

# Clonal Organisms and the Evolution of Mutualism

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## INTRODUCTION

The adaptive significance of clonality has been explored for organisms that are threatened by physical factors, competitors, herbivores, or predators, or that make their living by colonizing patchy or ephemeral resources (e.g., Stebbins 1960; Williams 1975; Harper 1977; Jackson 1977, this volume; Buss 1979; Cook 1979, 1983, this volume; Francis 1979; Werner 1979; Abrahamson 1980; Price 1980). Although at least one of the partners in many important mutualistic symbioses is a clonal organism (lichens, corals-dinoflagellates, orchids-mycorrhizal fungi, termite-gut flagellates, rumen bacteria, etc.), the relationship between clonality and mutualism has not been discussed. Here I will examine this relationship not in terms of the adaptive significance of clonality to organisms that participate in mutualisms, but rather from the complementary viewpoint of clonality as a trait that may facilitate the evolution of mutualism.

The evolution of a mutualistic symbiosis may be assumed to be divided into two steps: (1) the initial development and maintenance of an association between two organisms and (2) the transition of that association into one that is mutually beneficial. I will contrast the likelihood of evolving through each of these steps for clonal versus aclonal organisms and then compare predictions from this verbal model with observed patterns of association of clonality with mutualism in the multicellular invertebrates.

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*Clonality* as I use it here encompasses cases of propagation by growth processes such as budding, fragmentation, gemmulation, and rhizome growth. *Mutualism* is defined as an interspecific association from which all participants benefit (e.g., Ricklefs 1973; Krebs 1978). Here I am specifically concerned with those associations in which the organisms interact continuously throughout some part of their lives, thus excluding intermittent associations, such as most pollination, seed dispersal, and cleaning interactions, and concentrating attention on associations in which the partners maintain close physical contact, including cases in which one organism lives within another. By *symbiosis* I mean any continuous interspecific association, regardless of its effect on participating individuals.

Although many aspects of the integration and reconstitution of mutualistic symbioses have been elucidated by excellent experimental work, investigators have dealt, for obvious reasons, almost exclusively with organisms that have long been in mutualistic association with each other or else they have substituted a similar species for one of the normal partners (see Trench 1979 for a review of experimental treatments of plant-animal mutualisms). In such cases one or both of the subjects have already made substantial adaptations to a mutualistic life-style. Consequently, the bulk of this work does not directly address the question of how organisms originally come to be involved in a mutualism. Thus many of my arguments here will, by necessity, be made by analogy with processes about which more information is available.

The evolution of mutualism has been considered theoretically in a cost-benefit model by Roughgarden (1975), and the potentially related development of decreased virulence in a parasite has also been considered formally (e.g., see discussions by May and Anderson and by Roughgarden in Futuyma and Slatkin 1983). As Slatkin (1983) has pointed out, evolutionary models based on optimization or game theory represent a valuable approach, but such models require specification of possible phenotypes and include no means by which to test assumptions of what phenotypes are available—that is, what can or will evolve in a particular organism. Some constraints on the evolution of an optimum trait may simply not be predictable from formal mathematical models, and for a balanced view of the processes of evolution, processes other than adaptation must also be considered (e.g., Gould and Lewontin 1979). It is this complementary problem with which I tangle here in comparing the relative probabilities that organisms that differ in their propagative options will be in positions in which traits related to participation in mutualism can be selected, if they are available. My purpose is to provide a simple and informal selective model, to which refinements can be added later, and an examination of patterns in what has evolved in organisms living now.

A hypothetical case of clonal and aclonal organisms that are otherwise the same, perhaps a polymorphism in an imaginary species, will best serve for

comparison in the following verbal model summarized in table 12.1. Examples presented in the model are meant to be primarily illustrative, not exhaustive. Throughout I use *within* to describe the position of guest organisms with respect to hosts, and although this implies emphasis on endosymbionts, many points are more generally applicable. When the predictions of the verbal model are explored for living organisms, other ways, besides propagative options, in which clonal and aclonal organisms may differ from each other and which may be relevant to the evolution of mutualism will become obvious, and these will be discussed in the final section.

