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FUNCTIONAL MORPHOLOGY AND DEVELOPMENT OF SEGMENTAL INVERSION IN SABELLID POLYCHAETES

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Sabellid polychaetes have exceptional capacities for repeated reconstitution of missing parts anteriorly and posteriorly from any level of the body (Berrill, 1931), even from single segments (Okada, 1934). Although the morphogenetic processes involved are presumably under ultimate genetic control, the developmental processes, as such, remain elusive. The organism, however, is both a present and an historical entity, consisting of primary organizational (phyletic) features and superimposed adaptive modifications and specializations. A clear picture of the phenotype is necessary to the unraveling and understanding of the formative processes. The following account, mainly of *Branchiomma nigromaculata* (Baird) is made with this in mind. Nevertheless, any living organism has its own intrinsic interest as a going concern.

Sabellids live in a mucus-lined tube, with the prostomial crown of tentacles usually extended beyond the distal end of the tube. This complex food-collecting apparatus has been well described by Nicol (1931) for *Sabella pavonina*. Her observations are confirmed for *Branchiomma nigromaculata*, although they are peripheral to the main interest here, which concerns the significance of parapodial inversion of thoracic, compared with abdominal, segments. In sabellids and serpulids the segmental parapodia typically bear both a bristle bundle (setae) and a torus, or ridge with a row of hooks (uncini), which serve for locomotion and anchorage within the tube. The setae and uncini are respectively dorsal and ventral in anterior, thoracic segments, but are respectively ventral and dorsal in all abdominal segments. Why this is so, is the problem, with regard to both development and function.

In the sabellid long known as *Branchiomma vesiculosum* (Montagu), but now commonly referred to as *Megalomma vesiculosum*, the postlarval stage, according to Wilson (1936), elongates by addition of new segments posteriorly that are already thoracic in character, until the full number of eight thoracic segments have been formed. Only then are abdominal-type segments added. He concluded that this procedure is typical of sabellid development, in contrast to serpulid development, where eggs are typically small (about 80 microns in diameter) and form larvae with initially only three thoracic segments, additional thoracic segments being formed later by conversion of abdominal segments. A comparative study of

