Keeping A Flow Profile:
The Fluid Dynamics and Biomechanics of Trilobite Genal Spines

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ABSTRACT

Arthropods are well known for being extraordinarily diverse. Variation of form and niche-occupation in arthropods relies on specialized appendages and regionalization of a common bauplan. In the marine realm, ancient trilobites exhibit extreme exoskeleton disparity. It is commonly accepted that much of the variety of trilobite evolution, particularly in the head, reflects adaptation to assorted environments. Here, I demonstrate the relationship between cephalon morphology and fluid flow through turbulence and drag force. I examine the effect of genal spine length on (1) degree and position of turbulence relative to the trilobite body along with (2) amount of drag felt on the organism. General morphology of Devonian *Eldredgeops* (Trilobita: Phacopida) was used as a template. I do not suggest that *Eldredgeops* may have possessed cephalic spines, but rather, models were constructed with varying lengths of genal spines as a proof of concept. Trilobite models were constructed with five different genal spine lengths, from absent genal spines to spines extending past the rear of the body. In a flow tank, the forms were analyzed with dye stream tests to identify minimum turbulence and with a force transducer to measure drag forces. Laser techniques were used to visualize flow. Results address biomechanics of trilobite cephalon morphology as they affect the fluid dynamics around the entire body. I discuss ecological implications of these findings.

INTRODUCTION

Foreshadowing the ubiquitous nature of modern arthropods, Paleozoic trilobites occupied a vast ecomorphospace. Unlike recent arthropods however, trilobite morphology did not support their propagation with specialized appendages. Instead, their morphological disparity comes from variation in body segments and ornamentation. The evolution of the trilobite head, or cephalon, coevolved closely with feeding and locomotion techniques (Fortey 2004). Trilobite cephalization reflects a correlation between body function and the surrounding environment. The underlying interaction between the trilobite and the environment in which it lived through fluid dynamics and biomechanics will be discussed here.

Postulated trilobite ecology and environmental interaction is largely based on facies interpretation of the rock record and modern analogs. As a whole, trilobites were presumed to occupy just about every available niche space in the marine realm. Of these occupations, pelagic planktonivores and filter feeders have received much attention in terms of biomechanics and functional morphology. Pelagic forms have been tested for streamlining and drag with biomechanical models (Fortey 1985). Similarly, functionality of large spines on filter feeding forms has been hypothesized (Fortey and Owens 1999).

Ornamentation on the trilobite cephalon includes horns, tubercles, or even elaborate spines. A posteriorly directed spine off the lateral border of the trilobite cephalon is called a genal spine. The angle and length of the genal spine can vary greatly between clades. Ecological significance of this spine has been postulated as a tool for sexual selection (Knell and Fortey 2005) or hydrodynamic support structure (Whittington 1957). In some cases, genal spines are absent altogether, such as the Devonian *Eldredgeops*.

Genal spines on the cephalon can greatly alter the type of flow and fluid dynamics experienced by the trilobite. Within fluid dynamics, turbulence, drag, and lift may be the most influential for a benthic organism. Turbulence refers to the chaotic movement of the water while drag is a force that may limit the movement of the organism in a fluid. Here, I report observed effects of genal spine length on turbulence and drag and present potential biomechanics interpretations of how these affect the fluid dynamics of a trilobite.

METHODS

Five trilobite computer models were constructed in the software Autodesk Maya 2013. The body model was based on *Eldredgeops* awho does not possess genal spines. However, *Eldredgeops* does provide a standard body plan with which to experiment. Before adding genal spines, the original size was scaled (55.2044 mm x 94.3051 mm x 20.0406 mm) to work reasonably in a large flow tank. Spines were added to the head of the model to produce four additional arrangements and lengths. Spines terminated at positions 0.3, 0.5, 1.0 and 1.3 on the overall length of the trilobite body and were used as designations for the models (Figure 1).

Models were printed using ZPrint software and a rapid prototype 3D printer. Powdered models were excavated from the printer and excess powder was blown off. After being coated in epsom salt solution, the models were baked at 75°C for at least an hour. Once dried, models were coated in flat black spray paint. The black matte was chosen to reduce refractive and reflective surfacing when visualizing dye flow with a laser.

Tests were conducted in a Research Water Tunnel Model 1520 (manufactured by Rolling Hills Research Corporation). All experiments in the flume were done in freshwater. Positional turbulence experiments were conducted on all five models on speeds up to 0.2 m/s (Table 1). Fluid velocities were chosen based on speculated ranges that a benthic Paleozoic fauna may encounter. For the same reasons, models were placed on the bottom of the flume. Dye was directed at the anterior-most part of the cephalon and allowed to flow around the body. Measurements from the tip of the cephalon to the point were turbulence began were recorded for all five speeds (Figure 2). This technique enabled a qualitative measure of minimum flow around the trilobite. Lastly, the change from streamline to turbulent flow was visualized with a laser. Laser observations included dye streams around the genal spines and over the body.

