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Fluid mechanics of bloodmeal uptake by *Leishmania*-infected sandflies

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Summary

The fluid mechanics of blood flow in the pharynx and cibarium of *Phlebotomus papatasi* are described using a simple static model. The flow is characterized as viscous laminar. The Hagen-Poiseuille equation is used to assess the effects of attached parasites in the foregut of *Leishmania*-infected sandflies on blood flow. The reductions in flow rate imposed by parasite colonization of the pharynx and cibarium will reduce the ability of an infected fly to take a bloodmeal, thus encouraging further probing, enhancing transmission. Regurgitation of the contents of the foregut is also possible. This will aid the deposition of infective forms from the foregut. Transmission by means of regurgitation of parasites from the midgut is considered unlikely.

Key words: sandflies; *P. papatasi*; feeding behaviour; *Leishmania*; transmission; fluid mechanics; blood flow; viscous flow.

Introduction

Many authors have noted the difficulty which sandflies infected with *Leishmania* often experience in obtaining a bloodmeal (Smith et al., 1940; Adler and Ber, 1941; Chung et al., 1951; Strangeways-Dixon and Lainson, 1966; Williams, 1966; Killick-Kendrick et al., 1977, 1985a; Beach et al., 1984, 1985). Killick-Kendrick et al. (1977) found that 14 out of 17 *Lutzomyia longipalpis* infected with *Leishmania mexicana amazonensis* experienced difficulty in taking a second bloodmeal. Many probed repeatedly but took only a small meal.

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Analysis of the data of Chung et al. (1951), by the same authors showed that *Phlebotomus chinensis* was able to transmit *L. donovani* to hamsters with greater success when flies probed but took no blood. The chances of transmission were significantly lower when flies took a bloodmeal. Recently Beach et al. (1985) have provided strong evidence that infections anterior to the midgut are necessary in order to adversely affect feeding behaviour.

Shortt et al. (1926) and Shortt and Swaminath (1928) found that the foregut of infected flies anterior to the oesophagus appeared to be blocked by parasites. Smith et al. (1940) identified blocked flies as those that pierced the skin of the host, but were unable to obtain blood. Of 58 infected *P. argentipes*, 49 were found on dissection to be heavily infected with flagellates of *L. donovani*. The role of the occlusion of the foregut by parasites in the alteration of sandfly feeding behaviour has been largely overshadowed by the possible implications for the transmission of *Leishmania*. Transmission by regurgitation has received support from a number of authors (Smith et al., 1940; Napier, 1946; Parrot and Donatien, 1952; Bray, 1974; Lainson et al., 1977). However, Adler and Theodor (1934, 1957) rejected this idea, pointing out that the pharynx and buccal cavity (= cibarium) have powerful dilator muscles which they inferred would increase their internal diameter sufficiently to allow the ingestion of blood, even when heavily infected with parasites. These authors also provided convincing evidence that transmission of *Leishmania* is accomplished by the transfer of promastigote "proboscis forms" from the fascicle of the fly into the skin of the host (Adler and Theodor, 1929, 1931, 1934).

Killick-Kendrick et al. (1977) suggested that parasites in the cibarium block the pores of chemoreceptors responsible for the initiation of engorgement, thereby increasing the frequency of probing in infected flies. However, no direct evidence of this has been put forward.

Recent studies of vector-parasite interactions between *Glossina* and salivarian trypanosomes (Jenni et al., 1980; Livesey et al., 1980) prompted Killick-Kendrick and Molyneux (1981), to suggest that proper functioning of the pharyngeal and cibarial pumps may be adversely affected by the presence of parasites in the foregut, which may impede the flow of blood.

In this paper an attempt is made to determine the effects of attached parasites within the foregut of *Leishmania*-infected sandflies on the uptake of blood, applying the principles of fluid mechanics. The procedure used was adapted from that of Livesey et al. (1980). *Phlebotomus papatasi* was chosen as the subject of this study as all the data necessary for the calculation of bloodflow were available from published literature.

