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What Molecular Phylogenies Tell Us about the Evolution of Larval Forms¹

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SYNOPSIS. There is interest in assembling a robust hypothesis of animal relationships based on molecular and other character-based evidence, but even if a high degree of phylogenetic resolution is available, there remain challenging problems for postulating ancestral larval traits. This distinction between hypotheses of genealogies and our knowledge of specific traits is illustrated with specific examples of the portion of variable larval traits that are homoplastic (*i.e.*, they require convergences, parallelisms, or character reversals) with respect to specific molecular-based genealogical hypotheses. Corresponding molecular studies suggest (1) maximal incongruity in larval form and metamorphosis for extant echinoderm classes, (2) convergences in larval size and form associated with coloniality in ascidians, (3) multiple losses of the locomotory larval tail in molgulid ascidians, (4) multiple losses of larval feeding and gain of apomictic parthenogenesis within a genus of bivalves, (5) multiple losses of larval feeding in echinoids, (6) alternative explanations of the distribution of feeding and non-feeding larvae among gastropods, and (7) recent modifications in embryonic and larval development of echinoids following prolonged stasis. These examples show that inferences from phylogenetic studies will ultimately be limited by the extent to which homoplasy and polarity can be unambiguously assessed for larval traits. These limitations are illustrated by alternative hypotheses for larval trait synapomorphies among phyla, evolution of feeding with opposed prototrochal and metatrochal ciliary bands, and the retention or reacquisition of the locomotory nauplius of the Euphausiacea and Dendrobranchiata. Inferences on the evolution of larval traits require other sorts of evidence, perhaps including information on the evolution of genes that play important roles in morphogenesis and their sites of expression.

BACKGROUND: PREVALENT PRACTICES IN EVOLUTIONARY MORPHOLOGY

A phylum tree was sought by three
(with a hey-down homoplasy)
And the first employed anatomy

(with a plesio-, apo-, synapomorphy
and a day-down-dilly);

A hopper was filled with textbook traits
and the algorithm cranked in haste
for a tree to please traditional tastes
(with a plesio-, apo-, synapomorphy
and a day-down-dilly).

¹ From the symposium *Evolutionary Morphology of Marine Invertebrate Larvae and Juveniles* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December, 1993, at Los Angeles, California.

The second used a molecular tool
(with a hey-down homoplasy)
with a sequence long from each animalcule

(with a plesio-, apo-, synapomorphy
and a day-down dilly);

From an ATT and GCC
there emerged a fine and robust tree
with, alas, originality

(with a plesio-, apo-, synapomorphy
and a day-down-dilly).

The third had studied development
(with a hey-down homoplasy)
and wanted the embryos congruent;
Without a doubt and without a fear
and without review from panel or peer,
he drew the tree we all hold dear;
For the larvae fit, and we wanted that
clear

(with a plesio-, apo-, synapomorphy
and a day-down-dilly).

INTRODUCTION

Comparisons of information-rich molecules have greatly expanded the set of characters used to infer relationships among organisms. Molecular data have helped resolve some long-standing controversies about relationships among metazoans by favoring or opposing hypotheses that were only weakly supported by combinations of morphological, embryological, and paleontological data. In some other cases, molecular data sets have been less robust than other sets of data (as in Eernisse and Kluge, 1993). If one is nevertheless optimistic that our estimates of metazoan phylogeny are improving, then one can consider what this improved knowledge of relationships will tell us about the evolution of larval forms of marine animals. Will it only tell us how character histories can be mapped most parsimoniously on our best estimate of phylogeny, or are there other approaches that employ molecular data to point more directly to the evolution of larval structures? Partial answers to these questions are already available.

Our discussion is based on examples. The first examples are cases in which molecular data force us to examine remarkable cases of convergence in the evolution of larvae. Next are applications of phylogenetic trees in studies of evolutionary transitions between modes of development, especially evolutionary loss of function. Patterns of

evolutionary transitions, differential speciation and extinction, and durations of stasis and change are considered. Then we examine some controversies that would not be resolved by perfect knowledge of relationships of extant species. Finally, we mention evidence from molecules that play important roles in morphogenesis and thereby offer a different basis for inferences on the evolution of marine larvae.

