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Research Articles

The astrorhizae of fossil stromatoporoids closely approximate an energetically optimal fluid transport system

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Abstract. Direct measurements on 375 million year old stromatoporoid sponges show that the astrorhizal canals (excurrent flow channels) have a near-optimal architecture; they are configured such that the energetic costs to construct and operate these fluid transport systems averaged only 2.54% above those of equivalent Murray's Law systems, the theoretical minimum. The average cost incurred by the fluid transport system in stromatoporoids was a factor of three closer to the Murray's Law optimum than are vessel networks in the circulatory system of mammals.
Key words. Murray's Law; hydrodynamic forces; optimality; Porifera.

Murray's law[1-3] is a theoretical relationship which specifies the design which minimizes the total energetic expenditure of building and running a system of vessels to carry a given volumetric flow. This relationship is derived by simultaneously minimizing both the cost of pumping a fluid in laminar, fully developed flow through a circular pipe and some cost (e.g., capital investment and/or maintenance) proportional to the total volume of the system. The derived design rule specifies that the volumetric flow rate through any given vessel should be proportional to the vessel's radius cubed. Because total volumetric flow is conserved at a branch point in a system of vessels, at any branch point in a Murray's Law system the radius of the parent vessel (r_0) cubed is equal to the sum of the cubes of the radii (r_1, r_2) of the daughter vessels[2,4]; i.e., $r_0^3 = r_1^3 + r_2^3$. This branching rule is a good descriptor of the architecture of a number of fluid transport systems in biology[4] including the excurrent astrorhizal canals of Middle Devonian stromatoporoid sponges[5,6].

Flow or junction exponents either greater or less than the theoretical value of 3.0 imply an increased total cost (in volume-related costs of the system or increased resistance to flow). Even if the mean exponent for the branch points in a fluid transport system is not significantly different from three, the system as a whole may incur a cost significantly higher than the ideal. Theoretical analyses[7-9] indicate rather small (less than 5%) energetic penalties for individual junction exponents ranging from 1.5 to over 10.0, but energetic penalties rise sharply as larger portions of the system depart from Murray's Law. Although the hydrodynamic simplifications inherent in the derivation of Murray's Law yield a highly idealized model[3,5], Murray's Law represents a reasonable standard of comparison for biological fluid transport systems and permits evaluation of the architecture of biological fluid transport systems directly in energetic terms. Here I show that systems of astrorhizal canals in fossil stromatoporoids are configured such that their total energetic costs averaged only a few percent above those of Murray's Law systems of the same volume and geometry.

Materials and methods

The fossils used in this study were described elsewhere[5]. Fifteen astrorhizae from five stromatoporoids were selected on the basis of quality of preservation; a total of 91 branching astrorhizal canal systems, each with 3–43 vessel segments (fig. 1), were measured. Vessel radii were taken from the data set described in LaBarbera and Boyajian[5]; vessel lengths were measured off camera lucida drawings of the astrorhizae using a digitizer and

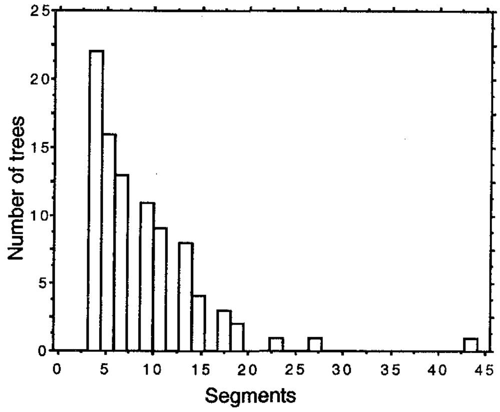

Figure 1. Frequency distribution of the number of segments (vessels between branch points) in the measured astrorhizal trees of five speciments of Middle Devonian stromatoporoids (see LaBarbera and Boyajian[5]).

microcomputer. Astrorhizal tree volume was calculated assuming that individual vessel segments were circular cylinders. Equivalent Murray's Law systems (i.e., a network of vessels with the same volume, geometry, and asymmetry ratio of vessel branches as the measured system, in which the relationships between vessel radii at branch points follows Murray's Law) were constructed for each astrorhizal canal system following Sherman et al.[9]; symbols here follow their conventions. According to Sherman et al.[9], construction of an equivalent Murray's Law system may be initiated using either the root or terminal vessels of the measured system. For systems with highly asymmetric branching, such as those studied here, beginning with the terminal vessels in constructing an equivalent Murray's Law system may result in situations where it is impossible to both satisfy Murray's Law at a junction and maintain vessel radius asymmetry ratios. Thus, all calculations of equivalent systems in the present study used the root vessel of the measured system as the starting point.