To test drag forces acting on the models, the models were fitted with attachment screws and connected to a 5000 g load cell. Models were suspended from the force transducer and submerged to 0.3 m depth. All fives forms were tested across thirteen different flow velocities (Table 2). Force acting on the models was collected in LabVIEW software and coefficients of drag were calculated in Microsoft Excel 2011. The equation used to calculate coefficient of drag (C_d) was:

$$C_d = \frac{2F}{\rho v^2 A_{proj}}$$

Where F is the force measured from the force transducer, ρ is the density of freshwater (1000 kg/m^2), A_{proj} is the projected area relative to flow, and v^2 is the velocity of the fluid.

RESULTS

Minimum turbulence across the trilobite displayed two different trends (Figure 3). Models with shorter genal spine lengths (0.0, 0.3, and 0.5) follow a pattern with increasing minimum turbulence up to a point, after which it quickly drops to zero. On the other hand, forms with spine lengths longer than the body of the trilobite (1.0 and 1.3), increase minimum turbulence rapidly before reaching the absolute minimum turbulence. The peak minimum turbulence is the same for forms with spines equal to the length of the body (1.0) and longer (1.3). The absolute minimum appears consistently at v = 0.062 m/s for all five models. After this absolute minimum is reached, the streamlining in the system quickly disappears. This is because positions of turbulence origination after this peak quickly move back up the body of the trilobite until turbulence dominates the entire system. Before this tipping point is reached, vortices began swirling at the tips of the genal spines. The minimum turbulence position increases with genal spine length until the spines are equal the length of the body (Figure 4) at which point it no longer increases.

A range was found in the drag forces acting upon the differing trilobite morphologies. The shortest genal spine lengths (0.0 and 0.3) experienced approximately equal drag forces across all velocities. The longest genal spine lengths (1.0 and 1.3) also experience approximately equal drag forces. However, the median genal spine length (0.5) experienced forces directly between the two extremes (Figure 5). Coefficients of drag for forms with long genal spines (1.0 and 1.3) were 1 to 1.5 times greater than those of the shorter genal spines (0.0 and 0.3). Again, the model with intermediate spine length (0.5) fell right in the middle. At higher velocities the coefficients of drag leveled out as they became dominated by higher flow speeds (Figure 6). The coefficients of drag, even at high velocities (Figure 7), seem unusually high for these models and may be incorporating other forces, such as lift into the measurements.

DISCUSSION

In certain flow regimes, trilobite genal spines have a direct effect on turbulence and drag forces and therefore the fluid dynamics acting on the organism. In moderate flow speeds and intermediate spine lengths, genal spine directly contribute to minimum turbulence and drag forces. With regards to turbulence, genal spine length has a direct effect on the transition from streamlining to turbulent conditions surrounding the animal. Once water speed becomes too high ($v > 0.062$ m/s here), however, fluid velocity in the boundary layer overcomes any morphological advantage. This tipping point velocity appears constant across all morphologies. The point of minimum turbulence may be significant for benthic organisms dependent on kicking up sediment either for burial and defense or for filter feeding. Too much turbulence would not be beneficial to the organism as the animal may become permanently buried.

Streamlines that were not directed by the lateral border of the cephalon down to the genal spine were directed over the nose of head shield. The rounded morphology at the posterior-most margin when flattened against the sediment would act like an air dam on a car, directing flow over the body. Minimizing flow under the body of the organism would be critical for reducing lift and keeping the trilobite on the ocean floor. Dorsally armored trilobites were likely keen to keep pressed against the substrate because they would not want to be flipped up, thus exposing their soft underbelly to predation.

Beyond considerations of lift, the other fluid dynamic effect acting on trilobites would be forces of drag. The drag forces induced on the models with increasing flow produced a range of results. Specifically, cases of short or absent genal spines yielded similar forces results. On the other hand, genal spines equal to or longer than the length of the body produced approximately equal results. These extreme cases bookend a potential range of spine lengths along the body. The range between the extremes is indicative of forces that could be experienced by trilobites with intermediate genal spine lengths (0.3-1.0). When calculating the coefficient of drag, the projected area is relatively constant (Table 2) even though the trilobites possess distinct morphologies. This emphasizes the importance of drag force and morphology over area and fluid velocity.

I conclude that genal spine length affects by flow only so long as the spines extend the body length of the trilobite. Extremely long or short genal spines have no added benefits to drag. While turbulence along the body can be minimized with longer spines, the effect can only be effective up until the spines reach the length of the body. Therefore, I interpret exaggerated spine form (>1.0) to be driven by factors beyond drag and turbulence in fluid flow. Possible factors include stabilization in flow or defense against predation. While trilobites with shortened or elongate genal spines are informative for interpreting the extremes, forms with intermediate genal spine length need additional analysis. If intermediate spine length corresponds to the environmental flow conditions observed in the force vs. velocity relationship, it may be possible to predict the underlying interaction between the trilobite and its environment. Furthermore, we could match these biomechanics inferences with facies interpretations of the habitat.