DISCOVERY OF CONVERGENCE IN LARVAL TRAITS

Phylogenetic analyses of molecular traits have indicated convergent similarities that are quite surprising. One possibility is that some of these surprises are not genuine. None of the authors of molecular studies have attempted to integrate their studies with other available data in a combined analysis of all pertinent data. We have resorted to comparing the separate results of somewhat arbitrarily-divided data sets, in contrast to a "total evidence" stance (Miyamoto, 1985; Kluge, 1989; Barret *et al.*, 1991; Eernisse *et al.*, 1992; Wheeler *et al.*, 1993). Our justification is that we are less concerned here with strength of evidence for topological details of our examples than with the problems of inference created when a particular hypothesis implies homoplasy for larval traits.

Relationships among echinoderm classes have long been controversial, and this is a perfect example of a controversy badly in need of a combined data analysis. Separate analyses of larval forms, metamorphic transitions, and adult forms suggest three different unrooted trees for the four eleutherozoan classes (Fig. 1) (Strathmann, 1988). Different sets of morphological data and molecular sequence characters analyzed in separate gene data sets have yielded numerous branching arrangements, with authors emphasizing their own preferred character sets. The difficulty in determining this branching order is not surprising because the classes diverged during a relatively brief time over 450 million years ago (Smith, 1989, 1992). Smith pessimistically concluded that there were likely to be few informative shared evolutionary novelties pres-

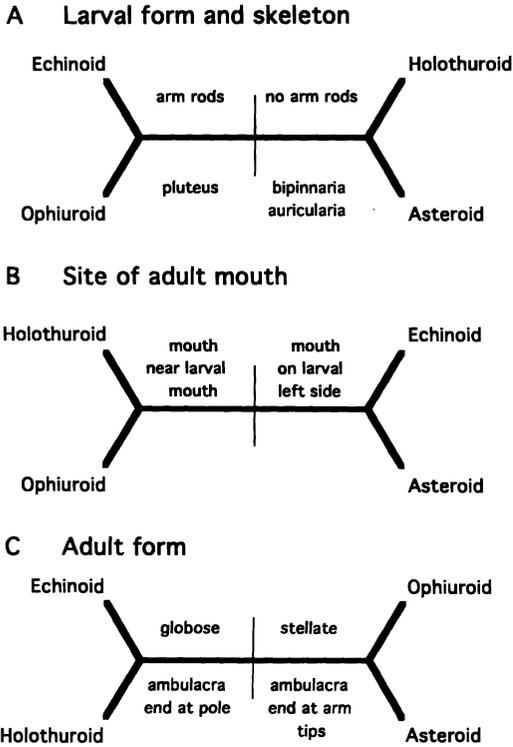


FIG. 1. Unrooted trees, each based on a single trait, for four classes of echinoderms known to have feeding larvae (after Strathmann, 1988). An inversion in mitochondrial DNA supports the relationships in C, thus maximizing incongruities in the larval traits of A and B.

ent by the time major echinoderm lineages had first diverged, and these have had ample opportunity to be confounded by homoplasy during the nearly half a billion years following these early divergences. The lack of close living outgroups presents another obstacle to reconstructing echinoderm phylogeny.

It is not known whether more complete and diverse sequence comparisons will eventually converge on robust support for a particular hypothesis, but the discovery of promising new evidence has revived hope of a molecular resolution of the problem. An initial discovery of differing arrangements of mitochondrial DNA (mtDNA) gene order of asteroids, in contrast to that in echinoids or vertebrates, offered a different approach (Jacob *et al.*, 1988) that gained significance when Smith *et al.* (1993) discovered the same "asteroid" mtDNA gene

