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Hydrodynamical strategies in the morphological evolution of spinose planktonic foraminifera

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APPENDIXES

1 The Reynolds Number Re

The Reynolds number Re is the ratio of inertial to viscous forces acting on an infinitesimal fluid element (Reynolds, 1883), and is defined by

$$Re = \frac{\rho L W}{\mu} \quad (A1.1)$$

where ρ is the density of the fluid, L is a characteristic linear dimension of the system, W is a characteristic fluid velocity, and μ is the dynamic viscosity of the fluid. For a coordinate system centered on a body immersed in a fluid involving steady, relative motion between them, W normally is taken as the free-stream velocity far from the body. In the present context, W is equal in magnitude to the settling speed. The choice of the dimension L is somewhat arbitrary, so long as it is applied consistently. When comparing geometrically similar systems, L is a geometrically corresponding dimension common to the systems. In the case of spheres, which are by definition geometrically similar, L is usually taken as the sphere radius or diameter. In the case of a foraminifer, it is convenient to choose the radius R .

2 The Coefficient of Drag C_D

Dimensional analysis leads to the result that the total surface force on a body immersed within

a fluid due to steady relative motion between the body and fluid and acting in the direction of the relative motion--the drag force F_D --can be written in terms of a dimensionless coefficient of drag C_D . This coefficient can be defined more than one way (for example, Tritton, 1988, p. 93-95; Furbish, 1997, p. 128-130), and it is a matter of convenience to choose a form that can be readily applied to both small and large Reynolds numbers. Whereas the work presented in this paper is largely concerned with small Reynolds number (viscous) flows, we also are interested in flows near (and greater than) a Reynolds number of unity. The coefficient C_D , then, is formed as the ratio of the drag force F_D to the product of the dynamic pressure of the flow $\frac{1}{2}\rho W^2$ and the square of the characteristic length, that is L^2 . Constants in this dimensionless quantity are arbitrary, so it is customary to replace L^2 by a characteristic area, the silhouette area normal to the flow, which involves the constant π in the case of a sphere. We therefore define C_D by (2) in the text using $L = R$. Note that it is not essential for the quantity πR^2 in the denominator of (2) to equal the true silhouette area of a foraminifer. This condition, however, is satisfied in the limiting case of a spherical test (and surrounding protoplasm) without spines.

Substituting (1) for Re in (3), then equating the resulting expression with (2) and solving for F_D , one obtains the result of Stokes (1851), that $F_D = 6\pi\mu RW$.

3 Statistical Similitude

A foraminifer has the shape of a sphere, and therefore possesses spherical symmetry, in the limit where n , l or r approaches zero. With one to three spines, however, associated planes of symmetry do not separate a foraminifer into hemispheres having spherical symmetry. This means, for example, that the drag on a foraminifer that is settling parallel to a plane containing three spines is in general different than the drag when it is settling normal to this plane, because the test-spine silhouettes normal to the relative fluid motion are different. Dynamical similitude is not satisfied for arbitrary rotation of the foraminifer. In contrast, a tetrahedral geometry (four spines) begins to render a sense of quasi-spherical symmetry; test-spine silhouettes normal to W are, for arbitrary rotations, more nearly alike than in the

three-spine case such that the total drag varies less with different orientations relative to the settling motion. With an increasing number of spines, we expect that the exact orientation of a foraminifer during settling becomes less significant in terms of its influence on the total drag. The relation between total drag and the symmetry of settling objects is fully examined by Happel and Brenner (1986, p. 159-234).

4 Qualitative Assessment of the Exponents a , b and c

Consider the drag associated with an isolated spine. The drag force per unit length of a spine (treated as a right circular rod) oriented normal to the flow varies approximately with $r^{1/5}$ over the domain $0.01 \leq Re \leq 1$. (Appendix 10 provides an exact expression for the relation between drag and Re .) Therefore the drag force on a spine with length l varies with $lr^{1/5}$, and the total drag on n independent spines oriented normal to the flow varies with $nlr^{1/5}$. If spines acted independently and additively, drag would therefore increase with the first power of n and l , and the $1/5$ power of r , neglecting effects of spine orientation relative to the mean motion.

