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An Atlas of Malformed Trilobites from North American Repositories
Part 1. The Indiana University Paleontological Collection

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ABSTRACT

Malformed trilobites have been well documented within the arthropod fossil record and serve as valuable evidence for illustrating aspects of trilobite paleoecology associated with development, predation, and pathologies. Ongoing efforts to comprehensively document these malformations have uncovered important, often unique records for the extinct group, shedding light on post-malformation recovery processes and potential predators. A key means of recording new examples of these specimens has been the examination of historically important paleontological collections. To expand this approach, we examined the Deiss collection in the Indiana University Paleontology Collection and present four examples of malformations from Cambrian (*Asaphiscus wheeleri*, *Dorypyge bispinosa*, *Wanneria walcottana*), and Ordovician (*Isotelus iowensis*) species. These specimens reveal evidence of injuries, failed predation, and developmental complications. We explore the possible explanations for malformations and consider the current state of the art for evaluating trilobite malformations. Finally, the Deiss collection history and its ongoing contributions to Paleozoic fossils are presented.

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INTRODUCTION

Malformed trilobites are arguably the most well-documented examples of abnormal arthropods in the fossil record (Šnajdr, 1981, 1985; Owen, 1985; Babcock, 1993; 2003; 2007). The abundance of these aberrant specimens reflects the preferential preservation of trilobites due to their biomineralized exoskeleton (Webster, 2007) and extensive taxonomic treatment of the group (Webster, 2007; Paterson et al., 2019). The significance of these specimens has resulted in ongoing efforts to comprehensively record trilobite malformations. Moreover, recent shifts in understanding trilobite malformations at the population level (Pates et al., 2017; Bicknell et al., 2019, 2022a, 2023a; Zong et al., 2023) have reinvigorated the documentation of these specimens.

Reviews of paleontological collections across the globe have consistently uncovered new examples of malformed trilobites (see Pocock, 1974; Alpert and Moore, 1975; Rudkin, 1979, 1985; Vorwald, 1984; Conway Morris and Jenkins, 1985; Owen, 1985; Jell, 1989; Babcock, 1993, 2003; Zamora et al., 2011; Fatka et al., 2021; Zong, 2021). These specimens present novel insights into (1) the position of trilobites in their ecosystems (Rudkin, 1979; Babcock, 1993, 2007; Bicknell and Paterson, 2018; Vinn, 2018; Pates and Bicknell, 2019; Fatka et al., 2021, 2022; Bicknell et al., 2022a), (2) pathological development in trilobite exoskeletons (Lochman, 1941; Šnajdr, 1978; 1979a; Conway Morris, 1981; Bicknell et al., 2023a), and (3) malformation recovery (Ludvigsen, 1977; Šnajdr, 1979b; Capasso and Caramiello, 1996; Babcock, 1993, 2003; Jago and Haines, 2002; Fatka et al., 2015; Pates et al., 2017; Zong and Bicknell, 2022). They have also been used to explore malformations at the species level (Pates et al., 2017; Bicknell and Smith, 2021; Bicknell et al., 2022a, 2023a; Zong et al., 2023), across the taxonomic scope of the group (Owen, 1985; Babcock, 1993), and over deep time (see tables in Owen, 1985; Bicknell and Paterson, 2018; Bicknell and Smith, 2021, 2022). Continued documentation of these important specimens therefore adds to the growing literature on malformations. To extend the assessment of trilobite malformations, we present four new examples here—unique records of *Asaphiscus wheeleri* Meek, 1873, *Dorypyge bispinosa* Walcott, 1905, *Isotelus iowensis* (Owen, 1852), and *Wanneria walcottana* (Wanner, 1901). This article represents a component of an ongoing series intended to expand the documentation of malformed trilobites in scientific literature, presenting the raw data needed to more thoroughly understand these aberrant morphologies.

METHODS

Trilobite specimens within the Indiana University Paleontology Collection (IUPC), Bloomington, were examined for malformations. Specimens identified to have malformations were coated with ammonium chloride sublimate and photographed under LED light with an Olympus E-M1MarkIII camera with 12–45 mm and 60 mm macrolenses. Images were stacked using OM Capture. Measurements of specimens were gathered using digital calipers.

TERMINOLOGY

Injury: Exoskeletal breakage through accidental injury, attack, or molting complications (Owen, 1985; Babcock, 1993, 2003). Injuries are usually L-, U-, V-, or W-shaped indentations across the exoskeleton (Owen, 1985; Bicknell et al., 2022a, 2023a). They can also be expressed as the reduction and rounding of exoskeletal sections (Conway Morris and Jenkins, 1985; Nedin, 1999; Bicknell et al., 2022a, 2022b). These features can show cicatrization and/or segment repair and regeneration (Rudkin, 1979, 1985; Babcock, 1993, 2003, 2007). Occasionally, injured exoskeletal areas recover abnormally, resulting in fusion of exoskeletal sections, or a lack of segment expression (Owen, 1985; Bicknell et al., 2022a, 2023a).

Pathology: Malformed exoskeletal sections resulting from parasitic activity or infections. These structures are often expressed as circular to ovate swellings (Šnajdr, 1978; Owen, 1985; Babcock, 1993, 2003, 2007; De Baets et al., 2022).

Teratology: External expressions of developmental, embryological, or genetic malfunctions (Owen, 1985; Babcock, 1993, 2003, 2007). These morphologies include addition or removal of nodes, segments, and spines, as well as abnormally developed structures (Owen, 1985; Babcock, 1993, 2003, 2007; Bicknell and Smith, 2021).

GEOLOGICAL CONTEXT

The holotype of *Wanneria walcottana* (Wanner, 1901) (cast figured here) was collected from the Emigsville Member of the Kinzers Formation, ~4.8 km north-northwest of York, Pennsylvania (Wanner, 1901; Resser and Howell, 1938; Skinner, 2005). Here the unit is dominated by light-gray to light-blue, mixed siliciclastic-carbonates shales with small amounts of limonite (Stose and Stose, 1944). The member has been interpreted as a deposit within a debris fan, distal to a carbonate shelf (i.e. the "Impure Carbonate Facies" of Skinner, 2005), likely under exaerobic conditions (Savrda et al., 1984). *Wanneria* is relatively widespread (occurring widely in North America and Greenland), and here it is a marker for the middle *Bonnia-Olenellus* Zone (Palmer and Repina, 1993), approximately equivalent Cambrian Series 2, Stage 4 on the global scale (Peng et al., 2020).

