

A trilobite cluster from the Silurian Rochester Shale of New York: predation patterns and possible defensive behavior

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ABSTRACT

Evidence of predator-prey interactions in the fossil record offers important insights into extinct ecosystems. As direct predator-prey relationships are rarely preserved, records of failed predation upon prey species are often considered. The biomineralized exoskeleton of trilobites is exemplary for recording injuries that have resulted from predation. Despite the extensive documentation of trilobite injuries, abnormal specimens are often documented in isolation, with examples of injuries among clustered individuals being poorly known. Here we document a well-preserved body cluster of 18 individuals of the large lichid trilobite *Arctinurus boltoni* from the mid-Silurian (Wenlock) Rochester Shale of New York, with eight specimens showing injuries. Landmark geometric morphometrics of the specimens is used to explore possible patterns between injured and noninjured specimens. Results of the morphometric analysis indicate that injured and noninjured specimens do not show any systematic difference in overall shape of the exoskeleton, but many of the larger specimens have injuries. The majority of injuries are posteriorly located and right-side dominant, highlighting the possibility of predator or prey lateralization. Biostratinomic evidence suggests that the cluster represents a biological aggregation that was rapidly buried in situ. Potential reasons for this gregarious behavior are discussed, including the possibility that individuals of *A. boltoni* grouped together to provide “safety in numbers” against predatory attack.

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INTRODUCTION

Predator-prey interactions are a key aspect of some biologically driven evolutionary processes, such as escalation (Babcock, 2003; Vermeij, 2013). Unfortunately, very few unambiguous examples of predator-prey interactions are preserved in the fossil record (e.g., when the predator is “caught in the act” of attacking, consuming, or digesting its prey; Baumiller et al., 1999). As such, palaeobiologists interested in exploring predator-prey dynamics are usually limited to either documenting injuries on biomineralized prey without knowing the identity of the predator, or investigating the functional morphology of predators while speculating about their victims (Zacai et al., 2016; Bicknell and Paterson, 2018; Bicknell et al., 2018a). Records of predation on Phanerozoic invertebrates are dominated by drill holes in biomineralized shells and exoskeletons (Smith et al., 1985; Brett, 2003; Kelley and Hansen, 2003; Klomp-maker et al., 2017; Bicknell et al., 2018b), as well as evidence of shell crushing (durophagy), particularly on molluscs (Alexander and Dietl, 2003; Nagel-Myers et al. 2009, 2013) and trilobites (Owen, 1985; Babcock, 1993a; Bicknell and Paterson, 2018).

Trilobites are an ideal group for studying predation in deep time, due to their extensive fossil record (from the early Cambrian to the end of the Permian) and biomineralized (low-Mg calcite) exoskeletons that can preserve evidence of failed attacks. A major issue with interpreting trilobite injuries is that they may have occurred in different ways, either through complications during molting, instances of accidental trauma (e.g., Rudkin, 1985), as well as failed predation (Rudkin, 1985; Babcock, 1993a; Pates et al., 2017; Bicknell and Paterson, 2018; Pates and Bicknell, 2019). Two major criteria have therefore been suggested to identify injuries that most likely reflect predation activity: (1) signs of cicatrization (defined as healing through scar formation, e.g., calluses; see discussion in Babcock, 1993a; Bicknell et al., 2018b); and (2) the presence of distinct U-, V-, W-, or L-shaped embayments across multiple exoskeletal sections and/or substantial single spine injuries (SSIs) (Owen, 1985; Bicknell et al., 2018b; Pates and Bicknell, 2019). Using these criteria, many records of failed predation on trilobites have been identified, especially in the Cambrian (Owen, 1985; Babcock, 1993a; 2003; Bicknell and Paterson, 2018; Vinn, 2018; Bicknell and Pates, 2019). However, the vast majority of these published examples are represented by isolated individuals (perhaps as a result of collection bias), and little is known about predation on trilobites in a quantitative sense, particularly within single deposits (Pates et al., 2017; Pates and Bicknell, 2019) or indeed geological snapshots, such as individual bedding planes.

Arctinurus boltoni (Bigsby, 1825) is a large (150+ mm long) lichid trilobite from the mid-Silurian (Wenlock) Rochester Shale of New York: a deposit known for several trilobite-rich horizons, with articulated specimens of many species (including *A. boltoni*) highly sought after by fossil collectors (Whiteley et al., 2002; Chinnici and Smith, 2015). Injured specimens of *A. boltoni* have been previously documented (table 1), as well as specimens bearing epibionts (e.g., brachiopods, bryozoans, worm tubes) that are attached to the dorsal and ventral sides of the exoskeleton (Tetreault, 1992; Taylor and Brett, 1996; Brett, 2015). *Arctinurus boltoni* was therefore subject to both commensalism and potentially predation. Here we document a slab of Rochester Shale containing a cluster of 18 fully articulated individuals of *A. boltoni*, eight of

TABLE 1. Records of previously documented *Arctinurus boltoni* specimens with injuries.

Reference	Injury	Possible predator
Rudkin, 1985: fig. 1A, B	Truncated right posteriormost pygidial spine forming cicatrized W-shaped injury	None suggested
Babcock, 1993b: 36 [no figure number]	Large U-shaped injury on posterior right thorax extending onto pygidium	None suggested
Whiteley et al., 2002: pl. 21; refigured in Chinnici and Smith, 2015: fig. 434	U-shaped injury on left side of cephalon, asymmetrical V-shaped injury on left anterior thorax, W-shaped injury on left posterior thorax, and U-shaped injury on right-side of pygidium	None suggested by Whiteley et al., 2002; cephalopods: Chinnici and Smith, 2015
Chinnici and Smith, 2015: fig. 432	Large U-shaped injury on anterior right thorax and truncated, left-side pygidial spines	Cephalopods
Chinnici and Smith, 2015: fig. 433	U-shaped injury on posterior cephalon and SSI on fourth thoracic spine on right side	Cephalopods

which show injuries. We also explore the potential predatory origin of these injuries and predator preference among the associated individuals, and the possible reasons why these individuals clustered together.

