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ADAPTIVE STRATEGIES LEADING TO THE ECTOPROCT GROUND-PLAN

JACK D. FARMER, JAMES W. VALENTINE, AND RICHARD COWEN

Abstract

Farmer, J. D., Valentine, J. W. and Cowen, R. (Dept. Geol., U. Calif., Davis, 95616). 1973. *Adaptive strategies leading to the ectoproct ground-plan*. *Syst. Zool.* 22:233-239.— Ectoprocts may have descended from a vermiform, burrow-dwelling lophophorate ancestor that would probably be classed with the Phoronida if it were living. Stripped of their adaptations for small size, coloniality, and skeletonization, ectoprocts closely resemble phoronids. We propose that ectoprocts probably arose from a lineage that became epifaunal, reproducing asexually to form tangled aggregations on hard substrates. Under these circumstances the disadvantages of aggregation, chiefly related to crowding, were mitigated through the development of small body size and by adoption of colonial habit. Coloniality was favored because it regulated intraspecific competition by controlling dispersion patterns and the spacing of individuals. It permitted coordinated manipulation of the environment in feeding and waste disposal, enhanced protection, and provided the opportunity for functional differentiation among individuals, thus promoting efficiency. Miniaturization led to the loss of distinct circulatory and excretory systems, while coloniality and eventual skeletonization led to a vast morphological and therefore ecological potential for the group. These factors appear to underlie the important place gained by ectoprocts in many benthic communities from the early Paleozoic until the present time. [Ectoprocts; Phoronida; adaptive strategies.]

INTRODUCTION

An understanding of the origin of higher taxonomic categories and the clarification of relationships among major phylogenetic lines have long been classic goals of the life sciences. The lophophorate phyla Phoronida, Ectoprocta and Brachiopoda form a close-knit group, with strong similarities in body plan. The relationship of these phyla to other groups is puzzling, for although they show some embryological features which would seem to ally them most strongly with the protostomes (Clark, 1964), they possess other features which suggest deuterostomatous affinities (see Emig, 1971). In this respect they are of special interest as they seem to represent a link between two major evolutionary lines.

In a similar way, relationships among the lophophorate phyla have been difficult to resolve. Hyman (1959), while considering it impossible to delimit precise relationships between the phyla, regards the Phoronida as nearest to the ancestral lophophorate. Clark (1964) considers the un-

attached condition of infaunal tubicolous Phoronida to be ancestral, the attached condition of the ectoprocts and brachiopods being derived secondarily. However, Jägersten (1972), reasoning from a theoretical and observational model of larval phylogenies, derives the lophophorates from a common sessile ancestor, with the Brachiopoda arising first, and then the Phoronida and Ectoprocta appearing successively from subsequent ancestral branches. This phylogeny fails to account for the functional origin of many important adult features, such as the coelomic cavity, and when such features are taken into consideration a model is generated that closely resembles Clark's, with phoronids standing nearest to the ancestral lophophorate lineage.

Schemes for lophophorate phylogeny that are based on embryological or larval similarities are subject to additional criticism in that they rely upon validity of the "biogenetic law" of recapitulation (see Jägersten, 1972), the general applicability of which is doubtful. Other phylogenies

(e.g., Termier and Termier, 1970) are based upon comparisons of a few isolated characters unrelated to the basic groundplan of the organism and apparently reflecting evolutionary convergence. No previous phylogenies have attempted to identify reasonable evolutionary pathways between lophophorate groups to account for the observed differences by adaptation to changing modes of life.

Although it is perhaps possible to envision alternate adaptive pathways, the preferred pathway should be the one that explains fundamental morphological differences most efficiently. For example, in an elaboration of the suggestion by Nichols (1962, 1967) of a sipunculid ancestry for the lophophorates, Ryland (1970) emphasized similarities between the Sipunculida and Ectoprocta in order to reconstruct a plausible ectoproct ancestor. Although a general kinship between the sipunculids and lophophorates is not unreasonable, we feel that a much more direct connection can be demonstrated between the Phoronida and Ectoprocta. Any pathway between the Sipunculida and Ectoprocta would probably involve an intermediate form closely resembling a phoronid in basic body plan and behavior.