## MODEL

### DEVELOPMENT OF A PERSISTENT ASSOCIATION

#### *Initial Colonization of a Potential Host by a Free-living Organism*

Entry of a potential symbiont, that is, any alien organism, into an intimate association with a living system may be accomplished by physical or chemical disruption of barriers by the invader, by feeding of the host on the invader, or by some other inducement for the host to allow the invader to enter. Whereas established symbionts may have evolved a variety of specialized means by which they enter and live within or on their host, most naive invaders will be physiologically unable to survive within the host or even to enter the host without damaging themselves.

An invader that does happen to be competent to enter and live in the new environment inside the host may, if clonal, be able to propagate itself without further ado, producing more competent symbionts. By contrast, for an aclonal invader that is able to live within the host to produce more competent symbionts, it must be an inseminated female or it must find a mate that also happened to invade and survive in the same host. In either case, young produced must be able to develop within the host.

The advantage that a clonal organism has in its initial invasion of a new host organism may be analogous to the adaptive association of clonality with colonization of patches of habitat such as islands, disturbed sites, and host organisms with which an association has already developed (e.g., see Stebbins 1960; Coates and Oliver 1973; Jackson 1977; Abrahamson 1980; Price 1980). In such situations, the ability to propagate asexually allows the colonizing individual rapidly to increase its size (in units that are connected or not), thereby increasing its chances of successful colonization by better buffering itself against local extinction.

When the patch of habitat colonized is a living organism, the response of the

**Table 12.1.** Summary of model for the evolution of mutualism.

	GUESTS	
	Aclonal Guests	Clonal Guests
<b>A. Development of a persistent association:</b>		
1. Initial colonization	Colonization by a mate or mating prior to colonization is required for a colonist to build a population in the host; recombination products may not be viable in the host	A population can be built up within the host by a single colonist that is able to proliferate there
2. Continuity and spread of the association	Progeny of the colonists must find a new host individual before the colonists die or their original host dies	A large population can be established within the host before dispersal to another host is required; if the host is also clonal, host and guest can proliferate in tandem
<b>B. Transformation of an association into mutualism:</b>		
1. Value of a host individual to the symbiont	Host value declines with guest reproductive values because of the mortality of guest individuals and dispersal of their progeny to other host individuals	Guests can maintain a population in a host individual as long as it lives, increasing the value of each host individual and providing selective impetus to prudent host use
2. Intra-specific competition among guests and decreased guest virulence	Competition among guests within the host may select for those which convert host into guest progeny most rapidly, i.e., increased guest virulence	Selection for prudent host use is possible if all guests within a host individual are of the identical genotype (e.g., a clone)
3. Effects of interspecific competition within host	Although symbiont species may ultimately sort out spatially and temporally, selection will favor individuals that are best at converting the host into their progeny	Because clones appear to be effective competitors a single clone can gain control of a host individual, protecting the host from interlopers and possibly preventing selection for increased guest virulence
4. Reinfection	Movement from one host individual to another may be risky; populations of symbionts depleted by gifts to host progeny are not internally renewable; the host may have little control over symbiont population size, which depends on rates of entry and death	Tandem proliferation is possible if the host is also clonal; supplies of symbionts can be replenished within host parents after gifts to host offspring; symbiont population size can be controlled by the host

Hosts	
Aclonal Hosts	Clonal Hosts
<p>A. Development of a persistent association:</p> <ol style="list-style-type: none"> <li>1. Initial colonization</li> <li>2. Continuity and spread of association</li> </ol>	<p>If a host is damaged by the invasion of a guest it has only its own resources to bolster its response</p> <p>Each fresh host is a physically separate and genetically different patch</p> <p>A host damaged by guest invasion may be aided by attached clonemates; guests can live intercalated between units</p> <p>A clonal host can increase in tandem with a clonal guest</p>
<p>B. Evolution of mutualism:</p> <ol style="list-style-type: none"> <li>1. Host value</li> <li>2. Reinfection</li> </ol>	<p>Guests that use their host prudently are more likely to have a selective advantage in a host of high value, such as a relatively long-lived clonal organism</p> <p>A clonal host can increase in tandem with a clonal guest</p> <p>Inevitable host mortality, especially in short-lived species, may give little selective advantage to guests with decreased virulence</p> <p>Coordination of life histories of guest and host must develop for reinfection to be ensured</p>