Cephalon biomechanics of trilobites has much room for expansion. These ancient arthropods occupied numerous ecospaces with a relatively standard morphology, making them prime candidates for correlating form, function and environment. Within their morphology, the genal spine has been considered here, but not to its fullest potential. For example, many trilobites molt by releasing their librigenae, or free cheeks, which include the genal spines. One wonders how fluid dynamics would change around the cephalon once these spines were removed or temporarily softened? While many large-scale questions may be asked about trilobite biomechanics, minor morphological modifications that confound from and function may also be of interest.

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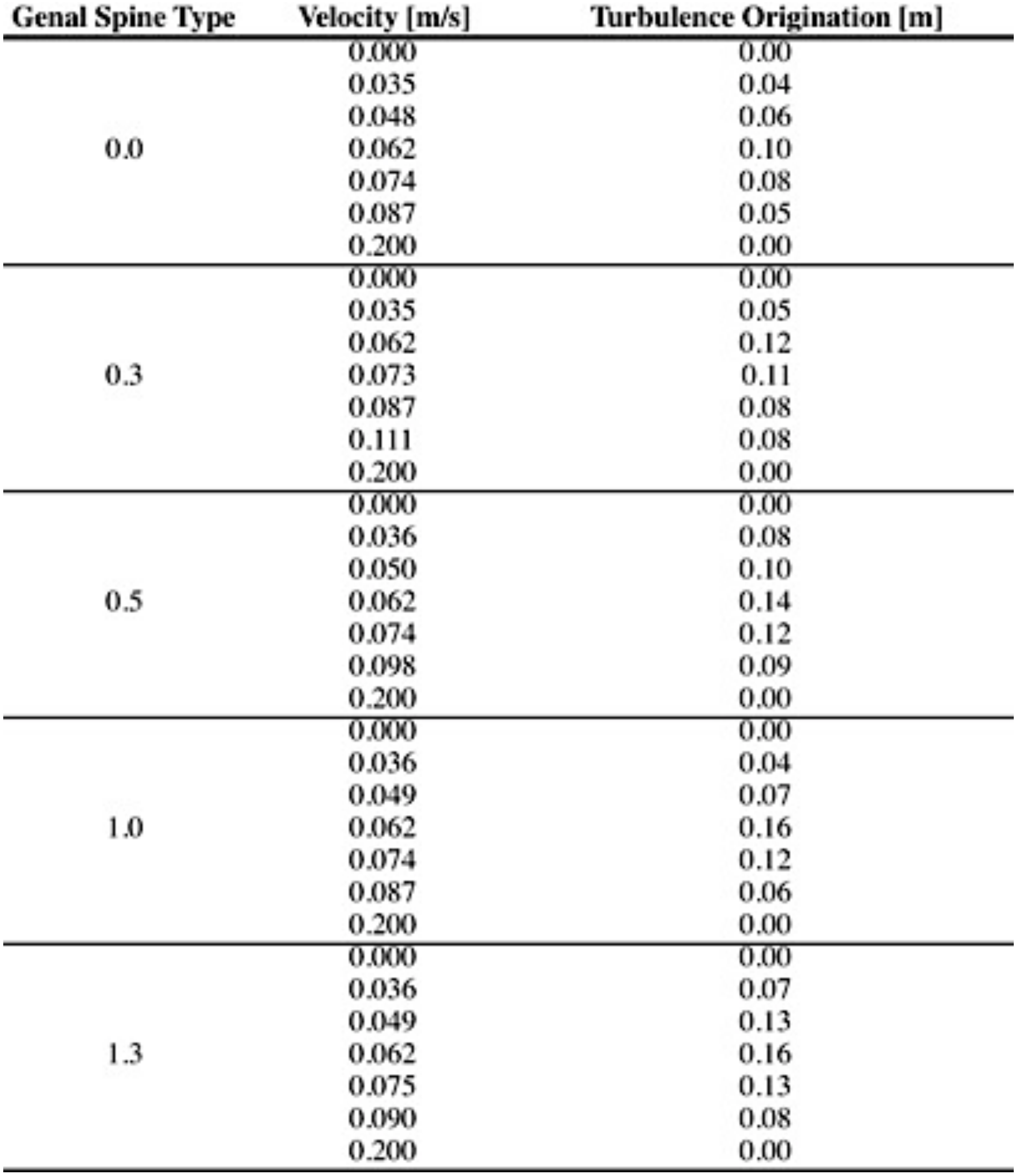
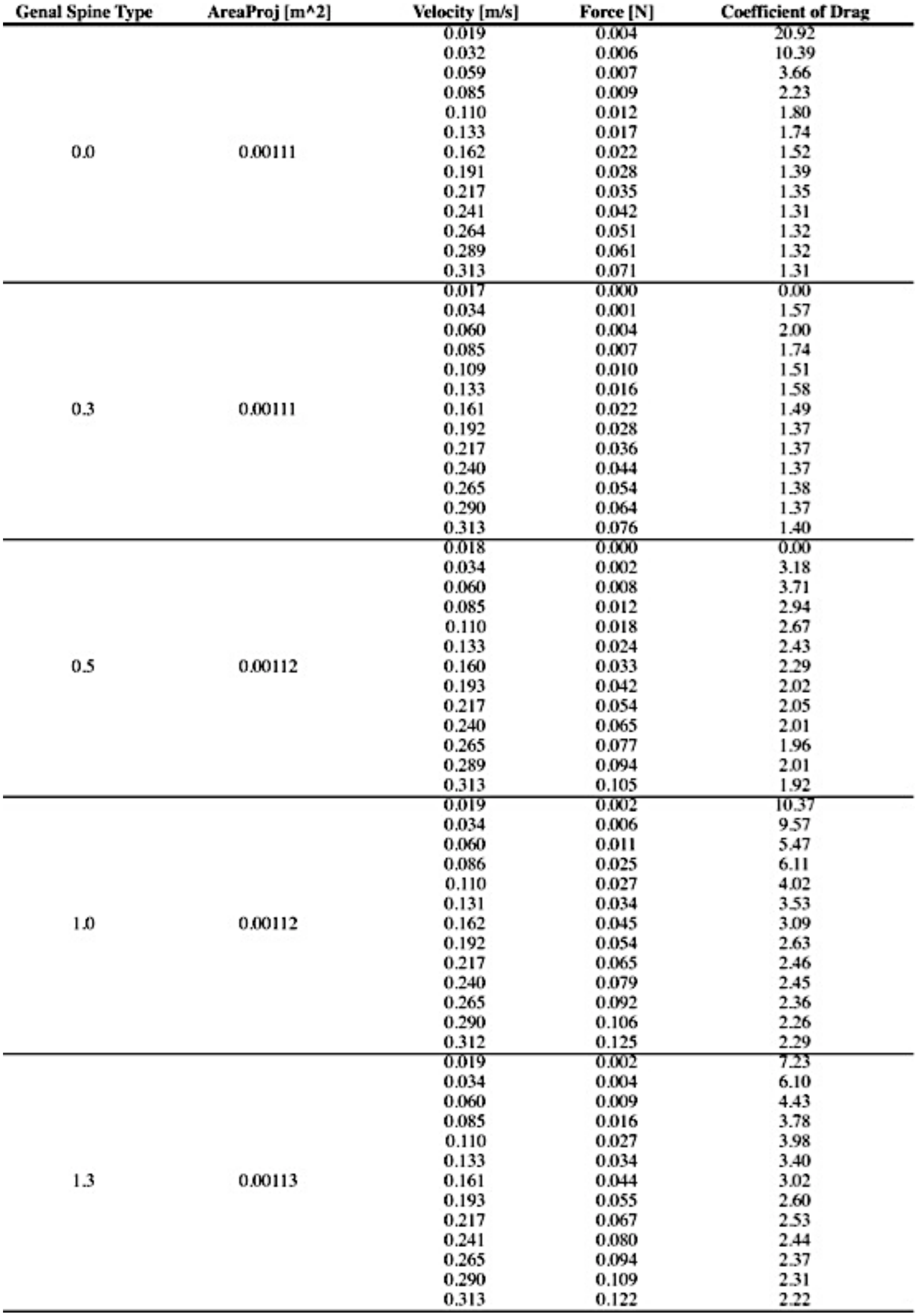
TABLE 1. Table showing distance of turbulence origination from anterior-most tip of cephalon with corresponding fluid velocity.