We examine here the question of the ancestry of the Ectoprocta and attempt to identify the adaptive pathway along which this phylum is likely to have arisen. We propose a model which traces the ectoprocts from a phoronid ancestor through an adaptive strategy based on the advantages of coloniality and small size.

GENERAL FEATURES OF THE PHORONIDA AND ECTOPROCTA

A detailed comparison of Phoronida and Ectoprocta is unnecessary here, and only a summary of the major adult features of each group is given. Much of the following information was taken from Hyman (1959), Ryland (1970), and Emig (1971).

The Phoronida are vermiform coelomates (usually 80–250 mm), with a tentaculate horseshoe-shaped lophophore which is non-

retractable. The Ectoprocta are much smaller (less than 0.5 mm) and are characterized by a circular or crescentic lophophore which is retractable. In both groups the digestive tract is distinctly regionated and U-shaped, the lophophore embracing the mouth, but the anus being located mid-dorsally, outside the lophophore. In both groups the coelom is divided into two distinct regions, mesocoel (anterior) and metacoel (posterior), by an imperfect septum located at the base of the lophophore. Phoronids possess a closed circulatory system and a pair of metanephridia that also function as gonoducts. Ectoprocts lack nephridia and do not have a closed circulatory system. In both groups the nervous system consists of a plexus throughout the body wall with a main ganglionic mass situated dorsally between the mouth and the anus, continuous with a nerve ring encircling the lophophore. In the lophophore of the Phoronida, ciliated tentacles arise in single rows along two ridge-like extensions of the body wall, separated by a ciliated buccal groove. The paired lophophore arms coil spirally away from the mouth, the buccal groove being continuous along each limb. The mouth is mid-ventral between the two lophophoral ridges and forms a crescentic aperture continuous with the buccal grooves. The mouth is covered dorsally by a crescentic fold of the body wall—the epistome. Although differing in detail, the general constructional features of the ectoproct lophophore closely resemble those seen in the Phoronida. In the Stenolaemata and Gymnolaemata the lophophore is a circular ridge of body wall bearing a single row of ciliated tentacles, encircling the mouth which is located centrally at the base of the tentacular crown. In the Phylactolaemata (fresh-water ectoprocts) the lophophore is generally crescentic or horseshoe-shaped, much like the phoronid lophophore.

Phoronids secrete a cylindrical, chitinous tube within which they can move freely. The secretion is initially soft and sticky, and, in appropriate sediments, particles

such as sand grains or shell fragments adhere to it to form a rigid, agglutinated tube. Phoronids usually occur in aggregations that in some species are partly propagated by asexual reproduction (Emig, 1971). Most species are infaunal and the tubes are straight and erect. However, in some species aggregations of tubes form entangled masses cemented to some hard substrate, such as rocks or pilings. An unusual habit of boring into hard substrates, such as mollusk shells or calcareous rock, is documented for two species, *Phoronis ovalis* and *P. hippocrebia* (Emig, 1971). Phoronids may be hermaphroditic or dioecious. Embryos are most often brooded within the concavity of the lophophore, but may be released directly into the water or attached to the interior of the tube. They develop into characteristic actinotroch larvae. Emig (1971) documents the occurrence of asexual reproduction in *P. ovalis* by transverse fission, by budding, or by the regeneration of a detached lophophore.

Ectoprocts are strictly colonial, the colonies originating by asexual budding of a single founding individual derived from the metamorphosis of a sexually-produced larva. The colony is composed of individuals (zooids), each enclosed in an exoskeletal case (zoecium) which may be composed of a flexible chitinous cuticle or, more commonly, calcium carbonate. Asexual reproduction is usually accomplished by lateral partitioning of the body wall, with growth and development of the bud to form a functional zooid. Mature ectoproct colonies also reproduce sexually; the majority are hermaphroditic (monoeocious), but the dioecious condition is known to exist in some forms. This has led to confusion concerning the dominant mode of fertilization in ectoprocts. According to Hyman (1959), most specialists believe the majority of ectoprocts to be self-fertilizing. But observation of sperm release into sea water by some species (Silén, 1966; Bullivant, 1967) and the detection of high genetic variability in populations of other species (Gooch and Schopf, 1970)

suggests that outbreeding is probably the general rule. Fertilized eggs are shed directly into the water or, in most marine forms, are brooded to the larval stage within specialized zooids modified for reproduction.