Materials and Methods

Calculation of foregut dimensions: the sizes of the partially and fully expanded cross-sections of the pharynx and cibarium of *P. papatasi* were estimated from the dimensions of the corresponding collapsed lumen, illustrated in Adler and Theodor (1926). Scale drawings were then made and the

necessary calculations performed, assuming triangular and circular cross-sections for the partially and fully expanded foregut lumens, respectively.

Calculation of increased pressure drop: for circular cross-sections the increased pressure drop ($-\Delta p$) was calculated according to Poiseuille's law as the inverse of the fourth power of the diameter (see Livesey et al., 1980). The pressure drop in tubes of various cross-sectional shapes can be determined from the fRe factor. For triangular ducts where $h/b > 0.5$, as in all examples considered here, $fRe \approx 13$ (Shah and London, 1978). For a circular duct $fRe = 16$. The increased ($-\Delta p$) for a triangular cross section is thus $13/16$ of that of a circular duct of the same hydraulic diameter.

Results

In order to estimate the effects of parasites attached within the pharynx and cibarium it is first necessary to characterize the type of flow encountered. The foregut, pumping chambers of the sandfly have distensible walls and change in both shape and dimensions as blood is pumped toward the midgut. A rigorous analysis of unsteady flow, i.e. a uni-directional flow with a superimposed oscillating pressure gradient in a tube with non-rigid walls, is not possible, as flow

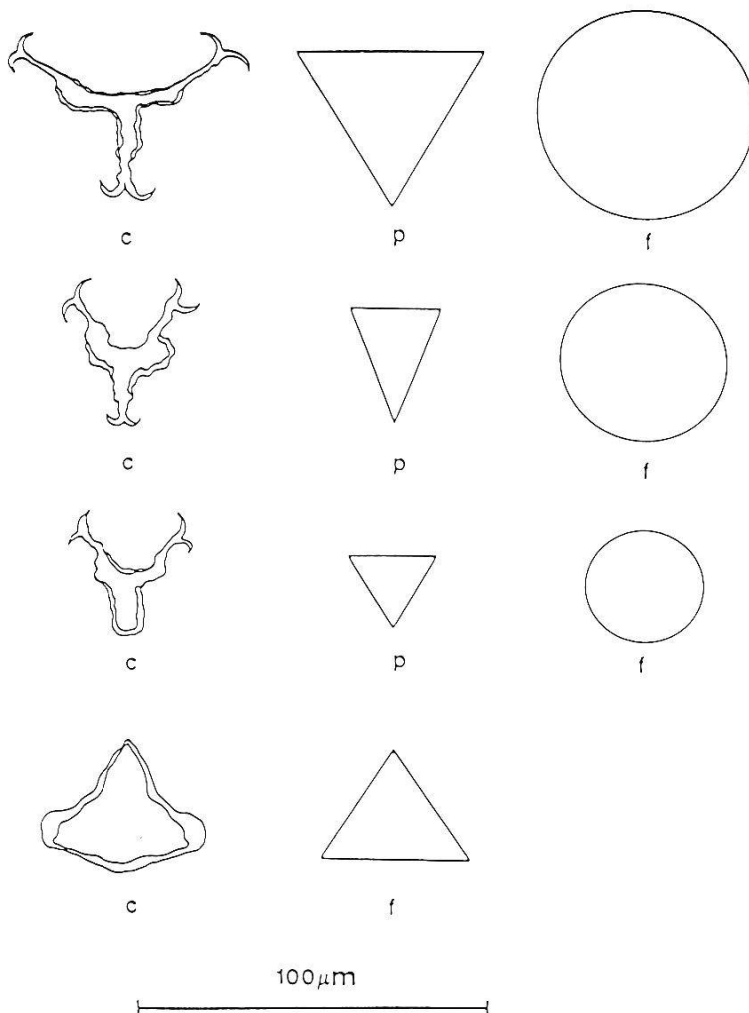


Fig. 1. Cross-sections of the pharynx and cibarium of *P. papatasi*. a) Posterior region of pharynx behind brain; b) mid-region of pharynx; c) anterior end of pharynx; d) mid-region of cibarium. Key: c = shape of collapsed cross-section; p = partially expanded lumen; f = fully expanded lumen.

