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An Adaptive Model
for the Evolution
of the Ectoproct Life Cycle

JACK D. FARMER

I. INTRODUCTION

The phylogenetic relationships among higher taxa pose some of the most intriguing and challenging problems of evolutionary biology. The lophophorate

basis of morphology—a knowledge that at present appears to be far more complete for the adult stage than for earlier phases of the life cycle of most groups. An incomplete knowledge of the adaptive basis of larval morphology and behavior in many groups makes it difficult to identify the features that may be important to considerations of phylogeny. Far higher metazoan taxa, phylogenies based on strictly embryological or larval features may only be tested in a strict historical sense where they are borne out independently by patterns of morphological change in the fossil record of the adult. For these reasons, a comparison of adult morphologies is believed to be *the most* reasonable starting point for considerations of the origin of higher categories.

II. THE GROUND PLAN CONCEPT AND ITS BEARING ON THE ORIGIN OF PHYLA

At progressively higher levels in the taxonomic hierarchy, organisms share a more inclusive set of characters and the basic body plan shared by all individuals is increasingly more generalized (Ghiselin, 1972). At the phylum level, the definition of similarity is based on a suite of characters shared by a large number of species and which group particular subsets of species (genera, families, etc.) into that phylum. These features are embodied in what has been called the "ground plan" of the phylum (e.g., see Valentine, 1973a, p. 51). Ground plans need not include only aspects of adult morphology, and in fact each phylum *is* characterized by larval or embryological features that also participate in the definition of the phylum. These features are fundamental in a taxonomic sense and equally, therefore, in the reconstruction of phylogeny. But more than that, they may reflect a suite of adaptations that were present in the ancestral stocks that originally gave rise to the phylum.

The goal of **most** systematists is a usable classification that also reflects phylogeny and an important assumption **is** that the morphological similarities used in constructing a taxonomic framework more often reflect common ancestry than convergence. The characteristics comprising the ground plan are important in the detection of convergence in that all subsequent adaptations must develop within the constraints imposed by earlier adaptations, representing variations on the major morphological theme imposed by the ground plan.

Although morphological similarities are fundamental in determining phylogeny, differences in morphology play an equally important role, and one that goes beyond providing a basis for the detection of convergence. Because morphological differences are assumed to be underpinned by differences in biological function, they also **possess** paleoecological value in providing the basis for reconstructing and understanding the possible evolutionary pathways that groups may have followed since their divergence.

III. THE POSITION OF THE ECTOPROCTA IN LOPBOPWORATE PHYLOGENY

Recent proposals that concern the relationship of the Ectoprocta to the other lophophorate phyla may be considered in light of the dichotomy of approach mentioned earlier. Most authors who have made comparisons of adult morphology regard the Phoronida as possessing the greatest number of primitive lophophorate characters, thus placing them nearest to the ancestral lophophorate stock (e.g., Silén, 1944; Marcus, 1958; Hyman, 1959). An interesting argument for this is found in the work of Clark (1964, pp. 235–238), who traces the evolutionary trend among the lophophorates from the infaunal, tubicolous habit of the Phoronida to the sessile, epibenthic habit of living Ectoprocta and most Brachiopoda. This model is based on Clark's belief that the primitive function of the coelom was as a hydrostatic skeleton in burrowing, and that elaboration of the role of the coelom in locomotion among early metazoan precursors was the basis for the adaptive radiation and early differentiation of these phyla. It seems likely that this radiation occurred in late Precambrian time (Valentine, 1973b). Among the lophophorates, the hydrostatic system of the Phoronida has probably been modified least from this assumed primitive condition, serving in burrowing, but primarily in moving the animal within its tube. In the ectoproct adult, the hydrostatic system has undergone changes to accompany a completely sessile existence,

Cowen (1974) has pointed out recently that respiration may have played an equally important role in early metazoan evolution in association with the locomotory functions stressed by Clark (1964). Among deeper burrowing, metamerically segmented coelomates, respiratory exchange would have been accomplished by currents set up by peristalsis associated with active burrowing. However, among the more sedentary oligomerous groups (such as the Phoronida), incapable of prolonged active burrowing, alternative adaptations for effective respiratory exchange may have been required. One possible adaptive solution to this problem could have been the development of a specialized tentaculate organ which functioned in both respiration and suspension feeding.

Nielsen (1971; Chapter 16, this volume) derives the ectoprocts from a solitary, entoproct-like ancestor based upon a consideration of both larval and adult features. Although this work represents a noteworthy contribution toward a phylogeny based on entire life cycles, it dismisses the significance of several differences in the adult ground plans of ectoprocts and entoprocts that have led others (e.g., Hyman, 1951, 1959; Hadzi, 1958; Brien, 1970; Jägersten, 1972) to place the Entoprocta in a separate phylum, much nearer the annelid line of evolution. The view of these later authors is adopted here because of the marked difference in the body cavity architectures of adult ectoprocts and entoprocts. It is by no means clear that the similarities between ectoprocts and entoprocts identified by Nielsen (1971, pp. 315–331) cannot be accounted for by conver-

gent evolution in light of *the* strong similarity in the life **styles** of the two groups.

Jägersten (1972, pp. 25—64) derived **a** model for lophophorate phylogeny, based primarily on larval ontogenies, that **traces** the entire group to a **sessile,** "protentaculate" ancestor that possessed a cyphonautes-type larva. In this scheme, the Brachiopoda arose first, with the Phoronida and Ectoprocta appearing successively from later evolutionary branches. This model fails to consider the functional origin of important adult features, such as *the* coelom. Furthermore, it rests in large part on the assumption that the cyphonautes larva of the ectoprocts is primitive among all lophophorates. The cyphonautes is viewed by Jägersten (1972, **p.** 40) **as** being poorly adapted to a pelagic existence owing to the presence of features in its ground plan {notably, a bivalved shell and ciliated oral creeping "foot"—the pyriform organ) that are alleged to have evolved in the benthonic adult stage **of** a remote ancestor, and were gradually shifted to the larval stage by "adult pressure" to speed metamorphosis. The work of Atkins (1955b) and Strathmann (1973) suggest, however, that the cyphonautes is, in fact, highly adapted to a planktotrophic existence. In view of the high estimates of larval mortality rates (>99%) that characterize many benthic invertebrate species with planktotrophic larvae (Thorson, 7946; Mileikovsky, 1971), there seems to he little reason to suspect that selection prior *to* metamorphosis in these groups should be less effective in eliminating poorly adapted traits than selection in the adult stage. Considering the types and intensities of selection that appear to operate during the pelagic **larval** stage of the life cycle (see Vance, 1973), it seems unreasonable *to* suggest, as Jägersten does, that ancient adult characters which lack functions beyond the acceleration of metamorphosis should persist there at all, particularly where they are no longer present in the adult **stage.**

Accepting in principle **Clark's** (I 964) proposal for lophophorate phylogeny and remaining **within** the theoretical framework developed previously, the following model **is** an extension of recent **work** by Farmer *et al.* (1973) that derives the ectoprocts From a phoronid ancestor by adaptation leading to coloniality and small size. In developing this hypothesis further, the implications of the proposed phylogeny for evolutionary trends at the larval stage will also be considered.

IV. GENERAL FEATURES OF THE PHORONIDA AND ECTOPROCTA

A. General Statement

In order to postulate a phoronid ancestry for the ectoprocts, all major morphological differences in the ground plans of the **two** groups must be

accounted for in a reasonable and efficient way by adaptation along evolutionary pathways that at every step contain viable intermediate forms operating in appropriate modes of life. **As** a first step in the development of this model, a general comparison of living Phoronida and Ectoprocta is necessary in order to elucidate the important differences in the adult ground plans of the two groups. The account that follows is based largely on the reviews of Hyman (1959). Ryland (1970), and Emig (1971).

