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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

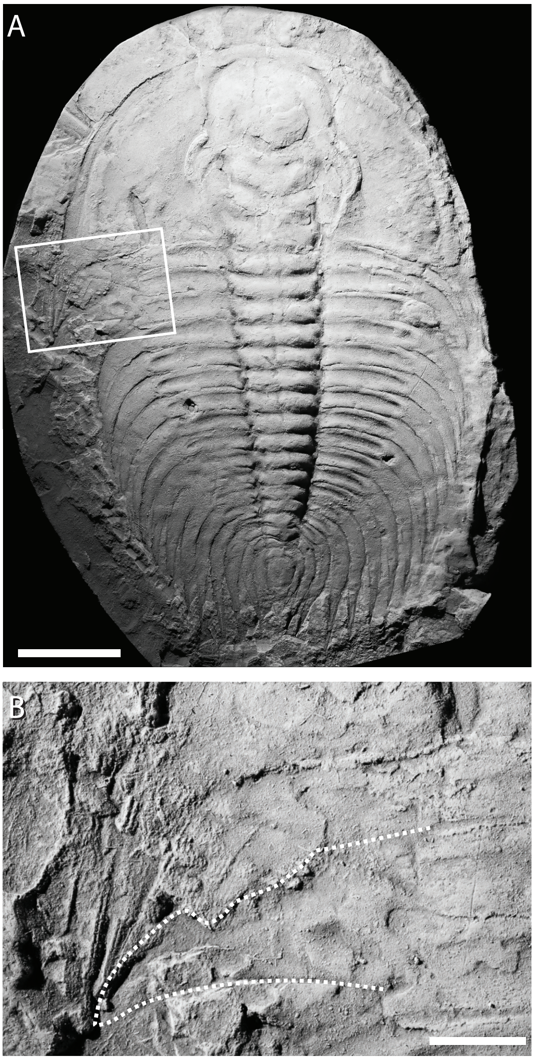

FIGURE 1. Cast of malformed *Wanneria walcottana* from the Kinzers Formation (Cambrian Series 2, Stage 4). IUPC C-158. **A.** Complete specimen. **B.** Close up of box in A, showing malformed pleural spines (dotted line). Specimen coated in ammonium chloride. Images converted to grayscale. Scale bars: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

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).

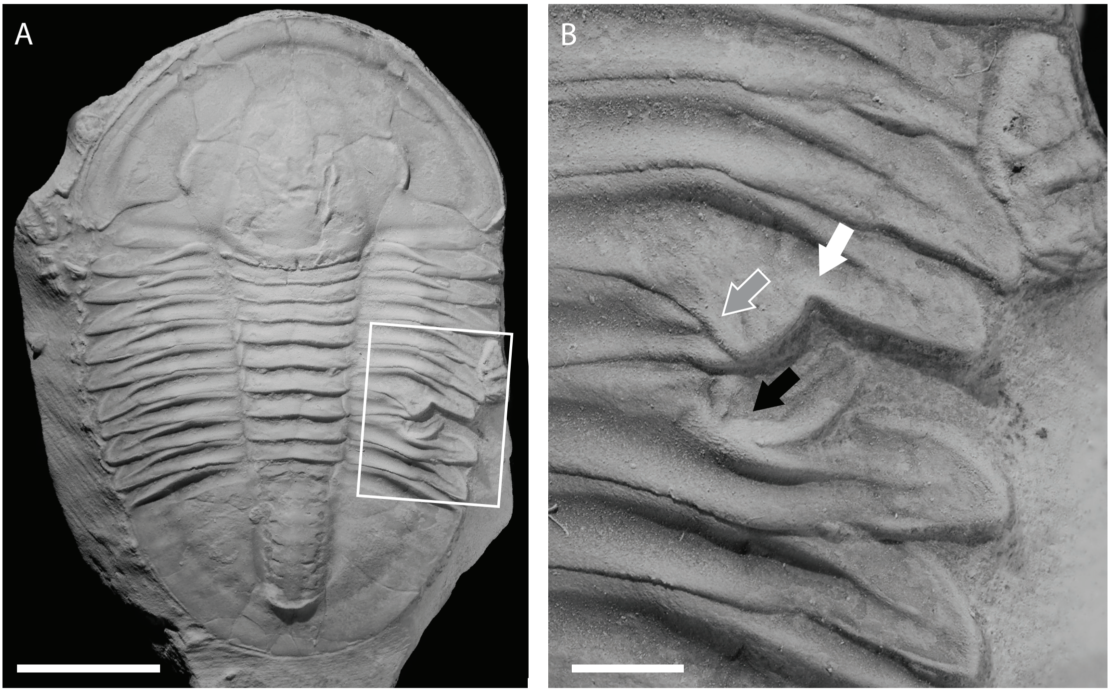

FIGURE 2. Malformed *Asaphiscus wheeleri* from the Wheeler Formation (Drumian, Miaolingian). IUPC 101527. **A.** Complete specimen. **B.** Close up of box in (A), showing V-shaped indentation in the sixth pleural segment (white arrow), the reduced seventh pleural segment (gray arrow) and bifurcation 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.

