occipital bands inflated, extend from ophthalmic ridges to genal spine termini. Prosomal-thoracetrone hinge 15.3 mm wide, 1.5 mm long.

Thoracetrone trapezoidal, 17.1 mm long, 19.8 mm wide anteriorly, tapering to 7.4 mm posteriorly. Reduced free lobe with nodes on both sides of free lobe. Medial thoracetrone lobe 13.9 mm long with medial thoracetrone ridge, five nodes along ridge, and pronounced node on ridge terminus. Left pleural lobe 17.8 mm long, 7.3 mm wide, tapering posteriorly



FIG. 7. — Further exceptionally preserved *Paleolimulus mazonensis* n. sp. specimens: **A**, CM 53793a, part, showing small movable spines (**white arrows**) and medial thoracetrionic nodes; **B**, CM 53794a, part, showing medial thoracetrionic nodes, part; **C**, **D**, Private Specimen 1, largest known *P. mazonensis* n. sp. specimen showing pronounced M-shape ophthalmic ridge joint: **C**, part; **D**, counterpart. Image credits: Scott McKenzie. Scale bars: 10 mm.

to terminal spine. Right pleural lobe has 1.2 mm wide rim, is 18.1 mm long, 7.7 mm wide, tapering posteriorly to terminal spine. Four small moveable spines along right pleural lobe. Telson 7.3 mm long, has weak keel, terminates at rock edge.

CM 53794

Articulated prosoma, thoracetrion, and partial telson (Fig. 7B). Specimen 38.3 mm long. Prosoma parabolic in outline, 13.7 mm long at midline, and 32.1 mm wide at widest part.



FIG. 8. — *Paleolimulus mazonensis* n. sp. specimens showing prosomal and thoracetrone sections: **A**, CM 53795a, part; **B**, CM 53796a, part. Image credits: Scott McKenzie. Scale bars: A, 10 mm; B, 5 mm.

Prosomal rim 0.9 mm wide. Both ophthalmic ridges straight, 8.2 mm long, converging anteriorly into an M shape. Cardiac lobe 5.9 mm wide posteriorly, tapering anteriorly into a triangle, terminates at ophthalmic ridge joint, is 10.5 mm long, with pronounced cardiac ridge. Both genal spines terminate within first quarter of thoracetrone. Left genal tip 15.4 mm from midline. Angle between left genal spine and left thoracetrone side 79.8°. Right genal spine 16.8 mm from midline. Angle between right genal spine and right thoracetrone side 60.2°. Occipital bands inflated, extend from ophthalmic ridges to genal spine termini. Prosomal-thoracetrone hinge pronounced, 14.2 mm wide, 1.1 mm long.

Thoracetrone trapezoidal, 16.3 mm long, 16.9 mm wide anteriorly, tapering to 3.9 mm posteriorly. Medial lobe 12.8 mm long with medial thoracetrone ridge with three nodes along a medial thoracetrone ridge. Left pleural lobe 14.8 mm long, 5.5 mm wide, tapering posteriorly, with rim 0.8 mm wide. Right pleural lobe 14.5 mm long, 7.2 mm wide, tapering posteriorly, with 1.0 mm wide rim. Rim margin crenulated, indicating movable spine notches. Terminal spines posterior directed. Telson 8.3 mm long, with keel, terminates at rock edge.

Private Specimen 1

Articulated prosoma, thoracetrone, and partial telson (Fig. 7C-D). Specimen 75.4 mm long. Prosoma parabolic in outline, 42.0 mm long at midline, 70.3 mm wide at widest section. Prosomal rim 1.5 mm wide. Both ophthalmic ridges straight, 27.0 mm long, converging anteriorly into an M-shape. Cardiac lobe 30.7 mm long, 18.6 mm wide

posteriorly, tapering anteriorly into triangle, terminating at ophthalmic ridge joint. Both genal spines terminate within first quarter of thoracetrone. Left genal tip 33.6 mm from midline. Angle between left genal spine and left thoracetrone side 50.6°. Right genal spine 34.7 mm from midline. Angle between right genal spine and right thoracetrone side 55.5°. Occipital bands inflated, extend from ophthalmic ridges to genal spine termini.

