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Application of the Hagen–Poiseuille Equation to Fluid Feeding Through Short Tubes

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ABSTRACT   The Hagen–Poiseuille equation has been widely applied to the study of fluid feeding by insects that have sucking (haustellate) mouthparts. However, the equation is valid only when the length of the cylinder is much longer than the *entrance length* (the length of the entrance region within which the flow is not fully developed). To estimate under what circumstances the flow through short tubular mouthparts would be slower than predicted from the Hagen–Poiseuille equation, we determined the empirical relationship between the relevant parameters using physical models made of glass micropipets. Fluid flow was measured while applying known pressure differences to cylinders of different geometries for a range of entrance lengths. We found a simple relationship between the flow and the entrance length in dimensionless terms for the range of experimental conditions (length:diameter range, 5:1–150:1; *Re* range, 18–1100). Thus, it is now possible to estimate easily correction factors resulting from the effects of the entrance region. The resistance to flow within the entrance region is sufficiently high that if the entrance length is one-half of the total length, the expected flow is only ≈80% of that predicted from the Hagen–Poiseuille equation. Reported flow rates through channels in insect mouthparts are sufficiently slow that the predicted entrance lengths are extremely small relative to their total lengths. Therefore, with the possible exception of some gigantic extinct insects, the Hagen–Poiseuille equation may be applied safely to fluid flow through even short feeding tubular structures (when the other assumptions are satisfied).

KEY WORDS   Hagen–Poiseuille, fluid feeding, fluid mechanics, mouthparts, haustellate

FLUID-FEEDING EVOLVED IN the insects often, probably 200–300 million years ago (Labandeira 1997). Some fluid-feeding insects pass fluid along cylindrical channels in their mouthparts, and for these cases there is a classic fluid mechanical equation available that describes the quantitative relationship among the geometry of the channel, the rate of flow, the physical properties of the flowing fluid, and the pressure difference along the length of the channel that causes the fluid to move. This equation, the Hagen–Poiseuille equation, is

$$Q = \frac{\pi \, \Delta P \, r^4}{8 \, \mu \, L},$$ [1]

where Q is the volume flow rate (m^3/s in SI units), ΔP is the pressure difference between the ends of the cylinder (Pa), r is the internal radius of the cylinder (m), μ is the dynamic viscosity of the fluid (Pa s), and L is the length of the cylinder (m) (Vogel 1994). This equation (or an appropriate modification) has been applied to studies of fluid feeding in a diverse group of insects, including water uptake in the large milkweed bug *Oncopeltus fasciatus* (Dallas) (Mittler 1967); blood uptake in the assassin bug *Rhodnius prolixus* Stål (Bennet-Clark 1963); sap uptake in the aphid *Tuberolachnus salignus* (Gmelin) (Mittler 1957); xylem uptake in the leafhopper *Homalodisca coagulata* (Say)

(Andersen et al. 1992); blood uptake in the mosquito *Aedes aegypti* (L.), the bed bug *Cimex lectularius* L., and the body louse *Pediculus humanus* L. (Daniel and Kingsolver 1983); and nectar uptake in the butterflies *Colias eurytheme* Boisduval, *Danaus plexippus* (L.), and *Pieris rapae* (L.) (Kingsolver and Daniel 1979, Daniel et al. 1989). For reviews and additional references see Raven (1983) and Kingsolver and Daniel (1993).