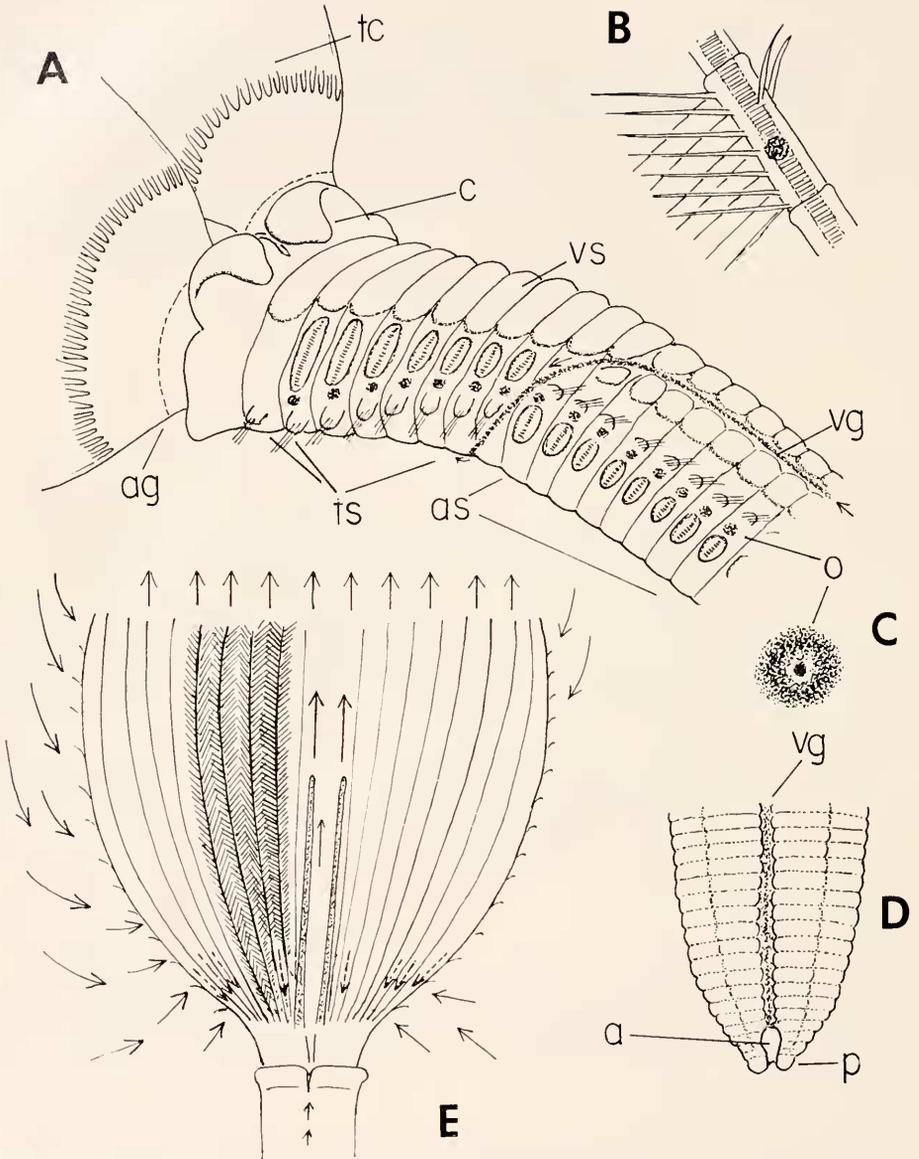


FIGURE 1. External structure of *Branchiomma nigromaculata*: A, anterior region in ventrolateral view showing base of crown of tentacles, collar, thoracic segments, and anterior abdominal segments; the ciliated ventral groove is seen to pass to the dorsal (lower) surface at the junction of thorax and abdomen; uncinigerous tori and setigerous bundles of abdominal segments are inverted compared to those of thoracic segments; B, a segment of a tentacle, showing internal skeleton of choroidal tissue, seven pairs of ciliated filaments, a pair of external processes and one of a pair of ocelli; C, ocellus of segment at same magnification as that of tentacle, showing central cavity; D, posterior region of worm showing ventral groove and pygidium; and E, bilateral crown of tentacles, with pair of palps, with arrows indicating direc-

several sabellid species, however, shows that the developmental procedure varies considerably and can be correlated with the size of the egg.

MATERIALS AND METHODS

A somewhat confusing situation persists concerning the names employed for two well known sabellid genera. According to Johannson (1927) the generic name *Branchiomma* should be used for species having a series of regularly spaced ocelli along each tentacle, or radiole, and that *Megalomma* be substituted for species with a single, large, subterminal ocellus on each radiole. This usage has become widely, but not universally, accepted; for example, it is adopted in Hartman's (1959) *Catalogue of the polychaetes of the world* but not in the 1957 edition of the *Plymouth marine fauna*. The Johannson nomenclature is used here. Thus, species of *Dasychone* become species of *Branchiomma*. Of the species described here, *Branchiomma nigromaculata* (Baird), an unnamed dwarf species, and *Potamethus clongatus* (Treadwell), were studied at the University of Hawaii Marine Institute, Kaneohe Bay, Oahu, Hawaii; while *Potamilla neglecta* (Sars) and *Fabricia sabella* (Ehrenberg) were studied at Boothbay Harbor, Maine. The late Dr. Olga Hartman confirmed the species identifications.

Branchiomma nigromaculata is notable for the ability of individuals removed from their tubes to secrete a new tube immediately, attach to any available surface, and to do so repeatedly. The whole worm becomes encased in a transparent mucoid tube open distally and by a small pore near the posterior end. The activities of the worm within its tube become clearly observable, which is rarely the case in other species. Developing embryos were obtained in this species and in others from natural spawnings, and glass slides with newly settled postlarvae were suspended in sea water in sheltered locations, where rapid growth occurred.

RESULTS

Form and function

An obvious feature in *Branchiomma nigromaculata* is a segmental series of dark pigment patches on both sides of the body, each patch overlying an ocellus. The patch lies between the medial end of the torus and bristle bundles in thoracic and abdominal segments alike, forming a single series (Figs. 1A, 3A). This may be taken as a stable point of reference for all segments. In other species, pigment patches alone may be present, e.g., in *Sabella pavonina*.

A deep, ciliated, midventral groove, dividing a prominent ventral glandular shield into a right and left part in each abdominal segment, extends forward to the thoracico-abdominal junction. From there it passes up the right side of the body to the dorsal surface, and there continues in a less well-defined form to the anterior end of the worm (Fig. 1A). The ventral shield continues forward from the junction as an undivided glandular mass in each segment. The groove is strongly ciliated and carries feces from the anus to a point of discharge dorsal to the mouth. The turn-over of the groove and the parapodial inversion give the illusion that

tion of currents produced by ciliary activity. Abbreviations are: a, anus; ag, autotomy groove; as, abdominal segments; c, collar; o, ocellus; p, pygidium; ts, thoracic segments; vg, ventral groove; and vs, ventral glandular shield.

the worm is twisted through 180 degrees at the junction between abdomen and thorax.

The tentacular crown of sabellids is light-sensitive, with receptors commonly spaced along each tentacle radiole. In *Branchiomma nigromaculata* they are multicellular, multilenticular ocelli, with up to 29 per tentacle in the largest individual, with tentacle number up to 40 in each half crown. Any rapid change in light intensity, as produced by a moving hand or the approach of a predator, induces the "shadow reflex" resulting in instant withdrawal within the tube. The action is mediated by a pair of giant axons originating in the dorsal cerebral ganglion and extending along the ventral nerve cord the whole length of the body. (In the largest sabellids, namely, *Myricola infundibulum*, *Eudistylia vancouverensis*, and *Sabellastarte magnifica*, in fact, when a worm is removed naked from its tube and held in a closed hand out of water, sudden contractions are felt as definite thuds.) The contraction of the body is complete, every segment being shortened antero-posteriorly to maximum degree and at the same time widened to maximum extent. The shortening and widening, however, affects the posterior portion of the body first, so that the body tends to lodge in the tube posteriorly and to be drawn there as a whole (Fig. 2A, F).

As seen within the transparent tube of *Branchiomma nigromaculata*, such contractions are followed by a regular cycle of further action. After a variable period of contraction, the body slowly extends, the anterior end moving forward to take up the slack without much change in the position of the posterior region that previously served as an anchor (Fig. 2B). During the process of re-emergence of the head, viewed from the open-end of the tube, the crown may be seen to undergo one or two full rotations. When fully extended, with crown protruded and collar flush with the distal margin of the tube, the thorax itself becomes anchored, with the remainder of the body now hanging free (Fig. 2C).