B. Comparative Analysis

The Phoronida are small (most adult species range from 80–250 mm in length), vermiform coelomates possessing a tentaculate horseshoe-shaped lophophore that is nontractable (Fig. 1B). The phylum is small, consisting of approximately a dozen species distributed among **two** genera (Emig, 1974b). The Ectoprocta are a much larger phylum consisting of an estimated 4000 living
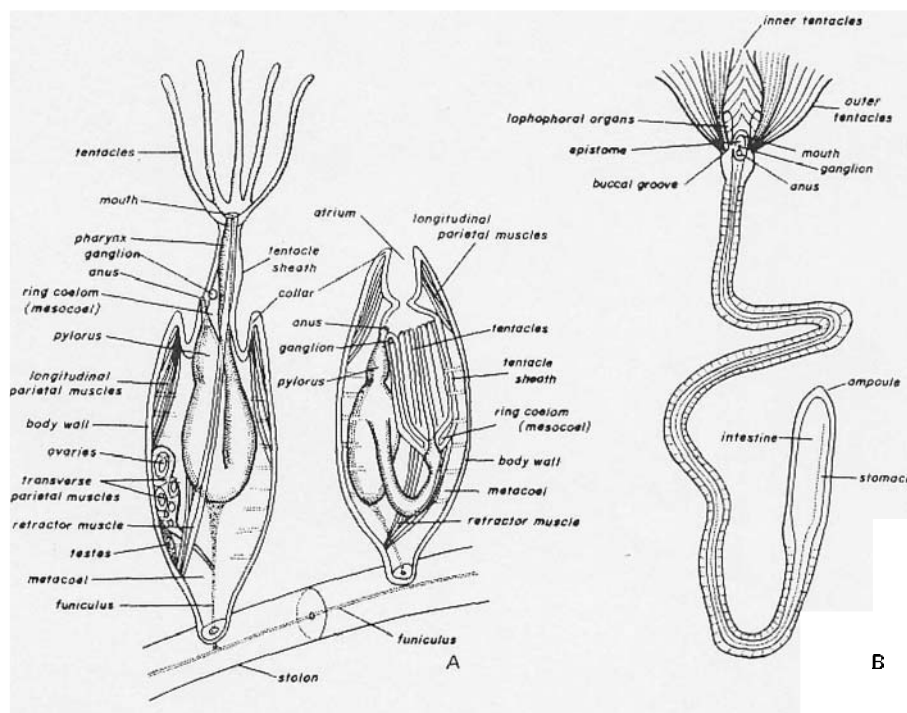

Fig. 1. Comparative **adult** morphology of **the** Phoronida and Ectoprocta. **(A)** Schematic **diagram** of **a** portion of an ectoproct colony **showing** an autozooid with the lophophore everted for feeding (left) **and a** nonfeeding zooid with the lophophore retracted (right). (B) Schematic **diagram** of **a** phoronid **(based on** Cori, 1939).

species and perhaps four times as many fossil species. They are smaller in size (usually <0.5 mm), are coelomate, and possess a crescentic or circular lophophore that is retractable (Fig. 1A). In both groups the digestive tract is distinctly regionated and U-shaped with the mouth being located within the circlet of tentacles and the anus "mid-dorsally," outside the lophophare.

In the phoronid lophophore, ciliated tentacles arise in single rows from two ridgelike extensions of the body wall which are separated along their length by a ciliated buccal groove, The paired arms of the lophophore coil spirally away from the mouth, which consists of an oval or crescentic aperture that is located between the two lophophoral ridges and which is continuous with the buccal grooves on either side. The mouth is covered dorsally by a crescentic flap of body wall called the epistome.

Although differing in detail, the general constructional features of the ectoproct lophophore are remarkably similar to those seen in the Phoronida. In the stenolaeinate and gymnolaemate ectoprocts, the lophophore is formed from a circular ridge of the body wall, bearing a single row of tentacles which encircle the centrally located mouth. In the phylactolaemate (freshwater) ectoprocts, the lophophore is generally crescentic or horseshoe-shaped and the mouth is covered dorsally by a crescentic epistomal flap of body wall, similar to that of phoronids.

Although controversy exists concerning the details of food particle capture and transport, several authors (Bullivant, 1968;Strathmann, 1973; Winston, this volume) have noted strong similarities in the feeding methods of all the lophophorate phyla. In phoronids, ciliary currents enter between the double rows of tentacles, passing outward at their base. Food particles impinging on the frontal surfaces of the tentacles are captured and transported by ciliary action into the buccal grooves, and eventually carried to the mouth. In the ectoprocts, currents enter at the top of the tentacle crown, exiting radially between the tentacle bases. Apparently mucus has not been demonstrated to play a role in the trapping or transport of food particles in the lophophorates. Bullivant (1968) coined the term "impingement feeding" to describe the mechanism of fond particle capture in the lophophorate phyla, by which particles entering the tentacle crown are carried across flow lines by their own momentum and essentially "thrown" at the mouth. But Strathmann (1971) doubts the effectiveness of the impingement mechanism in food capture because most particles are only slightly denser than water and possess negligible momentum of their own. As an alternative explanation, Strathmann et al. (1972; Strathmann, 1973) suggest that most food particle capture and transport in these groups is accomplished by the intermittent reversal of the beat of lateral cilia which directs the particles toward the frontal surface of the tentacle.

In both groups a spacious coelom is divided into two distinct regions, an anterior mesocoel and posterior metacoel, by a septum located at the base of the lophophore; this septum is complete in phoronids. but incomplete in bryozoans.

The presence of a third division of the coelom, corresponding to the protocoel of other oligomerous grou_ , is believed by some authors to be represented by the epistome present in the phoronids and phylactolaemate ectoprocts.

In both the phoronids and ectoprocts, the nervous system consists of a plexus throughout the body wall, with a main ganglionic mass situated between the mouth and anus that is continuous with a nerve ring that encircles the base of *the* lophophore. In *most* phoronid specks, *there* is generally a giant nerve fiber that passes from the mid-dorsal region of the nerve ring to the left side, where it descends within the epidermis at the attachment site of the left-lateral mesentery. In a few species, a second giant nerve is present in a complementary position on the right side. Each of the giant fibers gives off throughout its length transverse branches that enter the basement membrane of the muscular region of the trunk.

Phoronids possess a circulatory system of the closed type and a pair of metanephridia that also function as gonoducts. In contrast, circulatory **and** nephridial systems axe absent in ectoprocts.

Phoronids secrete a cylindrical, chitinous tube within which they can move freely. The secretion is initially soft and sticky and in appropriate sediments **picks** up grains of sand or shell fragments that adhere to it, forming a rigid, agglutinated structure, Most species live infaunally in soft, sandy to muddy substrates of the littoral zone, where the tubes stand vertically within the sediment. However, in some species aggregations of tubes form entangled masses attached to some hard substrate, such as rocks or pilings. An ususual habit of boring into hard calcareous substrates, such as mollusk shells or limestone, is known for three species, *Phoronis hippocrepia, P. ijimai,* and *P. ovalis.*

The Ectoprocta **axe** strictly colonial, the colonies originating by asexual budding of a single founding individual or ancestrula, derived from the metamorphosis of a sexually' produced larva. The colony is composed of individual zooids, each enclosed in an exoskeletal case (zooecium) composed of chitinous cuticle, or more commonly, cuticle and calcite. Functional differentiation and specialization among the individuals of the colony is a common feature of ectoprocts. In living cheilostomes, a high degree of polymorphism has been achieved through the specialization of individuals for feeding, reproduction, protection, etc. (see Silén, this volume, Chapter 6).

Phoronids may be hermaphroditic or dioecious. In many species, embryos are held within the concavity of the lophophore of the parent and in one species, within the parental tube, where they are brooded to larval stage. In a few species, no brooding is observed and all development occurs externally in the water. Embryos of all but one species develop into the characteristic actinotroch larva. Phoronids tend to be gregarious, occurring in aggregations that in some species are propagated in part by asexual reproduction (see Harmer, 1917; Marcus, 1949; Emig, 1972).

The majority of ectoproct species are hermaphroditic (monoecious), but the d ecious condition **is** also known. The hermaphrodotism is protandrous and this led to confusion among early workers regarding the dominant mode of fertilization in the group. However, observations of sperm release in a number of gymnolaemate and stenolaemate ectoprocts (Silén, 1966, 1972; Bullivant, 1967; Ström, 1969) and the detection of **high** genetic variability in populations of other species (Gooch and Schopf, 1970) suggest that outbreeding is probably the general rule. Fertilized eggs are shed directly into seawater where they rapidly develop into the distinctive cyphonautes larval form or, in most marine forms, *are* brooded to the larval: stage within the maternal coelom, or externally attached to the parent in specialized reproductive structures.

The Phoronidn exhibit remarkable powers of regeneration of the anterior end in particular, and they regularly cast off their lophophores and regenerate new ones following the *onset* of unfavorable conditions. The Ectoprocta show similar powers of regeneration as polypides undergo regular cycles of degeneration and regeneration due to natural senescence, the onset of unfavorable conditions, *or* in association with sexual reproduction. The powers of regeneration generally exhibit a gradient within the colony, being greater in the younger, more distal regions. Marcus (1926) explained degeneration not associated with **sexual** repro-*duction* as a method of excretion resulting from the accumulation of substances in the stomach epithelium. Capabilities for regeneration are not confined to the polypide alone, and the repair of structural damage to the colony or replacement of feeding zooids by specialized polymorphs has also been observed.

