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Title: Assessing the morphological impacts of ammonoid shell shape through systematic shape variation

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Short Abstract:

A substantial body of research has been accumulated around ammonoids over several decades. A core aspect of this research has been attempts to infer their life mode from analysis of the morphology of their shells and the drag they incur as that shell is pushed through the water. Tools such as Westermann Morphospace have been developed to investigate and scaffold hypotheses about the results of these investigations. We use Computational Fluid Dynamics (CFD) to simulate fluid flow around a suite of 24 theoretical ammonoid morphologies to interrogate systematic variations within this space. Our findings uphold some of the long-standing expectations of drag behavior; conch inflation has the greatest influence over ammonoid drag. However, we also find that other long-standing assumptions, such as oxyconic ammonoids being the best swimmers, are subject to substantial variation and nuance resulting from their morphology that is not accounted for through simple drag assessment.

I. Introduction

Ammonoid cephalopods were the most abundant meat-eaters (presumed based on modern cephalopod diets) in ancient marine ecosystems for more than 300 million years (Ritterbush et al. 2014, Klug et al 2015, Villanueva et al. 2017). Their abundant fossil shells are used to track geologic time worldwide, and the animals' possible roles in marine ecology are hotly debated. Quantification of lifestyles available to ammonoids – swim speeds, metabolic rates, trophic levels – requires data beyond the scope of traditional paleontological and experimental methods due to lack of preservation of soft tissue. Recent advances, however, now marshal integration of legacy data (e.g. Raup 1967; Ritterbush et al. 2014; Ritterbush 2015; Whalen and Briggs 2018), new fossil discoveries (e.g. Landman et al. 2012, Jattiot et al. 2016, Becker et al. 2019, Naglik et al. 2019), and digital analyses (e.g. Kruta et al. 2013, Lemanis et al 2016, Hoffman et al. 2018, Tajika et al. 2020, Peterman et al. 2019a; 2019b) to explore new interpretations of ancient ecosystems (Ritterbush et al. 2014, Whalen and Briggs 2018, Tajika et al. 2020). An avenue ripe for reinvestigation is the dynamism of fluid flow around different shapes of ammonoid shells (hereafter referred to as conchs).

Ammonoids produced conchs with extreme variation in shape and size. Substantial changes in conch traits accompanied regional and global bio-events, for which paleontologists' explanations often invoke evolutionary and ecological significance to conch shape (e.g. Dera et al. 2010, Smith et al. 2014, Pietsch et al. 2019). Like all living cephalopods, ammonoids presumably propelled a jet of water away from their body exposed at the aperture, requiring water to flow around their conch edge-on as their primary mode of locomotion. Predictable consequences of conch shape include greater fluid drag for broadly inflated forms, and reduced drag for streamlined forms (Chamberlain 1976, Jacobs 1992, Ritterbush and Bottjer 2012); these and more nuanced consequences of conch shape, such as trade-offs between material and metabolic efficiency or the stability and recovery of the conch following a jetting action, are well-supported by analyses (Tendler et al. 2015, Hammer and Bucher 2006), experiments (Jacobs 1992, Seki et al. 2000, Peterman et al. 2019) and simulations (Peterman et al. In Press, Hebdon et al 2020). Interpretive tools compare hydrodynamic perspectives to ammonoid conch shape data (Ritterbush and Bottjer 2012, Smith et al. 2014, Tendler et al. 2015).

Westermann Morphospace is a ternary diagram that projects common ammonoid conch shapes into distinct corners, and was framed explicitly to match fluid dynamics interpretations to fossil observations (Ritterbush and Bottjer 2012, Ritterbush et al. 2014, Ritterbush 2015). Based on clear differences in hydrodynamic drag measured for distinct ammonoid conch shapes (Ritterbush 2015, Hebdon et al. 2020), we predict gradients in efficiency for intermediate forms. Any increase in conch inflation or umbilical exposure should add drag to a conch, while any increase in whorl expansion rate should reduce drag. We predict that varying these three conch shape parameters (umbilical exposure, whorl expansion, and thickness ratio; Figure 1) together, and individually, will reveal coherent gradients, thresholds, and trade-offs that are consistent across the morphospace. Gradients and thresholds in swimming efficiency can be used to interpret the ecological consequences of ontogenetic and phylogenetic paths, and of ecological-evolutionary explanations for major bio-events.

