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C. Drew Harvell

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THE EVOLUTION OF POLYMORPHISM IN COLONIAL INVERTEBRATES AND SOCIAL INSECTS

C. DREW HARVELL

*Section of Ecology and Systematics, Cornell University
Ithaca, New York 14853 USA*

ABSTRACT

Morphological polymorphism is widespread in colonial marine invertebrates and social insects. The polymorphs originate as variants on the basic units that comprise the colonies and are often induced by local environmental cues. This review examines (1) the incidence of polymorphism within invertebrate phyla and social insects, (2) the cues triggering polymorphs in the colonial marine invertebrates and the social insects, (3) the roles of heterochrony and genetic assimilation in the origins of polymorphs, and (4) the factors favoring the maintenance of polymorphism.

The incidence of developmental polymorphism is high, but episodically distributed in three phyla of colonial marine invertebrates, the Cnidaria, the Bryozoa, and the Urochordata. Although polymorphism is well known in the social insects, the incidence appears lower than in some clades of colonial marine invertebrates. I suggest that the high incidence of polymorphism in some taxa of colonial marine invertebrates results from both unusually high origination rates and strong natural selection favoring division of labor in colonies where the units are isogenic. Four features of colonial marine invertebrates make them particularly susceptible to high origination rates of morphological novelties: (1) the iterated developmental process, (2) the late differentiation of the germ line, (3) the lability of signal transduction pathways, and (4) the potential for partially functioning "hopeful monsters" to be nurtured by the colony. Origination rates of morphological novelties may also be high in colonial marine invertebrates owing to a propensity for environmentally induced heterochronic shifts: All colonial invertebrates produce the units of the colony through an iterated developmental process that allows environmental stimuli to differentiate the functions and morphologies of the units from each other. A small difference in growth rate among the units can be translated into large shifts in morphology. Genetic assimilation of environmentally induced variants may be facilitated by the late time of differentiation of germ cells and the redifferentiation of germ cells in each newly budded zooid.

Environmental induction is common in the triggering of polymorphic transformations. The evolutionary lability of these signal transduction pathways is indicated by the diversity of different combinations of extrinsic and intrinsic cues activating morphological switches. Despite general interest in the evolution of phenotypic plasticity, the particular selective factors maintaining these inducible polymorphisms in nature remain poorly known.

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POLYMORPHISM, the morphological specialization of different units within a colony, represents the highest level of integration in colonial organisms. Polymorphism is characterized by the division of labor and resource sharing among the units of a colony. In colonial marine invertebrates, polymorphism is defined as discontinuous variation in the morphology of zooids within colonies (Boardman et al., 1973). These polymorphs are often bizarrely proportioned, morphologically specialized forms relative to the plesiomorphic or ancestral condition. Similarly, in social hymenopterans, polymorphism is defined as nonisometric relative growth occurring over a sufficient range of adult size variation to produce individuals of distinctly different proportions (Oster and Wilson, 1978). Thus the varying morphologies of the different castes of some social hymenopterans, such as soldier castes in the leaf-cutter ants, are examples of such polymorphism. Since polymorphs can often be induced from nonvariant forms, these are examples of the type of phenotypic modification termed developmental plasticity (Smith-Gill, 1983) or developmental polyphenism (West-Eberhard, 1989).

Similarities between social insects and colonial marine invertebrates that might be related to the evolution of polymorphism are (1) a modular, hierarchical organization into colonies; (2) an iterated developmental process by which the units of the colony are produced that may be particularly susceptible to developmental error; (3) a high degree of genetic relatedness among the units of a colony; and (4) the ability to share resources among units of a colony. However, while both the colonies of marine invertebrates and social insects have been called superorganisms (W. M. Wheeler, 1928; Gould, 1985; Seeley, 1989), this is really a less appropriate term for the colonial marine invertebrates, in which the units are isogenic, than for the social insects, where the units are genetically related but not identical. The collaborative biology of such a genetic mosaic seems more appropriately considered a superorganism than the subdivided, regionalized biology of a genetically homogeneous organism.

Despite apparent benefits associated with the division of labor and morphological spe-

cialization among colonial invertebrates, there is high variation in the incidence of polymorphism among groups. This raises the question of what factors favor and what factors constrain the evolution of polymorphism. The incidence of polymorphism is high in some orders of three phyla of colonial marine invertebrates, the Bryozoa, the Cnidaria, and the Urochordata, and essentially absent in the other phyla of colonial marine invertebrates (Table 1). Schopf (1973) conservatively estimated the rate of polymorphism in tropical cheilostome bryozoan faunas as 77 percent. The incidence of polymorphism, however, is relatively low among social hymenopterans, despite its spectacular expression in a few genera, such as the leaf-cutter and army ants. Only 44 of 263 living ant genera have a prominent degree of polymorphism within the worker caste (Oster and Wilson, 1978).

I will review the developmental, physiological and phylogenetic aspects of the biology of polymorphism that provide insight into the evolution of polymorphism in the social insects and colonial invertebrates. First, the polymorphs are often induced by environmental cues: I examine the types of cues that trigger developmental shifts in form and functions among the units of these colonies. This is a critical issue, because in both groups there are inducible and fixed expressions of polymorphism and there is a high diversity of cues activating the polymorphs. The inducible polymorphs may even give rise to fixed variants.

Second, I examine the developmental basis of polymorph formation and, in particular, how shifts in developmental timing give rise to morphological variants. In both groups, heterochrony seems to be an important mechanism by which variants arise. M. L. McKinney and McNamara (1991) estimate that most morphological novelty is the product of heterochrony, and Bonner (1982: 8) states that "everyone agrees that the most effective way to elicit big phenotypic changes with the least genetic fuss is by heterochrony." Heterochrony is defined as a change in the timing or rate of a developmental event relative to that of an ancestor (Gould, 1977). When applied to colonial invertebrates, the study of heterochrony has an added dimension. All aspects of the biology of colonial invertebrates are pervaded

TABLE 1
Classification of colonial marine invertebrates and social insects

Colonial marine invertebrates	
Phylum: Cnidaria	p +
Class: Hydrozoa	p +
Order: Trachylina	np
Order: Hydroida	p +
Order: Actinulida	np
Order: Siphonophora	p +
Order: Hydrocorallina	p
Class: Scyphozoa	np
Order: Stauromedusae	
Order: Coronatae	
Order: Semaestomeae	
Order: Rhizostomeae	
Class: Cubomedusae	np
Class: Anthozoa	p
Subclass: Octocorallia (Alcyonaria)	p
Order: Gorgonacea	p
Order: Pennatulacea	p
Order: Alcyonacea	p
Order: Stolonifera	np
Order: Telestacea	np
Order: Helioporacea	np
Subclass: Zoantharia	np
Order: Zoanthidea	
Order: Actiniaria	
Phylum: Rotifera	p
Phylum: Entoprocta	np
Phylum: Bryozoa	p +
Class: Phylactolaemata	np
Class: Stenolaemata	p
Order: Cyclostomata	p
Class: Gymnolaemata	p
Order: Ctenostomata	p
Order: Cheliostomata	p +
Suborder: Anasca	p +
Suborder: Ascophora	p +
Suborder: Cribrimorpha	p
Phylum: Hemichordata	np
Phylum: Urochordata	p +
Class: Ascidiacea	np
Class: Thaliacea	p +
Class: Larvacea	np
Social insects	
Phylum: Arthropoda	
Class: Insecta	p +
Subclass: Apterygota	np
Subclass: Pterygota (winged insects)	p +
Order: Isoptera	p +
Order: Homoptera	p
Order: Hymenoptera	p +
Order: 20 other orders	p

Note: np = no polymorphism; p = 1 or 2 polymorphic types per colony; p + = >2 polymorphic types.

by their hierarchical organization of zooids within colonies. Thus not only does each zooid have its own ontogenetic sequence, but the succession of zooids within the colony also has an ontogenetic sequence or astogeny (Anstey, 1987; Pandolfi, 1989). Thus heterochrony can occur at two levels in colonial invertebrates.

The study of heterochrony at the colony level (astogeny) is similar to the more traditional study of heterochrony among species in three ways: (1) the comparison is between the morphology of an ancestor (early budded) zooid and descendant (later budded) zooid that can be unequivocally aged; (2) there is the potential for reversals in the normal order of astogeny; and (3) the general tendency is for the astogeny of colonies to proceed from small, simpler zooids to larger, more complex zooids (Anstey, 1987). This hierarchy of developmental timing within the colony may well promote unusually fertile ground for the origination and propagation of variant morphologies.

Third, I discuss how initially inducible variants may become genetically fixed, through a process Waddington (1953a) termed genetic assimilation, "the genetic fixation of initially inducible traits." The challenge to understand the interplay between epigenetic and genetic factors is nowhere greater than in the study of environmentally induced characters, as Waddington realized so long ago. This discussion of genetic assimilation and the evolution of environmentally induced threshold characters grades naturally into a consideration of the selective factors favoring polymorphism. Thus the episodic appearance of polymorphism in the different clades of colonial marine invertebrates and social insects may be due both to variation in origination rates and variation in factors maintaining polymorphism once it arises.

DESCRIPTION OF POLYMORPHISMS

The categorization of taxa as solitary or colonial in the invertebrate metazoans is not agreed upon by all. According to Boardman and Cheetham (1973) the designation "coloniality" requires that (1) the organism be comprised of asexually produced modules, (2) the modules retain an organic connection such that resources can be shared among the mod-

ules, and (3) there be some degree of coordination among the modules. This definition is also consistent with Mackie's (1986) usage. The Cnidaria, Rotifera, Bryozoa, Hemichordata, and Urochordata are dominated by colonial forms. By this definition, groups of asexually reproducing invertebrates such as clonal anemones are clearly not colonial. Furthermore, even organisms such as tapeworms and syllid polychaetes, which propagate new members asexually and occasionally persist as a connected aggregate, are not truly colonial because there is no resource sharing among the modules. The tapeworms and syllid polychaetes, however, do share the property of serial homology with colonial invertebrates. By this definition, the social insects are also not, strictly speaking, colonial, because the modules are not isogenic and there are not organic connections among the modules. The units do share resources, however, and are behaviorally integrated and share many properties with colonial invertebrates, including the phenomenon of polymorphism. I will include them in this review because of the properties shared with colonial invertebrates (including polymorphism) and because the developmental control of polymorphism is well described in social insects and sheds useful light on the phenomenon in colonial marine invertebrates. In my review of polymorphism I will emphasize phenomena in the social insects and the three phyla of marine invertebrates with the best-developed polymorphism.

Polymorphism in the Bryozoa

Although there are five phyla containing colonial representatives, polymorphism is best developed in the Bryozoa, the Cnidaria and the Urochordata. I adopt here Boardman and Cheetham's (1969) definition of polymorphism as *discontinuous variation in zooid form*, but it is important to note that the crux of the definition is that the variation is discontinuous. Thus slight shifts in zooid size and shape are not considered polymorphisms, even though occasionally there may be functional significance to zooid size and shape variation. Even some sharply discontinuous morphologies are considered by some not to be polymorphisms. For example, Schopf (1973) counted only rad-

ically transformed morphologies (depicted in Fig. 1) as polymorphisms, whereas Silen (1977) and Cheetham and Cook (1983) clearly include less extreme forms as polymorphs. Furthermore, some types of polymorphs, such as spines, are almost indistinguishable from ornamentation on the exterior walls. In the Bryozoa, a true polymorphism is distinguished from these extrazoidal elaborations by the presence of a pore plate (Bobin, 1977) separating the two body cavities (Cheetham and Cook, 1983). Finally, it has also been suggested that even the pore plates themselves are polymorphs (Silen, 1944; Banta, 1969; Lidgard, 1985), although this idea remains speculative.

Incidence and Description of Polymorphs

Analysis of the evolution of polymorphism would benefit from a rigorous phylogenetic analysis of the incidence of polymorphism in the different invertebrate families and orders within phyla. This effort, mapped onto accurate phylogenies, would reveal the relationship between the incidence of polymorphism and phylogeny. Although such an effort is beyond the scope of this review, I have indicated in Table 1 the distribution of polymorphism among various higher taxa within the major colonial phyla. In the Conclusions section, I discuss the relationship between the distribution of polymorphism and the current phylogenies of the groups.