Genal Spine Type	Velocity [m/s]	Turbulence Origination [m]
0.0	0.000	0.00
	0.035	0.04
	0.048	0.06
	0.062	0.10
	0.074	0.08
	0.087	0.05
	0.200	0.00
0.3	0.000	0.00
	0.035	0.05
	0.062	0.12
	0.073	0.11
	0.087	0.08
	0.111	0.08
	0.200	0.00
0.5	0.000	0.00
	0.036	0.08
	0.050	0.10
	0.062	0.14
	0.074	0.12
	0.098	0.09
	0.200	0.00
1.0	0.000	0.00
	0.036	0.04
	0.049	0.07
	0.062	0.16
	0.074	0.12
	0.087	0.06
	0.200	0.00
1.3	0.000	0.00
	0.036	0.07
	0.049	0.13
	0.062	0.16
	0.075	0.13
	0.090	0.08
	0.200	0.00

TABLE 2. Values needed to calculate coefficient of drag for models in freshwater.



Genal Spine Type	AreaProj [m^2]	Velocity [m/s]	Force [N]	Coefficient of Drag
0.0	0.00111	0.019	0.004	20.92
		0.032	0.006	10.39
		0.059	0.007	3.66
		0.085	0.009	2.23
		0.110	0.012	1.80
		0.133	0.017	1.74
		0.162	0.022	1.52
		0.191	0.028	1.39
		0.217	0.035	1.35
		0.241	0.042	1.31
		0.264	0.051	1.32
		0.289	0.061	1.32
		0.313	0.071	1.31
0.3	0.00111	0.017	0.000	0.00
		0.034	0.001	1.57
		0.060	0.004	2.00
		0.085	0.007	1.74
		0.109	0.010	1.51
		0.133	0.016	1.58
		0.161	0.022	1.49
		0.192	0.028	1.37
		0.217	0.036	1.37
		0.240	0.044	1.37
		0.265	0.054	1.38
		0.290	0.064	1.37
		0.313	0.076	1.40
0.5	0.00112	0.018	0.000	0.00
		0.034	0.002	3.18
		0.060	0.008	3.71
		0.085	0.012	2.94
		0.110	0.018	2.67
		0.133	0.024	2.43
		0.160	0.033	2.29
		0.193	0.042	2.02
		0.217	0.054	2.05
		0.240	0.065	2.01
		0.265	0.077	1.96
		0.289	0.094	2.01
		0.313	0.105	1.92
1.0	0.00112	0.019	0.002	10.37
		0.034	0.006	9.57
		0.060	0.011	5.47
		0.086	0.025	6.11
		0.110	0.027	4.02
		0.131	0.034	3.53
		0.162	0.045	3.09
		0.192	0.054	2.63
		0.217	0.065	2.46
		0.240	0.079	2.45
		0.265	0.092	2.36
		0.290	0.106	2.26
		0.312	0.125	2.29
1.3	0.00113	0.019	0.002	7.23
		0.034	0.004	6.10
		0.060	0.009	4.43
		0.085	0.016	3.78
		0.110	0.027	3.98
		0.133	0.034	3.40
		0.161	0.044	3.02
		0.193	0.055	2.60
		0.217	0.067	2.53
		0.241	0.080	2.44
		0.265	0.094	2.37
		0.290	0.109	2.31
		0.313	0.122	2.22

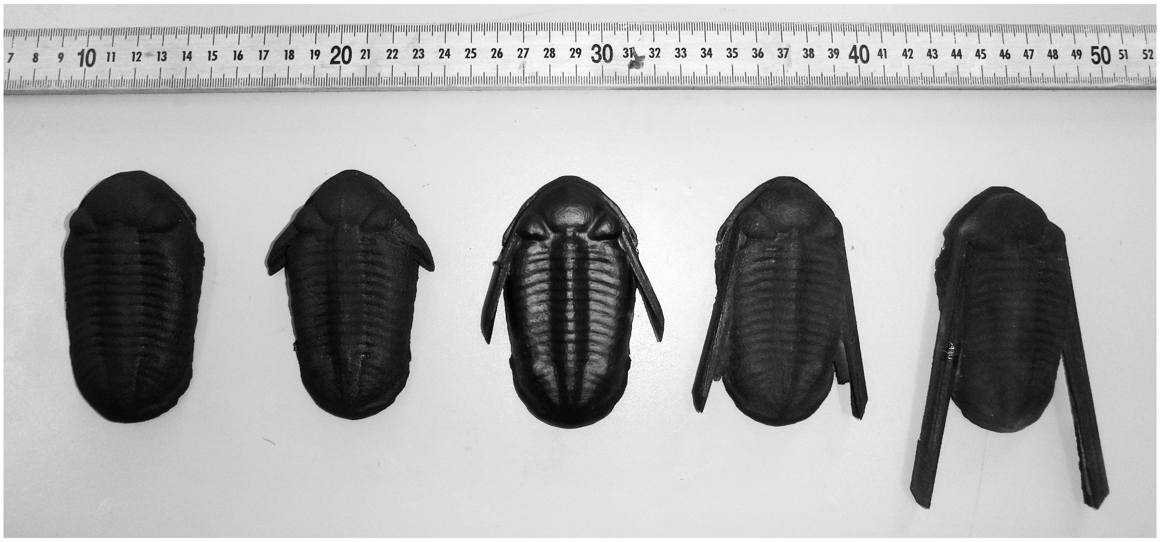


FIGURE 1. Five black trilobite models with genal spines of increasing length. From left to right, spine designations: 0.0, 0.3, 0.5, 1.0 and 1.3.