V THE ADAPTIVE BASIS OF MORPHOLOGICAL DIFFERENCES IN THE ADULT STAGE OF PHORONIDS AND ECTOPROCTS

Based on the preceding comparison, it is apparent that the major differences in adult morphology that separate living ectoprocts from living phoronids include a colonial habit, small size, differences in lophophore complexity and feeding, *the* absence of nephridial and closed circulatory systems, and the hydrostatic function of the coelom. In developing an evolutionary model linking phoronids and ectoprocts, the possible adaptive basis of each of these differences in adult morphology will now be considered.

Colonial organisms have been defined as associations in which the interests of the individual are subordinated to those of the group (Barrington, 1967, p. 443). The advantages of coloniality are **well** understood and are generally considered to include the regulation of competition among individuals (Knight-Jones and Moyse, 1961); coordinated manipulation of the environment, as in the generation of colonial feeding currents to function in feeding or waste disposal (Cowen

and Rider, 1972; Banta *et al.*, 1974); protection of the colony by specialized sensory (see Thorpe *et al.*, 1975) or protective devices; and the potential for differentiation and specialization among individuals to perform such functions as colony sup ort, reproduction, protection, etc., resulting in increased efficiency (Mackie, 1 53).

The adaptive basis of small size is more difficult to assess, although a possible advantage in small colonial organisms like ectoprocts is that the individuals may not **grow** large enough during ontogeny to encounter the problems associated with allometric size/area/volume increases in such functions as feeding and respiration. Small individual body size may hold disadvantages for some other colony functions: however, where late astogenetic developments in many erect colonies include the "nvercalcification" of older individuals in proximal regions of the colony *in* order to strengthen the colony against mechanical stresses during growth (see Cheetham, 1971, p. 12).

The small size of ectoprocts is also correlated with other facets of their biology. Hyman's (1959, p. 500) suggestion that the absence of nephridial and closed circulatory systems in ectoprocts may be associated with their small size is appealing, considering that the efficiency of closed systems for the transport of nutrients and **wastes** must decline in relation to that achieved by direct exchange, as size decreases.

The implication of Clark's (1964) **work** is that differences in the hydrostatic systems of phoronids and ectoprocts can be understood in terms of differences in individual mobility, Phoronids are mobile creatures that can burrow or move freely within their tube, while ectoprocts lack this ability. The highly integrated colonial habit of ectoprocts, in which organic contact between zooids is maintained implies a **loss** of mobility for the individual. The body wall of each zooid **is** stationary, being attached to the substrate or to rigid skeletal walls of the zoarium and the lophophore is everted relative to this fixed surface. The function of the hydrostatic system presumably h a been modified to accompany this sessile mode of life. It seems reasonable, therefore, that the retractable lophophore and difference in hydrostatic function of the coelom in ectoprocts may be interpreted as coadaptations to colonial life.

VI. A MOREL FOR THE ORIGIN OF THE ADULT FEATURES OF THE ECTOPROCT GROUND PLAN

It seems apparent that the differences between phoronids and ectoprocts represent a suite of characters, all associated in a general way with two contrasting modes of life. Phoronids are relatively large, somewhat mobile creatures which live an individualized existence, while ectoprocts **are** small, sessile, **and** colonial. Rased upon the differences that characterize the ground plans of these

phyla Ectoprocta, Phoronida. and Brachiopoda are of special interest in this regard, for although a majority of authors consider them to form a close-knit clade (e.g., Marcus, 1958; Hyman, 19.59; Brien, 1960; Zimmer, 1964, 1973; Jägersten, 1972), the exact relationship of these phyla to other metazoan groups is unclear. This confusion sterns in part from the fact that, as a group, the lophophorates share features common to both the Protostomia and Deutero-stomia and appear to lie close to the divergence of those two major evolutionary lines. Nielsen (1971; Chapter 16, this volume) considers bryozoans to be proto-stomes closely related to entoprocts and isolated from the brachiopods and phoronids. However, other recent work (Zimmer, 1964, 1973; Emig, 1973, 1974a) suggests that the lophophorates in actuality share a larger proportion of features with the Deuterostomia, of which they may represent an early evolu-tionary offshoot.

Interestingly, the phylogenetic relationships among the lophophorate phyla have also been difficult to resolve, as evidenced by the diversity of opinion that currently exists in the literature. This **derives** in part from the fact that compari-sons based on early stages of development: are often in opposition to those based only on a con. irison of adult features. Consequently, most authors have emphasized only one stage of the life cycle in framing hypotheses of lophophor-ate phylogeny. Considering the developmental patterns among the lopho-phorates (Zimmer, 1964, **p.** 267), such inconsistency is not entirely unexpected. Despite the strung similarities in cleavage (but see Rattenbury, 1954), regulative potential, and in the adult coelomic architecture, **few** similarities appear to exist among these phyla with regard to mesoderm formstion and its early differentia-tion during larval development.

During evolutionary change, natural selection may operate independently and in **quite** dissimilar ways at different stages of the life cycle. Therefore, a desired approach in reconstructing phylogeny **is** one in which the entire life cycle is considered (Jägersten, 1972, p. 250). Hypotheses that involve all aspects of the life cycle, although they are difficult to construct, possess greater explanatory power than those based on only one stage. This should be especially *true* for benthic marine invertebrate groups, such as the lophophorates, which have a planktonic larval stage. Prior to metamorphosis in these group.;, larval develop-ment and behavior are subject to a totally different regime of natural selection than is the adult stage (see Vance, 1973). Thus, evolution in such groups may have followed adaptive pathways in the larval stage quite independent of those in the adult. For groups where morphological divergence between stages of the life cycle has been extreme, a total reorganization at metamorphosis (such as **that** observed in the Ectoprocta) is not unexpected.

Most taxonomy is based upon morphological features of the adult, and these **axe** the features that are commonly preserved in the fossil record, In addition, phylogenetic speculation ideally proceeds from a knowledge of the functional

two groups, a model is proposed that accounts for the observed differences within a framework of adaptive evolution.

The common lnphophorate ancestor in the model is envisioned as a tubicolous, infaunal, vermiform coelomate very similar in adult morphology and behavior to living Phoronida. At least by late Cambrian–early Ordovician time one or more lineages of this primitive stock became epifaunal, some propagating asexually on hard substrates to form entangled masses of tubes. This trend toward an epifaunal existence may have been correlated with the general expansion and diversification of other higher taxa of epifaunal filter feeders that occurred in the lower Ordovician, perhaps the result of an overall amelioration of global marine climates (Valentine and Moores, 1970). The disadvantages of intraspecific competition associated with crowding in the early gregarious lineages were gradually overcome by the regulation of spacing and dispersion patterns among individuals **with** the adoption of a colonial habit. As a preadaptation to colonial life, the hydrostatic system underwent change to function in the eversion of the lophophore. This implies a loss of individual mobility prior to the development of coloniality, **perhaps** also associated with crowding or the development of a bnring habit similar to that observed in some living species of *Phoronis* (see Section VIII). Associated with the change toward a sessile, colonial existence was a trend toward decreasing size, perhaps related to trophic specialization in the early epifaunal lineages. Decreasing size was accompanied by the simplification of the lophophore and feeding system and the loss of nephridial and closed circulatory systems.

VII. HISTORICAL EVIDENCE BEARING ON THE MODEL

The Ectoprocta first appear in the fossil record of the early Ordovician and rapidly diversified into the major taxa which dominated the remainder of the Paleozoic (Larwood *et al.*, 1967; Ross, 1964). Due to the almost simultaneous appearance of early ectoproet lineages, phylogenetic relationships are unclear. Among the earliest reported genera is a stoloniferous ctenostome, *Marcusodictyon*, preserved as excavations in brachiopod shells from the early Ordovician of Estonia (Bassler, 1953). The explosive appearance of several well-delineated groups in the lower Ordovician may reflect the contemporaneous appearance of skeletonization in several soft-bodied lineages that were well-differentiated by at least early Ordovician time.

As might be expected in the absence of a hard skeleton, body fossils of phoronids are unknown. However, trace fossils that may be attributable to phoronid activities have been referred to the ichnogenus *Skolithos* (Fenton and Fenton, 1934, Alpert, 1974), some members of which have been reported from rocks in Australia dated at *790* million years (Glaessner, 1969). Anvimeleck

(1955) reported trace fossils attributed to the **genus** *Phoronopsis* from Maestrichtian limestones, **as** well as a boring species—possibly *Phoronis hippocrepia*—in hard, calcareous substrates in the late Cenomanian, early Turonian. and early Pliocene of Israel.

Evidence for the presumed existence of phoronids in the Precambrian or early Paleozoic awaits further study. Results **so** far suggest **an** approach emphasizing a comparative analysis of burrow morphology in living phoronids and their potential fossil representatives to be a fruitful line of research. The smaller boring species of *Phoronis* may well have older fossil records that have heretofore gone unnoticed. This is certainly deserving of further study.