The *Asaphiscus wheeleri* Meek, 1873 specimen figured here (IUPC 101527) was collected from the Wheeler Formation near the Wheeler Amphitheater, southeast of Antelope Springs, in the House Range, Millard County, Utah. The unit here consists of alternating thin bands of gray, olive, and pink limestone, and shales (Hintze and Davis, 2002, 2003). Previous work suggests the Wheeler Formation was deposited along a mixed carbonate-siliciclastic ramp infilling the House Range Embayment. The latter being a deep-water Cambrian subbasin structure bound by a normal fault along the modern southeastern margin (Robison, 1960, 1982; Kepper, 1976; Rees, 1986; Foster and Gaines, 2016; Bicknell et al., 2022b). Within the House Range, *A. wheeleri* occurs in the lower *Bolaspidella* Zone on the North American scale (Robison, 1964). This is equivalent to *Ptychagnostus atavus* Zone in the nearby Drum Mountains, which has been designated the standard stratotype-section and point (GSSP) for the base of the Drumian, Miaolingian (Babcock et al., 2004; Babcock and Peng, 2007; Peng et al., 2020).

The holotype of *Dorypyge bispinosa* Walcott, 1905 (cast figured here), was collected from the Changhia Formation south of Yanzhuang, Xintai district, Shandong, North China. Here the unit is composed of gray thick-bedded, massive, and occasional algal limestone, interbedded with black thin-bedded oolitic limestone and shale (Blackwelder, 1907; Bi, 1965; Zhang, 1996; Xiang and Zhu, 2005). Previous interpretations suggest the unit was deposited as part of an extensive epeiric sea that covered the North China craton (Meng et al., 1997). Various distinct environments have been recognized as part of the Changhia Formation, although *D. bispinosa* material was likely preserved in deep subtidal facies (Yan et al., 2017). Zhang and Jell (1987) placed the holotype within the *Amphoton* Zone of North China. This has been correlated with the *Amphoton* Zone of South Korea (Kang and Choi, 2007), and the upper *Ptychagnostus atavus* to lower *Goniagnostus nathorsti* zones of South China (Peng and Robison, 2000). Globally this places the occurrence somewhere within the Drumian, Miaolingian (Peng et al., 2020).

The *Isotelus iowensis* (Owen, 1852) specimen figured here (IUPC 18400-5) was collected from the Elgin Member of the Maquoketa Formation, Pike County, Missouri. This species is restricted to the lower beds of the member, giving its name to the lowest trilobite zone of Parker et al. (1959). This zone is up to 10 m thick, consisting of alternating blue, fine grained limestones and blue-gray shales. Previous authors have suggested these beds were deposited on the outer shelf of an empiric sea, within well-oxygenated waters below the storm wave base (Kolata and Graese, 1983; Raatz and Ludvigson, 1996). Graptolites from the formation suggests the Elgin Member ranges through the *Amplexograptus manitoulinensis to Dicellograptus complanatus* zones, both within the North American Richmondian Stage (Goldman and Bergström, 1997). This agrees with the boarder age range provided by conodonts (Kolata and Graese, 1983, and references therein). ^{40}Ar/^{39}Ar geochronology of sanidine crystals isolated from K-bentonites within the member, approximately 5 m above the base (at Rifle Hill, Chatfield, Minnesota), indicate an age of 447.9 ± 1.8 Ma (Smith et al., 2011). This would place it within the Katian of the Upper Ordovician on the global scale (Goldman et al., 2020).

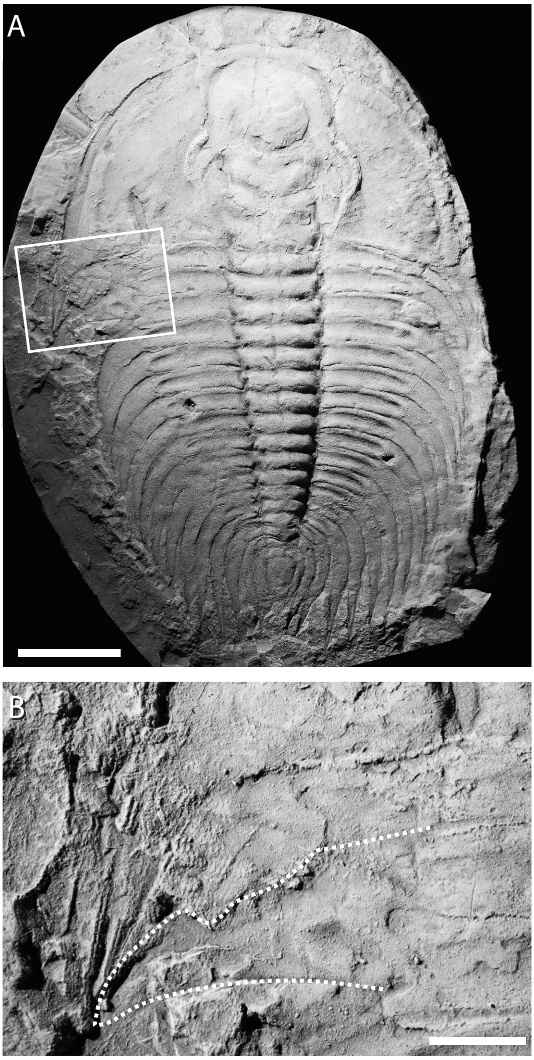

FIGURE 1. Cast of malformed *Wanneria walcottana* from the Kinzers Formation (Cambrian Series 2, Stage 4). IUPC C-158. **A.** Complete specimen. **B.** Close up of box in A, showing malformed pleural spines (dotted line). Specimen coated in ammonium chloride. Images converted to grayscale. Scale bars: A, 20 mm; B, 5 mm.