Among the three classes of Bryozoa, polymorphism is absent in the Phylactolaemata, present in the Stenolaemata, and well developed in the Gymnolaemata (Table 1). The absence of polymorphism in the phylactolaemates has been ascribed to their primitive position and to the fact that they are exclusively freshwater forms (Silen, 1977). To this I would add that the architecture of the phylactolaemates is unusual when compared to that of the other two classes. Phylactolaemates have a continuous body coelom shared by all polyps. In contrast, both the stenolaemates and gymnolaemates are highly compartmentalized. The compartmentalization must facilitate zooid functional autonomy and may enhance the evolution of division of labor. Within the gymnolaemates, polymorphism is poorly developed in the ctenostomes and well established in the

GLOSSARY

- ancestrula*—initial zooid in a bryozoan colony
autozooid—bryozoan zooid with a fully functioning polypide
avicularium—bryozoan heterozooid with an enlarged operculum
dactylozooid—cnidarian defensive polyp
entocodon—epidermal blastema in developing hydrozoan bud
ergatoid—insect functional male or female without wingbuds
fundatrix—viviparous parthenogenetic aphid female from fertilized egg
gastrozooid—cnidarian nutritive polyp
gonozooid—cnidarian or bryozoan reproductive zooid
heterochrony—a change in the timing or rate of a developmental event
heterozooid—bryozoan zooid without a functional polypide
hypermorphosis—peramorphic morphology produced through a late offset of growth
interzooid—small heterozooid acting as a spaceholder
kenozooid—same as heterozooid
larva—early insect nymph without wingbuds
nanozooid—reduced cyclostome bryozoan autozooid with only a single tentacle
nectophores—swimming bells of siphonophores
neoteny—paedomorphic morphology produced by reducing the growth rate relative to an ancestor
nymph—older insect nymph with wingbuds
paedomorphosis—reduced adult morphology relative to an ancestor
palpons—cnidarian polymorph specialized for defense
peramorphosis—“shape beyond”; enhanced morphology relative to an ancestor
polymorphism—discontinuous variation in morphology
polyp—feeding, tentacled animal inside the bryozoan zooecium; unit of a cnidarian colony
pore plate—communication pores connecting the zooids of a bryozoan colony
postdisplacement—paedomorphic morphology produced by advancing the age of growth onset
pseudergate—regressed insect from a nymph stage by a molt that eliminates wingbuds
rhizozooid—modified bryozoan kenozooid similar to a stolon
soldier—insect nymph with a conspicuously enlarged head sometimes armed with a frontal gland
spinozooid—bryozoan heterozooids forming spines
stolons—elongate bryozoan heterozooids formed at colony edge
worker—insect larval form that builds nest and provides food
zooecium—calcareous box that houses a bryozoan polypide
zooid—unit of a bryozoan or cnidarian colony

cheilostomes. The cheilostomes are viewed as expressing the greatest complexity of polymorphism within the Bryozoa (Silen, 1977).

Silen (1977) hypothesized that polymorphism originated independently in the gymnolaemates and stenolaemates because the polymorphs of the two groups result from different budding patterns. The most comparable polymorphs between the two groups are those specialized for reproduction, and these clearly do have independent origins. The gonozooids (or ooecia) of the stenolaemates are large structures, housing multiple embryos, and are perhaps com-

prised of several zooids (Fig. 1F). There are typically one to a few per colony. The ooecia of the gymnolaemates are small, can be associated with each zooid in a colony (Fig. 1E), and each receives oocytes from a single zooid, although they are cooperatively constructed from both the proximal and distal zooid (Silen, 1977).

There are two main types of polymorphs in the Bryozoa (Fig. 1; Silen, 1977): Autozooidal polymorphs possess a functioning feeding apparatus but are specialized in one or more aspects. All of the other polymorphic types are termed

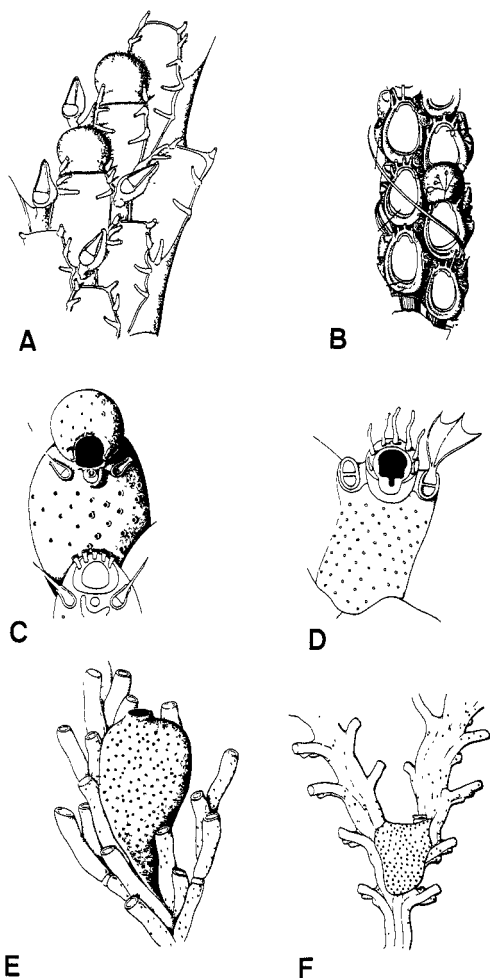


FIG. 1. THE MAIN CLASSES OF ZOOID
POLYMORPHISM IN THE BRYOZOA

A. *Dendrobeania murrayana*. Stalked avicularia, ovicells and spinozooids (Ryland and Hayward, 1977). B. Spinozooids, vibracularia, avicularia, and ovicells (from Hyman, 1959). C. *Microporella marsupitata*. Adventitious avicularia with elongated, pointed mandible. Ovicell distal to operculum (Osburn, 1952). D. *Mastigophora pesanseris*. Adventitious avicularia with elongated, flared mandible. Spines surrounding the operculum (Osburn, 1952). E. *Crisia*. Cyclostome gynozoooid among autozooids (Osburn and Soule, 1953). F. *Tervia brevovicella*. Location of cyclostome gynozoooid at branching point in the colony (Silen, 1951).

heterozooids, based on the lack of a feeding structure and the requirement that they be nourished by autozooids. These heterozooids, lacking musculature and other internal organs, are also sometimes called kenozooids (Cheetham and Cook, 1983). To facilitate discussion of the developmental control of polymorphic transitions, I will describe the different polymorphic types in some detail. All of the polymorphs are considered derived forms of plesiomorphic autozooids. The main types of polymorphs in the Bryozoa are:

(1) *avicularia* and *vibracularia*. Found only within the cheilostomes (Gymnolaemata), both the avicularia and the vibracularia are formed from zooids with a modified operculum; only cheilostomes have an operculum (Silen, 1977). The vibracularium differs from the avicularium in the prolongation of the operculum into a seta (Fig. 1). There are three main types of avicularia based on their position and size: Vicarious avicularia are formed by a similar budding process as an autozooid, hold a similar place in the budding sequence as an autozooid, are close in size to an autozooid, and are capable of budding an autozooid (Silen, 1977). The adventitious avicularia are situated as small interzooids on the front and lateral sides of an autozooid (Fig. 1) and are incapable of further budding. Interzooidal avicularia are small avicularia formed as lateral buds that are wedged in small spaces between autozooids. They also appear incapable of further budding.

(2) *nanozooids*. Only present in the cyclostomes (Stenolaemata), these are a reduced autozooid with a single tentacle; they are believed to function in sweeping the surface of the colony clear of detritus (Silen, 1977). Some of these may also be specialized as male zooids.

(3) *spinozooids*. The spines that occur in the gymnolaemates and some stenolaemates are called spinozooids (Fig. 1) and are classified as kenozooids because they lack a polypide and are incapable of budding. Many of the spines of the gymnolaemates are considered polymorphs, but there also appear to be spine-like forms that are simply extrazoooidal extensions, not separated from the main coelom by a pore plate and therefore do not represent reduced zooecia. For example, the corner spines

of *Membranipora membranacea* do appear to be true spinozooids because there is a reduced chamber at their bases, pierced by pore plates. The membranous spines that grow out of the frontal membrane, however, appear to be extrazoooidal extensions (Figs. 2, 3).

(4) *kenozooids*. The simplest form of kenozooids are those odd-shaped zoecia, lacking a polypide and musculature, that appear at colony margins and at budding disruptions (Fig. 4).

(5) *rhizooids*. Some flexible cheilostome species have modified kenozooids that grow geotropically or negatively phototropically from the underside of the colony to anchor it to the substrate (Silen, 1977).

(6) *stolons*. Stolons are similar to rhizooids in morphology and in having no polypide, but differ in being less rigid. They are common in the ctenostome gymnolaemates, but also occur in cheilostomes at the borders of interacting colonies (Fig. 2; Harvell and Padilla, 1990).

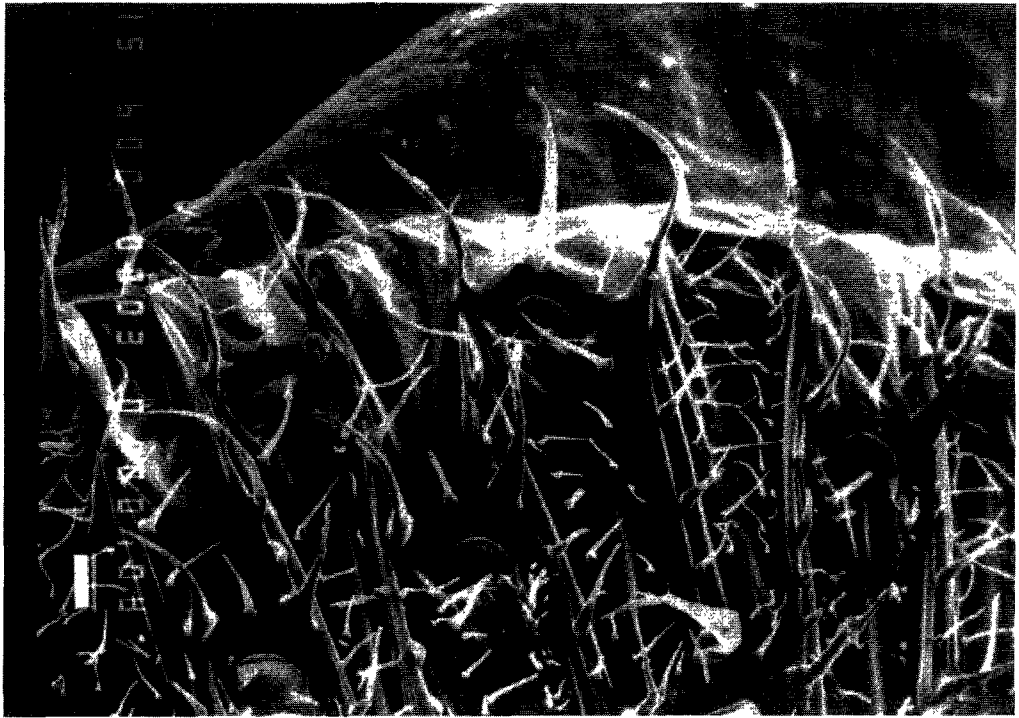
(7) *gonozooids*. All bryozoan colonies are hermaphrodites, but in some colonies male and female function is expressed sequentially in single zooids, in others male and female zooids differ morphologically. The most prominent gonozooids in the Bryozoa are the communal brood chambers of the stenolaemates (Fig. 1). These are large chambers that can house hundreds of genetically identical eggs produced by polyembryony (Silen, 1977). Many of the ovicells of the cheilostomes (Fig. 1) are also spectacular, particularly in view of the fact that they can be constructed by the coordinated growth of the proximal and distal zooid and in some also by the lateral zooids (see Cheetham and Cook, 1983). For example, the ooecium of *Bugula* is a heterozooid emanating from the zooid distal to the maternal zooid. The maternal zooid produces the egg to be brooded in the ooecium (Woollacott and Zimmer, 1975).