Fossil remains of temporally intermediate forms would provide the strongest evidence for the model proposed. However, such "missing links" are notoriously absent in the fossil record of most groups and the model suffers for a lack **of** testability in this regard. The model is, nonetheless, potentially testable and, hopefully, will serve to direct attention to the fossil record for evidence that may permit a more critical evaluation of the proposed relationships.

VIII. THE VIABILITY OF INTERMEDIATE MODES OF LIFE

Even in *the* absence of intermediate fossil forms linking phoronids and ectoprocts, it **is** still possible *to* evaluate the viability of intermediate modes of life predicted by the model in the light of some living phoronid species. Such modes of life are believed to be represented in the aberrant phoronid species, *Phoronis ovalis.* The fallowing account *of* the biology of this interesting species is based on the observations of Harmer (1917), **Marcus** (1949), Silén (1954). and Emig (1970, 1974b, personal. communication).

The smallest known living phoronid (usually <6 mm in length), *P. ovalis,* bores into hard, calcareous substrates where it reproduces extensively **by asexual** fission, achieving densities of up to 150 individuals/cm^2. The lophophore of *P. ovalis* is highly simplified in relation to other species of the genus, consisting of a single indented ring of ciliated tentacles, much reduced in number (15–28) which arise from a single oval ridge of body wall that surrounds a centrally located, owl mouth. An epistome is present but is much reduced in size, originating as a slight fold in the body **wall** at the base of the tentacles and projecting toward the mouth. The nephridial system is also simplified, but the closed circulatory system is apparently more complex, as it includes a second accessory vessel not found in other phoronid species. The giant fibers **of** the nervous system that characterize larger phoronid species are absent in *P. ovalis,* the muscular part of the body wall being supplied with only a diffuse nerve plexus. In *P. ovalis* bundles of strong longitudinal muscles are restricted to a

relatively short proximal part of the metasome. The distal end of the metasome, bearing the lophophore, possesses an extremely thin body wall which lacks the strong longitudinal muscles found in the proximal part of the **trunk.** *Phoronis ovalis* is capable of completely retracting its lophophore and tentacles into a shallow introvert formed by the invagination of *the* **thin** distal portion of the body wall into the thickened posterior muscular region of *the* trunk (Harmer, 1917, **pp. 139–141). Apparently,** no retractor muscles comparable to those in ecto-**procts** have been documented in *P. ovalis* and the exact method of lophophore retraction and eversion needs further study. It **is** envisioned that lophophore retraction probably involves shortening of longitudinal muscles in the proximal region of the trunk, with eversion being accomplished by muscular deformation of the coelomic cavity to create a positive internal hydrostatic pressure similar to the mechanism found in ectoprocts. Individuals of P. *ovalis* excavate shallow burrows more or Less parallel to the surface of the substrate, **which is** often the shell of a mollusk. During feeding only the tentacles are protruded from the tube. It is conceivable that the adaptations for lophophoral retraction in *P. ovalis* have developed as a consequence of a lack of individual mobility associated with the boring habit and of crowding due to the high population densities commonly achieved by **asexual** reproduction. *Phoronis ovalis* also reproduces sexually, and the large, yolky embryos are retained in the distal end of the tube where they are brooded to the larval stage. Immediately prior to sexual reproduction, the lophophore is cast off and fertilized **eggs** apparently exit from the temporary opening created at the anterior end of the body. The parent then retracts to the proximal end of its tube, entering a stage of dormancy until the larvae escape, at whirh time a new lophophore is generated and feeding resumes. This behavior is similar *to* the cycles of degeneration and regeneration exhibited by some ectoprocts during sexual reproduction.

The intermediate morphological and behavioral patterns exhibited by *P.* ovalis—many of them apparently associated with coadaptations for small size and the opportunistic use of hard substrates—correlate nicely with those pre-dicted by the model and provide an indication of the nature and viability of possible intermediate adult forms linking phoronids and ectoprocts.

IX. EVOLUTION OF THE LARVAL STAGE OF THE LIFE CYCLE

In benthic marine invertebrates that **possess** a pelagic larval stage, she life cycle may be subdivided into larval and adult phases that are linked to each other by only those processes that operate at metamorphosis. The adaptive demands placed on each of these stages of development clearly differ and evolutionary divergence in the adult stage may follow adaptive pathways quite

independent of those in the larval stage. In theory, this observation offers a potential for approaching phylogenetic hypotheses along **two** lines of inquiry and improves our chances of arriving at **a** model with the highest **possible** explanatory power.

In developing the previous evolutionary model linking ectoprocts and phoronids, only morphological features of the adult stage of the life cycle have been emphasized, for reasons discussed earlier (see Section I). In the absence of supporting evidence from the fossil record, the problem of directionality in evolution has been approached indirectly on theoretical grounds, based on the assumed primitive function of the coelom in the metazoa (Section III), and the advantages of a colonial life style (Section VI). But, for the larval stage of the life cycle, where the relative adaptive advantages of morphological differences are less clear, it is more difficult to visualize a theoretical framework that will independently impose directionality to the course of evolution. However, **an** attempt can be made to evaluate the consistency of the interpretations of adult morphology with morphological and behavioral patterns in the larval stage. To accomplish **this,** it is necessary to delineate the salient features of the larval ground plans of phoronids and ectoprocts and to evaluate the probable adaptive basis of morphological differences in these groups. Much of the account of larval biology which fallows **is** based on reviews by Hyman (1959) and Zimmer (1964).

X. THE ACTINOTROCH LARVA OF THE PHORONIDA

The fully differentiated actinotroch larva of the phoronids is characterized by an elongate (1–4 mm) tripartite body **plan** (Fig. 2A). **At** the anterior end, a large hoodlike feature—the preoral lobe—projects downward over the ventral surface of the larva, covering the mouth. **At** the **apical** pole of the larva, in the central region of the hood, is a thickened plate of ectoderm bearing long cilia. This apical plate functions as a sensory organ and constitutes the main nervous center **of** the larva. Posterior to the preoral lobe, slanting ventrally beneath it, is the collar region of **the larva.** Along the posterior margin of this collar. a girdle of tentacles arises from **a** ridge **of** thickened ectoderm that encircles the vestibule formed beneath the overarching hood. The vestibular cavity changes size and shape with movements of the hood and is confluent with the mouth, located anteriorly (and dorsally), The tentacles. and the ridge bearing them, are heavily ciliated and in advanced larvae apparently function primarily to generate feeding currents that enter the vestibule (Lebour, 1922; p. *666;* Strathmann, 1973; **p.** 133). Proximal to the tentacular girdle is an elongate trunk region. The **trunk** terminates in a heavily ciliated ectodermal thickening that surrounds the anus and functions as the principal locomotory organ of advanced larvae.
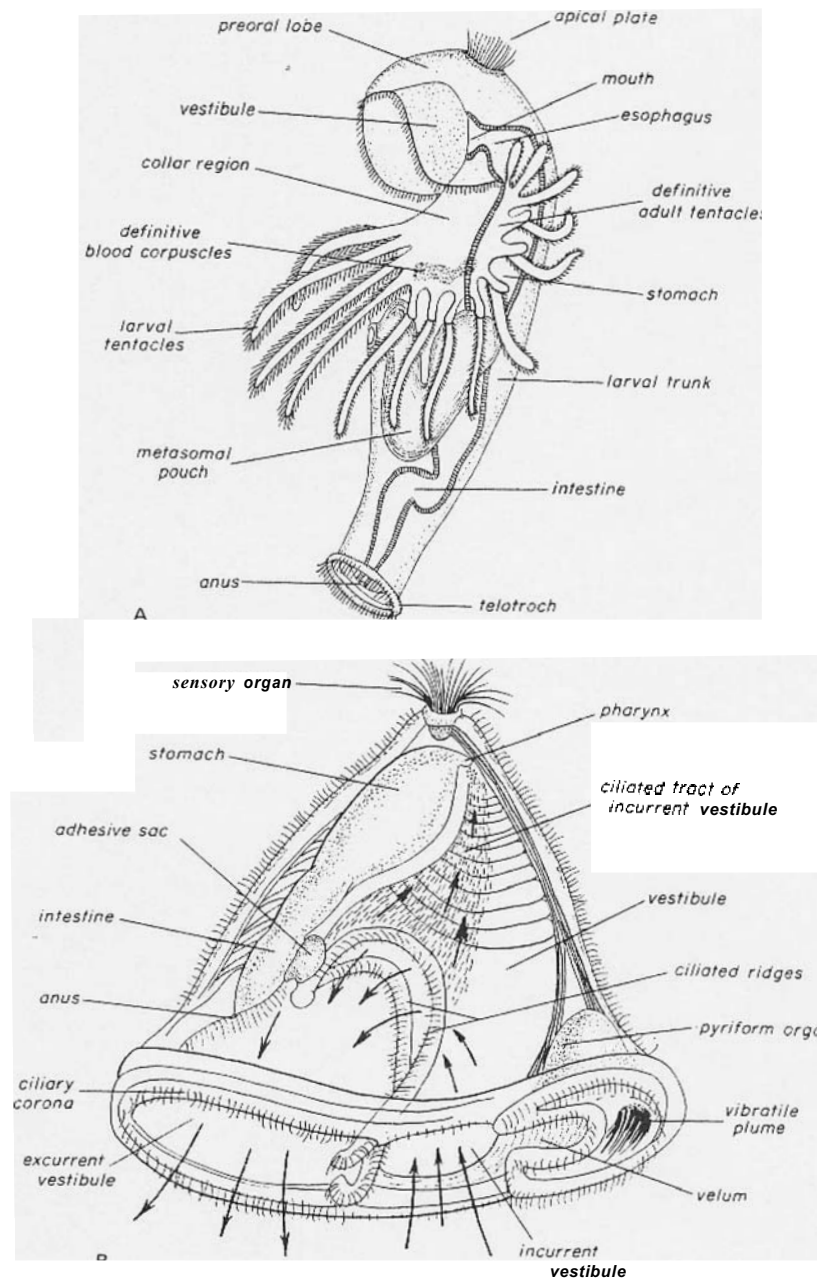
Fig. 2. Comparative morphology of planktotrophic larval forms in the Phoronida and Ectoprocta. **(A)** Schematic showing the major features of the actinotroch **larva** of **the** Phoronida **(based** on Hyman, 1959; and Jägersten, 1972). (B) Schematic showing the major features of the cyphonautes larva of the Ectoprocta (based on Atkins, 1955b).

