POLYCHAETE PHYLOGENY:
A PROBLEM IN PROTOSTOME EVOLUTION[1]

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Abstract

Fauchald, K. (Allan Hancock Foundation, University of Southern California, Los Angeles, California 90007) 1975. Polychaete phylogeny: a problem in protostome evolution. Syst. Zool. 23:493–506.—The evolution of the protostome coelom is an adaptation to burrowing as is segmentation in the annelids. The burrowing ancestral polychaete resembled in body-form recent terrestrial oligochaetes. Recent polychaete families originated in an adaptive radiation following the migration of the ancestral annelids into the flocculent detrital layers in shallow marine muds and from there onto hard bottoms and other specialized environments. [Polychaetes; phylogeny; protostomes.]

At present about seventy-five polychaete families are known (Fauchald, in preparation). Most families can be defined on morphological characters and recognized by non-specialists once the terminology is mastered. Attempts at grouping the families into acceptable higher taxa have been uniformly unsuccessful. Clark (1969) remarked that most polychaete taxonomists have overlooked all attempts and continued to use two old concepts: sedentary and errant polychaetes, vaguely identified as orders, but not really used as such and only rarely defined (but see Hartmann-Schröder, 1971). The two "orders" are practical groupings that subdivide the families into two equally large groups.

The lack of success in erecting higher taxa can be traced to two distinct complexes of causes. First, the variability of structure within each family has been poorly known (cf. Orrhage, 1966). Second, an interpretation of the phylogeny of any group depends on knowledge of the origin of the group with a consequent distinction between primitive and advanced traits. Interpretation of the polychaete phylogeny is thus dependent on an understanding of the origin of the segmentation and thus of the secondary body-cavities. This implies knowledge of the origin of the mesoderm and ultimately the origin of the metazoans.

One has to account for the living conditions of the organisms to interpret their phylogeny (Clark, 1964; 1969). Proposed hypothetical animals will have to be capable of performing all tasks of a living organism; they should also be at least as well adapted to their environment as contemporary organisms.

A number of morphological studies have demonstrated the limits of variability within several polychaete families (cf. Orrhage, 1964; 1966; Mettam, 1967; 1971 and others). Major synthetic papers have considered both morphological (Storch, 1968) and overall phylogenetic interpretations (Clark, 1969). A very important review of the eversible pharyngeal structures in polychaetes by Dales (1962) started a series of new investigations into these structures (but see Orrhage, 1973b).

A modified definition of primitive and advanced features in annelids and a new phylogenetic pattern for the polychaetes is given below. Theories on the origin of the secondary body-cavities and segmentation have been briefly reviewed to clarify the structure of the most primitive annelids.

ORIGIN OF COELOM AND SEGMENTATION

Three current theories attempt to account for the phylogenesis of the secondary body cavities. These include the gonocoel theory, the enterocoel theory and Clark's hydrostatic theory (cf. Hyman, 1951; 1959; Jägersten, 1955 and Clark, 1964; 1969). The coelomates are assumed to be monophyletic

by most authors. This assumed monophyly has created a major block to our understanding of these topics. The ontogenesis of the secondary body cavities follows usually either a schizocoelous or an enterocoelous pattern. These patterns are correlated with other developmental features such as spiral or radial cleavage, teloblastic or enterocoelous mesoderm and protostomous or deuterostomous condition in the derivation of the adult mouth. The postulated monophyletic origin of the coelomates assumes not only that one of the theories on coelom-formation is correct, but also that the whole set of correlated features can be accounted for, so that one pattern is derived from the other. Some groups should thus show a pattern or a set of patterns intermediate between the two major ones. The three lophophorate phyla (Brachiopoda, Bryozoa and Phoronida) superficially appear to bridge the gap between the protostomes and the deuterostomes; they have usually been considered early offshoots of the protostome evolutionary line (cf. Hyman, 1959; Jägersten, 1972). This situation is due to the usual definition of the two groups. If the adult mouth formed from the blastopore, or at least in the area where the blastopore should have been, an organism would be considered a protostome. If the adult mouth formed anywhere else, the organism *per definitio* was considered a deuterostome. This has the advantage of being simple, but as pointed out by Zimmer (1973), each group has a distinct set of features forming a pattern. Zimmer demonstrated that the lophophorate phyla are deuterostome and not at all intermediate between the two groups. The lophophorates fit very well with Romer's (1972, p. 150) concept of a pre-chordate ancestor (but see Jollie, 1972). The relegation of the lophophorates to the deuterostomes has left both groups reasonably uniform in terms of major ontogenetic patterns. The protostomes include, in addition to the spirally cleaving coelomates, all triploblastic acoelomates and pseudocoelomates. All deuterostomes are coelomate.