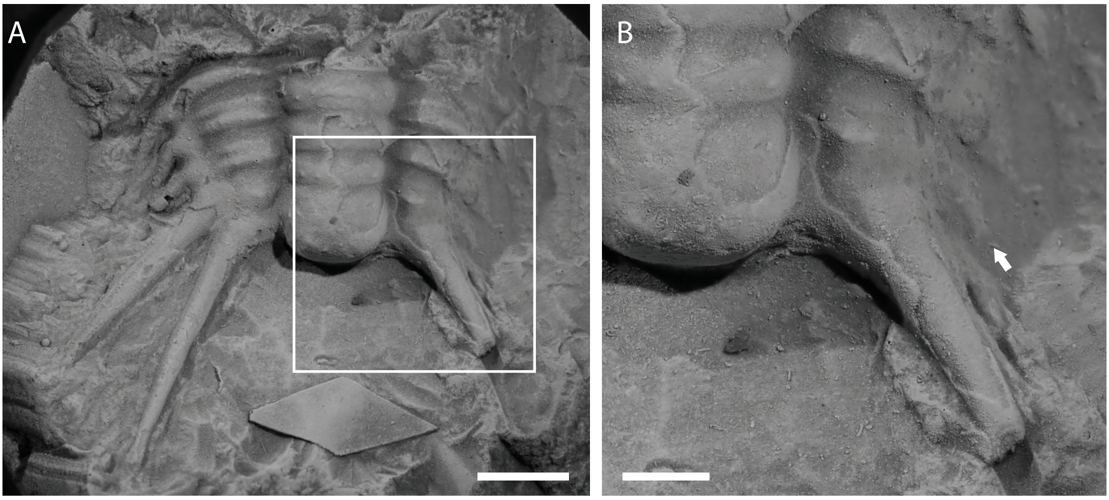

FIGURE 3. Cast of malformed *Dorypyge bispinosa* from the Changhia Formation (Drumian, Miaolingian). IUPC C-145. **A.** Complete specimen showing reduced fourth right pygidial spine. **B.** Close up of box in A, showing reduced spine (white arrow). Specimen coated in ammonium chloride. Image converted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

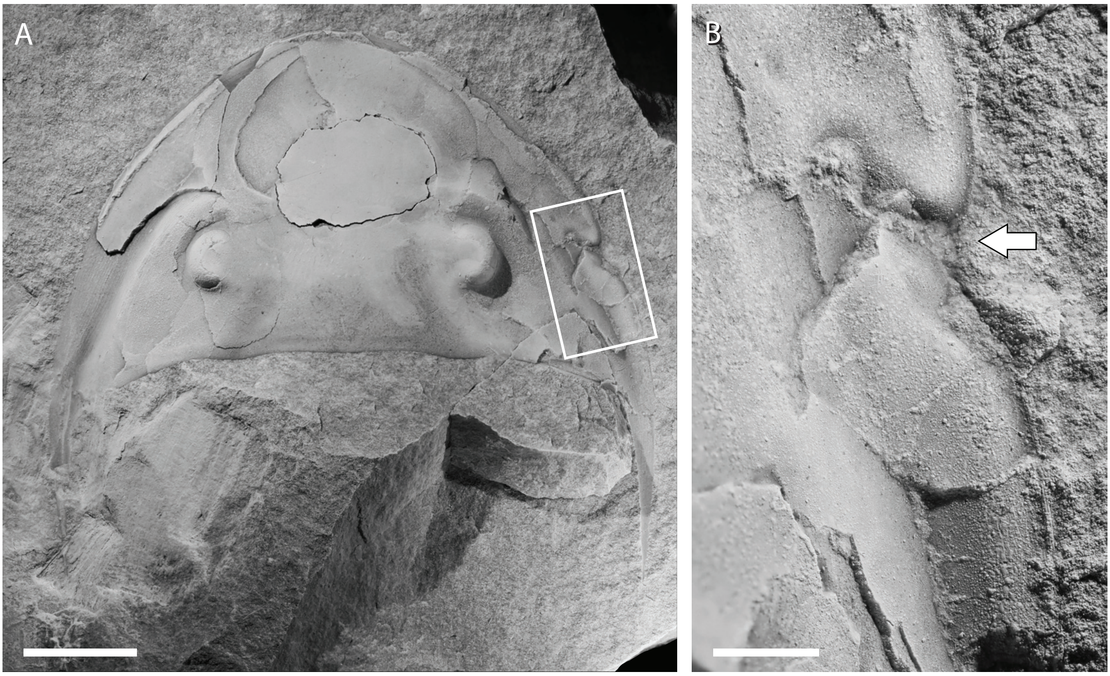

FIGURE 4. Malformed *Isotelus iowensis* from the Elgin Member, Maquoketa Formation (Upper Ordovician, Katian). IUPC 18400-5. **A.** Complete specimen. **B.** Close up of box in A, showing W-shaped indentation in cephalon (white arrow). Specimen coated in ammonium chloride. Images converted to grayscale.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