Almost immediately following, a variable but small number of peristaltic waves, commencing at the anterior region of abdominal segments, pass down the length of the worm, without any accompanying change in body length as a whole (Fig. 2D). At first the waves pass about halfway along the worm. Successive waves pass further and further, until the whole worm is involved. They serve for irrigation of the tube contents, for at least some respiration, and, in this species, there is some movement of water out through the posterior tube aperture. After the irrigation waves cease, the whole body becomes somewhat drawn up, and almost the entire lateral surfaces become applied to the inner wall of the tube (Fig. 2E).

As already noted, parapodia in sabellids each consist of a bulb carrying a bundle of setae, and a more elongate torus bearing a row of hooks (Fig. 1A, 3A). In *Branchiomma nigromaculata* their operation within a newly formed tube is readily seen. The setigerous bundles serve for "walking" forward and backward, and the uncingerous tori exclusively for holding position, either for the whole worm or a portion thereof.

In all sabellids examined, large and small, of both subfamilies, as well as in serpulids, the hooks throughout the body all point forward, in thoracic and abdominal segments alike. Individually, hooks are minute and ineffective. In aggregate their holding effect is considerable. In the largest species already mentioned

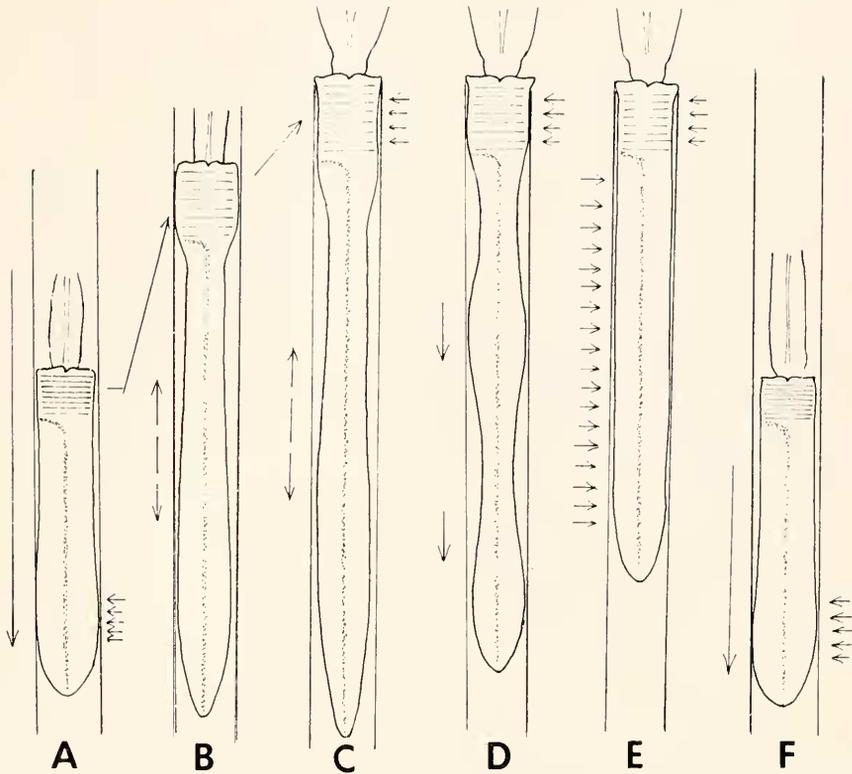


FIGURE 2. Cycle of movement of body of *Branchiomma nigromaculata* within the tube, seen from ventral side (points of anchorage indicated by horizontal arrows; direction of movement by vertical arrows): A, individual fully withdrawn, anchored posteriorly; B, body extending from contracted state; C, body fully extended, and anchored in thoracic region; D, fully extended with peristaltic irrigation waves passing posteriorly along the body from the anterior end of the abdominal region; E, body in full anchored state during stable filter-feeding, *i.e.*, anchored throughout both thorax and abdomen; and F, fully contracted state, induced by external disturbance or shadow initiating giant axon reflex.

they may amount to several thousand. In *Branchiomma nigromaculata* and many other species, the hook has a main fang with several smaller teeth above it, all directed forward (Fig. 3C). The main fang especially is capable of catching in the mucoid inner lining of the tube. In the resting, extended state the parapodia are pressed against the wall of the tube, and the tori with their rows of hooks become engaged and resist any tendency of the worm to slip forward.

During the resting, feeding state, firm anchorage of the anterior thoracic end of the worm, with collar flush with the rim of the tube, is required. Relating to this, the tori of the thoracic segments are longer more anteriorly, with correspondingly larger numbers of hooks. Nevertheless, the capacity of the hooks alone to securely anchor the body, or a part thereof, is limited.

Thoracic setal bulbs of most sabellid species carry two series of setae of somewhat different character. In *Branchiomma nigromaculata* an upper series has