The only eumetazoan phyla not included in either group are the Cnidaria and the Ctenophora. Members of these two phyla are structurally simple; what features can be studied suggest a closer association with the deuterostomes than with the protostomes.

The presence of clearly protostome acoelomates and pseudocoelomates suggests that the two major groups were distinct before the coelom was formed. The coelomic cavities may thus have arisen in a different manner in each group. The enterocoel theory, perhaps as modified by Jägersten (1955), is acceptable for the deuterostomes. Where identifiable the ontogenesis of the coelom always follows the enterocoelic pattern, with pouches from the archenteron; frequently it is obscured by the presence of yolk or other secondary modifications of the reproductive pattern.

The gonocoel theory is widely held. This theory assumes that the coelomic cavities represent emptied, partially sterilized gonads, where the sterilized walls have been retained as the peritoneal lining. This theory is not inconsistent with what information is available about the protostomes, but cannot justifiably be applied to the deuterostomes in view of the ontogenesis of the coelom in members of that group. An ontogenetic justification is not possible for the gonocoel theory; the coelomic cavities form as splits in solid masses of mesoderm in the protostomes (Hyman, 1951, p. 23). The justification of the gonocoel theory is exclusively on historical or speculative grounds and on the usual connection between the secondary body-cavity and the gonads. Clark (1964, pp. 6–7) reviewed some of the major objections to the gonocoel theory. Thus, the germ cells are not invariably associated with the coelom; the association between coelom-formation and segmentation assumed by most proponents of the gonocoel theory makes it difficult to account for the non-segmented coelomates, such as the echiurids. Other objections listed by Clark would be valid if the gonocoel theory is assumed to be the only way

to account for the coelom formation. Clark pointed out, correctly, that none of the objections are fatal to the theory, which could be considered acceptable because it cannot be irrevocably rejected. Clark did however, propose an alternative theory emphasizing the functional aspects of the secondary body cavity and appearing to be in very much better agreement with what functional, embryological and anatomical observations can be made on recent organisms.

Clark's theory emphasizes the hydrostatic function of the coelom. He tends to assume that when the ontogenesis so indicates, the cavity arose as a schizocoel during phylogenesis (Clark, 1964, p. 216); Clark very clearly pointed out however, that the coelomic cavities in the animal kingdom *per se* are polyphyletic and that the evolutionary pressures could lead to similar results through different mechanisms.

The position taken here is that the coelomic cavities in the protostomes arose as hydrostatic devices along lines suggested by the schizocoel theory, *i.e.*, as fluid-filled spaces between cells in mesodermal blocks. This accounts for the formation of the coelom in most recent protostomes. The common connection between the coelom and the gonads can be explained by reference to other coelomic functions. It is a storage area for nutrients, a nephridial structure and a homoeostatic device and since its contents are easily displaced, the cavity is an excellent storage area for gonadal products. Connections between coelom and gonads are also present in the deuterostomes; there is thus no necessary relation between the acceptance of any given theory of coelom formation and the position of the gonads.

The gonocoel theory, the enterocoel theory and most other theories about the coelom formation have tied the formation of the coelom to the presence of metameric segmentation. Consequently the earliest coelomates were considered segmented (cf. Clark, 1964). The nonsegmented coelomates became very difficult to explain.

Attempts were made to demonstrate that the sipunculids and echiurids show traces of a previous segmented condition (cf. Hyman, 1959, p. 657 and Newby, 1940, pp. 144–145); the priapulids have apparently never been considered segmented (cf. van der Land, 1970). All these attempts have failed; we have to account for the three different, completely unsegmented groups.

The modified Clarkian theory of coelomformation does not refer to metameric segmentation in the earliest protostome coelomates. Following Clark (1964, 1969) it is here suggested that the coelom arose first, as an adaptation to burrowing in soft marine muds. The three recent non-segmented phyla "represent" this stage in the evolution of effective soft-bottom burrowers. Later, the same environmental pressure led to the formation of segments as aids in peristaltic burrowing.

Coelom and segmentation arose in burrowing and not as modified archenteric pockets (as the enterocoel theory would have it) or as emptied gonads (as the gonocoel theory requires). Segmentation is thus primarily a feature of the locomotory apparatus, not involving any other organsystems, except secondarily. This theory makes it possible to postulate the presence of morphologically pre- and postsegmental regions. It does not assume the sharp distinction between ecto- and entomesoderm as does the gonocoel theory. Ecto- and entomesoderm can be separated with ease only in isolecithal embryos, and usually only for a short period of time (cf. MacBride, 1914 and Kume *et al.*, 1968). Later in development, the embryos become opaque and the recruitment of cells to each organ becomes less distinct as the remnants of the blastocoel are obliterated. The distinction between ecto- and entomesoderm may be important, but in terms of the evolution of the coelom and segmentation suggested above, it is irrelevant to know the provenance of every cell in each organ-system.