host "island" to the invader further complicates colonization. Since most metazoans have a recognition and defense system of some sort (see Cooper 1976; Marchalonis 1977, for reviews), they may attack an invader. Those whose defense systems include memory components may be able to mount an even more effective defense against a repeat invader. Vertebrates can become "immunized" not only against a variety of viral and unicellular pathogens, but also against metazoan parasites such as nematodes, cestodes, and trematodes (Kennedy 1975 for a review). Defense systems of a variety of invertebrates, such as sponges (Evans, Curtis, and Kerr 1979), corals (Hildemann, Bigger, and Jokiel 1979), annelids (Cooper 1969), crabs (A.E. Taylor, Taylor, and Collard 1964), and others (Cooper 1976; Hildemann, Bigger, and Jokiel 1979), also appear to include memory components that, although short-term and un-specific in most cases, nevertheless could be effective against a repeat invader. Similarly, some plants can be induced through attacks by herbivores to increase the levels of toxic compounds in their tissues in preparation for subsequent onslaughts (Whittaker and Feeny 1971, and references therein). Some orchids are stimulated to produce fungicides by the invasion of their mycorrhizal fungi (Nüesch 1963) and, after an initial viral infection, beans show increased resistance to subsequent invasions by viruses (Wheeler and Pirone 1969). Thus an organism that attempts to colonize another living organism may be greeted by a system that not only can recognize it as alien and attempt to kill or evict it, but that may also make difficult the invasion of the mate required by an aclonal invader in order to build a population within the host. If host defenses are arrayed such that entry is the critical point for an invader, a single clonal organism that is able to slip through may be able to build a population within the host.

Many successful symbionts appear to be able to trick or avoid the defenses of their hosts altogether, preventing either phagocytosis or digestion following phagocytosis (e.g., Read 1970; Cheng, Cali, and Foley 1974; Trench 1979, 1980). If a naive invader bears a mutation conferring ability to evade the normal host response to invaders, the trick will be automatically (barring somatic mutation) shared with clonal offspring. But if the invading individual lacks the ability to propagate itself, the mutation may be lost if the invader fails to reproduce, or it may be lost in recombination.

Clonality in the potential host organism may also increase the chances that a new association will persist. If members of a clone maintain connections with each other, they may be able to rely on each other for nutritional and other support (e.g., Pitelka and Ashmun, this volume), thereby increasing their tolerance of damage from the entry or feeding activities of an invader. Clearly, if the host dies when a potential symbiont invades, the interaction has no future as a partnership.

Physical disruptions of a clonal host in which units stay-together may also be

lessened if the symbiont can live intercalated between the units. Even though the units may not normally live completely autonomously, they may be sufficiently capable of independent living that they are relatively unaffected by the physical presence of the symbiont among them. An example of such an arrangement is the mutualistic association of the cheilostome bryozoan *Cella-poraria brunnea* and the hydroid *Zanclaea*. The hydroid, which gains substratum space from the association and confers protection from spatial competitors on its host, lays down its stolons between the zooids of the bryozoan, thereby minimizing physical disruption and eliminating physiological disruption of its host altogether (Osman and Haugsness 1981).

Clonal organisms may also live longer than aclonal relatives (Cook 1983, this volume; Jackson, this volume). The prediction that clonal hosts will have increased chances of developing persistent associations with symbionts is therefore consistent with Roughgarden's (1983) prediction that, all else being equal, more obligate symbionts will come to be associated with longer-lived host organisms.

#### *Maintenance of a New Association beyond the First Generation*

Even if a new association is maintained successfully throughout the lives of the instigators, it will not be able to develop further if it is not reconstituted in subsequent generations. Elaborate mechanisms for ensuring continuity, such as accurate host detection and synchrony of reproductive cycles between host and guest, have become important aspects of many symbiotic associations. However, these are, presumably, adaptations to established associations, and associates that are new to each other must reconstruct their association without them.

The probability that a new symbiont that has not developed special mechanisms for locating a fresh host will successfully colonize a fresh host will increase with both the size of the population of competent symbionts and with the time available for colonization. A new clonal invader can build a large population of competent symbionts before having to attempt a relatively risky step such as sexual reproduction or dispersal, and it can maintain that population while continuing to attempt to disperse. A new aclonal invader, which for reasons detailed above may be less likely to be able to build and maintain a population indefinitely within its original host, will therefore be more likely to go extinct within that host before it has a chance to produce sufficient propagules to ensure that a fresh host is colonized.