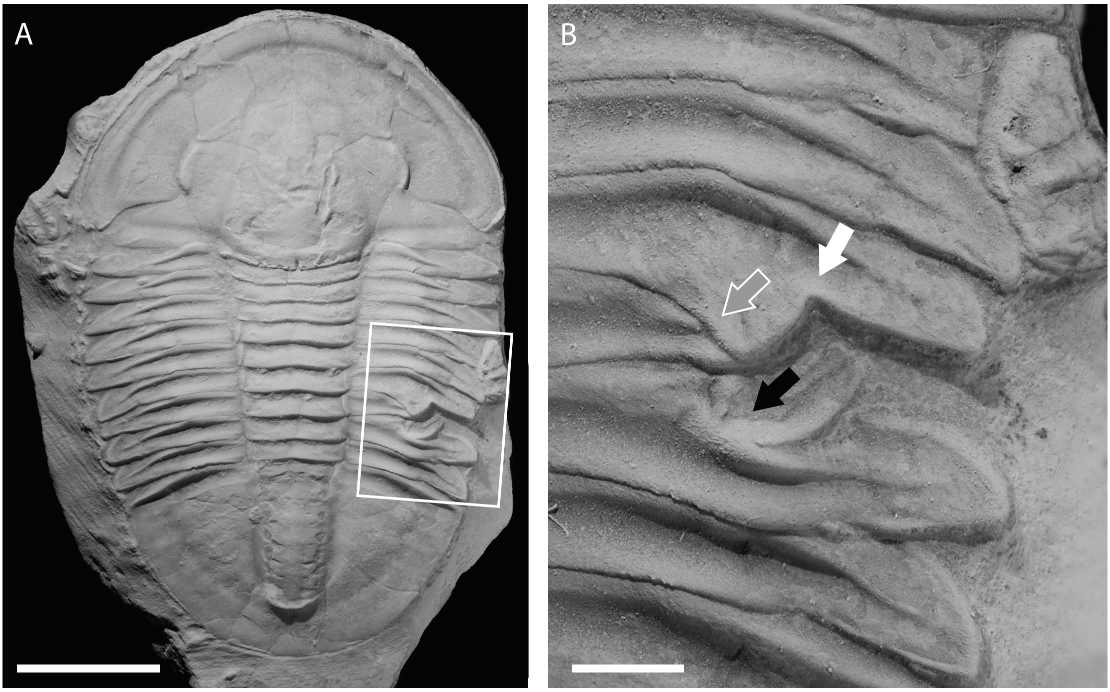

FIGURE 2. Malformed *Asaphiscus wheeleri* from the Wheeler Formation (Drumian, Miaolingian). IUPC 101527. **A.** Complete specimen. **B.** Close up of box in (A), showing V-shaped indentation in the sixth pleural segment (white arrow), the reduced seventh pleural segment (gray arrow) and bifurcation in the eighth pleural segment (black arrow). Specimen coated in ammonium chloride. Images converted to grayscale. Scale bars: A, 10 mm; B, 1 mm.

RESULTS

Cambrian

Wanneria walcottana (Wanner, 1901), IUPC C-158, cast of holotype in Wanner (1901, pl. xxxi, fig. 1, United States National Museum [USNM] 56807), Emigsville Member, Kinzers Formation (Cambrian Series 2, Stage 4), Pennsylvania (fig. 1).

Specimen is a cast of the original. It is complete, flattened, 115.21 mm long (sag.) and 77.42 mm (tr.) across the posterior cephalon margin. The specimen shows a malformation on the left side. The distal sections of the second and third pleural spines are fused into one spine, 16.82 mm from the axial lobe. This fused section extends laterally to the genal spine and is 14.61 mm long (tr.).

Asaphiscus wheeleri Meek, 1873, IUPC 101527, Wheeler Formation (Drumian, Miaolingian), House Range, western Utah (fig. 2).

The specimen is complete, 45.51 mm long (sag.) and 30.34 mm (tr.) across the posterior cephalon margin. The sixth to eighth right thoracic pleurae and associated spines are malformed, showing a V-shaped indentation that extends 4.5 mm toward the axial lobe. The sixth pleural segment has a section that is 3.47 mm longer (exsag.) than the rest of the segment.

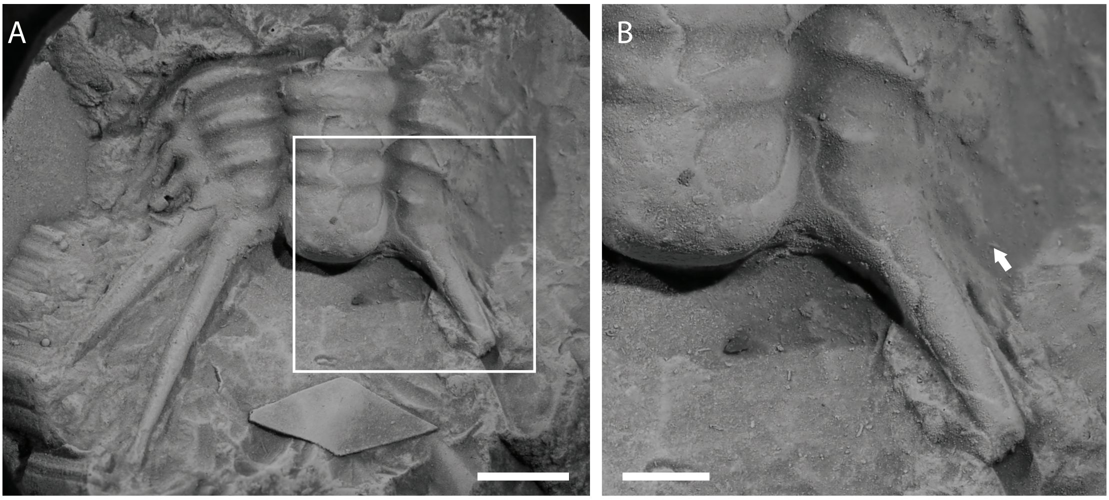

FIGURE 3. Cast of malformed *Dorypyge bispinosa* from the Changhia Formation (Drumian, Miaolingian). IUPC C-145. **A.** Complete specimen showing reduced fourth right pygidial spine. **B.** Close up of box in A, showing reduced spine (white arrow). Specimen coated in ammonium chloride. Image converted to grayscale. Scale bars: A, 5 mm; B, 2 mm.

Lateral to this is a 1.3 mm (exsag.) long V-shaped indentation. The seventh segment is reduced by 4.5 mm (exsag.) and terminates at the overlengthened section of the sixth segment (tr.). The eighth segment has a bifurcation 4.08 mm (tr.) from the axial lobe, resulting in an additional, 2.49 mm long (tr.) spine that is deflected anteriorly.

Dorypyge bispinosa Walcott, 1905, IUPC C-145, cast of holotype in Walcott (1905, pl. 8, fig. 3, USNM 57886), Changhia Formation (Drumian, Miaolingian), Shandong, North China (fig. 3).

Specimen is a cast of a partial pygidium, 10.2 mm long (sag.), 17.03 mm wide (tr.) at the anterior margin. The fourth right pygidial spine is 1.19 mm long (exsag.) compared with the fourth pygidial spine on the left side that is 10.15 mm long (i.e. only 11.7% the exsag. length). This reduced spine also appears to be partially fused with the fifth right pygidial spine at its base.

Ordovician

Isotelus iowensis (Owen, 1852), IUPC 18400-5. Elgin Member, Maquoketa Formation (Upper Ordovician, Katian), Missouri (fig. 4).

Specimen is an isolated cephalon, 30.38 mm long (sag.) and 55.26 mm wide (tr.) across the posterior margin. Specimen has an asymmetrical W-shaped indentation on the right side. The indentation extends 4.10 mm from the lateral border. The anteriormost section of indentation shows rounding. The lateral border width (tr.) is consistent along the malformation margin.