The derivation of the Hagen–Poiseuille equation relies on conditions that must be approximately satisfied to produce predictions with an acceptable uncertainty. The most useful discussions on these conditions or limitations describe methods for evaluating the magnitude of the different physical phenomena rather than simply dismissing them as negligible: the complication of non-Newtonian fluids such as blood (μ is not constant, Daniel and Kingsolver 1983), consideration of unsteady effects (Loudon and Tordesillas 1998), a changing diameter of the food canal (Kingsolver and Daniel 1979), the potential mechanical failure of the sucking apparatus (Kingsolver and Daniel 1979, 1993), the influence of gravity (Kingsolver and Daniel 1979), the role of capillary feeding (Kingsolver and Daniel 1993), and the problem with assuming a constant suction produced by muscular pumps such as the cibarial pump in the insect (Daniel et al. 1989).
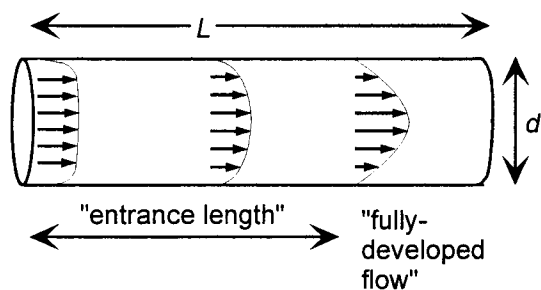
Fig. 1. As fluid moves downstream from the entrance to a channel, its speed distribution or velocity profile changes in shape until it becomes fully developed. The length of an arrow indicates the magnitude of the flow velocity at the location of the base of the arrow.

One assumption that has not been addressed quantitatively in this context is that the Hagen–Poiseuille equation is valid only for the condition of fully developed flow, where the parabolic velocity profile is no longer changing with distance along the cylinder (Fig. 1). For some distance downstream of the entrance to the cylinder, the velocity profile will be changing with distance (Fig. 1). The *entrance length* usually is defined as the distance from the entrance to the location where the velocity at the center of the cylinder has approached 99% of the value in the center of the fully developed flow downstream. The entrance length, L_E, may be estimated easily as

$$L_E = 0.058 \, Re \, d, \qquad [2]$$

(Vogel 1994), where Re is the dimensionless Reynolds number,

$$Re = \frac{\rho \, d \, u}{\mu}, \qquad [3]$$

d is the internal diameter of the cylinder (m), ρ is the density of the fluid (kg/m³), and u is the average velocity of the fluid inside the cylinder (m/s). Therefore, entrance length will increase with flow rate. So, for example, the entrance length in the case of water ($\rho = 998 \, \text{kg/m}^3$, $\mu = 1.002$ by 10^{-3} Pa s at 20°C) flowing through a cylinder of 1 mm internal diameter at 1 cm/s would be 0.6 mm. Although equations (2) and (3) suggest that as the flow approaches zero ($u \rightarrow 0$), the entrance length also will approach zero ($L_E \rightarrow 0$); in practice the entrance length approaches a lower bound of 0.6 d as seen mathematically in more complex formulas given for entrance length (e.g., White 1991, p. 293). That is, in very low Re flow ($Re \ll 1$)], where the diameter is very small or the flow is very slow or both, the flow will be become fully developed within ≈1 radius from the entrance. See White (1991) for review of both theoretical and experimental research on this subject.

The channels within sucking mouthparts of extant insects often are extremely long relative to their diameters (length/diameter ratios around 100:1 or greater) and may have very tiny lumens ($d \ll 1$ mm). For example, the length/diameter ratio is 83:1 for the food canal in the leafhopper *Homalodisca coagulata* (Say) (stylets 2 mm long, internal diameter 24 μm, Andersen et al. 1992), 750:1 for the aphid *Myzus persicae* (length 300 μm, internal diameter 0.4 μm, Auclair 1963), and 667:1 for the bug *Oncopeltus fasciatus* (length 6 mm, internal diameter 9 μm, Forbes 1976). Thus, the entrance lengths of the developing flow within these sucking insect mouthparts may be expected to be small relative to their overall lengths. However, the relative sizes of these anatomical features by themselves do not reveal the magnitude of the effect of the entrance region on the overall fluid flow rate. Complex formulas for calculating the excess resistance to flow in the entrance region are available in the fluid mechanical literature (e.g., White [1991], pp. 291–292), but they are written in a form more appropriate for engineering applications of high flow rates, using constants that vary in unpredictable ways with flow speed in the slower flow range more relevant to insect feeding rates ($Re < 500$). Examples of Re for the flow through sucking insect mouthparts are $Re = 10$ for the leafhopper *Homalodisca coagulata* feeding on xylem (calculated from data supplied in Andersen et al. 1992) and $Re = 0.06$ for the aphid *Myzus persicae* feeding on phloem (calculated from data supplied in Auclair 1963). In addition, derivations of these formulas usually assume a flat velocity profile at the entrance to the tube, although it has been shown experimentally using laser Doppler velocimetry that for $Re < 60$, the parabolic velocity profile begins to form in a fluid reservoir upstream of the entrance to the tube (Kawata et al. 1974). Therefore, to uncover the quantitative relationship between the overall flow and the events in the entrance region, physical modeling was used to determine empirically the relationship between the rate of fluid flow, the geometry of the cylinder, the applied pressure difference, and the characteristics of the fluid. The purpose is to make predictions of the circumstances within which changes in morphology, behavior, or environmental conditions may have unexpected effects on the rate of fluid feeding, as well as to provide guidelines for the appropriate application of the Hagen–Poiseille equation. The experimental Re range was 18–1100; this includes the higher end of the Re range for fluid-feeding insects where entrance effects are anticipated to be the most significant ($Re > 10$).

