TRILOBITE 'PELOTONS': POSSIBLE HYDRODYNAMIC DRAG EFFECTS BETWEEN LEADING AND FOLLOWING TRILOBITES IN TRILOBITE QUEUES

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Abstract: Energy saving mechanisms in nature allow following organisms to expend less energy than leaders. Queues, or ordered rows of individuals, may form when organisms exploit the available energy saving mechanism while travelling at near-maximal sustainable metabolic capacities; compact clusters form when group members travel well below maximal sustainable metabolic capacities. The group size range, given here as the ratio of the difference between the size of the largest and smallest group members, and the size of the largest member (as a percentage), has been hypothesized to correspond proportionately to the energy saving quantity because weaker, smaller, individuals sustain the speeds of stronger, larger, individuals by exploiting the energy saving mechanism (as a percentage). During migration, small individuals outside this range may perish, or form sub-groups, or simply not participate in migratory behaviour. We approximate drag forces for leading and following individuals in queues of the late Devonian (*c.* 370 Ma) trilobite *Trimerocephalus chopini*. Applying data from literature on *Rectisura herculea*, a living crustacean, we approximate the hypothetical walking speed and maximal sustainable speeds for *T. chopini*. Our findings reasonably support the hypothesis that among the population of fossilized queues of *T. chopini* reported in the literature, trilobite size range was 75%, while the size range within queues was 63%; this corresponds reasonably with drag reductions in following positions that permit *c.* 61.5% energy saving for trilobites following others in optimal low-drag positions. We model collective trilobite behaviour associated with hydrodynamic drafting.

Key words: trilobite, peloton, drafting, hydrodynamic drag, collective behaviour, group sorting.

THE fossil record reveals that some trilobite species formed aggregations (Speyer & Brett 1985; Karim & Westrop 2002; Radwański *et al.* 2009). Queuing behaviour, the tendency to form single-file rows of individuals, has been observed in Early Ordovician *Agerina* and *Ampyx* trilobites (Chatterton & Fortey 2008), the giant Middle Ordovician trilobites *Bathycheilus*, *Salterocoryphe* and/or *Retamaspis* (Gutiérrez-Marco *et al.* 2009), the blind Late Devonian phacopid *Trimerocephalus chopini* (Kin & Błażejowski 2013; Błażejowski *et al.* 2016), fossilized enigmatic Cambrian arthropods (Hou *et al.* 2008, 2009) and in living spiny lobsters (Bill & Herrnkind 1976). Fossilized 'beaten' trackways of probable eurypterids indicate similar queueing behaviour (Draganits *et al.* 1998, fig. 6; Braddy 2001).

The focus of this study is on *Trimerocephalus chopini*, for which the highest number of trilobites in collected fossilized queues was 19 (Błażejowski *et al.* 2016). Most queues were composed of the largest individuals, while the smaller individuals were in short queues of two individuals (Błażejowski *et al.* 2016). Queues were organized in straight single-files, or slightly twisted, or arched, either separated with no contact, or with head-to-tail contact and overlap to varying degrees (Radwański *et al.* 2009; Błażejowski *et al.* 2016) as shown in Figure 1C, D. Queues have also been described in zig-zag or wavy patterns (Gutiérrez-Marco *et al.* 2009). Of course, such queuing behaviour is almost certainly under-represented in the fossil record as very special conditions of synchronous mortality and rapid burial without seafloor disturbance are required to preserve such rows.

In addition to queue formations, aggregations of trilobite fossils appear in more compact non-linear 'clusters', which Speyer & Brett (1985) defined as 'a group of three or more trilobites along a single bedding plane in which adjacent individuals are no more
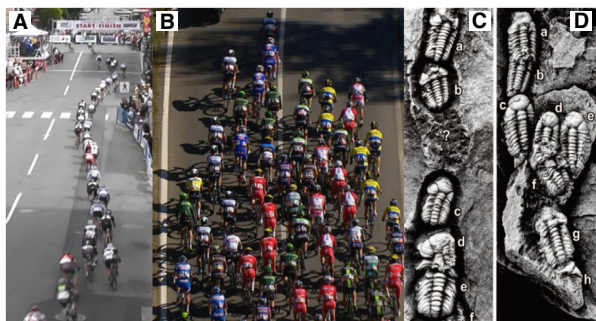
FIG. 1. A, cyclists in single-file travel at near maximal sustainable outputs. B, cyclists in unidirectional compact formation travel at below maximal sustainable outputs (from Trenchard & Perc 2016, figs 5B and 13A, with permission from the publisher). C, the trilobite *Trimerocephalus chopini* in single-file queue suggests trilobites travelling at speeds approaching maximal sustainable outputs (Radwański *et al.* 2009, pl. 4; CC BY). D, formation somewhat more compact than in image C, which may show a transition state in which leaders are decelerating and being passed laterally by followers, producing an increasingly compact formation; or an acceleration by leaders producing increased queue stretching. Colour online.

than two centimetres from one another' (p. 90). The authors reported clusters of between three and more than 200 randomly oriented individuals. Speyer & Brett (1985) proposed that fossilized cluster assemblages revealed synchronous moulting and possibly mating behaviour. Because of random orientations and evidence of moulting within clusters, these groupings probably do not record active migration, although aggregation itself implies some, at least local, migration. However, other trilobite clusters with non-random directions of cephala could represent a distinct type of migratory behaviour.

Migration may be defined as 'the directional movement of individuals of one species between distinct locations. The timescale on which these movement cycles occur can span hours, days, months or years, or it can be multigenerational' (Liedvogel *et al.* 2011, p. 562, box 1). Dingle & Drake (2007) identified migration as one category of animal collective movement, which 'can be divided into those that occur within the home range and those that take the individual more or less permanently beyond it' (p. 116). Trilobite queuing behaviour may have occurred during both short range commutes within the home range to and from spatially separated resource patches or roost sites, and long distance migration permanently away from the initial home range.

With respect to single-file formation as a mode of collective locomotion, extant spiny lobsters form queues (Bill & Herrnkind 1976) when travelling ocean floors. Bill & Herrnkind (1976) demonstrated that spiny lobsters obtain

c. 65% reductions in energy expenditure while travelling along ocean beds in single-file formations.

Spiny lobster queue formations are unique among benthic crustaceans (Herrnkind *et al.* 1973) but single-file travelling formations have been observed among other arthropods, including ants (e.g. Wilson 1959; Hansen & Klotz 2005, p. 135), juvenile spiders (Reichling 2000), whirligig beetles (Heinrich & Vogt 1980), weevil larvae (Fitzgerald *et al.* 2004) and a variety of caterpillars (Steinbauer 2009). Among these, ant single file formations have been modelled and studied in terms of energy optimization (Chaudhuri & Nagar 2015), but we found no reports quantifying the energy savings obtained by such formations.