MATERIALS AND METHODS

The studied slab of Rochester Shale (fig. 1) was collected by Ray Meyer in 2006 from the historic Caleb Quarry in Orleans County, western New York state, and is currently housed at the American Museum of Natural History (AMNH), New York. Preparation of the slab prior to acquisition by the AMNH included some minor reconstruction visible under UV light. Specimens of *Arctinurus boltoni* (AMNH-FI-101514 to AMNH-FI-101531) were visually assessed under normal and UV light for records of possible injuries and any examples were noted. The overall shape of each specimen was then quantified using geometric morphometrics to assess any morphological pattern of injured and noninjured specimens. Photographs of specimens were taken with a Canon PowerShot G15, and the software tpsDIG2 (v. 2.26, <http://life.bio.sunysb.edu/morpho/index.html>) was used to digitize 12 landmarks (fig. 2, table 2) that summarize the overall exoskeletal shape from the photographs (supplementary file 1, available at: <https://doi.org/10.5531/sd.sp.35>). Landmarks were collected for 17 of the 18 specimens on the slab; AMNH-FI-101524 was excluded as it is partially covered by another specimen. The symmetric component of variation was extracted following the Klingenberg et al. (2002) method for object symmetry. Briefly, a mirror image was generated from each landmark configuration and then superimposed onto its original configuration and averaged, yielding a consensus configuration that is bilaterally symmetric for each specimen. All the symmetric configurations were then superimposed jointly. Potential morphological differences between injured and noninjured specimens were visually assessed using a principal components analysis (PCA) of the Procrustes tangent coordinates. Procrustes tangent coordinates were plotted against logged-centroid size values to assess any patterns in specimen size. Finally, statistically significant differences between the mean shape of

TABLE 2. Description of landmarks used here. See figure 2 for depiction of these points.

Landmark number	Description of landmark
1	Intersection of anterior border furrow and anterior-posterior axis
2	Intersection of anterior facial suture with anterior margin of cephalon (left side)
3	Intersection of anterior facial suture with anterior margin of cephalon (right side)
4	Intersection of posterior border furrow and occipital furrow (left side)
5	Intersection of occipital furrow and anterior-posterior axis
6	Intersection of posterior border furrow and occipital furrow (right side)
7	Junction point between posterior margin of fifth tergite (= thoracic segment) and axial furrow (left side)
8	Junction point between posterior margin of fifth tergite (= thoracic segment) and axial furrow (right side)
9	Junction point between posterior margin of the 11th tergite (= thoracic segment), axial furrow, and anterior margin of pygidium (left side)
10	Junction point between posterior margin of the 11th tergite (= thoracic segment), axial furrow, and anterior margin of pygidium (right side)
11	Narrowest point along axial furrows, typically expressed just posterior to terminal axial piece (left side)
12	Narrowest point along axial furrows, typically expressed just posterior to terminal axial piece (right side)

injured vs. noninjured specimens were tested using Procrustes ANOVA. All analyses were carried out in R (R Development Core Team 2018) using the “geomorph” package (Adams and Otárola-Castillo, 2013). These plots were augmented with measurements of maximum length that were plotted as a histogram (raw data output in supplementary file 2, available at: <https://doi.org/10.5531/sd.sp.35>).

RESULTS

Eight of the 18 *Arctinurus boltoni* (44%) specimens display an injury (figs. 3–6), and the UV light was critical for distinguishing between injuries and reconstruction (see, for example, fig. 5C, D). Injuries are located on the trunk, most commonly on the pygidium, but none were observed on the cephalon of any specimen. AMNH-FI-101521 displays a slight truncation of the second pygidial spine on the left side and a subtle, cicatrized, W-shaped injury on the left posteriormost pygidial spine (fig. 3A, B). AMNH-FI-101527 has an SSI on the first pygidial segment (right side) (fig. 3C, D). AMNH-FI-101528 has a slightly cicatrized U-shaped injury on the posterior right side of the pygidium (fig. 3E, F). AMNH-FI-101529 has a large, slightly cicatrized W-shaped injury on the right posteriormost pygidial spine (fig. 4A, B). AMNH-FI-101530 has an SSI on the right side of the pygidium, forming part of a W-shaped injury (fig. 4C, D). AMNH-FI-101531 has a slightly cicatrized W-shaped injury on the posterior right side of the pygidium (fig. 4E, F). AMNH-FI-101518 has a substantial SSI on the second, right side thoracic spine: the spine is ~25% shorter than the left side (fig. 5A, B). Finally, AMNH-FI-101520 is extensively injured along the right side of the trunk (fig. 6A, B). The thorax shows two slightly cicatrized V-shaped injuries across thoracic segments 1–2 and 7–9. Spines on the



FIGURE 1. Slab preserving a cluster of 18 fully articulated individuals of *Arctinurus boltoni* (AMNH-FI-101514–101531) from the mid-Silurian (Wenlock) Rochester Shale, New York state. Stars indicate injured specimens. Scale bar = 10 cm.

posterior region of the pygidium are truncated and slightly cicatrized. In sum, 87.5% of the injured specimens have right-sided injuries only.

Results of the morphometric analysis show that there is no morphological difference between injured and noninjured specimens of *Arctinurus boltoni* (fig. 7), as confirmed by Procrustes ANOVA ($F = 1.0864$, $p = 0.372$, iterations = 999); the only specimen excluded from the analysis (AMNH-FI-101524) did not have any visible injuries. Plotting log-centroid size against regressed Procrustes ANOVA scores shows a similar interspersal of injured and noninjured specimens, though the two largest specimens have injuries (fig. 8).