The ectoprocts underwent a rapid diversification in the later part of the early Ordovician (Larwood et al., 1967; Ross, 1964) with the almost simultaneous appearance of all major Paleozoic groups. Among the earliest known genera is the stoloniferous ctenostome *Marcusodictyon*, preserved as excavations in brachiopod shells in the Lower Ordovician of Estonia (Bassler, 1953). Of the stenolaemate ectoprocts, major groups appear more or less simultaneously, making it difficult to resolve the precise biostratigraphic relationships among taxa (Larwood et al., 1967). The explosive appearance of ectoproct lineages in the early Ordovician suggests that they may have evolved from several unskeletonized ancestral stocks that were well established at least by latest Cambrian or earliest Ordovician time. As might be expected in the absence of a hard skeleton, no body fossils of the Phoronida are known. Although body fossils of unskeletonized invertebrates occur sporadically in the fossil record, their absence should not be taken as evidence that soft-bodied organisms were not present.

ANALYSIS

General Statement

If we are to postulate the derivation of ectoprocts from a phoronid-like ancestor, we must establish that all major differences between the two groups can be explained by adaptation and modification along reasonable evolutionary pathways, i.e., pathways which at every point contain viable organisms operating in appropriate modes of life.

Clark (1964) traces the evolutionary trend among the lophophorates from the infaunal tubicolous habit, seen in the living Phoronida, to the sessile epibenthic habit,

seen in living ectoprocts and brachiopods (except for linguloids). Clark believes that the coelom functioned initially as a hydrostatic skeleton in burrowing. In the Phoronida the hydrostatic system serves both for burrowing and for moving the animal within its tube, but has probably been modified least from the primitive condition. In the Ectoprocta the hydrostatic system has undergone modification to accompany a completely sessile existence, and functions only in the eversion and retraction of the polypide. Despite modification, however, the body wall musculature has remained largely unchanged, retaining the basic design seen in the Phoronida.

In an attempt to extend Clark's analysis, we offer a model which accounts for all major differences between the phoronids and ectoprocts within a framework of adaptive evolution. Five major adult features separate living phoronids and ectoprocts: colonial habit, small size, the lack of nephridia, the lack of a closed circulatory system, and a retractable lophophore.

Colonial Strategy

Colonial organisms are defined as associations in which the interests of the individual are subordinated to those of the group (Barrington, 1967:443). Colonial habit can also be considered in terms of the degree of integration and differentiation of the individuals making up the association (Cowen and Rider, 1972). At higher levels of integration, individuals are commonly closely related as in social insects, or genetically identical as in colonies propagated by asexual reproduction. In such situations, the potential for continuity of physiological response is great, and cooperative, "altruistic" behavioral patterns can take on a high selective advantage (Wilson, 1971). The advantages of the colonial strategy in such circumstances generally include regulated competition among individuals (Knight-Jones and Moyse, 1961), coordinated manipulation of the environment in feeding and in waste disposal, protection by structural or sen-

sory devices, and the potential for functional differentiation and specialization among individuals leading to increased efficiency (Mackie, 1963).

The advantages of the colonial strategy are well understood, and where higher levels of integration are achieved, a new order of individuality emerges—that of the compound organism. It is clear that constructional features of many ectoproct zoaria include structures such as roots, spines, and supports which are of no direct value to the individual, but which are advantageous to the colony as a whole (Tavener-Smith, 1969). In a compound skeletal structure like that of ectoprocts, important advantages are gained by secretion of a comparatively large zoarium capable of providing greater support and protection for the whole group. The colonial strategy involves a modular construction (Vermeij, 1970) in which various subunits are arranged to form an integrated functional whole. In applying this principle, Cowen and Rider (1972) suggest that the fenestellid cryptosomes may have had sophisticated cooperation among groups of zooids (functional units) in generating colonial feeding currents. Similarly, in the living ectoproct, *Plumatella*, the water currents generated by individuals are coordinated to benefit the colony as a whole.

