Kinetics of swimming in some smooth-bodied polychaetes

R. B. Clark and Colin O. Hermans*

Department of Zoology, University of Newcastle upon Tyne

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(With 2 plates and 4 figures in the text)

The opheliids Ammotrypane and Armandia have very small parapodia bearing few chaetae, and these are pressed back against the body when the animals swim; the archiannelid Polygordius lacks parapodia and chaetae. All three worms have smooth bodies and swim by retrograde sinusoidal movements in the same way as other long, narrow, smooth-bodied animals, unlike nereidiform polychaetes in which the parapodial beat provides the driving force and the body undulations travel in the same direction as that of locomotion.

The wavelength of the undulations is comparable to the body length of these smooth polychaetes and this generally results in pronounced yaw. The kinetics of swimming are similar to those observed in nematodes and the amphioxus, and these polychaetes have comparable structural and mechanical features. A thick cuticle containing a spiral fibre system and lacking circular body-wall muscles is comparable to the situation in some nematodes, but in these polychaetes transverse muscles antagonize the longitudinal muscles and may allow adjustment of the internal hydrostatic pressure—and hence the stiffness of the body—as in the notochord of amphioxus which has similar swimming characteristics.

Like amphioxus, these polychaetes leave and re-enter the substratum in which they live. The small archiannelid Protodrilus has a similar muscular anatomy to that in Polygordius, but has a thin cuticle without spiral fibres. Protodrilus has not with certainty been observed to swim.

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Introduction

Analysis of the kinetics of swimming in polychaetes has hitherto related to species of Nereis, Platynereis and Nephtys (Gray, 1939; Taylor, 1952; Clark & Tritton, 1970). In these nereidiform worms, the body is thrown into lateral sinusoidal waves that travel forward along the body as the worm swims forward. Superimposed on this motion, the parapodia execute a backwardly-directed stroke as the crest of an undulation reaches them.

In long, slender animals such as eels or snakes which have smooth bodies and swim by sinusoidal waves travelling along the body, the normal component of forces acting on the advancing surface of any part of the body performing this motion provides the driving force, and the tangential component drags. In this case the undulations travel along the

*Present address: Department of Biology, California State College, Sonoma, Rohnert Park, California 94928, U.S.A.
body in the opposite direction to that of locomotion, i.e. from head to tail when the animal is swimming forward. In rough-bodied animals the tangential component of forces acting on the body is large and may be sufficiently great that it drives the animal with the normal component of the forces dragging. The undulations then travel along the body in the same direction as that of locomotion, as in nereidiform polychaetes. In the particular circumstances of the nereids and nephtyids that have been examined, however, the body waves are such that they generate little or no driving force of any kind and propulsion, instead, is by the beat of the parapodia (Clark & Tritton, 1970).

Although nereids and nephtyids might be considered “typical” of errant polychaetes and many polychaetes produce undulatory movements of the body as they swim, not all possess large, laterally directed parapodia. In this paper we examine the kinetics of swimming in some relatively smooth-bodied species: the opheliid Ammotrypane aulogaster Rathke in which the parapodia consist of a finger-like cirrus and a small papilla bearing a few slender chaetae, and the archiannelid Polygordius lacteus Schneider, which lacks parapodia and chaetae altogether. We have also examined in less detail the locomotion of the opheliid Armandia brevis (Moore) and the archiannelid Protodrilus rubropharyngeus Jägersten.

Kinetics of swimming

The locomotor movements of Ammotrypane, Polygordius and Protodrilus have been analysed from ciné records filmed at 16 or 32 frames per second. Ammotrypane often swims spontaneously, but under the conditions of lighting needed for cinematography it sometimes required stimulation before it would swim. Polygordius swam only when stimulated by a fine paint brush or mounted hair and then performed only brief swimming excursions.

Fig. 1. Successive positions of swimming Ammotrypane at $\frac{1}{16}$ sec intervals, taken from ciné film.

In all these worms the lateral waves into which the body is thrown travel from anterior to posterior as the worms swim forward. Despite the presence of parapodia and chaetae in Ammotrypane and Armandia, these opheliids swim like smooth-bodied animals. During swimming the parapodia are folded back along the body which is laterally compressed by contraction of the transverse muscles (see below).
The body of the opheliids (*Ammotrypane*) accommodates no more than one complete body wave and often less (Plate I(a), Fig. 1). The archiannelids (*Polygordius*) throw their bodies into $1\frac{1}{4}$ waves (Plate I(b), Figs 2 and 3). As in other animals in which the wavelength of the undulations is not much different from the body length, lateral forces generated by the swimming motion do not equilibrate along the body throughout the locomotory cycle and this results in pronounced yaw. In *Ammotrypane*, which presents an extreme example, this is manifested as a sharp side-to-side jiggle in each half-cycle (Fig. 1).

