Clustered and injured *Pseudogygites latimarginatus* from the Late Ordovician Lindsay Formation, Canada

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With 3 figures

Abstract: Insight into how extinct animals responded to injuries developmental malfunctions and pathologies can be derived by examining malformed specimens. Trilobites are an ideal group for understanding how a completely extinct group of arthropods responded to and recovered from these conditions, as their biomineralised exoskeletons preserves malformations. Here we consider a slab containing eight individuals of the asaphid trilobite *Pseudogygites latimarginatus* from the Collingwood Member of the Lindsay Formation, Canada. Examining this slab, two individuals with malformations are documented. These malformations are considered injuries and used to demonstrate how *P. latimarginatus* recovered from failed predation attacks, allowing us to consider possible predator groups. The cluster is interpreted as possible evidence for an *in situ* biological aggregation that was preserved prior to a moulting event. Implications for this gregarious behaviour are considered, presenting more insight into the palaeoecology of Ordovician asaphid trilobites.

Key words: Ordovician, injuries, trilobites, Lindsay Formation, Collingwood Member, predation, clusters.

1. Introduction

Trilobites are extinct marine arthropods with an exceptional fossil record ranging from the Cambrian to the end-Permian extinction (HUGHES 2007; PATERSON et al. 2019; SUÁREZ & ESTEVE 2021). Their biomineralised exoskeletons aided preservation, in addition to giving them protection and support during life (WEBSTER 2007). This same exoskeleton is ideal for preserving malformed trilobites in the fossil record (OWEN 1985; BABCOCK & ROBISON 1989; BABCOCK 1993; BABCOCK 2003; BABCOCK 2007; BICKNELL & PATERSON 2018). There is therefore a wealth of data on trilobite injuries (ŠNAJDR 1979a, ŠNAJDR 1979b, BABCOCK 1993; FATKA et al. 2015; BICKNELL & PATES 2020; FOSTER 2021; ZONG 2021; BICKNELL et al. 2022b; BICKNELL et al. 2022c; ZONG & BICKNELL 2022), teratologies (BERGSTRÖM & LEVI-SETTI 1978; OWEN 1985; BICKNELL & SMITH 2021; BICKNELL et al. 2023), and neo-

plasms (ŠNAJDR 1978; OWEN 1985; BICKNELL et al. 2022a; DE BAETS et al. 2022). Despite this literature, malformations are commonly considered as isolated examples (see tables in OWEN 1985; BICKNELL & PATERSON 2018; BICKNELL & SMITH 2021; BICKNELL & SMITH 2022; FATKA et al. 2022). However, a shift to considering malformations at the population level has occurred recently (PATES et al. 2017; BICKNELL et al. 2019a; PATES & BICKNELL 2019; BICKNELL & SMITH 2021; BICKNELL & SMITH 2022; BICKNELL et al. 2022a; BICKNELL et al. 2023). This new direction has allowed patterns in prey size to be uncovered (BICKNELL et al. 2022a), presented insight into injury recovery in trilobites (PATES & BICKNELL 2019), and highlighted patterns of teratological development for the group (BICKNELL & SMITH 2022).