The larval coelom also exhibits a tripartite construction, consisting *of* a preoral protocoel arid postoral mesocoel and metacoel (see Zimmer, 1964; pp. 275–278 for discussion). The trunk coelom or metacoel is spacious, and is separated from the space of the collar region by a **septum** at the base of the tentacular girdle.

The metasome *is* occupied largely by the digestive tract, which is essentially straight and regionated into an esophagus, elongate stomach, and intestine. Located midventrally immediately below the tentacular girdle is an epidermal invagination called the metasomal pouch. This invagination elongates throughout larval development, eventually forming a large, tubular structure infolded into the coelomic space surrounding the gut.

A larval protocoel occupies much of the preoral lobe of the young actinotroch. During growth of the larva there *is a* gradual flattening of the hood, the protocoel being reduced (commonly to a small vesicle lying beneath the apical plate of the larva) or even obliterated (see Zimmer, 1964, pp. 225–278). Most of the hood cavity of the advanced larva is blastocoelic space that in some species, at least, becomes tilled with a gel-like substance probably secreted by amoeboid mesenchymal cells. The significance of this substance is debatable, hut it may in part function in supporting the preoral lobe (Zimmer, 1964, p. 277). The remaining preseptal space **is** occupied by a hollow blastocoelic cavity in the collar region. This collar blastocoel persists throughout larval life, but prior to metamorphosis it is partially replaced by a horseshoe-shaped collar coelom, the larval mesocoel. This coelom forms at the level of the tentacular girdle, just anterior to the collar–trunk septum.

The protonephridia of the actinotroch larva originate as a single midventral ectodermal invagination just posterior to the tentacle ridge. This primordium soon bifurcates and the paired protonephridia eventually come to lie on either side of the stomach. The nephridiopores remain just below the tentacular girdle and most of the solenocytes project into the preseptal blastocoelic space of the collar region.

The actinotroch larva is provided with a complex musculature, the details of which **vary** considerably between species. Major elements that **are** often present include a pair of longitudinal muscles spanning the trunk coelom on the ventral and/or dorsal sides from anterior attachments in the collar region to posterior attachments near the anus; hood and apical organ retractors, arising beneath the apical plate and traversing the preseptal space to attachments in the dorsal region of the collar; hood levators arising on the dorsal surface of the hood and attaching to the dorsal wall of the collar and trunk; tentacle levators and depressors; radial and concentric muscles of the preoral lobe; and outer circular and inner longitudinal muscles of the trunk and metasomal sac.

The principal nervous center of the actinotroch larva is a ganglion situated beneath the apical plate in the center of the dorsal surface of the preoral lobe. In

addition, the larva is provided with an intraepidermal nervous plexus that is continuous with the ganglion through several discrete nerve tracts. The latter are subject to considerable interspecies variation wi .regard to their location and design, but commonly present are longitudinal tracts arising from the ganglion, traversing the ventral and dorsal margins of the hood, and connecting to a nerve ring at the base of the tentacular girdle; a sensory element located on the midventral surface of the hood, associated with thickenings of the ventral longitudinal tracts; longitudinal dorsal or ventral nerves of the trunk; and a nerve ring encircling the anus.

The actinotroch larva possesses no functional circulatory system, but the major elements of the adult system are anticipated at the larval stage. The details of the larval system vary between species, but one or two longitudinal vessels—actually channels between the stomach wall and lining of the metacoel which are continuous with *the* preseptal collar blastocoel—are generally present in dorsal (and dorsolateral) positions along the stomach. The lophophoral ring vessels of the adult originate from the larval collar blastocoel during the transformations at metamorphosis. Definitive blood corpuscles occur as discrete aggregates, usually attached to the body wall of the collar region or in the preoral lobe. The circulatory elements of the **larva** and adult are considered to be blastocoelic in origin, *but* become lined by mesenchymal cells after metamorphosis (Zimmer, 1964, p. *322).*

Late in the larval development of some species, the definitive tentacles of the adult appear as buds at the base of the larval tentacles. These tentacle buds are associated with evaginations of the horseshoe-shaped mesocoel that develops in the collar cavity late in larval development. In other species, the larval tentacles are retained in the adult, but also become invaded by tubular extensions of the mesocoel prior to metamorphosis. Metamorphosis of the actinotroch larva is usually accomplished very rapidly(15–25 minutes), due lo the high degree of preformation of the adult (Hyman, 1959, p. 259; see also Silén, 1954, p. 251). Following the selection of a suitable substrate, the larva everts its metasomal pouch through convulsive contractions of the larval trunk. Shortening of the longitudinal retractor muscles of the trunk presumably generates high hydro-static pressures within the larval metacoel that assist in forcing the metasomal pouch to evert. With eversion of the metasomal pouch, the digestive tract is carried out and thrown into a U-shaped configuration; shortening of the larval trunk brings the anus and mouth into proximity at the future distal end of the adult. As a consequence, the everted metasomal pouch becomes the definitive trunk of the adult, while the preoral lobe shrinks and is cast off down to near the level of the definitive lophophoral coelom. The larval tentacles may be retained in the adult, but are sometimes cast off with the preoral lobe, the tentacle buds of the adult growing and rapidly increasing in number. The origin of the adult ganglion is unclear; it is generally believed to arise later as an

ectodermal thickening, but in some **species** the larval ganglion may be retained in
, the adult (Zimmer, 1944; p. 313). *The* cavities which form the larval circulatory
system are retained in the adult and become functional as the associated
corpuscular masses break down during the contractions that occur with eversion
of the metasomal pouch. The pratocoel—or epistome—is generally believed to
form later **as** a fold in the dorsal body wall. However, it has been suggested that
in some species, part of the larval protosome and protocoel may be retained
through metamorphosis to form the epistome and its corresponding coelomic
division in the adult (Zimmer, 1964; pp. 279–280).