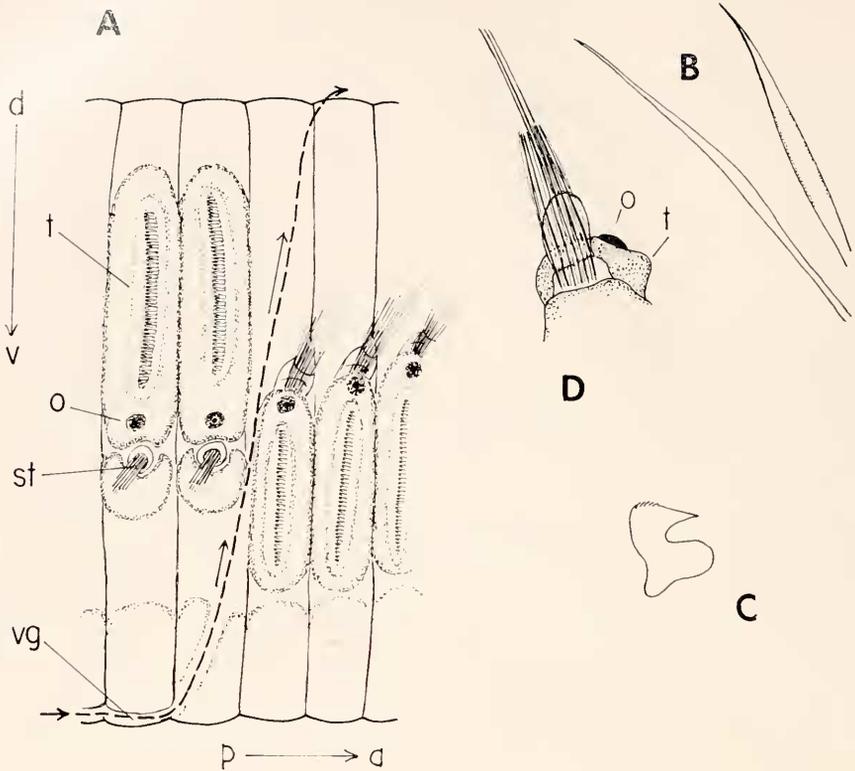


FIGURE 3. Parapodial structure and orientation in thoracic and abdominal segments of *Branchiomma nigromaculata*: A, abdominal segments with ventral setigerous bundle in mid-lateral region, and torus with hook row and ocellus in dorso-lateral region; and thoracic segments with ventro-lateral torus with hook row and ocellus, and setigerous bundle directed dorsally and forward; B, setae, typical of thoracic segments; C, uncinus, typical of both abdominal and thoracic segments, with hook pointing anteriorly; and D, abdominal para-podium in ventral view showing setigerous bundle consisting of fleshy lobe with about a dozen regular setae and several relatively long setae emerging through it, together with ventral end of torus bearing the segmental ocellus (in silhouette) projecting directly outward from mid-lateral region of segment. Abbreviations are: d-v dorsoventral; o, ocellus; p-a, antero-posterior axis, anterior to the right; st, setigerous bundle; t, torus; and vg, ventral groove.

short, tapering winged tips and more elongated striated shafts, while a lower series has broader striated wings, serrated at the edges (Fig. 3B). In abdominal segments the setae occur in small tufts, the upper setae with much elongated tips and the lower with distinct wings. In other species the differences may be greater, with one kind of seta more slender and the other more paddle-like below the fine tip. Such are the actual instruments employed to maneuver the body forward or backward or to rotate the anterior end. In operation the more or less wingless, slender setae may penetrate the mucoid lining of the tube to a considerable extent, while the winged setae penetrate only to the extent of the tip beyond the wings.

Muscles inserting on the setal bulbs move the base of the bundles and, thus,

cause the setae to exert leverage against the tube lining in which they impinge, as in the use of oars. As a rule, and *Branchiomma nigromaculata* is no exception, the thoracic bundles with their associated segmental muscles are somewhat larger and more powerful than the abdominal bundles, although this difference is offset by the relatively small number of thoracic segments. The thoracic setigerous bundles function primarily in walking, or levering the body forward. When at rest, the thoracic bundles point dorsally, outward and slightly forward from the segmental body wall (Fig. 3A). When the parapodial and segmental longitudinal muscles contract, the setae are protruded and engage the lining of the tube, and an effective backward stroke is produced, moving the segment forward. The parapodium then swings forward to the original position and the setae are released.

A stepping wave of contraction of the segmental longitudinal muscles passes down the whole worm, the two sides of the worm being out of phase with one another. This results in a spiral advance of the worm and a twisting of the anterior, thoracic region relative to the abdominal region which is free to unwind. The forward motion of the worm resulting from the action of the thoracic segments is resisted to some extent by the forward-pointing hooks, which are seen to catch in the tube lining and to be pulled free. The thoracic setae also serve to anchor against movement of the body posteriorly, particularly when the worm is not in active movement, for when anchored anteriorly and hanging freely in the tube, it cannot be pulled back through the posterior end of a cut tube without pulling the worm apart, usually. On the other hand, stimulation of the posterior end of a worm causes emergence from the front end of the tube, but rarely farther than the posterior end of the thorax.

Abdominal setigerous bundles are employed for walking backward. Abdominal bundles move in continuous series with the thoracic bundles but on close scrutiny do not appear to do any effective work with regard to forward progression. At rest, the setae extend outward, ventrally, and backward from the segmental wall (Fig. 3A). In walking the body, each setigerous bundle engages in the tube lining and strokes forward, causing the segment to move backward. At the end of the stroke the setae are disengaged. The cycle is similar to that of thoracic setigerous bundles but is concerned with differently oriented structures. In *Branchiomma nigromaculata* between fifty and a hundred abdominal segments are thus involved. The overall activity causes the worm to migrate to the posterior end of the tube, which is seen in circumstances that induce withdrawal without triggering the shadow reflex. In some species, such as *Sabella pavonina*, which may have tubes imbedded in mud to a depth of two feet, with up to one foot of tube standing above the mud, descent to the lower end of the tube is necessary at times in order to dredge up tube-building material. However, the much more vital function of the reversed action of the abdominal setae appears to be the capacity of the abdominal setigerous bundles, individually and collectively, to resist strongly any forward pull exerted on the body, greatly augmenting the combined effect of the forward-pointing hooks of all the segments.