Development of Polymorphs

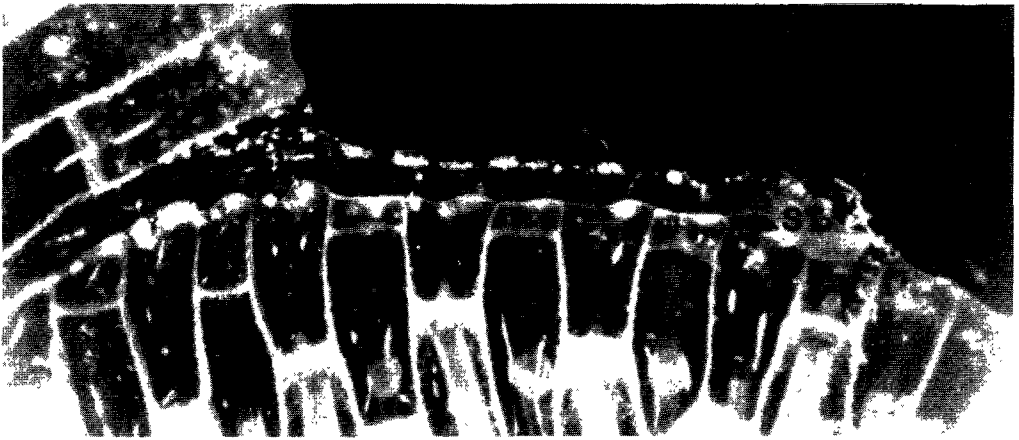
Since many of the polymorphs of bryozoans represent morphological variants on a basic zooidal theme, understanding the developmental basis for polymorph formation will reveal some of the mechanisms by which morphological novelty arises in this group. One

focus of this effort should be in determining how heterochrony (shifts in developmental timing) gives rise to variants. Although DeBeer (1958) clearly described most of the developmental phenomena associated with heterochrony that are important to this paper, the categorization of heterochrony will rely on the more recent terminology developed by Alberch et al. (1979). The important innovation in their scheme was to define separate parameters for growth rate changes and variations in the timing of growth initiation and offset (Fig. 5). Paedomorphic descendants are those with reduced morphologies relative to ancestors, and peramorphic descendants are those with enhanced morphologies relative to their ancestors. Paedomorphic morphologies can result from decreases in growth rate (neoteny), early growth offset (progenesis), or delayed growth onset (postdisplacement). Peramorphic morphologies can result from increases in growth rate (acceleration), early growth onset (hypermorphosis), or delayed growth offset (pre-displacement). In reality, many morphological changes, particularly in colonial organisms, are combinations of different heterochronic processes. These heterochronic complexes are termed mosaic heterochronies (M. L. McKinney and McNamara, 1991). In practice these can be impossible to distinguish. Furthermore, since most studies of heterochrony in Bryozoa have emphasized fossil species and attempted to infer the growth processes underlying a particular pattern, we cannot know which type of heterochrony is involved in most of the transformations (G. B. Muller, 1990). Studies of growth trajectories with extant taxa are needed to verify these heterochronic processes.

Furthermore, the developmental processes within a colony that give rise to some of the polymorphs are very complex. For example, each autozooidal bud in the gymnolaemates can be produced by fusion of three buds: one from the proximal zooid and the others from each proximolateral zooid (Silen, 1977; Cook, 1979). The inducible polymorphs are of particular significance in the effort to understand these developmental processes because they can be experimentally manipulated, allowing examination of how intrinsic and extrinsic cues affect morphology. As an example of approaches that can be used with inducible polymorphism,



A



B

FIG. 2. THE INDUCIBLE SPINES AND STOLONS OF *MEMBRANIPORA MEMBRANACEA*

A. Scanning electron micrograph (SEM) of the four-zooid-wide edge of a colony. The center zooid shows extensive corner and membrane spine development. B. Photograph of the interaction zone between two colonies, focusing on a large stolon formed by the upper left colony and growing across the front of the attacked colony (from Harvell and Padilla, 1990).

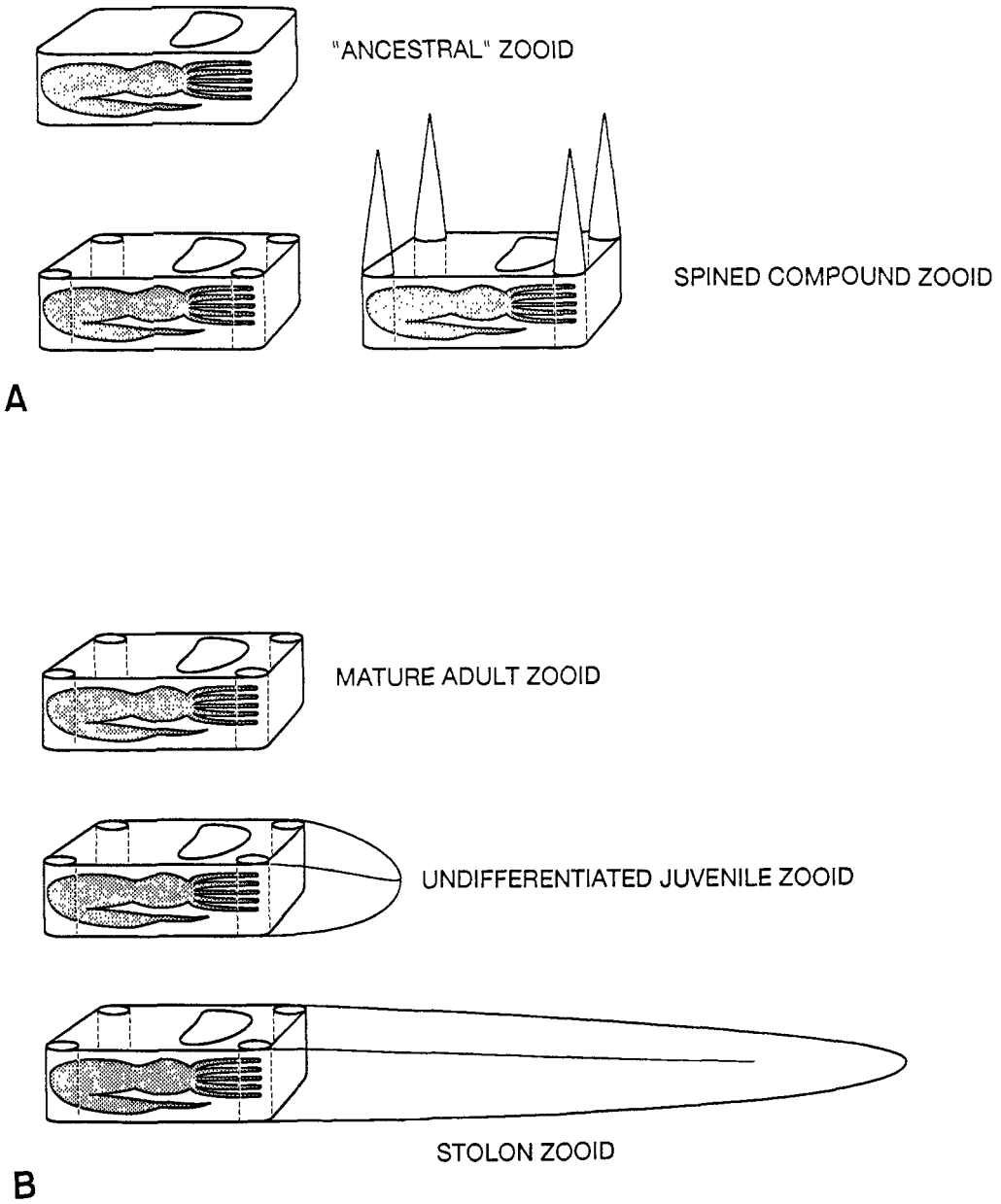


FIG. 3. HETEROCHRONY AND THE INDUCIBLE SPINES AND STOLONS OF *MEMBRANIPORA MEMBRANACEA*. A. The relationship between the plesiomorphic (ancestral) condition of bryozoan zooids and the compound spine-forming zooids of *Membranipora membranacea*. B. The relationship between mature adult zooids of *Membranipora membranacea*, normal undifferentiated zooids produced at the edges of colonies, and stolon zooids, also produced at the edges of colonies.

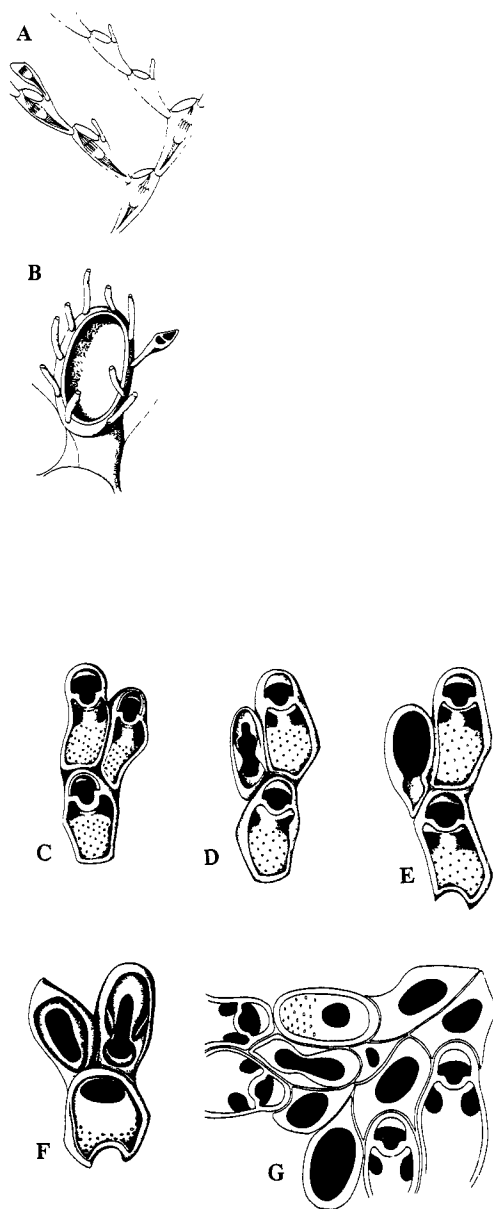


FIG. 4. THE EFFECT OF LOCATION AND BUD SIZE ON TYPE OF POLYMORPH EXPRESSED (from Silen, 1977)

A-B: Facultative development of identically situated buds into different zooid types. A. Scruparia. Facultative formation of autozooids and spinozooids in identical frontal positions. B. *Cauloramphus cymbaeformis*. Adventitious avicularium in same position as spinozooid (redrawn from Osburn, 1950). C-G (redrawn by Silen, 1977, from Powell and Cook, 1966). A hierarchy autozooid-avicularium-

I will give a case history of two inducible polymorphs of *Membranipora membranacea*.

The Inducible Polymorphs of *Membranipora membranacea*

The variant zooids produced by *Membranipora* are kenozooids, stolons and spinozooids. All of these morphs are heterozooids, that is, they possess no functional, feeding polypide. All of these morphs also require extrinsic stimuli to be activated, except for the spinebuds, which occur as reduced interzooids on all autozooids.

Spines. The spines of *Membranipora* are of two morphologies: large chitinous corner spines and more reduced chitinous spines protruding from the frontal membrane (Fig. 2A). Only the corner spines are strictly polymorphs with chambers at the bases of the spines and the ability to bud other zooids. The evolution of spinozooids is thought to be similar (Harvell, 1991) to the evolution of avicularia (described by Banta, 1973). The spine chambers are likely to be reduced interzooids, which are reduced forms of autozooids that have migrated to their corner positions (Fig. 3). The spine chambers of the ancestrulae are capable of budding other autozooids (C. D. Harvell, unpub.). The spines themselves are most likely elongated opercula or a chitinized frontal membrane itself (Harvell, 1991). Thus each spined zooid is a compound form consisting of an autozooid and four associated interzooids.

In comparison to the plesiomorphic condition of simple autozooids, the compound autozooids have likely arisen through a process of heterochrony. In this case, the heterochrony involves several different characters and is thus termed a mosaic heterochrony (M. L. McKinney and McNamara, 1991). First, the com-

kenozooid is directly related to the gradation of the reduction of body size or the deformation of the body. A distolateral bud at a zooid row bifurcation can form either an autozooid (C), avicularium (D), or kenozooid (E), or both buds can be reduced, resulting in formation of a kenozooid and an avicularium (F). Disturbance of the colony budding pattern such as by an obstruction can result in an irregular distribution of avicularia and kenozooids (G).