II. Methods

We simulate fluid flow around simple ammonoid models, using a Computational Fluid Dynamics (CFD) model (Ansys® Fluent 2017; 2019, v 18; v 19.2). First, we produced 24 theoretical ammonoid conch morphologies using a custom conch generation program created in Unreal (Unreal Engine 2019, v 4.22). We used Bezier curves to set aperture shape, which was then rotated from a focal point through three iterated spiral whorls, while reflecting user defined variation in umbilical exposure and whorl expansion. The central umbilicus was filled with a depressed cylinder to approximate fine inner whorl flanks (for which the variation in size of the center is beyond our model resolution). Finally, thickness ratio was applied as a ratio of conch width vs diameter from aperture to venter (Figure 1). Completed conchs represent first-order external geometry only, and lack ornament (ribs, tubercles, etc.) or internal features (chambers, density gradients, etc.). We then export the models from Unreal to Blender (Blender - a 3D modelling and rendering package 2018 v 2.79c) to assign a consistent conch diameter and orient the aperture 30° angle (Saunder and Shapiro 1986). In this study, we produce all specimen models at a conch diameter of five centimeters, consistent with a majority of ammonoid sizes through time (Raup 1967). In addition, models were fitted with a tapered "body" extending 1 cm from a flush contact to the aperture to represent soft tissue occupation and to remove artefacts caused by leaving the aperture flat or open (after Jacobs, 1992). Of these 24 models, 16 form transects along the three midlines of Westermann Morphospace, and an additional 8 which form single-parameter gradients (one set alters only umbilical exposure; the other set alters only whorl expansion; Figure 2).

Following Hebdon et al. 2020, the model conchs were simulated as a solid body at a fixed position in a 285 cm X 155 cm X 155 cm flume, with the model's midpoint placed at 32.5 cm away from the flume inlet and otherwise centered in the domain (Figure 3). In addition, the mesh was refined in an area around the conch to better resolve our flow field of interest. Refinement was chosen through a grid independence study done on the moderate serpenticone conch model, which possessed the median thickness ratio of models (Figure 4). This resulted in a grid size within the refinement area of 4mm and total element counts of approximately 4 million elements being used across the simulations.

We used the ANSYS Fluent solver (Ansys® Fluent 2017;2019, v 18;v 19.2) with the Shear Stress Transport (SST) k-ω turbulence closure model as per Hebdon et al. (2020).Boundary conditions were assigned following the recommendations of Hebdon et al. 2020; a symmetry boundary condition at the external walls of the fluid domain, velocity specified at the inlet, and a constant zero pressure at the outlet. The ammonoid surface within the flume was given a no-slip condition. Finally, the fluid in the domain was defined using Fluent's default properties for liquid water (density of 1 g/cm^3 and viscosity of 0.01003 g/cm-s). Finally, we set the stream velocity of the water within our simulated tank. As in a physical flume experiment, stream velocities in these simulations are proxies for the animal pushing through the water at the specified velocity and not ambient velocity of their environment. Simulations for each conch were done with stream velocities of 20 cm/s (approximately 4 body lengths per second) and 5 cm/s (approximately 1 body length per second) and the subsequent drag forces and coefficients were calculated and recorded. These speeds are well within the range of modern swimming cephalopods with 20 cm/s being relatively slow for rapid swimmers such as squid (Chamberlain 1981). These specific speeds were chosen based on previous work by Hebdon et al. (2020) where these speeds bookend the inflection around which the behavior of the drag force trend changed for all conch morphologies and thus represent the two places where differences in adaptive optima were assumed to be most visible. These speeds are also typical among the few previous experimental ammonoid hydrodynamics studies facilitating easy comparison across studies (Jacobs 1992, Seki et al. 2000)

Coefficient of drag (C_d) and Reynolds number (R_e) values were calculated for each shell-speed combination following Jacobs (1992). C_d is formulated as:

Eq 1. $C_d=2D_f/A\rho U^2$

In this formulation D_f is the drag force (which is taken from each completed simulation), A is the characteristic area term of the target (the model conch), ρ is the density of the fluid and U is velocity. For this study we follow Jacobs (1992) and use $V^{2/3}$ (volume) as our characteristic area term.