Amid the fossil record, there is evidence of high density (*c.* 150 per m^2) trackways of unidirectional migration among Late Jurassic isopods from the Crayssac Lagerstätte of France, thought to have been imprinted in soft-to-firm mud of a temporarily emerged tidal flat (Gaillard *et al.* 2005, fig. 11B). Given their high density and apparent near proximity to each other during locomotion, the trackways suggest compact collective configurations like those observed among bicycle pelotons, as shown in Figure 1B, although it is difficult to interpret such isopod collective motion as involving hydrodynamic drafting.

Bicycle peloton (group of cyclists) formations are generated largely by the energy saving mechanism of aerodynamic drafting. Drafting, either aerodynamically or hydro-dynamically, occurs when bodies, following in the wake of leading bodies, encounter reduced drag (Hoerner 1965). For cyclists, riding in zones of reduced air drag permits weaker cyclists, who may otherwise be incapable of such speeds in isolation, to sustain the same speeds as stronger cyclists (Olds 1998; Trenchard *et al.* 2014, 2015).

Although driven in part by human-based competitive strategy, pelotons exhibit self-organized collective behaviours that emerge largely as a function of the metabolic outputs of the individuals within the group, and the power output reductions afforded by drafting (Trenchard *et al.* 2014). As cyclists approach their maximal sustainable capacities, formations stretch into single-file lines (queues); below a certain output threshold, single-file lines tend to collapse into compact unidirectional formations, as shown in Figure 1A, B (Trenchard *et al.* 2014, 2015; Trenchard 2015).

Similar energy saving mechanisms involving hydrodynamic media have been demonstrated for a broad range of organism body sizes, which mechanisms facilitate generally unidirectional aggregations. For example, grey mullet fish (*Liza aurata*) with body lengths of *c.* 12 cm obtain an energy saving of up 19%, where optimal energy saving positions are at angles to nearby fish (Marras *et al.* 2015). Mysid shrimp (*Paramesodopsis rufa*) with body lengths of 0.9–1.3 cm, generate flow wakes and reduced

energy requirements for those following in wakes (Ritz 2000). Wakes of similar-sized krill are shown also to project at angles to body orientation (Yen et al. 2003). At still smaller scales, drafting dynamics have been demonstrated for spherical inanimate particles in liquid, of diameter 0.1–0.2 cm, following directly behind leading particles (Wang et al. 2014). For a review of energy reduction mechanisms in a variety of biological and non-biological circumstances, exhibited across the entire range of animal sizes from bacteria to whales, see Trenchard & Perc (2016).

Hydrodynamic drafting appears to be a physical mechanism not yet considered in the trilobite literature as a driving mechanism of aggregative trilobite behaviour, even though it has been demonstrated for modern arthropods travelling in queues (Bill & Herrnkind 1976). Here we consider the presence of hydrodynamic drag, drafting opportunities, and energetic differentials among trilobites in leading and following positions within queues.

We consider the behavioural consequences of these differentials, and their effects on the relative sizes of individual trilobites. In this context, certain scaling rules are applicable: except for birds and very large animals, speeds tend to scale with body mass (Garland 1983); speed is also proportionate to body length, a rule that applies across the range of running and swimming organisms from bacteria to arthropods to whales (Meyer-Vernet 2015) and as indicated by Jamieson et al. (2012); this is discussed in detail below. Moreover, juveniles tend to be slower, weaker and less agile than adults of the same species (Carrier 1996). It is thus reasonable to assume that larger trilobites were capable of higher speeds than smaller trilobites. Also, because drafting generates reductions in metabolic and power requirements, it is reasonable to conclude that smaller trilobites could sustain speeds by drafting that were otherwise unsustainable when travelling in isolation. In this paper we model these effects.

Furthermore, we argue that published *T. chopini* size ranges and queue behaviours are consistent with the variation range hypothesis raised by Trenchard & Perc (2016). The variation range hypothesis posits that the size range among individuals in groups corresponds proportionately to the energy saving quantity (as a percentage) because weaker, smaller, individuals sustain the speeds of stronger, larger, individuals by exploiting the energy saving mechanism. We determine size range using

$$SR = [(BL_{max} - BL_{min})/BL_{max}] \times 100 \qquad (1)$$

where *SR* is size range, and *BL* is body length. As discussed further below, this allows comparisons of size ranges and energy saving as a percentage, shown as Equation (8).

Individuals too small to fit within this range become isolated from the group and may perish, or form sub-

groups with narrower size ranges, as has been modelled by Trenchard et al. (2015) in the context of bicycle pelotons. In the wider context of migration as a factor that drives speciation (Winker 2000), we consider the possibility that this form of group-sorting may contribute to migratory divergence and to reproductive isolation, as proposed by Delmore et al. (2012).

Speyer & Brett (1985) reported that individuals within trilobite groups generally fall within a rather narrow size range, a finding which tends to support the variation range hypothesis. Moreover, the presence of any similarly sized trilobites of other species mixed with clusters of another species also tends to support the variation range hypothesis, since such individuals would probably have possessed similar power and speed capacities.

For example, Robison (1975) reported that several agnostid species (Wheeler formation, Utah) were aggregated within comparatively narrow size ranges in which inter-species' maximum pygidial length ratios were measured at between 1.0 and 1.54. Hickerson (1997) reported mixed trilobite species associations in the Middle Devonian Little Cedar Formation (Illinois) (c. 44% mixed), in which clusters tended to be size-sorted. Some clusters included a specimen that was significantly smaller than the others and, in a few clusters, a size range was evident, although the specific size range was not reported (Hickerson 1997). Hickerson (1997) did report an instance of a 1.75 cm *Dechenella? prouti* on top of three c. 3.5 cm *Phacops iowensis iowensis* (50% range), well within the range predicted by the variation range hypothesis. It is not known, however, whether these species engaged in queueing behaviour or otherwise exploited hydrodynamic drafting during collective locomotion.

METHOD

Trilobite queue formations may be understood as a relationship between the power output of the leading trilobite in the high-drag position, the energy reduction afforded by the energy saving mechanism, and the maximal sustainable power output of the following trilobite. Power output may be approximated in terms of speed assuming constant environmental conditions. Thus:

$$TCR = (S_{front} \times D)/MSO_{follow} \qquad (2)$$

where TCR is 'trilobite convergence ratio'; S_{front} is the speed of the trilobite in the high drag position, which sets the pace for followers; *D* is the drafting coefficient, or the proportion of power (here considered in terms of speed) required for a trilobite in a low drag (drafting) position relative to the power required for the trilobite in the leading, high drag, non-drafting position ($(1 - D)$ is the

energy saving benefit to the following trilobite as a percentage); MSO_{follow} is the maximal sustainable speed of following trilobites in reduced drag following positions. MSO_{follow} varies according to the distance over which a given speed is sustained, and may also be reduced by fatigue.