Now, for moderate to large n , the drag on a foraminifer due to spines is much greater than the drag associated with a test that is otherwise isolated from its spines. As n , l or r increases, the fluid therefore "sees" less of the test, and more of the spines; the total drag is essentially equal to that which would occur if the spines radiated from a point. A settling foraminifer drags a blob of liquid with it. Near the test, therefore, differential motion between fluid and spines is minimal, and only the outer parts of spines contribute to increasing drag directly associated with viscous fluid motion around the spines. The spines contribute indirectly to increasing drag, however, by increasing the size of the settling system—the test and spines plus fluid blob—such that viscous forces operate over a larger fluid volume.

For given R , l and r , an incremental increase in the number of spines when n is small leads to a significant increase in the total length of spines l contributing directly to drag, and in the size of the fluid blob. However, the proportion of l of an individual spine contributing directly to drag decreases,

because the region of small differential motion between fluid and spines near the test is enlarged. A similar incremental increase in the number of spines when n is large, in contrast, does not enlarge the fluid blob as much, whereas the region of small differential motion between fluid and spines near the test is enlarged. The net effect is likely to give $a \leq 1$. For given R , n and r , short spines are essentially enclosed within the fluid blob associated with the test, and an incremental increase in l does not add significant drag. As l increases, the proportion of the spine length that adds directly to drag increases, because the outer parts of spines become increasingly separated and extend into a region of greater differential motion between the fluid and spines. The fluid blob also grows. The net effect is likely to give $b \geq 1$. Of the three effects associated with increasing n , l and r , the effect of increasing r (for given R , n and l) should be most like that expected for an isolated spine, because an increase in drag associated with an increase in r is likely to be most significant near the outer parts of the spines. We therefore may anticipate that $c < 1$.

5 Regression Analysis

Equation (13) can be linearized to

$$\ln\left(\frac{C}{12} - 1\right) = \ln C_0 + a \ln(n - n_1) + b \ln \Lambda + c \ln P \quad (\text{A5.1})$$

For constant Λ and P , the last two terms are absorbed into the constant term. Simple linear regression involving measured values of the left side of (A5.1) and values of $\ln(n - n_1)$ then retrieves a as the estimated regression coefficient. The value of n_1 is selected by systematically varying this coefficient until it provides the "best" fit to the data (Figure 3a). These estimates are $n_1 = 4.5$ and $a = 0.476$. For constant n and P , terms involving a and c are absorbed into the constant term. Simple linear regression then retrieves the estimate $b = 1.992$ (Figure 3b). After pooling the data in Figure 3, multiple linear regression using the full model (A5.1) retrieves the estimates $C_0 = 0.584$, $n_1 = 4.5$, $a = 0.478$, $b = 1.992$ and $c = 0.596$. This fit gives a coefficient of determination equal to 0.998; although this provides

a qualitative measure of the closeness of the fit, statistical significance should not be placed on it. In this regard, the standard error of the estimate of a is 0.0189, which is about a four percent change in a . We report this here only for the purpose of translating variations in a to variations in settling velocity at large n (see text).

6 Zero Relative Settling Speed

The ratio $(W - W_R)/W_R$ is formed from (12), where W_R , denoting the settling speed of a spherical test (and protoplasm) without spines, is obtained by setting Λ in (12) to zero. Setting the ratio $(W - W_R)/W_R$ to zero gives

$$\frac{3(\rho_s - \rho_p)(R - R_t)}{4(\rho_R - \rho)R} nP^2 + \frac{3(\rho_s - \rho)}{4(\rho_R - \rho)} n\Lambda P^2 - C_0(n - n_1)^a \Lambda^b P^c = 0 \quad (\text{A6.1})$$

which is independent of fluid viscosity. The solution of (A6.1) defines the set of n - Λ coordinate pairs for which a spinose foraminifer settles at the same rate as an otherwise identical foraminifer without spines.