DISCUSSION

NATURE OF THE INJURIES

The injuries observed here mostly fulfill the criteria for failed predation (sensu Pates et al., 2017; Bicknell and Pates, 2019; Pates and Bicknell, 2019): they are commonly cicatrized, exhibit typical injury shapes, and are mostly posteriorly located. *Arctinurus boltoni* unlikely experienced injuries from problematic molting as the pleural spines along the trunk are short and spatulate, so the emerging soft-shelled individual would have had little issue removing its

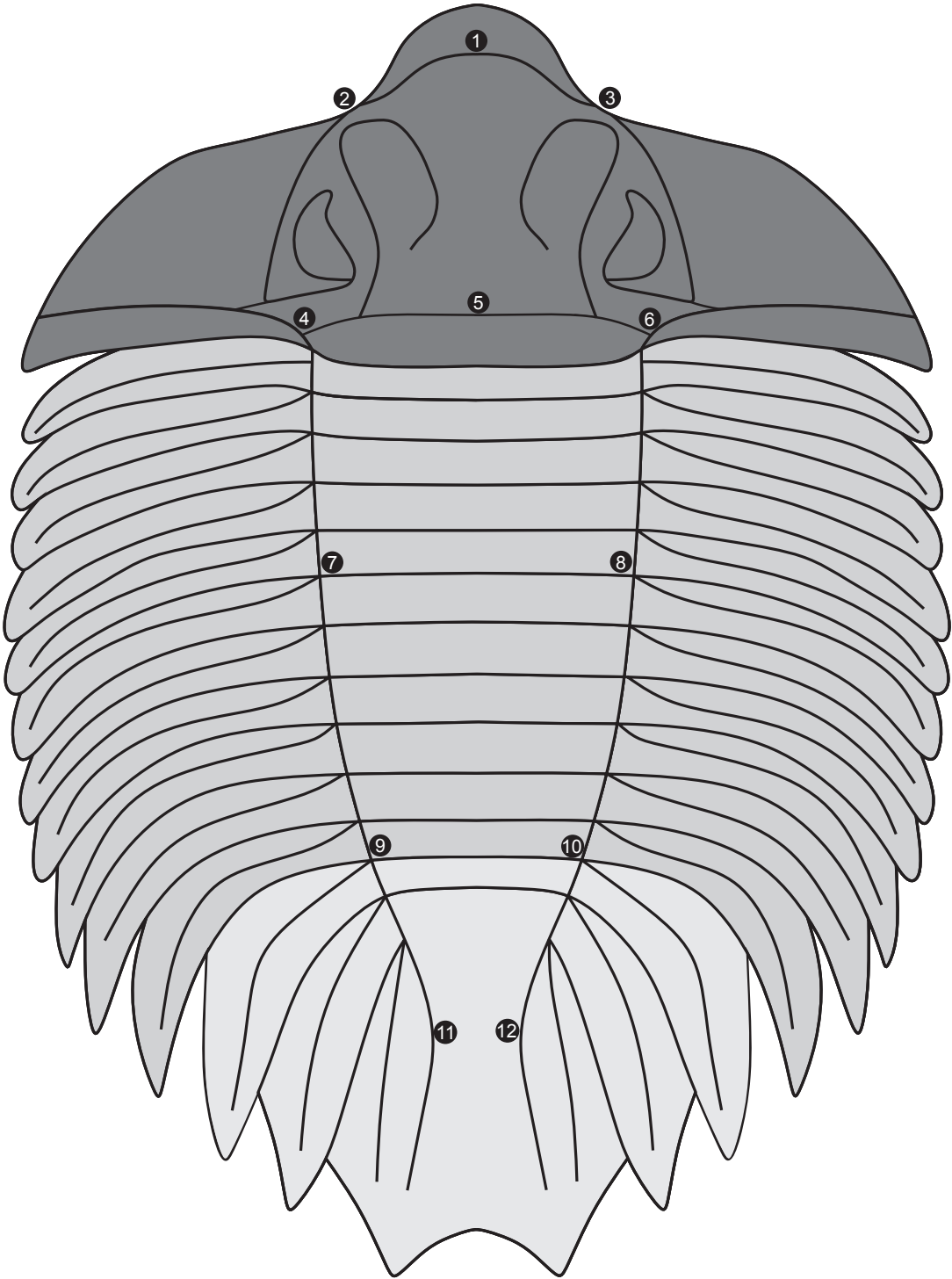


FIGURE 2. Diagram of 12 landmarks selected to describe the overall shape of the exoskeleton of *Arctinurus boltoni*.