Segmental transformation

The eggs of *Branchiomma nigromaculata* are mostly from 130 to 135 microns in diameter and appear well-packed with yolk granules. Unlike the trochophore

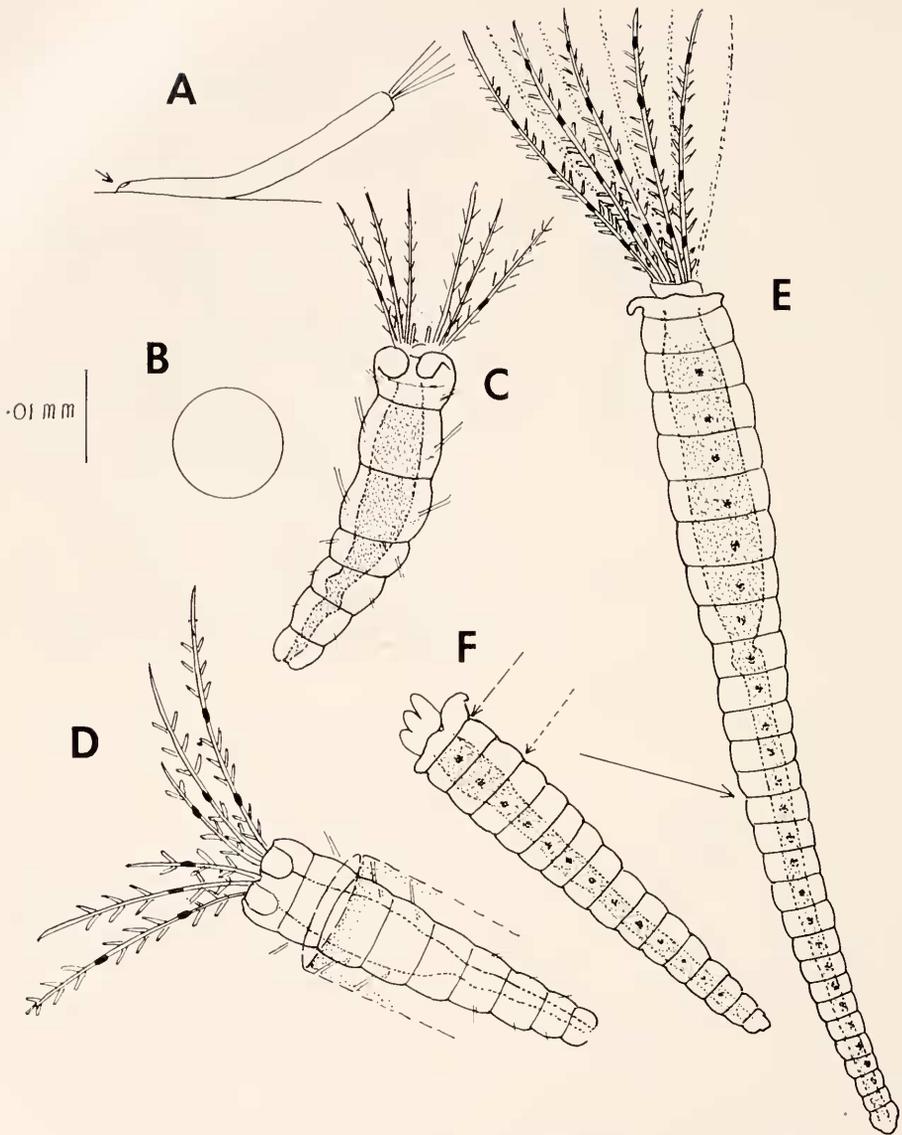


FIGURE 4. Postlarval development of *Branchiomma nigromaculata* (parapodial setae and hooks are not shown in E and F): A, attached juvenile, 7-10 days, showing characteristic elevation of anterior part of the tube, and posterior aperture; B, egg, at same magnification as juvenile stages; C, initial stage (first week) exhibiting bilobed collar (ventral) with 3 thoracic and 3 abdominal segments; D, somewhat older juvenile (10 days) with 4 thoracic and 3 abdominal segments; E, fully formed juvenile, from side, with 8 thoracic and 19 abdominal segments; and F, abdominal piece cut from stage in E, after five days, showing a regeneration of new tentacles, collar, and beginning of thoracic transformation of two most anterior abdominal segments. The intestine is indicated by dotted lines and the wide thoracic region is seen to be coextensive with the thorax. Pigment patches in E and F represent ocelli in lateral body

larvae of serpulids, which develop from an egg of about 80 microns in diameter, the free-swimming sabellid trochophore stage does not feed, and a functional planktonic phase is brief. Newly-settled metamorphosed larvae immediately secrete a delicate tube of mucus, which has a small posterior opening and an elevated anterior part (Fig. 4A). The completely metamorphosed and functioning postlarval stage exhibits three tentacular radioles on each side, with lateral filaments (pinnules) and, on two tentacles, a single eye spot (Fig. 4C). At this stage the body consists of the collar, three thoracic segments, three or four abdominal segments, and the terminal pygidium (Fig. 4C). Following the addition of one or two more abdominal segments, the foremost abdominal segment loses its setae and hooks (Fig. 4D), and later acquires new setae and hooks in the inverse or thoracic disposition. This procedure is repeated until altogether eight thoracic segments are present, five of which have resulted from successive transformations of the most anterior abdominal segments (Fig. 4E).