Pseudogygites latimarginatus HALL, 1847 from the Late Ordovician (Katian, Cincinnatian Regional Series) Collingwood Member of the Lindsay Formation
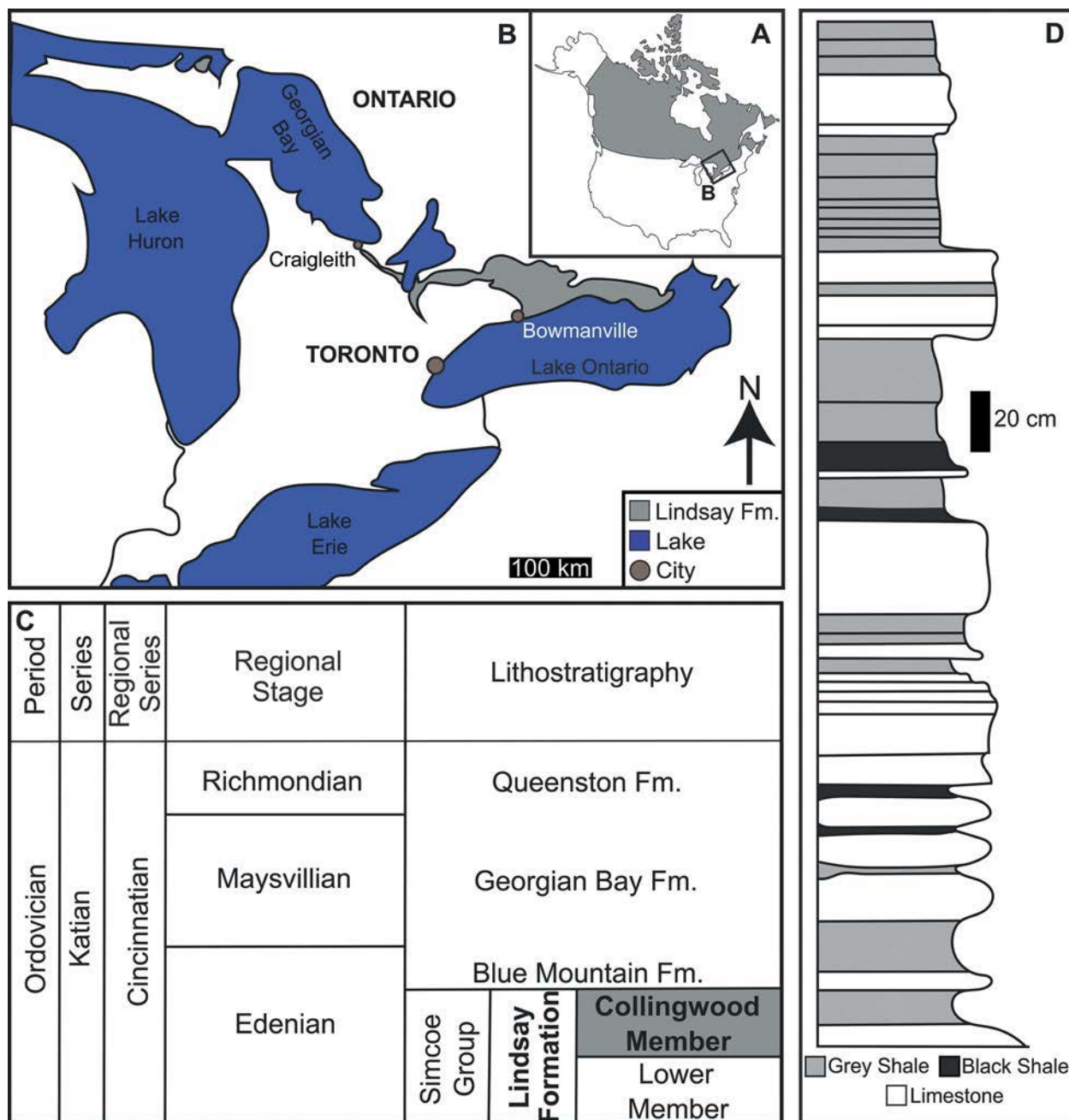
Fig. 1. Geographical and geological context for the Collingwood Member. **A** – Map of North America showing area of interest in box. **B** – Locality map. The slab comes from a quarry in Bowmanville, east of Toronto, Ontario. **C** – General lithostratigraphy of Upper Ordovician strata in southern Ontario, Canada. **D** – Stratigraphic section of the lower Collingwood Member at the Bowmanville. Figure elements for (**B**–**D**) after BRETT et al. (2006) and GBADEYAN & DIX (2013).

represents a possible target for documenting malformed trilobites within a larger population context. This is because injured (OWEN 1985; RUDKIN 1985) and teratological (BABCOCK 1993) specimens have previously been reported. Developing on this previous research, we considered museum collections housing other examples of this species. In this search, a slab of Collingwood Member preserving a cluster of eight, fully articulated

individuals of *P. latimarginatus* was identified. Importantly, two individuals on this slab show malformations. In documenting this slab, we explore the origin of these malformations and explanations for the cluster.