Functional differentiation and specialization among the individuals of a colony is a common feature of the ectoprocts. In living cheilostomes a high degree of polymorphism has been achieved through the specialization of individuals in feeding, reproduction, protection, and so on.

Small Size, Feeding, Circulatory and Nephridial Systems

Small size is a common, but not universal, corollary of colonial life. Seemingly, this relationship is more than coincidental, having obvious adaptive advantages for the organism. Small individuals are metabolically cheap to produce, maintain, and replace, and therefore are relatively ex-

pendable. In organisms like ectoprocts, which frequently have an accretionary skeleton, the individual may not grow large enough to encounter the problems associated with allometric size/area/volume increases (see Vermeij, 1970). In short, the colonial strategy involves a modular construction, and therefore the size of the constituent modules is small in relation to the colony.

The small size of ectoprocts is correlated with other facets of their biology. Ectoproct lophophores are relatively simple in their construction, a feature appropriate to a small organism. The lophophore is not involved directly in food collection, sorting or transport, but serves only to generate water currents which "throw" particles directly at the mouth (Bullivant, 1968). The food resources are not well known, but are probably in the lower size range of suspended matter (phytoplankton, suspended detritus) possibly supplemented by dissolved nutrients at times (Schopf, 1969).

It seems clear (Hyman, 1959:500) that the lack of nephridia and of a closed circulatory system in ectoprocts can also be attributed to small size.

Retractable Lophophore

Clark (1964) suggests that differences in the hydrostatic system of the phoronids and ectoprocts can be understood in terms of differences in individual mobility. Whereas a phoronid can move freely within its tube, an ectoproct lacks this facility. The highly integrated colonial habit of the ectoprocts, in which organic contact between zooids is maintained, implies a loss of mobility for the individual. The body wall of the zooid is firmly attached to the zoarium, and the lophophore is everted and retracted relative to this fixed surface. The hydrostatic system has undergone modification to accompany the change toward a sessile mode of life. The retractable lophophore of an ectoproct can thus be interpreted as a coadaptation to colonial life.

ORIGIN OF THE ECTOPROCT GROUND-PLAN

It is apparent to us that the differences between phoronids and ectoprocts represent a suite of characters, all associated in a coadaptive way with two different life strategies. Phoronids are relatively large, motile animals which live an individualized existence; ectoprocts are small, sessile animals which form highly integrated colonies. We must now construct an adaptive model which will link these two strategies in a reasonable way.

Historically, we envision a late Precambrian tubicolous infaunal vermiform lophophorate descended from actively-burrowing coelomate ancestors (Fig. 1). We would probably identify such a form as a phoronid, were it living. Near the beginning of Cambrian time, one or more lophophorate lineages became epifaunal, some of them giving rise to the brachiopods (Cowen and Valentine, in press). Other epifaunal lophophorates, propagating asexually, aggregated on hard substrates.

The disadvantages of aggregation, chiefly related to crowding, were overcome by the development of a smaller individual body size and by the regulation of spacing and dispersion patterns of individuals through the adoption of a colonial habit. As a preadaptation to a sedentary colonial existence, the hydrostatic skeletal system underwent modification to function primarily in the eversion and retraction of the lophophore. Genetic identity among individuals of the colony promoted intercommunication among individuals and functional differentiation led to increased efficiency in controlling the environment. Miniaturization was accompanied by the loss of distinct circulatory and excretory systems, along with simplification of the lophophore and feeding mechanism.