Trilobites' sustainable relative speeds and their corresponding metabolic requirements are unknown. However, modern analogues provide some insights. For example, it is known that ghost crab endurance time as a function of speed drops rapidly as speeds increase and, in general, smaller animals attain maximum oxygen consumption at lower speeds than do larger animals (Full 1987). Similarly, it has been shown that when travelling up to 12 h a day, terrestrial red crabs tend to travel at mean walking speeds near their maximum aerobic speed, using a mixed migration strategy in which pauses are interspersed with periods of locomotion that exceed crabs' maximum aerobic speed (Adamczewska & Morris 1998). By comparison, for human cyclists, the 'power output profile' consists of five sustainable capacities: explosive, or 'sprint' speeds, sustainable for c. 10 s; lactic tolerance speeds, sustainable for c. 30 s; maximal aerobic power, sustainable for c. 5 min; anaerobic threshold, sustainable for between 20 and 60 min; and endurance, sustainable for up to several hours (Pinot & Grappe 2010).

With respect to queue formations, the durations for which trilobite queues were sustained are unknown. However, extant arthropods (spiny lobsters) are known to travel in queues for many hours (Bill & Herrnkind 1976) so we may consider that the maximal sustainable speed of following trilobites occurred over several minutes to hours before substantial output reductions were required. In long range migrations, we may expect short periods of 'explosive' or lactic tolerance speeds during flight from predators, and relatively longer periods of endurance output. Or, like terrestrial red crabs, we may expect periods during which speeds exceeded maximum aerobic capacities, interspersed with pauses to rest or to feed. Moreover, if trilobites tended to migrate at mean speeds close to their maximum aerobic speeds as do terrestrial red crabs (Adamczewska & Morris 1998) then this would support the energy saving advantage of travelling in queues. Regardless, because data are not available to determine accurately the trilobite 'power profile', we adopt a singular MSO_{follow} that corresponds to mid-range sustainable outputs and is constant for each trilobite individually in correspondence with their size, as discussed subsequently.

Our objective is thus to derive *T. chopini* travelling speeds and their maximal sustainable outputs (MSO_{follow}) and to evaluate whether observed size ranges for *T. chopini* within queues (Kin & Błażejowski 2013) are consistent with the variation range hypothesis.

Our analysis involves three primary steps. First, we demonstrate the availability of hydrodynamic drafting for trilobites. We determine a drafting coefficient (D) by applying the drag coefficient from Hoerner (1965) for a streamlined half-body, which approximates the lateral profile of *T. chopini*, as indicated in Figure 2. Figure 2 shows the outstretched profile of a *Trimerocephalus interruptus*, a species of the same genus as *T. chopini*. This profile is consistent with inferred outstretched profiles of *T. chopini* shown by Kin & Błażejowski (2013) and Błażejowski *et al.* (2015).

Secondly, we determine realistic trilobite travelling and maximal sustainable speeds. For this we reconstruct speeds determined empirically for *Rectisura herculea*, a living crustacean of similar morphology to *T. chopini* and between about 2.5 and 5 times the size of *T. chopini* (Jamieson *et al.* 2012), to obtain a regression polynomial equation. We apply this equation to extrapolate travelling and maximal sustainable speeds of *R. herculea* for *T. chopini* body length (*BL*) range 0.5–2.0 cm (75% range), as reported by Radwański *et al.* (2009). We note that Błażejowski *et al.* (2016) reported a similar *BL* range of 0.7–1.9 cm (63% range) for *T. chopini* in queues.

Thirdly, we model trilobite collective behaviours, including the physical and physiological conditions underlying queuing behaviour and group sorting.

RESULTS

Hydrodynamic drafting availability for trilobites

We have approximated drag forces for both the front trilobite and the drafting trilobite. Here 'front trilobite' refers to a trilobite in the high-drag leading position, and 'drafting trilobite' refers to a following trilobite that enjoys the energy saving of drafting. Drag force, F_d, is (Hoerner 1965):

$$F_d = \frac{1}{2}(C_d \times p \times S \times V^2) \qquad (3)$$

where C_d is the drag coefficient (dimensionless) and is equal to 0.07 for a streamlined half-body placed on a wall
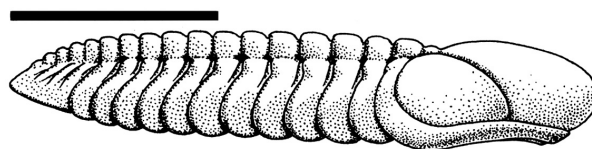

FIG. 2. Outstretched *Trimerocephalus interruptus* (modified from Berkowski 1991, fig. 4B; CC BY), with streamlined half-body morphology similar to that of *T. chopini*. Scale bar represents 1 cm.

(Hoerner 1965, ch. 8, p. 8-4), characteristic of a benthic trilobite in locomotion on an ocean bed, and where the streamlined half-body shape is similar to *T. chopini* morphology, as shown in Figure 2; *p* is fluid density = 1027 kgm^{-3} for seawater at 16°C; *S* is frontal surface area (m^2) which we determined for a holaspid (late stage) *T. chopini* as 2.7×10^{-5} m^2 by applying scaled length and height dimensions from Kin & Błażejowski (2013) (their fig. 4B) to a simplified cross-sectional elliptical shape; *V* is relative velocity of fluid (ms^{-1}), equivalent to the velocity of the trilobite moving through water.

C_d is largely a function of body shape, orientation, surface smoothness and position relative to other bodies (Hoerner 1965; Denny 1989); flow velocity is less important (Chamberlain 1976). Hydrodynamic drag coefficient of a streamlined body approximately corresponds to aerodynamic drag coefficients (Hoerner 1965, ch. 10, p. 10-14).

Drag coefficients consistent with those reported by Hoerner (1965) were reported for cephalopod shells with maximum diameter 12.7 cm (Chamberlain 1976) and are independent of body size (Hoerner 1965), while drag force scales with the size of the organism (Denny & Blanchette 2000).

We could not find reported drag coefficients for an in-wake streamlined half-body, but we may estimate that coefficient by reference to reported drag coefficients for two cylinders in tandem, where C_d for the in-wake cylinder is 0.45 (Igarashi 1981) and C_d for the cylinder in the leading high-drag position is 1.17 (Hoerner 1965, ch. 8; Igarashi 1981). The ratio of these two drag coefficients, 0.45/1.17, yields the drafting coefficient, *D*, 0.385 (dimensionless).