In *Polygordius*, though not *Ammotrypane*, the amplitude of the waves often increases markedly towards the posterior end of the body (Fig. 2) and this manoeuvre reduces yaw considerably although it is still about $20^\circ$ on each side of the axis of locomotion. The extreme lateral movement of the posterior end of the body sometimes results in it “overshooting” and at the extreme displacement it exerts a forward thrust on the water, drawing the more anterior part of the body backwards (Fig. 2(b)).

*Ammotrypane*, *Armandia* and *Polygordius* swim for short distances in one plane with the dorsal side uppermost. The epitokes of *Armandia* swim for an extended period by a series of short bursts, making about three undulations in the horizontal plane and then turning on one side or the other to make about three more in the vertical plane. This worm swims
in a very distinctive manner, listing alternately from side to side and gliding every few seconds.

We are not certain that we have observed swimming in *Protodrilus*. When crawling by cilia it is a very mobile, active worm and the body is often thrown into irregular bends and waves. In one filmed sequence a specimen produced a series of more or less regular

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<td>Relative velocity and pitch of locomotory waves in smooth-bodied polychaetes</td>
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<tr>
<th></th>
<th>$V$ mm/sec</th>
<th>$U$ mm/sec</th>
<th>$V/U$</th>
<th>$B$ mm</th>
<th>$\lambda$ mm</th>
<th>$\alpha = \tan^{-1} 12\pi B/\lambda$</th>
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<td>Ammotrypane</td>
<td>47.2</td>
<td>82.6</td>
<td>0.58</td>
<td>3.8</td>
<td>10.0</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>29.9</td>
<td>56.5</td>
<td>0.53</td>
<td>2.6</td>
<td>9.9</td>
<td>60</td>
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<tr>
<td></td>
<td>22.4</td>
<td>44.8</td>
<td>0.50</td>
<td>3.0</td>
<td>17.3</td>
<td>48</td>
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<td>Polygordius</td>
<td>36.5</td>
<td>68.5</td>
<td>0.53</td>
<td>3.7</td>
<td>4.8</td>
<td>78</td>
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<tr>
<td></td>
<td>14.7</td>
<td>20.2</td>
<td>0.73</td>
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<td>3.3</td>
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<td>1.8</td>
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<td>68</td>
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<tr>
<td>Protodrilus</td>
<td>2.00</td>
<td>2.56</td>
<td>0.78</td>
<td>0.2</td>
<td>1.9</td>
<td>33</td>
</tr>
</tbody>
</table>
undulations which travelled backwards along the body (Fig. 3) but it is possible that the worm was not detached from the substratum and that these waves were simply an accompaniment to ciliary creeping. The speed attained in this excursion (2-00 mm/sec, Table I) was no greater than that often observed (up to 2-57 mm/sec) when the same individual was creeping without throwing the body into waves.

Table I shows the velocity of the animal \( (V) \) and the velocity relative to the head \( (U) \), wavelength \( (\lambda) \) and amplitude \( (B) \) of the body undulations in swimming excursions by different specimens of species for which we have measurements. In \textit{Ammotrypane} the measured amplitude discounts the lateral movement attributable to yaw. In \textit{Polycorpus} the two velocities have been averaged over several undulatory cycles in each swimming excursion and the wavelength and amplitude are those of the middle two-thirds of the body,

![Diagram](image)

**Fig. 3.** Successive positions at \( \frac{1}{10} \) sec intervals of \textit{Protodrilus}, \( X \) marks the backward transmission of undulations along the body.

i.e. neglecting if necessary the relatively small amplitude at the anterior end and the very large amplitude at the posterior end of the body. This gives approximately the same value of the amplitude as averaging the lateral displacements of the anterior, middle and posterior parts of the body, which is the treatment adopted by Taylor (1952) in arriving at a representative figure for a swimming grass snake \textit{Natrix}, another species in which the body waves increase in amplitude towards the posterior end.