XI. LARVAL DEVELOPMENT IN THE ECTOPROCTA

In the gymnolaemate ectoprocts, larval forms are quite varied, hut may be
grouped into two main types: the cyphonautes, a planktotrophic form that
develops from nonbrooded eggs that are shed directly into the sea, and a
lecithotrophic form, quite unlike the cyphonautes, that develops from brooded
eggs. The vast majority of living gym laemate ectoprocts brood their eggs and
lecithotrophic forms are therefore the dominant larval type. Silén (1944) be-
lieves such brooded forms to be primitive in the Ectoprocta. However, some
authors (Atkins, 1955a; Brien, 1960; Jägersten, 1972; Zimmer and Wollacott,
this volume, Chapter 3) have viewed the cyphonautes **as an** archaic, and
presumably primitive form within the Ectoprocta, lecithotrophic types having
been derived secondarily with specializations for the brooding of the young. But
the strength of any assumption about larval phylogeny is difficult to evaluate in
view of the strong dependency of **larval** biology on reproductive "strategy" in
living species. The observed decrease in the number of benthic marine inverte-
brate species **possessing** pelagic larvae, from equator to poles, and with increasing
depths in modern oceans underlines the important role of the environment in
patterning the optimal reproductive "strategies" of living species (Thorson,
1946; Miliekovsky, 1971). Arguing by homology, a case can **perhaps** be made for
the cyphonautes being a primitive **larval** form within the Cheilostomata. A-
though **known** for several species of the Ctenostomata, typical planktotrophic
cyphonautes are essentially restricted to certain malacostegoid genera believed to
be primitive to Cheilostomata, based on functional criteria and supported by
evidence from the fossil record (see Cheetham, 1971, **pp.** 11–15 for discussion;
Pohowsky, 1973). However, we have no evidence for extending this same
argument to the entire phylum, which *is* today dominated by lecithotrophic
forms, The implication is that historically, larval biology may have depended
more on the geographic site of evolution than on phylogeny. For example, if
ancestral ectoproct lineages first appeared in seasonal environments such as those
that occur at **high** latitudes today, evidence from living systems would suggest

brooded lecithotrophic forms to be the primitive larval type. Alternatively, if ancestral lineages appeared in stable environments such as those that characterize low latitudes today, the same reasoning would *suggest* planktotrophic forms to be primitive to the phylum. It is of interest in this context that *the* earliest reported record of the Bryozoa (the ctenostome *Marcusodictyon*), is from the lower Ordovician of Estonia, which during that period in geologic history **is** believed from paleomagnetic and geologic evidence to have been positioned within 10"–30" of the paleoequator (see Briden *et al.,* 1974). Unfortunately, our present knowledge of paleobiogeography and the history *of* global marine climate precludes any choice between these alternatives on purely empirical grounds.

In expanding the model for ectoproct origins to encompass the early stages of 'he life cycle, we therefore assume the directionality of evolution arrived at from ⌐ consideration of adult. morphology. The characteristic larval form of the Phoronida *is* planktotrophic, and because the purpose here is only to investigate the plausibility of the actinotroch as an ancestral larval form for the ectoprocts, comparison is, of necessity: confined to the planktotrophic form of the ecto-procts—the cyphonautes.

XII. THE CYPHONAUTES LARVA

The described species of cyphonautes larvae exhibit a range of variability in size (usually 0.2–0.8 mm in length) and in certain details of their morphology (see Ryland, 1965). However, they share in common a bilaterally compressed body plan, and are enclosed between a bivalved shell of chitinous composition (Fig. 2B). This distinctive morphology, along with the presence of a functional gut, Serves to distinguish the cyphonautes from the more common lecithotrophic larval forms found in the vast majority of living ectoproct species.

The chitinous valves of the cyphonautes are generally triangular in outline and may be transparent or minutely agglutinated in structure. The apex of each valve is truncated and often flared to accommodate a knoblike sensory organ that bears tufts of long cilia. Basally the valves gape, and the mantle along the shell margin is thickened and heavily ciliated. This mantle thickening consititutes the ciliary corona which functions as the principal locomotory organ of the larva. Enclosed between the valves is a large mantle cavity, or vestibule, that is divided into anterior incurrent and posterior excurrent regions by two ciliated ridges that project toward each other across the vestibular space.

The digestive system is U-shaped and regionated into ciliated pharynx, stom-ach, and intestine. The funnel-shaped inhalent chamber extends from the base of the shell to near its apex. The pharynx **is** confluent with the heavily ciliated apical region of the incurrent chamber, while the anus opens posteriorly within

the excurrent chamber. Ciliation is weak or absent in the excurrent chamber, although in some species a ciliated tract is present, leading from the anus to the mantle edge (Atkins, 1955a, p. 457).

The shell margin is also regionated into excurrent and incurrent areas by modifications of the structure of the corona that encircles it. Coronal cilia, which function primarily as locomotory devices, beat downward, away from the apex. Along the excurrent margin of the vestibule, ciliation of the corona is heavier, and there the ciliary beat assists the current exiting from the exhalent chamber. **But** along the incurrent margin, where the beat **of** coronal cilia generates currents opposed to those entering the inhalent chamber, cilia are reduced in *size* and number (Atkins, 1955a, **pp.** 455–456). This variation in the size and density of cilia along the coronal margin may have an additional function in governing the attitude of the larva during swimming, as the cyphonautes is **observer!** to carry the apical organ forward during swimming (Ryland, 1965, **p.** 4) further differentiation of the mantle margin with regard to trophic function is provided by a delicate, epidermal fold (the velum) that is present on the corona surrounding the inhalent aperture. This epidermal fold is provided with circular muscles that regulate the **size** of the inhalent aperture and fanlike groups of cilia **that** probably function as a sieve (Atkins, 1955a, p. 454).

The ciliated ridges that divide the mantle cavity into incurrent and excurrent areas bear three longitudinal tracts of cilia that generate the principal feeding current and function in food collection (see Atkins, 1955a, **pp.** 458–461; Strathmann, 1973). Food particles **entrapped** on the medial tract **of** cilia are conveyed up the ridges **by** frontal cilia, and eventually pass onto a ciliated tract that crosses the upper part of the incurrent mantle cavity. Some food particles also reach this tract directly, due to the strong beat of the cilia located in this region of the mantle. The food particles are carried along the ciliated tract and accumulate in an unciliated region in front of the mouth before being **swallowed.**

Situated near the oral surface are two organ systems that are common to all gymnolaemate ectoproct larvae. In an anterior position near the oral surface, immediately in front of the inhalant region of the mantle cavity is the pyriform organ—a complex of glandular cells associated with a ciliated invagination. Near the anterior end of this invagination **is** the vibratile plume—a tuft of long sensory cilia (or flagella). In a posterior position, situated between the vestibule **and anus, is** the adhesive sac—another invagination that is lined by columnar cells that also have a secretory function. Both of these organs increase in size during growth, eventually occupying much of the larval volume in later development.

The cyphonautes larva is equipped with a complex musculature that serves chiefly to retract the corona and various organ systems into the protection of the valves and to regulate closure of the valves (Kupelweiser, 1905; Hyman, 1959, **p.** 349). The muscle **system** of the cyphonautes is intimately associated

with the major elements of the larval nervous system and is commonly united with the latter by a single neuromuscular system. Most major muscles originate from attachments beneath the apical sensory organ and associated ganglion. Spanning a narrow blastocoelic space between the pharynx and outer body wall, an anterior branch descends to the pyriform organ where it forks, sending strands to the vibratile plume and adjacent corona. Posterior dorsal branches ascend to attachments in the apical organ itself, or descend between the body wall and intestine where they supply the posterior region of the corona. Pairs of lateral muscles also extend from medial attachments on the inner surfaces of the valves to insertions in the adhesive sac or the anterior and posterior regions of the corona. Closure of the valves is accomplished by transverse adductor muscles that span the anterior region between the adhesive sac and vestibule, probably assisted by a circular muscle band that is present in the corona, Circular muscles are also present in the pharynx where they function in peristalsis, in the velum where they effect changes in the size of the inhalant aperture, and in the pyriform organ where: they assist in its protrusion.

Metamorphosis of the cyphonautes larva occurs following an often extended planktonic existence that may last as long as two months (Marcus, 1940, **p. 334).** Just before settlement, the larva hovers over the bottom using the vibratile plume in a sensory capacity fox the selection of a substrate for attachment. When a suitable substrate is found, convulsive contractions cause the adhesive sac to evert and then flatten out over the substrate, adhering *to* it by the secretions it produces. Simultaneously, the two **valves** separate by rupturing of the adductor muscles, and then flatten out, covering the mass (Kupelwieser, 1905; Hyman, 1959, **p.** 352). The valves are retained for one to several days and would seem to take on a secondary protective function during the early stages of metamorphosis, prior to the secretion of the definitive cuticle of the ancestrula (see Atkins, 1955b). **All** exclusively larval organs are retracted into the interior of the mass and disintegrate. The result is a flattened mass of loose cells and debris, which is enclosed within an epidermis.

The first definitive adult: organs begin to form from cells ofectodermal origin derived from the apical plate of the larva which invaginate into the interior and eventually separate from the exterior to form a hollow vesicle. This vesicle becomes covered by mesenchymal cells which differentiate from ectoderm to form peritoneum. The initial vesicle enlarges rapidly and by constriction forms a smaller secondary vesicle. The distal **part** of the first vesicle differentiates to form the definitive tentacle sheath, while its proximal **part** gives rise to the adult tentacles and pharynx. The tentacle buds on *the* ventral side arise before those on the dorsal side, imparting an early bilateral symmetry to the developing lophophore. The smaller secondary vesicle differentiates to form the rest of the digestive tract. The main divisions of the coelom became defined through the rearrangement of mesenchymal cells which line the larval blastocoel. Muscles of

the adult also differentiate from mesenchymal cells and the adult ganglion soon forms from an epidermal invagination. Communication is eventually established between the two developing parts of **the** polypide, and the tentacle sheath becomes associated with **an** epidermal thickening that eventually breaks through to form an orifice. **At** this **stage** in development, the polypide of the ancestrula is essentially complete and colony formation proceeds by growth of the primary zooid to form one or more buds. The time elapsed between attachment and development to this stage varies, but generally falls within the range of one to six days (Hyman, 1959, **p.** 354).