Thus, to approximate C_d for the drafting half-streamlined body, we apply $D = 0.385$, where $0.07 \times 0.385 = 0.0269$. Introducing $C_d = 0.0269$ into Equation (3) for the drafting trilobite, and $C_d = 0.07$ for the front trilobite,
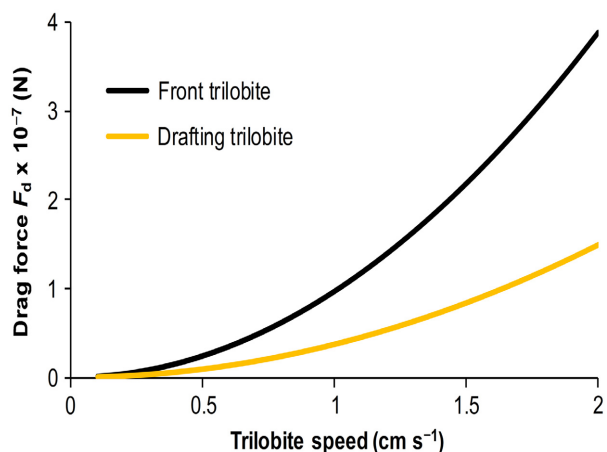

FIG. 3. Drag forces (N) for trilobite in front, non-drafting position (upper curve) and for drafting trilobite (lower curve). Colour online.

we determine respective drag forces, F_d (N), for the front half-streamlined body and the following half-streamlined body to approximate these values for trilobites over a range of travelling speeds up to 2.0 cms^{-1}, as shown in Figure 3.

$D = 0.385$ may now be introduced into Equation (2). The corresponding energy saving $(1 - D)$ is 0.615 (61.5%).

The approximated energy saving quantity of 61.5% is in reasonable agreement with Bill & Herrnkind's (1976) finding that spiny lobsters generate 65% energy savings by hydrodynamic drafting. It is also similar to the 63% maximum energy saving that Fish (1995) reported for ducklings swimming in a decoy wake compared to solitary swimming.

Determining T. chopini *travelling speeds and maximal sustainable speeds*

We used data from Jamieson *et al.* (2012), illustrated in Figure 4, for *R. herculea*, a living crustacean with a body length between 2.5 and 5 times that of *T. chopini*, to derive an approximate range of speeds for *T. chopini* for a range of body lengths (BL). To achieve this, for both sub-maximal and maximal sustainable walking speeds, we obtained a linear polynomial regression correlation between body length and walking speeds for *R. herculea*, which permits us to extrapolate speeds for the shorter *T. chopini* body lengths. We could find no data in the literature for arthropods closer in size, morphology and speed to T. chopini for this purpose.

Jamieson *et al.* (2012) also reported a single individual *R. herculea* with a high size-specific speed of 0.33 cms^{-1}BL^{-1} relative to the mean 0.19 cms^{-1}BL^{-1}. This particular specimen accelerated to 1.2 cms^{-1} as an aversion response in the presence of a fish, as shown in Figure 4 (Jamieson *et al.* 2012). We consider this aversion response to be within mid-range sustainable capacities described as a maximal sustainable aerobic speed, sustainable for *c.* 5 min; or an anaerobic threshold speed, sustainable for between 20 and 60 min (see foregoing discussion on the 'power profile') for *R. herculea* (but not a maximum explosive speed, for which Jamieson *et al.* (2012) reported considerably higher backward jump escape speeds). From this aversion response speed, we approximated a scaled corresponding maximal sustainable aerobic power, or anaerobic threshold, speed for *T. chopini*.

Applying regression polynomial $y = 0.2163x - 0.0796$, we extrapolated the following: sub-maximal sustainable walking speeds for trilobites between 0.1 and 2.0 cm long, and aerobic power, or anaerobic threshold, maximal sustainable walking speeds based on a maximum size-specific speed of 0.33 BLs^{-1}, as shown in Table 1. To model coupling effects and thresholds, values from the third column
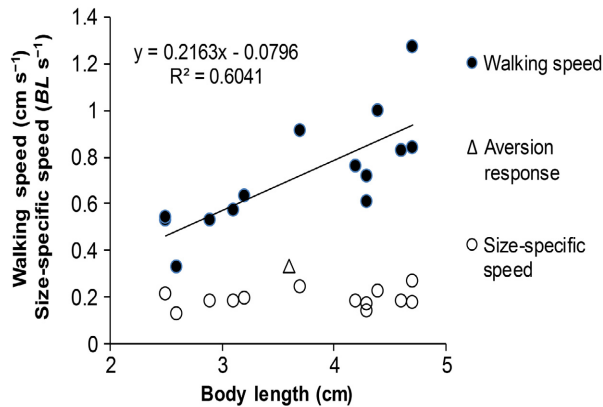
FIG. 4. *R. herculea* absolute walking speeds (black circles) and size-specific speeds (open circles). Data reconstructed from Jamieson *et al.* (2012). Triangle denotes acceleration due to aversion response to fish nearby (corresponding maximum speed of 1.20 cms^{-1} not shown and discounted from regression polynomial to obtain best fit for normal, unperturbed, walking speeds). Data applied to approximate maximal sustainable aerobic power, or anaerobic threshold, travelling speeds, and sub-maximal sustainable *T. chopini* travelling speeds. Colour online.

are thus applied to establish realistic MSO_{follow} and S_{front} speeds, as shown in Figures 5–7.

Modelling group coupling and sorting behaviour

We can now model aggregate trilobite coupling and sorting behaviour in terms of Equation (2). We define trilobite coupling as the energetic or metabolic requirements of two trilobites whose outputs are determined by the speed set by the non-drafting trilobite, and the relative drag forces for the given position they occupy, whether non-drafting or drafting. Trilobites are optimally coupled when a following trilobite achieves maximum energy saving by hydrodynamic drafting. Varying degrees of coupling may occur depending on the distance between trilobites and the angle between leading and following positions, but trilobites remain coupled when drafting trilobites are TCR <= 1. If a weaker trilobite follows a stronger trilobite which sets a pace faster than the weaker trilobite's maximal sustainable speed, the weaker trilobite can sustain the pace of the stronger by drafting. De-coupling occurs when TCR > 1. Coupling between two trilobites extends globally to larger aggregates.

In Figures 5–7 we show the effects of varying the three parameters: maximal sustainable speed of the following trilobite (MSO_{follow}); speed set by the front trilobite (S_{front}); and the drafting coefficient, D, recalling that $D = 0.385$ is the ratio of drag coefficients of an in-wake cylinder to a leading cylinder, 0.45/1.17, and the energy saving quantity is $1 - D = 0.615$.

TABLE 1. Estimated *T. chopini* travelling speeds using regression polynomial equation obtained from data for *R. herculea* by Jamieson *et al.* (2012).