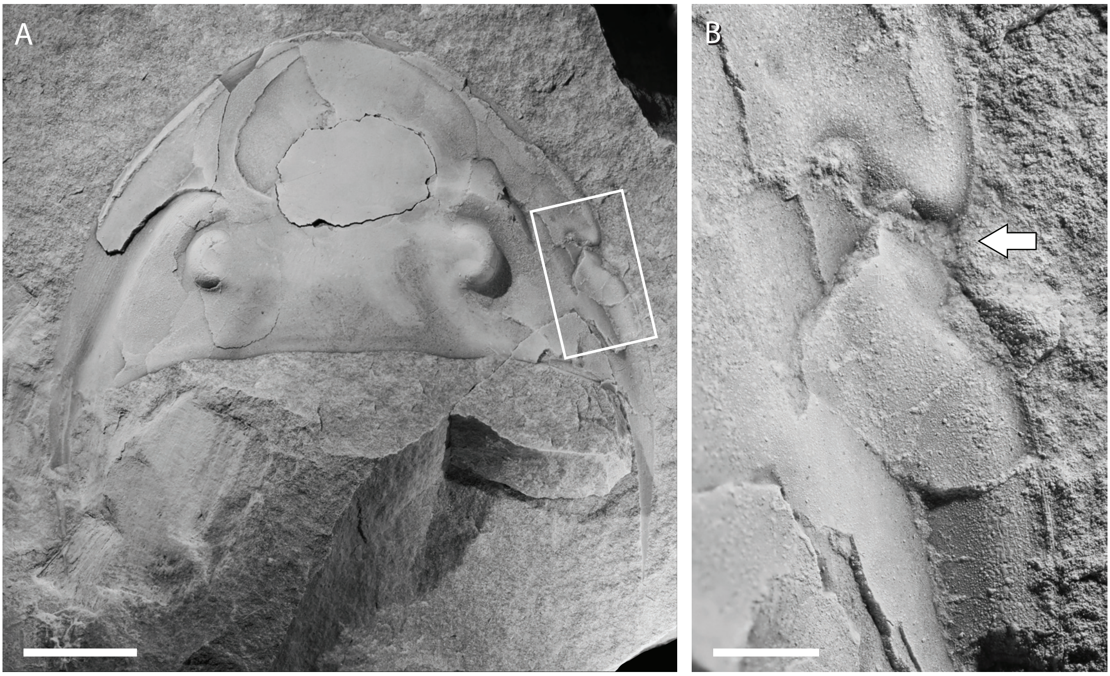

FIGURE 4. Malformed *Isotelus iowensis* from the Elgin Member, Maquoketa Formation (Upper Ordovician, Katian). IUPC 18400-5. **A.** Complete specimen. **B.** Close up of box in A, showing W-shaped indentation in cephalon (white arrow). Specimen coated in ammonium chloride. Images converted to grayscale. Scale bars: A, 10 mm; B, 2 mm.

DISCUSSION

On the Malformations

Malformations are split into three main sections: injuries, teratologies, and neoplasms (Owen, 1985; Babcock, 1993, 2003, 2007; see above, Terminology). Here, we see no evidence for round or ovate structures, excluding the possibility of neoplasms in the examined material (Babcock, 1993, 2003, 2007; De Baets et al., 2022). We document examples of injuries in the form of reduced and malformed spines and indentations, and possible evidence for teratological structures. The nature of these examples is discussed below.

Wanneria walcottana has a single malformation on the left side of the thorax—distal fusion of the second and third pleural spines (fig. 1). There is no clear indication of an indentation or possible callusing proximal to the malformation. This seems to reflect abnormal recovery and fusion of the spines, as the original injury is no longer observable (see Šnajdr, 1981, Owen, 1985 and Bicknell et al., 2022a, for other examples).

Dorypyge bispinosa is diagnosed by the presence of the considerably longer (sag.) and proximally much wider (tr.) fourth and fifth pygidial spines (Palmer, 1968; Zhang and Jell, 1987). The holotype of the taxon (fig. 3A); however, has a reduced fourth right pygidial spine that is merged at the base with the fifth. Two possible explanations for the malformation are presented:

(1) The fourth right pygidial spine was damaged and is recovering, resulting in the reduced spine and fusion at the base. In this case, the malformation may reflect complications from molting or predation.

(2) The fourth left pygidial spine is teratological, similar to spine malformations in *Thysanopeltis speciosa* (Hawle and Corda, 1847), *Acanthopyge bifida* (Edgell, 1955), and *Sanbernardaspis excalibur* Smith and Allen, 2023. These examples show similarly exaggerated or duplicated spines (Owen, 1985).

At present, both options are possible. The means of determining which is more likely necessitates more material from the type locality. This research direction is pertinent as the taxon has been considered only briefly beyond the original work (Walcott, 1905; Zhang and Jell, 1987; Wasserman, 1999; Peng et al., 2006), reflecting the limited collected material.

V-shaped indentations are commonly considered evidence of failed predation (Rudkin, 1979; Conway Morris and Jenkins, 1985; Rudkin, 1985; Nedin, 1999; Bicknell and Paterson, 2018; Bicknell et al., 2022b). The indentation in IUPC 101527 (fig. 2B) suggests an example of failed predation, aligning with other examples of malformed *Asaphiscus wheeleri* (Vorwald, 1982; 1984; Owen, 1985; Babcock, 1993; Eaton, 2019; Bicknell et al., 2022b), and bolstering the record of thoracic injuries on *A. wheeleri* (see Bicknell et al., 2022b). We can therefore consider possible predator groups within the Wheeler Formation. Artiopodans with gnathobasic spines on the protopodal regions of the walking legs (Whittington, 1975, 1980; Bruton, 1981; Stein, 2013; Zacaï et al., 2016; Bicknell and Pates, 2020), priapulid worms (Conway Morris and Robison, 1986), and radiodonts (Vorwald, 1984; Babcock, 1993; Bicknell and Holland, 2020) have commonly been highlighted as possible predators. As Cambrian priapulid worms were smaller than documented examples of injured *A. wheeleri* specimens (Conway Morris, 1979; Vorwald, 1984), we can exclude this group. Biomechanical, fluid dynamic, and kinematic analyses of *Anomalocaris canadensis* Whiteaves, 1892, have demonstrated that select radiodont frontal appendages were ineffective at handling biomineralized prey (De Vivo et al., 2021; Bicknell et al., 2023b). However, other radiodonts within the deposit may have been capable of processing trilobite exoskeleton (see Pates and Daley, 2017; Pates et al., 2018, 2021; De Vivo et al., 2021). Functional morphological (Bruton, 1981; Stein, 2013; Zacaï et al., 2016; Bicknell et al., 2018a, 2021; Holmes et al., 2020) and biomechanical models (Bicknell et al., 2018a, 2021) of artiopodans with gnathobases on their walking legs have demonstrated that a selection of these morphologies could have processed re-enforced prey. We propose that arthropods with gnathobasic spines on walking legs, or radiodonts, such as *Caryosyntrips* Daley and Budd, 2010, were the likely predators of *A. wheeleri* (Briggs et al., 2008; Pates and Daley, 2017; Pates et al., 2018, 2021).

The *Asaphiscus wheeleri* specimen also presents unique data regarding injury recovery. Reduction in the seventh pleural spine width (tr.) is accommodated by the overdevelopment of the sixth and the eighth pleural spines (fig. 2B). These segments may have had additional resources allotted to them to fill in the space. This demonstrates compensatory exoskeletal hypertrophy in trilobites (Babcock, 1993, 2003, 2007).