Materials and Methods

Physical Models. Glass micropipets (25 and 50 μl, FisherBrand) were used for the cylindrical physical models. The internal diameters of the micropipets were 0.60 and 0.85 mm for the 25 and 50 μl micropipets, respectively (calculated from the marked lengths corresponding to the indicated internal volumes). Glass micropipets were cut to different lengths to provide different length/diameter ratios: 25:1, 50:1, and 100:1 for the 25 μl micropipets and 5:1, 13:1, 25:1, 50:1, and 150:1 for the 25 and 50 μl micropipets. Three or 4 replicates (different micropipets of identical geometry) were averaged for any flow measurement at
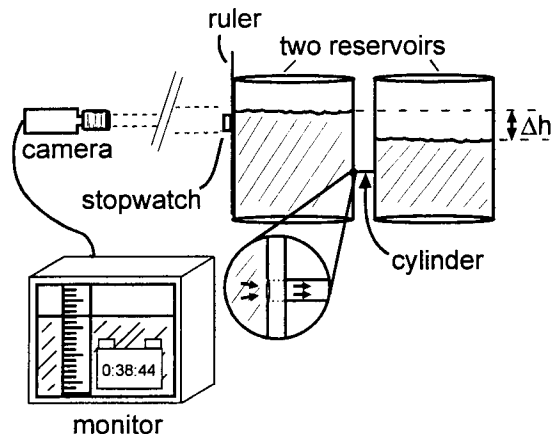
Fig. 2. Apparatus for applying a known pressure gradient to a cylinder and measuring the resulting volume flow rate through the cylinder.

a given pressure difference. Seventy-six different combinations of pressure differences and cylinder morphology were used. The micropipets were attached in a horizontal orientation between 2 reservoirs such that the opening edge of the micropipet was flush with the inner surface of the rubber septum holding the pipet in place (Fig. 2). The internal diameter of a reservoir was at least 10 cm. The fluid used was distilled water. The difference in water level height between the 2 reservoirs supplied the pressure difference along the cylinder causing the flow (Fig. 2). The experimental *Re* range was 18–1100.

Determination of Volume Flow Rate. The volume flow rate was determined by videotaping the fall of the meniscus of the air-water interface using a video camera (Panasonic CCD WV-CL50 with a 8–80 mm television lens; VHS video format) which allowed a vertical field of view of 4–6 cm (Fig. 2). A ruler and a stopwatch located outside of the reservoir also were in the field of view of the video camera. The video camera was positioned 1 m away to reduce parallax caused by the distance between the ruler and the center of the meniscus. Comparisons of measurements at the top and bottom of the field of view indicated that the measurement error caused by parallax was on the order of 4 μm for a change in meniscus height of 1 mm. The pressure difference between the 2 ends of the cylinder was calculated from the difference in height of the water level of the 2 reservoirs. The videotapes were played back frame by frame to determine the time at which the meniscus reached a given height in the reservoir as measured on the ruler. The precision of the meniscus height measurement was determined by repeated blind frame selections; the standard deviation of 10 selections was 0.05 mm (calculated from the known rate of change in meniscus height). Because the total volume of water and the dimensions of the 2 reservoirs are known, the height of fluid in 1 reservoir could be used to calculate the height in the other reservoir. The time for a change of water height

