Swimming and burrowing in *Limulus* and *Mesolimulus*

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In the swimming of *Limulus polyphemus*, the development of an unstable, recirculating vortex within the prosomal vault is an important factor determining swimming orientation, swimming speed, and stroking rate of appendages. Experimental evaluation of the characteristics of vortex formation in *Mesolimulus walchi* gives us a good estimate of its swimming orientation, speed, and stroking rate. The highly vaulted prosoma of *Limulus*, which limits its speed as a swimmer, contributes to its proficiency as a burrower. Similarly, the mechanics of the femoral-patellar joint indicate greater swimming abilities for *Mesolimulus* and greater burrowing abilities for *Limulus*. The morphology of each species represents a compromise between the conflicting requirements imposed by swimming and burrowing.


The swimming and burrowing of Recent horseshoe crabs is of special interest to those of us concerned with the ethology of fossil merostomes and trilobitomorphs. As Eldredge (1970) has pointed out, the very general similarities in form between these groups tempt us into studies of comparative functional morphology. In making such comparisons, however, it is extremely important that we do not simply note specific correlations between form and behavior, but rather that we go on to understand the precise, physical reasons for these correlations. This approach leads us to focus directly on the physical basis of the relationship between form and movement.

The following analysis of swimming and burrowing is very limited in its goals. It will consider only a few aspects of each activity, and only a few sorts of evidence supporting an interpretation of each. It should, however, have some intrinsically interesting results and also show something of the power of techniques that directly investigate the physical consequences of ethological and morphological patterns. The adaptive relationship between form and movement constitutes one of the most fruitful approaches to the reconstruction of the behavior of fossil animals. In an extended sense, movement is really only another dimension of morphology, one may thus speak of the shape of movement. However, movement, with its peculiar evanescence, places the burden of its documentation on static form. It is with this, then, that we must begin.

**STATIC MORPHOLOGY OF *LIMULUS POLYPHEMUS* AND *MESOLIMULUS WALCHI***

The morphology of the Recent *Limulus polyphemus* is well enough known to require little more than a mention of the features which will be compared in our two species. The morphological knowledge of the Jurassic *Mesolimulus walchi* is based on study of material from the Solnhofen limestone, some of which has been prepared by a specially developed acid technique. This work is part of a larger scale investigation of the morphology and evolution of horseshoe crabs which is in preparation by the author. Pertinent morphological details are presented in Fig. 1. Of importance for the following discussion are the difference in prosomal width and height, the different angular relationships of podomeres when withdrawn into the prosomal vault, and the difference in the robustness of podomeres.
Swimming is probably the most complex of the activities in the behavioral repertoire of *L. polyphemus*. A full understanding of the precision and coordination of swimming movements and the several phases of swimming behavior would involve a number of different sorts of physical analyses. However, at present, I wish to consider only three facets of swimming behavior: (1) orientation of the body relative to the horizontal, (2) swimming speed, and (3) stroking rate of the appendages. I shall refer to these as \( \Theta \), \( v \), and \( f_s \) respectively. I will deal with these factors only in the context of unaccelerated swimming in a horizontal direction, well above the surface of the sediment, and below the surface of the water. Furthermore, I will limit the discussion of investigative techniques to experiments involving visualization of the pattern of fluid flow about a swimming horseshoe crab, especially in the region of the ventral prosomal vault.

The basic motions of horizontal swimming in *L. polyphemus* have been described, with various degrees of accuracy, by numerous authors. The most recent descriptions are by Vosatka (1970), Knudsen (1973), and Fisher (1971). The following analysis, however, rests on only a few simple observations, based on work with individuals one to five centimeters in prosomal length (Fisher, 1971).

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Fig. 1. Transverse cross sections of *L. polyphemus* (A) and *M. walchi* (reconstructed) (B), through the lateral compound eyes, and perpendicular to a plane defined by the post-opthalmic branches of the opthalmic ridges. The plane of the appendages has been rotated somewhat to lie in this transverse plane of the body. Both are drawn to the same scale and represent animals 4.5 cm in prosomal length. P, body cavity of prosomal carapace; Pv, prosomal vault; c, coxa; t, trochanter; f, femur; p, patella; b, tibia; r, tarsus.

**SWIMMING**

Fig. 2. A swimming horseshoe crab. Movement is in a horizontal direction, as indicated by the arrow. Swimming orientation (\( \Theta \)) is defined as the angle, measured in a vertical longitudinal plane, between the post-opthalmic branches of the opthalmic ridges and the direction of movement. The prosomal appendages have just begun their power stroke.
(1) a. During unaccelerated horizontal swimming the body moves in a generally anterior
direction, with the ventral surface uppermost.
b. The body is inclined in such a way that a plane described by the post-opthalmic
branches of the ophthalmic ridges lies at 20°–30° to the horizontal, measured in the
direction of motion (Fig. 2).

