Internal Flows and the Propulsion of Mucus

It appears that the primary difficulty regarding internal flows (and a number of external flows (Jahn *et al.* 1965, Jahn & Hendrix 1969, Winet & Jones 1975) in organs with ciliated epithelia is that the fluid usually is non-Newtonian. This fluid virtually always consists of mucus or some other association of glycoproteins. Such systems are called mucociliary systems. When the concentration of these long-chain polymers in the colloidal system is greater than about 1% (wt/vol), the system invariably displays significant viscoelastic, shear-thinning, or thixotropic effects. At higher concentrations gel particles and eventually gel networks form. At all mucin concentrations up to and including the ones that produce gelation (the network- formation process) liquefaction (gel to sol transformation) will occur under applied stress (see Frey-Wyssling 1952, Eliezer 1974, Litt 1970, Hwang, Litt & Forsman 1969).

The propulsion of mucus in mammalian trachea is one such situation that appears to be dominated by viscoelastic effects. The conventional view is that a blanket of highly viscoelastic mucus lining the airway is propelled by cilia that are surrounded by a much less viscous fluid (serous fluid). The cilia appear to move the blanket by contacting it only during the effective stroke (Cheung & Jahn 1975). Experiments by Sade *et al.* (1970) have indicated that the propulsion of mucus is quite sensitive to the form and state of the mucus, with optimum propulsion occurring when the concentration of glycoprotein is close to that of the sol to gel transformation. Ross & Corrsin (1974) constructed a theoretical two-fluid-layer model (inner serous-fluid layer and outer viscoelastic blanket of mucus) for mucus transport employing an envelope model for the cilia/serous fluid interaction. Their calculations indicate that propulsion is enhanced when the mucus is fairly rigid and when the ciliary tip loci have predominantly horizontal motions. Blake (1975) has also applied his sublayer method to model the interaction of the cilia and the serous fluid (see also Miller 1969 and Barton & Raynor 1967) and the subsequent propulsion of a solid slab representing the mucus blanket; he also gives a qualitative discussion of the effects of the elasticity of the slab.

However, the observation by Cheung & Jahn (1975) of more direct mechanical propulsion of the mucus blanket appears to require a reevaluation of the fluid mechanics of tracheal mucus propulsion. If the cilia penetrate the mucus only during the effective stroke, this provides a much more direct mechanism for mucus propulsion. Furthermore, such a mechanism would not require any particular organization of the metachrony of the cilia, unlike most of the fluid-mechanical models. Indeed, some confirmation of this direct-contact mechanism is provided by the fact that propulsion seems to take place in the absence of organized metachronism (Cheung & Jahn 1975), which is often hard to observe in tracheal cilia. The observations suggest that the cilia attached to each ciliated cell (which are usually interspersed with secretion cells) beat in synchrony but that any relationship between the phase of the cilia on different cells is not readily apparent. It should be noted, however, that the tissue utilized for this study was observed in vitro (i.e. removed from its site in the organism and macerated to create a layer thin enough for observation on a thin slide preparation), and in vivo influences on ciliary motion such as the nervous effect described by Murakami & Takahashi (1975) could hot have been taken into account.

In mucociliary systems where mucus is an incidental component of the propelled object (e.g. the mammalian oviduct in which ova and perhaps spermatozoa are the primary objects of ciliary activity), the role of mucus is not clear. It has long been assumed, for example, that mucus acts as a lubricant for the transport of ova down the isthmus of the oviduct. No quantitative test of this assumption appears to have been conducted in situ. A model system utilized recently for measuring the lubrication effect (Winet 1976) consists of a ciliated spheroid swimming down a mucin-filled tube. Observations of this system indicate not only a lubrication effect for small clearances but also an optimized drag reduction effect at larger

clearances. Although we have concentrated here on tracheal mucus flows, we should mention in closing that there are many other internal flows in ciliated tubes such as the ductus efferentes and the oviduct for which some modification of an infinite-sheet model may suffice (e.g. Blake 1975).

In closing we should emphasize again that, although we have concentrated in this review on the fluid mechanics of cilia and flagella, a complete understanding of the life functions of these biological systems requires much more than fluid mechanics. At the same time, fluid mechanics is an integral component of any quantitative analysis for the contraction processes and indicates where ciliation and flagellation give selective advantages to organisms not only in terms of their ability to propel fluids but also in terms of biosynthesis and concentration. Indeed, the ubiquity of these systems would itself be a worthy study by comparative physiologists.