During this transformative period of juvenile development, the number of tentacles on each side, in each half crown, increases from three to five, each tentacle now possessing four ocelli. An ocellus also appears on the body wall of each side of each segment, located between the setae and hooks in thoracic and abdominal segments alike (Fig. 4E). It is, however, absent on the segment adjoining the collar.

Also evident, in such small transparent juvenile stages, is that the thoracic gut extends posteriorly coexistent with the posterior extension of the thoracic parapodial, segmental character (Fig. 4C, D, E). In the case of the individual shown in Fig. 4E, the posterior abdominal region consisted of fifteen abdominal segments, which, when cut off, regenerated a new head consisting of crown and collar (Fig. 4F), with evidence (enlargement of the gut) of the two anterior segments transforming into thorax. The anterior regenerative-reorganizing capacity typical of sabellids is accordingly present at a somewhat surprisingly early stage of growth.

The progressive conformation of thoracic gut and parapodial character is more dramatically shown in Figure 5. In this species, at least, gut transformation appears to precede conversion of abdominal to thoracic parapodial type, inasmuch as full enlargement of the gut appears posteriorly, before thoracic setae and hooks are visible in the respective segments. Parapodial transformation is already underway in such segments, however, as indicated by the loss of the previously present abdominal parapodial structure (Table 1). The question whether thoracic gut extension truly precedes and perhaps induces parapodial conversion cannot, therefore, be determined from these observations. What is evident is the successive manner of transformation of segments along the anteroposterior axis. Moreover, this developmental procedure in *Branchiomma nigromaculata*, which is very similar to that reported for serpulids, and different from that of *Megalomma vesiculosum*, suggests that some cause other than familial inheritance is responsible for the differences.

In addition to the relatively detailed accounts of the contrasting postlarval

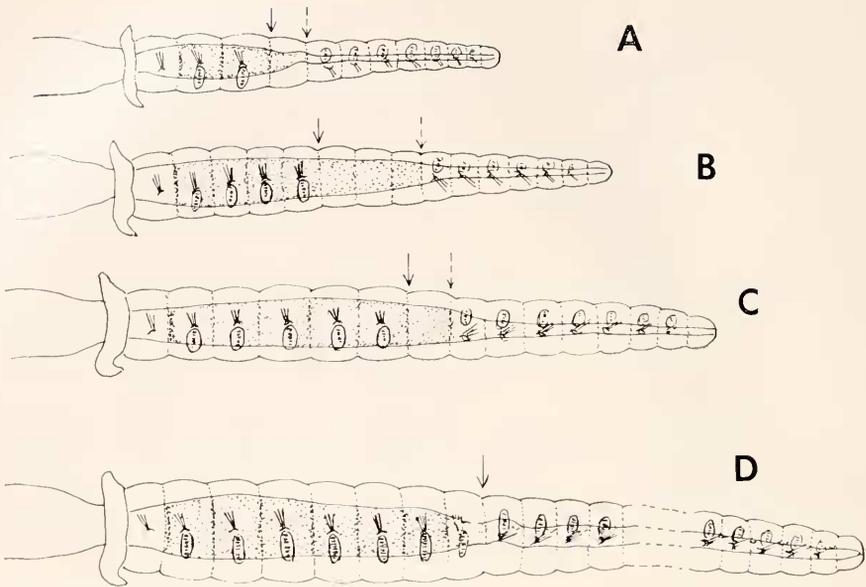


FIGURE 5. Correlation between segmental parapodial transformation and thoracic gut extension in juvenile *Branchiomma nigromaculata*: A, juvenile with 3 thoracic, one transforming and 7 abdominal segments; B, juvenile with 5 thoracic, 3 transforming, and 6 abdominal segments; C, juvenile with 6 thoracic, one transforming, and 7 abdominal segments; D, juvenile with 8 thoracic, none transforming and 19 abdominal segments. Thoracic setae are dorsal, hooks ventral; abdominal setae are ventral, hooks dorsal. In the transforming region between thoracic and abdominal segments, the abdominal segments lose abdominal parapodial structures as the thoracic gut extends at the expense of abdominal gut. Solid arrow indicates posterior limit of fully transformed segments, broken arrow indicates posterior limit of transforming segments.

development of *Megalomma* [*Branchiomma*] *vesiculosum* given by Wilson (1936) and *Branchiomma* [*Dasychone*] *nigromaculata* presented here, the little that is known concerning postlarval development in five other species is somewhat illuminating.

In *Potathemus elongatus*, a species with eggs of about the same size as those of *Branchiomma nigromaculata*, the newly settled postlarva (Fig. 6A) has two segments with thoracic type parapodia and three abdominal, with thoracic gut extending through the first two segments and partially through the third. In the dwarf species, as previously recorded (Berrill, 1977), and seen here in Fig. 6B, five thoracic segments are initially present, with four or five abdominal segments. Eggs are approximately the same size as in the two species just mentioned (Table II).

In the remaining species the egg size is much larger, more than three times greater in volume, of the order of 200 microns or more in diameter. In all three species the full number of thoracic segments form directly, with abdominal segments being added posteriorly later. In *Potamilla neglecta* (Fig. 6C) new abdominal segments are successively added during later growth until sixty to seventy have been formed.

