

Waukeshaaspis eatonae n. gen. n. sp.: a specialized dalmanitid (Trilobita) from the Telychian of southeastern Wisconsin

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Non-technical Summary.—A new genus and species of dalmanitid trilobite, *Waukeshaaspis eatonae*, is here described based on ~200 exoskeletons that were recovered from bedding plane clusters that were part of the Silurian soft-bodied Waukesha Biota. This form has a notable embayment in the posterior margin of the posterior trunk tergite (pygidium) where a long spine is commonly found in this form's close relatives. This structure might have enhanced respiration while the animal was in an enrolled posture.

Abstract.—A new dalmanitid trilobite is described from the early Silurian (Telychian) Waukesha Biota in Wisconsin, USA, best known for its variety of exceptionally preserved arthropods. *Waukeshaaspis eatonae* new genus new species is the most common trilobite found in the Waukesha Biota, numbering ~200 specimens, allowing a thorough description of the dorsal exoskeleton. This new taxon has a combination of characters unique to the Dalmanitidae, including a distinct embayment on the posterior margin of the pygidium. Embayments are rare for dalmanitids, most species having instead a caudal spine. The lengthening of the genal spines might have served a similar function to that which a caudal spine would have served, allowing the embayment to fulfill a different function, related to keeping an opening when enrolled. The abundance at the preservation site suggests physiological tolerance at the habitation site.

UUID: <http://zoobank.org/50a214e3-72f0-4ca2-b8f1-4ad4460bc1d4>

Introduction

The Waukesha Biota (aka, Brandon Bridge Lagerstätte or Waukesha Lagerstätte) is a Telychian assemblage of fossils, which lies within the lower beds of the Brandon Bridge Formation (Moore et al., 2005; Braddy et al., 2023). The biota is thus far known only from two quarries in southeastern Wisconsin; one located in Waukesha, and the other in Franklin, 25 km to the southeast (Mikulic et al., 1985b; Kluessendorf and Mikulic, 1996a). This biota has been shown to include various exceptionally preserved arthropods, palaeoscoleoids, annelids, lobopodians, conodont animals, cycloneuralians, and other soft-bodied and lightly biomineralized invertebrates, many of which have been found nowhere else (Mikulic et al., 1985a, b; Smith et al., 1987; Moore et al., 2005; Haug et al., 2014; Jones et al., 2016; Wendruff et al., 2020a, b; Pulsipher et al., 2022; Braddy et al., 2023).

An unusual aspect of this biota is the paucity of most of the more heavily biomineralized taxa and individuals that are typically preserved in other Paleozoic biotas (Mikulic et al., 1985b; Wendruff et al., 2020a). Most of the trilobites, which have only been found in the Waukesha locality (Kluessendorf and Mikulic, 1996a; Wendruff et al., 2020a), are uncommonly or

rarely preserved. A significant exception is *Waukeshaaspis eatonae* new genus new species, the only trilobite species from the Waukesha Biota thus far found in exceptionally large clusters of articulated exoskeletons (Mikulic et al., 1985a, b; Wendruff et al., 2020a).

Also noteworthy is the consistent absence of a caudal spine or pointed posterior margin in *Waukeshaaspis eatonae* n. gen. n. sp., a contrast to most other dalmanitid taxa, with a posterior embayment at the midline of the pygidium. Herein, we describe this taxon and elaborate on its unusual occurrence and the potential functional relationships between its pygidial and other morphological features.

Geologic setting

The Brandon Bridge Formation in southeastern Wisconsin lies below the Wenlockian Waukesha Formation and above the Llandoveryan Manistique Formation (Fig. 1; Pulsipher et al., 2022, fig. 1). The Waukesha Biota occurs in an interval (up to 1 m thick) of finely planar laminated carbonate mudstone beginning 2 m above the disconformity with the Manistique Formation. Most of the trilobites from this biota were preserved in the lower 12 cm of the interval (Wendruff et al., 2020a). The biota has been assigned to the *Pterospathodus eopennatus* Superzone (Telychian) (Kleffner et al., 2018). The sediment in this interval was deposited in sediment traps under conditions

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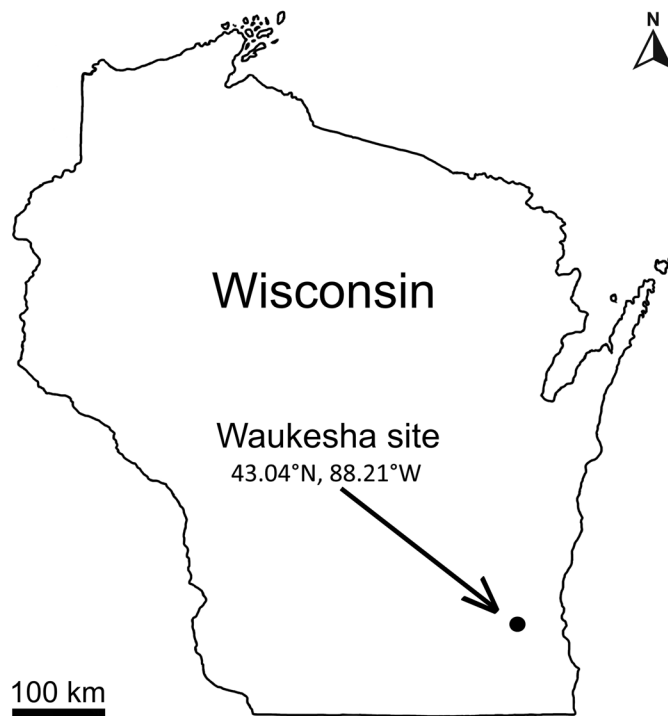


Figure 1. Map showing where the trilobites of the Waukesha Biota were collected.

interpreted to be peritidal (Wendruff et al., 2020a; Pulsipher et al., 2022). The lithology of the interval differs from most other parts of the Brandon Bridge Formation in the generally darker color and relatively consistent presence of planar, rather than wavy, laminations in the former (Anderson et al., 2021). Kluessendorf and Mikulic (1996b) and Wendruff et al. (2020a) provided further details.

Materials and methods

A Canon EOS Rebel T7i camera with an EFS 18–55 mm macro lens and polarizing filter and a Canon EOS Rebel T3i camera with an EFS 60 mm lens were used to photograph most of the fossils. Terminology relating to systematic placement, morphology, and orientation follows Whittington and Kelly (1997). In the description of the pygidial terminal piece, we counted any furrow that indicates segmentation, including those barely impressed (see discussions by Campbell, 1977).

Repository and institutional abbreviation.—The fossils examined in this study are deposited in the University of Wisconsin Geology Museum (UWGM), Madison, Wisconsin.