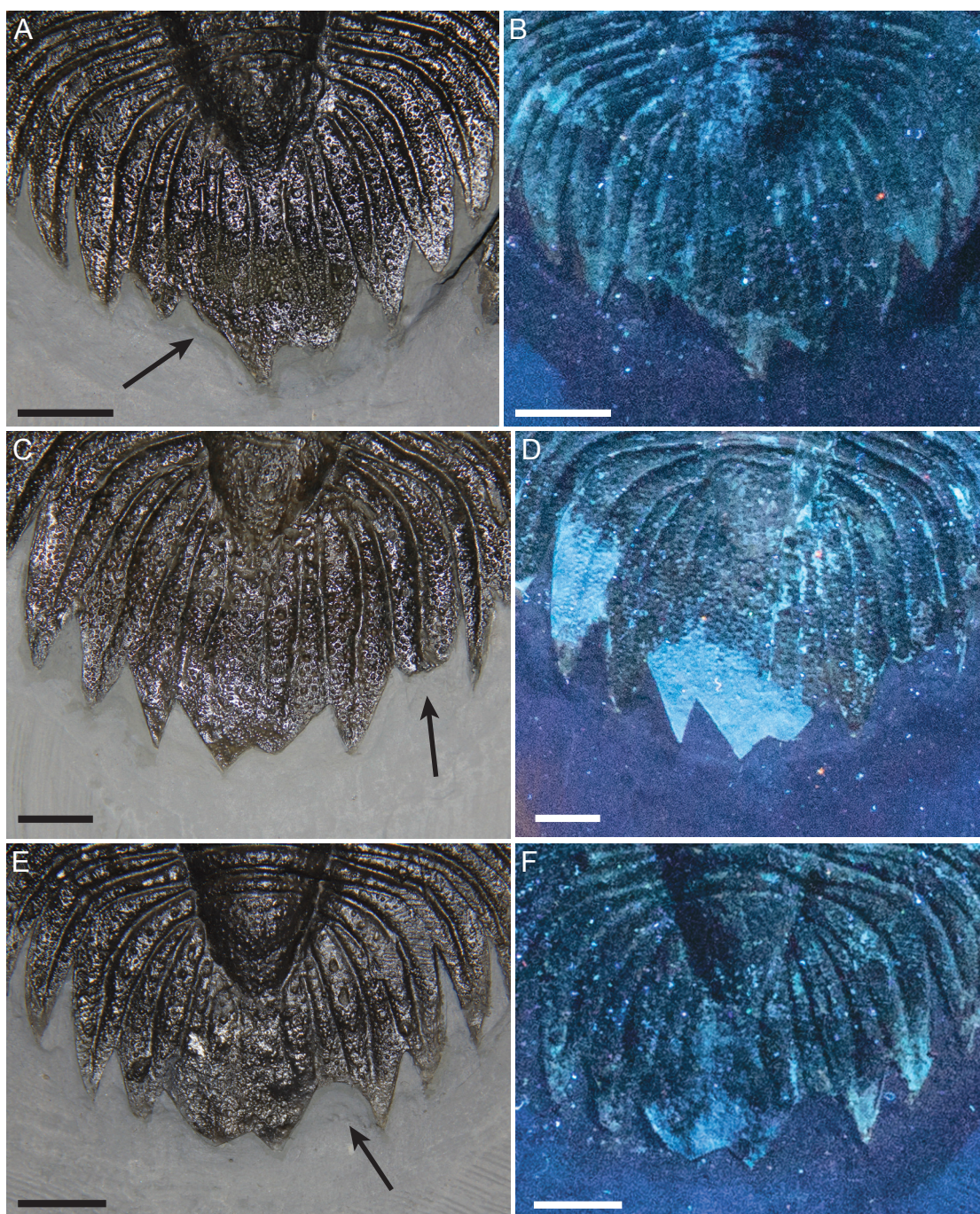


FIGURE 3. Specimens of *Arctinurus boltoni* with injuries to the pygidium, under plain and UV light (with brighter areas indicating parts of reconstructed exoskeleton). Arrows point to injuries described in the text. Scale bar = 1 mm. **A–B**, AMNH-FI-101521. **C–D**, AMNH-FI-101527.