cannot be time-averaged over the pumping cycle. However, an approximation of flow in such a passage can be arrived at by considering flow through a typical cross-section during different stages of the pumping cycle. In the present analysis a single cross-section of the cibarium and 3 separate cross-sections of the pharynx are used to illustrate flow (Fig. 1).

Flow regime

In a rigid tube of constant cross-sectional area the flow regime is characterized by the Reynolds number (Re). A parameter termed the Womersley number (α) is used to assess the effects of an oscillating pressure gradient superimposed on a fully developed steady flow (Womersley, 1955; Uchida, 1956).

Reynolds number: $Re = VD_h/\nu$

where: D_h = hydraulic diameter of food canal
 V = velocity of blood
 ν = kinematic viscosity of blood

Hydraulic diameter (D_h): the dimensions of the expanded cross-sections of the cibarium and pharynx of *P. papatasi* are shown in Fig. 1. D_h is calculated from the following relationship:

$$D_h = \frac{4 \times \text{cross-sectional area}}{\text{perimeter}}$$

This can be used to determine the hydraulic diameter of passages of a wide variety of cross-sectional shapes. For a circular tube of radius r , this reduces to $2r$, which is the actual diameter.

Velocity (V): the velocity of the blood is calculated from the relationship: $AV = Q$

where: A = cross-sectional area of food canal
 Q = volume flow rate

The volume flow rate is equivalent to the amount of blood taken per second, i.e. the volume divided by the duration of the bloodmeal.

Theodor (1936) gives an average first bloodmeal weight of 0.45 mg for *P. papatasi*. Dividing by the density of blood ($\rho = 1.06 \text{ mg/mm}^3$) this gives a bloodmeal volume of 0.42 mm^3 . The duration of the bloodmeal is about 2 min 30 sec (Whittingham and Rook, 1923).

Kinematic viscosity (ν): Livesey et al. (1980) used a value of $3 \times 10^{-6} \text{ m}^2\text{s}^{-1}$ for the kinematic viscosity of blood.

Womersley parameter: $\alpha = D_h \times \sqrt{\omega/\nu}$

where ω = radian or circular frequency ($= 2\pi \text{ Hz}$).

Adler and Theodor (1926) observed that the cibarial pump of *P. papatasi* contracted up to 120 times per minute, a frequency of 2 Hz.

The resultant Reynolds and Womersley numbers for each cross-section considered are shown in Table 1. The magnitude of the Reynolds numbers ($Re \ll 1$) reveals that the flow is markedly laminar and that viscous forces predominate. In addition the values of α ($\alpha < 1$) confirm that the unsteady component of the flow, caused by the action of the cibarial and pharyngeal pumps, will not seriously alter the velocity distribution, which will remain in phase with the pressure fluctuations (Livesey et al., 1980).

Table 1. Characterization of the flow regime in the pharynx and cibarium of *P. papatasi*