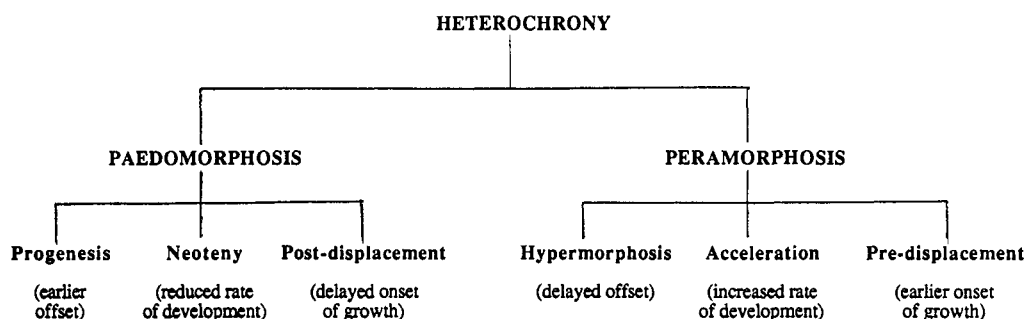


FIG. 5. A CLASSIFICATION OF HETEROCHRONY
Modified from McNamara (1986).

pound zooid must have evolved through reduction in zooecium size of the four interzooids and loss of the polypides (Fig. 3). This process would be termed paedomorphosis, although we cannot distinguish whether the reduction occurs by growth rate or onset-offset changes (Fig. 5). The corner spine itself is an example of peramorphosis, however, because it is overdeveloped relative to its ancestor with no spine (Fig. 3). It could have arisen through hypermorphosis or acceleration of the operculum growth relative to the growth of the interzooid. Since the growth rate of the induced spine is so rapid, there is clearly acceleration involved, but growth offsets may also have shifted.

The spines are activated by exposure to the chemical exudate of a particular species of dorid nudibranch, *Doridella steinbergae*. *Doridella steinbergae* is a trophic specialist, feeding only on *Membranipora membranacea*. Spines grow from spine buds within 36 to 48 hours of exposure to the chemical cue (Harvell, 1984). The delayed development of the spine until receiving the cue results in a delayed onset of growth (postdisplacement). Spines can also be activated by some kinds of hydrodynamic environment. In still water, colonies from Southern California grow spines (C. D. Harvell and G. Trager, unpub.). The functional consequences of these spines in different hydrodynamic environments are not known. The intrinsic control of spine induction is not known, but it appears that different kinds of environmental stimuli can activate the same developmental pathway.

Production of the spines is associated with

a reduced colony growth rate. Colonies exposed weekly to nudibranch extract grew more slowly in the field than control colonies (Harvell, 1992). The growth reduction in induced colonies was even more dramatic in short-term laboratory experiments (Harvell, 1986, 1992). Grünbaum (1992) also detected a slower growth rate in spine-making colonies. This is a conservative result with respect to the issue of whether polymorphisms are costly because the spined zooids of *Membranipora* are capable of feeding, unlike many of the polymorphs.

Stolons. The stolons of *Membranipora membranacea* are heterozooids (lack a feeding polypide) and may be considered to be kenozooids. Unlike the spine buds, they are not constitutive but are only present when induced by specific types of competitive environments. Colonies produce stolons in response to contact with conspecifics (Harvell and Padilla, 1990). The extrinsic cue inducing stolons is contact with a nonclonemate (D. K. Padilla et al., pers. commun.). Stolons are differentiated from peripheral, undifferentiated buds (Fig. 2B). By producing a stolon that obstructs the growing edge of a competitor, colonies reduce the amount of space occupied by conspecifics. In addition to having no polypide, stolons differ from autozooids in the capacity to grow proliferatively. Stolons grow 3 to 4 times the rate of a normal bud and may end up 5 to 6 times the length of a normal autozooid. The heterochronic process producing stolons appears to be a combination of paedomorphosis and peramorphosis. The development of the polypide is reduced relative to an ances-

tor, probably caused by an early offset (progenesis) of polyp differentiation. The growth rate of the stolon itself is increased relative to the ancestral zooid (acceleration) and may also have a delayed offset (hypermorphosis) (Fig. 3).

Cues Inducing Polymorphs

The expression of polymorphism in bryozoans appears to be hierarchical with both intrinsic and extrinsic cues operating. For example, some of the polymorphs, particularly the avicularia, do not appear to require an extrinsic cue for activation. These must rely solely on intrinsic control. In the situations where polymorphs are activated by an extrinsic cue, there is the potential for both extrinsic and intrinsic signal transduction pathways to activate the same developmental pathway. The ubiquity of extrinsic cues in polymorph induction suggests that intrinsic signal transduction pathways can be readily activated by extrinsic factors. It is plausible that the intrinsic mechanism involves the amount of some type of morphogen that is very sensitive to zooid size or growth rate. Although there is yet no evidence for any morphogens regulating these pathways, I will review what is known about the operation of extrinsic and intrinsic cues in the production of polymorphs.

The most important factors governing whether a particular zooid in a colony will become an autozooid or some form of polymorph appear to be size and age. In *Thalamoporella* (Silen, 1938; Powell and Cook, 1966), zooids in a defined location can turn into autozooids, avicularia, or kenozooids, according to the size of the zooecium (Fig. 4). The unexpected appearance of an avicularium in place of a spine resembles the homeotic mutants of *Drosophila*. Indeed, it is possible that, like some of the homeotic mutants, the fate of a particular bud is determined by timing of differentiation, rather than bud size. In this view, the fate of the bud is likely controlled by the amount of some morphogenlike substance.

Silen (1977) invoked two kinds of environment to explain the variation: the colonial environment (e.g., ontogenetic and size environment) and the extrinsic environment. In budding accidents, such as where a zooidal bud is not quite large enough to form an auto-

zooid, usually the dwarfed zooids become polymorphs: "this restriction of the body volume influences the primordium of the interior organs, the polypide bud. . . . This absence or transformation of the polypide bud, has an inductive effect on the further differentiation of the zooid as a whole, the end result being a kenozooid, an avicularium, etc." (Silen, 1938). Silen (1977) hypothesized a morphogenetic substance that induced discontinuous variation and viewed the induced formation of polymorphs as secondary, since it only occurred in forms already possessing polymorphs. There is still no information about the role of morphogens in the induction of polymorphs in bryozoans.

Observation of budding patterns in actively growing colonies of *Membranipora membranacea* reveals the role of zooid age and size in the expression of polymorphs. Zooid age also seems to affect the response to extrinsic inducing cues. For example, newly budded zooids close to the growing edge are most sensitive to extracts from nudibranch predators. In this case, zooid age alone appears to determine competence to respond to an extrinsic inducer (Harvell, 1991). Zooid size is also a major determinant of zooid morphology. Zooid size is highly sensitive to environmental factors that cause budding disruptions. In *Membranipora*, if a zooecium is below a particular size threshold, it forms an interzooid with no feeding polypide. This situation most commonly occurs adjacent to budding disruptions, such as when a colony is damaged or runs into an obstruction (Fig. 4). This induced use of kenozooids to fill space has been described for other bryozoan species (Stebbing, 1973; Silen, 1977). These kenozooids are also formed in a more regular manner at the border between two colonies and were termed guard cells by Stebbing (1973). If zooids are above particular size thresholds, then a single zooecium with two functional polypides can result (see description of double lophophores in *Factors Promoting High Originational Rates of Morphological Novelty*, p. 176).

The evolution of stolon morphology through heterochrony adds an interesting insight into the zooecium size hypothesis. In the case of an incipient stolon, the zooecium is large enough to form a polypide, and yet polypide formation is suppressed. Thus the zooecium size

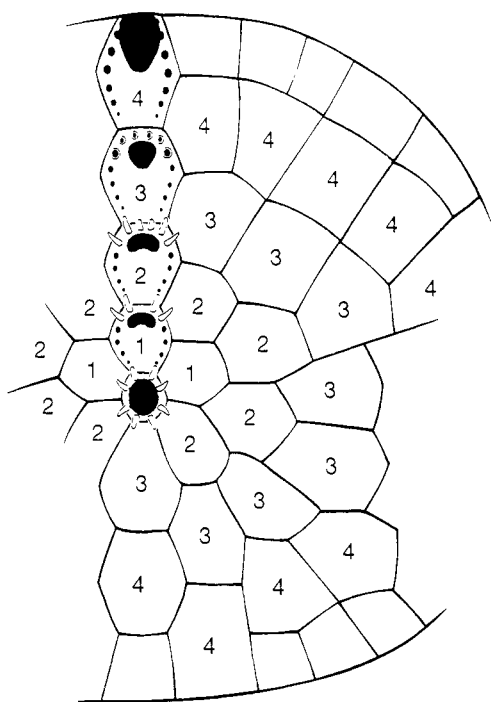


FIG. 6. ONTOGENY AND ASTOGENY OF A BRYOZOAN COLONY (modified after Boardman and Cheetham, 1973)

The numbers represent the order in which zooids are budded. The filled-in zooids depict the changes that can occur in successively younger zooids relative to older zooids.

model alone is not sufficient to account for the presence or absence of a polypide and there must also be substances capable of inhibiting polypide formation in an actively growing stolon. In normally developing buds, the polypide does not begin to differentiate until the walls begin to calcify. Since a stolon never calcifies, it may be that both polypide formation and calcification are cued by the same developmental environment, or are dependent in some way.

In the Bryozoa, the recognition of polymorphism must not be confused with variation among zooids arising owing to zooid ontogeny and colony astogeny. For example, in Figure 6, the difference in lengths of filled-in zooids 2 and 3 is astogenetic, but their differences in

orifice shape and spine length are ontogenetic. With further growth, the spines and orifice of zooid 3 would come to look like those of zooid 2, but the lengths of zooids 2 and 3 remain permanently characteristic of the budded generation to which they belong. The ancestrula (the initial zooid of the colony) could be considered a polymorph in Figure 6, because its morphology is radically different from the other zooids. Polymorphism is, however, most unambiguously identified among zooids of the same generation.

Polymorphism in the Cnidaria

Incidence and Description of Polymorphs

Polymorphism is only well developed in the Hydrozoa, conspicuously absent in the Scyphozoa, and rare in the Anthozoa (Table 1). Within the Hydrozoa, polymorphism is spectacularly developed in the orders Hydroida and Siphonophora and virtually absent in the others (Table 1). The Hydroida and Siphonophora provide particularly interesting examples of polymorphism because hydroid colonies are bottom dwelling and siphonophore colonies are pelagic; thus polymorphism is not dependent upon the sessile mode that is characteristic of most colonies. In part, the basis for polyps of different morphology in these colonies is the integration into a single colony of two zooid types (polyps and medusa) that, in the plesiomorphic condition, followed in sequence in the life cycle (Berrill, 1949, 1950). The less derived forms of hydrozoan colonies consist of a monomorphic polyp stage that alternates with a pelagic medusoid stage. In highly derived colonies, such as the benthic *Podocoryne carnea* and *Hydractinia symbiolongicarpa* or the pelagic *Physophora hydrostatica*, the colony is populated by both medusa derivatives and polyp derivatives (Fig. 7).

In *Hydractinia symbiolongicarpa* or *Podocoryne carnea* there are five types of modified units: *gastrozooids*: polypoid—specialized for feeding; *gonozooids*: medusoid—specialized for reproduction; *dactylozooids*: polypoid—short tentacles with nematocyst barriers, specialized for defense; *tentaculozooids*: polypoid—single hypertrophied tentacle with nematocysts; and *stolons*: specialized for defense.

In *Physophora hydrostatica* there are five types of modified units: *gastrozooids*: polypoid—

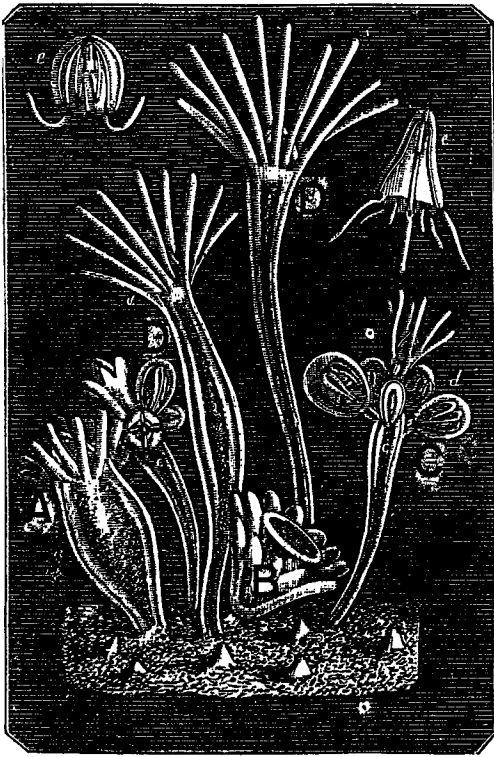


FIG. 7. EXAMPLES OF POLYMORPHS IN THE HYDROZOA (*Podocoryne carnea*, from Perrier, 1881)

A, B. Contracted feeding polyps; C. gonozooids; D. expanded feeding polyps.

specialized for feeding; *palpons*: polypoid—specialized for defense; *nectophores*: medusoid—specialized for swimming; *gonozooids*: medusoid—specialized for reproduction; and *dactylozooids*: polypoid—specialized for defense.