Body length (cm)	Estimated sub-maximal sustainable walking speed* (cms^{-1}) = 0.216 × BL − 0.0796	Estimated maximal sustainable walking speed[†] (cms^{-1})
0.1	−0.058	0.033
0.2	−0.0364	0.066
0.3	−0.0148[‡]	0.099
0.4	0.0068	0.132
0.5[§]	**0.0284**	**0.165**
0.6	0.05	0.198
0.7	0.0716	0.231
0.8	0.0932	0.264
0.9	0.1148	0.297
1	0.1364	0.33
1.1	0.158	0.363
1.2	0.1796	0.396
1.3	0.2012	0.429
1.4	0.2228	0.462
1.5	0.2444	0.495
1.6	0.266	0.528
1.7	0.2876	0.561
1.8	0.3092	0.594
1.9	0.3308	0.627
2	**0.3524**	**0.66**
2.1	0.374	0.693
2.2	0.3956	0.726
2.3	0.4172	0.759
2.4	0.4388	0.792
2.5	0.4604	0.825

*Estimated sub-maximal sustainable speeds for *T. chopini* of varying body length.
[†]Estimated maximal sustainable walking speed trilobites of varying body length, scaled according to aversion response size-specific speed of 0.33 cms^{-1}BL^{-1} from Jamieson *et al.* (2012) for the extant crustacean, *R. herculea*.
[‡]Negative values due to imprecision in regression equation and may be discounted for the model proposed.
[§]Max. and min. body length values as reported by Kin & Błażejowski (2013) shown **bold**.

The greater the maximal sustainable capacity of a follower relative to the speed set by the leader, the longer the follower remains coupled to the leader. The smaller the energy saving value, the faster a stronger leader outpaces a follower; conversely, the greater the energy saving value, the longer the follower 'sticks' with the leader.

Thus, it is apparent that if the MSO_{follow} of a weaker trilobite exceeds the speed set by the front trilobite (S_{front}), as reduced by D, then the weaker trilobite can sustain the speed of a stronger trilobite by drafting. This is shown by the inequality,
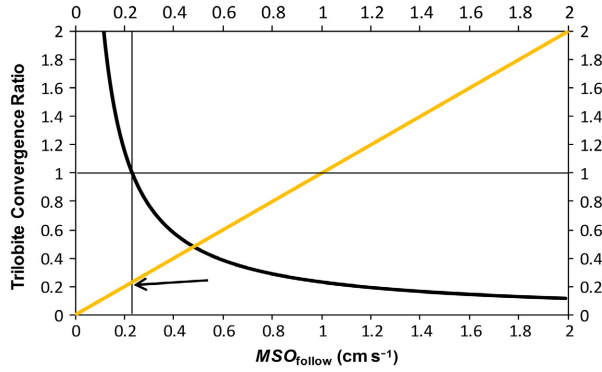
FIG. 5. Coupling threshold for variable maximal sustainable output of drafting trilobite (MSO_{follow}). MSO_{follow} is a variable between 0 and 2.0 cms^{-1} (diagonal). Trilobite convergence ratio = $(S_{front} \times D)/MSO_{follow}$ (non-linear black curve). S_{front} is constant at 0.6 cms^{-1}, and the drafting coefficient, D, is constant at 0.385 (energy saving quantity $1 - D = 0.615$). Arrow indicates threshold MSO_{follow} (0.23 cms^{-1}), when TCR = 1. For all $MSO_{follow} > 0.23$ cms^{-1} to right of vertical line when TCR < 1, trilobites are coupled; for all $MSO_{follow} < 0.23$ cms^{-1} to left of vertical line, when TCR > 1, trilobites are de-coupled. Colour online.
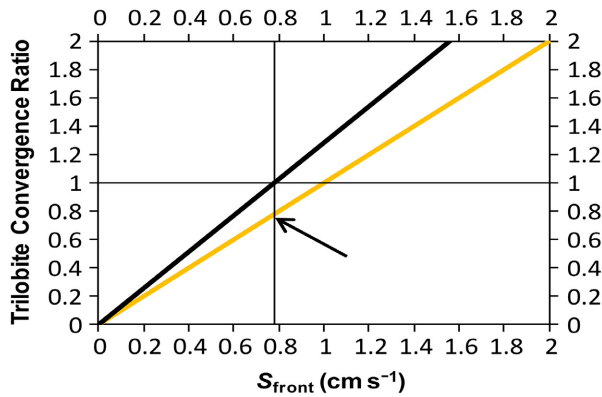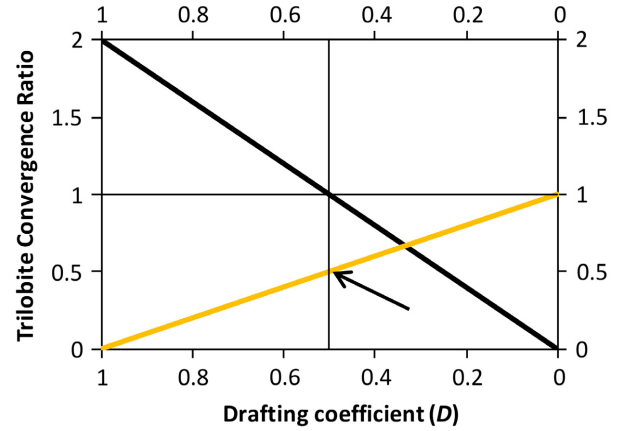

FIG. 7. Coupling threshold for variable D. D varies between 0 and 1.00 (lower diagonal); S_{front} is constant at 0.6 cms^{-1}; MSO_{follow} is constant at 0.3 cms^{-1}. Trilobite convergence ratio = $(S_{front} \times D)/MSO_{follow}$ (upper black diagonal). Arrow indicates the threshold $D = 0.501$, when TCR = 1. For all $D < 0.501$ to the right of vertical line, when TCR < 1, all trilobites are coupled; for all $D > 0.501$, when TCR > 1, to the left of the vertical line, trilobites are de-coupled. Colour online.

FIG. 6. Coupling threshold for variable speed of leading trilobite (S_{front}). S_{front} is a variable between 0 and 2.0 cms^{-1} (right diagonal). Trilobite convergence ratio = $(S_{front} \times D)/MSO_{follow}$ (left black diagonal). MSO_{follow} is constant at 0.3 cms^{-1}, and D is constant at 0.385. Arrow indicates threshold speed of the leading trilobite ($S_{front} = 0.78$ cms^{-1}), where TCR = 1. For all $S_{front} < 0.78$ cms^{-1}, left of vertical line when TCR < 1, trilobites are coupled; for all $S_{front} > 0.78$ cms^{-1} to the right of vertical line when TCR > 1, trilobites are de-coupled. Colour online.

$$MSO_{follow} \geq S_{front} \times D \qquad (4)$$

This condition is demonstrated in Figure 5, where MSO_{follow} is varied, S_{front} is constant at 0.6 cms^{-1} and $D = 0.385$: all trilobites with $MSO_{follow} \geq 0.23$ cms^{-1} are coupled with S_{front} trilobites, and TCR < 1; all trilobites with $MSO_{follow} < 0.23$ cms^{-1} are de-coupled from S_{front} trilobites, and TCR > 1.