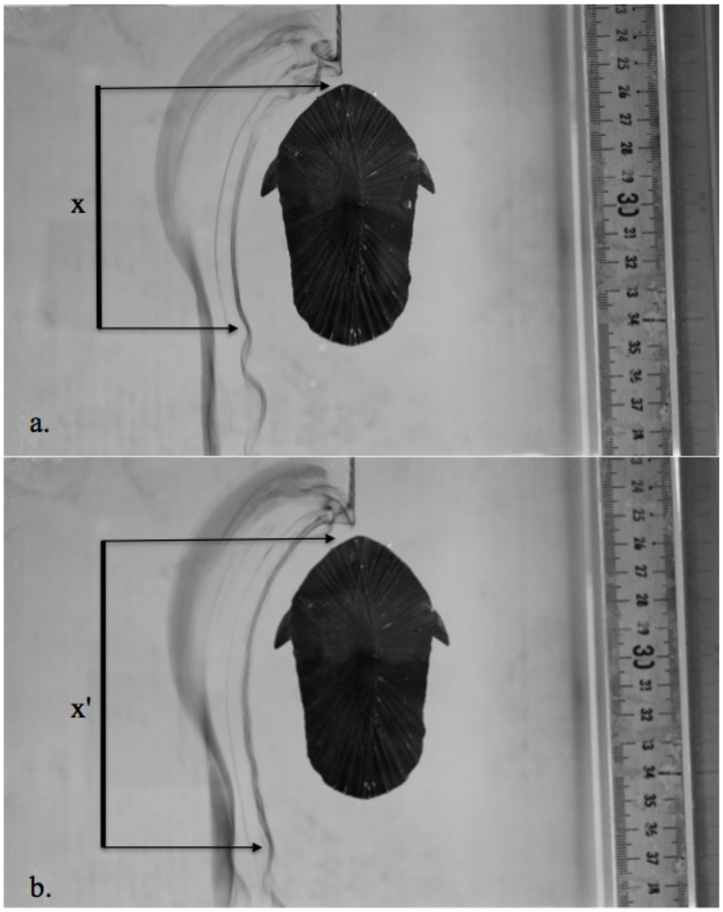


FIGURE 2. Dye stream method used to determine point of turbulence origination at a.) low velocities and again at b.) higher velocities.