(2) Swimming speed usually ranges between 10 and 15 cm sec⁻¹.

(3) a. Swimming is powered by the motions of the prosomal and opisthosomal appendages,
which consist of power and recovery phases of a stroking cycle.
b. This cycle has a frequency of 2.0–2.4 sec⁻¹.

(4) The opisthosomal appendages and the sixth prosomal appendages stroke in a metachronal
rhythm, the wave of activation passing anteriorly. Prosomal appendages 2–5 move in
phase with one another, and begin their stroking cycle immediately after the sixth pro-
somal appendages.

(5) During their power stroke, the prosomal appendages extend ventrally and move posterior-
ly. During their recovery stroke, they withdraw into the prosomal vault and move anteri-
orly, their distal elements approximated to the ventral surface of the prosoma.

We would now like to investigate the quantitative aspects of the foregoing description of swim-
mapping in order to understand the specific values of \(O, v,\) and \(f_s\) that are observed in \(L. pol-
yphemus\) and to reconstruct values of each of these factors for \(M. walchi.\)

The qualitative aspects of a similar description of swimming movements for \(M. walchi,\)
and the rather basic assumption that \(M. walchi\) swam at all, will be dealt with in detail else-
where (Fisher, in preparation). Briefly, the argument is as follows.

Despite the differences in shape between \(L. polymphemus\) and \(M. walchi,\) it can be shown
that their carapaces have a similar relative spatial distribution of centers of mass-buoyancy
and lift (as determined for any swimming position). These observations, coupled with data
from the measurement of the forces acting on a swimming horseshoe crab, indicate that if
\(M. walchi\) swam, it also swam on its back — i.e. item (1) a. applies to \(M. walchi.\) Similarly, ana-
tomical and energetic-mechanical considerations of appendage movement allow the trans-
position of items (3) a. and (4). Furthermore, the best interpretation of such anatomical details
as the course and development of the ophthalmic ridges of \(M. walchi\) (also based on force
measurement data not given here) involves the assumption of swimming in \(M. walchi.\) This line
of reasoning, together with evidence from trace fossils and details of preservation, supports the
assumption that \(M. walchi\) swam and that its general manner of swimming was similar to that
exhibited by \(L. polymphemus.\)

Materials and methods

It is standard practice, in studies of fluid mechanics, to simulate the conditions of an object
moving through a quiescent fluid, by setting up the dynamically equivalent situation of a
stationary object immersed in a flowing fluid. For this study, models of horseshoe crabs were
mounted in a flume which supplied a non-turbulent flow, whose velocity could be regulated
between 0 and 70 cm sec⁻¹, through a test section measuring 45 cm by 45 cm. The flume was
built, and is maintained by, the Division of Engineering and Applied Physics, Harvard Uni-
versity.

Models of \(L. polymphemus\) were made by sealing the anterior exuviation suture of dried
molts. Prosomal and opisthosomal appendages were removed and the resulting openings into
the body cavity were plugged. For \(M. walchi,\) a reconstruction of the carapace (without
appendages) was sculpted in wax, molded in silicone rubber, and cast in polyester resin. Both
models have a prosomal length of 4.5 cm.

The removal of appendages from the models was originally done in order to study how
the carapace itself would tend to influence the development of flow patterns. It later became
clear that the motion of the appendages during swimming was such as to reinforce the patterns
set up by carapace shape, not obliterate them. Unless a mechanism were developed for accurate
animation of model appendages, their motionless presence on a model would constitute more of
a distortion of the ‘real’ situation than their absence.

We must next raise the question of how accurately a model reproduces the control of
flow patterns that the real carapace would exercise. In morphological detail, the models are
probably excellent representations of the real animals. The molt of *L. polyphemus* gives us as near perfect a model, in this respect, as could be desired. In fact, flow visualization experiments on plastic models representing progressively more simplified abstractions of the carapace morphology of *L. polyphemus* show that it is its general shape, rather than minute surface details, which is significant for explaining the flow patterns that will be dealt with here.

Some attempts to model organisms for hydrodynamic study are confounded because of the difficulty of reproducing the elastic and textural properties of biological surfaces. For the present study, this problem is of minimal importance. For our purposes, the smooth, stiff, chitinous exoskeleton is effectively simulated by rigid plastics.