The ability of clonal organisms to increase and maintain their local representation by simply growing into adjacent or newly available resources, thereby using the local resource to its fullest before dispersing, has been pointed out many times. Clonal plants can grow out over sand dunes (Ogden 1964) or

onto fresh badger mounds in the prairie (Platt 1975), and they respond most quickly to newly available space in old fields (Allen and Forman 1976). Clonal animals inhabiting the undersurfaces of foliaceous corals can grow into the new space provided as the edges of the plates grow (Jackson 1977) or as previous occupants are removed by predators (Palumbi and Jackson 1982). By contrast, aclonal organisms must reproduce and the propagules must settle successfully in order for them to increase or even maintain a local population.

Maintenance and spread of the initial association may be facilitated still more when both the host and symbiont are clonal organisms because they can grow in tandem, the symbiont simply proliferating into expanding host tissue. For example, as a hermatypic scleractinian coral grows, it produces more tissue that can be infiltrated by asexual propagation of its symbiotic zooxanthellae. If the coral fragments, each new physiological unit already includes symbionts. Thus, the association may be propagated as many independent units, decreasing the risk of mortality (e.g., Cook 1979, 1983; Janzen 1977) of the symbiont before its propagules can colonize another host.

#### CLONAL ORGANISMS AND THE EVOLUTION OF MUTUALISM

An intimate association between two previously unassociated species is unlikely to have an immediate positive effect for both participants but may start out as a neutral or even parasitic interaction. Clonality in the symbiont or in both the symbiont and host may increase the probability that a new association will develop into a mutually beneficial partnership as adaptations to the association develop in the participating species.

##### *Value of the Health of the Host to Symbionts*

Efficient use of hosts by a symbiont depends upon a trade-off between the value of an individual host and the difficulty of locating and invading a fresh host. The location and entry of a fresh host by a symbiont is an especially hazardous step in many host-parasite systems (e.g., Price 1980; Barrett 1983) and, judging by the elaborate mechanisms for locating hosts and the phenomenal fecundities exhibited by many symbionts, this may be the case for symbionts in general. Symbionts should therefore attempt to get as much as possible out of each host individual colonized, within constraints (detailed below) imposed by the relative life spans of the host and symbiont species.

For a symbiont that can propagate itself within its host, the value of the current host is high since, as long as the host remains alive and healthy, the symbiont has a home in which it can build and maintain a population and from which it can send forth dispersing propagules. Thus the selective value of



decreased virulence or even a beneficial effect on its host for a clonal symbiont may be high. Only rarely do aclonal metazoan symbionts reproduce within animal hosts. Although larval stages of some helminth parasites reproduce asexually or by parthenogenesis within the host (e.g., Holmes 1983), and although aclonal symbionts may produce massive numbers of propagules [e.g., 10,000 eggs per day per female *Haemonchus contortus* (Kennedy 1975)], the propagules are not normally able to remain within the current host and must pass out and infect a fresh host before they can develop. The value of its current host to an aclonal (mortal) symbiont will therefore decline as the reproductive value of the symbiont declines and end when the symbiont dies. Since it is of no consequence to a dead symbiont or its dispersed progeny whether the host remains healthy or dies, the evolution of decreased virulence ("prudence" in host use) is less likely among aclonal than among clonal symbionts.

When the host is also a clonal organism, indefinitely producing more tissue into which a clonal symbiont can expand, its value to a symbiont is increased still more, further facilitating the evolution of mutualism. In contrast, the certain mortality of an aclonal host may give less selective impetus to a symbiont, whose efforts cannot prevent the inevitable demise of its current host, for making a positive contribution.

Thus, mutualism is more likely to develop when the symbiont, or both the symbiont and host, are clonal organisms because in these cases a symbiont can expect its host to be able to provide a home for a longer time, allowing selection for symbionts with gentler approaches to turning host biomass into symbiont biomass. This is in agreement with Roughgarden's (1975) prediction that it will be advantageous for an association to develop into a mutualism if the guest can improve its own fitness by helping its host.

