

Trilobite “pelotons”: Possible hydrodynamic drag effects between leading and following trilobites in trilobite queues

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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 per cent), has been hypothesized to correspond proportionately to the energy saving quantity because weaker, smaller, individuals sustain speeds of stronger, larger, individuals by exploiting the energy saving mechanism (as a per cent). During migration, small individuals outside this range may perish, or form sub-groups, or simply not participate in migratory behavior. We approximate drag forces for leading and following individuals in queues of the late Devonian (~370 Ma) trilobite *Trimerorhynchus chopini*. Applying data from literature of *R. herculea*, a living crustacean, we approximate the hypothetical walking speed and maximal speeds for *T. chopini*. Findings reasonably support the hypothesis: among the population of fossilized queues of *T. chopini* reported by Kin & Błażejowski (2013), trilobite size range was 75% while the size range within queues, was 63%; this corresponds reasonably with drag reductions in following positions that permit ~61.5% energy saving for trilobites following others in optimal low-drag positions. We model collective trilobite behavior associated with hydrodynamic drafting.

INTRODUCTION

The fossil record reveals that some trilobite species formed aggregations (Speyer & Brett 1985, Karim & Westrop 2002, Radwański et al. 2009). Queuing behavior, 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 *Bathyscheilus*, *Salterocoryphe* and/or *Retamaspis* (Gutiérrez-Marco et al. 2009), the blind Late Devonian phacopid *Trimeroccephalus chopini* (Kin & Błażejowski 2013; Błażejowski et al. 2016), fossilized enigmatic Cambrian arthropods (Hou et al. 2008; Xian-Guang et al. 2009), and in living spiny lobsters (Bill & Herrnkind 1976). Fossilized “beaten” trackways of probable eurypterids indicate similar queueing behavior (Draganits et al. 1998, (their Fig. 6); Braddy 2001).

The focus of this study is on *T. 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 Fig. 1C, D. Queues have also been described in zig-zag or wavy patterns (Gutiérrez-Marco et al. 2009). Of course, such queueing behavior 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 than two centimeters from one another” (p. 90). The authors reported clusters comprising from three individuals to over 200, in which individuals were randomly orientated. Speyer & Brett (1985) proposed that fossilized cluster assemblages revealed synchronous moulting and possibly mating behavior. 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 cephalia could represent a distinct type of migratory behavior.

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) identify 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 queueing behavior may have occurred both during short range commutes within the home range to and from spatially separated resource patches or

roost sites, or during 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 ~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. Hansen & Klotz 2005, p. 135; Wilson 1959), 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 (Chadhuri & 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 (~150 per m²) trackways of unidirectional migration among Late Jurassic isopods from the Crayssac Lagerstätte, of Germany, thought to have been imprinted in soft-to-firm mud of a temporarily emerged tidal flat (Gaillard et al. 2005, their 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 Fig.1B, although it is difficult to interpret such isopod collective motion as involving hydrodynamic drafting.



Figure 1A. 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; Creative Commons Attribution License (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.