of 1 mm in 1 reservoir was used to calculate the volume flow rate; these time intervals ranged from 12.5 to 1,016 s. The average pressure differential (during the 1-mm change in height) was used as the representative pressure differential for that measured volume flow rate. The height difference between the 2 reservoirs was always >3 mm. Water in the reservoirs was always allowed at least 5 min to become still after a mechanical disturbance such as adding water.

Viscosity of Water. The viscosity of the water was estimated from the temperature (Weast 1988). The temperature of the water varied by <1°C within any set of measurements, although the temperature of the water in the reservoirs varied between days of measurement (total range, 18.2–25.0). The results were all normalized to a standard temperature of 20°C; the predicted flow at 20°C is obtained by multiplying the measured volume flow rate by the ratio of the viscosity of water at that experimental temperature to the viscosity of water at 20°C. The water in the reservoirs was always within 1°C of the room temperature to minimize the exchange of heat between the apparatus and the room. The reservoirs were loosely covered with plastic wrap; evaporation is estimated to be an insignificant source of error under the experimental conditions.

Statistics. The regression and test for homogeneity of slopes were performed on Minitab software using the General Linear Models procedure (Minitab 1996).

Results

General Predictive Equation. When the entrance length was much less than the total length of the cylinder, the Hagen–Poiseuille equation closely predicted the volume flow rate (Fig. 3A). As the entrance length approached the order of magnitude of the total length of the cylinder, the deviation from predictions of the Hagen–Poiseuille equation became very pronounced (Fig. 3B). Uncovering a general physical relationship requires identification of the appropriate dimensionless parameters (McMahon and Bonner 1983, Pennycuick 1992). We reasoned that the ratio of the measured flow, Q_{meas}, to the flow predicted using the Hagen–Poiseuille equation, Q_{calc}, might scale with the ratio of the total length, L, to the calculated entrance length, L_E, in the following way:

$$\frac{Q_{meas}}{Q_{calc}} = \frac{L/L_E}{(L/L_E) + R}, \qquad [4]$$

where R is an excess resistance caused by the influence of the entrance region. This general equation fit the data very well for the complete experimental range of Reynolds numbers and length/diameter ratios (Fig. 4). Linear regression performed on the variables (transformed to generate a linear relationship) allowed an empirical estimate for R of 0.52. Thus, the best fit of equation 4 to the data is

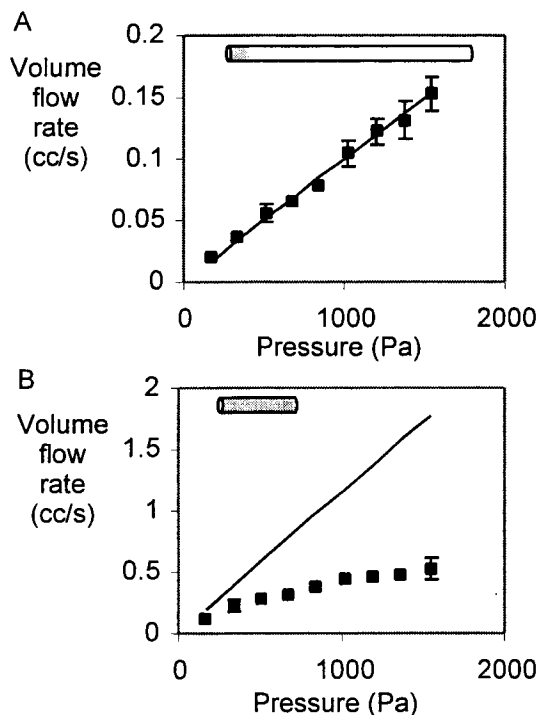$$\frac{Q_{meas}}{Q_{calc}} = \frac{L/L_E}{(L/L_E) + 0.52}, \qquad [5]$$