Cross-section ¹			Dimensions of cross-sections (μm) ²			Cross-sectional area (m ²)	Perimeter (m)	D _h (m)	Re	α
			b	h	D					
Pharynx	a	p	52	45	–	1.17×10 ⁻⁶	1.56×10 ⁻³	3.0×10 ⁻⁵	2.4×10 ⁻²	6.1×10 ⁻²
		f	–	–	60	2.83×10 ⁻⁶	1.88×10 ⁻³	6.0×10 ⁻⁵	1.9×10 ⁻²	1.2×10 ⁻¹
	b	p	25	33	–	4.12×10 ⁻⁷	9.4 ×10 ⁻⁴	1.7×10 ⁻⁵	3.9×10 ⁻²	3.5×10 ⁻²
		f	–	–	46	1.66×10 ⁻⁶	1.44×10 ⁻³	4.6×10 ⁻⁵	2.6×10 ⁻²	9.4×10 ⁻²
	c	p	24	21	–	2.52×10 ⁻⁷	7.2 ×10 ⁻⁴	1.4×10 ⁻⁵	5.2×10 ⁻²	2.9×10 ⁻²
		f	–	–	32	8.04×10 ⁻⁷	1.0 ×10 ⁻³	3.2×10 ⁻⁵	3.7×10 ⁻²	6.5×10 ⁻²
Cibarium	d	f	41	32	–	6.56×10 ⁻⁷	1.17×10 ⁻³	2.2×10 ⁻⁵	3.1×10 ⁻²	4.5×10 ⁻²

¹ Letters correspond to the drawings in Fig. 1

² b = base width; h = height; D = diameter; m = metre

The viscous nature of blood flow in blood feeding has been confirmed by studies with various groups of haematophagous arthropods (Daniel and Kingsolver, 1983; Jefferies, 1984). Furthermore any possible error in the magnitude of the values used to calculate the above parameters, such as the size and duration of the bloodmeal, will not alter the nature of the flow. The Re number could be increased 100-fold and α 10-fold and the flow would remain viscous laminar.

Thus the Hagen-Poiseuille theory can be applied to the time-averaged flow and time-averaged pressure gradient when assuming a constant cross-sectional area, i.e.

$$Q = \frac{\pi D_h^{-4}}{8\mu} \times \frac{(-\Delta p)}{L}$$

where: μ = dynamic viscosity (= ν × ρ)
 (-Δp) = negative pressure drop
 L = length of food canal

Clearly the pressure drop (-Δp) required to maintain a given flow rate will be most affected by changes in the diameter of the food canal, as the flow rate is inversely proportional to the fourth power of the diameter.

Effects of attached parasites on flow

Molyneux and Killick-Kendrick (in press) state that paramastigote forms of *Leishmania* found attached in the foregut are typically 5–10 microns in length and 4–6 microns wide. Taking a conservative view of the occlusion of the lumen of the pharynx by parasites, the reduction in hydraulic diameter of each cross-section shown in Fig. 1, assuming an average parasite length of 7.5 microns, has been used to estimate the factor by which the pressure drop must be increased in order for the fly to feed normally. Or conversely, the factor by which the flow

Table 2. Occlusion of foregut lumen by attached parasites

Cross-section ¹			D _h (μm)			Proportion unoccluded	Factor of increase in (-Δp)
			f Re	un-occluded	occluded		
Pharynx	a	p	13	30	15	0.5	13.0
		f	16	60	45	0.75	3.2
	b	p	13	17	2	0.12	3920
		f	16	46	31	0.67	5.0
	c	p	13	14	0	0	∞
		f	16	32	17	0.53	12.7
Cibarium	d	f	13	22	12 ³	0.54	9.5

¹ Letters and numbers correspond to the drawings in Fig. 1

³ Estimated with only dorsal wall colonized i.e. $\frac{2}{3}$ reduction in diameter compared with that of the pharynx.

rate will be reduced if (-Δp) remains the same (Table 2). In infections of the cibarium, paramastigotes normally colonize only the roof or dorsal wall (Killick-Kendrick, 1979). Hence, the extent of occlusion is estimated accordingly.