In the Anthozoa, polymorphism is rare, but appears in the Pennatulacea, the Gorgonacea, and the Scleractinia. Pennatulaceans are highly modified colonies with polyps specialized for support (stem and leaf polyps) and water flow (siphonozooids). There is only one polymorph type reported for either the Gorgonacea or the Scleractinia. Polyps in both groups produce sweeper tentacles in response to encroachment by competitors. The gorgonacean sweeper tentacles are quite highly modified and consist of tentacle elongation, differentiation from a pinnate to a smooth tentacle, and elaboration

of nematocyst batteries (Sebens and Miles, 1988). The scleractinian sweepers are simply elongated tentacles with nematocyst elaboration (Wellington, 1980; Chornesky, 1983).

Cues Inducing Polymorphs and Development of Polymorphs

In the Hydroida, both intrinsic and extrinsic factors inducing polymorphism are known. Polymorphs can be induced by vibration of the substrate (Bravermann, 1974), contact with competitors (Ivker, 1972), or carbon dioxide increases mediated by locally high polyp densities (Bravermann, 1974). In the hydrozoan *Podocoryne*, pattern in the distribution of polymorphic polyps is produced when sexual polyps are induced from nonsexual hydranths by high concentrations of carbon dioxide. In gymnoblastic hydroids, temperature differences can trigger the change between a stolon-dominated colony and a hydranth and gonangium-dominated colony (Bravermann, 1974). In *Hydractinia echinata*, nematocyst-filled stolons proliferate at the margins of contacts with conspecifics. These hyperplastic stolons only differentiate at non-self contacts (Ivker, 1972; Buss and Grosberg, 1990).

Both inhibitory and activating morphogenetic factors control the allocation of growth to stolons and hydranths (W. A. Muller et al., 1987). Inhibitory substances are produced by the hydranths, limiting the proximity of new hydranths to a minimum distance from existing ones. Similarly, the location of branching in the stolon systems appears to be regulated by inhibitory and activating substances. In *Hydractinia*, the stolon tip is the source of an inhibitory substance, Proportion-Altering Factor (PAF), which spreads proximally in decreasing concentration. The inhibitor prevents stolon formation in its immediate vicinity (W. A. Muller and Plickert, 1982). Also in *Hydractinia*, stolon branching is induced by a morphogenetic inducer, Stolon-Inducing Factor (SIF) (Lange and Muller, 1991). SIF was isolated from the exudate of whole hydranths, and when applied locally to a stolon, induced a new tip. In addition, globally applied SIF induced abnormal stolons from the body of hydranths and induced secretion of periderm over the body of the hydranth. Periderm nor-

mally forms only over the stolons (Lange and Muller, 1991). The ability of a hydranth to sprout stolons and secrete periderm again emphasizes the small degree of differences in control required to shift from one morphotype to another.

Relative metabolic activity seems to also affect heterochronic changes in morphology of cnidarian colonies. Treatment of developing colonies of the hydroid *Podocoryne carnea* with 2,4-dinitrophenol (DNP) accelerates the usual trajectory of polyp and stolon production; treated colonies produce more and denser polyps and are considered peramorphic (Blackstone and Buss, 1992, 1993). DNP is an uncoupler of oxidative phosphorylation and therefore controls the rate of energy metabolism. In the loosely coupled DNP-treated colonies, the volumetric flow of gastrovascular fluid declined initially. Blackstone and Buss (1992) suggest that the decreased energy resources in DNP-treated colonies, causing decreased gastrovascular flow, are compensated by producing more polyps to pump gastrovascular fluid. A closely related species, *Hydractinia symbiolongicarpus*, shows a similar pattern of peramorphosis and gastrovascular flow as the DNP-treated *P. carnea*. The implication is that metabolic differences can be a cause of heterochronic patterns varying across species.

Polymorphism in the Urochordata

There are three classes in the Urochordata, but polymorphism is present only in the Thaliaceans (Table 1). Polymorphism is present to some degree in all three orders of thaliaceans: the pyrosomes, the doliolids, and the salps. The doliolids show the most striking variety of polymorphs (Berrill, 1958): *gonozoid*: solitary sexual individual; *oozoid*: acts as a nurse zooid for a generation of blastozooids, loses feeding capability; *blastozooids*: procure nutriment for the nurse zooid; *gastrozooids*: feeding blastozooids—gonads are absent and muscle bands are greatly reduced; *phorozooids*: develop into gonozooids.

Polymorphism is not generally known from the *Salpa*, but they do exist in two forms, a solitary and a gregarious phase. In the gregarious phase, the oozoid has a budding stolon but no gonads, while the blastozooid has go-

nads but no budding stolon. There is virtually nothing known about induction and development of the polymorphs in the Urochordata.

Polymorphism in the Social Insects

Incidence and Description of Polymorphs

Polymorphism in the social insects is a similar but not identical phenomenon to that in the marine invertebrate colonies. Colonies of social insects, such as ants, are composed of related, but not genetically identical, individuals. The individuals comprising colonies of social insects are usually at least 1/4 related and can be as much as 3/4 (Wilson, 1971). In most cases, the units comprising colonies of marine invertebrates are genetically identical (but see Buss, 1983, 1987; Rinkevich and Weissman, 1989; Rinkevich et al., 1993). The polymorphs of ant colonies represent different castes in a division of labor. Individuals within a colony of leaf-cutter ants may be specialized for defense, leaf-gathering, or tending the fungus gardens, and the queen is a specialized reproductive form. Although there are genetic differences among the individuals within a nest of social insects, the basis for morphological divergence among members of different castes is environmental rather than genetic. Thus the range of morphologies (castes) expressed among workers of leaf-cutter ants is induced by particular environmental conditions. Virtually all examples of variation in morphology among castes of the social insects are determined physiologically rather than genetically (Oster and Wilson, 1978). These are thus true polyphenisms.

All of the examples of complex polymorphisms occur in two orders of social insects, Isoptera and Hymenoptera. There are other cases of polymorphism I will discuss in the Homoptera. The termites have the most complex system of polymorphism and multiple castes in the social insects, with eight morphologically differentiated stages: *larva*: early nymphs without wingbuds; *nymph*: older nymphs with wingbuds; *pseudergate*: regressed from a nymph stage by a moult that eliminates wingbuds; *soldier*: highly modified nymph with a conspicuously enlarged head sometimes armed with a frontal gland, has a defense function; *worker*: larval form that builds nest and provides food; *primary reproductive*: fully winged; *second-form re-*

productive: functional male or female with wingbuds; considered neotenous (Matsuda, 1987); *third-form reproductive* (ergatoid): functional male or female without wingbuds; considered neotenous.

The ants are the most conspicuous in degree of structural differentiation among castes, which include the queen, haploid male, soldier, worker, and ergatogyne. The queen and male have deciduous wings, all others are wingless. The worker is an individual diverted from the normal queen course of development by having part of its adult system shut down. Some of these workers may differentiate into soldiers, distinguished by an enlarged head and mandibles; some may differentiate into an ergatogyne, an intermediate between worker and queen (Matsuda, 1987).

Among the insects, the induction of polymorphism in the aphids most closely approximates that in marine colonies. Aphids live in clonal aggregates and individuals in the clone can be induced to different forms. For example, enlarged soldier aphids can be induced in an otherwise monomorphic clone (Aoki, 1982), and, similarly, winged reproductive morphs, called alates, are induced by local crowding (Harrison, 1980).

One of the interesting aspects of polymorphism in the social insects is that it has evolved so sporadically. Systems of physical subcastes, the differentiation of the workers into minors and majors (soldiers), are essentially absent in the bees and wasps, but are present in the ants. Even in the ants, highly complex systems are present only in four genera — *Eciton*, *Atta*, *Daceton*, and *Pheidole* — and each contains no more than three distinct forms. Of the 263 living ant genera, only 44 contain species with a prominent degree of polymorphism within the worker caste (Oster and Wilson, 1978).

Polymorphism occurs rarely in other arthropods. One striking example is a trophic polymorphism of an herbivorous caterpillar (Greene, 1989). The external morphology and coloration of the caterpillar change with diet. Another example is the induced spine produced by cladocerans in response to waterborne cues from predators (J. J. Gilbert, 1966). Similarly, barnacles grow in a bent-over morphology when exposed to predators (Lively,

1986). To date, these examples of polymorphism in noncolonial organisms are rare and usually not extreme transformations.

Cues Inducing Polymorphs and Development of Polymorphs

Wilson (1953) distinguishes five steps in the evolution of morphologically differentiated castes: (1) monomorphism, (2) monophasic allometry, (3) diphasic allometry, (4) triphasic and tetraphasic allometry, and (5) complete dimorphism. Different types of polymorphism are produced by different growth transformation rules. The simplest mechanism is one where small differences in initial larval size are transformed into large differences in final size by correlated growth rate changes. A more complex mechanism involves the introduction of thresholds or decision points in growth. If a larva is above a certain size threshold halfway through growth, it becomes a major; otherwise it develops into a minor (Oster and Wilson, 1978). The scheduling of receptiveness to caste-biasing stimuli varies with individual species. The later the decision point, the more flexible is the system. All of the transformations are governed by a small set of rules that operate during larval growth and adult development within the pupa. Thus the evolution of caste systems in the ants appears to consist of relatively few steps.

The relationships between intrinsic and extrinsic mechanisms governing polymorphic transformations are known in social insects. The intrinsic control of polymorphism is through the relative levels of two hormones that affect transitions between instars. The larval stage is maintained by high levels of both ecdysone and juvenile hormone (JH). If maintained at a high level past the normal time of metamorphosis, the result is an abnormally large and perhaps bizarrely proportioned larval specimen (M. L. McKinney and McNamara, 1991). A drop in levels of JH triggers metamorphosis to the next stage. Ecdysone promotes development of adult tissues. The importance of JH in affecting polymorphs was shown by applying it to the last larval instar of an ant species (Nijhout and Wheeler, 1982; D. M. Wheeler and Nijhout, 1983). The JH delayed metamorphosis and prolonged a growth stage, resulting in production of a soldier ant

instead of a worker ant. Soldier ants differ in being larger and having hypertrophied jaws. JH also initiates and coordinates the expression of queen development. In the absence of sufficient JH, larvae will develop as workers (D. M. Wheeler, 1986, 1990, 1991).

There is interaction between extrinsic and intrinsic factors in the control of polymorphic transitions. For example, the timing of divergence in morphology determines the magnitude of the difference generated between castes (Michener, 1974). In *Myrmica rubra*, only larvae that have undergone winter chilling in the last larval stage can become queens. The queen determines whether larvae overwinter and hibernate, or hatch directly. Further, after hibernation, the queen still determines gyne development by stimulating workers to underfeed large, bipotential larvae, thus preventing additional queens from developing. However, if nutrition has been adequate, JH induces gyne differentiation (Brian, 1975).

There are two major thresholds in the evolution of morphologically variable castes in the social insects: species that have only queen-worker dimorphisms, and species with queen-worker dimorphism and multiple worker castes. These polymorphic transitions are regulated by six potential classes of cues: larval nutrition, winter chilling, temperature, caste self-inhibition, egg size, and age of queen (Oster and Wilson, 1978). Because ants are the only social hymenopterans with morphologically variable worker castes, and thus possess the most complex systems of morphological divergence (with the exception of the termites), I will focus on mechanisms cuing the morphological shifts in ants. Nutritional factors are important in most systems of gyne determination. Nutrition and development are linked by a nutritional switch; if nutrition is sufficient, JH levels rise.

Ants are exceptional among the social Hymenoptera in having multiple worker castes. Despite the morphological complexity of multiple worker castes in the two largest genera, *Pheidole* and *Campanotus*, only 44 of 263 known ant genera have any polymorphic worker castes (Oster and Wilson, 1978). D. M. Wheeler (1986) suggests that the relative rarity of worker polymorphisms may be explained by a constraint imposed by the system of worker determina-

tion. Only in cases where the worker-queen dimorphism is determined early in development is there any potential for the subsequent development of complex worker castes. In both ants and termites, complex worker castes occur only in species with early gyne determination (D. M. Wheeler, 1986).

Roisin (1988) demonstrated that the caste system of a termite species was based on the timing of metamorphosis among workers and that the developmental system is very plastic. Late larvae can give rise to (1) wing-padded nymphs, or (2) the next larval instar, or (3) neotenic reproductives. Nymphs can (1) moult directly to alates, or (2) revert to workerlike individuals, or differentiate into (3) soldiers or (4) neotenic reproductives. This degree of developmental flexibility in both the sequence and the timing of appearance of stages is unusual even among the social insects.