Average values for \textit{Ammotrypane} and \textit{Polycorpus}, and the dubious record for \textit{Protodrilus}, are plotted in Fig. 4 on Taylor’s (1952) diagram relating the pitch of the body waves \( (\alpha = \tan^{-1} \frac{2\pi B}{\lambda}) \) and the ratio of the velocities \( (\frac{V}{U}) \). Two boundaries are indicated in the diagram. Line A marks the condition for maximum speed for a given energy output calculated by Taylor (1952, fig. 4) and line B is the limit above which all parts of the body move forward during swimming. Between this line and the \( x \)-axis, parts of the body, performing a sinusoidal motion, move in a direction opposite that of locomotion at some stage in the cycle and this is a region of ineffective swimming (Clark & Tritton, 1970).
In all three species, the form of the body waves is such that they are capable of producing effective locomotory forces (i.e. the average points lie above line B). The average values for *Polygordius* and *Ammotrypane*, far to the right of line A denoting theoretical maximum velocity for a given energy output, indicate that they bend their bodies a good deal more than would be expected were the most economical movements being made. *Polygordius* in practice swims less efficiently than the average results suggest because, as we have observed, the exaggerated sweep of the posterior end of the body which is far removed from the

![Graph showing relationship between velocity of swimming (V) and velocity of locomotory waves along the body (U) to pitch of locomotory waves α (= tan⁻¹ 2πB/λ where B is amplitude, λ wavelength). Line A is the condition for theoretical maximum speed for a given energy output (Taylor, 1952), line B is the lower limit for efficient swimming (Clark & Tritton, 1970). Values for *Natrix*, *Hirudo*, ceratopogonid from Taylor (1952), *Branchiostoma* from Webb (1973), *Panagrellus*, *Haemonchus*, *Turbatrix* from Gray & Lissmann (1964).](image)

theoretically sinusoidal wave-form of the body and is neglected in these calculations, causes the whole body to move backwards for a brief part of each cycle.

The very low value of α, coupled with high \( \frac{V}{U} \) observed in *Protochilus* suggest that if it indeed swims by body undulations it does so with unparalleled efficiency and is comparable to a vertebrate. This is incredible and provides an additional reason for suspecting that the undulations were an accompaniment to ciliary creeping and had no connexion with locomotion.

The corresponding value for *Branchiostoma* has been calculated from Webb’s (1973) fig. 1 and is indicated in Fig. 4; it is close to the average values for *Ammotrypane* and *Polygordius*. The significance of this correspondence is discussed below. The figure also includes the observed values for a swimming snake, *Natrix*, the leech *Hirudo* and a ceratopogonid larva recorded by Taylor (1952) and for the nematodes *Haemonchus*, *Turbatrix* and *Panagrellus* (Gray & Lissman, 1964; Crofton, 1971).
Structural correlates

The sub-family Polyophthalminae, to which Armandia and Ammotrypane belong, represents an extreme among the Opheliidae, the three sub-families of which live in different habitats from one-another, use different locomotory techniques, and show a progressive change in the organization of the musculature.

The Travisiinae (Travisia is the only genus) are short, fat and grub-like. They live in fine, muddy benthic deposits and burrow by peristaltic locomotory waves which travel the
Plate II. (a) Transverse section through body of *Travisia*. (b) Transverse section through body of *Armandia*. (c) Cuticle stripped from *Ammotrypane* showing fibrillar structure. (d) Torn edge of stripped cuticle of *Ammotrypane* showing frayed out fibres.
whole length of the body. The circular body-wall muscles form a complete muscle coat and the weakly developed longitudinal muscles an almost complete coat, and both exist in all parts of the body. Slender transverse muscles suspend the ventral nerve cord in the coelom, free of the body wall (Plate II(a)).

The body of the Opheliinae (Ophelia, Euzonus) consists of an anterior “thorax” and a narrower, posterior “abdomen”. The former has complete circular and longitudinal body-wall muscles, but no transverse muscles. The abdomen has longitudinal and transverse muscles but no circular muscles. Members of this family live in coarse intertidal sands and burrow by peristaltic movements of the “thorax” in the same manner as Travisia, but the posterior “abdomen” is dragged along passively.

The Polyophthalminae (Polyophthalmus, Ammotrypane, Armandia) have no circular body-wall muscles at all. The transverse muscles are strongly developed and run from the lateral body-wall between the dorsal and ventral muscle blocks to the mid-ventral line (Plate II(b)). Their insertion is marked externally by pronounced grooves, giving the body a characteristic unequal trilobed cross-section which is also a feature of the “abdomen” of the Opheliinae where the organization of the musculature is similar. The Polyophthalminae inhabit benthic sediments which presumably they leave and re-enter periodically. Polyophthalmus and Armandia become pelagic as sexually mature epitokes (Fage & Legendre, 1927; Hermans, 1964). Swimming by retrograde undulatory movements is the only form of locomotion that has been observed in members of this sub-family.