Fig. 3. Examples of measured volume flow rates (squares; means ± 2 SEs, $n = 4$) compared with predictions from the Hagen–Poiseuille equation (solid line) as a function of applied pressure differences. (A) Entrance length (indicated by gray shading) is <10% of total length of the cylinder. Experimental conditions: length of cylinder is 127 mm, internal diameter is 0.848 mm, Re range is 25–250. (B) Entrance length is as long as the cylinder or longer. Experimental conditions: length of cylinder is 11 mm, internal diameter is 0.848 mm, Re range is 200–1,000.

($n = 76$, $r^2 = 0.97$ from linear regression on transformed variables where Q_{calc}/Q_{meas} is the dependent variable and L_E/L is the independent variable). This simple relationship (equation 5) allows general state-ments to be made about the quantitative influence of the entrance length on the total flow: a 5% decrease in flow rate ($Q_{meas}/Q_{calc} = 0.95$) is expected when the entrance length is 10% of the total length, and a 20% decrease in flow rate is expected when the entrance length is about half of the total length. Although a test for the homogeneity of slopes showed a significant effect of the length/diameter ratio when this geometric factor was treated as a categorical variable (the $(L_E/L)*$(length/diameter ratio category) term was significant to the 0.001 level), we believe that this is an artifact of the differences in ranges of this geometric variable along the x axis (Fig. 4). There was no trend in the relationship between flow rate and entrance length with the length/diameter ratio.

When Do Short Cylinders Approach the Behavior of Orifices? As the total length becomes small relative to the entrance length ($L/L_E \ll 1$, Fig. 4B), the curve more closely approximates a straight line intersecting the origin. This has the consequence that the flow rate becomes approximately independent of length; that is, an increase in length will not carry the usual consequence of reducing the flow seen in ordinary Hagen–Poiseuille behavior. This can be described mathematically as

$$\frac{Q_{meas}}{Q_{calc}} \propto \frac{L}{L_E}, \qquad [6]$$

or

$$Q_{meas} \propto \frac{L}{L_E} Q_{calc} = \frac{L}{(0.058\,Re\,d)}\left(\frac{\pi\,r^4\,\Delta P}{8\,\mu\,L}\right), \quad [7]$$

which, removing all terms except the morphological ones, simplifies to

$$Q_{meas} \propto r^2, \qquad [8]$$

because the Ls cancel. The loss of the dependence of volume flow rate on length is reminiscent of formulas for flow through orifices (Vogel 1994, Fung 1997), although note that this fluid behavior occurred for cylinders with lengths at least 5 times their diameter.
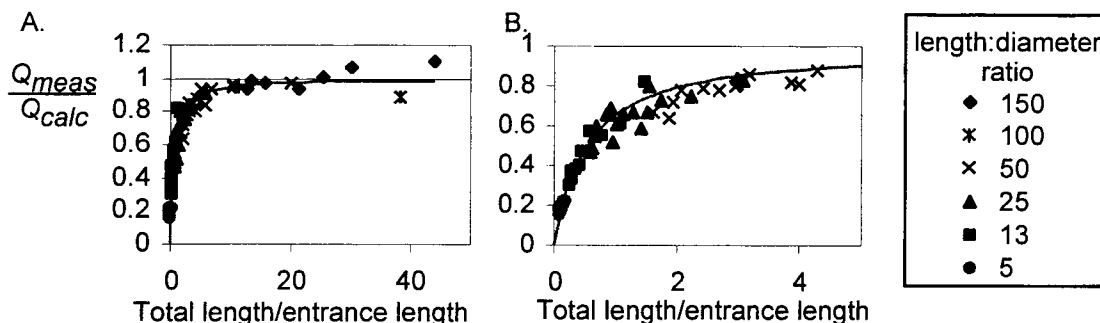