Polymorphism is also common in aphids, although not as well developed as in some true social insects. The situation in an aphid colony differs from social insects, but is similar to a marine colony, in that it is a true clone; all individuals are genetically identical. The units in the clone can take on different morphologies, depending upon their environment. Common morphologies include: the *fundatrix*: viviparous parthenogenetic female from fertilized egg; the *virginopara*: viviparous parthenogenetic female that produces only the same; the *ovipara*: female that lays hibernating eggs; the *gynopara*: vivipara that produces only oviparae; and the *sexupara*: vivipara that produces oviparae and males (Matsuda, 1987). As with other insects, JH has a juvenilizing effect in transformations: Aphids treated with a type of JH metamorphosed precociously and became reproductive at an earlier instar (Hales and Mittler, 1981, cited in Matsuda, 1987). Some aphids can also be induced to form a soldier caste. *Colophina clematis* produces nymphs with enlarged forelegs and middle legs that aggressively attack invaders (Aoki, 1982).

COMPARISON OF COLONIAL MARINE INVERTEBRATES AND SOCIAL INSECTS

Incidence and Complexity

Polymorphism is present in colonial marine invertebrates and social insects, but is largely absent in other groups that are serially

homologous but not colonial. For example, tapeworms and annelids not only asexually propagate new modules, but the clonal units persist as attached clones. These cannot be considered truly colonial, however, because there is no resource sharing among the modules. There is a form of reproductive polymorphism that occurs in the polychaete annelids, but it is not necessarily associated with asexual propagation. In several families, bottom-dwelling reproductive worms are hormonally induced to develop enlarged heads and enlarged paddle-shaped parapodia and take up a pelagic existence (Brusca and Brusca, 1990). The general absence of polymorphism in these groups may point toward the importance of resource sharing among units as a factor favoring the evolution of polymorphism. A limited type of inducible serial polymorphism, however, does occur in clonal aphids, rotifers and cladocerans (Harvell, 1990). An effect of resource sharing on the incidence of polymorphism is possible through the ability of a colony to subsidize partially functioning morphological variants. Thus resource sharing may affect the origin of polymorphism. Resource sharing could also mediate any costs of polymorphism and thus affect the extent to which polymorphs are maintained.

Polymorphism appears more widespread within groups of colonial marine invertebrates than in social insects. The Bryozoa and Cnidaria stand out as groups with the highest levels of polymorphism. Not only is the incidence uniformly high among entire orders within the Bryozoa and the Cnidaria, but the number of different polymorphic types within a colony can routinely exceed three and be as high as six. Not only is the incidence lower in social insects, but the number of potentially different stages is generally low except in a few genera of termites. Oster and Wilson (1978) earlier addressed the factors favoring the evolution of polymorphism in the social insects. They were also struck by the rarity of polymorphism in most groups and their inability to predict in which groups polymorphism would be prominent. They suggested that, in the ants, morphological specialization (polymorphism) is only one route to specialized function. While only a few groups of social insects show well-developed morphological specialization, be-

havioral specialization is common in all social insects. The colonial marine invertebrates differ sharply in that most are sessile, and thus options for behavioral specialization are more limited. Thus morphological specialization is the primary means of functional specialization in colonies of marine invertebrates.

The proportion of polymorphic species in some groups of the bryozoans is high. Schopf (1973) estimates that the percentage of polymorphic species is 77% in tropical bryozoan faunas and averages 26% (highest estimate 41.2%) in tropical ant faunas. The high rate of polymorphism in bryozoans is particularly striking in view of the fact that Schopf used a very conservative definition of polymorphism. Schopf (1973) suggests that the level of polymorphism in bryozoans is so much higher than in ants because the land is less well buffered to environmental fluctuations than the sea and because zooids are 100% related, but sisters of an ant colony are only 75% related at most. This does not explain the large variation in polymorphism among the classes and orders of Bryozoa nor the large variation among phyla of marine invertebrates. Furthermore, among ants, it is unlikely that high levels of polymorphism are correlated with high relatedness among a colony's members; in fact, the opposite appears more likely. For example, Sherman et al. (1988) described a correlation between colony size and low relatedness among members. Since caste polymorphism is best developed in large colonies, this suggests that caste polymorphism is better correlated with low than high relatedness.

Schopf (1973) also detected geographic variation in incidence of polymorphism in bryozoans. Species from the American arctic and the West Atlantic tropics had a comparable percentage of species with a single polymorph (counting only avicularia and vibracularia as polymorphs) (74.2 and 77.3%, respectively), but there was a higher incidence of two (16.6 versus 24.9%) and three (2.5 versus 8.4%), respectively, in the tropics. Several genera have species without avicularia in the arctic, but with avicularia in the tropics and the temperate zone. In addition, he analysed the frequency of vicarious (similar in size and shape of autozooids) and adventitious (adorned on top of existing zooids) polymorphs; among

species that exhibit polymorphism, vicarious polymorphs occur in 26.1% of tropical fauna but only 5.6% of arctic fauna. Adventitious polymorphs occur in more than 85% of both tropical and arctic fauna. The vibraculata, a very specialized form of avicularium, is 13.3% of tropical species with polymorphism and 2.2% of arctic forms. From this Schopf concludes that there is a higher incidence of polymorphism in tropical waters. Moyano (1979) found relatively high levels of polymorphism in Antarctic bryozoans and suggested that high levels of polymorphism in south polar and tropical marine bryozoans relative to arctic bryozoans was due to greater stability of the antarctic and tropical environments.

The incidence of polymorphism (defined as colonies possessing either ovicells or avicularia) also varies with colony growth form (F. K. McKinney and Jackson, 1989). The highest incidence of polymorphism occurs in recent, multiserial, multilaminate forms, although a high incidence also occurs in multiserial erect forms. In fossil bryozoans, the highest incidence is in multiserial, unilaminate forms. F. K. McKinney and Jackson (1989) attribute the increased polymorphism between fossil and recent forms as indicating a trend toward increasing morphological specialization.

Cues and Development

In both the social insects and the colonial marine invertebrates, environmental cues play a large role in the final form of the polymorph. These plastic morphological strategies allow large, potentially centrally organized "super-organisms" to be locally responsive to their environment. The form of polymorphs is sensitive to both extrinsic and intrinsic inducers.

Some general principles emerge from this review of cues:

(1) The functioning of cues is often hierarchical and involves combinations of intrinsic and extrinsic cues; examples of this are the queen-worker and worker-worker differentiation in social insects (D. M. Wheeler, 1991) and the induction of stolons in *Hydractinia* (Lange and Müller, 1991).

(2) Timing during development of cue reception is critical. For example, spines are only produced on young zooids within a bryozoan colony (Harvell, 1991), and the reception of a

cue activating a queen is only effective in early development (D. M. Wheeler, 1991).

(3) Signal transduction pathways appear very labile. The diversity of extrinsic and intrinsic cues inducing polymorphs suggests that the signal transduction pathways (STP) preceding the actual polymorph effectors are highly malleable evolutionarily. The significance of such labile transduction pathways preceding developmental switches was discussed by S. F. Gilbert (1991). He called the phenomenon of labile STP "transfer of competence" and stressed the lability of the pathways in the evolution of the vertebrate immune system and worker polymorphism in ants.

The importance of morphogens (such as JH) in activating polymorphisms in social insects, and the recent discovery of a morphogenlike inducer activating stolon branching in *Hydractinia* (Lange and Müller, 1991), indicates that morphogens or other growth factors may play an extensive role in polymorphic transformations of colonial invertebrates. Similarly, a morphogenetic inhibitor has been detected only in colonies of *Hydractinia* (Plickert, 1987, 1989), but such inhibitors are almost certainly widespread in other phyla of colonial invertebrates.

THE ORIGIN AND MAINTENANCE OF POLYMORPHISM

Overview

Although polymorphism is common in many colonial marine invertebrates, a number of clades within phyla with polymorphic representation are without polymorphs. One hypothesis to account for the episodic incidence is that the pattern of nonpolymorphic clades has a phylogenetic order. Thus if we find that all the clades without polymorphic representatives are actually considered the primitive clades, this might indicate that derived forms like polymorphs had not evolved in these plesiomorphic clades. I will examine the distribution of polymorphism relative to what is currently known about the phylogenies of bryozoans, cnidarians and urochordates.

The evolution of polymorphism in different phyla is characterized by four similarities. (1) Many of the morphologic changes are induced by environmental cues resulting in extensive epigenetic variation in morphology.

This leads to a discussion of how lability in signal transduction pathways is a key facilitator of diversity of polymorphs. (2) Most of the variation in morphology is caused by allometric changes and appears to be due to heterochronic shifts. This is particularly notable in the variation among zooids within a colony of marine invertebrates, and is detectable because unequivocal ancestor-descendant relationships are preserved in the colony-budding pattern. (3) Because iterated production of units is a pervasive theme in the biology of colonial marine forms, there is the potential for novelty to arise as budding mistakes. There is evidence that this potential is realized, particularly when biotic or abiotic factors disrupt the normal budding pattern. Examples include the kenozooids and double lophophores of bryozoans (discussed below). These novelties can persist and propagate even if they lack feeding organs, because they can be subsidized by the remainder of the colony. The lability of signal transduction pathways allows rapid genetic assimilation of initial budding mistakes. Furthermore, many populations of colonial invertebrates are potentially highly inbred (Jackson, 1986; Grosberg, 1987) and therefore likely have an excess of homozygotes. In a number of organisms there is a correlation between homozygosity and phenotypic plasticity owing to "developmental instability" (Lerner, 1954; Palmer, 1986). (4) Irrespective of the peculiarities associated with the origin and genetic fixation of these morphological novelties, the process by which the novelties and their phenotypically plastic expression are favored in natural communities remains a mystery as well. Indeed, selection is likely to play an important role in the process of genetic assimilation. Selection might act to shift the threshold of expression so that an initially inducible character can become expressed without the cue.

Each of these aspects of the evolution of polymorphism will be considered below in more detail.

The Role of Phylogeny in the Distribution of Polymorphism

Polymorphism is a derived character (Cheetham and Cook, 1983; Cuffy and Blake, 1991) found largely in the most derived clades of

the colonial phyla. In the Bryozoa, polymorphism is absent in the phylactolaemates and poorly developed in the ctenostomes, which are both considered more primitive than the cheilostomes (Silen, 1977; Cuffy and Blake, 1991). Stratigraphic data support the hypothesis of an earlier origination and diversification of the ctenostomes than cheilostomes (Cheetham and Cook, 1983). While this does not explain why derived characters did not originate in the phylactolaemates or radiate in the ctenostomes, it does support the notion that polymorphism is rare in older clades. The final resolution of this issue in the Bryozoa awaits the independent development of a cladogram based on molecular characters.

In the Cnidaria, the phylogenetic hypothesis at least explains the rarity of polymorphism in the scleractinian corals, which are members of the class Anthozoa. The Anthozoa are likely the primitive class in the Cnidaria on the basis of having linear rather than circular mtDNA (Bridge et al., 1992). Even this explanation is not without problems, however, since the pennatulaceans are an example of a clade in the Anthozoa with well-developed polymorphism. Within the family Hydractiniidae, the transition from free-living medusa to attached medusoid (gonozooid) appears to have occurred multiple times and independently of phylogeny (Cunningham and Buss, 1993).

In the Urochordata, polymorphism is strikingly absent in the ascidians, and well developed in the thaliaceans. Berrill (1958) considers the ascidians the most primitive class of the Urochordata. Once again, the absence of polymorphism appears as a plesiomorphic condition. These three examples raise the possibility that the absence of polymorphism in some clades may have little functional significance, and largely reflects timing of the diversification of the body plan. Testing this hypothesis requires a rigorous, properly controlled, phylogenetic analysis based on strongly supported cladograms.