Systematic paleontology

- Class Trilobita Walch, 1771
- Order Phacopida Salter, 1864
- Suborder Phacopina Struve in Moore, 1959
- Superfamily Dalmanitoidea Vogdes, 1890
- Family Dalmanitidae Vogdes, 1890
- Subfamily Dalmanitinae Vogdes, 1890

Remarks.—The recognition and definition of subfamilies within Dalmanitidae has been long discussed. Several genera particularly challenge the validity of Dalmanitinae (see Carvalho and Fonseca, 2007; Holloway and Carvalho, 2009; Randolfe et al., 2022). Because detailed analysis of the subfamily is beyond the scope of this study, we provisionally follow taxonomic proposals given by Campbell (1977) and Holloway (1981), together with additional taxonomic criteria drawn by Holloway and Carvalho (2009), thus including *Waukeshaaspis* new genus as a member of the Dalmanitinae.

Genus *Waukeshaaspis* new genus

Type species.—*Waukeshaaspis eatonae* n. gen. n. sp., by monotypy.

Diagnosis.—As for the type species, by monotypy.

Occurrence.—Quarry at Waukesha Lime and Stone Company, Waukesha, Wisconsin, 43.04°N, 88.21°W (Wendruff et al., 2020a, fig. 1A–C); Brandon Bridge Formation, Telychian.

Etymology.—Named for Waukesha, Wisconsin, where the material was collected.

Remarks.—*Waukeshaaspis* n. gen. can be differentiated from the majority of dalmanitids by the combination of the anterior branch of the facial suture not crossing the preglabellar furrow, the low visual surface, and the pygidium outline having a characteristic embayment, present in all pygidia studied with the posterior margin preserved. *Bessazon tenuimucronatum* (Whittard, 1938) from the Telychian of England is another Silurian dalmanitid with an embayment in the posterior pygidial margin of large adult specimens. *Bessazon* Curtis and Lane, 1998 shares with *Waukeshaaspis* n. gen. the apparent absence of conspicuous granulation, the low eyes, and the similar shape of the precranial median process. It is noteworthy that Curtis and Lane (1998), when defining *Bessazon*, did not consider it to have a precranial median process, which was later discussed by Chatterton and Ludvigsen (2004). *Bessazon* is easily differentiated from *Waukeshaaspis* n. gen. by the course of the anterior branch of *Bessazon*'s facial suture, immersed in the preglabellar furrow, the shorter (sag.) anterior cephalic border, the shorter (sag.) preocular area, the connection of the anterior and posterior cephalic border furrows near the genal area, the almost straight anterior pygidial margin, and the posterior embayment of the pygidium being present only in the larger specimens, with shorter specimens (considered early holaspids) having a more triangular pygidium with a caudal spine, clearly different from that of *Waukeshaaspis* n. gen. With all of the specimens known of *Waukeshaaspis* n. gen., it is possible to affirm that even early holaspids have the embayment. In addition to this, the assignment of pygidia with posterior embayments to *B. tenuimucronatum* was questioned (Sandford and Holloway, 2006). These pygidia, designated as type B by Curtis and Lane (1998), are not found in association with any cephalia. Those authors designated smaller pygidia as type A, which Sandford and Holloway (2006) considered a separate species. Resolving *Bessazon tenuimucronatum* is outside

the scope of the present work. *Waukeshaspis eatonae* n. gen. n. sp. is comparable to *B. tenuimucronatum* in cephalic characters, but only to type B in pygidial characters as defined by Curtis and Lane (1998). *Kasachstania* Maksimova, 1972 has a similar pygidial outline, but can be differentiated from *Waukeshaspis* n. gen. by the presence of a caudal spine and its pygidial pleural bands, which are slightly sinuous without the marked change in curvature seen in the middle course present in *Waukeshaspis* n. gen. Additionally, there are several cephalic differences, including the course of the anterior branch of the facial suture and the shorter (exsag.) preocular and postocular areas. *Preodontochile* Degardin and Pillet, 1984, known from the lower Silurian of Spain and Australia, is like *Waukeshaspis* n. gen. in the course of the anterior branch of the facial suture, anterior to the preglabellar furrow, the long genal spines with a longitudinal furrow, and the low granular surface. *Preodontochile* can be differentiated by the absence of a precranial median process, the extremely shorter (exsag.) eyes, the genal spines not reaching the height of the pygidium, and the more triangular pygidial outline, with a short caudal spine and a wider (tr.) axis. The number of pygidial segments is different in the species of *Preodontochile*. *Preodontochile springfieldensis* Sandford and Holloway, 2006, from the lower Silurian of Australia, shares the same number of axial rings with *W. eatonae* n. gen. n. sp.

Waukeshaspis eatonae new species

Figures 2, 3

- 1985a Undescribed dalmanitid trilobite; Mikulic et al., pl. 1, fig. 6.
 1986 Undescribed dalmanitid trilobite; Meyer and Gundersen, fig. 14.
 2020a Dalmanitid trilobites; Wendruff et al., figs. 3D–F, 9A–C, 10H, I, 11.
 2023 Undescribed dalmanitid; Gass and Braddy, fig. 2h.
 2024 Undescribed dalmanitid; Fatka et al., p. 57.

Holotype.—Dorsal exoskeleton UWGM 7447 (Fig. 2.2); Waukesha Biota, Telychian, Brandon Bridge Formation, quarry at Waukesha Lime and Stone Company, Waukesha, Wisconsin (43.04°N, 88.21°W).

Paratypes.—Dorsal exoskeletons (UWGM 5048 [Fig. 2.7], UWGM 7446 [Fig. 2.5; Gass and Braddy, 2023, fig. 2h], UWGM 7448 [Fig. 2.1], UWGM 7449 [Fig. 2.4], UWGM 7450 [Fig. 2.3], partial dorsal exoskeletons (UWGM 2927 [Fig. 2.6], UWGM 7460 [Fig. 3.1], UWGM 7461 [Fig. 3.2], UWGM 7462 [Fig. 3.6]); Waukesha Biota, Telychian, Brandon Bridge Formation, quarry at Waukesha Lime and Stone Company, Waukesha, Wisconsin (43.04°N, 88.21°W).

Diagnosis.—Dalmanitid with facial suture running anteriorly to, but not crossing, the preglabellar furrow. Cephalic border furrows not connecting in the genal area or extending into the genal spine more than the base. Short (sag.) anterior cephalic border. Lower visual surface, with no more than eight lenses per dorsoventral file. Long genal spines reaching the pygidial

anterior margin. Pygidial pleural bands and furrows with maximum anterior convexity at the midline. Pygidium heart-shaped, with short (sag.) posterior embayment located at its midline, with 10 axial rings plus a terminal piece and 10 pleurae.

Occurrence.—As for genus.