Malformed *Isotelus iowensis* have not previously been documented. Furthermore, records of malformed *Isotelus* DeKay, 1824, are rare within the literature (see note in Berg, 1992). Despite this, there is abundant evidence of malformed asaphid trilobites. Abnormalities on asaphids have been attributed to molting complications (Ludvigsen, 1979; Wandås, 1984; Bicknell and Smith, 2023), teratological development (Tjernvik, 1956), parasitic infestation (Ross, 1957; Owen, 1985), and failed predation (Tjernvik, 1956; Šnajdr, 1979a; Rudkin, 1985; Bicknell et al., 2023c; Bicknell and Kimmig, 2023; Zong et al., 2023). Within these, cephalic malformations have been considered evidence of injuries (Schmidt, 1906; Owen, 1985; Zong et al., 2023) and possible pathologies (Ross Jr, 1957; Owen, 1985). There are no other records of W-shaped injuries in asaphids. This injury shape is comparable to cephalic indentations attributed to failed predation on Cambrian trilobites (Hall, 1859; Babcock, 1993, 2003; Bicknell et al., 2018b). As such, we attribute this injury to possible failed predation. However, the injury size is minute compared to the cephalon. The specimen was likely attacked during a soft-shelled stage and was only slightly damaged. This aligns with the proposals that *Isotelus* species could have been targeted by Ordovician eurypterids using capture-basket-like raptorial appendages (Caster and Kjellesvig-Waering, 1964; Schmidt et al., 2022a, 2022b).

On Dark Collections

The examination of dark collections and dark specimens has become a core research theme for museums over the past decade (Smith and Blagoderov, 2012; Marshall et al., 2018). This examination has highlighted the historical nature of often underexplored material. Even more so, these collections house material from rare or completely inaccessible fossil sites, representing the only means of understanding understudied regions (Monfils et al., 2020). The Indiana University Paleontological Collection is one such example. During the early stages of the collection, the material was on display in a grand gallery. However, a series of catastrophes and unfortunate administrative decisions, including a fire, a "great housecleaning," and decades of neglect led to a marked decline (Lane, 2000; Sturgeon et al., 2019). Despite this, over the past 15 years, the paleontology faculty at Indiana University have renewed the curation, making the collection available to researchers once more.

One subsection contained within the IUPC is the Deiss material. Charles Deiss was the former chair of the department, state geologist, and director of the Indiana Geological and Water Survey (Lane, 2000). His collection of trilobites includes casts of types created from the holdings of museums around the world, and specimens from the northern Rocky Mountains. Deiss used the latter to build a biostratigraphic record for the Cambrian of North America (Deiss, 1936, 1938, 1939, 1940; Howell et al., 1944; Lochman et al., 1944). While the scope of his research was largely biostratigraphic, there are many lines of inquiry (such as injuries discussed herein) that can be assessed with this material. As the Deiss collection contains over 700 lower Paleozoic fossils, this material will continue to present more insight into animals from this time period.

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REFERENCES

Alpert, S.P., and J.N. Moore. 1975. Lower Cambrian trace fossil evidence for predation on trilobites. Lethaia 8: 223–230.

Babcock, L.E. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. Journal of Paleontology 67: 217–229.

Babcock, L.E. 2003. Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems. *In* P. Kelley, M. Kowalewski, and T.A. Hansen (editors), Predator-prey interactions in the fossil record: 55–92. New York: Springer.

Babcock, L.E. 2007. Role of malformations in elucidating trilobite paleobiology: a historical synthesis. *In* D.G. Mikulic, E. Landing, and J. Kluessendorf (editors), Fabulous Fossils–300 years of worldwide research on trilobites: 3–19. New York: University of the State of New York, State Education Dept., New York State Museum.

Babcock, L.E., and S. Peng. 2007. Cambrian chronostratigraphy: Current state and future plans. Palaeogeography, Palaeoclimatology, Palaeoecology 254: 62–66.

Babcock, L.E., M.N. Rees, R.A. Robison, E.S. Langenburg, and S. Peng. 2004. Potential global standard stratotype-section and point (GSSP) for a Cambrian stage boundary defined by the first appearance of the trilobite *Ptychagnostus atavus*, Drum Mountains, Utah, USA. Geobios 37: 149–158.

Berg, T.M. 1992. Trilobites featured in survey's GSA display. Columbus: Ohio: Ohio Department of Natural Resources: 6.

Bi, D.C. 1965. The study on Sinian, Cambrian and Ordovician of Huaibei. Acta Geologica Sinica 45: 12–29.

Bicknell, R.D.C., and B. Holland. 2020. Injured trilobites within a collection of dinosaurs: using the Royal Tyrrell Museum of Palaeontology to document Cambrian predation. Palaeontologia Electronica 23: a33.

Bicknell, R.D.C., and J. Kimmig. 2023. Clustered and injured *Pseudogygites latimarginatus* from the late Ordovician Lindsay Formation, Canada. Neues Jahrbuch für Geologie und Paläontologie 309: 199–208.

Bicknell, R.D.C., and J.R. Paterson. 2018. Reappraising the early evidence of durophagy and drilling predation in the fossil record: implications for escalation and the Cambrian Explosion. Biological Reviews 93: 754–784.

Bicknell, R.D.C., and S. Pates. 2020. Exploring abnormal Cambrian-aged trilobites in the Smithsonian collection. PeerJ 8: e8453.

Bicknell, R.D.C., and P.M. Smith. 2021. Teratological trilobites from the Silurian (Wenlock and Ludlow) of Australia. Science of Nature 108: 25.

Bicknell, R.D.C., and P.M. Smith. 2022. Examining abnormal Silurian trilobites from the Llandovery of Australia. PeerJ 10: e14308.

Bicknell, R.D.C., and P.M. Smith. 2023. Five new malformed trilobites from Cambrian and Ordovician deposits from the Natural History Museum. PeerJ 11: e16326.

Bicknell, R.D.C., et al. 2018a. Computational biomechanical analyses demonstrate similar shell-crushing abilities in modern and ancient arthropods. Proceedings of the Royal Society of London B, Biological Sciences 285: 20181935.

Bicknell, R.D.C., S. Pates, and M.L. Botton. 2018b. Abnormal xiphosurids, with possible application to Cambrian trilobites. Palaeontologia Electronica 21: 1–17.

Bicknell, R.D.C., J.R. Paterson, and M.J. Hopkins. 2019. A trilobite cluster from the Silurian Rochester Shale of New York: predation patterns and possible defensive behavior. American Museum Novitates 3937: 1–16.

Bicknell, R.D.C. et al. 2021. Biomechanical analyses of Cambrian euarthropod limbs reveal their effectiveness in mastication and durophagy. Proceedings of the Royal Society of London B, Biological Sciences 288: 20202075.

Bicknell, R.D.C., P.M. Smith, J. Bruthansová, and B. Holland. 2022a. Malformed trilobites from the Ordovician and Devonian. PalZ 96: 1–10.

Bicknell, R.D.C., P.M. Smith, T.F. Howells, and J.R. Foster. 2022b. New records of injured Cambrian and Ordovician trilobites. Journal of Paleontology 96: 921–929.