#### *Competition among Conspecific Symbionts within a Host*

The above comparison between an aclonal and clonal symbiont is, of course, oversimplified because, once an association has developed, the symbiont species may develop effective ways of locating hosts that make it less likely that a symbiont will be the sole colonist of its host. Competition among symbionts within the same host must therefore be taken into consideration.

Competition among conspecific aclonal symbionts within the same host may manifest itself in smaller sizes of individual symbionts, as for cestodes in mice (Moss 1971), or in a decline in egg production per individual and increase in generation time, as for digenean trematodes in sheep (Boray 1969). Although the proximate effect on a host of crowding of its symbionts may not be unfavorable, competition among conspecific symbionts may ultimately select for those which can grow faster and reproduce earlier and more. If the host is providing the raw materials for symbiont growth and reproduction, selection for

increases in the rate and amount of growth and reproduction of the symbiont cannot lead to amelioration of the effects of the symbiont on the host. In one case, schistosomes initially infecting a host appear to incorporate host antigens onto their surfaces, allowing the adults to live within the host without provoking it but triggering host immunity to subsequent infections (Smithers, Terry, and Hockley 1969). Depending upon the relatedness and numbers of schistosomes in the initial infection, such a parasite might evolve decreased virulence. In general, however, selection for prudent host use should be less likely among asexual symbionts, since the population of conspecific symbionts within a particular host is usually a temporary association resulting from numerous independent invasions of unrelated individuals that do not build a population by reproducing within that host. In contrast, although more than one strain (clone) of zooxanthella may colonize a host individual, Schoenberg and Trench (1980c) did not find more than one strain in any individual host. They suggest that ultimately the more productive strain will tend to exclude the others. If, in general, single clonal symbionts can fill their hosts with identical symbionts, selection may be allowed for prudence in host use. Selection acting on the symbiont through the host can favor symbiont clones that keep their hosts healthy.

Such evolution of decreased guest virulence, although derived by individual selection, may be considered an extreme example of previous models in which group selection has been used to explain decreased guest virulence (for reviews and discussions see May and Anderson 1983; Holmes 1983; Roughgarden 1983). From his analysis of the conditions under which group selection can occur, Leigh (1983) has suggested that populations of some parasites in their hosts may be the only groups for which group selection is able to overwhelm individual selection.

### *Competition among Symbionts of Different Species*

Competition within a host may also occur among symbionts of different taxa, although little is known of the mechanisms involved. Consistent differences in distribution within a host of asexual parasites of different taxa have been described (see Schad 1963; Crompton 1973, for a review), but experiments documenting competitive interactions have been performed in only a few cases. Acanthocephalans have been shown to inhibit growth of tapeworms and displace them from their preferred sites in rats (Holmes 1961); and one species of larval trematode may suppress cercarial release of another in double infections of the mud snail *Nassarius obsoletus* (DeCoursey and Vernberg 1974). In no cases, however, do internal asexual parasites appear to be able to evict other species from their host altogether.

Although information available regarding competition among clonal sym-

bionts is also scanty, interactions among them appear to be different. The "normal" algal symbionts of the acoel turbellarian *Convoluta roscoffensis* are not only able to prevent the establishment of other potential symbiont taxa if introduced into their host together, but can also evict previously established symbionts of other taxa (Provasoli, Yamasu, and Manton 1968). The *Chlorella* symbiont of *Paramecium bursaria* is also able to evict prior occupants of other taxa (Bomford 1965). The blood-digesting bacterial symbiont of the leech *Hirudo* prevents establishment of other symbionts in the gut of its host (Read 1970). *Escherichia coli* in the gut of germ-free guinea pigs, although not a normal symbiont, can prevent infection by *Shigella* and *Vibrio*, as can the normal guinea pig gut flora (Lev 1963). Finally, pure cultures of clonal symbionts in insects result from mixed infections (Brooks 1963).

Free-living clonal organisms may be superior at acquiring and maintaining control over localized resources (analogous to host organisms) in two types of situations. To the processes effective in these two situations, Werner (1979) has applied the terms *preemptive competition* and *interactive competition*.

In systems in which resources become available in patches, organisms that are not necessarily good competitors when in contact with other organisms may be able to preempt new patches of resource by filling them before others can colonize, thus maintaining a local advantage by preventing the colonization and concurrent use of the resource by potential competitors. One way of being successful at this "preemptive competition" is to propagate clonally following a single colonization event.