R_e is used to express the turbulence of fluid flow via the ratio of viscous and pressure forces, which provides the context for comparison when experiments span the range from viscous to turbulent conditions.

Eq 2. $R_e=Ul/v^2$

As before U is the velocity of the fluid, l is the characteristic length of the fluid which in this formulation is the total length of the ammonite model parallel to flow, and v is the fluid viscosity. By setting the characteristic length to the length of the shell it is the turbulence of the flow around the shell and not that of the flow within the whole of the simulated tank. It is the R_e functionally experienced by the shell when moving at a certain speed rather than that of the ambient water.

III. Results

Drag values for all 24 conchs are shown on filled contour plots of Westermann Morphospace for both velocities in Figure 5. Darker colors in both plots indicate higher drag forces. As hypothesized, these plots show a very strong association between drag force and thickness ratio. The highest drag forces occur in the spherocone region of the morphospace (the upper right portion) and the lowest occur along the left flank of the morphospace. Additional gradients or thresholds that occur along the left flank – that is, along the gradient between serpenticone and oxycone – are harder to distinguish amid the overwhelming thickness ratio signal. Figure 6 shows drag force plotted along the individual parameter gradients within the central part of this region.

The non-dimensionalized metrics (C_d and R_e) illustrate interactions between the underlying dynamics of fluid flow that are obscured just through observing raw drag forces. We show the morphospace contoured by C_d (Eq 1) in Figure 7, which removes size factors such as differences in volume or length caused by morphological variance (even when some factors of size are controlled such as conch diameter in this study). The highest C_d values occur in inflated spherocone shapes, but the minimal values have a more complex expression. In simulated stream flow of 5 cm/s (Figure 7A), minima appear near the extreme serpenticone, and moderate serpenticone-to-oxycone areas. In simulated stream flow of 20 cm/s (Figure 7B), minima shift more to the oxycone and platycone (a compressed intermediate shape) areas.

Finally, Figure 8 contours Westermann Morphospace with the logged ratio of C_d/R_e. Here, results for simulations at 5 cm/s differ dramatically from simulations at 20 cm/s. In stream flow of 5 cm/s (Figure 8a), minimum values occur for conchs with a moderate serpenticone or oxycone shape. In simulated flow of 20 cm/s (Figure 8b), these minima shift closer to the left flank of the morphospace, encompassing most, but not all, compressed shapes.

IV. Discussion

Westermann Morphospace was deliberately framed to compare and contrast planispiral conch shapes with demonstrated (or presumed) differences in hydrodynamic efficiency (Ritterbush and Bottjer 2012). Our simulations evaluate hydrodynamic consequences of conch shape across gradients between outstanding morphotypes (which differ from one another via changes in all three shape parameters), and largely support previous interpretations. Consistent with previous studies (experimental e.g., Saunders and Shapiro 1986, Jacobs 1992, Jacobs and Chamberlain 1996, Seki et al. 2000; and speculative, e.g., Westermann 1996, Ritterbush 2012, Smith et al. 2014, Tendler et al. 2015, Walton and Korn 2018), we find higher drag forces from spherocone shells (high inflation, low umbilical exposure, low whorl expansion); and lower drag forces from compressed shells (serpenticones, with high umbilical exposure; oxycones, with high whorl expansion). Conch shape traits typically co-vary in ammonoids (i.e., high whorl expansion typically occurs in fossil conchs with low umbilical exposure; see Thompson 1942), but testing distinct morphotypes does not resolve which, or how, specific shape characteristics influence drag force. Before presenting interpretations relevant to paleoecologists reconstructing the life-habits of ammonoids, we add scrutiny to individual parameters of conch shape.