Description.—Cephalon semicircular in dorsal view, with length/width index ~0.42–0.46. Cephalic anterior margin subcircular to slightly parabolic without indentations or crenulations. Anterolateral margin almost straight, with short (sag.) precranial median process convex anteriorly. Deep epiborder furrow, continuing to genal spine, almost reaching distal tip of genal spine. Glabella (excluding occipital ring) approximately as long as wide. Axial furrow wide (tr.), deep, shallower anteriorly to S3, almost straight at level of occipital ring, then weakly divergent anteriorly to occipital furrow, slightly bending outward, giving maximum divergence in front of L3. Preglabellar furrow short (sag.; exsag.), shallow. Posterior border furrow not reaching lateral border furrow. Lateral border furrow shallow in cranium, expanding toward base of genal spine, disappearing without extending into genal spine. Occipital ring moderately long (sag., exsag.), more extended than L1 laterally, slightly convex medially in lateral view. Occipital node absent. Occipital furrow only slightly impressed medially; occipital apodemes deep, short (tr.), in contact with axial furrows. S1 and S2 furrows transglabellar, shallow with narrow (tr.), deep apodemes without contact with axial furrows. S1 apodemes slightly curved backward medially. S2 apodemes practically transverse to the middle line. S3 furrows deep with distal portion strongly expanded exsagittally. L1, L2, and L3 lobes slightly convex dorsally. L1 and L2 subrectangular, of similar length (sag.), each corresponding to 10–13% of total glabellar length (sag.), excluding occipital ring. Frontal lobe subrhombic in outline, of width (tr.) comprising almost 36% of maximum cephalic width, convex dorsally, with two anteroposteriorly elongated and slightly depressed auxiliary impressions on either side of midline. Large (exsag.) palpebral lobes. Eyes situated with posterior edge opposite L1 and anterior edge opposite anterior part of L3. Palpebral furrow strongly curved in middle part, with anterior section slightly deeper than posterior section. Palpebral lobe elevated with respect to palpebral area, convex in transverse and exsagittal profile. Large (exsag.) eyes with steep, low visual surface. Shallow eye socle furrow. Preocular area elevated, convex dorsally. Visual surface outline semicircular in dorsal view, composed of 32 dorsoventral files, with maximum of eight lenses in some files. Anterior branch of facial suture running subparallel to and just laterally of axial furrow near lateral corner of frontal lobe of glabella, and anterior to preglabellar furrow on anterior border. Posterior branch of facial suture curving forward at level of S1, crossing genal field toward inner edge of lateral border reaching margin at level of L2. Posterior border narrow (exsag.), slightly shorter than lateral margin of occipital ring adjacent to axial furrow, tapering laterally until broadening markedly toward genal angle. Posterior border furrow deep, relatively broad (exsag.), markedly expanding toward base of genal spine, disappearing without extending into genal spine. Genal spines

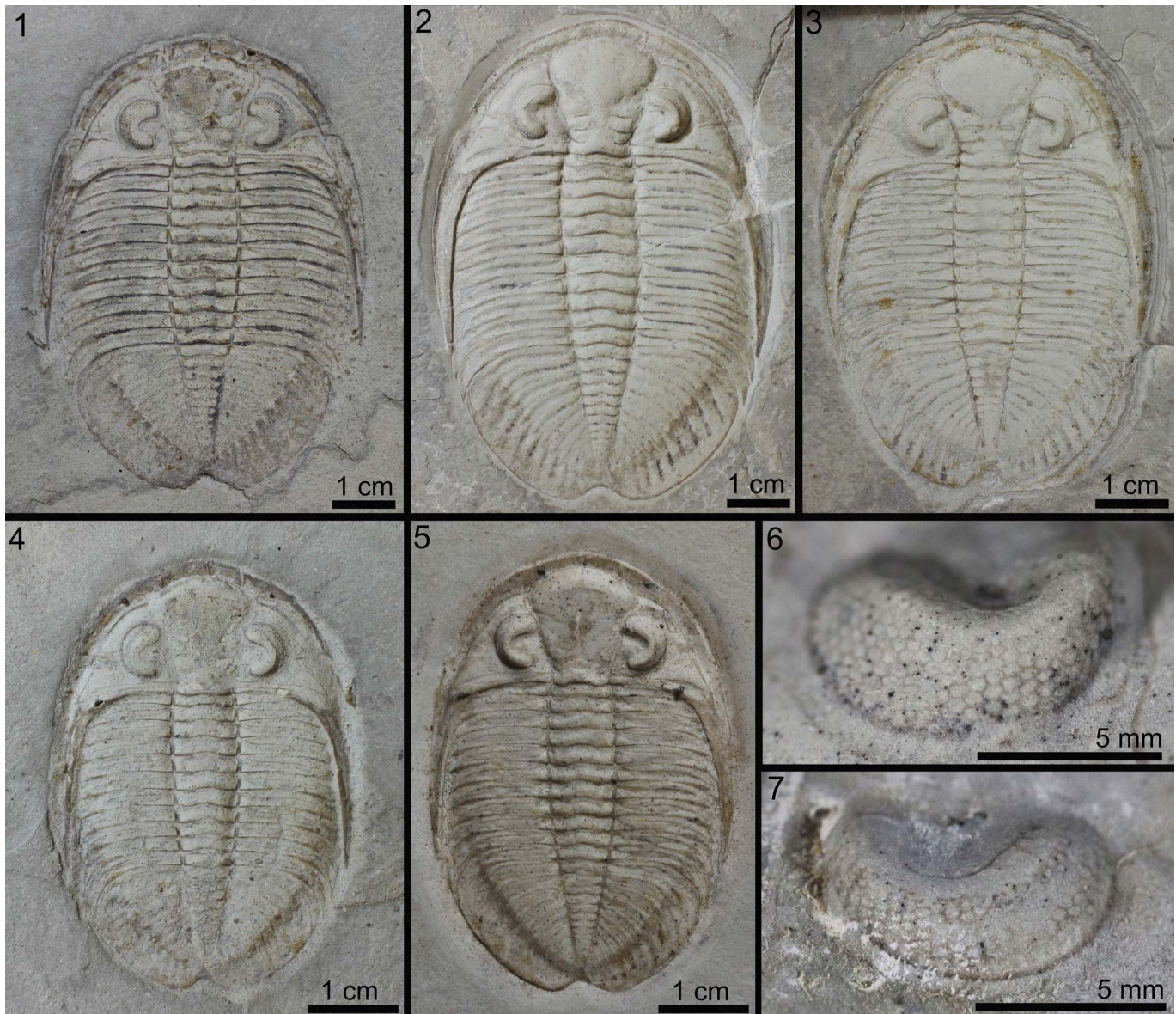


Figure 2. *Waukeshaaspis eatonae* n. gen. n. sp., early Silurian (late Llandovery; Telychian) Brandon Bridge Formation; Waukesha Lime and Stone Company quarry, Waukesha, Wisconsin, USA (43.04°N, 88.21°W): (1) UWGM 7448, paratype, dorsal exoskeleton; (2) UWGM 7447, holotype, dorsal exoskeleton; (3) UWGM 7450, paratype, dorsal exoskeleton; (4) UWGM 7449, paratype, dorsal exoskeleton; (5) UWGM 7446, paratype, dorsal exoskeleton; (6) UWGM 2927, paratype, dorsolateral detail view of left eye; (7) UWGM 5048, paratype, dorsolateral detail view of right eye.

robust, long (exsag.), flattened and elliptical in cross section, reaching anterior margin of pygidium. Cephalic doublure, as observed from ventral view, with length (sag.) $\sim 20\%$ of total cranidium length (sag.), nearly flat to barely concave. Anterior cephalic doublure with more depressed internal area $\sim 40\%$ of total doublure length (sag.).