The consequence of this view of the evolution of the coelom is that the earliest coelomates must have been rather large

animals, well beyond the size of the interstitial organisms (Clark, 1964). Clark also summarized the information available about the distribution of active burrowing in the animal kingdom and demonstrated clearly that peristaltic burrowing is a function of the size of the organisms. Below a certain body-size, such burrowing no longer takes place, but the animals move between the sediment particles and handle each particle individually rather than on a mass base as in peristaltic burrowing.

The presence of setae in the annelids has never been adequately explained. Setae are present in brachiopods, pogonophorans and echiurids as well, and the structure of all setae appears very similar (Orrhage, 1971; Gustus and Cloney, 1972). Functionally there are two distinct classes of setae.

Larval setae, both in the brachiopods and the annelids, can usually be erected. This will increase the flotation area of the larvae and may decrease predation by increasing the apparent size of the larvae. Larval setae are unknown in the pogonophorans and echiurids.

Functionally, adult setae vary strongly. They are anchoring points in burrowing and tubicolous forms. Some errant forms living on hard substrates use their notosetae for defense (Storch, 1968) and the neurosetae may be used for traction in a stepping motion (Mettam, 1971). The tubicolous pogonophorans use their setae as anchoring points as do burrowing and tubicolous echiurids.

The selective advantage of the setae follows from the suggestion that segmentation arose as an aid in burrowing; setae under these conditions are used as anchoring points in tubes or burrows. Setae probably evolved as roughened thickenings of the cuticle to increase the friction between worm and burrow. Later the thickenings continued into the body to give firmer anchorage and evolved musculature to increase the possibility of lateral pressure. The suggested process provides for a selective advantage of the setae while they are evolving. Other functions of the adult annelid setae are secondary; setae in the larvae represent an adultation to use Jägersten's (1972) term for the precocious development of adult features. The setae of brachiopods and annelids are analogous structures. The pogonophorans were up to recently considered deuterostomes, due to their apparent tripartite adult body structure and to Ivanov's (1960) interpretation of the larval development, but doubt has been raised as to the appropriateness of this placement (George, 1973; Orrhage, 1973a). If the pogonophorans are protostome, their setae are homologous to the annelid setae as are the echiurid setae. If the pogonophorans should remain deuterostomes, it is still possible that their setae evolved as suggested for the annelids, since they have the same selective advantage in both groups. Thus the presence of setae in the pogonophorans cannot by itself be used to clarify their systematic position (cf. Orrhage, 1973a).

POSITION OF ARCHIANNELIDA

The group Archiannelida, as presently accepted, consists of five distinct families, Dinophilidae, Nerillidae, Polygordiidae, Protodrilidae and Saccocirridae. Each contains a modest number of small annelids found in the mesopsammon in marine and partially in freshwater environments. The group has generally been considered the most primitive of the annelid groups (cf. Hatschek, 1893; Hermans, 1969).

This apparent primitiveness may be spurious. Swedmark (1964, pp. 6–8) set forth a set of morphological criteria that generally characterize mesopsammic organisms. Hermans (1969, pp. 97–99), using these criteria, demonstrated that the archiannelidan primitiveness was due to adaptations to life between sand-grains. Hermans felt that he had insufficient evidence to demonstrate whether these adaptations were primitive or secondarily derived from some other condition. Interstitial species are considered secondarily specialized rather than primitive in other phyla (Swedmark, 1964; Laubier, 1967).

The annelids are the most primitive of the clearly segmented protostomes. The acquisition of segmentation must have been a selective advantage to the evolving annelid. Segmentation is apparently of no advantage to small, mesopsammic organisms; most mesopsammic members of normally segmented groups (annelids and arthropods) tend to have reduced segmentation or have the segments fused into tagmata. Clark (1964) demonstrated that segmentation arose as an aid in burrowing in soft substrates and that burrowing organisms were considerably larger than the mesopsammic archiannelids. If Clark's argument is accepted, the small archiannelids cannot be considered as the primitive annelids. It is however, still quite possible that other traits of the archiannelids, apart from their small size, might be primitive.

These traits include the reduced anterior appendages, low number of segments in most forms, strongly developed external ciliation and reduction of septa. Characteristically, parapodia are also reduced or absent and the setation is poor or absent. Most of these characters are however, exactly those that adapt these organisms to life in the mesopsammon. These features could thus be either primitive or secondarily specialized and to resolve this problem one would have to get new evidence from features not usually considered in this context.

The characters listed are also used to define the group Archiannelida. One cannot first use this set of characters to demonstrate the close adaptation of these five families to life in the mesopsammon and then, secondarily, use them to demonstrate the close relationships between the contained members. A demonstration of the relation between the families will have to depend on other characters.