Similarly, if the speed of the front trilobite (S_{front}) does not exceed the maximal sustainable speed of the drafting trilobite as a ratio of the drafting coefficient, D, then it will not outdistance a drafting trilobite. This is shown by the inequality,

$$S_{front} \leq MSO_{follow}/D \qquad (5)$$

This condition is demonstrated in Figure 6, where S_{front} is varied and MSO_{follow} is constant at 0.3 cms^{-1} and $D = 0.385$: all S_{front} trilobites travelling ≤ 0.78 cms^{-1} are coupled with drafting trilobites, and TCR < 1; all S_{front} trilobites travelling > 0.78 cms^{-1} are de-coupled from drafting trilobites, and TCR > 1.

If drafting coefficient, D, is less than the drafting trilobite's maximal sustainable speed as a proportion of the speed set by the front trilobite, then a drafting trilobite can sustain the pace of a stronger front trilobite. This is shown by the inequality,

$$D \leq MSO_{follow}/S_{front} \qquad (6)$$

This condition is demonstrated in Figure 7, where D is varied, MSO_{follow} is constant at 0.3 cms^{-1} and S_{front} is constant at 0.6 cms^{-1}: for all $D \leq 0.501$, front and drafting trilobites are coupled, and TCR < 1; for all $D > 0.501$, front and drafting trilobites are de-coupled, and TCR > 1. The scenario in Figure 7, where $D = 0.5$, implies that a drafting trilobite which is half the size of the front trilobite can, by exploiting the drafting benefit, sustain a pace set by the front trilobite that is twice the drafting trilobites' maximal sustainable speed when it

travels alone. Here it should be recalled that as D diminishes, the corresponding energy saving, $1 - D$, increases.

In turn, if the energy saving quantity, $1 - D$, exceeds the difference between the speed set by the front trilobite and the maximal sustainable speed of the follower, as a ratio of the speed of the front trilobite, the drafting trilobite will sustain the pace of the front trilobite. This is shown by the inequality,

$$1 - D \geq (S_{\text{front}} - MSO_{\text{follow}})/S_{\text{front}} \tag{7}$$

where $S_{\text{front}} > MSO_{\text{follow}}$, and $1 - D = 0.615$.

The right-side term of Equation (7) is in the same form as Equation (1), which describes the size range (SR) for a set of trilobites. Since body length corresponds to strength, as discussed above, the basic inequality between the energy saving quantity and SR, foundational to the variation range hypothesis, is

$$1 - D \geq [(BL_{\max} - BL_{\min})/BL_{\max}] \tag{8}$$

Consequently, when the energy saving quantity, $1 - D$, exceeds the proportionately equivalent size range (SR) of a heterogeneous set of trilobites, the trilobites can remain coupled; conversely, trilobites outside SR (i.e. too small) become decoupled.

DISCUSSION

Weaknesses in the hydrodynamic drafting model

Although the energy saving quantity 61.5% is in good agreement with Bill & Herrnkind's (1976) finding that spiny lobsters generate 65% energy savings by hydrodynamic drafting, imprecision in our model exists due to the complexities of fluid dynamics. For instance, smaller trilobites will have had proportionately smaller frontal surface areas (S) than their larger counterparts. S is typically calculated using two different methods: first, total frontal surface area given a convoluted surface morphology ('wetted area'); second, the maximum cross-sectional area; each yield significantly different drag forces and it may be recommended that both methods be used for accuracy (Alexander 1990).

Our simplified model is based on cross-sectional frontal surface areas for leading and following trilobites that are equal, but where trilobite body length is varied. Since body length is the critical parameter that correlates to an organism's speed (Meyer-Vernet 2015), this permits us to discount frontal surface area in our simplified analysis.

Furthermore, the drafting coefficient $D = 0.385$ does not account for a region of negative drag (a 'suction zone') reported for a critical spacing up to 3.5 diameters between cylinders (Igarashi 1981). However, trilobite morphology is not cylindrical; rather it is an elongated streamlined profile that fills much of the suction zone that exists between cylinders. Therefore, we do not model the effect of the streamlined trilobite body on the magnitude of this suction zone.

A further consideration is the change in drag interaction between cylinders with respect to orientation angle (Dalton & Szabo 1977). Thus, for trilobites in moving queues, directional changes laterally and vertically will have had large effects on their drag forces and energetic demands. Moreover, the optimal drafting orientation was probably offset in the order of 30° laterally to the midline of the front trilobite; this is indicated for cylinders in tandem in which a free-floating drafting cylinder can overtake the one ahead (Tchieu et al. 2010), thereby also avoiding collision. Similar offset optimal drafting orientations are observed among fish species, although for different reasons (Marras et al. 2015).

A refined hydrodynamic model should also consider the costs of trilobite collisions and collision-avoidance, both of which appear to have occurred frequently, as shown in Figure 1D and in the fossil record as shown in Radwański et al. (2009).

In general, the fluid dynamics that may be considered for a refined hydrodynamic model of trilobites in motion relative to each other involve complex equations of motion and fluid turbulence (Borisov et al. 2007; Tchieu et al. 2010) which are beyond the scope of this paper. Future studies may account for these fluid dynamical complexities, and may also involve computer simulations or the use of physical 'toy' model trilobites to measure drag forces and optimal drag reducing positions, like the experiments of Bill & Herrnkind (1976) for spiny lobsters.

The 'trilobite convergence ratio' and implications for trilobite collective behaviour

The 'trilobite convergence ratio' (TCR) model allows several inferences about the collective behaviour of trilobites. As discussed, as trilobite speeds increase to approach their MSOs, the group may be expected to align into queues, as observed to occur among cyclists (Trenchard et al. 2014) and shown in Figure 1A. Because of the hydrodynamic drafting coefficient that permits trilobite energy saving up to c. 62%, we may expect correspondingly weaker trilobites to sustain the pace of stronger trilobites by exploiting drafting positions.

It should be noted that while cyclists gain substantial energy reduction advantages by remaining in pelotons, theirs is ultimately a competition in which the objective is to finish ahead of other cyclists. This is often achieved by intentionally seeking to separate oneself ahead of the

peloton. For trilobites, particularly blind forms such as *Trimerocephalus*, we may expect some advantage conferred by separating ahead of the aggregation for faster access to foraging resources, but this may have been outweighed by the cost of becoming permanently isolated from the group. Consequently, particularly for blind trilobites, the survival advantage of remaining in close contact may have outweighed any advantages to advancing ahead of the group. Also, as with modern spiny lobsters, trilobites may well have travelled with antennae in contact with the individual ahead to keep together for defensive, feeding and/or other functions. Antennae were revealed in *T. chopini* by X-ray microcomputed tomography (Kin & Błażejowski 2013) and the distances indicated in the fossil record are generally sufficiently short to permit antennae contact (Radwański *et al.* 2009, pls 1–5).