The Role of Heterochrony in the Development of Morphological Novelty

The hierarchical nature of development in colonial invertebrates, such that the developmental processes of the modules themselves and the colony are potentially decoupled, re-

sults in a complex series of possibilities for the level at which heterochrony can act. Pandolfi (1989) distinguished between ontogenetic heterochrony (involving the developmental processes of individual modules) and astogenetic heterochrony (involving the sequence of modules produced in the colony). Because the detection and correct categorization of heterochrony usually requires information about ancestor and descendant relationships, as well as relative developmental stage and age, colonial invertebrates present both unusual opportunities and problems. An example of an ontogenetic heterochrony is the process that produces an avicularium — the operculum grows large relative to the size of its zooecium. In this case, both paedomorphosis (reduction of the zooecium) and peramorphosis (enhanced size of the operculum) occur. An example of an astogenetic heterochrony involving the same character would involve changing its location within the colony. For example, avicularia can occur in both interzoooidal and suprazoooidal (adventitious) locations. The transition from interzoooidal to adventitious is an example of an astogenetic heterochrony. Similarly, the transition from one interzoooidal location to another would also be an astogenetic heterochrony. Another example of an ontogenetic heterochrony involves thecae of the graptolites *Monograptus halli* and *M. sedgwickii*. *Monograptus halli* has proximal thecae similar to *M. sedgwickii*, and distal thecae in which full growth of the hook is retarded (Rickards, 1977). This is a clear example of an ontogenetic paedomorphosis. It is also an example of an astogenetic peramorphosis, however, since the younger modules showed retardation of a character relative to older, more proximal modules (Pandolfi, 1989). Pandolfi (1989) suggested that astogenetic heterochrony is more common than ontogenetic: The sequence of buds in the colony changes more readily than the morphology of constituent zooids.

Variations in the morphology of the bryozoan ancestrula relative to the rest of the colony are common. Indeed, the ancestrula or founding zooid of the colony shows some of the most pronounced examples of heterochrony and polymorphism. There has been almost no investigation of the special biology of the ancestrula that allows its zooid to depart

from the morphological constraints imposed on the rest of the zooids. There are three morphological peculiarities of the bryozoan ancestrula:

(1) In a few species (including *Membranipora membranacea*), acceleration of budding is seen in the ancestrula. The larva metamorphoses into a twinned ancestrula with two reduced yet fully functioning autozooidal zooecia. In some related species a tripartite ancestrula is formed. These multiple-zooid ancestrulae are the only instances in which the normal rule of sequential budding of individual zooids is violated, and instead simultaneous budding occurs. These multiple-zooid ancestrulae illustrate how novel morphologies can arise from shifts in timing of budding.

(2) In a number of cheilostomes, a tata ancestrula (characterized by the presence of spines) is produced. These may be spined and have other specialized morphological structures, even when no other zooid in the colony expresses spination (Fig. 6). The tata itself may also be a recapitulation from a more primitive group of bryozoans. Ryland (1970) describes the tata ancestrula of ascophoran cheilostomes as resembling the morphology of the more primitive anascan cheilostomes.

(3) The ancestrula is usually much smaller than later zooids. The earliest zooids in general are smaller than later ones, but none to the extent of the ancestrula.

Because some of the more prominent groups of colonial invertebrates, such as corals and bryozoans, have skeletonized parts, they also have an excellent fossil record. Thus many of the documented examples of heterochrony involve fossil species (Anstey, 1987; Pandolfi, 1989). This is problematic because, for indeterminately growing organisms, age cannot be inferred from size. Thus it is difficult to use the classic methods of detecting heterochrony, such as making comparisons among or even within taxa concerning relative size differences, or to deduce rate differences from size differences. This attempt to infer process from pattern is tenuous in solitary and colonial organisms alike (G. B. Muller, 1990). Some of these difficulties could be explicated by measuring presumed heterochronic shifts against growth trajectories with extant colonies.

While it has long been known that hetero-

chrony is an important process by which morphological variation arises both between and within colonies of marine Bryozoa (reviewed by Anstey, 1987; Pandolfi, 1989), the importance of developmental thresholds and induction in determining the placement of novelties within colonies was only recently discussed by Harvell (1991). The importance of zooid age and size were, however, implicit in Silen's examination of factors affecting the placement of polymorphs in *Thalamoporella*.

*Factors Promoting High Origination Rates
of Morphological Novelty*

What clues does the distribution of polymorphism among phyla provide to factors favoring the evolution of polymorphism? If we relax our requirement of resource sharing as a necessary component of coloniality, then we could consider the clonal aggregates of tapeworms and polychaetes as colonies. These forms proliferate by budding and the buds remain physically attached, forming a colony of attached but nonintegrated units. As discussed earlier, there are no examples of polymorphism in the tapeworms, and reproductive polymorphisms are found only in the polychaetes (epitoky). One explanation that explains an association between polymorphism and resource sharing is that resource sharing allows the nurturing of partially functioning polymorphs. Thus resource sharing might act to increase the origination rates of polymorphs.

West-Eberhard (1989) emphasized that high phenotypic plasticity may facilitate and accelerate the origin of novelty, speciation and macroevolution. If so, the propensity for plasticity in the colonial invertebrates may predispose them to high origination rates of novelties. West-Eberhard suggests that intrinsically high plasticity can facilitate the evolution of novelty by allowing small genetic changes in a single character to be accompanied by large phenotypic shifts in other characters. One example she uses is that of Slijper's goat (Slijper, 1942). An otherwise normal goat was born with reduced forelegs. The goat learned to walk on its hind legs and as a consequence of the upright stance developed enlarged hind legs, a curved spine, an unusually large neck, and an oval thoracic cross-section. The ability to compensate phenotypically for the reduced

forelegs may allow a trait that would otherwise be lethal to persist.

One mechanism that might explain high phenotypic plasticity in the colonial marine invertebrates is an association between inbreeding (producing low heterozygosity) and phenotypic plasticity (Lerner, 1954; Palmer, 1986). Many colonial invertebrates are likely to be inbred, due to having a larval form that does not disperse far and in some, even behavioral mechanisms that promote aggregation of kin (Grosberg, 1987). Within the Bryozoa, some families considered to have low polymorphism (the Membraniporidae) are exceptional in having long-distance dispersal of larvae and no sign of inbreeding. The incidence of polymorphism is high in the groups that brood their larvae and hence are more likely to be inbred. In the Cnidaria, some of the highly polymorphic species like *Hydractinia* are also brooders. The larvae from ascidian colonies, however, are brooded and have limited dispersal, and yet there is no sign of polymorphism. This is an issue that requires further analysis to detect whether there is any likelihood that developmental instability, associated with low heterozygosity, is linked to the high propensity for polymorphism in some colonial clades.

The next, and more difficult, issue is one that pervades any analysis of the origin of morphological novelty. How does the genetic program for the variant zooids initially arise? How many steps and how much time are involved in the transition from a normal zooid to a reduced avicularium? There is very little evidence bearing on the question of whether the evolution of polymorphism proceeds gradually over long periods or is more saltational. The epigenetic model of change, however, would allow extremely rapid change. In this scenario, polymorphisms could initially arise as budding mistakes or mutations that become rapidly assimilated. The little evidence that exists suggests more gradual evolution. Cheetham (1973) used principal components analysis to examine progressive and regressive evolution of polymorphism in two genera of cheilostome bryozoans. His analysis is consistent with gradual transformation between monomorphic and polymorphic forms, and showed examples of both progressive (addition of polymorphs) and regressive (loss of polymorphs) evolution.

In bryozoans, morphological variants seem to arise frequently in response to budding mistakes. These are strictly epigenetic factors that produce morphological variants. Most colonial invertebrates (and many plants), however, are more susceptible to the incorporation of somatic mutants into the germ line than unitary organisms. In most colonial invertebrates, germ cells are redifferentiated from somatic cells in each new zooid bud that develops; therefore, somatic mutants could be propagated into future somatic cells and germ cells (Buss, 1983). The appearance of interzooids, for example (reduction in zooecium size and loss of polypide), appears to be a major step in the evolution of several different polymorph types, including spinozooids, avicularia and kenozooids. The transition from an autozooid to an interzooid readily occurs when the budding process is disrupted, such as when a colony is crowded or damaged. Although these are not genetically caused changes, if a propensity for interzooid propagation were selected for, this could form a foundation upon which polymorphs could develop. One can thus imagine that the initial origination of a genetically based interzooid required only a small genetic change.

Similarly, the expression of different polymorphs may be affected by environmental factors. Polymorphs often occur in consistent locations within colonies. It is not known whether the stereotypical placement is due to a genetically based astogenetic program or to a developmental propensity for expression of polymorphism at particular sites. In *Steginoporella magnilabrus* and *S. mandibulata*, there are three forms of variant zooids: B cells (with slightly enlarged opercula), interzoecial avicularia, and adventitious avicularia. The B cells usually occur on the zooid proximal to a zooid row bifurcation (Silen, 1977). These zooids are typically a little larger than normal (e.g., Fig. 6). The interzoecial avicularia typically occur on the zooid distal to a zooid row bifurcation; these zooids are typically a little smaller than normal. The adventitious avicularia are typically also on the enlarged zooids proximal to a zooid row bifurcation. Banta (1973) hypothesizes that these three forms represent a series in the development of avicularia and suggests their placement is controlled exclusively by zooecium size variation.

There are a number of similar examples of different polymorphs being substituted into a particular budding location. In *Thalamoporella* (Silen, 1938, 1977; Powell and Cook, 1966), zooids in defined positions can be autozooids, avicularia, or kenozooids, according to their size. The implication is that the series from one extreme in complexity to the other is controlled by size variation (Silen, 1977). Several other examples of these series of morphs appearing in defined positions are shown in Figure 4. In *Flustra* also, the avicularia are always in a particular location within the colony. However, they only appear at this location if the zooid is small. A normal-sized bud in that location becomes an autozooid (Silen, 1938). Thus zooecium size plays a major role in the type of morph expressed in a particular location. The zooecium size hypothesis, that the size of the zooecium directly determines its morphology, provides a simple explanation for how epigenetic influences can cause a continuously varying character like zooid size to produce discontinuous morphologies. A small zooid always becomes an interzooid or an avicularium, that is, a morph without a lophophore. Normal-sized zooids become autozooids. Perhaps more revealing to the zooid size hypothesis is the observation of what happens to zooids of *Membranipora membranacea* when the zooecium ends up larger than normal. Again, these larger than normal zooecia are usually produced adjacent to budding disruptions. In this case the opposite result can occur: Instead of a single lophophore in the zooecium, a double lophophore is produced. Again, the interpretation that it is the size of the zooecium alone that controls the final contents is supported by this observation. Thus we can imagine a simple model where the continuous variation in zooecium size is overlain by thresholds in size that determine whether the unit will become a kenozooid or a double lophophore form. The developmental link between zooid size and morphology is not known. In other organisms, however, small changes in initial size of developing blastemas are known to produce morphological discontinuities in resulting morphology. For example, the number of setigerous segments of regenerating worms appears owing to the initial size of the blastema (Oka, 1929, in Berrill, 1952). The ultimate determi-

nants of zooid size are unknown, but must often involve disruptions in growth rates and disruptions in growth onsets and offsets.

An unusual character found only in large zooecia of *Membranipora membranacea*, adjacent to budding disruptions, is a double lophophore. The appearance of these anomalies under some environmental conditions indicates that the genetic machinery underlying the novelty exists and is only expressed under particular circumstances. This example, however, is particularly interesting because there is a relationship between epigenetically induced novelties and genetically produced novelties. Double lophophores of *Membranipora membranacea* appear both as an apparent budding accident and a mutation. As discussed earlier, particular junctures in the astogeny of bryozoan colonies are most likely to express polymorphs. One of these presumptive locations is the last row before a bifurcation; this is usually a larger than normal zooid (e.g., Fig. 6). In some colonies that have undergone slight budding disruptions, a zooid with a double lophophore can be produced at this location (C. D. Harvell, unpub.). The novelty is not propagated and often does not reappear in the colony. The evidence that this type of novelty can also arise as a mutation is the discovery of an apparent mutant almost entirely populated by the double lophophore zooids (Fig. 8). The mutant is a true "hopeful monster" in that it is populated with several novelties that never appear in normal colonies. The novelties expressed in the monster are: (1) double lophophores, (2) sideways orientation of zooids, and (3) failure to bifurcate normally and thus increasing zooid size as colony circumference increases. It is imaginable that the novelties all arise as consequences of one small mutational change in the budding pattern in the same way that double lophophores sometimes arise in normal colonies with slight budding disruptions. Goldschmidt and Piternick (1957a, b) were particularly interested in the situation

where both environmentally induced and apparent mutational novelties arise. They called the environmentally induced examples of mutational changes "phenocopies."