It thus becomes doubly important to demonstrate the possibility of morphologically primitive features in the archiannelids and to demonstrate the relationship between the five archiannelidan families. A more systematic search is needed, but it appears that the pharyngeal apparatus and reproductive patterns in these forms may be useful. The different kinds of pharynges present are, in principle, as varied in these five families as in the whole class Polychaeta (Dales, 1962; see also Orrhage, 1973b). Reproductive patterns may vary even within one genus (Jägersten, 1952; Swedmark, 1954). No features indicate a particularly close relationship between the group Archiannelida and any given polychaete family or between the five archiannelidan families. Bubko (1973) came to a similar conclusion in that he separated the Dinophilidae from the rest of the archiannelidans and considered the Protodrilidae and Polygordidae in separate orders under a subclass Archiannelida. Archiannelida is here considered a polyphyletic group, secondarily adapted to life in the mesopsammon. The group must be broken up and the five families allied to their closest apparent relatives among the other polychaetes. Individual archiannelidan families do show resemblances to specific polychaete families or can be allied with these temporarily.

PRIMITIVE ANNELID AND PRIMITIVE POLYCHAETE

The polychaetes are almost universally considered the most primitive annelids, apart from the archiannelids (cf. Clark, 1969) and the oligochaetes and hirudineans have been derived from the polychaetes. There are several reasons for this. The polychaetes are mainly marine forms, they are usually structurally more complex than members of the other two groups and their reproductive habits are simpler in that they are dioecious, have gonads in numerous segments and simple gonoducts without copulatory devices, etc. They are only rarely hermaphroditic. The oligochaetes and hirudineans, which may be considered as one group for the present purposes, are mainly fresh-water, terrestrial or ectoparasitic forms. They are hermaphroditic and have gonads limited to a few segments. Complex glands are associated with the

gonoducts. Parapodia are always absent and setae may also be missing. Septation is either nearly complete (terrestrial oligochaetes) or absent (most freshwater oligochaetes and hirudineans).

These generalizations must be examined in some detail. The best arrangement of muscles for a burrowing organism is a well developed body-wall with layers of longitudinal and circular fibers. In annelids the longitudinal fibers are concentrated in four bundles. In the polychaetes the circular fibers are largely subverted to use in the parapodia (Mettam, 1971). Remnants of the circular muscles are limited to small areas and the hydrostatic pressure in the body is maintained by oblique or transverse muscles (Clark, 1964).

The parapodia and anterior appendages of the polychaetes are mechanically disadvantageous to burrowing organisms. The unadorned prostomium, the complete septation and the strongly developed body-wall muscles of the terrestrial oligochaetes are exactly what would be predicted of an ancestral annelid if it evolved primarily as a burrowing organism in shallow, soft-bottom marine environments. Furthermore, the structurally complex polychaetes, with well developed parapodia and strong anterior appendages are either associated with hard-bottom habitats (phyllodoeids, amphinomids and the scale-worms) or are tubicolous (onuphids, sabellids and serpulids). Burrowing polychaetes have reduced appendages and may lack acicula and prominent parapodia (lumbrinerids, capitellids, cirratulids, etc.). Some polychaetes are in fact structurally as simple as the oligochaetes (questids, cossurids and cirratulids).

Hermaphroditism is a condition considered related to the habitat of the organisms in which it occurs and is often related to abnormal reproductive habits. Normal in this context are dioecious organisms spawning small eggs and sperm directly into sea water. As a corollary of this, planktotrophic larvae that spend a long time in the plankton are considered normal. Lec-

ithotrophic larvae and direct development are considered secondary phenomena where they occur (Jägersten, 1972).

Hermaphroditism is an obviously adaptive pattern in environments where water is scarce or where the availability of partners is low, but the condition is not limited to such environments. Turbellarians in all environments are hermaphroditic. The phylogenetic pattern in gastropods indicates a decreasing dependency on the "normal" reproductive pattern, independent of environmental variables. It is difficult to use the presence of hermaphroditism in the oligochaetes to demonstrate the advanced condition of these organisms, since it is often the presence of the hermaphroditic gonads limited to a few segments that makes it possible to define a worm as an oligochaete, rather than a polychaete, this being the only *a priori* character that safely separates the two classes.

The degree of septation present in any worm has been associated with the habits of each species (Clark, 1964). Burrowing animals tend to have more complete septa than non-burrowers, but Mettam (1967; 1969; 1971) has demonstrated that septation may be retained for other purposes.

The structure of the postulated primitive annelid will depend on how and where it is considered originating. If it arose in a hard-bottom environment, it is quite possible that it resembled the structurally complex errant polychaetes as suggested by Storch (1968). The origin of the septation then becomes difficult to explain, since there appears to be no selective forces in this environment to make septation advantageous (Clark, 1964; 1969). Septation may be *retained* for reasons other than burrowing, but no satisfactory explanation of how septation could arise in any other way has been given.