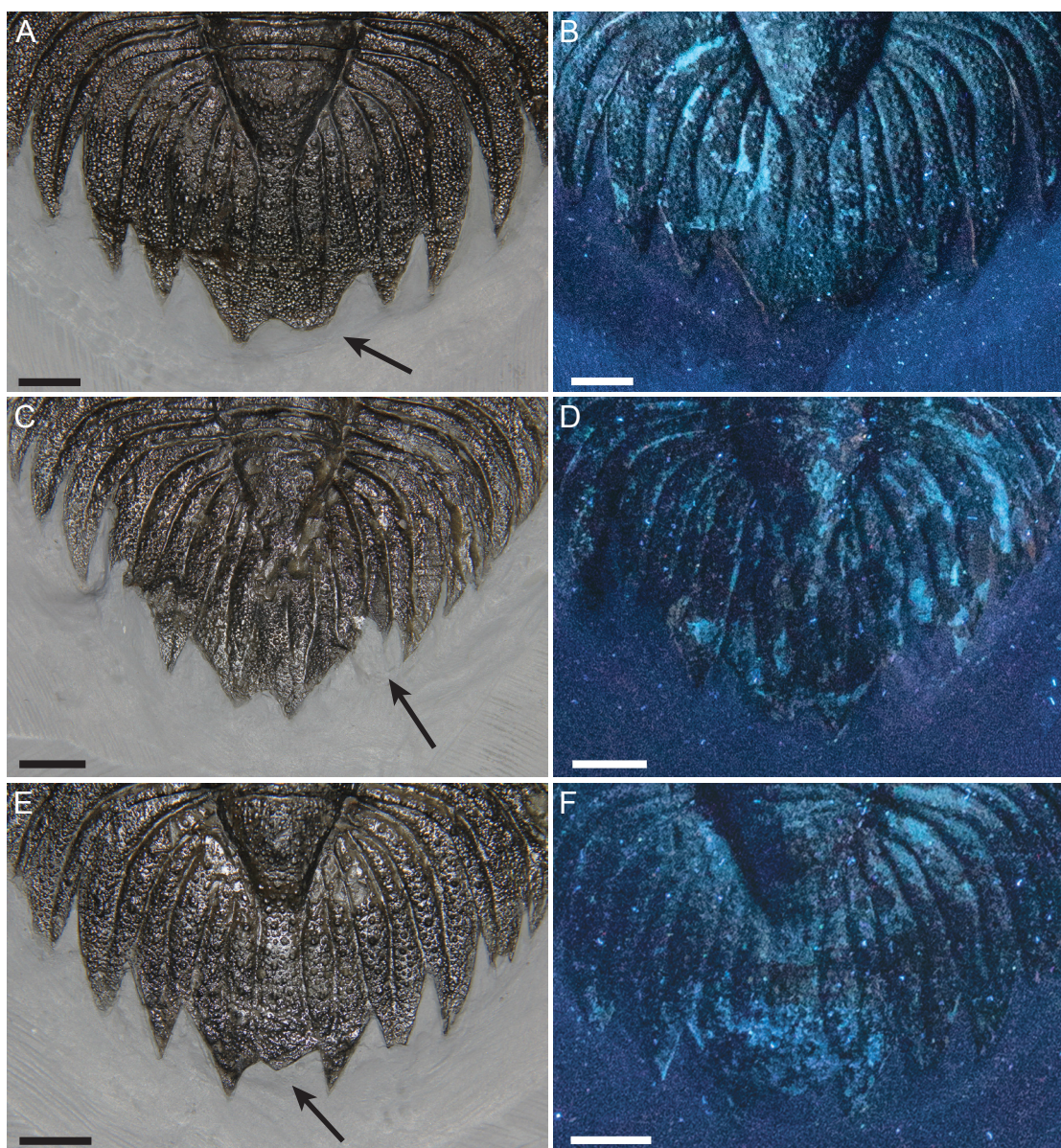


FIGURE 4. Further specimens of *Arctinurus boltoni* with injuries to the pygidium, under plain and UV light. Arrows point to injuries described in the text. Scale bar = 1 mm. A–B, AMNH-FI-101529. C–D, AMNH-FI-101530. E–F, AMNH-FI-101531.

spines from the old calcitic exoskeleton (Conway Morris and Jenkins, 1985; Daley and Drage, 2016). Furthermore, in the case of the cluster observed here, it seems improbable that around half of the preserved population would have undergone complications during ecdysis. Mechanical breakage due to transportation also seems unlikely, as the individuals appear to have been rapidly buried and preserved in situ (discussed further below).

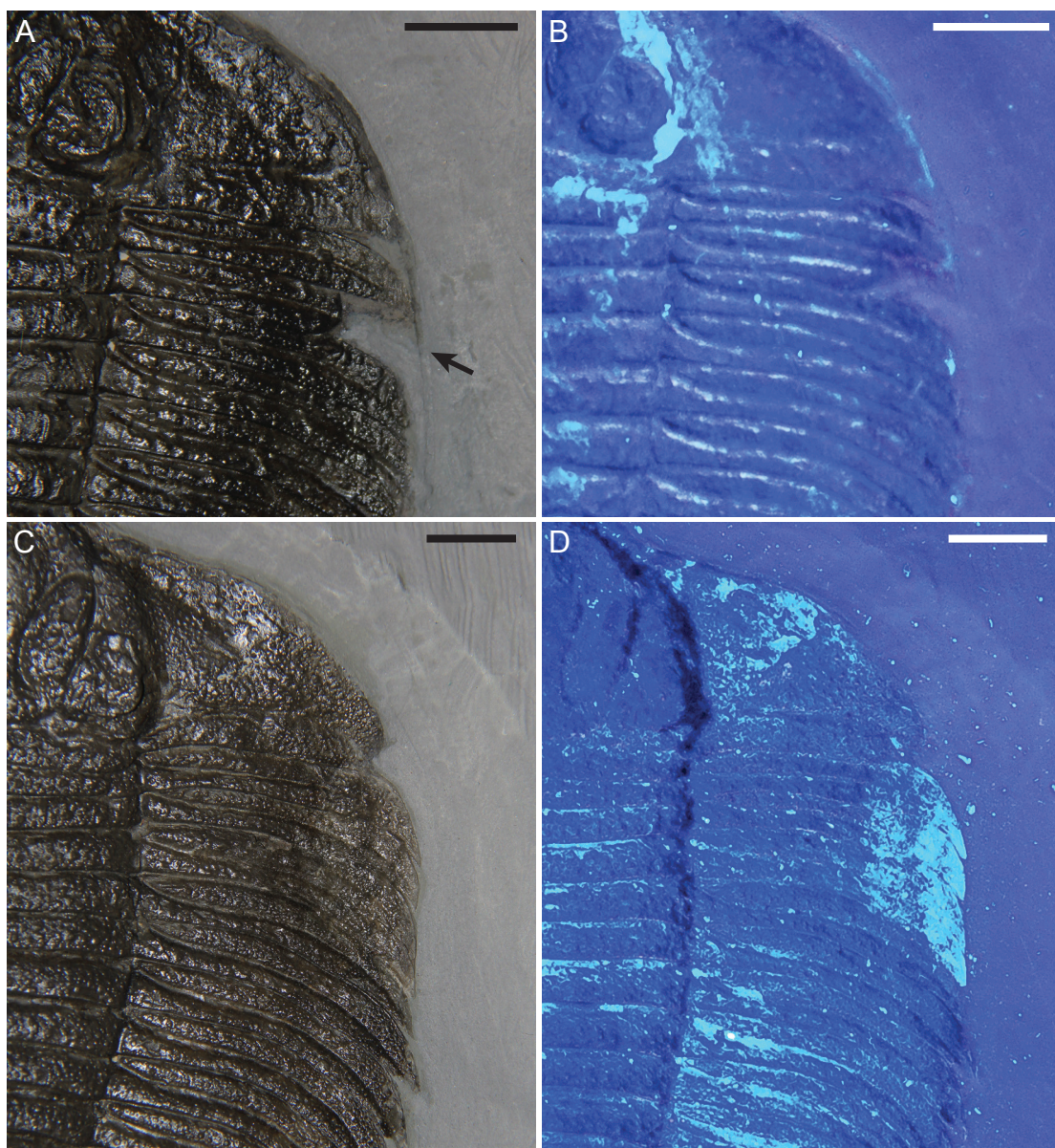


FIGURE 5. Specimens of *Arctinurus boltoni* with injuries to the thorax (A, B) and with reconstruction that mimics an injury (C, D), under plain and UV light. Arrows point to injuries described in the text. Scale bar = 1 mm. A–B, AMNH-FI-101518. C–D, AMNH-FI-101516.