The models were supported in the flume on the end of a brass rod, one quarter inch in diameter, mounted on the ventral surface of the model. The rod was held in a brace which could be rotated about the animal’s center of mass (Fig. 3). This varied the orientation of the model relative to the direction of fluid movement, without displacing the model within the test section. The similarity of the flow patterns, using this method of support, to those developed using other methods (not involving structures within the prosomal vault) indicates that the presence of the rod does not significantly affect flow patterns within the prosomal vault.

In order to trace the patterns of flow about the models, hydrogen bubbles were generated upstream of the models through the electrolysis of the flume water. The electrodes were fine wires mounted paradiametrically across a plexiglass hoop. In most cases, the cathode was platinum and the anode copper, resulting in a single linear source of H₂ bubbles.

The results of bubble tracking are obviously most significant when the terminal velocity of bubble ascension is very much less than the velocity of fluid flow. In these experiments terminal ascension velocity of the bubbles was usually 5–10% of the flow velocity. As bubbles were generated from a linear source, a planar sheet of bubbles was propagated downstream. In the presence of an object suspended in the flow, this sheet was deformed in a manner closely approximating streamline deformation around the object, thus giving a visible record of flow patterns.

Flow patterns developed for each of the models, at specified orientations and flow velocities, were recorded on 3” x 5” Polaroid film and on 16 mm cine film. Frame by frame analysis of the cine film provided a means for measuring the periodic structure of these patterns.

**Results**

The flow patterns illustrated by these experiments are caused solely by the interaction of carapace morphology and the moving fluid medium. The details of the flow pattern which are most informative concerning the aspects of swimming that we have chosen to analyse.
Fig. 4. Flow pattern near the prosoma (shown in longitudinal section through the interophthalmic region) of a swimming *Limulus polyphemus*. Vectors on the velocity profiles indicate direction and magnitude of the flow velocity at their origins on a vertical baseline. The curve b represents a streamline which, above the prosoma, marks the upper extent of the boundary layer. The curve v represents the locus of points with a velocity equal in magnitude to the maximum flow velocity in the anteriorly moving portion of the vortex. v may be taken as the size and shape of the fully developed vortex.

(orientation, speed, and stroking rate) are those concerning flow in the prosomal vault and in the wake behind it.

When fluid approaches the anterior prosomal margin, it either moves over the dorsal surface of the carapace or passes ventrally across the prosomal doublure. Fluid moving along this ventral path experiences an abrupt discontinuity in surface conformation, resulting in a flow separation at this margin. (The physics of flow separation are discussed in any fluid dynamics text. What concerns us here is only the resulting pattern of flow.) This fluid is deflected further ventrally in a smooth arc and then passes back into the wake. The space between this deflected flow and the ventral surface of the prosoma is occupied by a recirculating vortex which, when intact within the prosomal vault, has a roughly crescentoid shape. The 'dorsal' portion of this vortex is appressed to the ventral surface of the prosoma and the 'ventral' portion of the vortex grades into the body of deflected flow, occasionally incorporating some of this flow into its own recirculation (Fig. 4).

Another important feature demonstrated by the flow visualization experiments is that the vortex formed in the prosomal vault is not continually present or active there. Rather, vortices are periodically formed and shed into the wake behind the horseshoe crab. This may be expressed as a strong periodicity in the energy distribution of fluid moving in the separated region. This periodicity is superimposed on the more randomly variable energy distribution of turbulent flow in the wake (the unstable range of vortex shedding, in Roshko's terminology, 1954). This allows the period of individual formation-shedding cycles to vary somewhat, but does not obscure the strong periodic structure of the wake (Figs. 5 and 6).

Fig. 5. A single frame of the 16 mm cine film of flow visualization using a model of *M. walchi*. Bubbles moving below the model are $O_2$, formed at a platinum anode. $H_2$ bubbles formed at the cathode are of a small and large (due to particulate matter in the water) size class. The former are useful for tracing flow patterns, while the latter rise conspicuously. A vortex has just been shed, and the deflection in bubble paths which is seen just posterior to the opisthosoma represents a portion of its recirculating flow.
Vortex formation and shedding in and from the prosomal vault is characteristic of any generally horseshoe crab-like shape, at any of the orientations or flow velocities under consideration. However, a closer look at these flow patterns shows that the precise size and shape of the vortex is dependent on the orientation of the model and the velocity of the fluid. This dependency is illustrated in Figs. 7 and 8, matrices of orientation-velocity variation for each model. Dependency is mappable on a finer scale than the divisions of this matrix might suggest. However, the most unambiguous significance can be assigned to variation of this scale.