Bicknell, R.D.C., J.D. Holmes, D.C. García-Bellido, and J.R. Paterson. 2023a. Malformed individuals of the trilobite *Estaingia bilobata* from the Cambrian Emu Bay Shale and their palaeobiological implications. Geological Magazine 160: 803–812.

Bicknell, R.D.C. et al. 2023b. Raptorial appendages of the Cambrian apex predator *Anomalocaris canadensis* are built for soft prey and speed. Proceedings of the Royal Society of London B, Biological Sciences 290: 20230638.

Bicknell, R.D.C., P.M. Smith, and J.R. Paterson. 2023c. Malformed trilobites from the Cambrian, Ordovician, and Silurian of Australia. PeerJ 11: e16634.

Blackwelder, E. 1907. Stratigraphy of Shantung. Section 1, northeastern China. *In* B. Willis, E. Blackwelder, and R.H. Sargent (editors), Descriptive topography and geology research in China 1: 19–58. Washington DC: Carnegie Institution of Washington Publication 54.

Briggs, D.E.G., B.S. Lieberman, J.R. Hendricks, S.L. Halgedahl, and R.D. Jarrard. 2008. Middle Cambrian arthropods from Utah. Journal of Paleontology 82: 238–254.

Bruton, D.L. 1981. The arthropod *Sidneyia inexpectans*, Middle Cambrian, Burgess Shale, British Columbia. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 295: 619–656.

Capasso, L., and S. Caramiello. 1996. A healed injury in a Cambrian trilobite. Journal of Paleopathology 8: 181–184.

Caster, K.E., and E.N. Kjellesvig-Waering. 1964. Upper Ordovician eurypterids of Ohio. Palaeontographia Americana 3: 301–358.

Conway Morris, S. 1979. The Burgess Shale (Middle Cambrian) fauna. Annual Review of Ecology and Systematics 10: 327–349.

Conway Morris, S. 1981. Parasites and the fossil record. Parasitology 82: 489–509.

Conway Morris, S., and R.J.F. Jenkins. 1985. Healed injuries in early Cambrian trilobites from South Australia. Alcheringa 9: 167–177.

Conway Morris, S., and R. Robison. 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. University of Kansas Paleontological Contributions 117: 1–22.

Daley, A.C., and G.E. Budd. 2010. New anomalocaridid appendages from the Burgess Shale, Canada. Palaeontology 53: 721–738.

De Baets, K., P. Budil, O. Fatka, and G. Geyer. 2022. Trilobites as hosts for parasites: from paleopathologies to etiologies. *In* K. De Baets and J.W. Huntley (editors), The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques: 173–201. Cham, Switzerland: Springer International Publishing.

Deiss, C. 1936. Revision of type Cambrian formations and sections of Montana and Yellowstone National Park. Bulletin of the Geological Society of America 47: 1257–1342.

Deiss, C. 1938. Cambrian formations and sections in part of Cordilleran Trough. Bulletin of the Geological Society of America 49: 1067–1168.

Deiss, C. 1939. Cambrian stratigraphy and trilobites of northwestern Montana. Geological Society of America Special Papers 18: 1–135.

Deiss, C. 1940. Lower and Middle Cambrian stratigraphy of southwestern Alberta and southeastern British Columbia. Bulletin of the Geological Society of America 51: 731–793.

De Vivo, G., S. Lautenschlager, and J. Vinther. 2021. Three-dimensional modelling, disparity and ecology of the first Cambrian apex predators. Proceedings of the Royal Society of London B, Biological Sciences 288: 20211176.

Eaton, K. 2019. Lethal and sublethal predation on Cambrian trilobites from North America. Undergraduate thesis, Ohio State University, Columbus. [http://hdl.handle.net/1811/87602].

Edgell, H.S. 1955. A Middle Devonian lichid trilobite from south-eastern Australia. Paläontologische Zeitschrift 29: 136–145.

Fatka, O., P. Budil, and L. Grigar. 2015. A unique case of healed injury in a Cambrian trilobite. Annales de Paléontologie 101: 295–299.

Fatka, O., P. Budil, and O. Zicha. 2021. Exoskeletal and eye repair in *Dalmanitina socialis* (Trilobita): An example of blastemal regeneration in the Ordovician? International Journal of Paleopathology 34: 113–121.

Fatka, O., P. Budil, and R. Mikuláš. 2022. Healed injury in a nektobenthic trilobite: "octopus-like" predatory style in Middle Ordovician? Geologia Croatica 75: 189–198.

Foster, J.R., and R.R. Gaines. 2016. Taphonomy and paleoecology of the "Middle" Cambrian (Series 3) formations in Utah's West Desert: recent finds and new data. Utah Geological Association Publication 45: 291–336.

Goldman, D., and S.M. Bergström. 1997. Late Ordovician graptolites from the North American midcontinent. Palaeontology 40: 965–1010.

Goldman, D., et al. 2020. The Ordovician Period. *In* F.M. Gradstein, J.G. Ogg, M.D. Schmitz, and G.M. Ogg (editors), Geologic time scale 2020: 631– 694. Amsterdam: Elsevier.

Hall, J. 1859. Remarks upon the trilobites of the shales of the Hudson-River Group, with descriptions of some new species of the genus *Olenus*. Natural History of New York, Paleontology 3: 525–529.

Hawle, I., and A.J. Corda. 1847. Prodrom einer Monographie der böhmischen Trilobiten. Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften 5: 1–176.

Hintze, L.F., and F.D. Davis. 2002. Geologic map of the Tule Valley 30'x60' Quadrangle and parts of the Ely, Fish Springs, and Kern Mountains 30′ x 60′ quadrangles, northwest Millard County, Utah.

Hintze, L.F., and F.D. Davis. 2003. Geology of Millard County, Utah. Utah Geological Survey Bulletin 133: 1–305.

Holmes, J.D., J.R. Paterson, and D.C. García-Bellido. 2020. The trilobite *Redlichia* from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia: systematics, ontogeny and soft-part anatomy. Journal of Systematic Palaeontology 18: 295–334.

Howell, B., et al. 1944. Correlation of the Cambrian formations of North America. Bulletin of the Geological Society of America 55: 993–1004.

Jago, J.B., and P.W. Haines. 2002. Repairs to an injured early Middle Cambrian trilobite, Elkedra area, Northern Territory. Alcheringa 26: 19–21.

Jell, P.A. 1989. Some aberrant exoskeletons from fossil and living arthropods. Memoirs of the Queensland Museum 27: 491–498.

Kang, I., and D.K. Choi. 2007. Middle Cambrian trilobites and biostratigraphy of the Daegi Formation (Taebaek Group) in the Seokgaejae section, Taebaeksan Basin, Korea. Geosciences Journal 11: 279–296.

Kepper, J.C. 1976. Stratigraphic relationships and depositional facies in a portion of the Middle Cambrian of the Basin and Range Province. Brigham Young University Studies in Geology 23: 75–91.