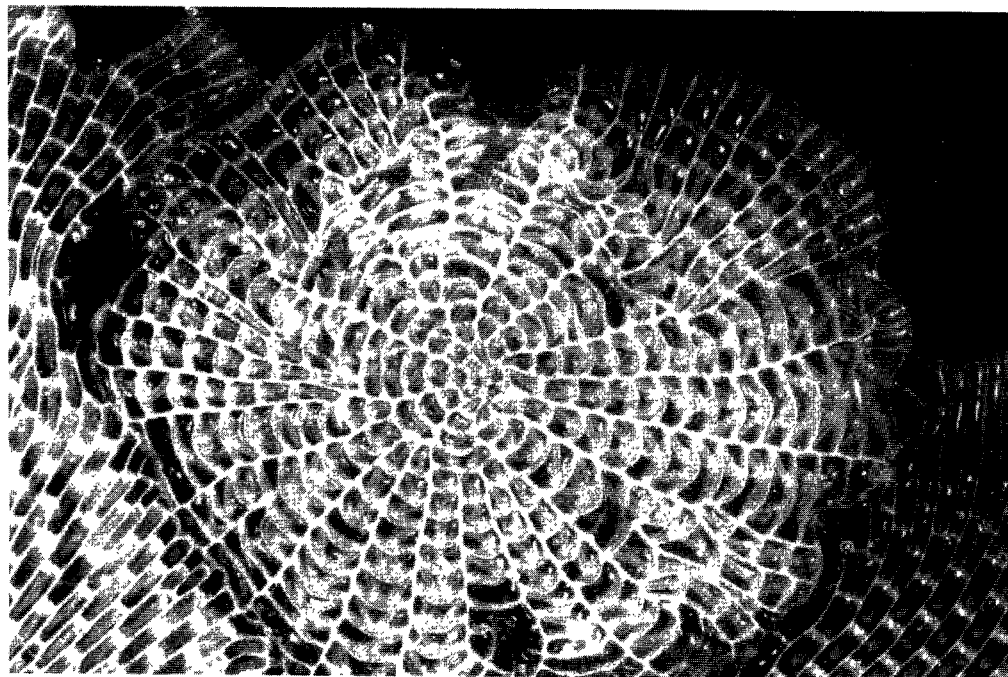
Genetic Assimilation of Threshold Traits

The distribution of both environmentally induced and constitutive polymorphisms in bryozoans and perhaps other colonial invertebrates indicates that constitutive variants could arise from environmentally induced variants through a process of genetic assimilation. For example, inducible spination may be a mechanism by which the timing and placement of fixed polymorphs can be expressed (Harvell, 1991). Waddington (1942, 1953a, b, c, 1959, 1961) defined genetic assimilation as the genetic fixation of a threshold character that originally could be obtained only by exposure to an environmental factor. Waddington's (1956a, b) and Bateman's (1959a, b) selection experiments with *Drosophila* exposed to cold, heat, or other treatments revealed that extreme phenotypes induced by the environmental shocks could be increased by selection and would eventually be spontaneously expressed without the environmental shocks. Similarly, the conversion of an inducibly spined colony to a constitutively spined one would be an example of genetic assimilation. It is also plausible that many of these polymorphs evolve from constitutive to inducible. In this case, genetic assimilation would not necessarily directly affect the character of interest, but only the receptivity of the cuing system. That these signal transduction pathways are labile is suggested by the variety of intrinsic and extrinsic cues that trigger morphological shifts. S. F. Gilbert (1991) discusses the lability of signal transduction pathways in the context of social ant polymorphisms.

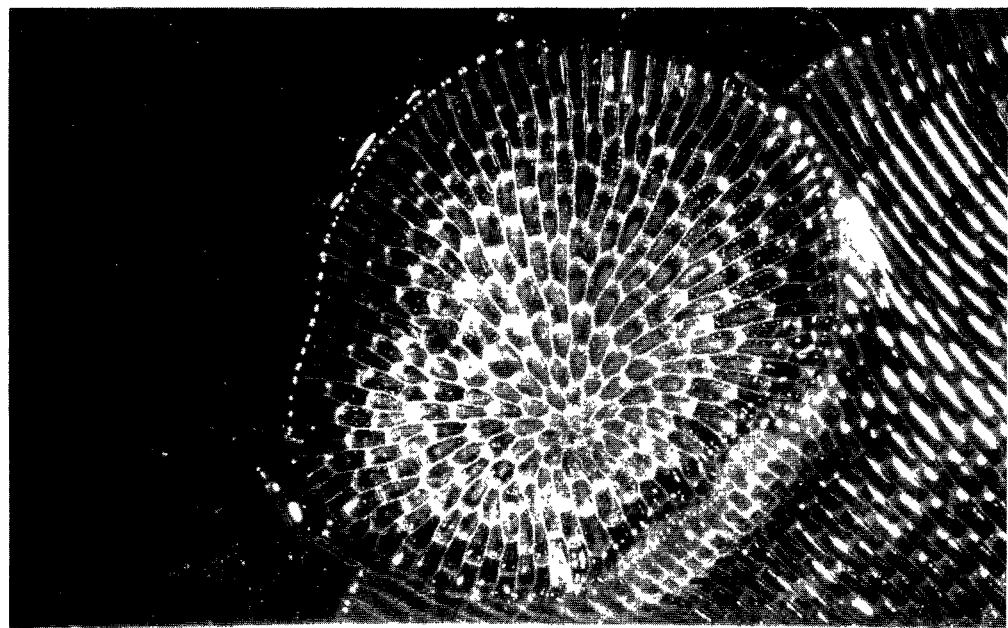
In the case of bryozoan spines, it is clear that the character, inducible spine length, is a trait with a genetically variable threshold for expression (Harvell, 1990, unpub.). In norm-

FIG. 8. THE ORIGIN OF MORPHOLOGICAL NOVELTY IN *MEMBRANIPORA MEMBRANACEA* THROUGH MUTATION

A. Mutant *Membranipora* colony. Abnormalities include double lophophores, sideways budding, and failure to bifurcate normally, resulting in gradually increasing zoecium size. B. Normal *Membranipora* colony.



A



B

of-reaction experiments, Harvell showed that different colonies (genotypes) had different thresholds of sensitivity in responding to the extrinsic inducing factor. In addition to the variation in whether a colony produced spines or not, the rate at which spines increased with increasing concentrations of inducer varied (Harvell, 1990, unpub.). The pattern of differential spination within a colony is also produced by a system of variable thresholds in sensitivity to the inducer—only the youngest zooids, near the outer edge of a colony, produce spines when exposed to the inducer (Harvell, 1991). Thus the evolution of the inducible spine response involves a shifting in the sensitivity of zooids to the inducer. The difference between a fixed, an inducible, and a nonpolymorphic colony is the sensitivity of the threshold to respond. A colony with fixed polymorphs expresses the trait without an inducer; a nonpolymorphic colony may actually be one with the capability to produce polymorphs but a very insensitive threshold.

The Maintenance of Polymorphism

One of the central benefits of division of labor and polymorphism in both social insects and colonial invertebrates is the capacity to conduct different operations concurrently rather than sequentially (Oster and Wilson, 1978). This system of parallel operation is the essence of coloniality. Thus the substantial benefits of polymorphism associated with coloniality are clear. What is problematic is explaining why some colonial forms have no well-developed polymorphism, such as the colonial ascidians, the ctenostome and phylactolaemate bryozoans, and the scleractinian corals. The absence of zooidal polymorphism in these large, speciose groups that are closely related to taxa with well-developed polymorphism is inexplicable, given our current notions of the benefits of polymorphism.

With the exception of Schopf's ergonomic model (1973), patterned after that of Wilson, there have been no previous considerations of the costs of polymorphism. One of the most obvious potential costs is of course the one discussed by Schopf, an energetic one. Because many of the polymorphs are nonfeeding, they must be subsidized by the other zooids of the colony. Although the notion that this is costly

seems clear, it is an assumption that must be tested empirically. Harvell (1992) showed a cost to induction of spined zooids in *Membranipora membranacea*, and Grünbaum (1992) showed a cost to maintaining polymorphic colonies of the same species in particular flow environments. In considering costs of polymorphism, *Membranipora* is a special case, because the defensive zooids still have a functional polypide, and thus the trade-off between defense and feeding is not as extreme as in the cases of feeding zooids that are replaced by nonfeeding defensive zooids. If there are detectable costs associated with the induction of polymorphs in this case, however, then they may be all the greater in species with a more complete division of labor. While this indicates the plausibility of cost as a factor in the maintenance of polymorphism, the evidence is still too limited to support the hypothesis that cost limits the distribution of polymorphism among taxa.

In a review of the evolution of developmental polyphenism, Moran (1992) emphasized the special relationship between the inducing environment and the selective environment. She suggested that a possible constraint in the evolution of these switches might be the availability and timing of appropriate cues. Appropriate cues are those that adequately reflect the selective environment. It is difficult, however, to understand how such a constraint would explain the type of episodic distribution of polymorphism within phyla that is seen in the colonial invertebrates, unless there were an associated aspect of the biology such as slowed growth rate or other life history attribute that reduced the response time to an inducing stimulus.

The evolution of polymorphism may also be limited by developmental costs, particularly if origination rates of polymorphs are high. These developmental costs could take the form of a high rate of nonoptimal morphs produced owing to the propensity of colonial invertebrates to spin off morphological novelties.

Why is polymorphism in the colonial invertebrates limited to a few groups, in which the incidence of polymorphism is so high? What reduces or prevents polymorphism in the clonal, social and colonial ascidians, the zoanthids, the ctenostomes, and the scleractinian corals? Are origination rates lower in these groups or is there strong selection against polymor-

phism? If a high incidence of polymorphism is associated with high origination rates owing to a less canalized developmental process, then it is possible that groups with high polymorphism all have a similar developmental syndrome. This could have arisen by chance in some groups and not in others. Or there may be a more adaptive explanation for the difference in incidence of polymorphism among major groups. In the colonial marine invertebrates, the only factor that seems to vary among groups and be associated with the incidence of polymorphism is the degree of compartmentalization among the units of the colony. As discussed earlier, the cheilostomes are the taxon with the highest degree of compartmentalization and the best-developed polymorphism within the Bryozoa. The Phylactolaemata, with no polymorphism, also lack compartmentalization. Similarly, the units of ascidian colonies are closely integrated and not compartmentalized; they share a blood vascular system and a coelom, but not a gut. This hypothesis is nullified, however, by examination of the Hydrozoa. The two orders containing highly polymorphic colonies, the Siphonophora and the Hydroida, are the most highly integrated and least compartmentalized of any colony, with component polyps sharing a common gut.

The hypothesis that energetic costs limit the expression of polymorphism also does not explain the distribution of polymorphism among groups. If energetic costs were the primary limitation on the expression of polymorphism, I would expect polymorphism to be best represented within the scleractinian corals. They are tropical in distribution and could be judged as having the largest energy budget, because they derive much of their carbon from photosynthetic algae living in their tissues. This algal-subsidized physiology may result in a greater energy budget. Yet polymorphism is conspicuously absent in the scleractinian corals. In contrast, bryozoans and hydrozoans, which are typically not subsidized by symbionts, have well-developed polymorphism in both tropical and temperate communities.

The only hypothesis remaining to explain the current distribution of polymorphism among higher taxa is one of phylogenetic constraint. The major groups discussed that do not have polymorphic representatives are all considered

less phylogenetically derived than those more derived groups with polymorphic representatives. In some cases, however, it is traits like polymorphism itself that contribute to the placement of the group within a phylogeny. The hypothesis therefore remains untested without phylogenetic trees derived independently of morphology.

CONCLUSIONS

The incidence of polymorphism is variable among colonial marine invertebrates and social insects, but appears much higher in some groups of bryozoans than in any group of social insects.

The higher rate of polymorphism in some groups of colonial marine invertebrates than in social insects may be explained by their monoclonal nature and consequent lack of conflict among the units of a colony. It is also possible that the iterative developmental process that produces the units is subject to readily producing and assimilating developmental novelties.

The apparent preponderance of polymorphism in the most derived clades and the relative paucity of polymorphism in ancestral clades of colonial marine invertebrates raises the hypothesis that the absence of polymorphism in many groups has little functional significance and is instead a plesiomorphic condition.

In both colonial marine invertebrates and social insects, extrinsic cues are largely responsible for controlling shifts in morphology. The role of juvenile hormone is of overwhelming importance in the proximate control of polymorphism in insects; there is the potential for morphogenetic inducers to play a similar role in colonial marine invertebrates.

Although the benefits of polymorphism appear large, opposing costs limiting the incidence of polymorphism have not been clearly identified. Costs of polymorph induction have been measured in bryozoans, and theorized in the social insects. No evidence yet suggests that there are developmental costs in having the ability to produce polymorphs.

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