The range of injuries documented here and noted in table 1 raises the question of predator identity. Based on the associated fauna within the Rochester Shale, Brett (2015) suggested that nautiloid cephalopods were the apex predators that attacked trilobites, with other suspects being phyllocarids or eurypterids (see Chinnici and Smith, 2015). More than one predator group may therefore have produced the variable record of injuries.

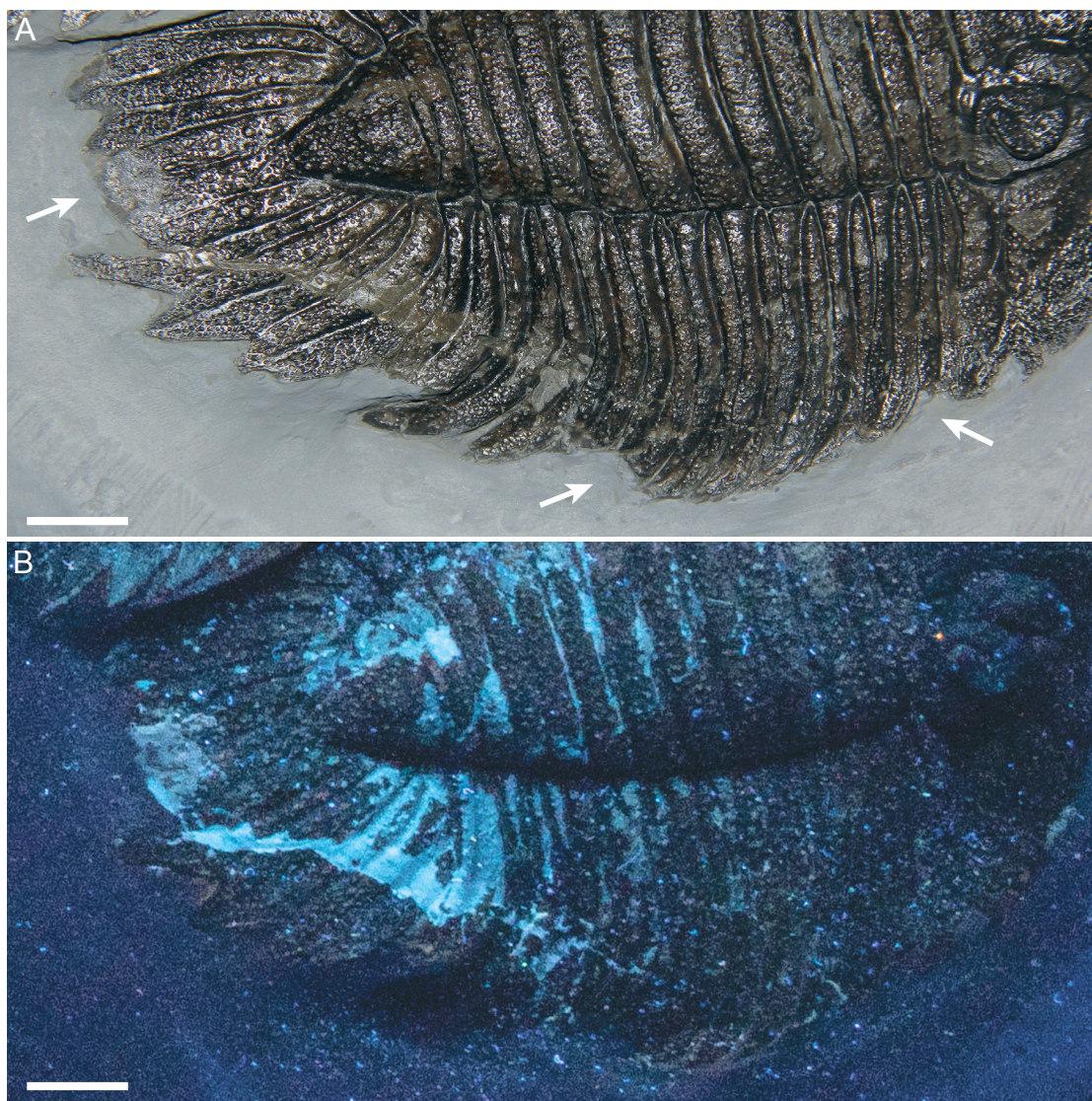


FIGURE 6. *Arctinurus boltoni* specimen AMNH-FI-101520 with injuries to the thorax and pygidium, under **A**, plain and **B**, UV light. Arrows point to injuries described in the text. Scale bar = 1 mm.

Using a broad dataset, Babcock (1993a) identified a preference for right-sided and posteriorly located injuries on Cambrian trilobites and also suggested that post-Cambrian injuries conformed less strongly to this pattern. Pates et al. (2017) and Pates and Bicknell (2019) reconsidered Babcock's ideas, but focused on single Cambrian-aged deposits and singular trilobite taxa within these deposits. They showed that there was no preference for which side the injury occurred, but confirmed that injuries are commonly posteriorly located. Contrasting both Pates et al. (2017) and Pates and Bicknell (2019), the Rochester Shale slab documented here shows strong right-sided injury dominance and preference for posterior locations. This demonstrates that either Rochester Shale predators potentially expressed a lateralized attack