If the annelids arose according to the theory suggested by Clark and repeated above, as burrowing organisms, structural simplicity will have been a key feature in the ancestral annelid.

This oligochaetoid ancestor may or may

not have been hermaphroditic; the reproductive pattern is irrelevant in terms of the origin of the annelid body-plan. It is likely, however, that the ancestral annelid was dioecious and did reproduce as suggested by Jägersten and others as the primitive mode of reproduction. The ancestral annelid is thus a polychaete, since the oligochaetes, by definition, have hermaphroditic gonads limited to a few segments. The ancestral annelid is referred to below as the ancestral polychaete, but it should be remembered that it differed from most recent polychaetes in that parapodia were absent or at most present as low ridges.

In summary, the ancestral polychaete is here considered to be a burrowing organism with complete septation and distinct segments. Setae and low parapodial folds evolved parallel to the evolution of the septation. The anterior end had a series of sensory endings, but probably no anterior appendages of any kind. The ancestral polychaete was marine and lived in shallow water. It was dioecious and spawned into the sea; the larvae were planktotrophic.

The phylogenetic schemes that have been set up to relate the different families of polychaetes to each other have not been particularly successful; reasons for this have been suggested above. Using the structure of the ancestral polychaete, it should be possible to achieve some semblance of order in the class. A short review of the morphological features used to separate the different families will be necessary to relate these features to the characters of the ancestral polychaete.

REVIEW OF MORPHOLOGICAL AND
ANATOMICAL FEATURES USED IN
TAXONOMY OF RECENT POLYCHAETES

The present review will cover only features of immediate importance for the following discussion. Most attention has centered on the degree of cephalization in the different families. Benham (1894, 1896) used the presence of a distinct prostomium as the basis for his grouping of the polychaetes into Gymnocephala and Crypto-

cephala. The numbers and kinds of anterior appendages in relation to the life habits of the worms are used for the traditional separation into errants and sedentaries and Dales (1962) focussed his attention on the development of the muscular parts of the stomodaeum.

Different categories of anterior appendages and the structure of the eversible proboscis have been used to define the families and superfamilies. Using these characters and the principal construction of the parapodia, each family can be easily defined. All anterior appendages are homologous developments within each family, but there has been considerable disagreement between different workers when the families have been compared with each other. The different categories of appendages, such as palps, antennae and tentacular cirri vary sufficiently in external morphology and position to lead to confusion in concept in addition to the usual confusion in terminology. Attempts have been made to base the definition of each category on the internal anatomy or on the ontogenesis and recent investigations into these two aspects have clarified the situation (Orrhage, 1966; 1973; Åkesson, 1961; 1962; 1963; 1967a; 1967b and 1968).

All anterior appendages appear to be formed embryologically in very much the same way (Åkesson, 1963). Ontogenetic evidence is thus not particularly helpful. It is possible to separate out one category of appendages on the adult innervation. With one notable exception, the palps are innervated in the same manner in all polychaetes investigated, irrespective of their position in adult organisms. Palps may be ventral or dorsal, frontal or occipital; they may be sensory or be used in feeding. Thus several classes of palps can be recognized, partly in terms of position, partly in terms of function. It is not possible to derive one kind of palp from any other; transitional conditions are absent in recent polychaetes. Spionid palps are always dorsal feeding appendages; aphroditid palps are ventral and sensory. The exception alluded to

above is in the superfamily Eunicea, where two of a set of maximally five occipital tentacles have the innervation pattern usually found in palps, but the structures called palps are embryologically formed as palps in other errant polychaetes (Åkesson, 1967a).

A definition of different categories of cephalic appendages based on the apparent limitations between the pro- and peristomium is difficult, partially because the fusion of these two parts may be complete, partially because the appendages will retain their original innervation even if they are positioned differently in adult organisms of different kinds. The presence of anterior appendages *per se* is taxonomically very important.

The anterior end of the digestive tract is specialized for ingestion in all polychaetes. The region is embryologically a stomodaeal invagination; it may contain various structures such as jaws, teeth and chitinized plates. The region often has specialized muscles associated with the eversion of the anterior end of the digestive tract. Dales (1962) demonstrated that the whole diversity of anterior modifications could be reduced to two basic constructions. In one of these, the lower lips contain plate muscles and are eversible. These lower lips may be large and balloon-shaped (*Magelona*), frilled or lobed (several orbiniids) or more modestly developed as a thickened lip (spionids, amphinomids).

The other kind of pharyngeal modification is the axial proboscis. The lining of the digestive tract just posterior to the mouth forms a symmetrically developed, thin-walled buccal tube that can be everted through the mouth. The buccal tube may be followed by a strongly muscular region, or special muscles may be absent. In the latter case, eversion of the buccal tube is effected by increasing hydrostatic pressure in the coelom (Clark, 1964; Pilgrim, 1966).