Thorax of 11 segments; axis moderately vaulted (tr.), increasing slightly in width and length until segment 7, then decreasing in width. Axial rings slightly vaulted, first one $\sim 24\%$ of maximum thorax width (tr.). Axial furrow deep, moderately narrow (tr.). Pleurae slightly oriented backward with respect to axis. Pleural furrows deep, wide (exsag.), lanceolate in outline, not reaching thoracic margin; anterior and posterior pleural bands narrower (exsag.) in median portion. Pleural tips curving backward distally to form sharp point.

Pygidium heart-shaped to widely subtriangular, length/width index $\sim 0.52\text{--}0.56$, with widely rounded anterolateral corners, evenly convex posterolateral margin, interrupted by medially located embayment in posterior margin. Axial furrows almost straight to barely convex laterally, narrow (tr.), moderately deep, diverging $\sim 10^\circ$ from sagittal line. Pygidial axis $\sim 20\%$ of maximum pygidial width, narrowing uniformly backward, with 10 well-defined axial rings plus terminal piece. Inter-ring furrows narrow (sag.), deepest laterally at apodemes, not in contact with axial furrows. Pleural field with 10 pleurae; pleural furrows narrow (exsag.), deep, gradually less impressed backward and more posteriorly directed. All pleural bands and furrows sinuous adaxially with marked maximum of anterior convexity midwidth, and laterally to it only slightly convex until almost reaching pygidial margin. Midwidth convexity



Figure 3. *Waukeshaaspis eatonae* n. gen. n. sp., early Silurian (late Llandovery; Telychian) Brandon Bridge Formation; Waukesha Lime and Stone Company quarry, Waukesha, Wisconsin, USA (43.04°N, 88.21°W): (1, 2) UWGM 7460 and 7461, paratypes, dorsal exoskeletons preserving gut tracts; (3, 4) UWGM 2576 and 5581, large clusters of mostly complete, microbially entombed dorsal exoskeletons; (5) UWGM 2868, microbially entombed partial cephalon; (6) UWGM 7462, paratype, partial dorsal exoskeleton (interior) showing cephalic doublure.

reduced in posterior segments, with pleural bands straighter, posteriorly directed. Interpleural furrows well-impressed, incised, symmetrical in cross section, becoming deeper and wider (exsag.) near pygidial margin. Posterior pleural bands slightly wider (exsag.) than anterior pleural bands near margin, extending more laterally and almost contacting pleural margin. Pleural field dorsally convex in general, but slightly concave near margin. Posterior embayment short (sag.), narrow (tr.), with straight lateral margin and curved forward medially.

Etymology.—Named after Carrie Eaton, Curator for the UWGM.

Other material studied.—22 dorsal exoskeletons (UWGM 2722 [Mikulic et al., 1985a, pl. 1, fig. 6], 2896, 2903, 2929, 2932, 2936, 3434, 3460, 3464, 3495, 3559, 3834, 5046, 5048, 5052, 5073, 5076, 5085, 5105, 5295, 5319, 7133), six partial dorsal exoskeletons (UWGM 3608, 4026, 4374, 5322, 5326, 5329), 19 cephalia (UWGM 2756, 2763, 2868, 2871, 2874, 2912, 2925, 2937, 3353, 3443, 3459, 3461, 3556, 3829, 3883, 5086, 5099, 5141, UWM 5306), two pygidia (UWGM 2915, 5077), seven slabs with multiple dorsal exoskeletons (UWGM 2340 [Wendruff et al., 2020a, fig. 3D, F], 2576, 2888, 2891, 2875, 3497, 5581), two slabs with parts from multiple individuals (UWGM 2933, 5289); Waukesha Biota, Telychian, Brandon

Bridge Formation, quarry at Waukesha Lime and Stone Company, Waukesha, Wisconsin (43.04°N, 88.21°W).

Taphonomy.—*Waukeshaaspis eatonae* n. gen. n. sp. is the most abundant and completely preserved trilobite in the Waukesha Biota, and it is one of the most common arthropods, surpassed only by leperditocopids. Many of the taxa, including *W. eatonae* n. gen. n. sp., preserve soft tissues including intestinal tracts (Fig. 3.1, 3.2). Fatka et al. (2024) recently considered this kind of preservation as infillings. Even though most of the fossils are flattened (least so, the trilobites), many are exceptionally preserved. Several factors, primarily taphonomic conditions, account for this abundance and exceptional preservation.

Evidence, e.g., common occurrences of alignment of the individuals on a surface, consistency of their up/down orientation, exceptional preservation, and paucity of trackways, indicates that the individuals preserved in the biota typically did not inhabit the site at which they were preserved, but were transported by currents as carcasses or molts from nearby areas to sediment traps, where they were typically microbially entombed (Mikulic et al., 1985a; Mikulic and Kluessendorf, 1998; Wendruff et al., 2020a). This entombment aided in the preservation of soft tissues by inhibiting decay, predation, and scavenging most likely due to low oxygen conditions, and hypersalinity (compare Allison and Briggs, 1991a, b; Gehling, 1999; Briggs, 2003; Wendruff et al., 2020a). Conditions were also conducive to the nonpreservation, absence or rarity of most organisms having biomineralized exoskeletons, the frequent decalcification of those that do, and the coating or replacement of some remains with calcium carbonate, calcium phosphate, or pyrite. Microbial entombment, the normal state of preservation in the trilobites at this locality, is generally indicated by an obscured appearance or ‘ghosting’ of the exoskeletal remains, whereas the degree of entombment is variable (Wendruff et al., 2020a; compare Fig. 2 with Fig. 3.3–3.5).