Now, of what importance to a swimming horseshoe crab is the formation of a vortex of a particular size and shape? One aspect of efficient swimming is efficient production of thrust. This, in turn, requires efficient appendage functioning in both power and recovery phases of the stroking cycle. It is during the recovery stroke that the vortex comes most directly into play. Efficient recovery means reduction of the drag forces acting on the appendages during recovery movements, since these forces would be oriented opposite to the direction of motion. One important way in which horseshoe crabs effect this drag reduction is to reduce the velocity...
of prosomal appendages relative to their surrounding fluid during the recovery, and one important method for doing this is to execute the recovery stroke via the 'dorsal' anteriorly moving portion of the prosomal vortex. Therefore, the vortex arrangement which would be most auspicious for efficient recovery stroking would be one in which there was a coherent backflow extending from the posteriormost portion of the excursion range of the prosomal appendages, forward to the anteriormost portion of their excursion—the edge of the prosomal doublure. This configuration is best obtained, for the models, under the conditions represented by the heavily framed squares of Figs. 7 and 8. These same conditions therefore constitute our prediction of Θ and v values for the swimming animals.

Indeed, for *L. polyphemus* these conditions of orientation and flow velocity are just those under which horizontal swimming occurs. This behavioral observation constitutes convenient and encouraging corroboration of our predictions of Θ and v based on the experiments. However, the predictions can be made just as strongly in the absence of observed values for these characters.

The coincidence of the path of movement of the prosomal appendages with the flow patterns observed on the *L. polyphemus* models, and the coincidence of observed values of Θ and v with the range of those values predicted from flow visualization, argue that flow patterns are an important control of swimming orientation and speed. In reality, there are other physical relationships which share in this control. The most important of these is the dependence of lift and drag forces on Θ and v. In the final analysis, though, these other controls simply serve to locate the actual values of Θ and v within the range prescribed by flow patterns.

As noted above, and as shown in Fig. 8, the values of Θ and v which result in the most 'helpful' vortex configuration for *M. walchi* are 0°–10° and 15–20 cm sec⁻¹. These results give us an experimental estimate of these characters for this fossil species.

Vortex shedding frequency (fᵥ) is dependent on the same variables as vortex shape and size. Thus, for the optimum conditions specified above, each model has a characteristic fᵥ.

In order for the relative velocities of prosomal appendages and their surrounding fluid to be minimized during their recovery stroke, it is obvious that the prosomal vortex must be intact and in place during recovery execution. If this relationship is to be preserved throughout consecutive stroking cycles, stroking frequency (fₛ) must equal fᵥ and vortex shedding must occur during the power phase of the stroking cycle.

This is not to say that stroking is absolutely constrained to coincide with vortex shedding as observed in the legless models. The energy input of appendage motion is great enough to
overcome the periodic energy distribution associated with the vortex. In fact, within certain limits, stroking frequency is probably able to control the actual rate of vortex shedding in the swimming animal. This is why there is no problem in coordinating phases of these two cycles, once their periods are equal. The point is simply this: when vortex shedding and stroking are coordinated, there is a savings of appendage energy which would otherwise be invested in setting up a periodic distribution of current energy different from that distribution which is potentially (i.e. independent of appendage motion) in force.

For the *L. polyphemus* model, the measured $f_v$ is about $2 \text{ sec}^{-1}$. This corresponds closely to the $f_s$ noted above, lending support to the hypothesis of control that has been set forth. This hypothesis would also argue that the measured $f_v$ for the *M. walchi* model ($1.7 \text{ sec}^{-1}$) indicates for that species a normal $f_s$ during horizontal swimming of $1.7 \text{ sec}^{-1}$. Again, we have an experimental determination of a swimming character for a fossil species that is independent of our knowledge of the value of that character in the Recent species.

To summarize this look at swimming, experiments involving the visualization of flow patterns around models of swimming horseshoe crabs allow one to explain or reconstruct swimming orientation, swimming speed, and stroking rate. *M. walchi* swam at a smaller angle to the horizontal, swim faster, and swim with a lower stroking rate than *L. polyphemus*. The full significance of the values for each of these characters will take form only in the light of other investigations on the swimming of horseshoe crabs. However, even at this point, the differences between *M. walchi* and *L. polyphemus* suggest greater swimming ability and endurance for the former.

If the carapace morphology of *M. walchi* is more specialized for swimming, what is the reason for the more highly vaulted carapace of *L. polyphemus*? Part of the answer becomes clear when we look at the burrowing behavior of horseshoe crabs.