Based on the construction of the proboscis, Dales subdivided the class into several "superorders"; supplementing this with characters from other organ-systems, Dales could define a series of orders. However, otherwise closely similar forms may have different kinds of proboscides. There is especially overlap between the occurrence of plate-muscle and non-muscularized axial proboscides (Orrhage, 1964, 1973b).

The structure of the cephalic ganglion has never formally been used in a phylogenetic scheme, but this possibility was discussed in a series of papers (Binard and Jeener, 1928; Hanström, 1928a; 1928b; 1930 and Gustafson, 1930). The debate was reviewed by Orrhage (1966). The brain may be a superficially smooth, rounded lobe or it may be separated into two or three distinct lobes, one after another (Heider, 1925; Hanström, 1928a; 1928b; Fauvel, 1958). There are generally four brain commissures (Orrhage, 1966) and several, perhaps most, polychaetes have double circumesophagal rings. Even when simple, these rings have two roots on each side. When the brain is superficially lobed, one root originates in the anterior lobe and another in the posterior (or median) part. Palps also have two roots, associated with the same parts of the brain and may be innervated from the circumesophagal ring rather than from the brain directly. This is the key difference between palps and antennae; palps have double roots, antennae do not. Collections of presumably associative cells, referred to as *corpora pedunculata* have been reported from several families of errants (Hanström, 1928a; 1928b). The *corpora pedunculata* of nereids and aphroditids are dense nuclei; similar cells are found scattered over the whole surface of the brain in eunicids. *Corpora pedunculata* are also present in serpulids, but appear otherwise limited to a few phyllodociform and aphroditiform families in addition to the families named above.

Interpretation of the observed differences in brain structure is intimately connected to the problem of the origin of the annelids, thus in turn to the origin of the coelom and the triploblastic metazoans. The prostomium is pre-segmental according to one group of workers (e.g. Hanström); others

claim that the polychaetes are completely segmented (Binard and Jeener). The former point of view is associated with the gonocoel, the latter with the enterocoel theory. The prostomium is here considered pre-segmental, derived from the episphere of the trochophore larva. There is evidence to show that the peristomium also may be pre-segmental (e.g. *Eunice*, Åkesson, 1967a). A stomatogastric ganglion is frequently added to the primitive brain: it represents a cephalized segment. There is no relation between the number of parts in the brain and the external lobation (Fauvel, 1958); the degree of cephalization of the stomatogastric ganglion and additional segments varies from one family to the next. It is difficult to associate the degree of cephalization with other morphological characters. Tubicolous animals tend to be more strongly cephalized than non-tubicolous ones.

The structure of the nephridia and the relationship between gonoducts and nephridial ducts has been used phylogenetically. Protonephridia are present in a few phyllodociform polychaete (Goodrich, 1945); all others have metanephridia. The two canals are more or less fused in all other polychaetes as nephromixia or mixonephridia. The detailed structure varies from one family to the next and even otherwise closely similar families may have rather different nephridial structures (e.g., nereids and syllids).

Strongly segmented polychaetes with complete septa are considered more primitive than animals with incomplete septa. The ancestral annelid is always depicted as having had complete septation (see above). Complete septation is associated with vagile habits and incomplete septation with sessile ones (Clark, 1964). However, septation may also function in peristalsis (Mettam, 1971) or in tube irrigation (Mettam, 1969) so the presence of complete septation may be related also to habits other than burrowing. Pseudosepta are present in a number of polychaetes with long, axial proboscides (Mettam, 1967); they resemble functionally the true septa; both are used to isolate pockets of coelomic fluid for hydrostatic purposes. Pseudosepta are developed from the oblique musculature and are best developed in burrowing forms. Again, the presence or absence of septa appears more related to the life habits of the individual species than to any other morphological feature.

The segments of polychaetes have been assumed to be of two different kinds (heteronomy). This theory was especially promulgated by Ivanov (1928). The first segments, according to Ivanov always three, are laid down more or less simultaneously in the pelagic larvae; these primary segments are considered different from all other segments which are added later from a prepygidial growth zone. The number of primary segments varies from one group to another and even within one group (Blake, 1969). The separation into primary and secondary segments would be needed if the enterocoel theory applied to the polychaetes; this is not the case and there is little reason to believe that the number of primary segments is anything more than a larval adaptation. It seems related to the amount of yolk present in the eggs and thus to the length of larval life.