Thoracetrone trapezoidal, 29.3 mm long, 32.5 mm wide anteriorly, tapering to 9.8 mm posteriorly. Medial lobe 30.3 mm long with six nodes present along axial ridge. Both pleural lobes broken. Telson 4.1 mm long, terminates at rock edge.

CM 53795

An articulated prosoma and thoracetrone (Fig. 8A). Specimen 37.4 mm long. Prosoma parabolic in outline, 19.8 mm long at midline, 34.5 mm wide at widest part. Prosomal rim 0.8 mm wide. Both ophthalmic ridges straight, 14.4 mm long, converging anteriorly into an M-shape. Cardiac lobe 11.9 mm long along medial ridge, is 8.7 mm wide posteriorly, tapering anteriorly into triangle, terminating at ophthalmic ridge joint. Left genal spine broken, right genal spine complete. Left genal spine terminates 15.4 mm from midline. Angle between left genal spine and left thoracetrone side 70.4°. Right genal spine tip 16.8 mm from midline. Angle between right genal spine and right thoracetrone side 63.5°. Occipital bands slightly inflated, extend from ophthalmic ridges to genal spine termini. Prosomal-thoracetrone hinge pronounced, 14.7 mm wide, 1.1 mm long. Impressions of proximal sections of prosomal appendage sections about midline.



FIG. 9. — Fragmentary *Paleolimulus mazonensis* n. sp. specimens: **A**, CM 53797a, part; **B**, CM 53798b, counterpart, showing impressions of prosomal appendages; **C**, **D**, CM 53799a, b: **C**, part; **D**, counterpart. C, D, converted to greyscale. Image credits: Scott McKenzie. Scale bars: 5 mm.

Thoracetrone trapezoidal, 17.6 mm long, *c.* 21 mm wide anteriorly, tapering to 4.6 mm posteriorly. Medial lobe 15.7 mm long, with six nodes present along an axial ridge. Three longitudinal ridges across posterior section of medial lobe.

CM 53796

Articulated prosoma, thoracetrone, and partial telson (Fig. 8B). Specimen 32.3 mm long. Prosoma parabolic in outline, 16.5 mm long at midline, 27.3 mm wide at widest part. Ophthalmic ridges straight, 8.9 mm long. Both genal spines terminate within first quarter of thoracetrone. Left genal tip 12.9 mm from midline. Angle between left genal spine and

left thoracetrone side 51.1° . Right genal spine 13.8 mm from midline. Angle between right genal spine and right thoracetrone side 48.0° . Occipital bands slightly inflated, extend to genal spine ends. Impressions of proximal prosomal appendages about prosomal midline.

Thoracetrone trapezoidal, 13.0 mm long, 14.2 mm wide anteriorly, tapering to 3.4 mm posteriorly. Medial lobe 12.9 mm long with a medial thoracetrone ridge. Left pleural lobe 12.2 mm long, 5.1 mm wide, tapering to posterior terminal spine. Right pleural lobe is 11.9 mm long, 4.8 mm wide, tapering to posterior terminal spine. Terminal spines posteriorly directed. Telson 2.8 mm long, terminating at rock edge.