XIII. DISCUSSION AND CONCLUSIONS

The strong simil: 'ties in coelomic architecture, construction of the lophophore, and other fea. ures of the ground plan of adult phoronids and ectoprocts have been previously interpreted **as** having a phylogenetic basis. In pursuing this suggestion, an evolutionary model **was** proposed (Farmer *et al.,* 1973) which derives the adult ground plan of the Ectoprocta from a phoronid ancestor by adaptation and evolutionary divergence leading to a colonial habit and small size. Directionality of evolution in the model is based on the assumption that the coelom functioned primitively **as** a hydrostatic skeleton in burrowing (Clark, 1964). Subsequent functional modifications for respiration and feeding in some early oligomerous stocks eventually led *to* the development of a primitive, protentaculate ground plan (Cowen, 1974), bearing a close resemblance to living Phoronida. Also inherent in this interpretation are the assumed advantages of a colonial "strategy" and small individual body size. Both of these adaptations have been acquired independently in the evolution of many unrelated phyla and would seem to have universal advantages under an appropriate selective regime, Intermediate modes of life linking phoronids and ectoprncts are regarded as viable in light of the biology of the aberrant phoronid species, *Phoronis ovalis.*

Consideration of the larval biology of phoronids and ectoprocts reveals that similarities in morphology, comparable to those observed in the adult ground **plans** of these **phyla,** are not apparent at the larval stage. Consequently, it is difficult to visualize a phylogenetic connection between the Phoronida and Ectoprocta based on larval morphology alone. Even if it were possible to associate the two larval forms on the basis of morphological similarity, we still **lack** an independent theoretical framework, comparable to that developed for the adult stage, which would impose directionality to the course of evolution. However, it does not seem reasonable to reject a relationship between phoronids and ectoprocts on the basis of negative evidence from the larval stage alone. In weighing the relative importance of the observed dissimilarities in the larval

morphology of phoronids and ectoprocts, careful consideration must be given to the adaptive basis of morphological differences in the two groups.

Perhaps the most interesting aspect of the ground plan of the phoronid larva is the high degree of preformation of the adult at the larval stage of the life cycle (see Silén, 1954, **p.** 251); indeed, many of the important morphological attributes of *the* actinotroch are best explained by "adulation" (Jägersten, 1972, p. **4**) or the shifting of adult characters into the larval stage which has facilitated an accelerated metamorphosis. Although the "package" of adaptations we associate with the actinotroch larva cannot be explained entirely from the viewpoint of the adult, they are believed to represent the best functional compromise for fulfilling the requirements of a successful pelagic life, on the one hand. and rapid metamorphosis linking the larval and adult stages of development, on the other. This suggests that in the Phoronida evolution at the larval stage has, in general, been closely linked to evolution at the adult stage as *a* consequence of a reproductive "strategy" that emphasizes the advantages of rapid metamorphosis.

In contrast, considerable differences exist between the larval and adult ground plans of the Ectoprocta. The cyphonautes larva is viewed as a **highly** coadapted planktotroph. capable of a sustained pelagic existence. In the Ectoprocta there seems to have been considerable independence in the evolution of the adult arid larval stages of the life cycle in that none of the features of the larva bear any clear relationship to those of the adult. In the case of the cyphonautes *larva, the* strong morphological divergence between the larval and adult stages is undoubtedly linked to a reproductive "strategy" which emphasizes the advantages of planktotrophy and long-range dispersal. In addition, the complex and prolonged metamorphosis that is characteristic of the Ectoprocta as a whole may be a necessary consequence of this evolutionary divergence of larval and adult stages *of* development during the early history of the group.

A noteable departure from the general pattern of larval development, behavior, and metamorphosis in the Phoronida has been observed for *Phoronis ovalis* (Silén, 1954). Morphologically, the larva of *P. ovalis* is highly divergent from the typical actinotroch larva of other phoronid species. The trunk region of *the* larva is considerably reduced in size relative to the preoral **hood,** and is ventrally flattened (see Silén. 1954, p. 245, Fig, 22). The larval stage of *P. ovalis* consists of two stages: an early pelagic lecithotrophic stage, serving in general dispersal, followed by a benthonic stage, serving in substrate selection and during which time the larva "creeps" over the substrate on the flattened ventral region of the body by ciliary action. assisted by mucous secretion. Compared to other phoronid species, the larva of *P. ovalis* is poorly differentiated upon settlement, sharing few features in common with the adult. Although the details **of** larval development in *P. ovalis* await study, the observations of Silén (1954, p. 248) suggest that metamorphosis is prolonged, involving a more complicated reorgani-

zation of larval structures than is required for other phoronid species, and approaching in many respects the style of metamorphosis obsesved in the Ectoprocta.

The degree of independence *of* larval and adult *stages* of the life cycle in evolution, and consequently the potential of morphological divergence of the two stages of development, is clearly linked to reproductive "strategy" in the Phoronida and Ectoprocta. Because reproduction in benthic marine invertebrates appears to be strongly patterned by spatial and temporal variations in biotic and abiotic factors of the environment, "strategies" of reproduction have certainly varied in the past in response to changing paleogeographies and marine climates. In light of the many complex events that have shaped the evolution of the biosphere and the long time spans involved, dissimilarities in larval biology alone do not seem to provide a strong basis *for* rejecting a relationship between the Phoronida and Ectoprocta.

In considering possible evolutionary trends at the larval stage, it is useful to identify the selection pressures that can operate to pattern the reproductive "tegy" of a species. Vance (1973; see also Underwood, 1974; Vance, 1974) has examined the common modes of reproduction in benthic marine invertebrates from a theoretical standpoint and arrived at some interesting conclusions regarding the selection of optimal reproductive "strategies." Because reproduction involves a nontrivial portion of the energy budget of a species. it is assumed that natural selection favors the pattern with the greatest efficiency. Of the common reproductive modes, planktotrophy and nonpelagic lecithotrophy may be considered as end members with regard to the relative duration of feeding and nonfeeding stages of larval development. For planktotrophic forms the nonfeeding period **is** regarded as trivial, while in lecithotrophic forms it encompasses the entire period of larval life. For organisms with comparable larval development times, an important advantage of planktotrophy over nonpelagic lecithotrophy is the capability for greater dispersal, which enhances the utilization of a patchy environment by the adult. An additional advantage of planktotrophy is that a large number of eggs can be produced for a **given** allocation of reproductive energy in that the larva does not depend on a supply of yolk from the parent for its development. The obvious disadvantdges are that larvae must depend solely on a planktotrophic food source throughout development and are subject to higher mortality rates due to planktonic predation. Nonpelagic lecithotrophy involves a greater investment of energy per egg as yolk. **Thus,** the number *of* eggs that can be produced for a given allocation of reproductive energy is lower, but the rate of planktonic predation is essentially reduced to zero. *An* important disadvantage of nonpelagic lecithotrophy is the lowered dispersal capability of brooded **larvae.** Flanktotrophic development is favored when (1) the distribution of habitats in space and/or time **is** "predictable," (2) when planktotonic predation is low, or *(3)* when planktonic food is abundant. Nonpelagic lecithotrophy

is favored when (1) planktonic predation is excessive, (2) planktonic food is limiting, or (3) when the distribution of habitats is "unpredictable," thereby favoring opportunistic use of habitat by the adult. Pelagic lecithotrophy represents a "strategic" compromise in allowing for independence from a pelagic food source and perhaps shorter exposure to planktonic predation compared to planktotrophy, and greater dispersal potential than nonpelagic lecithotrophy.