Kolata, D.R., and A.M. Graese. 1983. Lithostratigraphy and depositional environments of the Maquoketa Group (Ordovician) in northern Illinois. Illinois State Geological Survey Circular 528: 1–49.

Lane, G. 2000. Geology at Indiana University 1840–2000, Bloomington: Department of Geological Sciences, Indiana University.

Lochman, C. 1941. A pathologic pygidium from the Upper Cambrian of Missouri. Journal of Paleontology 15: 324–325.

Lochman, C., D. Duncan, W.C. Bell, and C.F. Deiss. 1944. Early upper Cambrian faunas of central Montana. Geological Society of America Special Papers 54: 1–181.

Ludvigsen, R. 1977. Rapid repair of traumatic injury by an Ordovician trilobite. Lethaia 10: 205–207.

Ludvigsen, R. 1979. The Ordovician trilobite *Pseudogygites* Kobayashi in eastern and arctic North America. Life Science Contributions Royal Ontario Museum 120: 1–41.

Marshall, C.R., et al. 2018. Quantifying the dark data in museum fossil collections as palaeontology undergoes a second digital revolution. Biology Letters 14: 20180431.

Meek, F.B. 1873. Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the ages of the rocks in which they were found. U.S. Geological Survey of the Territories, 6th Annual Report USGS Washington, DC: 429–518.

Meng, X., M. Ge, and M.E. Tucker. 1997. Sequence stratigraphy, sea-level changes and depositional systems in the Cambro-Ordovician of the North China carbonate platform. Sedimentary Geology 114: 189–222.

Monfils, A.K. et al. 2020. Regional collections are an essential component of biodiversity research infrastructure. BioScience 70: 1045–1047.

Nedin, C. 1999. *Anomalocaris* predation on nonmineralized and mineralized trilobites. Geology 27: 987–990.

Owen, A.W. 1985. Trilobite abnormalities. Transactions of the Royal Society of Edinburgh: Earth Sciences 76: 255–272.

Owen, D.D. 1852. Report of a geological survey of Wisconsin, Iowa, and Minnesota, and incidentally of a portion of Nebraska Territory, Philadelphia: Lippincott, Grambo & Company.

Palmer, A.R. 1968. Cambrian trilobites of east-central Alaska. U.S. Geological Survey, Professional Paper 559B: 1–115.

Palmer, A.R., and L.N. Repina. 1993. Through a glass darkly: taxonomy, phylogeny, and biostratigraphy of the Olenellina. University of Kansas Paleontological Contributions 3: 1–35.

Parker, M.C., F.H. Dorheim, and R.B. Campbell. 1959. Resolving discrepancies between surface and subsurface studies of the Maquoketa Formation of northeast Iowa. Proceedings of the Iowa Academy of Science 66: 248–256.

Paterson, J.R., G.D. Edgecombe, and M.S.Y. Lee. 2019. Trilobite evolutionary rates constrain the duration of the Cambrian explosion. Proceedings of the National Academy of Sciences of the United States of America 116: 4394–4399.

Pates, S., and R.D.C. Bicknell. 2019. Elongated thoracic spines as potential predatory deterrents in olenelline trilobites from the lower Cambrian of Nevada. Palaeogeography, Palaeoclimatology, Palaeoecology 516: 295–306.

Pates, S., and A.C. Daley. 2017. *Caryosyntrips*: a radiodontan from the Cambrian of Spain, USA and Canada. Papers in Palaeontology 3: 461–470.

Pates, S., R.D.C. Bicknell, A.C. Daley, and S. Zamora. 2017. Quantitative analysis of repaired and unrepaired damage to trilobites from the Cambrian (Stage 4, Drumian) Iberian Chains, NE Spain. Palaios 32: 750–761.

Pates, S., A.C. Daley, and B.S. Lieberman. 2018. Hurdiid radiodontans from the middle Cambrian (Series 3) of Utah. Journal of Paleontology 92: 99–113.

Pates, S., A.C. Daley, G.D. Edgecombe, P. Cong, and B.S. Lieberman. 2021. Systematics, preservation and biogeography of radiodonts from the southern Great Basin, USA, during the upper Dyeran (Cambrian Series 2, Stage 4). Papers in Palaeontology 7: 235–262.

Peng, S., and R.A. Robison. 2000. Agnostoid biostratigraphy across the middle-upper Cambrian boundary in Hunan, China. Journal of Paleontology 74: 1–104.

Peng, S., Babcock, L.E., Lin, H., 2006. Polymerid trilobites from the Cambrian of northwestern Hunan, China. Beijing: Science Press.

Peng, S., L.E. Babcock, and P. Ahlberg. 2020. The Cambrian Period. *In* F.M. Gradstein, J.G. Ogg, M.D. Schmitz, and G.M. Ogg (editors), Geologic Time Scale 2020: 565629. Amsterdam: Elsevier.

Pocock, K.J. 1974. A unique case of teratology in trilobite segmentation. Lethaia 7: 63–66.

Raatz, W.D., and G.A. Ludvigson. 1996. Depositional environments and sequence stratigraphy of Upper Ordovician epicontinental deep water deposits, eastern Iowa and southern Minnesota. *In* G.A. Witzke, G.A. Ludvigson, and J. Day (editors), Paleozoic sequence stratigraphy: views from the North American Craton 143–159. Special Paper, Geological Society of America 306.

Rees, M.N. 1986. A fault-controlled trough through a carbonate platform: the Middle Cambrian House Range embayment. Geological Society of America Bulletin 97: 1054–1069.

Resser, C.E., and B.F. Howell. 1938. Lower Cambrian *Olenellus* Zone of the Appalachians. Geological Society of America Bulletin 49: 195–248.

Robison, R.A. 1960. Lower and Middle Cambrian stratigraphy of the eastern Great Basin. *In* J.W. Boettcher and W.W. Sloan (editors), Guidebook to the geology of east central Nevada: 43–52. Salt Lake City, Utah: 11th annual field conference of the Intermountain Association of Petroleum Geologists.

Robison, R.A. 1964. Late middle Cambrian faunas from western Utah. Journal of Paleontology 38: 510–566.

Robison, R.A. 1982. Some Middle Cambrian agnostoid trilobites from western North America. Journal of Paleontology 56: 132–160.

Ross, R.J., Jr. 1957. Ordovician fossils from wells in the Williston Basin, eastern Montana. U.S. Geological Survey Bulletin 1021-M: 439–510, pls. 37–43.

Rudkin, D.M. 1979. Healed injuries in *Ogygopsis klotzi* (Trilobita) from the Middle Cambrian of British Columbia. Royal Ontario Museum, Life Sciences Occasional Paper 32: 1–8.

Rudkin, D.M. 1985. Exoskeletal abnormalities in four trilobites. Canadian Journal of Earth Sciences 22: 479–483.