Another feature of the Waukesha Biota likely related to its preservation in sediment traps where the remains were protected from decay, predation, and scavenging, as outlined above, is the common preservation of articulated dorsal exoskeletons of trilobites, particularly *Waukeshaaspis eatonae* n. gen. n. sp. (Mikulic et al., 1985a; Wendruff et al., 2020a). Of particular interest is that *W. eatonae* n. gen. n. sp. clusters of up to 49 mostly-articulated individuals occur on some bedding planes (Fig. 3.3, 3.4). This is not the case with the trilobites preserved in the other parts of the Brandon Bridge strata at the Waukesha site, and other Brandon Bridge localities, where articulated trilobites are uncommon and preserved as molds, and clusters are rare (Mikulic et al., 1985a; Watkins et al., 1994). Sorted molt parts from multiple individuals (e.g., specimens are all cephalae or all pygidia) of *W. eatonae* n. gen. n. sp., some sorted by size and/or orientation, have also been observed (Mikulic et al., 1985a; Kluessendorf, 1990, fig. 2-13D), but not to the extent at which sorted, articulated dorsal exoskeletons of that taxon occur. Clustering of trilobites has also been attributed to molting or mating behaviors (Speyer and Brett, 1985; Karim and Westrop, 2002). Loosely folded specimens of *W. eatonae* n. gen. n. sp. are rare and enrolled specimens are absent. Wendruff et al. (2020a) attributed this to either the individuals not

succumbing to quickly changing conditions, or being incapable of enrollment; however, the similarity in the outlines of the precranial median process and the embayment of the pygidium are consistent with the capacity for enrollment.

All known specimens of *Waukeshaaspis eatonae* n. gen. n. sp. are holaspids, and no known exoskeletons are estimated to be < 9 mm in maximum length. The next-smallest individual is 23 mm long, and most are much larger, with a mean length of ~60 mm (N = 178). This underrepresentation of larval individuals and small holaspid trilobites in this biota could be due to taphonomic bias.

The majority of specimens of *Waukeshaaspis eatonae* n. gen. n. sp. is housed in the UWGM. Numbering ~200 individuals, they far outnumber those of the other trilobite taxa from the Waukesha Biota in that museum, each taxon numbering < 10.

The other trilobite taxa preserved in the Waukesha Biota, all rare or uncommon, include *Arctinurus* Phleger, 1936, *Distryax* Lane, 1988, *Leonaspsis* Richter and Richter, 1917, *Mero-perix* Lane, 1972, *Scotoharpes* Lamont, 1948, *Stenopareia* Holm in Schmidt, 1886, a calymenid, at least two cheirurids, an otarionid, a phacopid, an encrinurid, and a proetid (Mikulic et al., 1985a; Gass et al., 1992; Wendruff et al., 2020a). The *Mero-perix* specimens appear to belong to a new species (Gass and Braddy, 2023, fig. 2j). Inadequate preservation and paucity of material of the other taxa preclude reliable specific determination.

The abundance of *Waukeshaaspis eatonae* n. gen. n. sp., in comparison to that of the other trilobites and most of the other organisms, with the exception of leperditocopids and conulariids, is notable and difficult to resolve. The size, shape, and life-style of the three organisms mentioned are different, as are the chemical compositions of their exoskeletons. Also puzzling is the rarity or absence of other heavily biomineralized organisms, e.g., brachiopods, mollusks, and echinoderms. Physiological intolerance at the habitation site, taphonomic bias, and other mechanisms were likely contributing factors.

Paleoecology and functional morphology.—Campbell (1977, p. 76) considered that enrollment in Silurian and Devonian dalmanitids, which is rarely preserved, would not be complete, because these trilobites lack coaptive structures that would allow a perfect closure. He postulated that incomplete enrollment most likely implies a need for openings, because the variety of morphologies made it “difficult to believe” that the margin would not be selected to have a perfect seal. These openings, including embayments, would allow water circulation, the exit of the antennae, and the expulsion of feces while the dalmanitid was enrolled (Campbell, 1977). The embayments more commonly are in the cephalon, laterally located to a precranial median process, as in *Huntoniatonia* Jell and Adrain, 2002 or *Synphoroides* Delo, 1940. Campbell (1977) pointed to *Coronura* Hall and Clarke, 1888, with a pygidial embayment slightly arched dorsally that would form an open tunnel during enrollment allowing the previously mentioned functions. Holloway and Carvalho (2010) considered a similar function for the pygidial embayment of *Chacomurus* Braniša and Vaněk, 1973, also slightly arched dorsally. The absence of enrolled specimens of *Waukeshaaspis* n. gen. n. or detailed specimens with ventral features preserved makes the

proposal of a similar function provisory. The flatness of the material also makes it impossible to determine whether the embayment has a dorsal arch, although in some specimens, a slight arch was observed (Fig. 2.1). This could be resolved if additional material is uncovered, because some trilobite taxa known to be capable of enrollment, e.g., most dalmanitids, are rarely preserved in an enrolled state (e.g., Budil et al., 2008, fig. 3).

The presence of a pygidial embayment contrasts with caudal spines, present in almost all other dalmanitids, and the two structures could not coexist. The function of the caudal spine in trilobites, although not extensively discussed, has been suggested to have assisted in enrollment and burrowing (Whittington and Kelley, 1997) or having a function similar to those proposed for glabellar spines or genal spines as protection, stabilizing, hydrodynamic streamlining, or as a sensory apparatus (Kloc, 1992; Knell and Fortey, 2005; Esteve et al., 2011). The common presence of the caudal spine along the entire history of dalmanitids suggests that it could fulfill an important function, e.g., overturning the individual. In cases of its absence, either that function is no longer necessary or it was performed by a different structure. *Coronura* and *Chacomurus* have an embayment with two posteriorly directed marginal spines situated on each side of the embayment, probably with an analogous function to a caudal spine (Fig. 4.1). Both genera also have other marginal spines in the pygidium shorter than these two posteriorly directed spines. Marginal spines are not present in any of the other taxa with an embayment. If caudal spines and genal spines served similar functions, long genal spines could replace a short or absent caudal spine. *Waukeshaspis* n. gen. bears long genal spines, remarkable for a Silurian dalmanitid. Other dalmanitids with long genal spines reaching or almost reaching the pygidium usually have short caudal spines, as seen in *Odontochile hausmanni* (Brongniart, 1822) from the Pragian of Czech Republic, or do not have a caudal spine, e.g., *Forillonaria dunbari* (Delo, 1940) from the Pragian of USA, and *Needmorrilla simoni* Holloway and Scott, 2023 from the Emsian-Eifelian of Australia. In the case of the other taxa with a pygidial embayment, the maximum size of the genal spines is unknown, making it impossible to estimate a relationship between the presence of embayment and the size of the genal spines. The absence of a caudal spine and presence of a long genal spine in *W. eatonae*

n. gen. n. sp. could therefore be evidence for the functional substitution of one structure (caudal spine) with a different one (long genal spines) that performs a similar function, like those already proposed by other authors.