7 Sensitivity Functions S_p , S_f and S_μ

The sensitivity functions S_p , S_f and S_μ are given by

$$S_p = \frac{dW}{d\rho_p} = \frac{2gR^2 \left[1 - (1 - \phi) \left(\frac{R_t}{R} \right)^3 - \frac{3}{4} \left(1 - \frac{R_t}{R} \right) nP^2 \right]}{9\mu [1 + C_0(n - n_1)^a \Lambda^b P^c]} \quad (\text{A7.1})$$

$$S_f = \frac{dW}{d\rho} = - \frac{2gR^2 \left(1 + \frac{3}{4} n\Lambda P^2 \right)}{9\mu [1 + C_0(n - n_1)^a \Lambda^b P^c]} \quad (\text{A7.2})$$

$$S_\mu = \frac{dW}{d\mu} = - \frac{W}{\mu} \quad (\text{A7.3})$$

where W in (A7.3) is given by (12). Notice that S_p is independent of the protoplasm density ρ_p , and S_f

is independent of the fluid density ρ .

8 Extrema of the Settling Speed W

Taking the partial derivative $\partial W/\partial n$ of (12) and setting this result to zero, any local extremum associated with variations in n for constant Λ and P must satisfy the condition:

$$(n - n_1)^a - a \left(n + \frac{4(\rho_R - \rho)}{3 \left[(\rho_s - \rho_p) \left(1 - \frac{R_t}{R} \right) + (\rho_s - \rho) \Lambda \right] P^2} \right) (n - n_1)^{a-1} + \frac{1}{C_0 \Lambda^b P^c} = 0 \quad (\text{A8.1})$$

The spine number n_{0W} associated with an extremum can be obtained from (A8.1) numerically. Taking the partial derivative $\partial W/\partial \Lambda$ of (12) and setting this result to zero, any local extremum associated with variations in Λ for constant n and P must satisfy the condition:

$$\Lambda^b + \left[\frac{4b(\rho_R - \rho)}{3(b-1)(\rho_s - \rho)nP^2} + \frac{b(\rho_s - \rho_p)}{(b-1)(\rho_s - \rho)} \left(1 - \frac{R_t}{R} \right) \right] \Lambda^{b-1} - \frac{1}{(b-1)C_0(n - n_1)^a P^c} = 0 \quad (\text{A8.2})$$

Our experiments suggest that $b = 2$. Then, the dimensionless spine length $\Lambda_{0W} = l_{0W}/R$ associated with an extremum can be obtained from (A8.2) using the quadratic formula. Namely,

$$\Lambda_{0W} = \left(\left[\frac{4(\rho_R - \rho)}{3(\rho_s - \rho)nP^2} + \frac{(\rho_s - \rho_p)}{(\rho_s - \rho)} \left(1 - \frac{R_t}{R} \right) \right]^2 + \frac{1}{(b-1)C_0(n - n_1)^a P^c} \right)^{\frac{1}{2}} - \left[\frac{4(\rho_R - \rho)}{3(\rho_s - \rho)nP^2} + \frac{(\rho_s - \rho_p)}{(\rho_s - \rho)} \left(1 - \frac{R_t}{R} \right) \right] \quad (\text{A8.3})$$

which is a positive real root. A similar condition can be written for extrema associated with variations in r ; however we do not consider this further.

More generally, (A8.1) and (A8.2) define two equations that must be satisfied simultaneously for existence of a global extremum in W over the full $n\Lambda$ -domain. Notice that, whereas W (and W_0) vary with both fluid and foraminifer properties according to (12), n_{0W} and Λ_{0W} are independent of fluid viscosity according to (A8.1) and (A8.2).