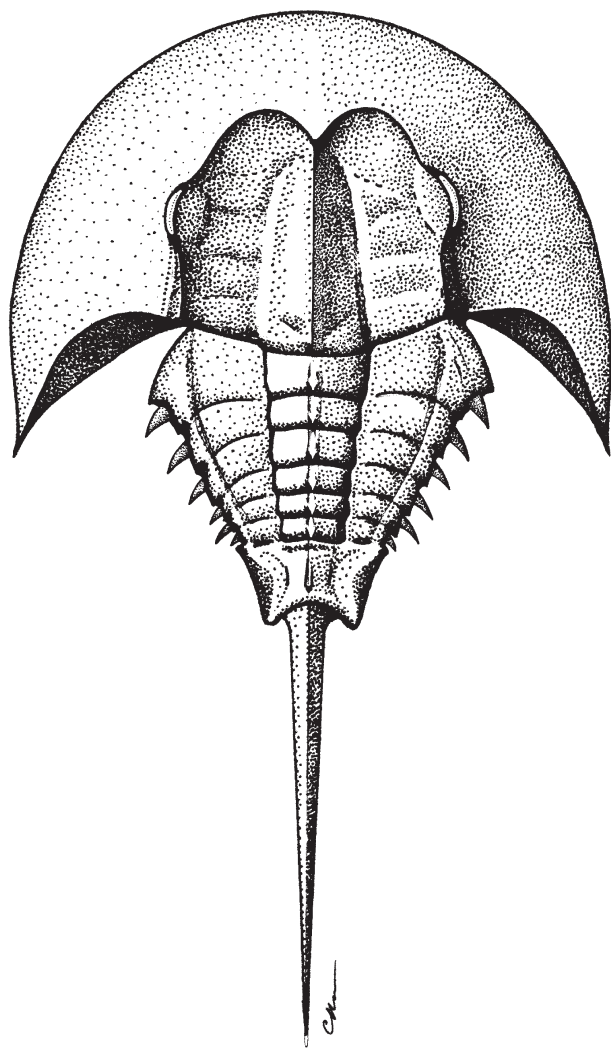


FIG. 10. — Idealized reconstruction of *Paleolimulus mazonensis* n. sp. Reconstruction credit: Serge Naugolnykh.

CM 53797

Articulated thoracetrone and telson (Fig. 9A). Specimen 33.8 mm long. Thoracetrone trapezoidal, 20.9 mm long, 20.8 mm wide anteriorly, tapering to 5.4 mm posteriorly. Reduced free lobe. Nodes on both sides of lobe. Medial lobe 16.0 mm long, with a medial thoracetrone ridge, and node at ridge terminus. Left pleural lobe 15.0 mm long, 6.4 mm wide, with 0.5 mm wide rim. Lobe tapers to posterior terminal spine. Right pleural lobe 15.0 mm long, 6.4 mm wide, with 0.9 mm wide rim. Lobe tapers to posterior terminal spine. Terminal spines posteriorly directed. Three *c.* 5 mm wide longitudinal thoracetrone ridges across pleural lobes noted. Telson 12.9 mm long, terminates at rock edge.

CM 53798

Articulated prosoma, thoracetrone, and partial telson (Fig. 9B). Specimen 28.3 mm long. Prosoma parabolic in outline, 14.5 mm long at midline, and 18.4 mm wide. Prosomal rim 0.6 mm wide. Left genal spine terminates within first quarter of thoracetrone, is 12.9 mm from midline. Angle between left

genal spine and left thoracetrone side 47.7° . Prosomal appendage impressions about prosomal midline.

Thoracetrone, trapezoidal, 10.1 mm long, 14.7 mm wide anteriorly, tapering to 4.3 mm posteriorly. Left pleural lobe 9.9 mm long, 3.5 mm wide, tapering posteriorly, with 0.8 mm wide rim. Right pleural lobe 9.4 mm long, 5.2 mm wide, tapering posteriorly. Telson 3.7 mm long, has keel, terminates at rock edge.

CM 53799

Anterior prosomal section (Fig. 9C, D). Specimen 19.8 mm long at midline, 26.0 mm wide at widest part. Prosomal rim 0.6 mm wide. Anterior ophthalmic ridges sections converge into an M-shape. Cardiac ridge 8.5 mm long.