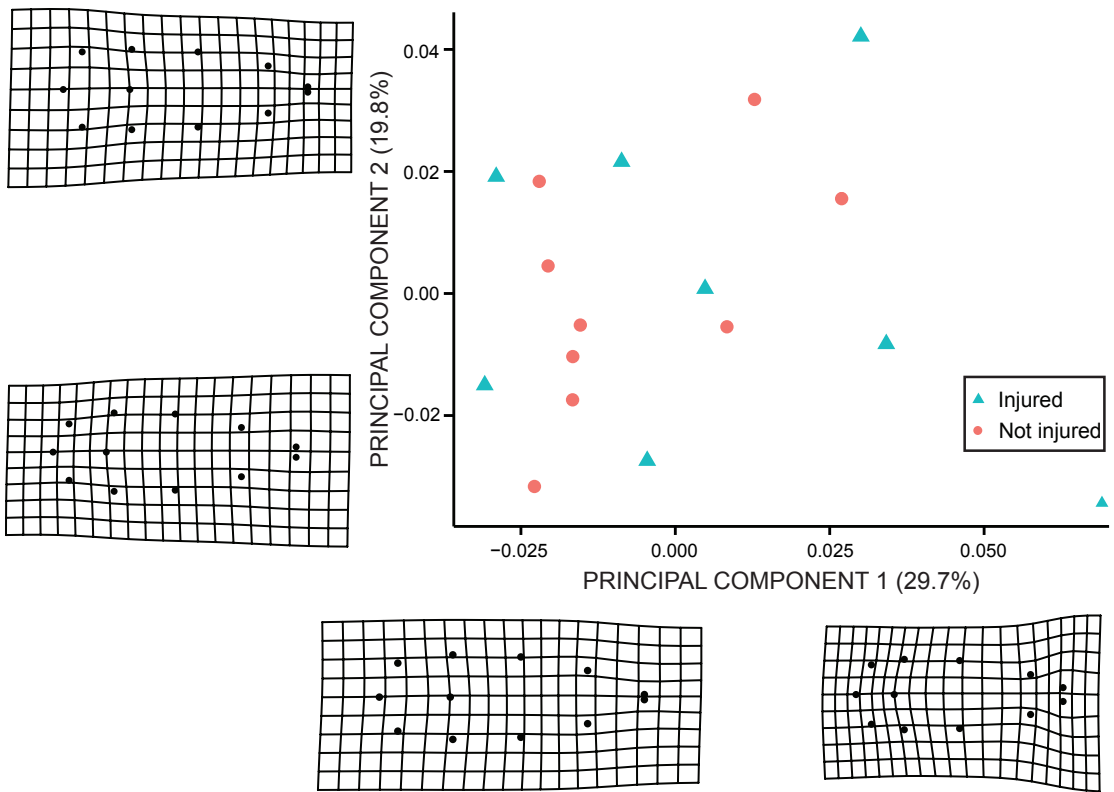


FIGURE 7. Principal components analysis of landmark data, with 49.5% variance in the data explained by the first two PCs (PC1=29.7%, PC2=19.8%). PC1 describes the variation in the intersection of the occipital furrow and anterior-posterior axis and junction points between posterior margin of the 11th tergite. PC2 mostly describes variation in cephalic width.

pattern, or *Arctinurus boltoni* had a lateralized defense strategy (see ideas in Babcock, 1993a). No grouping of injured and noninjured specimens was observed in PC space (fig. 7), but it seems that most of the larger specimens were injured (fig. 8). This may suggest a possible prey preference—with predators targeting larger and potentially less maneuverable individuals—but overall there is no strong support for any predatory choice. It is important to note that only eight associated injured specimens were considered in this study, so these conclusions are not supported statistically, but other previously illustrated examples of injured *A. boltoni* (table 1) seem to confirm some of the injury patterns observed here. More specimens are needed to build a large enough dataset to unambiguously confirm these ideas.

NATURE OF THE CLUSTER

Trilobite clusters that predominantly contain fully articulated individuals on single bedding planes are termed “body clusters” and record group mating, molting, or other gregarious activi-