In systems in which competitive ability is related to the ability to expand, the significance of clonality for the acquisition and maintenance of control over a resource is different. In such situations clonal organisms may be superior at "interactive competition." Jackson (1977, this volume) has drawn attention to this fundamental difference between solitary and clonal organisms that grow on marine hard substrata. Clonal organisms, such as encrusting bryozoans and sponges, can simply grow in order to acquire the substratum space that is the limiting resource. This expansion may run right over solitary organisms, such as barnacles and serpulid worms, which, by contrast, must grow to sexual maturity and produce young, which must then settle successfully in order to increase significantly their cover of that substratum.

Too little is known of the mechanisms of competition among symbionts within a host to determine if those used by clonal symbionts are analogous to those described above for free-living species. The blood-digesting bacteria of the leech produce an antibiotic that makes the host uninhabitable for other symbionts, but this is the only case for which a mechanism for the observed displacement is indicated. Whatever the mechanisms, however, competitive interactions among clonal symbionts appear to result in definite winners.

Several important consequences of the ability of clonal symbionts to gain

and maintain control of a host may increase the chances that a symbiosis involving clonal symbionts will develop into a mutualistic association.

First, if a clonal symbiont can keep control of its host, the value of an individual host organism will be higher, and the selective value of decreased symbiont virulence, or even of positive contributions to the host, will be increased.

Second, the ability of a clonal symbiont to rebuff or evict alien symbionts from its host may, as in some of the examples given above, serve to protect the host from harmful invaders. Increased survival of hosts that harbor such symbionts may confer selective value on host traits that encourage symbiont growth.

Third, a host that harbors a clonal symbiont may be more assured that the symbiont living within it is its "normal" one. Hosts may not be able to differentiate among similar symbiont species (e.g., Jolley and Smith 1980; and see Trench 1979 for a review of experimental cross-infections in plant-animal symbioses) and thus may allow alien symbionts to partake of benefits for which only their normal symbiont gives fair return. Effects of alien symbionts on hosts have been studied under laboratory conditions by presenting aposymbiotic hosts with unusual potential symbionts. Free-living strains of *Chlorella* and *Scenedesmus* support growth in *Paramecium bursaria* less well than does its normal symbiotic *Chlorella*, although they infect easily (Karakashian and Karakashian 1965). Likewise, the acel turbellarian *Convoluta roscoffensis* grows less rapidly when infected with algae other than its normal *Platymonas convolutae* (Provasoli, Yamasu, and Manton 1968). A host that leaks nutrients to or confers other benefits upon symbionts of whose identity it is not certain, and which may not provide services in return, may be selected against. If clonal symbionts eliminate alien symbionts from their host, the host may be assured that its guests are always of the same taxon and it may safely (with respect to selection) confer benefits on its guests commensurate with the selective advantage they contribute.

### *Certainty of Reconstitution of an Intimate Association*

For mutualistic integration to develop, a host and symbiont must not only be certain of each other's identity, but they must also be assured of each other's presence. The reconstitution of a symbiotic association can be greatly simplified, and therefore more assured, when the symbiont or both the symbiont and host are clonal organisms.

Reinfection of gut flora is accomplished by trophallaxis in termites (Brooks 1963); wood wasps stuff the holes in which they lay their eggs with pieces of their symbiotic fungus (Baker 1963); leaf-cutter ant queens carry pellets of their

fungus in their mouths on nuptial flights (Cooke 1977); and eggs from some corals, hydroids, and zoanths may be packed with a subsample of the zooxanthellae from the parent colony (e.g., Schoenberg and Trench 1980a). A clonal symbiont population can simply expand to replace those given to offspring, and the new populations in the offspring can expand as they grow. By contrast, a gift from parent to offspring of an aclonal symbiont may deplete parental supplies that are not internally renewable and may ultimately be insufficient for the needs of the growing offspring, anyway. Although aclonal symbionts often do infect the offspring of their hosts, this usually requires that life cycles become synchronized so that availability of infective symbiont offspring coincides with availability of host offspring. Such a requirement may further restrict the likelihood that mutualism develops.

When both the host and symbiont are clonal organisms, reinfection can become even more certain because the association can be propagated as a unit. For example, the *Chlorella* symbionts of *Hydra*, *Paramecium*, and *Spongilla* are simply divided among offspring produced by parental division (Trench 1979).