Radwański *et al.* (2009) observed that longer single-file trilobite lines were primarily formed of larger individuals, while smaller individuals were observed to comprise shorter queues, generally of two specimens. Although not without other explanations, in this case the fossil record may have captured the sorting process in action in which smaller trilobites were in the process of being isolated from larger ones. In circumstances of group separation like this, if the larger trilobites maintained speeds that established a separation between themselves and weaker trilobites, eventually the distance between themselves and the smaller ones may have been too great for the groups to reintegrate.

Despite being able to sustain the speeds of larger trilobites by exploiting hydrodynamic drafting, small following trilobites may be expected to have spent more time at near maximal sustainable outputs even in drafting positions. Larger trilobites, weakened during periods spent in high-drag positions, would be expected to be overtaken by other large trilobites, thus sharing the high-drag positions and maintaining a constant high collective speed while overtaken large trilobites would recuperate in drafting positions. This high-drag position sharing is a function of natural decelerations due to leader fatigue. The fatigued individuals are then passed by 'fresh' trilobites. This kind of self-organized passing behaviour is not due to any volitional motivation to share positions. Bill & Herrnkind (1976) observed similar positional sharing among spiny lobsters, although the authors did not quantify or explain the behaviour. Similar positional sharing has been observed among spiderlings travelling in single file, although the reasons for this behaviour have not been proposed (Reichling 2000). Positional sharing among cyclists in pelotons due to fatigue is well known (Olds 1998).

At corresponding low speeds, small trilobites may have been capable of overtaking weakening larger trilobites to assume a high drag position, but only with a drastic reduction in group speed. In these circumstances, larger trilobites would be expected to quickly overtake the smaller ones, returning the group to a higher speed. We may therefore expect that larger trilobites generally tended to set the aggregate pace.

Trilobite de-coupling and sub-group formation. In circumstances in which larger trilobites tended to set the aggregate pace, smaller trilobites probably weakened faster than larger ones even while exploiting drafting positions. In turn, eventually smaller trilobites would weaken to the critical threshold condition TCR > 1 and de-couple from the group of larger trilobites. Moreover, de-coupling may have occurred even when stronger trilobites accelerated the pace at their own sub-maximal sustainable speeds.

This greater fatigue rate among weaker trilobites could occur even while generally enjoying drafting advantages because weaker trilobites were likely to be highly susceptible to positional instabilities, even at intermediate speeds set by stronger front trilobites. If caught out of optimal drafting range or position, even momentarily, small trilobites would have been required to increase their output dramatically to sustain the speeds set by the leaders or to catch up again, and relocate to optimal drafting positions. Such a process would have been highly fatiguing, eventually producing the condition TCR > 1.

This describes the localized sorting process. Extended globally over the course of a migration period, we infer that groups underwent a continuous sorting process leading to the formation of sub-groups in which sub-groups tended to consist of members of similar strength, and corresponding size. This strength sorting principle was modelled by Trenchard *et al.* (2015) in the context of groups of cyclists. Trenchard & Perc (2016) proposed that this sorting process also depends partly on the number of group members, since the larger the group, the longer the sorting process.

Size ranges greater than the hypothesized variation range may indicate pre-migratory stages. Because the hypothesized sorting process probably occurred over a comparatively long time-span, trilobite aggregations whose size ranges exceeded the hypothesized variation range (equivalent to $1 - D$, or *c.* 62%) were likely in pre- or early migratory stages when the process of sorting by size was not yet underway or complete. Early instars probably did not participate in migrations, but may have been involved in short–range foraging commutes.

Such broad size ranges were most likely to occur if adults were mixed with much smaller (i.e. smaller than within the hypothesized *c.* 62% range) early stage instars after hatching, such as in the case where adults co-existed with juvenile 'nurseries', as suggested by Błażejowski *et al.* (2016).

A wide size range of this kind was reported by Lin & Yuan (2009) who studied a *Pagetia* trilobite cluster of 22 individuals from the Middle Cambrian Kaili Formation Guizhou (China). The cluster contained both degree 0 meraspids with cephalic length as short as 0.44 mm, and holaspids with cephalic lengths and long as 2.17 mm (80% range).

Similarly, Cederström *et al.* (2011) reported meraspid and holaspid individuals of the early Cambrian *Strenuaeva inflata* in the Tornesträsk area (Sweden) across a wide size range: for 3397 specimens, cranidia measurements ranged between *c.* 0.2 and 2.0 cm (90% range). The authors argued that the aggregations occurred for brooding purposes and that the absence of very small instars could be explained by earliest-stage development in brood pouches (Cederström *et al.* 2011). If, in fact, the reported aggregations were in a brooding and early developmental stage, this implies a pre-migratory stage with respect to early instars which would not yet have undergone migration (but post-migration for adults having arrived prior to brooding).

Size range less than or approximately equal to the hypothesized variation range indicates stopovers or post-migratory stages. Generally, the argument we present supports the proposition that queues occurred during migration (Radwański *et al.* 2009; Błażejowski *et al.* 2016), while non-linear clusters formed during sedentary 'stopover' periods, when moulting, brooding, or spawning.

Although non-linear clusters were probably not in a travelling phase, owing to their random orientations (Speyer & Brett 1985; Karim & Westrop 2002) it is reasonable to expect that the trilobites migrated to these clustering locations. It was during migratory periods when size sorting would occur, and so we would expect to see evidence among the clusters during 'stopovers' of size-sorting processes that occurred during migration periods. Narrow size ranges observed among spawning, brooding, or moulting clusters is just the sort of evidence that tends to support the variation range hypothesis.

Speyer & Brett (1985) reported size-segregated clusters of Middle Devonian *Phacops rana*, *Greenops boothi,* and *Dechenella rowi* from the Windom Smoke Creek Bed (Windom Shale, Hamilton Group) and from the Murder Creek Bed (Wanakah Shale) both from western New York State. The authors reported cephalon length ranges of 0.6–1.4 cm (57% range, where cephalon length correlates with body length; Trammer & Kaim 1997) and cephalon length ranges of 0.4–1.0 cm (60% range), respectively. Further, the authors reported spatially separated clusters of different mean size, indicating that specific instar classes associated among themselves to the exclusion of other classes.

In a similar finding, Karim & Westrop (2002) reported a non-linear cluster of Late Ordovician *Homotelus bromidensis* from the Bromide Formation, Dunn Quarry (Oklahoma) with cephalic lengths between 1.0 and 2.25 cm (56% range), and a second non-linear cluster with cephalic lengths between 1.0 and 2.75 cm (64% range).

These cases indicate that group members travelled together due to their approximate size equality, and suggest that groups of different mean speeds would arrive at stopover points at different times. This proposition does not challenge a gregarious behavioural explanation for instar segregation, but rather complements such an explanation while providing insight into the more primitive origins of gregarious segregation.