Remarks.—Pygidial embayments as a whole are a rare structure in dalmanitids (Fig. 4), present mostly in Devonian taxa considered to be of the subfamily Synphoriinae (*Chacomurus* [Fig. 4.1], *Coronura*, and *Schoharia* Lespérance, 1975). Silurian synphoriines characteristically have a subtriangular pygidium without embayment or caudal spine (for example, *Rickardsia* Storey, Thomas, and Owens, 2016). In the Silurian, the only dalmanitid with an embayment is the aforementioned *Bessazon tenuimucronatum* (Fig. 4.3), with the embayment being present only in large specimens, and specimens proposed as early holaspids bearing a caudal spine (Curtis and Lane, 1998). Although this character was included in the diagnosis of *Bessazon*, no other species included in the genus have an embayment, having instead a caudal spine. The posterior pygidial margin of *B. buttingtonense* Curtis and Lane, 1998 from the early Silurian of Wales is without spines or any other modification. Additionally, not all species assigned to *Coronura* have a pygidial embayment. As such, the expression and possible variation of the embayment was always treated as a diagnostic character at the species level. *Schoharia* was erected as a genus that includes different species of synphoriines not considered necessarily closely related (Lespérance, 1975), known only from pygidia, all with a posterior embayment. Each species has differences related to the grade of reentrance and outline. The embayment of *Waukeshaspis* n. gen. (Fig. 4.4) is more like that of *Schoharia quebecensis* Lespérance, 1975, from the Emsian of North America (Fig. 4.2), shorter (sag.) than the embayments of the previously mentioned taxa and with rounder anterolateral margins.

Conclusion

The most outstanding feature of *Waukeshaspis eatonae* n. gen. n. sp. is the posterior embayment of its pygidium (a rare character in the family), rather than the much more common caudal spine. The observed lengthening of its genal spines might have served the same function that a caudal spine would have served, allowing the embayment to fulfill a different function, related to keeping an opening when enrolled. The abundance of the new taxon, combined with sorting at the preservation site are probably the primary factors accounting for the observed occurrence of significant clustering.

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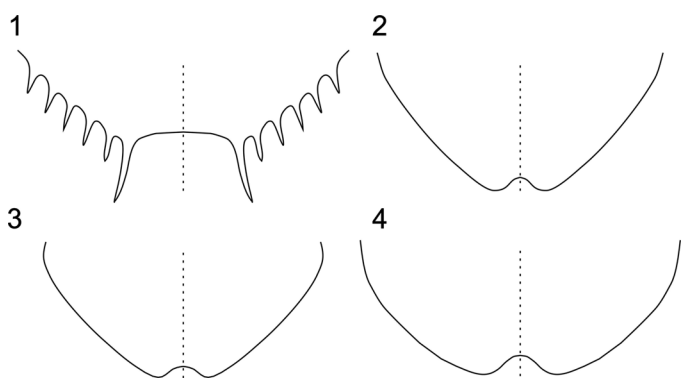


Figure 4. Schematic drawings of posterior margins of selected dalmanitids: (1) *Chacomurus confragosus* Braniša and Vaněk, 1973; (2) *Schoharia quebecensis* Lespérance, 1975; (3) *Bessazon tenuimucronatum* (Whittard, 1938); (4) *Waukeshaspis eatonae* n. gen. n. sp.

Declaration of competing interests

The authors declare none.