The loss of circular body-wall muscles is not unknown in polychaetes and circular muscles are totally lacking in nematodes and nematomorphs also. Various systems are employed in such worms to provide restoring forces for the longitudinal muscles. In Nephtys, dorso-ventral muscles in the basal parts of the parapodia are the principal antagonists of the longitudinal muscles (Clark & Clark, 1960); in Ascaris it is the high turgor pressure in the fluid-filled pseudocoel coupled with the anisotropic cuticle (Harris & Crofton, 1957). In Ammotrypane and Armandia it is likely to be the transverse muscles, although experimental proof of this is lacking.

From the geometry of these ophieliids it is evident that contraction of the transverse muscles reduces the cross-sectional area of the body by exaggerating the lateral grooves and by lateral flattening. This increases turgor pressure and may be compensated by extension of the longitudinal muscles. The greatest change of length of stationary Ammotrypane observed in the ciné records was from a minimum of 14.7 mm (width 1.2 mm) to maxima of 20.8 and 21.1 mm (widths 1.0 and 0.9 mm, respectively). The same worm swam fully extended with an average length of 21.9 mm.

The longitudinal muscles of ophieliids are as well developed as those of nereids. The dorsal blocks almost meet the ventral blocks at the side in the intersegmental parts of the body and here account for nearly 60% of the cross-sectional area (Table II). The dorsal blocks do not extend quite so far in the neighbourhood of the parapodia but even so, the longitudinal musculature here accounts for more than 38% of the cross-section of the body.

Ammotrypane has a superficial resemblance to some nematodes in its smooth body and lack of circular muscles, and this is enhanced by a multi-layered fibre system in the ophieliid cuticle (Storch & Welsch, 1970). In relaxed, fixed Armandia and Ammotrypane, the orientation of the fibres to the longitudinal axis of the worm is 55–65°, but if the cuticle of Ammotrypane is stripped from the underlying epidermis, the orientation of the fibres may be varied between 35° and 70° to the longitudinal axis, depending on tensions applied to it.
Table II
Cross-sectional area of muscles as percentage of cross-sectional area of body
(excluding parapodia)

<table>
<thead>
<tr>
<th></th>
<th>n*</th>
<th>Dorsal</th>
<th>Ventral</th>
<th>D/V</th>
<th>Total</th>
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<tbody>
<tr>
<td>Ammotrypane</td>
<td>max</td>
<td>8</td>
<td>47·2</td>
<td>12·6</td>
<td>3·75</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>8</td>
<td>25·6</td>
<td>12·6</td>
<td>2·04</td>
</tr>
<tr>
<td>Polygordius</td>
<td></td>
<td>7</td>
<td>15·0</td>
<td>14·4</td>
<td>1·05</td>
</tr>
<tr>
<td>Perinereis</td>
<td></td>
<td>7</td>
<td>34·0</td>
<td>22·2</td>
<td>1·54</td>
</tr>
</tbody>
</table>

* Number of determinations.

We have not examined the cuticular structure in detail and can add nothing material to the description of Storch & Welsch (1970), but the fibres appear to be loosely embedded in the cuticular matrix and insecurely or not at all attached to one-another where they cross, for they fray out readily from torn edges of the stripped cuticle (Plate II(c), (d)).

The lack of circular body-wall muscles, the development of transverse muscles and the existence of a thick cuticle with a geodesic fibre system are also features of Polygordius (Fraiport, 1887) and the superficial resemblance of this worm to nematodes is sufficiently great for the view to have been advanced at one time that it might be related to gordioidean nematomorphs (Schneider, 1868). Its longitudinal muscles are not as well developed as those of Ammotrypane and represent only 30% of the cross-sectional area of the body (Table II). Protodrilus is similar to Polygordius in lacking circular muscles and having transverse muscles (Pierantoni, 1908) but in this worm the cuticle is thin and no fibre system has been described in it.

While not representing a structural modification, the configuration of the body of swimming epitokal Armandia differs from that of any other polychaete and may account for its curious rotational swimming motion. The parapodia of the last five segments instead of being directed backwards are turned posteriorly and downwards towards the ventral midline. At the same time the longitudinal muscles of these segments are differentially contracted, shortening the dorsal part of them and the anal funnel points dorsally at about 45° from the longitudinal axis of the worm. The chaetae of the last five segments fan out directly to the rear. Mucus secreted by the epidermis and which normally forms a very thin tube around the worm covers the posterior chaetae and they then constitute a structure which is remarkably like a heterocercal caudal fin of a fish (Plate I(c)). This modification occurs only in sexually mature worms which become pelagic. Immature worms do not adopt this posture and although they can be excited to swim, appear to do so more slowly.