It is clear from the data that an infection in which a substantial length of the foregut is colonized by paramastigotes could seriously impair the ability of a sandfly to take a bloodmeal (Table 2). In the posterior region of the pharynx, where the lumen is at its largest, the pressure drop (-Δp) is increased at least by a factor of 3 when fully expanded, and by a factor of 13 when only partially expanded. However, this region of the pharynx, which lies behind the brain, only occupies a very short proportion of its total length. Along the greatest proportion of the length of the pharynx the dimensions are those of cross-section (b) (Fig. 1), tapering towards (c) (Fig. 1), at the anterior end (Adler and Theodor, 1926). Hence for the majority of its length (-Δp) in the pharynx is increased 5 to 13 fold, even when the walls are fully expanded. At other stages of the pumping cycle flow, to all practical extents and purposes, virtually ceases. Colonization of the cibarium causes a 10-fold increase in (-Δp) (Fig. 1, d), adding to the already considerable problems an infected fly may have in maintaining the rate of blood uptake at a comparable level to that of an uninfected fly.

An additional factor which must be considered is the effect of attached parasites on the pumping efficiency of the pharynx and cibarium. The power generated by the pharyngeal and cibarial dilator muscles is a product of the force produced by the contraction of the muscles, multiplied by the distance moved by the walls of these chambers. Occlusion of the lumen of the cibarium and/or the pharynx by parasites will effectively reduce the latter, decreasing the pumping power to an extent equivalent to the reduction in diameter of the lumen (see Table 2). Thus a pharyngeal infection would decrease the power output of the

pharyngeal dilator muscles by 25–50% were the same force exerted. Similarly in the cibarium the loss of power would be about 50%.

It is possible that an infected fly may generate greater force in distress. However, even if the force could be raised to the levels indicated as necessary by the required pressures to achieve the same flow rate as in normal feeding, the power requirements would be directly proportional to the required pressures (i.e. $\propto D^{-4}$). The maintenance of such power outputs is likely to be momentary at the factors quoted of say 5–10 fold or above. Thus the power losses experienced by a heavily infected fly will decrease pump performance and therefore prevent effective compensation for a reduced flow rate.

Discussion

Adler and Theodor (1934, 1957) rejected the theory that the foregut of an infected sandfly could be blocked to such an extent that the uptake of blood would be prevented, claiming that the pharynx and cibarium as pumping chambers with strong dilator muscles were capable of great distention which would allow the unimpeded passage of blood. The above analysis shows this argument to be invalid. Despite expansion, colonization by parasites will reduce flow through the foregut and decrease the power output of the cibarial and pharyngeal pumps to a significant extent.

It is now well documented that sandflies can transmit *Leishmania* by probing alone without engorgement (Killick-Kendrick et al., 1977, 1985a; Killick-Kendrick, 1979; Beach et al., 1984, 1985) by the inoculation of infective free-swimming promastigotes from the proboscis into the wound (Killick-Kendrick, 1979; Killick-Kendrick and Molyneux, 1981). The observation that infected sandflies indulge in multiple probing is explained by their inability to engorge as a result of effective blockage of the pharynx. Reductions in the sensory input to flow-detecting mechanoreceptors on the labrum and in the cibarium will induce a fly to break off probing, while the “hunger state” brought on by its inability to feed will ensure further probing attempts. Thus transmission will be enhanced as infective proboscis forms can be extruded at each probe (Beach et al., 1984, 1985; Killick-Kendrick et al., 1985a, b).

Killick-Kendrick et al. (1977) suggested that parasites attached in the cibarium might cover the pores of chemosensilla thought to be present in the cibarium, thus preventing engorgement and encouraging continued probing. However, the presence of chemoreceptors in the cibarium of sandflies has not been established (Jefferies, 1984; in preparation). If found, such receptors are likely to be on the ventral wall of the cibarium, their position in all other groups of Diptera examined (Rice, 1970). Parasites in the cibarium are attached mainly to the roof or dorsal wall (Killick-Kendrick, 1979), and would therefore be unlikely to interfere with the function of these sense organs. The only sensilla found within the cibarium to date (Lewis, 1984), appear to be mechanoreceptors

arising from the dorsal wall which possibly monitor the flow of blood within the cibarium (Lewis, 1975; Jefferies, 1984; in preparation). Direct interference with the function of these receptors is possible, as with trypanosome-mechanoreceptor interactions in the proboscis of *Glossina* (Jenni et al., 1980). However, once an infection has reached this site, such effects are likely to be of minimal importance compared to the effects of the occlusion of the pharynx.