Starting with the measured radius (r_0) of the root vessel of each tree, expected values for the daughter vessel radii (s_1^*, s_2^*) were calculated under the constraints that the asymmetry ratio, A, ($= r_1/r_2$) of the daughter vessels was the same as that in the measured tree and that the junction as a whole followed Murray's Law. These conditions were met using the relationships

$$s_1^* = \left(\frac{r_0^3}{(1+A^{-3})}\right)^{1/3} \quad \text{and} \quad s_2^* = \left(\frac{r_0^3}{(1+A^{3})}\right)^{1/3}$$

Using the calculated radii for the daughter vessels as new values for r_0, radii for the next vessels in the network were iteratively determined until the terminal vessels in the network were reached. The segment radii (s_i^*) were scaled by a factor, F, yielding predicted segment radii (r_i^*) in an ideal network of the same volume as the measured tree. F was calculated as:

$$F = \left(\frac{\sum_{i=1}^{n} r_i^2 l_i}{\sum_{i=1}^{n} s_i^{*2} l_i}\right)^{1/2}$$

where l_i equals segment length. Relative energetic cost (Ψ_T) of the astrorhizal tree was calculated using:

$$\Psi_T = \frac{\sum_{i=1}^{n} \Psi_i r_i^{*2} l_i}{\sum_{i=1}^{n} r_i^2 l_i}$$

where $\Psi_i = \frac{1}{3}(r_i/r_i^*)^{-4} + \frac{2}{3}(r_i/r_i^*)^2$. Derivations of the expressions for F and Ψ are given in Sherman et al.[9].

Results

The calculated energetic costs of these systems varied from 0.01–19.7% above those of equivalent Murray's Law systems (fig. 2); the average increase was $2.54 \pm 0.30\%$ (mean ± standard error of the mean). Average values for the sampled canal systems on individual stromatoporoid specimens ranged from 1.1–2.56%; average values for the sampled canal systems in individual astrorhizae ranged from 0.79–5.45%. ANOVA revealed no significant differences in energetic penalty for canal systems among specimens ($F_{4,86} = 0.629$; $p = 0.64$) or individual astrorhizae ($F_{14,76} = 0.857$; $p = 0.61$). The frequency distribution of energetic penalty values was strongly right skewed (fig. 2), implying that a simple mean was a poor measure of the central tendency of the distribution; a square root transformation effectively normalized the distribution. The (backtransformed) mean of the transformed values was 1.92% (95% CI = 1.50–2.41%); average values for individual stromatoporoid specimens ranged from 0.67–2.26%. ANOVA of the square root-transformed energetic penalty value again revealed no significant differences in energetic penalty for canal systems among specimens ($F_{4,86} = 0.795$; $p = 0.53$) or individual astrorhizae ($F_{14,76} = 0.839$; $p = 0.63$).

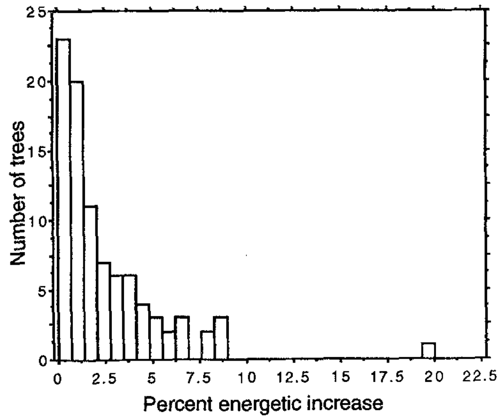

Figure 2. Frequency distribution of percentage energetic increase (energetic penalty) relative to an ideal Murray's Law network of the same volume and geometry for the 91 astrorhizal trees measured. The mean cost increase for the astrorhizal trees was 2.54%.

Discussion

It is important to realize that any differences in segment dimensions between the measured systems and the ideal equivalent systems would yield an increase in calculated cost. Actual differences in dimensions between the measured and ideal systems, measurement errors, and postmortem alterations of the stromatoporoid skeletons would all act to increase the calculated cost; the extremely low average cost calculated is thus particularly remarkable.