Postlarval development in *Potamilla neglecta*, however, shows another very significant feature. The extension posteriorly of the thoracic gut lags far behind the establishment of thoracic parapodial character. In *Sabella microphthalmia*, the full number of thoracic segments again is attained directly, with an indefinite number of abdominal segments subsequently added (Kerby, 1971). In *Fabricia sabella* the exceptionally large and yolky egg develops the full number of thoracic segments directly, while yet an embryo within the parental tube (Fig. 6D). Abdominal segments are added later posteriorly, but only to a total of three (Fig. 6E).

DISCUSSION

In sabellids, and in the closely related but much more specialized serpulids, the thoracic region, as defined by the dorso-ventral orientation of the setigerous and uncinigerous units of the parapodia, is generally limited to about eight segments. These segments are solely responsible for forward locomotion in the tube, and may represent the minimum number compatible for effective progression (*cf.*, Gray, 1939, for analysis of stepping waves of four to eight segments in *Nereis*). In other polychaetes, including the tubicolous terebellids (Thomas, 1940), the thoracic, dorso-ventral orientation of the parapodia extends posteriorly from the head throughout the length of the body. In no case is there any inversion as seen in sabellids and serpulids; all setigerous segments are employed in walking forward.

Apart from the particular, highly differentiated structure and function of the crown as a feeding organ, the outstanding morphological feature of sabellids is accordingly the inversion of the parapodial structure in so-called abdominal segments, together with the relatively great extent of the inverted segments, which may exceed 300 in some species, *e.g.*, in *Sabella pavonina* and *Sabella spirographis*.

Sabellids suffer severe predation by fish in spite of protective mechanisms and behavior, unlike serpulids which are encased in a cemented calcareous tube and can lose only parts of their tentacles. *Sabella pavonina*, for example, exists in huge populations on the northern Atlantic Continental Shelf and parts of them are found in large numbers in the stomachs of bottom-feeding fish. In any large sample of apparently intact worms dug from lowtide mud flats, about 30 per cent show internal evidence of reconstitution. This situation has persisted at least since the upper Silurian, inasmuch as fossil serpulids are known from that period

TABLE I

Postlarval development of Branchiomma nigromaculata (each category represents the range based on about 25 individuals).

Number of tentacle radioles	Eyespots per radiole	Setigerous thoracic segments	Transforming segments	Abdominal segments	Total number of segments
2 + 2	1 - 2	1 - 4	1 - 2	3 - 8	7 - 16
3 + 3	2 - 3	5 - 6	2 - 3	5 - 11	12 - 20
5 + 5	3 - 4	6 - 8	0 - 2	7 - 19	13 - 29
14 + 14	11 - 15	8	0	83	91
40 + 40	25 - 29	8	0	103	111