9 Extrema of the Sensitivity Functions S_p and S_f

Taking the partial derivative $\partial S_p / \partial n$ of (A7.1) and setting this result to zero, any local extremum associated with variations in n for constant Λ must satisfy the condition

$$(n - n_1)^a - a \left[n - \frac{4 - 4(1 - \phi) \left(\frac{R_f}{R} \right)^3}{3 \left(1 - \frac{R_f}{R} \right) P^2} \right] (n - n_1)^{a-1} + \frac{1}{C_0 \Lambda^b P^c} = 0 \quad (\text{A9.1})$$

The spine number n_{0p} associated with an extremum can be obtained from (A9.1) numerically. Numerical analysis indicates that the root n_{0p} occurs only at very large n ($n_{0p} \gg 10^4$) for realistic values of physical properties of foraminifera. Taking the partial derivative $\partial S_p / \partial \Lambda$ of (A7.1) reveals that local maxima of S_p occur in the limit $\Lambda = \Lambda_{0p} \rightarrow 0$. Thus the settling speed of a foraminifer with given R is most sensitive to changes in the density of its protoplasm when the exposed length of its spines l approaches zero.

Taking the partial derivative $\partial S_f / \partial n$ of (A7.2) and setting this result to zero, any local extremum associated with variations in n for constant Λ must satisfy the condition

$$(n - n_1)^a - a \left(n + \frac{4}{3 \Lambda P^2} \right) (n - n_1)^{a-1} + \frac{1}{C_0 \Lambda^b P^c} = 0 \quad (\text{A9.2})$$

The spine number n_{0f} associated with an extremum can be obtained from (A9.2) numerically. Numerical

analysis indicates that the root n_{0f} is effectively zero for all Λ . Taking the partial derivative $\partial S_f / \partial \Lambda$ of (A7.2), setting this result to zero and assuming that $b = 2$, the coordinate Λ_{0f} of any local extremum associated with variations in Λ for constant n can be obtained using the quadratic formula:

$$\Lambda_{0f} = \left[\left(\frac{4}{3nP^2} \right)^2 + \frac{1}{C_0(n - n_1)^a P^e} \right]^{\frac{1}{2}} - \frac{4}{3nP^2} \quad (\text{A9.3})$$

which is a positive real root. Because P is on the order of 10^{-3} for real (and modeled) foraminifera, the second term within the brackets generally is much smaller than the first term. Thus the root Λ_{0f} generally is very close to a value of zero for $n < 10^4$, and can be neglected.

10 Conditions of Spine Breakage

Consider a foraminifer with six spines possessing cubic symmetry, where the axes of four spines are normal to the settling motion. With $r \ll R$, there is negligible interaction among spines, and the "background" velocity field in the vicinity of the test is well approximated by that associated with a spherical test without spines. This field is, of course, locally modified in the immediate vicinity of each spine. Consider a coordinate system that moves with the foraminifer; the z -axis is parallel to the motion of the foraminifer, and the radial x -axis is normal to the motion. The origin of the coordinate system is centered on the foraminifer. The fluid velocity component w of the background field, parallel to the settling motion and in the plane of the origin ($z = 0$), is given by the solution provided by Stokes (1851):

$$w(x) = W \left(1 - \frac{3}{4} \frac{R}{x} - \frac{1}{4} \frac{R^3}{x^3} \right) \quad (\text{A10.1})$$

Here, W is the global far-field velocity, which is equal to the settling speed.

For a spine treated as a right-circular rod with radius r , it is convenient to define a coefficient of drag C_{Dr} for a unit length of the spine (for example, see Batchelor, 1967; p. 244-246):

$$C_{Dr} = \frac{F_s}{\rho r V^2} \quad (\text{A10.2})$$

where F_s is a drag force per unit length of spine and V is a characteristic fluid velocity. Theory and experiments suggest that (for example, see Batchelor, 1967; p. 244-246, 261)

$$C_{Dr} = \frac{4\pi}{Re_r \ln\left(\frac{3.7}{Re_r}\right)} \quad (\text{A10.3})$$

where the Reynolds number Re_r is

$$Re_r = \frac{\rho r V}{\mu} \quad (\text{A10.4})$$

The drag force F_s is then

$$F_s = \frac{4\pi\mu V}{\ln\left(\frac{3.7\mu}{\rho r V}\right)} \quad (\text{A10.5})$$

Each spine on a foraminifer that experiences fluid drag is mechanically equivalent to a cantilever. The largest background fluid velocities occur at positions $z = 0$. Moreover, the lever arm associated with the drag induced by these velocities has its maximum length when a spine axis is normal to the settling motion. For these reasons we may assume that such a spine experiences the largest torque due to fluid drag, and therefore has the greatest chance for failure if properties of mechanical strength are the same among spines. The conditions of failure of a spine oriented normal to motion therefore define the limiting conditions for which all spines remain intact.