Recently it has been shown that forms infective to the vertebrate host develop in the midgut of sandflies as early as day 3 post-infection and are especially virulent on day 5 after the bloodmeal has been passed (Sacks and Perkins, 1984, 1985). This clearly gives credence to the theory that regurgitation of parasites from the midgut is a possible mode of transmission (see Molyneux, 1977; Killick-Kendrick, 1979).

It was not possible to determine the effects of parasites in the midgut on flow as the dimensional data are lacking and flow into the midgut is difficult to model. However, indirect evidence suggests that midgut infections alone are not capable of regularly initiating infections in the vertebrate host. Adler and Theodor (1931, 1934) showed that only *P. perniciosus* flies which had proboscis infections of *L. infantum* deposited parasites when induced to feed in a Hertig apparatus.

Furthermore it appears that invasion of the anterior station is necessary to alter the feeding behaviour of infected flies (Smith et al., 1940; Beach et al., 1985). The latter authors found that flies with midgut only infections fed normally. This hardly fits in with the theory that transmission of *Leishmania* is analogous to the transmission of plague (Shortt et al., 1936; Shortt and Swaminath, 1928; Smith et al., 1940), where blockage of the proventriculus of the flea vector causes it to make repeated efforts to obtain blood and thereby regurgitate plague organisms into the wound (Bacot and Martin, 1914).

It appears from the work of Sacks and Perkins (1984, 1985) that were midgut forms readily transmissible to the vertebrate host then there would be no necessity for further development in the vector, which undoubtedly occurs (Killick-Kendrick, 1979). Killick-Kendrick (loc. cit.) has presented the strongest arguments to support the view that the transmission of *Leishmania* by bite is accomplished by the transfer of small free-swimming promastigotes from the fascicle of the fly into the tissues of the vertebrate host (Adler and Theodor, 1931, 1934, 1957). However, due to the occasional transmission of *Leishmania* in laboratory experiments in the apparent absence of proboscis forms (Lainson et al., 1977; Killick-Kendrick et al., 1985b), the impression that transmission can occur when parasites are regurgitated from other regions of the foregut has persisted (Killick-Kendrick, 1979).

Lainson et al. (loc. cit.) achieved transmission of *L. chagasi* to hamsters by the bite of *Lutzomyia longipalpis* from day 7 post-infection onwards. Although no proboscis infections were found by dissection until day 14, free-swimming promastigotes were observed in the pharynx of one fly 7 days after infection.

Any impairment of the feeding ability of an infected fly caused by the occlusion of the pharynx by parasites would increase the possibility of regurgitation of blood, together with parasites from the foregut. Thus although passive transfer of infective forms from the proboscis into the skin of the host is likely to be the normal mode of transmission (Killick-Kendrick, 1979), active expulsion of infective parasites from other regions of the foregut is a possibility.

It has been demonstrated that forms from the cibarium and pharynx (Adler and Theodor, 1957) and from the midgut (Sacks and Perkins, 1984, 1985) are infective for the vertebrate host when inoculated in large numbers. Promastigotes from the proboscis of the fly on the other hand, are likely to be inoculated in very low numbers. The ability of these forms to survive in the host is therefore of paramount importance. Thus the production of a morphologically distinct form, seen to arise initially in the thoracic midgut (*L. infantum* in *P. perniciosus*: Adler and Theodor, 1931) or the pharynx (*L. infantum* in *P. ariasi*: Killick-Kendrick, 1979; *L. chagasi* in *Lutzomyia longipalpis*: Lainson et al., 1977), which subsequently migrates to the proboscis, may represent an adaptation to a form more capable of surviving the transition to the vertebrate host, in a similar manner to the appearance of metacyclic forms of salivarian trypanosomes in the vector (Baker, 1977).

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