order in ophiuroids, and also found the presumed plesiomorphic condition (*i.e.*, more similar to vertebrate gene order) in holothuroids as well as in echinoids. These results are consistent with the hypothesis that asteroids and ophiuroids share a derived multigene inversion in mtDNA that is not present in echinoids, holothuroids, and vertebrates (Smith *et al.*, 1993). The gene order evidence thus supports the tree in Figure 1C, consistent with adult body shape and not with larval body form or changes in body axis at metamorphosis. If this is the true branching order, then the formation of the adult mouth at the lower left side of the larval body either evolved twice or reverted at least once to formation from the larval mouth. Also, either the plutei of echinoids and ophiuroids or the bipinnaria and auricularia forms of asteroids and holothuroids are convergently similar, or both. Pronounced homoplasy in both larval form and metamorphosis occurs in the phylogeny inferred from mtDNA gene order (Fig. 1C), more so than would have been required by competing hypotheses (Figs. 1A, B).

Solitary ascidians produce small and simple tadpole larvae and most are free-spawners. Colonial ascidians produce larger more complex tadpoles, usually with rudiments of postlarval structures more developed; nearly all colonial ascidians brood embryos and release swimming larvae (Berrill, 1950; Cloney, 1982). Given a presently accepted division of ascidians into two orders, based on adult morphology, the distribution of these larval traits would suggest some remarkable convergences, because each order includes both colonial and solitary representatives. Does the classification reflect phylogeny? Sequences of the central region of 18S rDNA suggest that it does at the ordinal level (Wada *et al.*, 1992). Species of *Ciona* (solitary), *Ascidia* (solitary) and *Perophora* (colonial) were placed in a monophyletic group distinct from another monophyletic group composed of *Styela* (solitary), *Halocynthia* (solitary), *Pyura* (solitary), *Polyandrocarpa* (colonial), and *Symplegma* (colonial). At least one evolutionary convergence in the combination of larval traits with colonial or solitary habit has occurred. Moreover, the relationships inferred from

the molecular data are inconsistent with the hypothesis that the common ancestor was polymorphic for these traits. The functional basis for this combination of traits is unclear to us. Brooding is associated with colonality in some but not all phyla (Strathmann, 1990; Knowlton and Jackson, 1993), and a larger larva with more developed rudiments of postlarval structures does not always accompany brooding, as demonstrated by brooding and non-brooding species of the solitary ascidian *Corella* (Lambert *et al.*, 1981). For solitary and colonial ascidians, the molecular and adult morphological analyses call attention to a remarkable and unexplained convergence in larval development that is associated with evolution of the colonial or solitary habit. Molecular data from more families of ascidians could strengthen the inference that there is a predictable pattern of homoplasy.

Some treatments of molecular traits have placed phyla in unexpected positions, but the inferred phylogenies have not yet forced a reinterpretation of evolution of larval traits. An example is the placement of the brachiopod *Lingula* in a clade with such spiralian phyla as molluscs and annelids and far from echinoderms and chordates in two studies based on 18s rRNA data (Field *et al.*, 1988; Lake, 1990; Eernisse, unpublished manuscript). This placement of a member of the lophophorate superphylum grouping (*i.e.*, brachiopods, phoronids, and bryozoans) implies either a remarkable convergence on traits of hemichordates and echinoderms or convergent evolution of many of the traits in the eutrochozoan phyla. Capture of particles upstream from a band of simple cilia (Nielsen and Nørrevang, 1985; Strathmann, 1987) and an oligomeric body plan (Zimmer, 1973) are among the synapomorphic traits of lophophorates, hemichordates, and echinoderms (and possibly other taxa) that are challenged by such a phylogeny. The alternative would be to challenge the remarkably similar cell lineages and larval locomotion by a preoral band of cilia that are among the synapomorphic traits for spiralian phyla that are lacked by brachiopods. Acceptance of this placement of a brachiopod would therefore force recognition of some remarkable con-

vergent similarities. Yet it could also account for similarities in the formation of setae of brachiopods and annelids (Long and Stricker, 1991). Once again, the discovery of which characters are best explained as homoplasies is a problem that can be empirically addressed with a combined phylogenetic analysis of all available data, and by more complete taxonomic sampling of sequences. In this case more complete sampling from lophophorates will be especially instructive.