We model subtle shape differences in umbilical exposure, and in whorl expansion, by producing two additional spectra of shell shapes (see Figure 3C). Along these subtle shape gradients, we find unexpected complexity in simulated drag force. First, the magnitude, and even direction, of drag force change does not appear to scale linearly with the altered shape parameter. For example, we can easily conclude that additional umbilical exposure generally adds drag to a conch (Fig. 6), but the magnitude of added drag force is difficult to predict. In contrast, conchs with increased whorl expansion generally yield reduced drag force, but the specific results are erratic (Figure 6). In fact, only inflation appears to behave predictably. To make sense of these overall results and develop a framework to better evaluate morphological alterations, we must look beyond direct drag estimates, and consider the dynamics of fluid flow around these complex shapes.

Because Westermann Morphospace orients specimens with respect to their relative expression of the three shape traits we alter here, we can illustrate gradients in our results as contour plots. Figure 5 shows results of drag force in Westermann Morphospace. Here, conch inflation clearly holds heavy influence on simulated drag force: at both simulated velocities (5 cm/s and 20 cm/s), inflated shells produce more drag than compressed shells. But the relatively low drag force values among compressed conch shapes bely complexity in the flow regimes that develop around these models. Estimates of drag in stream flow carry unscrutinized effects of size: even though our conchs are modeled with the same diameter, they have different volumes, surface areas, and cross-sectional areas. Our choice of a uniform diameter for the models is somewhat arbitrary; while it is intuitive to a paleontologist examining fossils in a drawer, an engineer or biologist might want to match the models' overall volume, or body chamber volume, etc. To acknowledge (and dismiss) the role size plays in drag force, we instead can view each shape's drag coefficient (C_d).

We find drag coefficients highlight the complexity of flow around varied serpenticone and oxycone shapes (Figure 7). The C_d is a non-dimensional number that expresses how each distinct shape contributes to drag force, when other conditions are held constant (size, turbidity conditions, etc.; Jacobs 1992). For simulations at 5 cm/s velocity, we note two distinct minima in C_d value: a moderate serpenticone with a highly exposed umbilicus (the maximum of the gradient tested here); and a moderate oxycone with a high whorl expansion rate (the maximum of the gradient tested here). Importantly, these specimens are not single-point outliers; we observe gradients surrounding each C_d value minima, due to intermediate results for adjacent conch shapes (those plotting nearby due to alteration of one or more shape parameters). Under the 20 cm/s simulation, minimal C_d values appear among more oxyconic shapes.

Turbulence and the general flow regime that an ammonoid faces are also crucial to consider. From an engineering perspective, all of our simulations at a single velocity (say, 5 cm/s) present the specimen with matching circumstances: the experimental orientation is the same, the velocity of the fluid is the same, etc. But if we consider a very small animal, in a very small shell, trying to jet propel its way through a space of open surface ocean, we must orient our attention to the conditions of turbulence from this frame of reference. One approach is to express the turbulence regime in terms that attend to the specimen, rather than to the simulated flow chamber.

Reynolds number (Re) assesses turbulence by relating momentum and viscosity. It is a relative and dimensionless variable. An object with little momentum in a high viscosity fluid will have a low Re, permitting laminar flow, and will be subject to friction drag along the object's flanks. An object with great momentum in a low viscosity fluid will have high Re and experience turbulent flow, which releases friction drag but retains pressure drag. Thus, the transition from low to high Re, the transition from laminar to turbulent flow, and the transition from friction to friction-less drag force, are crucial for an animal moving through water. Momentum, of course, relates to both size and velocity; if we consider the Re from the perspective of our animal, then we have an additional context in which the size of the conch is critical. But, as discussed with Cd, our conchs modeled at the same diameter still have different characteristic volumes, cross sectional areas, and surface areas, any of which may influence both Cd and Re.