The development of the parapodia is frequently used as a character to group and organize the diferent kinds of polychaetes. Parapodia are in principle biramous; vagile polychaetes tend to have well developed parapodia supported by acicula; sessile ones often have low parapodia and acicula are frequently missing. With very few exceptions, all polychaetes retain setae at least in the neuropodia, even if the fleshy parapodial structures may be absent. Tomopterids lack setae in body-segments, but parapodia are well developed and internal acicula are present in a pair of modified parapodia. Notopodia are often reduced and their locomotory role is negligible in several families. Remnants of the notopodia are frequently retained as supports for branchiae (e.g., onuphids) or the notosetae are used for defensive purposes (e.g., chrysopetalids and amphinomids. Internal noto-

podial acicula may be retained even if the whole external structure is missing (e.g., *Lumbrineris*); these internal acicula apparently function as muscle attachments.

Neuropodia of burrowing and tubicolous forms tend to expand laterally to form low welts (tori) and in some capitellids form nearly complete cinctures around the body. Sometimes the parapodia are reduced, but the setae form complete cinctures (*Chaetozone, Myxicola*). Tubicolous forms tend to have the setae arranged in single rows, transverse to the long axis of the body in at least one of the two rami; the other ramus may retain the original bundle arrangement. Tori are never supported by acicula and the parapodial muscles are represented by setal protractors and retractors.

The construction of the body-wall musculature was used to separate the groups of polychaete families by Storch (1968). He suggested that worms with the most complex systems (e.g., *Aphrodita*) should form the central type from which all other polychaetes could be derived by secondary simplifications and specializations. The methodology of Storch's study is based on Remane's homology considerations but also includes comparisons of similarity characteristics of numerical taxonomy. This combination of methods will, almost invariably, lead to the recognition of the most complex member of the contained taxa as the central group. Storch's study is very precise within the limits set. The method cannot be used to calculate the direction of the phylogeny and it is possible to interpret Storch (1968, fig. 30) to imply that evolution of the polychaetes led from the nereidiforms through the aphroditiforms to the phyllodociforms or *vice versa*; or from the aphroditiforms separately in both directions. The methodological difficulties can be solved only by direct evidence but no pertinent fossil evidence is available to support either interpretation.

The main problem in using the major body-wall muscles in interpreting the phylogeny of the polychaetes lies however not in the methodology for interpreting the data, but in that it disregards the muscles associated with the parapodia as pointed out by Mettam (1971, p. 490). The complexity of the parapodial muscles varies with the development of the parapodia and will strongly influence the patterns demonstrable in the body-wall muscles *per se*. The musculature furnishes valuable evidence of the relations between the different families and genera, but the structure cannot be used alone as a character to group the polychaete families.

PHYLOGENY OF POLYCHAETES: SOME PRINCIPLES

The proposed ancestral polychaete was a burrowing organism with setae, but without parapodia, adapted to burrowing in soft muds. Clark (1969, p. 45) indicated that parapodia arose as aids for crawling in soft substrates. At the interface between water and mud in the marine environment is an accumulation of flocculent detrital material. This material is too soft for peristaltic burrowing and too dense for efficient sinusoidal swimming. In shallow water it is one of the richest environments in the sea in terms of available energy. The detrital layer is largely composed of remnants of planktonic algae and other planktonic organisms and terrestrially derived materials. It is not easily available as food for a filter-feeding organism or for a true burrower, but organisms that can crawl through it will have ample resources.

Organisms known or assumed to be present at the time the annelids arose include sponges, cnidarians, ctenophores, turbellarians, probably some of the pseudocoelomate groups, sipunculids and echiurids. If any deuterostomes were present, they were probably sessile filter-feeders such as the lophophorates. Mollusks of various kinds may have been present. Most of these organisms are either small, sessile, or pelagic or a combination of two or three of these characteristics. None of them, including the mollusks, would be particularly well adapted to life in the detrital layer. Other

organisms, presently wholly extinct, may have been present. This does not seem likely: completely extinct phyla are rare in the fossil record and there is no *a priori* reason to assume that extinct phyla are any more common among the soft bodied organisms than among those that leave identifiable fossil traces. It thus appears probable that a food source was available for an organism that could move through the flocculent layer.

Both parapodial rami probably evolved equally well; they were probably more or less foliose, perhaps resembling the present nephtyids. Storch (1968) claimed that the original function of the notopodia was defensive. He postulated the aphroditids as the central polychaete group and cited the condition in the aphroditids *sensu latu*, the amphinomids and the euphrosinids as evidence that the notopodia were primarily defensive and secondarily locomotory devices. These three families are central in his phylogenetic scheme. Most polychaetes with modified notopodia are either tubicolous (e.g., onuphids) or are mainly found in hard bottom environments (e.g., polynoids, amphinomids, phyllodocids and syllids). Of the aphroditiform polychaetes, only the aphroditids *sensu stricto* and the sigalionids are characteristically soft-bottom forms. In these the notopodial setae may be developed as a felt (*Aphrodita*), be defensive (*Laetmonice*, etc.) or reduced (most sigalionids).