(Halanych [1993, personal communication] infers that the lophophorates are more closely related to protostomes than to deuterostomes on the basis of new data for 18S RNA sequences for an articulate brachiopod and a phoronid. We look forward to seeing his data and inferred phylogenies.)

EVOLUTIONARY TRANSITIONS INVOLVING LOSS OF FUNCTION

Evolutionary loss of function in larvae is widespread. Inferences of a predominance of losses over gains are best founded for cases in which the following conditions occur. The losses involve extensive changes, and the retained structures are highly similar, well coordinated, and complex, so that independent gain of these structures would require many fortuitous contingencies. Biases toward parallel or convergent changes on the basis of similar functional requirements or similar ancestral traits must be weak or absent. A particular larval function can certainly evolve more than once, but when the preceding conditions are met, the secondary larval traits are expected to differ from the original ones (Strathmann, 1978, 1993).

Loss of capacity for feeding or for locomotion is, for many forms, accompanied by dramatic changes in morphology. The events are well replicated, because such losses of function have occurred numerous times in numerous phyla. The losses are generally thought to occur more commonly than subsequent reversal resulting, once again, in fully integrated function. These evolutionary transitions in development of larvae have therefore provided useful systems for studies of constraint and flexibility, directional biases in transitions, levels of selec-

tion, the basis of stasis, and the roles of developmental processes and functional requirements in all these phenomena. Molecular evidence can be useful in several ways.

Number of parallel losses of function

When one sees numerous species with similar presumed reduction in larval structures, one wonders whether the losses evolved once or many times. In many clades, there are few morphological differences other than those in the embryos and larvae, and one does not know whether similar losses in function and changes in structure have resulted in closely parallel changes. Molecular evidence provides more characters presumed to be independent markers of homology and provides a correspondingly improved phylogenetic resolution.

Most ascidians produce tadpole larvae with tails, but the tail is absent in the development of some species. Larval locomotion clearly has been lost. Tailless species are known from at least two families of ascidians but are especially common in the Molgulidae (Berrill, 1931). On the basis of subfamily classifications inferred from the structure and arrangement of branchial sac and gonads, Berrill suggested that loss of the larval tail in the Molgulidae is polyphyletic and arose at least four times. It is not clear why losses of the tail should occur many times in molgulids but be rare in other ascidians. Berrill noted that loss of larval mobility is associated with ascidians that live on sedimentary surfaces. He noted this association within molgulids, as well as for ascidians in general. He suggested that neither swimming nor habitat selection would have a strong selective advantage when suitable habitats are readily available, whereas these behaviors would be highly favored in areas where suitable habitats are relatively rare. A possible exception to Berrill's generalization is the case of a tailless *Molgula* species recently discovered to be living in a wave-swept rocky habitat, with its eggs adhering to the rocks (Young *et al.*, 1988). If the larva's best chance of finding suitable habitat when released into a wave-swept environment is near its mother, then Berrill's explanation might still apply in general

but would not account for the concentration of tailless species in the Molgulidae, because species in other families occur in wave-swept habitats. Jeffery and Swalla (1992a) suggested that energetic economy contributed to loss of larval locomotion when locomotion was no longer essential, but it is not clear why locomotion should be less often essential for molgulids.

If Berrill's inference of multiple losses of the tail in molgulids were incorrect, then a possible explanation for the distribution of taillessness among ascidians would be rarity of tail loss and inheritance from a common ancestor. This alternative is not supported by recent molecular evidence, which instead agrees with Berrill's inference of a replicated evolutionary event. For a different but overlapping set of molgulid species than those analyzed by Berrill, four separate evolutionary losses of the larval tail are indicated by 50% majority-rule consensus trees inferred from data from 18s and 28s rDNA (K. A. Hadfield, B. J. Swalla, and W. R. Jeffery, unpublished observations). The molecular bases for this evolutionary change in development is under investigation in an attempt to determine the genetic bases for the changes in larval morphology (Jeffery and Swalla, 1992b; Swalla *et al.*, 1993).