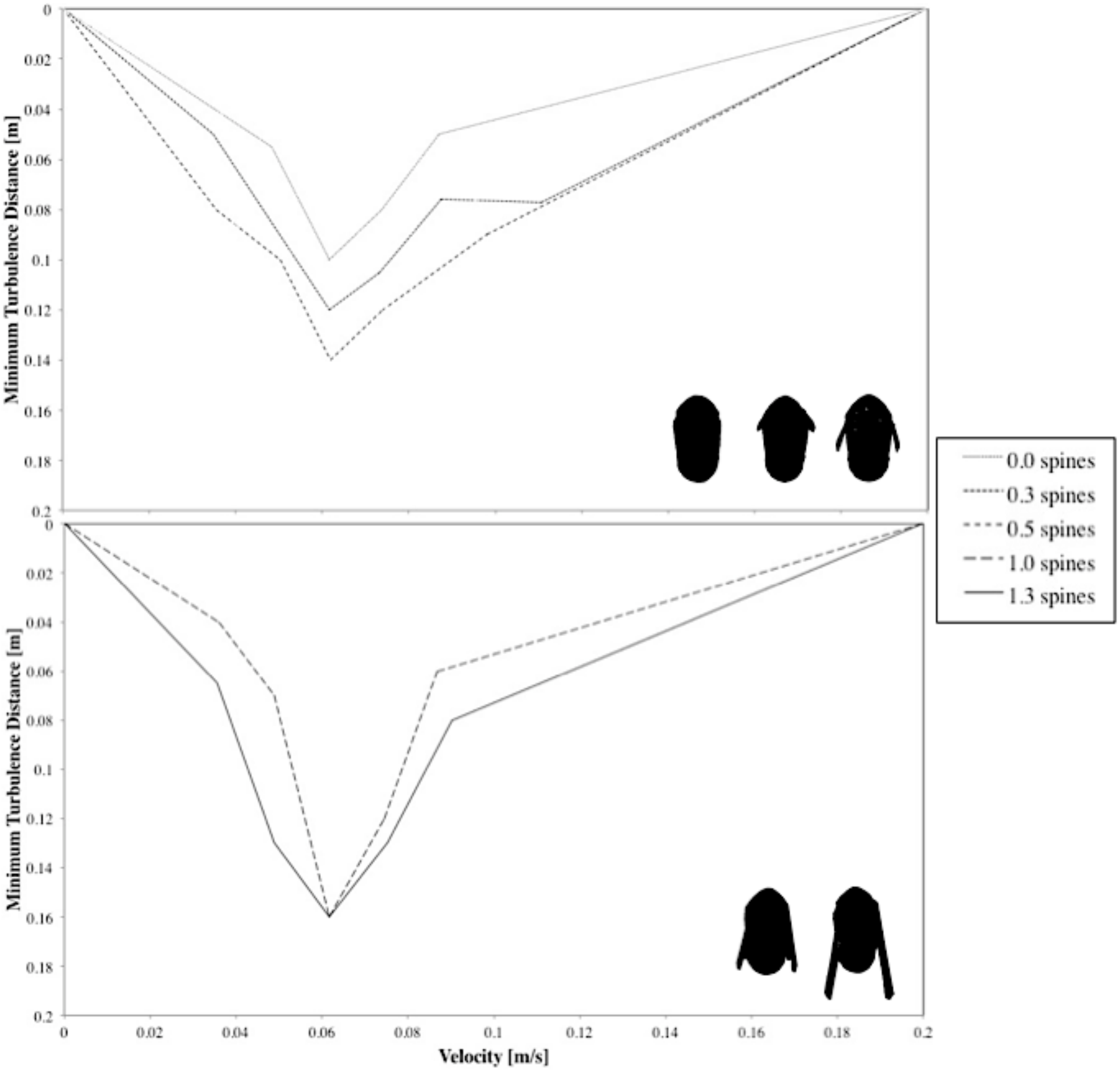


FIGURE 3. Minimum turbulence, measured from tip of cephalon to point of qualitative turbulence origination, against velocity for forms of lowest genal spine lengths (top) and long spine lengths (bottom). Two different trends were observed.

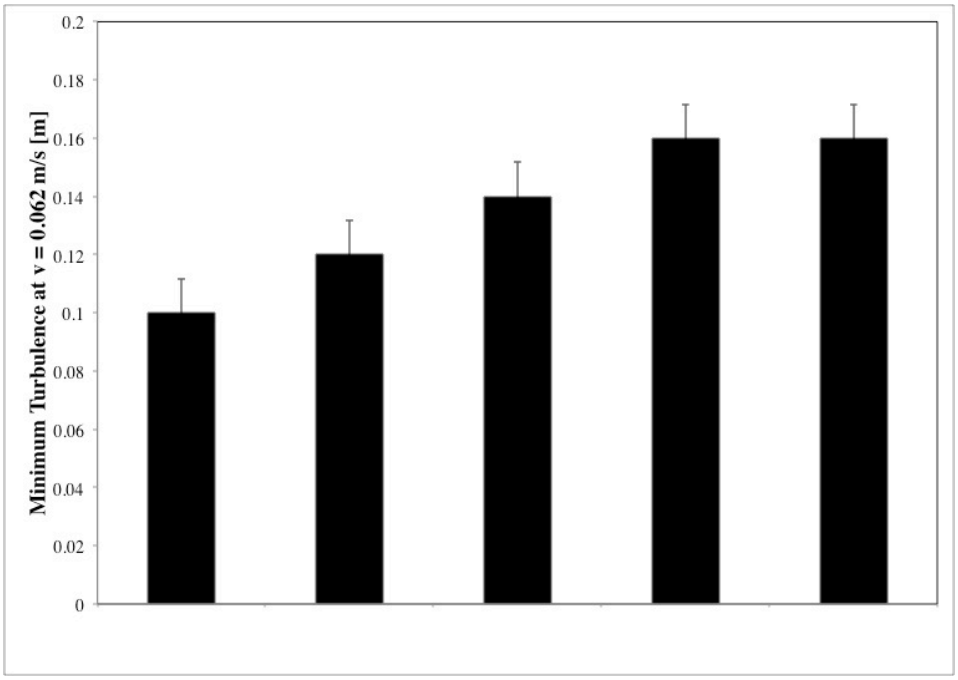