The more typical soft-bottom free-moving polychaetes have biramous parapodia (nephtyids, goniadids, lacydoniids, orbiniids, paraonids, in part spionids, questids, magelonids, flabelligerids, fauveliopsids, etc.). In most of these, the rami are subequal and participate in the locomotion. If the parapodia arose in soft-bottom polychaetes, it appears likely that the parapodial structures of recent soft-bottom organisms would resemble the original condition more closely than the same structures in recent hard-bottom animals or in animals living in special environments (e.g., commensals).

Highly developed anterior appendages will be of no great advantage to an animal moving through a flocculent layer of detritus. The early polychaetes with parapodia probably were sparsely equipped with short antennae and palps. The ancestral polychaete probably had a ventral plate-muscle proboscis. An axial proboscis probably evolved within several groups as a swallowing device. The ancestral polychaetes had only one peristomial segment. In the genus *Eunice* the pro- and peristomium is formed as a unit (Åkesson, 1967a) and the apparent segmentation is secondary. The muscles and the coelomic pouches associated with these parts of the body are derived from the first setiger. The eunicids are admittedly rather different from the ancestral polychaete both in habitat and structure. The ontogenesis of the anterior end may consequently be modified, but it is suggestive to find that what appears externally as three different "segments" (the prostomium and two peristomial segments in the usual terminology) are in fact formed as one unit and subdivided only when invaded by mesoderm from behind.

The evolution of the different polychaete families is here seen as a rapid radiation from several ancestors adapted to life in the semi-consolidated detrital layer above the sea bottom. It is probable that several distinct groups of similar, but not identical forms gave rise to different families. The radiation is seen mainly as a move from the detrital layer onto hard bottoms and into a burrowing or tubicolous existence. A radiation would explain the confusion in structure and numbers of anterior appendages in the different families, the odd distribution of nephridial structures and the varied development of the nervous system.

Theoretically a radiation is impossible (Hennig, 1966), but where the time span in which the differentiation took place is short relative to the time since the differentiation happened, even a nicely dichotomous splitting will appear as part of a radiation. Fossil materials of eunicid polychaetes are present in Ordovician remains

(Kielan-Jaworowska, 1962) and other identifiable polychaete remains are present in Cambrian materials (Glaessner, 1958; Glaessner and Daily, 1959). The early presence of eunicids, which are rather specialized hard-bottom and tubicolous forms, strengthens the supposition that the differentiation of the polychaete families followed a pattern best described as a rapid radiation. It probably took place in the main in Precambrian times.

In some respects this solution parallels the Alexandrian solution to the Gordian knot. Recent polychaetes can be analyzed for traits assumed primitive (i.e., adaptive in the flocculent layer) or advanced. However, it becomes impossible to relate the different groups of recent polychaete families to each other, and the question of which of the recent polychaete families is the most primitive becomes irrelevant, since each family will consist of a mixture of primitive and advanced traits. The adaptations to new environments may be profound or relatively minor, but the important point is that each organ system may react differently to similar environmental pressures. The nephtyids have retained their protonephridia (a primitive trait), but the septa have been lost and functionally replaced by pseudosepta (a highly advanced trait, Clark, 1964, pp. 138–139).

The interpretation of the polychaete phylogeny rests on the assumption that recent polychaetes evolved from a burrowing ancestor and that the evolution of the parapodia took place in the flocculent detrital layer above the shallow marine bottoms. It assumes that hard-bottom, or burrowing or tubicolous polychaetes evolved as a result of a radiation from an animal adapted to wriggling through the flocculent layer.

The suggested phylogeny implies parallel evolution of several important characters such as the anterior appendages, branchiae and partially nephridial structures. This is difficult to accept. However, if the ancestral polychaete was a complexly organized oligochaete-like animal with a finite set of

potentialities then similar evolutionary pressures would lead to similar, if not identical results in descendant groups. The ontogenesis of the anterior appendages demonstrates that they are homologous structures. The present scheme admits this basic homology, but avoids deriving structures found in one recent family from structures in any other family.

Previously suggested phylogenetic schemes have always depended on selection of one organ-system as being the most conservative or the most expressive of relations between the different groups. The schemes when completed showed a great deal of internal inconsistencies, if the taxa were defined at all.

It is possible to group recent polychaetes into a limited number of orders. It should be irrelevant in which sequence the orders are given, considering the view of the polychaete phylogeny suggested above. However, the traditional sequence has the advantage of demonstrating an increasing complexity in anterior structures and an increasing involvement of body-segments in the anterior end, a cephalization. Despite warnings by Hennig (1966, p. 70 ff), it is believed that this increasing morphological distance from the ancestral polychaete reflects one, if not the only evolutionary trend in the class.

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