Relationships inferred from mtDNA gene sequences indicate that, in the marine clam genus *Lasaea*, polyploid asexual lineages that lack a veliger stage evolved twice from diploid meiotic ancestors in a lineage for which a veliger stage is likely plesiomorphic (O'Foighil and Smith, 1994). The trees were inferred from comparing a 624 site alignment of part of the gene coding for COIII (with 203 sites informative under the conditions of parsimony). Each of two major branches included both a polyploid asexual lineage and a diploid meiotic lineage. One of the diploid meiotic lineages, and the outgroup employed, have a veliger larval stage. If it is assumed that the common ancestor of all had a veliger larval stage and that no lineage that had lost the larval structures reacquired them, then the free veliger stage was lost at least twice also. If it is assumed that the common ancestor of all was diploid and meiotic and that no polyploid asexual lineage became secondarily diploid and sex-

ual, then polyploidy and asexuality evolved twice. An interesting feature of this genus is that the congeners that lack a planktonic larva are cosmopolitan, whereas the species with a planktonic larval stage has a much more restricted distribution (O'Foighil, 1989).

Emler's (1990) analysis of loss of a feeding pluteus stage in echinoids increased estimates of the minimum number of losses to 14 (from a previous estimate of 6 to 9). The higher estimate resulted in part from increased resolution of relationships among species, not just increased sampling of species. Emler used updated inferences on relationships based in part on molecular data (Smith, 1988).

Conversion versus differential speciation and extinction as a cause of trends

Evolutionary trends toward fewer species with a feeding veliger stage have been noted for several clades of prosobranch gastropods (Hansen, 1982; Jablonski, 1986). In many gastropods the larval shell is retained at the apex of the adult shell. Evidence of larval growth and thus presence or absence of feeding can be inferred from a well preserved shell apex. The trend toward non-feeding and non-planktonic development could result from either (1) the bias in conversions from feeding to non-feeding or (2) differential speciation and extinction of species with the different kinds of development. Information on relationships is needed to distinguish these two macroevolutionary processes. A phylogeny for 11 species of turrnellid gastropods was inferred from about 300 base sequences of 16S mitochondrial ribosomal DNA in order to test the frequency of conversion *versus* differential speciation and extinction (Lieberman *et al.*, 1993). Planktonic development (and feeding larvae) was indicated for four of these species, non-planktonic development for five species, and type of development was unknown for two (Fig. 2). Under the assumption of the irreversibility of the loss of feeding development and the assumption that the inferred tree is correct, non-feeding and non-planktonic development evolved at least three separate times. Speciation in

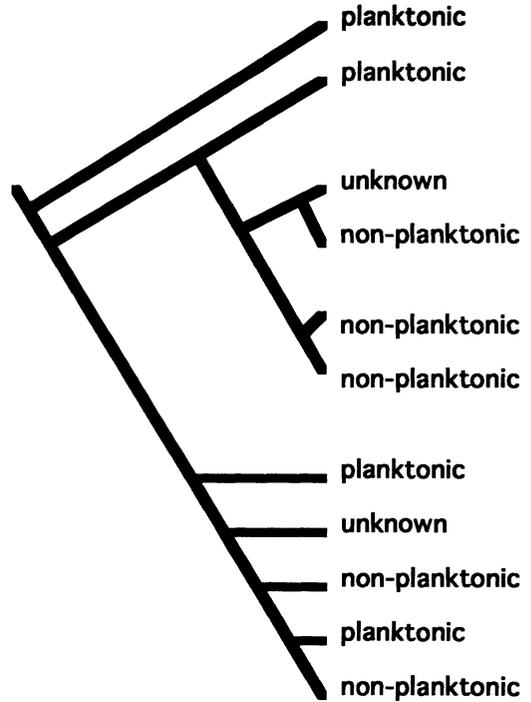


FIG. 2. A phylogeny inferred from DNA sequences for turrnellid species (after Lieberman *et al.*, 1993), testing the roles of conversions *versus* species selection in producing the distribution of the trait among the species.

a lineage with non-feeding development could have added up to two additional species with this mode of development. This branching pattern would then imply that conversion is at least as important as differential speciation and extinction.