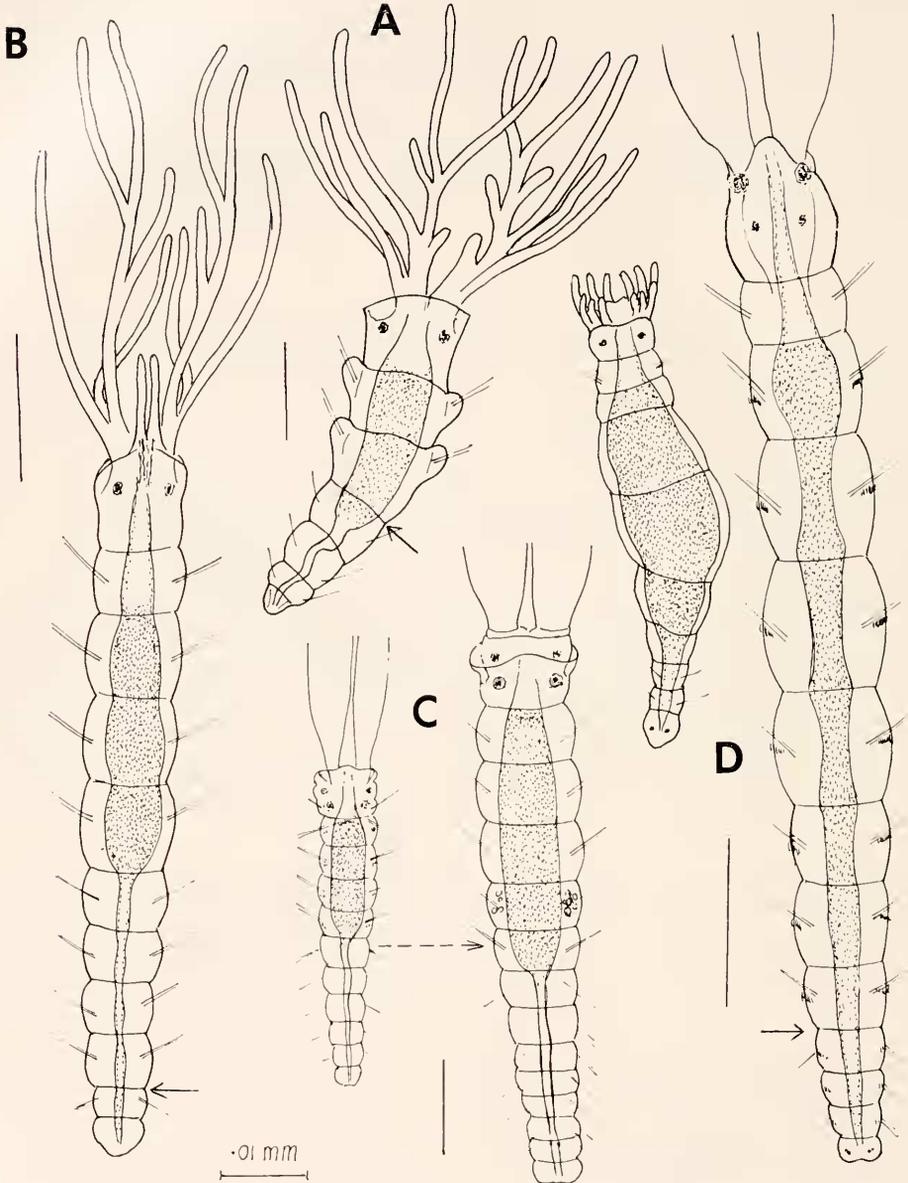


FIGURE 6. Settled juvenile (postlarval) stages of various sabellid species, showing correlations between number of thoracic segments initially formed and the size of the egg. Straight lines indicate diameter of respective eggs (see Table II). A, *Potamethus elongatus*, small egg size and postlarva with two primary thoracic segments and three abdominal segments, with thoracic gut already extending into first abdominal segment; B, *Potamilla neglecta* showing large egg size and postlarva with eight primary thoracic segments and one abdominal segment, with posterior extension of thoracic gut lagging relative to thoracic character of the body wall; C, egg size, first juvenile and incipiently sexually mature stages of a dwarf species, showing

TABLE 11

Egg size and number of initial thoracic segments.

Species	Egg diameter in microns	Number of thoracic segments initially formed
<i>Branchiomma nigromaculata</i>	135	3
<i>Potamethus elongatus</i>	110-150	3
Dwarf species (Berrill, 1977)	140	5
<i>Megalomma vesiculosum</i> (Wilson, 1936)	150	8
<i>Fabricia sabella</i>	200	8
<i>Potamilla neglecta</i>	200	8
<i>Sabella microphthalma</i> (Kerby, 1971)	250	8

and serpulids have undoubtedly evolved from a sabellid stock. The filtration-feeding crown of a sabellid, which is large relative to the size of the body (Dales, 1957), is necessarily ostentatiously displayed, and a considerable part of the worm in the distal part of the tube is likely to be bitten off, in spite of a fast shadow reflex, although autotomy of the crown may often be a saving grace.

The conversion of the greater part of the worm from forward-moving to backward-moving locomotory structure in each segment, with the concomitant digging-in of the parapodial heels, so to speak, virtually ensures that some of the more posterior portion of the worm will be left behind in the tube when the distal part is pulled from the front. This, combined with the extraordinary capacity, in sabellids, of abdominal segments, at all levels of the body, to regenerate a new head, and for the most anterior of the surviving abdominal segments to reorganize into thoracic-type segments, guarantees that a new individual forms from the one that was pruned.

From the observations on segmental transformation in *B. nigromaculata* and other species, it is evident that there are two dominant features in postlarval development and growth. Posterior extension of the body occurs by means of successive formation of abdominal segments from a zone of growth immediately anterior to the terminal pygidium. Thoracic segment character extends posteriorly from the metamorphosed larval head. Both processes vary from species to species. The final number of definitive abdominal segments, apart from any that may have become transformed to thoracic, ranges from three to about three hundred. The final number of thoracic segments is typically eight, but these may be all formed directly, or a smaller number may be formed directly and the remaining thoracic segments added through transformation of abdominal segments. Altogether these phenomena support the concept of two morphogenetic agencies working from

four primary thoracic segments and five abdominal segments in the juvenile stage, and the conversion of the first abdominal segment to thoracic both with regard to the gut and the parapodia (broken arrow); and D, egg size, advanced embryo, and fully developed stages of *Fabricia sabella*, showing heavily yolky endoderm of embryo, and direct formation of eight thoracic segments, with terminal three abdominal segments (the complete number) added to form the final condition.

opposite ends toward the middle, a concept long evident from experimental studies of regeneration and reorganization.

The extent of posterior abdominal growth, most simply expressed by the total number of abdominal segments successively produced, is a variable independent of other aspects of growth, and constitutes a major developmental problem. The nature of the "morphogenetic field" responsible for the imposition of thoracic character anteriorly is also a fundamental problem, but at least the variability expressed in this study indicates a correlation between egg size and initial extent of such a field of influence, *i.e.*, the larger the egg, the larger the larvae, particularly the anterior region. This in turn has a correspondingly greater dominance over posterior structure in the process of development.

SUMMARY

The structure and function of the external features of sabellid polychaetes are described, with special reference to the species *Branchiomma nigromaculata*. Form and function particularly are analyzed with reference to the ability of such worms to survive radical mutilation by predators. In addition to adaptive features already known, namely, "shadow reflex" withdrawal involving giant axon stimulation, autotomy of the crown, regeneration of a head, and reorganization of a new thorax from old abdominal segments, the crucial structural modification in the intact worm is the parapodial inversion of all segments posterior to the first eight or so anterior segments. This enables the parapodia to dig into the inner wall of the tube in such a way that a predator cannot pull an entire worm out of the tube. A posterior part is inevitably left behind to reconstitute a complete individual.

During postlarval growth, in several species, namely, *Potamilla neglecta*, *Sabella microphthalma*, and *Fabricia sabella*, all with comparatively large eggs, all thoracic segments (typically eight) are formed before any abdominal segments are produced. In other species, *Branchiomma nigromaculata*, *Potamethus elongatus*, and the dwarf species, all with comparatively smaller eggs, less than the full complement of thoracic segments are initially produced, and the remainder are subsequently formed by successive conversion of adjoining abdominal segments, in accordance with the procedure typical of the development of the small eggs of most serpulid polychaetes.

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