REMARKS

Paleolimulus traditionally represented one of the most oversplit xiphosurid genera (Bicknell 2019; Bicknell *et al.* 2020), outclassed only by *Euproops* and *Belinurus* (Anderson 1994; Bicknell & Pates 2020; Haug & Haug 2020). As such, we were tentative in erecting another *Paleolimulus* species. However, the lack of hypertrophied exoskeletal sections excludes the Mazon Creek Konservat-Lagerstätte material from Austrolimulidae (Lamsdell 2016; Bicknell 2019; Bicknell & Pates 2020), and the convergence of ophthalmic ridges into a prominent M-shape excludes them from Limulidae (Fisher 1979; Bicknell & Pates 2020). Finally, the overall morphological similarities and temporal congruence with other *Paleolimulus* species (Figs 10–12), as well as the results of a phylogenetic analysis (see Results), support the notion that the Mazon Creek Konservat-Lagerstätte specimens belong in *Paleolimulus*. In the light of these considerations, we have opted to follow the taxonomic thesis presented in McKenzie (2012) and erected a new species for this material within *Paleolimulus*. To justify this decision, we outline the combination of features that separate *P. mazonensis* n. sp. from other morphologically comparable paleolimulid species (*sensu* Bicknell & Pates 2020).

Paleolimulus signata (Fig. 11A–C) from the Fort Riley Limestone Member of the Barnston Limestone, Kansas, (Cisuralian, Wolfcampian), the Crouse Limestone, Kansas, (Cisuralian, Wolfcampian), the Wellington Formation, Kansas, (Cisuralian, Wolfcampian), and the Pony Creek Shale Member of the Wood Siding Formation, Kansas, United States (Pennsylvanian, Virgilian) has the longest fossil record of a *Paleolimulus* species. It is overall morphologically comparable to the Mazon Creek specimens (compare Figure 10 with Figure 11A–C). This likely explains why Babcock & Merriam (2000) synonymised the two forms. However, *P. signata* has a thoracetrone articulation, anterior to the telson; this feature is not observed in *P. mazonensis* n. sp. Furthermore, *P. signata* lacks the pronounced thoracetrone axial ridge observed in *P. mazonensis* n. sp.

Norilimulus woodae (Lerner, Lucas & Mansky, 2016) (Fig. 11D) from the Horton Bluff Formation, Nova Scotia, Canada (Mississippian, Tournaisian) is the oldest paleolimulid that is morphologically comparable to *Paleolimulus mazonensis* n. sp.



FIG. 11. — Examples of other morphologically comparable paleolimulid species: **A–C**, *Paleolimulus signata* (Beecher, 1904). **A**, Mostly complete specimen from Pony Creek Shale Member, Wood Siding Formation, Kansas, United States (Pennsylvanian, Virgilian); **B**, USNM PAL 484408, hypotype: complete specimen from the Wellington Formation, Kansas, United States (Cisuralian, Wolfcampian); **C**, MCZ 109538, hypotype: prosoma from Pony Creek Shale Member, Wood Siding Formation; **D**, USNM 484411, hypotype: *Norilimulus woodae* (Lerner, Lucas & Mansky, 2016) from the Horton Bluff Formation, Nova Scotia, Canada (Mississippian, Tournaisian); **E–G**, NSM005GF045.374, paratype *Paleolimulus kunguricus* Naugolnykh, 2017 from the Philippovian Formation, Urals, Russia (Cisuralian, Kungurian). **E**, Most complete specimen of the species. GIN PH-18, holotype; **F**, mostly preserved prosoma. GIN PH-9; **G**, thoracetrone section showing longitudinal ridges. GIN PH-19; **B**, Converted to greyscale. Image credits: A–C, Russell Bicknell; D, Allan Lerner; E–G, Serge Naugolnykh. Scale bars: A, E, 10 mm; B, D, 5 mm; C, 20 mm; F, G, 15 mm.