2. Geological content

The examined slab was collected from a quarry in Bowmanville, Ontario, Canada, east of Toronto (Fig. 1A, B), likely the Blue Circle Cement Ltd. Quarry or adjacent stream exposures. The material is from the Late Ordovician (Katian) in age Collingwood Member, formerly "Collingwood Formation" (RAYMOND 1912), within the Lindsay Formation (Fig. 1C, D). The Collingwood Member is up to 9 m thick and consists of black to brown carbonaceous and fossiliferous shale with limestone interbeds (ZHANG et al. 2011). The member has been interpreted as equivalent to at least part of the Utica Shale of eastern North America (ARMSTRONG & CARTER 2010; ZHANG et al. 2011). The shales are organic-rich and one of the earliest commercially exploited oil shale units (BRETT et al. 2006). The type section is near Craigleith Provincial Park, Georgian Bay (section 6; HAMBLIN 1999, figs. 2, 9). The Collingwood Member overlies the so-called 'Lower Member' of the Lindsay Formation and is overlain by the Blue Mountain Formation (BRETT et al. 2006; ZHANG et al. 2011).

The slab considered here originates from the black and grey shale facies of BRETT et al. (2006). Fossils in the shales are usually fragmentary, and trilobite fossils are usually represented by isolated cranidia or pygidia, However, there are rare horizons that yield articulated trilobites, including moults, similar to the slab considered here.

3. Material and methods

The studied slab of Collingwood Member (Fig. 2) is housed at the Palaeontological collection of the Staatliches Museum für Naturkunde Karlsruhe (SMNK-PAL), Karlsruhe, Germany. The slab was acquired in 1980 from R. HENZEL, Celle, Germany and assigned the specimen number SMNK-PAL 10390. *Pseudogygites latimarginatus* specimens were visually assessed under normal light for possible malformations. The slab and specimens were photographed normally and coated in ammonium chloride using a Canon EOS R5 camera mounted with an EF 100 f/2.8 Macro IS USM lens under white light. The colour, contrast, and brightness of the images were adjusted using Adobe Photoshop Lightroom. Specimen measurements were made from photographs in ImageJ (SCHNEIDER et al. 2012).

4. Terminology

Injury: Exoskeletal breakage because of injury, attack, or moulting issues (BICKNELL et al. 2022a). The malformations are commonly L-, U-, V-, or W-shaped indentations in the exoskeleton (BABCOCK 1993; BICKNELL & PATES 2019; BICKNELL et al. 2022a), or a 'single segment injury' (SSI; *sensu* PATES & BICKNELL 2019; BICKNELL & PATES 2020; BICKNELL et al. 2022a) and often show cicatrisation and/or segment regeneration. Rarely, exoskeletal areas can recover abnormally, resulting in exoskeletal section fusion and possible lack of segment expression (CONWAY MORRIS & JENKINS 1985; OWEN 1985; BICKNELL et al. 2022a; BICKNELL et al. 2023).

Malformation: Evidence for injuries, teratologies, or pathologies on the exoskeleton.

Teratology: The expression of genetic, developmental, or embryological malfunctions (OWEN 1985). Morphologies ascribed to teratologies include additional, removed, or offset spine bases, segments, and spines, as well as fusion or bifurcation of ribs, and abnormally developed exoskeletal structures (STRUSZ 1980; HOWELLS 1981; OWEN 1985; BICKNELL & SMITH 2021; BICKNELL & SMITH 2022).

Pathology: Malformations caused by infections or parasites. Swellings in constrained exoskeletal sections are often attributed to pathological infestation in trilobites (OWEN 1985).