Vessel trees with few segments are less likely to depart greatly in cost from an equivalent Murray's Law system of the same volume. Because approximately 24% of the trees measured had only three segments and about 42% had five or fewer segments (fig. 1), the possibility that these cost values are biased must be considered. While the shorter measured trees exhibit relatively low values

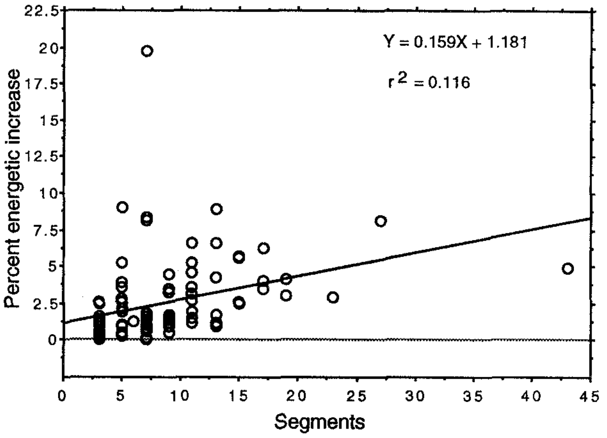

Figure 3. The influence of number of segments (vessels) in the 91 measured trees on the calculated energetic increase above an equivalent Murray's Law network. Segment number has only a weak influence on calculated energetic increase.

for cost increase (fig. 3), a least squares regression of cost increase against number of segments for the 91 trees analyzed explains only 12% of the variance of the data. The weak trend apparent in figure 3, although statistically significant ($p = 0.001$), seems as likely to result from the increased probability of measurement error in trees with many segments as from a bias resulting from the high proportion of trees with few segments.

In the only study directly comparable to the present work, Sherman et al.[9] calculated the relative energetic costs of 10 arteriolar trees in the sartorius muscle of rats; these trees had energetic penalties ranging from 1.6–24.3% above those of equivalent Murray's Law systems. The average cost increase for these arteriolar trees, $8.95 \pm 2.02\%$, stands in marked contrast to the average value determined here for the astrorhizae of stromatoporoids. While it is certainly possible that the difference in average efficiency between these fluid transport systems is artifactual, the most likely sources of error cannot account for the threefold difference in cost increase: a) Given that the circulatory system of mammals contains shunts to meet changing metabolic or thermoregulatory demands, it is possible that the arteriolar casts measured by Sherman et al.[9] may not have been full flow[2] systems. However, given the relatively small size (4–18 junctions) of these arteriolar trees, this possibility seems unlikely. b) The classic form of Murray's Law is predicted on the assumption that the fluid is Newtonian[2,4]; mammalian blood exhibits non-Newtonian behavior in vessels smaller than about 300 μm. A version of Murray's Law which explicitly took the viscosity of the fluid into account would maintain $\Sigma(r^3/\sqrt{\mu})$ (where μ = the effective dynamic viscosity of the fluid) rather than Σr^3 constant at each branch point[3]. The vessels analyzed by Sherman et al.[9] ranged from 5–32 μm in diameter, but, since effective blood viscosity should change only by a factor of 1.8 over this range of vessel diameters[10], the non-Newtonian behavior of blood maximally accounts for less than half the difference in average cost between the mammalian and stromatoporoid fluid transport systems. Thus, it seems likely that the differences in energetic efficiency between these fluid transport systems are real.

Stromatoporoid fluid transport systems more closely approached the ideal Murray's Law system either because 1) the selective pressures for increased fluid transport system efficiency were more intense in stromatoporoids (cost of pumping is likely to be the largest single item in a suspension feeding animal's energy budget), or 2) there were fewer conflicting constraints determining the architecture of stromatoporoid fluid transport systems. It is likely that all animals use the same mechanism to generate fluid transport systems approximating Murray's Law systems[3,4], a negative feedback system in which local shear stress (sensed by the cells lining the vessels) is the input variable and vessel diameter is the controlled output of the system. The present results imply that suspension feeding animals may provide clearer examples of this mechanism than the circulatory system of vertebrates and demonstrate that high efficiency fluid transport system designs were evolved by simple metazoans early in the Phanerozoic.

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