Consider a small interval dx on a horizontal spine at a radial distance x . With $r \ll R$, the boundary layer associated with the interval dx , viewed in isolation, has a "local" far-field velocity that is given by the background velocity $w(x)$ at the same radial distance x . This background velocity serves

as the characteristic velocity V in (A10.4) and (A10.5), and we therefore denote $V = w(x; W)$, where the appearance of W after the semicolon emphasizes the importance of this parameter.

The small quantity of drag dF_D on dx is $F_s dx$, and the contribution $d\tau$ to the total torque τ measured relative to the base of the spine is $d\tau = F_s(x - R_t)dx$. The total torque τ is therefore

$$\tau = 4\pi\mu \int_R^{R_t + l_s} \frac{w(x; W)(x - R_t)}{\ln\left(\frac{3.7\mu}{\rho r}\right) - \ln w(x; W)} dx \quad (\text{A10.6})$$

where $w(x; W)$ is given by (A10.1). The integral quantity in (A10.6) can be readily evaluated numerically.

The formulation of (A10.6) is based on the assumption that flow around a spine is everywhere two-dimensional in planes normal to the spine. This may be incorrect in the immediate vicinity of the test, where $\partial w/\partial x$ is large (if W is large); and it also is incorrect at the very tip of the spine. The formulation is reasonable for moderate-to-long spines where $w(x)$ is approximately uniform ($\partial w/\partial x \approx 0$) over much of their length. Indeed, long spines are of most concern here.

The maximum tensile stress σ within a spine occurs at the position of maximum torque τ , which is at, or very close to, the base of the spine. The stress σ is given by

$$\sigma = \frac{4\tau}{\pi r^3} \quad (\text{A10.7})$$

At failure, σ must be infinitesimally larger than the tensile strength T_s of the spine. Setting $\sigma = T_s$ in (A10.7), combining (A10.6) and (A10.7), and specifying the settling speed $W = W_b$ at which breakage occurs,

$$T_s - \frac{16\mu}{r^3} \int_R^{R_t + l_s} \frac{w(x; W_b)(x - R_t)}{\ln\left(\frac{3.7\mu}{\rho r}\right) - \ln w(x; W_b)} dx = 0 \quad (\text{A10.8})$$

The speed W_b (obtained from (A10.8) numerically) is realistic for the case of small n ($n \sim 10$ or less) where interaction among spines is negligible. It is much more difficult, however, to evaluate W_b for large n , because we do not have information regarding the velocity field in the vicinity of individual spines. Any approach therefore must be *ad hoc*.

As n increases, the region near the test of negligible differential motion between spines and fluid expands, and the radial position $x = R_0$ where the velocity is effectively zero increases. We thus define R_0 by $w(R_0; W) \approx 0$. The position $R_0 = R$ in absence of spines, and R_0 can be no greater than $R + l$. We assume for simplicity that the distance $R_0 - R$ varies with n and Λ in a manner that is similar to the relation between the drag on a spinose foraminifer, and n and Λ . Dimensional analysis then suggests that the ratio $(R_0 - R)/l$ can be expressed as

$$\frac{R_0 - R}{l} \propto \frac{\alpha}{\sqrt{Re}} C_0 (n - n_1)^a \Lambda^b P^c \quad (\text{A10.9})$$

where α is a dimensionless coefficient. To ensure that the upper limit of this ratio is unity, it can be normalized by dividing by $\beta + (\alpha/\sqrt{Re})C_0(n - n_1)^a\Lambda^bP^c$, where β is an arbitrary positive constant. Setting $\beta = 1$, performing this division and rearranging,

$$\frac{R_0 - R}{l} = \frac{C_0 (n - n_1)^a \Lambda^b P^c}{\frac{1}{\alpha} \sqrt{Re} + C_0 (n - n_1)^a \Lambda^b P^c} \quad (\text{A10.10})$$