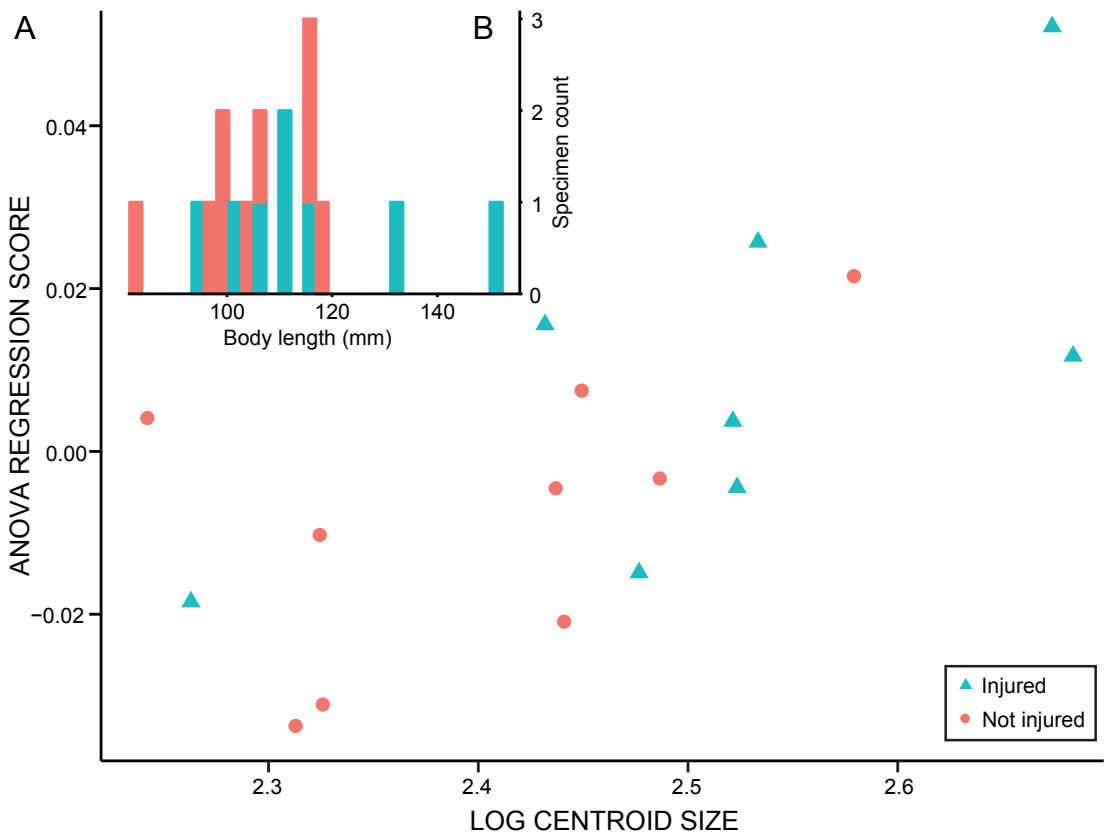


FIGURE 8. Plot of regressed PC coordinates against log-centroid size and histogram of maximum specimen length, coded for injured and noninjured specimens. **A**, Regressed PC coordinates against log-centroid size that shows no obvious pattern in injured and noninjured specimens, although many of the larger specimens are injured. **B**, Histogram of specimen length has an approximately normal distribution with the two largest specimens showing an injury.

ties that are preserved via rapid burial events, commonly induced by storms (Speyer and Brett, 1985; Karim and Westrop, 2002; Paterson et al., 2007, 2008; Gutiérrez-Marco et al., 2009; Brett et al., 2012; Brett, 2015; Schwimmer and Montante, 2019). As the Rochester Shale in the Orleans County area was deposited in a quiet, offshore shelf setting below normal wave base (Taylor and Brett, 1996; Whiteley et al., 2002; Brett, 2015), it is unlikely that the cluster represents a mechanical accumulation caused by strong bottom currents (Speyer and Brett, 1985; Brett et al., 2012). Biostratigraphic evidence, such as all the individuals being preserved in a prone position and with the same dorsoventral attitude on a single bedding plane (fig. 1), provides support that this cluster represents an *in situ* biological aggregation (or a “Type 1” assemblage, *sensu* Brett et al., 2012). Since the Rochester Shale depositional environment was subject to periodic storm disturbances (Taylor and Brett, 1996; Whiteley et al., 2002), this particular occurrence of clustered *Arctinurus boltoni* individuals was likely “buried in place by a heavy blanket of sediment” during a storm event (Whiteley et al., 2002: 41), although cause of death may have also involved asphyxiation (via temporary anoxic conditions) prior to burial.

Modern animal species congregate in groups for a variety of reasons and may occur through “self organization” (e.g., seasonal mating or migration) or result from a response to extrinsic factors, such as localized food sources or nearby predators (Allee, 1927; Alcock, 1993; Parrish and Edelstein-Keshet, 1999; Sumpter, 2006; Morrell and Romey, 2008; Sumpter, 2010). As noted above, trilobite body clusters have been interpreted as representing a variety of gregarious behaviors, with one of the most popular hypotheses for monospecific clusters being mass molting and synchronous reproduction (e.g., Speyer and Brett, 1985; Karim and Westrop, 2002; Paterson et al., 2007, 2008; Gutiérrez-Marco et al., 2009), as observed in modern arthropods such as the American horseshoe crab, *Limulus polyphemus* (Shuster Jr. et al., 2003). Although none of the individuals on the Rochester slab represent exuviae (see Daley and Drage, 2016 for criteria), they are monospecific, somewhat size segregated and, in some cases, partially overlapping, which are features used by Speyer and Brett (1985) in identifying body clusters that have formed just prior to mass molting and mating.

While the Rochester Shale body cluster may have assembled for the purpose of synchronous molting and mating, the noted absence of “molt clusters” in the Rochester Shale (Brett et al., 2012) and the considerable number of injuries among *Arctinurus boltoni* individuals provides evidence for another plausible explanation: group protection from predators. There is considerable evidence to suggest that trilobites clustered in cryptic places on the seafloor (e.g., within burrows or reef cavities, under or inside empty shells and exoskeletons, etc.) to perform a variety of gregarious activities (especially molting) while avoiding predators or environmental perturbations (see Chatterton et al., 2003; Gutiérrez-Marco et al., 2009; Fatka and Budil, 2014; Zong et al., 2016; references therein). However, the Rochester cluster was exposed on the seafloor prior to burial, so perhaps the only line of defense from predation was a “safety in numbers” approach. This is a common strategy among a huge variety of modern animals (Hamilton, 1971; Alcock, 1993; Morrell and James, 2007; Sumpter, 2010; Lehtonen and Jaatinen, 2016). Types of collective defense behaviors include: group vigilance (or the “many eyes” effect), where grouped prey can often detect predators more efficiently (e.g., faster) than solitary individuals (Treves, 2000; Beauchamp, 2015); the dilution effect, where, in general, the larger the group, the less likely a particular individual will be targeted by a predator (Foster and Treherne, 1981; Turchin and Kareiva, 1989; Ruxton and Sherratt, 2006); and the confusion effect, where large numbers of moving, phenotypically similar prey can reduce the ability of a predator to track an individual target (Landeau and Terborgh, 1986; Jeschke and Tollrian, 2007). While it is impossible to elucidate the specific gregarious behavior/s in the Rochester cluster, it is reasonable to suggest that trilobites, such as *A. boltoni*, living unprotected on the seafloor would have employed such a survival strategy.

ACKNOWLEDGMENTS

This research is supported by funding from an Australian Postgraduate Award and a Charles Schuchert and Carl O. Dunbar Grants-in-Aid Award (both to R.D.C.B.). We thank Paul Chinici and Carl Brett for useful discussions and providing pivotal literature. Furthermore, we

thank Carl Brett for his insightful comments that improved an early version of the text. Finally, we thank Olev Vinn and Oldřich Fatka for their helpful reviews.

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