Stasis and change

Under the assumptions for a molecular clock, molecular data offer a means of assessing stasis and rates of change in developmental processes and larval morphology.

As far as is known, all echinoids with feeding larvae share such features as micromeres produced by unequal cleavages, early ingression of primary mesenchyme, symmetrical inward movement of cells at gastrulation, similar parts of the embryo fated to be dorsal or ventral parts of the larva, skeletal rods initially formed at paired sites of calcification in the embryo, and skeletal rods supporting larval arms (Raff, 1992; Wray, 1992). Fossils of adults indicate that

lineages that share these traits diverged as early as the Triassic (*i.e.*, more than 200 Mya). The loss of a feeding larval stage is accompanied by changes in many of these traits, and *Heliocidaris erthrogramma* differs in all of them (Wray and Raff, 1991; Raff, 1992). Nevertheless, *H. erythrogramma* diverged from its congener *H. tuberculata* relatively recently, following this long period of stasis in embryonic and larval development. An estimate of 10 to 13 Mya was based on single-copy DNA distance (Smith *et al.*, 1990) combined with estimates of rates of molecular divergence for other sea urchins for which there is a fossil record (Britten, 1986). An estimate of 6 to 10 Mya was based on differences in mitochondrial DNA (McMillan *et al.*, 1992; Wray, 1992) with a further estimate of 2 Mya as an upper boundary for the evolutionary change in development, because of divergence of two populations of *H. erythrogramma* that have similar larval development. Thus molecular data indicate that remarkably extensive and relatively rapid evolutionary changes in early development can occur after remarkably long periods of stasis. These observations support a view based on comparative functional morphology: it is not primarily constraints associated with developmental processes but rather selection on performance of embryos and larvae that accounts for long periods of stasis and the conservatism of many features of development. Increases in nutritional reserves in ova permit relatively rapid evolutionary changes in other developmental processes and in larval form (Strathmann, 1975; Wray and Raff, 1991; Raff, 1992).

PROBLEMS REMAIN WHEN THE TREE IS KNOWN

In many cases, the relationships inferred from molecular traits are consistent with relationships inferred from other morphological traits, and thus uncertainty about evolution of larval traits remains unaffected.

Some hypotheses place the origins of many larval traits at the same time as the origins of different body plans within the Metazoa (Jägersten, 1972; Nielsen and Nør-

revang, 1985). A polyphyletic origin of the Metazoa could definitely reject parts of these hypotheses. Inferences based on partial 18S (Field *et al.*, 1988; Ghiselin, 1988; Patterson, 1990; Lake, 1990) or 28S (Christen *et al.*, 1991) rRNA sequence comparisons have varied, but Wainwright *et al.*'s (1993) comparison of complete, more taxonomically diverse, 18S rRNA sequences suggested a monophyletic origin of the Metazoa, including sponges. A monophyletic origin is consistent with many hypotheses of homology among larvae of different phyla. Thus the effect of this inference from molecular evidence is to keep these hypotheses in the running.

Inferences from 18s rRNA grouped annelids and molluscs in a monophyletic group that excluded arthropods (Field *et al.*, 1988; Lake, 1990; Eernisse *et al.*, 1992). A monophyletic "Eutrochozoa" is consistent with embryological and other morphological evidence that places several spiralian phyla with trochophore-like larvae (annelids, pogonophorans, echiurans, sipunculans, and molluscs) in a clade that is the sister group to arthropods (Eernisse *et al.*, 1992). A monophyletic Eutrochozoa is consistent, however, with varied interpretations of ancestral larval traits. Different authors continue to propose widely divergent interpretations of plesiomorphic larval traits for this group of phyla. Hypotheses for ancestral (plesiomorphic) larval traits include a broad field of cilia rather than a narrow prototrochal band (Ivanova-Kazas, 1985), a test-cell or pericalymma larva with a cover of ciliated cells enveloping the developing juvenile that will emerge at metamorphosis (Salvini-Plawen, 1980, 1990), or the ciliary bands of prototroch, metatroch, and food groove that characterizes many feeding larvae (Jägersten, 1972; Nielsen, 1987). It is not uncertainty about relationships that has kept controversy alive; it is uncertainty about direction and frequency of evolutionary transitions (Strathmann, 1993).