This ratio has the following desirable properties:

$$\frac{R_0 - R}{l} \rightarrow 0 ; \quad n \rightarrow n_1, \quad Re \rightarrow \infty \quad (\text{A10.11})$$

$$\frac{R_0 - R}{l} \rightarrow 1 ; \quad n \rightarrow \infty, \quad Re \rightarrow 0 \quad (\text{A10.12})$$

Solving (A10.10) for R_0 , the settling speed W_b is evaluated as above, where R in (A10.1), and in the limits of integration in (A10.8), is replaced by R_0 . The value of the coefficient α is estimated by matching values of W_b for small n obtained from (A10.8) using R and then using R_0 . This formulation retrieves a minimum value of W_b , because it does not fully account for hydrodynamic interaction among spines extending beyond R_0 . Finally, it is noteworthy that the effects of spine interaction as embodied in (A10.11) and (A10.12) are consistent with the analysis of Cheer and Koehl (1987) regarding the drag on bristled appendages (in particular, see points (1), (3) and (5), p. 26-27, in Cheer and Koehl).

Turning to the tensile strength T_s , Turner and others (1954) obtained three values for the elastic limit of calcite crystals in a state of extension parallel to the crystallographic c -axis, under rapid strain rates ($0.025\% \text{ sec}^{-1}$). These values are $9.3 \times 10^7 \text{ dyn cm}^{-2}$ and $2.0 \times 10^8 \text{ dyn cm}^{-2}$, both obtained at 20°C and a confining pressure of $1 \times 10^{10} \text{ dyn cm}^{-2}$; and $4.4 \times 10^7 \text{ dyn cm}^{-2}$ obtained at 300°C and a confining pressure of $5.1 \times 10^9 \text{ dyn cm}^{-2}$. The third value strongly reflects effects of high temperature. The first two values represent an upper limit of the tensile strength under a state of elastic fracture. (The experiments involved plastic deformation of the crystals.) The effects of confining pressure on the elastic limit are unknown; although T_s may be reduced by an order of magnitude at near-surface confining pressures, this is unlikely.

In addition, it is well-known that the strengths of many materials, when measured per unit size, increase with decreasing sample size of material. Explanations for this size-dependent behavior generally are grounded in the early statistically-based theories of Pierce (1926), Daniels (1945), Epstein (1948), Gumbel (1954) and others. These theories suggest that the essential reason for increasing strength with

decreasing size is that, for a given underlying distribution of structural flaw sizes, the probability that a material sample will contain large, weak flaws decreases as its size decreases. The potential implication for foraminiferal spines is that the largest flaw size is limited by spine diameter; by virtue of their small diameter, the tensile strength T_s of spines may be larger than that obtained for a "large" calcite crystal. The extent to which this size-dependent behavior occurs for crystalline spines, however, is unknown. For order-of-magnitude arguments, we therefore choose the $T_s = 1 \times 10^8$ dyn cm⁻² based on the experiments of Turner and others (1954), with the caveat that this value possibly is an underestimate of the actual strength of spines.

11 Boundary Effects During Settling

For a sphere with radius R settling along the axis of an infinite cylindrical container with radius R_c , the total drag F_c on the sphere, accounting for effects of the container, is given by (for example, Happel and Brenner, 1986, p. 318)

$$F_c = 6\pi\mu RWK_1 \quad (\text{A11.1})$$

where the factor K_1 , to four terms, is

$$K_1 = \left[1 - 2.10444\left(\frac{R}{R_c}\right) + 2.08877\left(\frac{R}{R_c}\right)^3 - 0.94813\left(\frac{R}{R_c}\right)^5 - \dots \right]^{-1} \quad (\text{A11.2})$$

It is then straightforward to demonstrate that experimentally determined values of the coefficient of drag C_D are given by

$$C_D = \frac{12}{Re} K_1 \quad (\text{A11.3})$$

which immediately indicates that, for geometrically similar sphere-container systems where R/R_c is a constant, boundary effects may systematically influence the value of the numerical factor in (A11.3), but not the inverse relation between C_D and Re . If similarity is not maintained, however, then the form of

the relation between C_D and Re may be affected, for example, as R is systematically varied, because R is common to both Re and K_1 .