Probably the earliest ectoprocts were relatively simple, soft-bodied types which encrusted hard substrates. It is interesting in this context that among the smallest known living phoronid species, *Phoronis ovalis* (Emig, 1971) bores into hard sub-

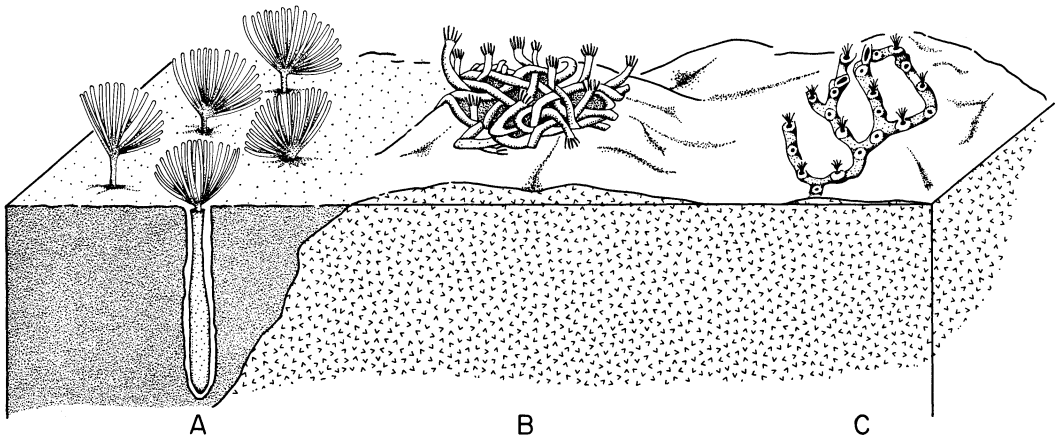


FIG. 1.—An adaptive model for the origin of the Ectoprocta. Early infaunal, tubicolous phoronid ancestors (1) gave rise to one or more epifaunal lineages (2) which formed entangled aggregations on hard substrates. In Cambrian times, these gave rise to one or more ectoproct lineages (3), initially simple soft-bodied forms which encrusted hard substrates. These early ectoproct lineages gave rise to a diversity of forms which, with the advent of skeletonization, appear in abundance in the fossil record of the early Ordovician.

strates forming aggregations of tubes which originate in large part by asexual reproduction. Apart from the difference in coloniality, this mode of life is not far removed from that of some modern stoloniferous ctenostomes and by analogy provides an indication of possible intermediate Cambrian forms. Calcification of zoaria in early Ordovician times may have been favored for reasons of increased structural support and protection. This permitted the exploitation of a variety of colony growth forms and led to a vast ecological potential for the group. Elaboration of the hydrostatic devices related to eversion and retraction of the lophophore, and increasing functional differentiation among individuals, gave rise to a variety of advanced ectoproct taxa. Their success in the benthic communities of the middle and late Paleozoic, interrupted briefly in Permian-Triassic times, continues today.

Our hypothesis of ectoproct origins is necessarily rather speculative, but nevertheless can be subjected to test and is even capable of being disproven. Evidence that would support our conclusions is expected to come chiefly from work on trace fossils

or from impressions of soft-bodied organisms such as are occasionally recovered from the fossil record. Our model assumes the existence of late Precambrian phoronids or protophoronids that, as suspension feeders, formed relatively permanent burrows in soft substrates. Examples of such burrows would stand a reasonable chance of preservation. Careful study of the burrows of living phoronids—which occur at times as clusters of vertical tubes with agglutinated walls—might provide the necessary basis for a comparative analysis of fossil forms. Trace fossils that may well represent the activities of phoronids have been referred to the ichnogenus *Skolithus*, some members of which are among the earliest trace fossils, having been recorded from the late Precambrian Buckingham sandstone of the Wessel Group, northern Australia, with a reported age of 790 m.y. (Glaessner, 1969). The discovery of late Precambrian body fossils of phoronids would also support our suggestion.

Disproof of our hypothesis would depend chiefly upon the establishment of a date of origin for phoronids late enough to preclude their ectoproct ancestry. The dis-

covery of fossil phoronids only after the early Ordovician, for example, would provide strong evidence against our hypothesis. Methods of protein sequencing, a recent outgrowth of advances in genetics, may provide another line of evidence in evaluating the hypothesis. We hope that this contribution will prompt a closer look at the question of ectoproct origins and that attempts to examine our hypothesis will be made by those with access to appropriate materials and methods.

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