Kin & Błażejowski (2013) reported that among 78 examples of Late Devonian (Famennian) *Trimerocephalus* queues from the Kowala Quarry (Poland), specimens ranged in size from 0.5 to 2.0 cm body length (75% range). Although this range exceeds the range of *c.* 62% predicted by the variation range hypothesis, the overall 0.5–2.0 cm body length (75% range) appears to represent the size range among all specimens in the study but does not distinguish between size segregated groups and narrower size-ranges among the queues themselves.

Following the Kin & Błażejowski (2013) study, Błażejowski *et al.* (2016) reported that for the same 78 queues, the size ranges for individual queues were between 0.7 and 1.9 cm (63% range), thus supporting the assertion that the 75% range reported by Kin & Błażejowski (2013) was for the entire sample population and not queue-specific.

It is also noteworthy that in their study of queues from the Kowala Quarry, Radwański *et al.* (2009) reported that 'The majority of queues are formed from the largest individuals. The smaller-sized individuals are arranged as a rule in short files consisting of only two individuals' (p. 467). From this it appears that the queues had indeed sorted themselves in much the way predicted by the variation range hypothesis. Kin & Radwański (2008) also reported specimens from the Kowala Quarry in files, of mature growth stage, between 1.8 and 2.4 cm (25% range).

We note that enrolled juvenile *T. chopini* smaller than within this range were reported by Błażejowski *et al.* (2016) situated a few millimetres above the queue formation bedding plane. However, the nearby presence in the fossil record of smaller enrolled juveniles presents a challenge to the variation range hypothesis in these circumstances, because it suggests queues were in travelling mode somewhat concurrently with the presence of nearby small juveniles which, according to the variation range hypothesis, would have been isolated and left behind by the travelling queues.

However, because they appear on a different bedding plane, the small enrolled juveniles may have arrived at their positions at a different time, or may have already been at their positions in 'nursery grounds' before the queues arrived as Błażejowski *et al.* (2016) tentatively explained, and probably did not migrate with the queues containing their much larger counterparts.

In another study, Gutiérrez-Marco *et al.* (2009) reported monospecific clusters of large Middle Ordovician trilobites *Ogyginus forteyi* and *Asaphellus* in Arouca Geopark (Portugal), 7–17 in number, of 'similar sized specimens' (p. 444), but the authors did not report precise ranges.

The energy reduction hypothesis for trilobite queueing behaviour does not exclude single-file formations observed in the fossil record for other reasons, such as trilobites having been constrained in linear burrows (Chatterton & Fortey 2008). However, it may be an alternative explanation to proposed chemosensory coordination for blind trilobites (Błażejowski *et al.* 2016). By exploiting energy saving positions behind leading trilobites, followers may have modified their positions according to sustainable metabolic outputs and naturally gravitated toward the 'easiest' positions. This principle of local self-organized behaviour would lead to queue formation at the aggregate level, as is observed to occur in bicycle pelotons (Trenchard *et al.* 2015). Moreover, because collective behaviour can emerge among inanimate objects in the presence of hydrodynamic drafting (Wang *et al.* 2014), it is possible the energy saving mechanism for queues preceded the development of trilobite chemosensory apparatus' in the evolutionary lineage.

CONCLUSIONS

We have proposed that by travelling in queues, trilobites could exploit the energy saving benefits of hydrodynamic drafting. Weaker trilobites could thereby sustain speeds, as set by stronger trilobites, which were otherwise unsustainable when travelling in solitary isolation. We have proposed that the degree to which trilobites could have been weaker (and therefore smaller in size) and still have sustained speeds of stronger trilobites, approximately corresponds with the degree of energy saved by drafting.

We have modelled certain parameters that define trilobite coupling and the sorting process, including the relationship between the pace set by the leading trilobite, the maximal sustainable output of the following trilobite, and the energy saving mechanism of hydrodynamic drafting.

We have proposed that the correspondence between trilobite strength (and size) and the energy saved by drafting, implies a process by which trilobite groups tended to sort into sub-groups of increasingly narrow size ranges. Consequently, during migration the maximum size range we would expect to observe is *c.* 62%, since this is approximately the quantity of energy saved by hydrodynamic drafting. Over extended migrations, we would expect this range to narrow increasingly because of a hypothesized faster fatigue rate for weaker trilobites, even with the availability of drafting, due to positional instabilities and their temporary exposure to high-drag positions. Conversely, we suggest that stronger trilobites, by self-organized continuous collective motion, may have shared drafting positions and distributed the time spent in high-drag positions among group members, thereby resulting in a net advantage for stronger trilobites over time. Consequently, the longer the migration, the more likely it was for trilobites to sort into groups of narrow size ranges.

Trilobites had to be adaptive to the various selection pressures at all growth stages because, of course, they could not reach adult sizes without first going through their instar stages and corresponding sizes. However, the proposed model, by which groups sort into narrow size ranges and by which those outside the threshold range may be de-coupled from the group and become reproductively isolated, is not in conflict with trilobite fitness at all instar stages. This is because de-coupling and size sorting would occur only during locomotion and migration periods of sufficient duration, and this process would be scaled in correspondence to the different mean sizes of each aggregation travelling independently.

It is likely that individuals among early instar stages up to a certain size did not participate in queues simply because they were not sufficiently mature to migrate. However, this raises the question as to why members of each instar stage would proceed through their growth stages within certain size ranges in the first place. The proposed model addresses this: because spawning or brooding trilobites, arriving after the proposed migratory sorting process had occurred, would naturally produce hatchlings whose sizes were consistent with the size range of those trilobites which survived the journey to spawn or brood. This suggests, therefore, that hatchlings would generally begin life within this approximate size range (as a percentage) and commence their own migrations as a group (when sufficiently strong to do so), scaled in sizes according to their instar stage and growing accordingly with the passage of time, but travelling separately from their larger adult counterparts. Thereupon the process would be repeated.

Alternatively, and perhaps concurrently, trilobites of varying sizes may have had different behaviours, and queue formation may have been a behaviour typical of individuals above a given size. This would be in line with variations in trilobite size ranges observed in different environments. In any case, the examples of fossilized

trilobite queuing behaviour are presently comparatively few, and more data are required to draw inferences with any degree of certainty. Fossil records in which trilobites were travelling unidirectionally, not in queues but in more compact formations, may also assist our understanding of the advantages of queue formations, in hydrodynamic terms or otherwise.

Future work may involve modelling more precisely the complex fluid dynamics involved in trilobite hydrodynamic drafting and its energetic consequences, including 'toy' model experiments. In addition, future work may include a more comprehensive review of the reported size ranges among fossilized trilobites and other species and an analysis of their corresponding migratory stages. The proposed model presents a novel palaeoecological framework in which to consider migration and size variation among trilobites, in addition to other fossil and extant organisms.

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