5. Results

Two malformed *Pseudogygites latimarginatus* are identified. The first individual is partly preserved, missing the right side of the exoskeleton. The individual therefore consists of a partial cranidium, thorax, and pygidium, and is 47.7 mm long (Fig. 3A, C). The

Fig. 2. Slab preserving a cluster of eight articulated *Pseudogygites latimarginatus* (SMNK-PAL 10390) from the Late Ordovician (Katian) Collingwood Member of the Lindsay Formation, Canada. Yellow stars indicate injured individuals. Image credit: MATHIAS VIELSÄCKER.

left side of the cephalon has a W-shaped indentation that is 6.1 mm long (Fig. 3C, black arrows). The region proximal to the indentation lacks the genal spine, and shows rounding (Fig. 3C, white arrow).

The second malformed individual is 50.2 mm long, completely preserved, and has two malformations (Fig. 3B, D, E). The left side of exoskeleton has a large V-shaped indentation that extends from the 7th thoracic segment to the pygidium (Fig. 3B, D). The indentation extends 4.5 mm from the exoskeletal edge and truncates the 7th and 8th thoracic segments. Pygidial terrace lines are not present proximal to the malformation. The second malformation is located on the right side of the pygidium (Fig. 3B, E). The seventh pygidial rib terminates 1.4 mm from the axial ring, contrasting all other the pygidial ribs. Additionally, the pygidial border proximal to this malformation is asymmetrical, albeit subtly, compared to other specimens on SMNK-PAL 10390.
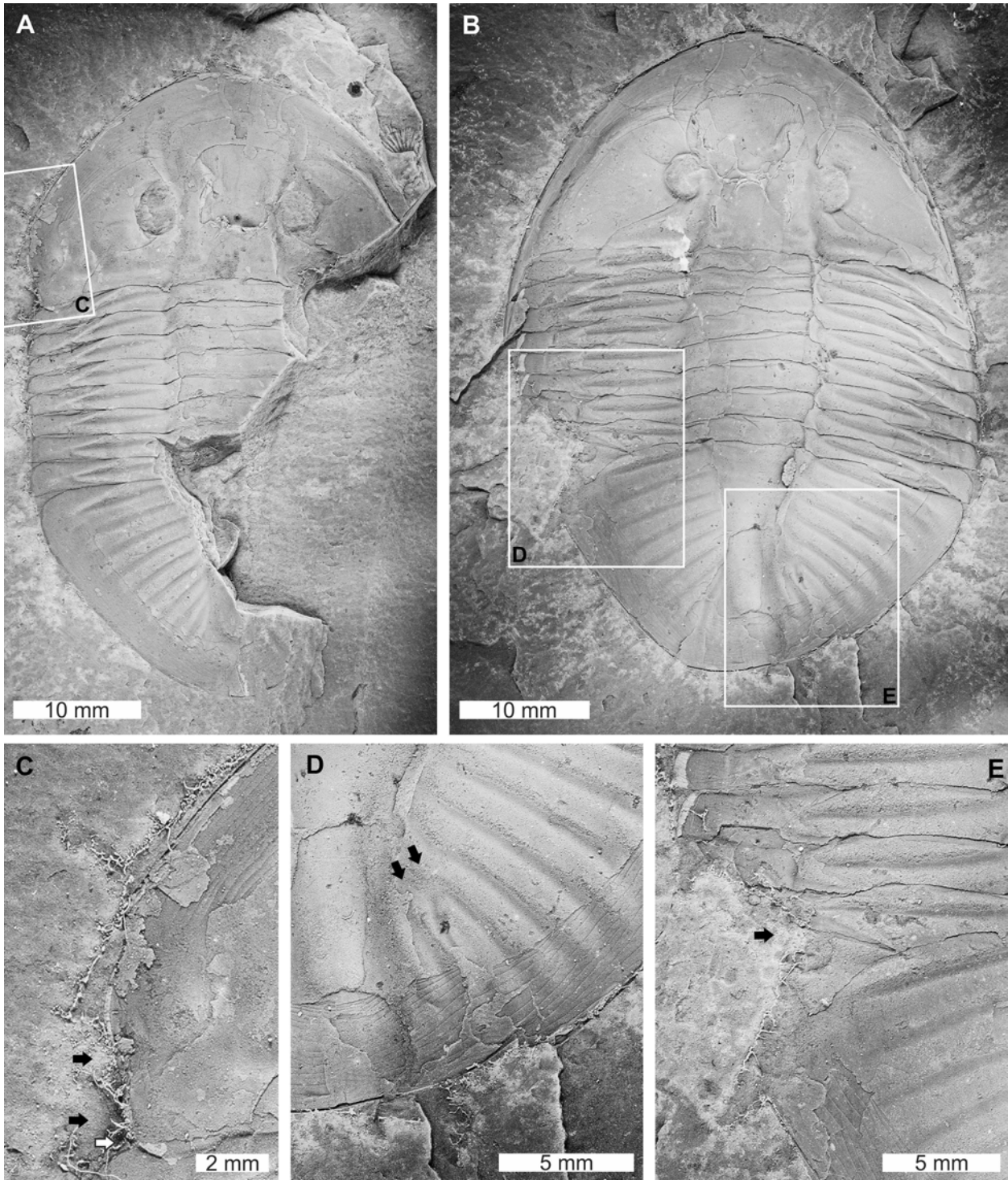
Fig. 3. *Pseudogygites latimarginatus* specimens with injuries. **A, C** – Partial specimen with a W-shaped injury to the left cephalic region. A: Complete specimen. C: Close-up of injury. **B, D, E** – Complete specimen with two injuries. B: Complete specimen. D: Close-up of V-shaped injury to thorax and pygidium. E: Close-up of malformed pygidial ribs. Black arrows in (**C–D**) indicate malformations described in text. White arrow in (**C**) indicates injury rounding. Trilobites coated in ammonium chloride before imaging. All images converted to greyscale. Image credit: MATHIAS VIELSÄCKER.