Fig. 4. The ratio of the measured volume flow rate (Q_{meas}) to the calculated volume flow rate (Q_{calc}) as a function of the ratio of total length to entrance length. Similar trends were seen for all cylinder geometries (as indicated by different symbols for the 6 length/diameter ratios) and Re's (Re range from 18 to 1,000). (A) The measured flow rate asymptotically approaches the calculated volume flow rate as the length of the cylinder becomes very long relative to the entrance length. (B) Detail of the lower range of ratios of total length/entrance length.
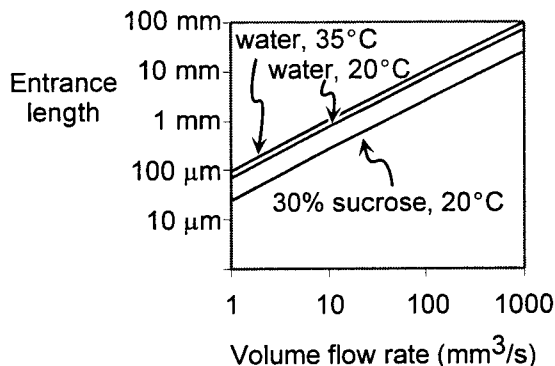
Fig. 5. The predicted entrance length increases with volume flow rate for any fluid. Three representative fluids are illustrated. Most biologically relevant aqueous solutions will lead to a smaller entrance length than found for water of the same temperature flowing at the same rate. The fluid densities and viscosities are from tables in Weast (1988).

Entrance Length As a Function of Volume Flow Rate. The predicted entrance length may be calculated solely from the volume flow rate and the physical properties of the fluid (Fig. 5). This relationship follows from combining equations 2 and 3 and noting that $Q_{meas} = \pi r^2 u$:

$$L_E = \frac{0.074 \, Q_{meas} \, \rho}{\mu} \qquad [9]$$

Note that for a given volume flow rate, the entrance length is independent of tube diameter (keeping in mind that L_E has a lower bound of 0.6 d).

Discussion

We have supplied a simple method for estimating when the length of a tube is sufficiently short relative to the entrance length to cause a significant decrease in flow rate relative to the predictions of the Hagen–Poiseuille equation (equation 5; Fig. 5). Most reported fluid feeding rates for insects fall below 1 mm^3/s (=1 μl/s), but some of the rates in the literature may be underestimates if they were averaged over a long time period that included nonfeeding time as well. Examples of feeding rates include 5×10^{-4} mm^3/s is the maximal reported volume flow rate for a range of aphid species feeding on phloem (Auclair 1963); 0.19 mm^3/s is the maximum recorded for the adult leafhopper *Homalodisca coagulata* (Say) feeding on xylem (Andersen et al. 1992); 0.34 mm^3/s is the average reported for 5th instars of the assassin bug *Rhodnius prolixus* feeding on rabbit blood (Bennet-Clark 1963a); and 2.5 mm^3/s is the average reported for puddling male *Gluphisia septentrionis* moths (Smedley and Eisner 1995). For fluid feeding at rates below 1 mm^3/s for water or more viscous fluids, the entrance length is <100 μm (Fig. 5), so the flow should be within 5% of that predicted by the Hagen–Poiseuille equation for food canals of lengths on the order of 1 mm or more. Therefore, for most extant insects, a

significant departure from the predictions of the Hagen–Poiseuille equation caused by entrance effects is not expected.

Extinct insects may be another matter. Sucking mouthparts probably evolved from the elongation of modified chewing mouthparts held close to each other (Snodgrass 1935, Chapman 1982). That is, the channels through which the fluid flows are usually formed by aligned indentations of juxtaposed modified mouthparts. Therefore, it is reasonable to assume that at some point in the past, insects ancestral to extant fluid-feeding insects had shorter and wider (presumably more irregular) channels to direct the fluid. In addition, some extinct paleodictyopterans had large beaks (1 report of 3.1 cm long) that probably fed on plant sap (Labandeira 1997). Certainly if these extinct insects had sufficiently high feeding rates, the effect of the entrance region could lower the penalty of a slowed flow that would otherwise occur during the development and evolution of longer sucking mouthparts.

Acknowledgments

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