The problems are well illustrated by the varied views on the evolution of feeding veliger larvae within the molluscs (Salvini-Plawen, 1990; Strathmann, 1993). Feeding veliger larvae are known from such disparate clades as lamellibranch bivalves, mo-

notocardian gastropods, and neritoidean gastropods. The capacity and requirement for larval suspension feeding is undemonstrated for other molluscs. Some malacologists have been struck by the similarities among non-feeding larvae of taxonomically widespread molluscs, including those traditionally referred to as aplacophorans, polyplacophorans, scaphopods, protobranch bivalves, and archaeogastropods. By current estimates of molluscan phylogeny, the two or more clades that include feeding veligers are separated by numerous branches that lead to clades with nonfeeding larvae. These observations suggest that feeding larvae have arisen separately in gastropods and bivalves through convergent evolution. In contrast, some invertebrate zoologists have emphasized similarities of the opposed prototrochal and metatrochal ciliary bands of feeding larvae of polychaetes, echiuroids, and entoprocts and the feeding veligers of molluscs (*i.e.*, all eutrochozoans). This emphasis, plus arguments about the implausibility of independent acquisitions of the highly similar opposed-band feeding structures, have been used to suggest a common ancestor for molluscs with feeding larvae. Disagreement results from different interpretations of characters and different opinions on biases in evolutionary transitions. There is no consensus on interpretation of characters or polarities for transitions among character states, and thus there is no consensus on conditions for parsimonious inferences on evolution of characters. Evidence of relationship will not resolve this controversy to the satisfaction of those making different assumptions about character transformations (Strathmann, 1993).

Presence or absence of locomotory naupliar stages has a peculiar distribution among crustaceans. Many crustaceans hatch as nauplii with 3 pairs of appendages that function in locomotion and often also in feeding. These crustaceans also have holoblastic cleavage in early embryos. Many other crustaceans hatch with a larger number of functional appendages. In these, the nauplius stage is reduced to an "egg nauplius" represented by the development of three pairs of limb rudiments before the rudiments of

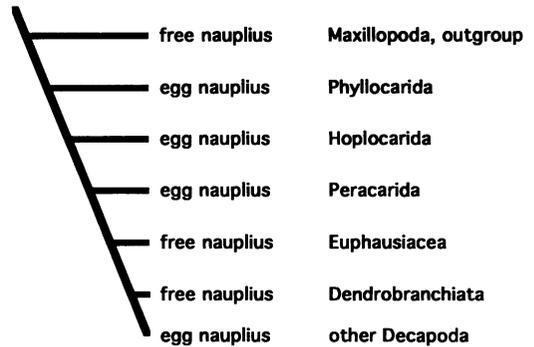


FIG. 3. A phylogeny inferred from morphology for some malacostracan crustaceans. The isolated position of free nauplii of the Euphausiacea and Dendrobranchiata implies a remarkable reversal or multiple convergent evolution of egg nauplii.