Savrda, C.E., D.J. Bottjer, and D.S. Gorsline. 1984. Development of a comprehensive oxygen-deficient marine biofacies model: evidence from Santa Monica, San Pedro, and Santa Barbara basins, California continental borderland. AAPG Bulletin 68: 1179–1192.

Schmidt, F. 1906. Revision der ostbaltischen silurischen Trilobiten, St. Petersberg: Académie impériale des sciences de St.-Pétersbourg.

Schmidt, M., R.R. Melzer, and R.D.C. Bicknell. 2022a. Kinematics of whip spider pedipalps: a 3D comparative morpho-functional approach. Integrative Zoology 17: 156–167.

Schmidt, M., R.R. Melzer, R.E. Plotnick, and R.D.C. Bicknell. 2022b. Spines and baskets in apex predatory sea scorpions uncover unique feeding strategies using 3D-kinematics. iScience 25: 103662.

Skinner, E.S. 2005. Taphonomy and depositional circumstances of exceptionally preserved fossils from the Kinzers Formation (Cambrian), southeastern Pennsylvania. Palaeogeography, Palaeoclimatology, Palaeoecology 220: 167–192.

Smith, M.E., B.S. Singer, and T. Simo. 2011. A time like our own? Radioisotopic calibration of the Ordovician greenhouse to icehouse transition. Earth and Planetary Science Letters 311: 364–374.

Smith, P.M., and H.J. Allen. 2023. Early Ordovician trilobites from Barnicarndy 1 stratigraphic well of the southern Canning Basin, Western Australia. Alcheringa 47: 234–291.

Smith, V.S., and V. Blagoderov. 2012. Bringing collections out of the dark. ZooKeys 209: 1–6.

Šnajdr, M. 1978. Pathological neoplasms in the fringe of *Bohemoharpes* (Trilobita). Věstník Ústředního ústavu geologického 53: 49–50.

Šnajdr, M. 1979a. Patologické exoskeletony dvou ordovických trilobitů z Barrandienu. Časopis Národního muzea v Praze 148: 173–176.

Šnajdr, M. 1979b. Two trinucleid trilobites with repair of traumatic injury. Věstník Ústředního ústavu geologického 54: 49–50.

Šnajdr, M. 1981. Bohemian Proetidae with malformed exoskeletons (Trilobita). Sborník geologických věd – Paleontologie 24: 37–61.

Šnajdr, M. 1985. Anomalous exoskeletons of Bohemian encrinurine trilobites. Věstník Ústředního ústavu geologického 60: 303–306.

Stein, M. 2013. Cephalic and appendage morphology of the Cambrian arthropod *Sidneyia inexpectans*. Zoologischer Anzeiger 253: 164–178.

Stose, A.I., and G.W. Stose. 1944. Geology of the Hanover-York District, Pennsylvania. U.S. Geological Survey, Professional Paper 204: 1–84.

Sturgeon, P.R., N.B. Mowery, and M.G. J. 2019. Resurrecting Megajeff: uncovering the hidden history of IU's lost *Megalonyx jeffersonii*. Online resource (https://legacy.igws.indiana.edu/megajeff).

Tjernvik, T.E. 1956. On the early Ordovician of Sweden: stratigraphy and fauna. Bulletin of the Geological Institution of the University of Uppsala 36: 107–284.

Vinn, O. 2018. Traces of predation in the Cambrian. Historical Biology 30: 1043–1049.

Vorwald, G.R. 1982. Healed injuries in trilobites—evidence for a large Cambrian predator. Proceedings of the Geological Society of America, Abstracts with Programs 14: 639.

Vorwald, G.R. 1984. Paleontology and paleoecology of the Upper Wheeler Formation (late Middle Cambrian), Drum Mountains, west-central Utah. Ph.D. dissertation, Department of Geology, University of Kansas, Lawrence.

Walcott, C.D. 1905. Cambrian faunas of China. Proceedings of the U.S. National Museum 29: 1–106.

Wandås, B.T.G. 1984. The Middle Ordovician of the Oslo region, Norway. 33. Trilobites from the lowermost part of the *Ogygiocaris* series. Norsk Geologisk Tidsskrift 63: 211–267.

Wanner, A. 1901. A new species of *Olenellus* from the Lower Cambrian of York County, Pennsylvania. Proceedings of the Washington Academy of Sciences 3: 267–270.

Wasserman, G.J. 1999. Middle-upper Cambrian trilobite biostratigraphy of slope deposits, Paibi, western Hunan Province, China. Ph.D. dissertation, Graduate School, Ohio State University, Columbus.

Webster, M. 2007. A Cambrian peak in morphological variation within trilobite species. Science 317: 499–502.

Whiteaves, J.F. 1892. Description of a new genus and species of phyllocarid crustacea from the Middle Cambrian of Mount Stephen, B.C. Canadian Record of Science 5: 205–208.

Whittington, H.B. 1975. Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. Fossils and Strata 4: 97–136.

Whittington, H.B. 1980. Exoskeleton, moult stage, appendage morphology, and habits of the Middle Cambrian trilobite *Olenoides serratus*. Palaeontology 23: 171–204.

Xiang, L.-W., and Z.-L. Zhu. 2005. Cambrian. *In* X.-F. Wang and X.-H. Chen (editors), Stratigraphic division and correlation of China: 67–100. Beijing: Geological Press.

Yan, Z., J. Liu, Y. Ezaki, N. Adachi, and S. Du. 2017. Stacking patterns and growth models of multiscopic structures within Cambrian Series 3 thrombolites at the Jiulongshan section, Shandong Province, northern China. Palaeogeography, Palaeoclimatology, Palaeoecology 474: 45–57.

Zacaï, A., J. Vannier, and R. Lerosey-Aubril. 2016. Reconstructing the diet of a 505-million-year-old arthropod: *Sidneyia inexpectans* from the Burgess Shale fauna. Arthropod Structure and Development 45: 200–220.

Zamora, S., E. Mayoral, J. Esteve, J.A. Gámez-Vintaned, and A. Santos. 2011. Exoskeletal abnormalities in paradoxidid trilobites from the Cambrian of Spain, and a new type of bite trace. Bulletin of Geosciences 86: 665–673.

Zhang, W.-T., and P.A. Jell. 1987. Cambrian trilobites of North China, Chinese Cambrian trilobites housed in the Smithsonian Institute. Beijing: Science Press.

Zhang, Z.-Q. 1996. Cambrian-Ordovician. *In* Z.-Q. Zhang and M.-W. Liu (editors), Lithostratigraphy of Shandong Province. Wuhan: China University of Geosciences Press.

Zong, R.-W. 2021. Abnormalities in early Paleozoic trilobites from central and eastern China. Palaeoworld 30: 430–439.

Zong, R., and R.D.C. Bicknell. 2022. A new bilaterally injured trilobite presents insight into attack patterns of Cambrian predators. PeerJ 10: e14185.

Zong, R., R. Fan, and Y. Gong. 2023. Predation bias of Ordovician predators on trilobites. Journal of the Geological Society 180: jgs2023–019.

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