Our final step is to contour Westermann Morphospace with the contrast of drag coefficient and turbulence: $\log(C_d/R_e)$; Figure 8. This metric effectively isolates each shape's contribution to viscous drag force. At last, we can consider our results as a proxy for shape efficiency as a response to flow conditions: how much a conch shape will frustrate the animal trying to jet propel through seawater will depend on both size and speed. When we evaluate raw drag force, our 5 cm/s simulations imagine an animal moving one conch-diameter per second. A literal interpretation is that an oxycone shell generates the least drag force (Figure 5). But if we imagine that our animals will jet propel and experience a mild acceleration to a slightly higher velocity (but same size), the moderate serpenticone, and moderate oxycone, are going to get the most bang-for-their buck. In this range, for a given increase in turbulence (Re, caused by the added velocity after accelerating), the contribution of shape to drag force (Cd) is quite small for both the moderate serpenticone and for the moderate oxycone. Next, let us imagine each animal will increase the size of its conch slightly by growing a bit (isometrically, for the purpose of discussion), and will still try to move at the same 5 cm/s velocity. Each animal will experience, again, slightly elevated turbulence right around its conch. Again, the moderate serpenticone and moderate oxycone will each have low Cd in this exchange, so that the slight increase in conch size does not generate much increase in drag force, compared to their differently-shaped peers. The same principals, but different outcomes, apply to our simulations at 20 cm/s. Now, the extreme oxycone specimens will have it easy. If all our animals experience a slight increase in turbulence (via all moving quicker; or via each growing isometrically a bit), the extreme oxycone is the shape that should impart the least drag force increase. If an animal will experience this generally-more-turbulent flow regime, then the most extreme oxycone conch shape is going to have the least drag gain per unit of speed (or size) gain. Our moderate serpenticone, and moderate oxycone, will fare about as well as our central, generic ammonoid; in this more-turbulent situation, they offer nothing special.

First-order hydrodynamic trade-offs in conch shape provide a useful framework to interpret past bio-events in Earth history. The abundance of small spherocone conchs in

Paleozoic seas (Raup 1967, Dera et al. 2010, Whalen and Briggs 2018) may have best-served very modest jet-propelled activity; based on our results, their shells would be strikingly difficult to propel with any size or speed increase. Many Early Triassic species produced small conchs of moderate serpenticone or oxycone shapes. Applying our results, each shape would benefit from a slight increase of turbidity to release friction drag, and so we propose that these conch shapes might have supported generally active (though perhaps intermittent or infrequent) jet-propelled swimming. This may help explain why these morphotypes become the most common in the time of dinosaurs (Ritterbush 2015, Pietsch et al. 2019). In the Early Jurassic particularly, species produced medium-to-large conchs with serpenticone shapes, which would automatically put the adult animals into higher turbulence regimes. Applying our results, we suggest that swimming efficiency was probably not a selective driver of this shape trend (Guex 1995, Smith et al. 2014). Finally, we interpret that only the more oxyconic conch shapes would have enjoyed substantial locomotory benefits as size and speed increased the turbulence of their flow regime (McGowan 2004, Brosse et al. 2013, Ritterbush et al. 2014, Pietsch et al. 2019). If any ammonoids used jet propulsion for vigorous swimming (be it persistent activity, or intermittent-but-repeated escape bursts), we suggest the oxycone conchs, especially large oxycone conchs, offered the best chance of efficiency.

V. Conclusions

Our results are consistent with previous interpretations of ammonoid life modes and hydrodynamics but increase the nuance of these interpretations. We show that high thickness ratio conchs are indeed inefficient swimming morphologies but less so than may have previously been speculated, even being comparable to their counterparts at low Reynolds number. However, we show that efficiency among these morphotypes in particular rapidly decreases as swimming velocity increases. On the other hand, oxycone and serpenticone morphs retain at least modest efficiency as they approach multiple body lengths per second speeds. This serves as a reasonable explanation for their decline through ammonoid history as more streamlined forms became more common in marine ecosystems and possibly necessitated with increased competition from other organisms.

The dynamics of the space characterized by whorl expansion and umbilical exposure are even less straightforward. There appear to be multiple efficiency peaks within this region and the areas of peak efficiency at high flow velocity reverse to become areas of decreased efficiency with low velocities. This dynamic efficiency optimum supports previous hypotheses that particular morphologies best serve particular life modes but the actual shape of those regimes is drastically more complex than has been previously suspected. Our analysis shows that even small shifts in the morphology of these animals had observable impacts on the potential life modes of ammonoids. This creates the foundation upon which the challenges and advantages of ammonoid shape can be examined across environmental, ontogenetic and phylogenetic perspectives. Additionally, our models do not include any surface variations such as ribbing or ornamentation. This facilitates future comparative studies investigating the development of these features, their effect on swimming performance, and the drivers behind their development.