FIGURE 4. Peak turbulence (at v = 0.062 m/s) for all genal spine lengths. Genal spine lengths ≥ 1 peak at the same point.

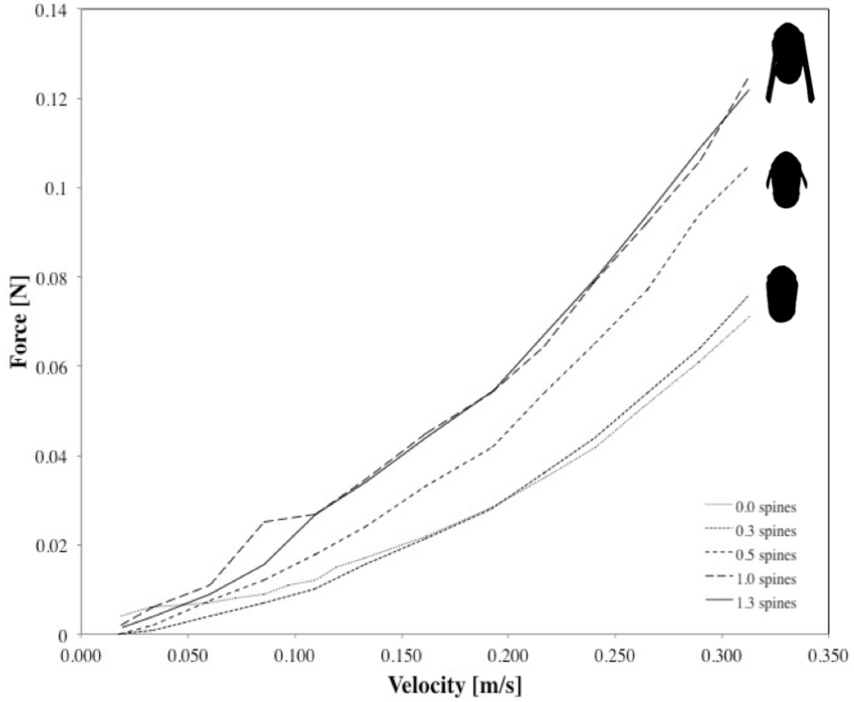


FIGURE 5. Force against velocity for all five trilobite forms. Genal spine lengths of similar extremes cluster together revealing a range in between.

