An asymptotic solution of the Stokes Flow equations for a self-propelling filament is presented. An explicit expression for the propulsive velocity is obtained for the case of an infinite filament undergoing small amplitude sinusoidal motions. The asymptotic solution is then used to obtain drag coefficients to be used in a simpler approximate analysis which can be applied to experimentally observed motions.

Introduction. A study of the hydrodynamics of swimming spermatozoa can provide estimates of the internal forces and bending moments in the flagellum and of the energy dissipated by the flagellum against external forces. This estimate of the energy dissipated can be used to obtain a lower limit to the biochemical energy which must be available in the flagellum. Further, the knowledge of the internal forces and bending moments will help give insight into the nature of the contractile mechanisms of the flagellum (Blum and Lubliner, 1973).

Estimates of the energy dissipated and of the internal bending moments have been obtained previously by a number of investigators (e.g., see, Gray and Hancock, 1955; Carlson, 1959; Brokaw, 1965, 1970; Holwill and Sleigh, 1967; Holwill and Miles, 1971). These investigators used an approximate analysis first introduced by Gray and Hancock in which the viscous loading on an infinitesimal element of the flagellum or filament is described phenomenolo-
gically in terms of normal and tangential drag coefficients $C_N$ and $C_T$ respectively. Hancock's earlier paper (1953) showed that for a vanishingly thin filament, $C_N$ and $C_T$ are constants, independent of the form of the motion of the filament, and that $C_N/C_T = 2$. Although the Gray and Hancock expressions for the propulsive velocity of a filament undergoing sinusoidal swimming motions are valid for motions of arbitrary amplitude, the dependence on the filament thickness is not included. Other investigators (Brokaw, 1966a, 1966b, 1968, 1971; Gray, 1958; Holwill and Burge, 1953; Holwill, 1966; Machin, 1958; and Rikmenspoel, 1965), have considered more realistic planar swimming motions, while Chwang and Wu (1971), Coakley and Holwill (1972), and Schreiner (1971) have extended the analysis to three-dimensional helical tail motions; however, all these papers have the same fundamental hydrodynamic limitations of the original Gray and Hancock formulation.

In a recent experimental study Yun et al. (1974) applied the general two-dimensional analysis of Brokaw (1970) to study the motions of sea urchin, rabbit, and bull spermatozoa. From experimental data on the form of the tail motions, trajectories of the moving spermatozoa were calculated and compared with the experimentally observed trajectories. The agreement between the theoretical and experimental trajectories was satisfactory for sea urchin spermatozoa, but not for the mammalian sperm. These results suggest that the simplified analysis of Gray and Hancock may not be adequate for an analysis of the hydrodynamics of many spermatozoa. The limitations may be both geometric—the restriction to two-dimensional motion—and hydrodynamic—the drag coefficients for the infinitely thin filaments are not adequate to describe the viscous loading on a filament of finite thickness.

In an attempt to extend the range of applicability of the simplified analysis of Gray and Hancock, we present in this paper a vector derivation of the planar analysis which is easily extended to include three-dimensional motions, and we suggest how corrections to the drag coefficients to account for the finite thickness of the filament may be obtained by an extension of the analysis of Cox (1970).

**Equilibrium Analysis.** Much of the earlier work on swimming spermatozoa has assumed that the tail motions could be adequately described by uniform sinusoidal or helical motion. However, the motion of many spermatozoa cannot be described in terms of a simple uniform flagellar motion, for example, the tail motion of an immature rabbit spermatozoon. Analyses of simple non-uniform motions have been presented by Rikmenspoel (1965) and Holwill and Miles (1971), but the first analysis valid for arbitrary planar motions of a finite flagellum is due to Brokaw (1970). We present an alternative derivation of Brokaw's formulation below.