Beyond ammonoids, this analysis illustrates the stark differences that can arise if a morphological problem is being interrogated from an insufficiently constrained perspective. It is possible to under examine the influence of the morphology in question and, in doing so, incorrectly characterize the influence of different attributes. Along the same lines it is easy to mischaractize a morphospace based on its complex morphological shifts when the underlying, simpler geometry changes may reveal unexpected dynamics at play.

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Figure Captions

Figure 1: Overview of anatomical terminology used within Westermann Morphospace and frequently throughout this paper (top). Formulations for the three primary metrics that define Westermann Morphospace are shown coordinated with the terminology above. Each image below a formulation shows what an exemplar of that feature might look like.

Figure 2: All Shells used in this study plotted in Westermann Morphospace A) Shells comprising the three midline transects highlighted B) Shells within the serpenticone transect, which strongly vary umbilical exposure (pink), and spherocone transect, which strongly varies thickness ratio (blue) C) Shells comprising the oxycone transect, which strongly varies whorl expansion (gray), and two individual gradients varying a single parameter: whorl expansion (shown in green) and umbilical exposure (shown in pink).

Figure 3: Cross-section through the meshed fluid domain. The length of the domain totals 285 cm. The inlet and corresponding outlet are squares with an individual side length of 155 cm. The model's midpoint is placed 32.5 cm from the inlet with the body approximation facing away from the inlet to simulate a typical, forward moving jet. The white box around the shell shows

the area of the inset (lower right). This shows the structure of the refinement area around the shell, which incorporates 10 layers of prismatic mesh to simulate the fluid boundary layer.

Figure 4: Results of the mesh independence study on the median serpenticone model. The X-axis shows the number of elements in the mesh (in millions of elements), the y-axis is the corresponding drag coefficient result. The green star highlights the selected grid size for the mesh where we begin to see stabilization and asymptotic behavior relative to large increases in mesh size. This selection balances computational efficiency while maintaining a grid size that provides a reasonably accurate solution.

Figure 5: Drag values contoured across Westermann Morphospace at 5 cm/s (A) and 20 cm/s (B). Darker colors show increasing drag values. The signal contoured in this way is dominated by a single transect, the spherocone axis (varying thickness ratio). The 24 models are plotted as black points within the space with white points highlighting models with the lowest drag forces. The morphology corresponding to the highlighted points is shown to the left arranged top to bottom corresponding with their points.

Figure 6: Drag values plotted against individual Westermann parameter gradients. A) Drag along the umbilical exposure gradient at 5 cm/s and C) 20 cm/s. B) Drag along the whorl expansion gradient at 5 cm/s and D) 20 cm/s. Drag along these gradients, generally, does not behave in a predictably linear fashion. This also highlights that shifting a single parameter does not consistently yield changes of the same magnitude or even the same sign (positive/negative) as when that trait is accompanied by smaller shifts along one or more of the other axes. The inset ternary diagram in the upper left of each plot shows the line these shells occupy in Westermann Morphospace (the coloring of this line also corresponds with Figure 2 for reference)

Figure 7: Coefficient of Drag values contoured across Westermann Morphospace at 5 cm/s (A) and 20 cm/s (B). Darker colors show increasing drag values. The spherocone transect still shows the strong gradient but now some of the underlying nuance between the oxycone and serpenticone corners of the morphospace are made clearer. The 24 models are plotted as black points within the space with white points highlighting models with the lowest C_d values. The morphology corresponding to the highlighted points is shown to the left arranged top to bottom corresponding with their points.

Figure 8: Log transformed C_d/R_e values contoured across Westermann Morphospace at 5 cm/s (A) and 20 cm/s (B). Darker colors show increasing drag values. The shape of the contouring when examining the morphospace in this way is slightly more nuanced, particularly in the areas where the highest values were seen in the previous contour plots (Figures 5 and 7). The 24 models are plotted as black points within the space with white points highlighting models with the lowest values. The morphology corresponding to the highlighted points is shown to the left arranged top to bottom corresponding with their points.

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