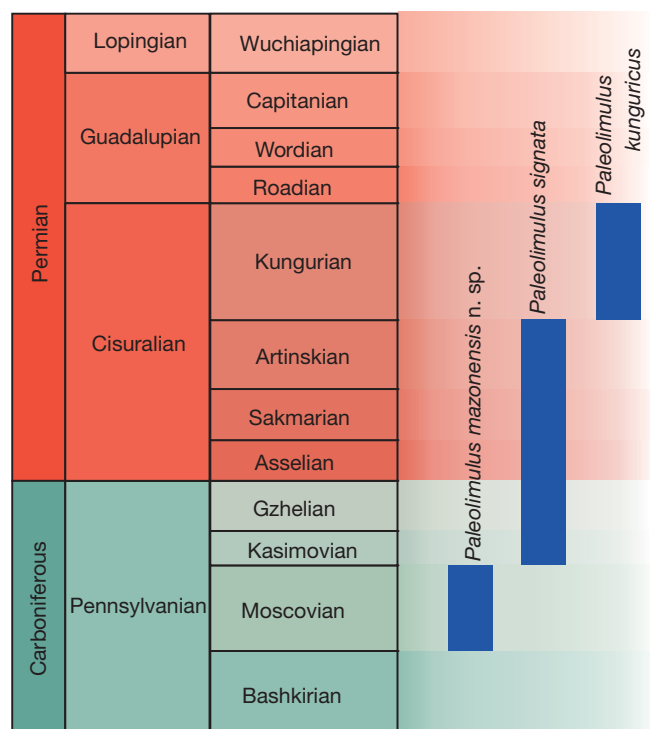


FIG. 12. — Temporal distribution of *Paleolimulus* species.

Norilimulus woodae specimens have fewer pronounced features than other comparable paleolimulids. Of particular note, *N. woodae* lacks a prominent cardiac lobe ridge, pronounced occipital bands, and nodes along the thoracetronic ridge. The presence of these features in *P. mazonensis* n. sp. precludes the placement of the Mazon Creek specimens in *Norilimulus*.

Paleolimulus kunguricus Naugolnykh, 2017 (Fig. 11E-G) from the Philippovian Formation, Urals, Russia (Cisuralian, Kungurian) is the youngest *Paleolimulus* species. Similar to *P. signata*, *P. kunguricus* has many morphological similarities to *P. mazonensis* n. sp. The key differentiating features are the lack of pronounced cardiac and thoracetronic ridges and an un-pronounced M-shaped ophthalmic ridge joint in *P. kunguricus*. We therefore conclude that erecting a new species within *Paleolimulus* is valid and justified. As such, *P. mazonensis* n. sp. represents the oldest documented *Paleolimulus* species (Fig. 12).

RESULTS

The phylogenetic analysis resulted in four most parsimonious trees of length 734 (CI: 0.468; RI: 0.878). The topology of the strict consensus tree (Appendix 3) is comparable to studies that have used this matrix (Lamsdell 2016; Bicknell 2019; Bicknell & Pates 2019). The key difference is that *Paleolimulus mazonensis* n. sp. resolves as sister to *P. signata*. Further, *Limulitella henkeli* (von Fritsch, 1906), *Valloisella lievinensis* Racheboeuf, 1992, *Xaniopyramis linseyi* Siveter & Selden, 1987 and the stem leading to *Paleolimulus* are resolved

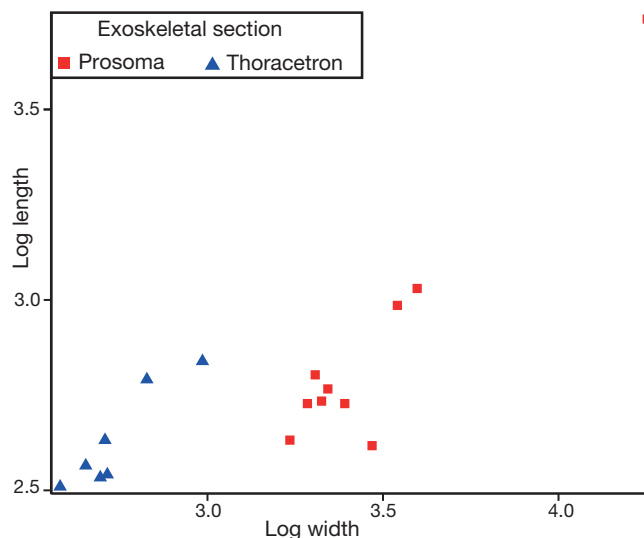


FIG. 13. — Bivariate plot of measured *Paleolimulus mazonensis* n. sp. prosomal and thoracetronic sections. Three main groups are identified, suggesting a possible ontogenetic trajectory. Data associated with this plot is found in Appendix 2.

within a polytomy outside of Austrolimulidae and Limulidae (Lamsdell, 2016).