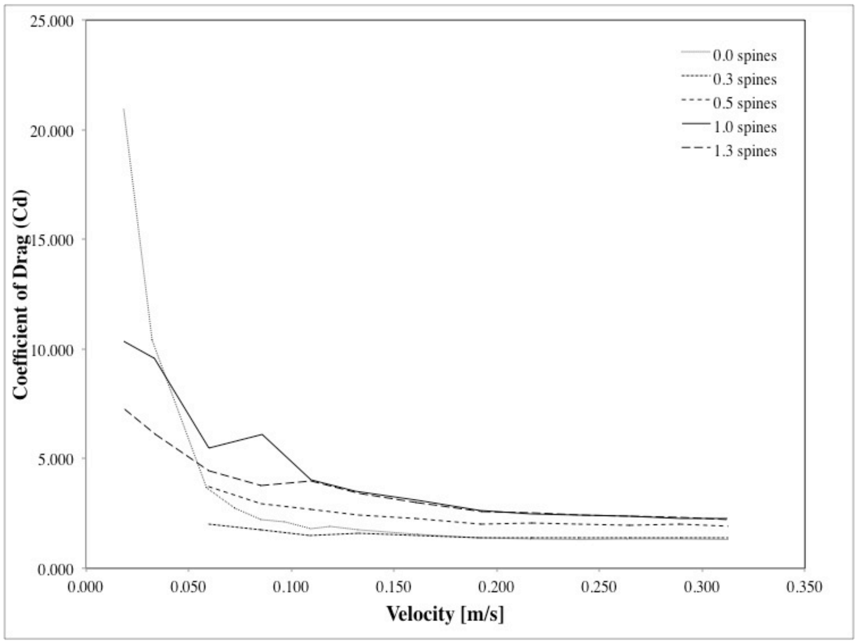


FIGURE 6. Calculated coefficients of drag for all five trilobite forms for all velocities.

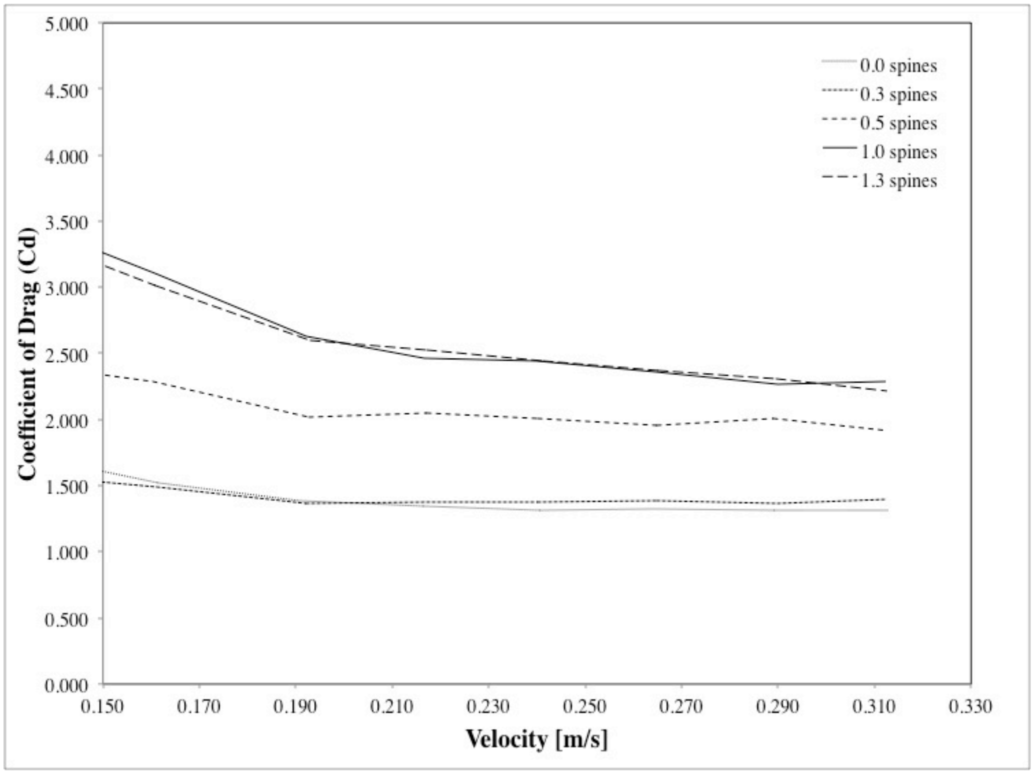


FIGURE 7. Calculated coefficients of drag for all five trilobite forms at highest velocities.