Analogous conclusions pertain to model foraminifera due to their quasi-spherical symmetry, although the factor K_1 cannot be used directly to correct for boundary effects. Nonetheless, one may envision that each model possesses a nominal radius, analogous to R in (A11.2), that is greater than the test radius R_t but less than the total radius $R_t + l_s$. Then, with the model and container dimensions used, "actual" values of the drag coefficient for models ideally settling in an unbounded fluid would be as little as six percent, to as much as 70 percent, less than the observed values of C_D , based on (A11.3). Moreover, the fit of data in Figure 2 suggests that the boundary "sees" a nominally spherical object, not the details of the spine geometry, such that for models with similar overall dimensions, boundary effects are systematic. The settling system—the model plus cylindrical container—is approximately geometrically similar (or boundary effects are negligible) such that an inverse relation between C_D and Re is maintained among replications in the two sets of experiments, a result that would not otherwise occur. More generally, we suspect that boundary effects are likely to systematically affect estimates of the exponents in (8), but not the basic power form of (8). This is indirectly reflected in the very good fit of data in Figure 5, including the data that were not used in developing (8).

NOTATION

a	empirical exponent associated with spine number n
b	empirical exponent associated with dimensionless spine length Λ
c	empirical exponent associated with dimensionless spine radius P
C	constant associated with coefficient of drag C_D
C_D	coefficient of drag
C_{Dr}	coefficient of drag for spine treated as right-circular rod
C_0	empirical coefficient

F_c	total drag on sphere settling in cylindrical container
F_D	drag force
F_s	drag force per unit length of spine
g	acceleration due to gravity
K_1	boundary correction factor for drag on sphere settling in cylindrical container
l	length of spine extending beyond protoplasm
l_s	length of spine
l_{ow}	spine length associated with settling speed extremum
L	characteristic linear dimension
n	number of spines
n_{op}	spine number associated with extremum of S_p
n_{ow}	spine number associated with settling speed extremum
n_{of}	spine number associated with extremum of S_f
n_1	empirical coefficient
r	spine radius
R	radius of test and protoplasm combined; sphere radius
R_c	radius of settling container
R_t	radius of test
R_0	effective radius of zero velocity surrounding foraminifer
Re	Reynolds number defined by $\rho RW/\mu$
Re_r	Reynolds number defined by $\rho rV/\mu$
S_p	derivative of settling speed W with respect to protoplasm density ρ_p
S_μ	derivative of settling speed W with respect to fluid viscosity μ
S_f	derivative of settling speed W with respect to fluid density ρ

T_s	tensile strength of calcite for planes normal to crystallographic c -axis
V	characteristic velocity of flow around spine
w	fluid velocity component parallel to settling motion
W	settling speed
W_b	settling speed at which spines break
W_R	settling speed of spherical test without spines
W_0	maximum (or minimum) settling speed
x	coordinate axis normal to settling motion
z	coordinate axis parallel to settling motion
α	dimensionless coefficient
β	arbitrary positive constant
Λ	dimensionless spine length equal to l/R
Λ_{0p}	dimensionless spine length associated with extremum of S_p
Λ_{0w}	dimensionless spine length associated with settling speed extremum
Λ_{0f}	dimensionless spine length associated with extremum of S_f
μ	dynamic viscosity of liquid
ρ	liquid density
ρ_p	density of protoplasm
ρ_R	effective density of test and surrounding protoplasm without spines
ρ_s	density of spine
P	dimensionless spine radius equal to r/R
σ	maximum tensile stress within spine
τ	torque on spine
ϕ	total porosity of test

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