The distribution of *Paleolimulus mazonensis* n. sp. prosomal and thoracetronic measurements in bivariate space shows three major groups (Fig. 13). These clusters preclude a sexual dimorphic explanation for the distribution and suggest that three possible ontogenetic stages may be present within the sampled specimens. The limited number of specimens produced large gaps between the two largest stages.

DISCUSSION

Horseshoe crab species are commonly described from singular specimens within deposits; often representing unique genera. It is therefore exceptional when multiple genera are known from a single formation (Table 1). The Mazon Creek Konservat-Lagerstätte is an especially intriguing example of a horseshoe crab-rich deposit as it preserves a generically diverse array of xiphosurids (see Table 1; Figs 1, 14). This likely reflects the combination of freshwater and marine environments that are preserved within the Konservat-Lagerstätte. The deposit preserves multiple ecotopes: shallow water shoreface grading into freshwater influenced off-shore conditions, allowing for fluvial taxa to be preserved (Baird 1997). In particular, the northeast zone of the Mazon Creek biota includes xiphosurid remains associated with plant megafossils (ferns, pteridosperms, and sphenophytes) and marine organisms adapted for change/alternation of salinity (xenacanth sharks, estheriids, and syncarids). Similar estuarine palaeoenvironments are found observed in other Konservat-Lagerstätten, such as the Pennsylvanian of France (Poplin & Heyler 1996; Racheboeuf *et al.* 2002), the lower Permian of the Urals, Russia (Naugolnykh 2020), and the Triassic of France (Gall 1996; Bernier *et al.* 2014). These deposits are characteristic of semi-closed lagoon basins with