more posterior limbs. In many but not all species with an egg nauplius, the early nuclear divisions occur without cleavage, and in later development the embryo differentiates as a blastodisc on one side of the large mass of nutrient reserves. The similarities within either type of development are striking. Nevertheless, the distribution among taxa indicates that an egg nauplius (and elimination of early cleavages) evolved multiple times, or there was a reversion to locomotory nauplii (and holoblastic cleavage), or both. For illustration (Fig. 3), we use a phylogeny accepted by many authors (Siewing, 1963; Dahl, 1983; Hessler, 1983). The life histories are reviewed by Schram (1986). An alternative phylogeny that removes the Phyllocarida from the Malacostraca (Schram, 1986) would not eliminate the problematical distribution of egg nauplii and free nauplii within the remaining Malacostraca. There appears to be no plausible position for the Euphausiacea and Dendrobranchiata that is not bracketed by branches leading to nuclear divisions without cleavage, an egg nauplius, and postnaupliar hatching. If there is no bias in direction of transitions, the most parsimonious interpretation is atavism ("resurrection") of a free nauplius from an egg nauplius at least once. If this is what happened, then evolutionary changes in embryonic and larval development can be reversed to a remarkable extent in the crustaceans. But do developmental processes or functional con-

straints on naupliar locomotion indicate a basis for reversibility? Reacquisition of holoblastic cleavage is indicated by its presence in amphipods and epicaridean isopods (Anderson, 1973), but these peracarids did not regain a free nauplius. Reacquisition of a locomotory larval stage from a brooded one has been suggested for a pterasterid asteroid (Strathmann, 1974; McEdward, 1992), but in this case there have been extensive modifications relative to larvae of other asteroids (Janies and McEdward, 1993). In contrast, the free, locomotory nauplii of eucarids share enough traits with other nauplii that Sanders (1963) could group them on the basis of morphology with nauplii of cirripedes, copepods, mystacocarids, and cephalocarids as distinct from the nauplii of branchiopods. D. Walossek (personal communication) considers multiple evolution of egg nauplii more plausible than "resurrection" of a free nauplius from an egg nauplius. The evolution of free nauplii and egg nauplii among crustaceans deserves attention, but better inferences on relationships will not answer the remaining questions.

EVIDENCE FROM GENES INVOLVED IN MORPHOGENESIS

As the molecular basis for morphogenesis becomes clearer, other kinds of comparative molecular studies will aid studies of the evolution of larval forms. The evolution of genes that play an important role in morphogenesis can provide information beyond relationship and branch lengths in phylogenetic trees. Other kinds of evidence on homology or homoplasy of larval structures or on direction of evolutionary changes may soon be available. Much of the current research in developmental biology is applicable but cannot be reviewed here. Homeobox genes are especially intriguing. Structural and functional similarities of homeobox genes among distantly related animals have prompted the hypothesis that homeobox genes have been involved in axial patterning since the origin of metazoans (McGinnis and Krumlauf, 1992) and also prompted hypotheses on evolutionary changes in these genes and their roles in development (Holland, 1992). Structure,

function, and spatial expression of these and other genes involved in morphogenesis may add comparable traits for distantly related animals and improve inferences on direction of evolutionary changes, relationships, and homology.

A sample application is a search for homologous regions in larval cephalochordates and vertebrates (Holland *et al.*, 1992). Comparisons of the anterior limit to expression of homologous homeobox genes in developing nerve cords suggested homology between the vertebrate brain and an extensive anterior region of the nerve cord of cephalochordates, not just the cerebral vesicle of cephalochordates.

CONCLUSION

In studies of the evolution of larvae, molecular data have strengthened some inferences on relationship. These inferences suggest surprising convergences in larval traits, including multiple parallel evolutionary losses of function. Inferences on relationship can distinguish between processes involving different levels of selection, a larval example being hypotheses of conversion *versus* differential speciation and extinction as causes of trends in proportions of species with feeding or non-feeding larvae. Molecular data used as a clock have contributed to studies of rapid evolution of morphogenesis following extreme stasis. Many controversies about evolution of larvae would not be resolved, however, even if perfect knowledge of relationships and branch lengths were attainable. Prior assumptions on direction of changes (based on other kinds of evidence) have been used in many of the interpretations of character evolution. There is hope that structure, function, and sites of expression of genes with important roles in developmental processes could provide both molecular and morphological data that would be useful where divergence of clades was ancient, morphological differences of extant larvae are great, and useful characters have been few.

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