6. Discussion

Malformations observed here show little evidence of abnormal genetic developments and no indications of neoplasms (refer to Terminology section). These malformations are also broadly comparable to malformed Cambrian (Owen 1985; Bicknell & Paterson 2018, Bicknell et al. 2022a) and Ordovician trilobites considered to have injuries (see Sinclair 1947; Hessin 1988; Zong 2021; Bicknell et al. 2022b). As such, the malformations here are classed as injuries. The rounding of the injuries in Fig. 3 also indicates that these individuals were able to recover from these injuries in subsequent moulting events (Owen 1985; Bicknell et al. 2022a).

The W-shaped indentation in the cephalon shows a rare example a cephalic injury that likely did not result in death of the individual. There are two explanations for this injury. The first option is that the injury records failed or complicated moulting. While unlikely, this is possible as *Pseudogygites latimarginatus* has long genal spines that may have complicated moulting (Conway Morris & Jenkins 1985; Daley & Drage 2016). However, one would expect a stunted genal spine (see Hessin 1988; Bicknell et al. 2023) as opposed to complete spine removal and localised rounding of the injury. Furthermore, this injury is comparable morphologically to other examples of W-shaped indentations to the cephalic region (see Resser & Howell 1938; Babcock 1993; Bicknell et al. 2018d; Bicknell et al. 2022a). As such, while we cannot completely discount moulting, it seems more likely that this cephalic injury reflects failed predation.