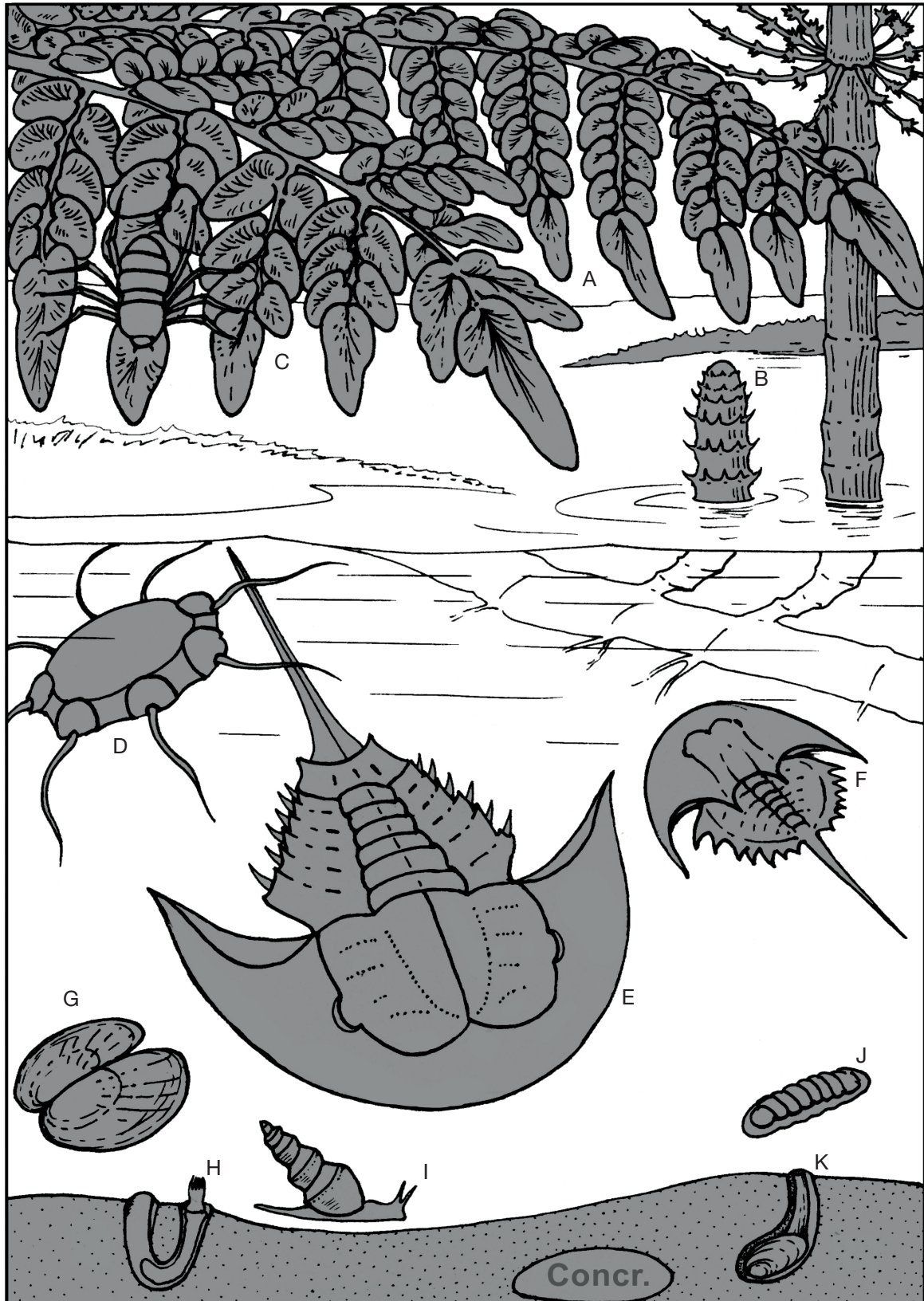


FIG. 14. — Palaeoecological reconstruction of the Mazon Creek Konservat-Lagerstätte (modified from Clements *et al.* 2019): **A**, *Neuropteris* sp., fronds of the medullosalean pteridosperms (Pfefferkorn *et al.* 1984; Naugolnykh & Jin 2014); **B**, *Calamites* sp., hydrophilous equisetophytes inhabiting a shallow-water to tidal zones (Pfefferkorn *et al.* 2001); **C**, *Poliochera* sp. hidden in the pteridosperm foliage; **D**, *Octomedusa pieckorum* (Johnson & Richardson Jr., 1968); **E**, *Paleolimulus mazonensis* n. sp.; **F**, *Euproops danae* (Meek & Worthen, 1865); **G**, postmortem position of '*Solemya*' *radiata* Meek & Worthen, 1860; **H**, *Flabelligeridae* sp. indet; **I**, gastropod *Hypselentoma* sp. feeding; **J**, *Glaphurochiton concinnus* (Richardson Jr., 1956); **K**, *Edmondia aspinwallensis* Meek, 1871. Abbreviation: **Concr.**, concretion within sediment. Note that metazoans, with the exception of *P. mazonensis* n. sp., are modelled after Shabica & Hay (1997). Reconstruction credit: Serge Naugolnykh.

gradual transition to marine environments that are strongly influenced by cyclic additions of fresh and marine water sources (Odum 1971). Extant limulids range in habitat during ontogeny: tropical lagoon basins near river mouths, marshlands, and shallow sea bottoms in the near-tidal zone (sub-littoral) (Shuster Jr. 1982). The presence of such varied palaeoenvironmental conditions suggest ideal conditions for the proliferation of multiple xiphosurid groups.