References

- Allison, P.A., and Briggs, D.E.G., 1991a, Taphonomy of nonmineralized tissues, in Allison, P.A., and Briggs, D.E.G., eds., Taphonomy: New York, Plenum Press, p. 25–70.
- Allison, P.A., and Briggs, D.E.G., 1991b, Taphonomy of soft-bodied animals, in Donovan, S.K., ed., The Processes of Fossilization: London, Belhaven Press, p. 120–140.
- Anderson, E.P., Schiffbauer, J.D., Jacquet, S.M., Lamsdell, J.C., Kluessendorf, J., and Mikulic, D.G., 2021, Stranger than a scorpion: a reassessment of *Parioscorpion venator*, a problematic arthropod from the Llandoveryan Waukesha Lagerstätte: *Palaeontology*, v. 64, p. 429–474, <https://doi.org/10.1111/pala.12534>.
- Braddy, S.J., Gass, K.C., and Tessler, M., 2023, Not the first leech: an unusual worm from the early Silurian of Wisconsin: *Journal of Paleontology*, v. 97, p. 799–804, <https://doi.org/10.1017/jpa.2023.47>.
- Braníša, L., and Vaněk, J., 1973, Several new trilobite genera of the superfamily Dalmanitacea Vogdes, 1890 in the Devonian of Bolivia: *Vestník Ústředního Ústavu Geologického*, v. 48, p. 95–101.
- Briggs, D.E.G., 2003, The role of decay and mineralization in the preservation of soft-bodied fossils: *Annual Review of Earth and Planetary Sciences*, v. 31, p. 275–301, <https://doi.org/10.1146/annurev.earth.31.100901.144746>.
- Brongniart, A., 1822, Les Trilobites, in Brongniart, A., and Desmarest, A.-G., *Histoire Naturelle des Crustacés Fossiles, Sous les Rapports Zoologiques et Géologiques*: Paris, F.-G. Levrault, p. 1–65, pl. 1, 2.
- Budil, P., Thomas, A.T., and Hoerlinger, F., 2008, Exoskeletal architecture, hypostomal morphology and mode of life of Silurian and Lower Devonian dalmanitid trilobites: *Bulletin of Geosciences*, v. 83, no. 1, p. 1–10, <https://doi.org/10.3140/bull.geosci.2007.01.027>.
- Campbell, K.S.W., 1977, Trilobites of the Haragan, Bois d'Arc and Frisco formations (Early Devonian) Arbuckle Mountains Region, Oklahoma: *Oklahoma Geological Survey Bulletin*, v. 123, p. 1–227.
- Carvalho, M.D.G.P. de, and da Fonseca, V.M.M., 2007, The Trilobite '*Dalmanites*' *Maecuria* Clarke, 1890 (Middle Devonian, Amazon Basin, Brazil) and the new genus *Amazonaspis* (Synphoriidae): *American Museum Novitates*, no. 3591, p. 1–14.
- Chatterton, B.D.E., and Ludvigsen, R., 2004, Early Silurian trilobites of Anticosti Island, Québec, Canada: *Palaeontographica Canadiana*, v. 22, no. 22, p. 1–264.
- Curtis, N.J., and Lane, P.D., 1998, The Llandovery trilobites of England and Wales, part 2. Monograph of the Palaeontographical Society, London, v. 152, p. 51–101.
- Degardin, J.-M., and Pillet, J., 1984, Nouveaux trilobites du Silurien des Pyrénées centrales espagnoles: *Annales de la Société Géologique du Nord*, v. 103, p. 83–92, pl. 5.
- Delo, D.M., 1940, Phacopid trilobites of North America: *Geological Society of America Special Paper* 29, 135 p.
- Esteve, J., Hughes, N.C., and Zamora, S., 2011, Purujosa trilobite assemblage and the evolution of trilobite enrollment: *Geology*, v. 39, p. 575–578, <https://doi.org/10.1130/G31985.1>.
- Fatka, O., Budil, P., and Mikuláš, R., 2024, Remains of the alimentary tract in the Late Ordovician trilobite *Dalmanitina* (Prague Basin, Barrandian area, Czech Republic): *Rivista Italiana di Paleontologia e Stratigrafia*, v. 130, no. 1, p. 575–578, <https://doi.org/10.54103/2039-4942/20845>.
- Gass, K.C., and Braddy, S.J., 2023, The Waukesha biota: a wonderful window into early Silurian life: *Geology Today*, v. 39, p. 169–176, <http://doi.org/10.1111/gto.12447>.
- Gass, K.C., Edgecombe, G.D., Ramsköld, L., Mikulic, D.G., and Watkins, R., 1992, Silurian Encrinurinae (Trilobita) from the central United States: *Journal of Paleontology*, v. 66, p. 75–89, <https://doi.org/10.1017/S0022336000033497>.
- Gehling, J.G., 1999, Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks: *Palaios*, v. 14, p. 40–57, <https://doi.org/10.2307/3515360>.
- Hall, J., and Clarke, J.M., 1888, *Palaeontology, Volume 7: Trilobites and other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, and Chemung, and Catskill groups*: Albany, New York Geological Survey, 236 p.
- Haug, C., Briggs, D.E.G., Mikulic, D.G., Kluessendorf, J., and Haug, J.T., 2014, The implications of a Silurian and other thylacocephalan crustaceans for the functional morphology and systematic affinities of the group: *BMC Evolutionary Biology*, v. 14, p. 1–15, <https://doi.org/10.1186/s12862-014-0159-2>.
- Holloway, D.J., 1981, Silurian dalmanitacean trilobites from North America and the origins of the Dalmanitinae and Synphoriinae: *Palaeontology*, v. 24, p. 695–731.
- Holloway, D.J., and Carvalho, M.D.G.P. de, 2009, The extraordinary trilobite *Fenestraspis* (Dalmanitidae, Synphoriinae) from the Lower Devonian of Bolivia: *Palaeontology*, v. 52, p. 933–949, <https://doi.org/10.1111/j.1475-4983.2009.00878.x>.
- Holloway, D.J., and Carvalho, M.D.G.P. de, 2010, The trilobite *Chacomurus* (Dalmanitidae, Synphoriinae) from the Lower Devonian of Bolivia: *Memiors of the Association of Australasian Palaeontologists*, v. 39, p. 71–83.
- Holloway, D.J., and Scott, B.M., 2023, *Needmorella*, a new trilobite genus of the Synphoriinae (Dalmanitidae) from the Lower-Middle Devonian of West Virginia: *Journal of Paleontology*, v. 97, p. 355–365, <https://doi.org/10.1017/jpa.2022.96>.
- Jell, P.A., and Adrain, J.M., 2002, Available generic names for trilobites: *Memiors of the Queensland Museum*, v. 48, p. 331–552.
- Jones, W.T., Feldman, R.M., and Schweitzer, C.E., 2016, *Ceratiocaris* from the Silurian Waukesha Biota, Wisconsin: *Journal of Paleontology*, v. 89, p. 1007–1021, <https://doi.org/10.1017/jpa.2016.22>.
- Karim, T., and Westrop, S.R., 2002, Taphonomy and paleoecology of Ordovician trilobite clusters, Bromide Formation, south-central Oklahoma: *Palaios*, v. 17, p. 394–402, [https://doi.org/10.1669/0883-1351\(2002\)017<0394:TAPOOT>2.0.CO;2](https://doi.org/10.1669/0883-1351(2002)017<0394:TAPOOT>2.0.CO;2).
- Kleffner, M.A., Norby, R.D., Kluessendorf, J., and Mikulic, D.G., 2018, Revised conodont biostratigraphy of lower Silurian strata of southeastern Wisconsin: *Geological Society of America, North-Central Section Meeting, 52nd, Abstracts with Programs*, v. 50, no. 4, <https://doi.org/10.1130/abs/2018NC-312921>.
- Kloc, G.J., 1992, Spine function in the odontopleurid trilobites *Leonaspis* and *Dicranurus* from the Devonian of Oklahoma: *The Paleontological Society Special Publications, Volume 6, North American Paleontological Convention, Abstracts with Program*, p. 167, <https://doi.org/10.1017/S2475262200007279>.
- Kluessendorf, J., 1990, Depositional and taphonomic aspects of a Silurian (Brandon Bridge, Llandovery-Wenlock fossil Konservat Lagerstätte) from Waukesha, Wisconsin (U.S.A.), predictability of North American Silurian fossil Konservat Lagerstätten, and some insights into ichnofacies [Ph.D. dissertation]: Urbana-Champaign, University of Illinois, 115 p.
- Kluessendorf, J., and Mikulic, D.G., 1996a, Discovery of a new deposit of the Silurian soft-bodied Waukesha Biota and implications for the origin of fossil Konservat Lagerstätten: *The Paleontological Society Special Publications, Volume 8: North American Paleontological Convention, 6th, Abstracts of Papers*, p. 213, <https://doi.org/10.1017/S247526220000215X>.
- Kluessendorf, J., and Mikulic, D.G., 1996b, An early Silurian sequence boundary in Illinois and Wisconsin: *Geological Society of America Special Paper* 306, p. 177–185, <https://doi.org/10.1130/0-8137-2306-X.177>.
- Knell, R.J., and Fortey, R.A., 2005, Trilobite spines and beetle horns: sexual selection in the Palaeozoic?: *Biology Letters*, v. 1, p. 196–199, <https://doi.org/10.1098/rsbl.2005.0304>.
- Lamont, A., 1948, Scottish dragons: *The Quarry Manager's Journal*, v. 31, p. 531–535.
- Lane, P.D., 1972, New trilobites from the Silurian of Northeast Greenland, with a note on a trilobite faunas in pure limestones: *Palaeontology*, v. 15, p. 336–364.
- Lane, P.D., 1988, Silurian trilobites from Peary Land, central North Greenland: *Rapport Grønlands Geologiske Undersøgelse*, v. 137, p. 93–117.
- Lespérance, P.J., 1975, Stratigraphy and paleontology of the Synphoriidae (Lower and Middle Devonian dalmanitacean trilobites): *Journal of Paleontology*, v. 49, p. 91–137.
- Maksimova, Z.A., 1972, [New Devonian trilobites of the Phacopoidea]: *Paleontologicheskij Zhurnal*, v. 14, p. 88–95. [in Russian].
- Meyer, R.C., and Gunderson, G.O., 1986, Discovering a new Silurian soft-bodied fauna: *Rocks and Minerals*, v. 61, p. 310–319, <https://doi.org/10.1080/00357529.1986.11768462>.
- Mikulic, D.G., and Kluessendorf, J., 1998, Sequence Stratigraphy and Depositional Environments of the Silurian and Devonian Rocks of Southeastern Wisconsin: Waukesha, Wisconsin, Society of Economic Paleontologists and Mineralogists Great Lakes Section and Michigan Basin Geological Society, 84 p.
- Mikulic, D.G., Briggs, D.E.G., and Kluessendorf, J., 1985a, A new exceptionally preserved biota from the lower Silurian of Wisconsin, USA: *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, v. 311, p. 75–85, <https://doi.org/10.1098/rstb.1985.0140>.
- Mikulic, D.G., Briggs, D.E.G., and Kluessendorf, J., 1985b, A Silurian soft-bodied biota: *Science*, v. 228, p. 715–717, <https://www.science.org/doi/10.1126/science.228.4700.715>.
- Moore, R.A., Briggs, D.E.G., Braddy, S.J., Anderson, L.I., Mikulic, D.G., and Kluessendorf, J., 2005, A new synzyphosurine (Chicerata: Xyphosura) from the late Llandovery (Silurian) Waukesha Lagerstätte, Wisconsin,