The individual with the V-shaped indentation on the left side of the exoskeleton and the malformed pygidial ribs is an example of one specimen recording two possible events. The V-shaped injury is comparable to other recorded examples of trilobites with V-shaped indentations considered evidence of failed predation (see Rudkin 1979; Owen 1985; Bicknell et al. 2022a for examples). We therefore confidently ascribe this injury to failed predation. The malformed pygidial ribs and pygidial border could reflect failed predation, a complicated moulting event, or possible genetic malfunctions. However, as both the ribs and pygidial border are disrupted, a genetic explanation seems less likely. In this situation, we would expect to see fused ribs, without marked disruption of the border (Owen 1985). Regardless though, the ribs and pygidial border were disrupted and recovered abnormally.

The injuries from failed predation documented here and in Rudkin (1985) prompt some consideration of possible predators. The Collingwood fauna houses two groups of animals that could have been predators: nautiloids and trilobites (Russell & Telford 1983; Rudkin 1985; Brett et al. 2006). Nautiloid cephalopods are traditionally considered the primary injury producers in the Collingwood Member (Rudkin 1985; Nedin 1999). This is a perspective that seems likely. Furthermore, recent three-dimensional biomechanical analyses have presented strong evidence that trilobites and other artiopodans could have crushed biomineralised shell with gnathobasic spines on sets of walking legs (Bicknell et al. 2018b; Bicknell et al. 2021). This is akin to durophagous predation by modern day horseshoe crabs (Botton 1984; Bicknell et al. 2018a; Bicknell et al. 2018c). We therefore propose that both trilobites and large cephalopods produced these injuries. It is important to note that there are Ordovician predator groups that could have caused these injuries that may not be preserved within the fossil record of the Collingwood Member (see Brett 2003) or may not have been collected (Whitaker & Kimmig 2020). Further examination of the deposit may therefore uncover new evidence of other predators.

Trilobite clusters consisting of mostly fully articulated individuals preserved on the same bedding plane are termed 'body clusters' that record mating, moulting, or other gregarious activities that are preserved through rapid burial events, commonly storms (Speyer & Brett 1985; Karim & Westrop 2002; Paterson et al. 2007; Paterson et al. 2008; Gutiérrez-Marco et al. 2009; Brett et al. 2012; Brett 2015; Schwimmer & Montante 2019; Corrales-García et al. 2020). Large monospecific clusters of smaller trilobite species have also been considered evidence for exaerobic specialist inhabiting low-oxygen conditions (Gaines & Droser 2003; Paterson et al. 2016; Holmes et al. 2021). The Collingwood Member beds that preserve *Pseudogygites latimarginatus* are considered to represent deep to moderately deep muddy substrates, that ranged between dysoxic to fully oxic, and had limited influence of distal storms (Brett et al. 2006). Given this depositional environment and the fully articulated nature of the individuals, the trilobite cluster considered here shows little evidence for mechanical accumulation by bottom currents. Furthermore, preservation of individuals in the same dorsoventral attitude on the same bedding plane (Fig. 2) supports the interpretation of this cluster as an *in situ* biological aggregation. Finally, as *P. latimarginatus*

is larger than forms commonly considered exaerobic specialist (see GAINES & DROSER 2003; PATERSON et al. 2016; HOLMES et al. 2021) and lived within dysoxic to oxic conditions, evidence of exaerobic forms can likely be discounted. As such, we consider this aggregation to be a 'body cluster'. Trilobite 'body clusters' are thought to be reflect behaviours such as mass moulting, or synchronous reproduction (see SPEYER & BRETT 1985; SPEYER 1987; HUGHES & COOPER 1999; KARIM & WESTROP 2002; PATERSON et al. 2007; PATERSON et al. 2008; GUTIÉRREZ-MARCO et al. 2009; BICKNELL et al. 2019a). Similar clustering events are observed in modern and fossil horseshoe crabs (SHUSTER JR. 1982; SMITH et al. 2002; SHUSTER JR. et al. 2003; MCGOWAN et al. 2011; BICKNELL et al. 2019b). The monospecific individuals on the Collingwood slab with no evidence of moulting indicates that the 'body cluster' reflects a possible moulting and mating event that was preserved before the moulting began (SPEYER & BRETT 1985).

Acknowledgements

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