Discussion

In both swimming characteristics and certain structural features, the Polyophthalminae and Polygordius bear some resemblance to swimming nematodes and Branchiostoma. All long, slender animals that swim by undulations of the body require for the success of this type of locomotion a means of resisting axial compressive forces (Gray, 1953). In chordates this compressive member is the notochord or vertebral column, but in worms it can only be provided by turgor of the whole body. The way it is generated and maintained varies in
detail and depends on the configuration and mechanical properties of the musculature and other structural elements in the body wall.

The nematode *Ascaris* for example, has a high internal hydrostatic pressure at all times and to contain it there is a thick cuticle containing several layers of collagenous fibres arranged in such a way that the muscular-fluid-cuticular system is very resistant to shortening: muscle contraction increases turgor rather than reducing the length of the animal (Harris & Crofton, 1957). This nematode system represents a special case of the musculo-fibrous system analysed by Clark & Cowey (1958) for nemerteans and turbellarians. Both these worms lack a cuticle and the fibre system in question is that of the sub-epidermal basement membrane, but the constraints it places on changes of shape are the same if it is in the cuticle, as it is in *Ascaris*, many polychaetes and most other worms.

Like the fibres in the nemertean basement membrane and in the cuticle of other worms, the cuticular fibres of polychaetes are collagenous (Kimura, 1971a, b; Michel, 1972) and are virtually inextensible. Following the argument of Clark & Cowey (1958), for a cuticle of this nature to permit changes of the length or girth of the animal that involves extension or compression of the epidermis, the fibres must be arranged obliquely to the longitudinal axis and their inclination to it change as the worm changes in length. If at greatest elongation or contraction, the animal has a circular cross-section, it is the fibre system which prevents further change of length.

This may be true under some circumstances in the archiannelids, but the cross-sectional shape of *Ammotrypane* and *Armandia* is complicated by the presence of deep lateral grooves and the worms are never circular in cross-section. Limits to changes of length which might be imposed by the cuticular fibre system are therefore never reached. Although the worms swim fully extended, turgor is maintained by the differential contraction of the antagonistic transverse and longitudinal muscles.

The maintenance of turgor usually demands the maintenance of body volume, and the hydrostatic skeleton of most animals is effectively sealed. This is not so in spawning *Armandia*. The gut is extensively histolysed when the worms are sexually mature and becomes confluent with the coelom. The epitokes leave the benthos, become pelagic and swim throughout spawning. As the eggs are shed through the genital openings on the 10–13th segments, the worms would lose volume and be unable to swim but for the peristalsis of the anal funnel which pumps water into the gut and thence into the coelom (Hermans, 1964).

The relationship between the pitch of the locomotory waves and the ratio of the speed of swimming to the relative velocity of the undulations is shown in Fig. 4. In view of the greatly simplified assumptions and approximations in the analysis that Taylor (1952) was obliged to make, close agreement between theory and the actual performance of animals cannot be expected. Effective swimming becomes impossible and, indeed Taylor's theoretical analysis does not apply at small values of $\frac{V}{U}$. The nematodes *Haemonchus*, *Paragrellus* and *Turbatrix* are all near this limit, unlike *Ammotrypane* and *Polygordius* which have high values of $\frac{V}{U}$. Their swimming characteristics in fact have more in common with the chordate *Branchiostoma* than with any other invertebrates that have yet been examined.

In addition to similarities in the kinetics of swimming between these polychaetes and *Branchiostoma*, there are mechanical parallels which may be of some significance. The axial compression strut in *Branchiostoma* is the notochord consisting of transverse paramyosin muscular plates in a thick connective tissue sheath. The contained fluid pressure and hence
the stiffness of the notochord can be changed, and Guthrie & Banks (1970) have suggested that an increase in stiffness is important for fast swimming. It is also possible that differential changes of stiffness may be made along the notochord and Webb (1973) suggests that changes of stiffness at the anterior and posterior ends, depending on whether the animal swims head- or tail-first, are important in penetrating the substratum.

While archiannelids retain intersegmental septa, the coelom of Ammotrypane and Armandia is not subdivided (save for a pair of anterior septa which are probably related to proboscis eversion). It is unlikely that differences of turgor and hence stiffness could be generated in different parts of the body of the opheliids, but the transverse muscles provide a mechanism whereby the overall stiffness of the animal could be adjusted.

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