**BURROWING**

The discussion of swimming has involved a consideration of the direct interaction between the dome-like prosoma of a horseshoe crab and the external environment; here, let us look at a more indirect interaction. During burrowing, the ventral surface of the prosoma and the substrate define a closed space, the prosomal vault, within which the prosomal appendages operate. The ventral surface of the prosoma corresponds precisely to the surface form of an abstract three-dimensional body defined as the locus of all appendage positions. This relationship means that during burrowing, the limb elements of *M. walchi* cannot obtain the acute angulation of those of *L. polyphemus* (see Fig. 1).

During burrowing, part of the first phase of propulsive movements of the prosomal appendages consists of flexion at the femoral-patellar articulation. This flexion takes place about an axis defined by two points of articulation on the dorsal surface of the joint. It is accomplished largely by muscles in the femur which insert on an arcuate sclerite embedded in the ventral arthrodiatal membrane of this joint (Ward, 1969). As can be seen in Fig. 9, the moment arm of these muscles acting about the femoral-patellar articulation is greatest when the angle between the femur and patella is small. When the length of this moment arm is maximized (holding other variables constant), so is the force which can be generated, at the distal end of the appendage, against the substrate. Thus, the prosoma of *L. polyphemus* allows greater force production, in this respect, than that of *M. walchi*.

We may also look at the shape of podomerones themselves. The femur and patella of *L. polyphemus* are much deeper dorso-ventrally and of greater cross-sectional area than those of *M. walchi*. Besides being able to accommodate a larger muscle mass, this means that at any possible limb orientation the arcuate sclerite is located farther from the femoral-patellar articulation in *L. polyphemus*. Again, this represents an increase in the moment which can be developed for flexion at this joint. These observations are only brief examples of the sort of differences that exist between the mechanical system of burrowing in *L. polyphemus* and *M. walchi*. Other indications of specializations for burrowing behavior in *L. polyphemus* have been noted by Eldredge (1970) and will be dealt with further elsewhere.

Before leaving the matter of appendage morphology, it is important to note that the joint mechanics of *M. walchi* are not without their advantages. The shorter moment arm of muscles acting at its femoral-patellar joint means that for a given rate of displacement of the muscle insertion, the appendage tip will move at a greater linear velocity. This is important because flexion at the femoral-patellar joint also occurs during the power stroke of the
swimming cycle of the prosomal appendages, and because the propulsive force generated by the appendage varies as the square of its linear velocity. In general, the appendages of *M. walchi* are 'designed' for quick action against relatively small forces of resistance, while those of *L. polyphemus* are 'designed' for more powerful action against larger resistance. These alternate strategies may be interpreted as specializations for swimming and burrowing respectively.

**CONCLUSIONS**

A hydrodynamic and mechanical analysis of swimming and burrowing in horseshoe crabs can help to explain and reconstruct precise details of their morphology and behavior. This discussion has dealt with only a few aspects of each of these activities. Many activities (e.g. walking, scuttling, feeding, enrolling, righting) have not even been mentioned. However, further work on these and other activities supports the specific determinations made here, the importance of swimming and burrowing to each of the species considered, and the general view of relative swimming and burrowing proficiencies.

It is interesting that each morphological character discussed (general prosomal shape, appendage angulation, and appendage robustness) is influenced, in each species, by conflicting selective pressures that are related to the divergent mechanical requirements of two important activities. The state of any one of these morphological characters thus reflects a compromise representative of the relative importance of the activities. Certainly there are instances of morphological change, in the evolution of horseshoe crabs, that are related to real innovations in their behavioral repertoire. However, at least some of the differences between *M. walchi* and *L. polyphemus* seem rather to be the result of a shift in the balance of importance between two mechanically competing activities — swimming and burrowing.

*Fig. 9. Moment of a femoral-patellar flexor (muscle represented by dashed lines). Axes or points of articulation are shown as small circles. f, line of force production, or line of muscle action in a flexed position (A); f', line of muscle action in a more extended position (B); m, moment arm of muscle acting in the flexed position (A); m', moment arm for the more extended position (B); ac, arcuate sclerite.*
ACKNOWLEDGEMENTS. — Part of this work was completed during tenure of a National Science Foundation Graduate Fellowship. I am particularly grateful to Richard I. Land and D. James Baker for advice and equipment pertaining to technical aspects of the experimentation. I have also appreciated discussions of the material presented here with Niles Eldredge, Stephen J. Gould, Thomas A. McMahon, Jane A. Peterson, and Leif Størmer.

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