- USA: *Journal of Paleontology*, v. 79, p. 242–250, [https://doi.org/10.1666/0022-3360\(2005\)079<0242:ANSCXF>2.0.CO;2](https://doi.org/10.1666/0022-3360(2005)079<0242:ANSCXF>2.0.CO;2).
- Phleger, F.B., 1936, Lichadian trilobites: *Journal of Paleontology*, v. 10, p. 593–615.
- Pulsipher, M.A., Anderson, E.P., Wright, L.S., Kluessendorf, J., Mikulic, D.G., and Schiffbauer, J.D., 2022, Description of *Acheronauta* gen. nov., a possible mandibulate from the Silurian Waukesha Lagerstätte, Wisconsin, U.S.A.: *Journal of Systematic Palaeontology*, v. 20, p. 1–24, <https://doi.org/10.1080/14772019.2022.2109216>.
- Randolfe, E.A., Rustán, J.J., and Bignon, A.M.J., 2022, New dalmanitid trilobite taxa from the Lower Devonian of Argentina: comments on spinosity in endemic taxa from southern high paleolatitudes: *Comptes Rendus Palevol*, v. 21, p. 17–38, <https://doi.org/10.5852/cr-palevol2022v21a2>.
- Richter, R., and Richter, E., 1917, Über die Einteilung der Familie Acidaspidae und über einige ihrer devonischen Vertreter: *Centralblatt für Mineralogie, Geologie und Paläontologie*, v. 1917, p. 462–472.
- Salter, J.W., 1864, A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations, part 1: *Monograph of the Palaeontographical Society*, v. 16, p. 1–80, pl. 1–6.
- Sandford, A.C., and Holloway, D.J., 2006, Early Silurian phacopide trilobites from central Victoria, Australia: *Memoirs of Museum Victoria*, v. 63, no. 2, p. 215–255, <https://doi.org/10.24199/J.MMV.2006.63.17><https://doi.org/10.5852/cr-palevol2022v21a2>.
- Schmidt, F., 1886, Revision der ostbaltischen silurischen Trilobiten, Abtheilung 3, Die ostbaltischen Illaeniden: *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg*, ser. 7, v. 33, p. 1–173.
- Smith, M.P., Briggs, D.E.G., and Aldridge, R.J., 1987, A conodont animal from the lower Silurian of Wisconsin, U.S.A., and the apparatus architecture of panderodontid conodonts, in Aldridge, R.J., ed., *Palaeobiology of Conodonts: British Micropalaeontology Series*, Chichester, Ellis Horwood, p. 91–104.
- Speyer, S.E., and Brett, C.E., 1985, Clustered trilobite assemblages in the Middle Devonian Hamilton Group: Lethaia, v. 18, p. 85–103, <https://doi.org/10.1111/j.1502-3931.1985.tb00688.x>.
- Storey, A.J., Thomas, A.T., and Owens, R.M., 2016, The deep-water trilobite association of the Silurian Coldwell Siltstone Formation of northern England and its wider significance: *Proceedings of the Yorkshire Geological Society*, v. 61, p. 1–23, <https://doi.org/10.1144/pygs2015-352>.
- Struve, W., 1959, Suborder Phacopina, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha*: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. O461, O462.
- Vogdes, A.W., 1890, A bibliography of Paleozoic Crustacea from 1698 to 1889, including a list of North American species and a systematic arrangement of genera: *U.S. Geological Survey Bulletin* 63, p. 1–177.
- Walch, J.E.I., 1771, *Die Naturgeschichte der Versteinerungen, Dritter Theil: Nuremberg, Germany*, Paul Jonathan Felstecker, 235 p.
- Watkins, R., Kuglitsch, J.J., and McGee, P.E., 1994, Silurian of the Great Lakes region, part 2: paleontology of the Upper Llandoverly Brandon Bridge Formation, Walworth County, Wisconsin: *Milwaukee Public Museum Contributions in Biology and Geology*, v. 87, p. 1–53.
- Wendruff, A.J., Babcock, L.E., Kluessendorf, J., and Mikulic, D.G., 2020a, Paleobiology and taphonomy of exceptionally preserved organisms from the Waukesha Biota (Silurian), Wisconsin, USA: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 546, n. 109631, <https://doi.org/10.1016/j.palaeo.2020.109631>.
- Wendruff, A.J., Babcock, L.E., Wirkner, C.S., Kluessendorf, J., and Mikulic, D.G., 2020b, A Silurian ancestral scorpion with fossilized internal anatomy illustrating a pathway to arachnid terrestrialization: *Scientific Reports*, v. 10, n. 14, <https://doi.org/10.1038/s41598-019-56010-z>.
- Whittard, W.F., 1938, The upper Valentian trilobite fauna of Shropshire: *Annals and Magazine of Natural History*, v. 11, p. 85–140.
- Whittington, H.B., and Kelly, S.R.A., 1997, Morphological terms applied to Trilobita, in Kaesler, R.L., ed., *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Volume 1: Boulder, Colorado*, Geological Society of America (and University of Kansas Press), p. O313–O329.

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