Recent research has accelerated the taxonomic organisation of *Paleolimulus*. As a result, supposed *Paleolimulus* specimens have been moved into Austrolimulidae, or considered to be representative of stem austrolimulid groups (Bicknell 2019; Bicknell & Pates 2020; Bicknell *et al.* 2020; Lamsdell 2020). Furthermore, specimens lacking the diagnostic features to confidently place them within the genus have been removed from the group (Bicknell *et al.* 2020). With the genus effectively organised after almost a century, there are new directions that should be explored to further understand *Paleolimulus*. One particular area is the ontogenetic development of *Paleolimulus*, following approaches developed by Haug *et al.* (2012), Haug & Rötzer (2018), and Haug & Haug (2020). In examining the *P. mazonensis* n. sp. sample collated here, three possible ontogenetic groups were uncovered. However, the limited number of complete specimens precludes a more detailed insight at this point. Furthermore, as *P. mazonensis* n. sp. is rare compared to other Mazon Creek Konservat-Lagerstätte xiphosurids, extensive sampling would be needed for a more complete developmental record to be explored. In the light of this limitation, *P. signata* from the Pony Creek Shale should be examined, as more than 100 specimens have been documented from this deposit (Babcock & Merriam 2000; Babcock *et al.* 2000; Leibach *et al.* 2020). Related to this point, we highlight that the specific epithet of *P. signatus* must be *P. signata*, *contra* Babcock & Merriam (2000). This reversion to the original spelling by Beecher (1904) follows Article 32.5.1. of the ICZN (ICZN 1999) outlines that “incorrect latinization must not be corrected, and the original spellings be maintained” (Krell *et al.* 2017: 8).

In exploring paleolimulids, comparisons to other horseshoe crab clades can be made. Of particular note, there is marked morphological similarity between paleolimulids and limulids, especially when compared to members of Austrolimulidae and Belinurina (Bicknell & Pates 2020; Bicknell *et al.* 2021a). This similarity likely reflects the occupation of predominately marine niches by paleolimulids and limulids. Paleolimulidae were not subject to the selective pressures that resulted in hypertrophy or reduction of exoskeletal features observed in groups that occupied freshwater conditions (Bicknell 2019; Bicknell *et al.* 2021b). As such, the morphology observed in extant horseshoe crabs was observed in these Paleozoic forms.

Acknowledgements

This research was supported by funding from a Research Training Program scholarship (to R.D.C.B.), a University of New England Postdoctoral Fellowship (to R.D.C.B.), a Charles Schuchert and Carl O. Dunbar Grants-in-Aid award

(to R.D.C.B.), and the State Program no. 0135-2019-0044 of the Geological Institute of Russian Academy of Sciences “Phytostratigraphy, palaeofloristics, crises events in Cenozoic, Mesozoic, and Palaeozoic of the various regions of Eurasia; palaeoclimatic, palaeophytocoenotic and palaeophytogeographical reconstructions”. We thank Allan Lerner and Jessica Tashman for photographs of specimens figured here. We thank the YPM IP and USNM for the use of their camera equipment. Albert Kollar, Jessica Utrup, Mark Florence, and Susan Butts are thanked for help with collections. We thank the McKenzie family for access to Private Specimen 1. TNT is made freely available thanks to a subsidy from the Willi Hennig Society. We thank Michel Laurin for translating the abstract to French. Finally, we thank the two anonymous referees for their constructive reviews that improved the direction and scope of the text, and the associate editor, Annalisa Ferretti.

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Submitted on 27 October 2020;
accepted on 11 January 2021;
published on 28 April 2022.

APPENDICES

APPENDIX 1. — NEXUS file of the analysed phylogenetic matrix modified from Bicknell (2019). Originally presented in Lamsdell (2016): https://doi.org/10.5852/cr-palevol2022v21a15_s1

APPENDIX 2. — Prosomal and thoracetrone measurements used in Figure 13: https://doi.org/10.5852/cr-palevol2022v21a15_s2

APPENDIX 3. — Phylogenetic tree from strict consensus of the four most parsimonious trees. *Paleolimulus mazonensis* n. sp. shown in **bold**. Pycnogonia, Synziphosurines, Chasmataspida, Euryptera, and Arachnida were collapsed as these are unchanged from other works that have used the matrix. https://doi.org/10.5852/cr-palevol2022v21a15_s3