An interesting framework for considering the implications of the proposed model for evolution at the larval stage is provided by Fig. 3A–D, in which possible morphological homologies between the actinotroch and cyphonautes larval forms through two hypothetical intermediate forms are presented. *The* interpretations are based on Jägersten (1972, p. 58), who proposed an evolutionary trend that traces the actinotroch from a cyphonautes ancestor. It seems equally reasonable, however, to interpret the sequence in the apposite sense, based upon the directionality suggested by the model for the adult stage— namely, the derivation of the cyphonautes larval form from an actinotroch ancestor by specialization for planktotrophy. Some major morphological
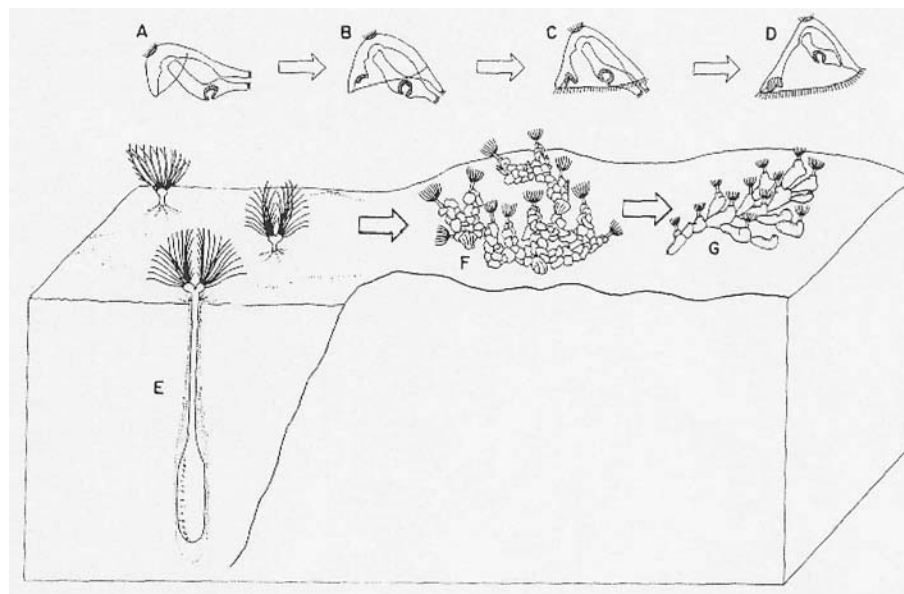

Fig. 3. Diagrammatic representation of the proposed model for evolution *of* the ectoproct life cycle. (A–D) Evolution at the larval *stage* of the life cycle tracing the cyphonautes larval form (D) to an actinotroch ancestor (A) through two hypothetical intermediate morphologies (B and C) by specialization for planktotrophy and long-range dispersal ability (diagram based on Jägersten, 1972; p. 58). (E–G) Evolution *at* the adult stage of the life cycle tracing the Ectoprocta to a phoronid ancestor through an intermediate epifaunal form by specialization for a colonial habit and small size (based on Farmer *et al.*, 1973).

changes required by such specialization include (1) a shortenting of the larval trunk of the actinotroch and modifications in the biological role of the preoral lobe to function not only in feeding, but also as the principal locomotory organ in the cyphonautes; (2) a change in the biological role of the metasomal pouch as the preadult trunk of the actinotroch to function in attachment of the cypho-nautes to the substrate prior to metamorphosis; (3) bilateral compression and an associated reduction in the coelomic and blastocoelic body cavities, with acquisi-tion of a bivalved shell in the cyphonautes; (4) the development of the pyriform complex in the cyphonautes to function as the principal organ in substrate selection; and (5) the elaboration of certain neuromuscular systems to function in retraction of various organ systems into the protection of the bivalved shell of the cyphonautes. It is of interest in this context that morphological and developmental divergence within the living Phoronida, as exemplified by *P. ovalis,* is of a nature and magnitude such that the changes suggested by Fig. 3 A–D do not appear unreasonable from an evolutionary standpoint.

Perhaps the most serious objections to an evolutionary model linking phoro-nids and ectoprocts are those of Nielsen (1971, pp. 309–3111), which concern the developments at metamorphosis in the **two** groups. *Assuming* a solitary, protentaculate ancestor in which the alimentary canal and larval tentacles are retained in the adult, Nielsen finds difficulty in deriving the typical ectoproct life cycle from that which characterizes living phoronids. Although the general features of the phoronid ground plan fulfill the requirements for a probryozoan ancestor **very** well, problems arise in achieving a functional phoronid adult through an ectoproct-type of metamorphosis. In the Phoronida, the adult tentacles develop from, or in contact with, the metatroch of the actinotroch larva. However, in the metamorphosis of the ectoproct larva, the Comparable region becomes enclosed beneath the episphere of the larva which eventually expands to contact the substratum- Clearly, a functional adult would be impossi-ble to obtain in an ancestor with this type of metamorphosis. Rut this interpreta-tion **relies** on the assumption that the ectoproct style of *metamorphosis* had already evolved in the early probyrozoan lineage. It seems reasonable, however, to envision an intermediate form linking phoronids and ectoprocts which was colonial, but in which *the* first individual of the colony developed by a phoro-nid type of metamorphosis, thus yielding a functional adult. Nielsen (1971, pp. 310–311) rejects **this** notion of **an** ancestral probryozoan which was already colonial because budding in the Ectoprocta is from the episphere of the cypho-nautes **larva,** a region believed by him to be homologous in position to a narrow region inside the ring of tentacles of the adult phoronid. Clearly, budding from such a position in the adult phoronid seems incompatible (functionally) with general phoronid organization. But the specific location and orientation of budding in the two groups **is** critical to Nielsen's argument. Nielsen (1971, **p.** 309) points out the difficulties in assigning an orientation *to* the polypide in the

ectoproct adult. Orientation cannot be based on embryological evidence, as the gut of the polypide has nothing *to do* with the gut of the cyphonautes larva, the Former having an independent origin at metamorphosis. In light of the problems of interpreting the embryological evidence, *the* traditional orientation of the ectoproct adult is based on comparisons with adult phoronids. The phenomenon of budding in the Phoronida awaits detailed study, but the observations of Marcus (1949, p. 164) for *Phoronis ovalis* suggest that buds originate on the ventral (oral) side of the adult animal in the nonmuscular region of the trunk, and *not* within the tentacle ring, as suggested by Nielsen (1971, p. 310) on embryological evidence. In the Ectoprocta such oral budding occurs in the Phylactolaemata, while budding in the Gymnolaemata and Stenolaemata *is* in an anal direction (Marcus, 1949; Jebram, 1973).

The derivation of the ectoproct life cycle from that of a colonial probryozoan with a phoronid-type of metamorphosis seems reasonable using adult criteria for orientation. But we are left with the problem that the shift to an ectoproct type of metamorphosis would have to have been abrupt in that no intermediate style of development has been envisioned that is capable of producing a functional adult. In the evolutionary trends represented in Fig. 3A–D, an ectoproct style of metamorphosis would seem to be necessitated by shortening of the larval trunk of the actinotroch larval form whereby eversion of the metasomal pouch (adhesive sac) would begin to occur beneath the expanded preoral lobe (corona), making it increasingly difficult *to* achieve a functional adult by a phoronid style of metamorphosis (the details of larval development and metamorphosis in *Phoronis ovalis* may prove enlightening in exploring this aspect of the problem, arid arc certainly deserving of study). But such an abrupt change in the style of metamorphosis may have held considerable adaptive advantages for those populations in which it first appeared. Under an appropriate selective regime considerable evolutionary potential may have been gained with the appearance of an ectopsocf-type of metamorphosis in that the larval ground plan would have *been* freed from restrictions placed on it bv the adult stage for accelerating metamorphosis. The morphological trends represented in Fig. 3A–D. interpreted to represent specialization for planktrophy at the larval stage, actually Seem to necessitate increased flexibility in larval development and metamorphosis by a decoupling of the larval and adult stages of the life cycle through a shift away from adultation. The appearance of this novel style of metamorphosis. regardless of ancestry, may in part underlie the rapid evolutionary advances made by the Ectoprocta *in* the Lower Ordovician.

If we are to accept *the* proposed model linking phoronids and ectoprocts at the adult stage, we must be willing to accept the possible evolutionary changes implied for the larval stage as wall.. We also must accept the conclusion that evolution at the larval stage of the life cycle in this system has been less conservative to morphological change than evolution at the adult stage. That the

larval stage is a highly adaptable part of the life cycle in living groups is apparent from observations that larval behavior in **many** aquatic invertebrates varies significantly between closely related species, between populations of single species, and **even** within single populations (Meadows and Campbell, 1972, p. 351).

Based on these interpretations, an evolutionary model linking the life cycles of phoronids and ectoprocts is derived which emphasizes specialization for planktotrophy and long-range dispersal at the larval stage (Fig. 3A–D), and independent trends in the evolution of the adult stage leading to small size and a colonial habit (Fig. 3E-G). Evolutionary trends at both stages of the life cycle may have been guided by selection for trophic specialization. The general and widespread diversification of filter feeders in the lower Ordovician, suggestive of an abundance of planktonic food, and the widespread stabilization of marine climates is favorable to such an interpretation. *An* interesting corollary to this interpretation is that *the* later evolutionary history of the Pctoprocta has witrssed a widespread shift in reproductive mode to the pelagic, lecithotrophic dev..opment that characterizes the phylum today.

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