In order for some mutualistic interactions to work for the benefit of the host, the host requires not only infection but also a certain population size of symbionts in residence. For instance, the light organs of squid must be filled with sufficient bacteria actually to emit light in order for the association to benefit the squid (Buck 1978). Selection for hosts that facilitate symbiont residence, and thus the development of mutualism, may depend in these cases upon assurance that the host always has a sufficiently large population of symbionts. A single infection of a clonal symbiont can supply the gut of a termite with sufficient microorganisms for cellulose digestion or the light organ of a squid with sufficient bacteria to emit light. By contrast, since the population of aclonal symbionts within a host may be a function of the rate of entry of individual symbionts and the lengths of their lives, and thus dependent upon external variables over which the host may have no control, the population sizes of aclonal symbionts are less likely to be consistent from host to host and time to time. The interdependence of host and symbiont that is a feature of mutualistic associations is less likely to develop under such circumstances. Furthermore, if the symbiont has unlimited potential to increase its population size within its host, then the host can more readily control the size of the symbiont population, evicting extras or preventing further increases. Such control may not be possible for a host that must rely on chance recruitment to gain a particular number of symbionts.

Another aspect of this last point relates to special structures that function solely in the mutualistic association of a host and its symbiont. Selection for the development of special structures, such as bacterial light organs in some teleosts and squid and the fungus-carrying pouches of ambrosia beetles, is unlikely if full complements of symbionts are not consistently assured.

## CORRELATION OF CLONALITY AND MUTUALISM

The above predictions may be best evaluated by observing patterns among the multicellular invertebrates because among them representatives of a wide variety of feeding methods, developmental plans, and degrees and types of motility can be found on both sides of the clonal-aclonal and mutualistic-not mutualistic dichotomies.

The orders of invertebrates were tabulated with indications of which include members that are clonal or that participate, as hosts or guests, in mutualistic associations (see Appendix 12A). An order was counted as clonal if mention is made of propagation by budding or fragmentation in textbook or monographic treatment on the familial or ordinal level. Participation in mutualism was credited to an order if at least one member participates as host in an association for which there is documentation for or strong suggestion of mutual benefit.

Analysis on the level of orders was made as a compromise between a manageable number of taxa and relative homogeneity of morphology, development, and chemistry within a group. Analysis based on a lower taxonomic grouping might on initial consideration appear to be more refined and, therefore, more meaningful. However, mutualisms in a number of related lower taxa are frequently a reiteration of essentially the same interaction. That is, each mutualism does not represent a new partnership between previously naive species, but rather the result of one or a series of speciation events or the simple expansion of the host or symbiont into an association with a relative of the original partner [e.g., see Mitter and Brooks (1983) for a recent discussion of association by descent]. For example, the association of zooxanthellae with corals of the order Scleractinia is unlikely to have developed independently in each genus or family and therefore, with respect to the evolution of mutualism, should be considered a single case of mutualism. Of course, not all orders are homogeneous with respect to the symbionts they harbor. Nevertheless, the ordinal level appears to be the best compromise for observation of patterns in the initiation of new mutualisms. Detailed analysis of lower taxa with respect to the evolution of mutualism is bound to be interesting (e.g., Roughgarden 1975), but such an approach seems more applicable to the very different question of the relative costs and benefits of participating in a mutualistic association.

## THE PATTERN

All forty invertebrate orders that harbor mutualistic symbionts include members that harbor clonal guests. Four of these orders (Actiniaria, Scleractinia, Decapoda, and Hymenoptera) also include members that harbor aclonal symbionts. No order includes only members with aclonal symbionts. Members

of the order Sacoglossa harbor symbiotic chloroplasts, which could be considered aclonal symbionts but, as chloroplasts are not independent organisms, these were not included in this analysis. The clonal symbionts are members of a wide variety of groups, including bacteria, cyanobacteria, green algae, dinoflagellates, hydroids, zoanthids, demosponges, scleractinian corals, and fungi. Results are summarized in table 12.2. As hosts, members of 28 percent (22/80) of the clonal orders have developed mutually beneficial associations with symbionts, whereas only 8 percent (18/236) of aclonal orders have developed such associations (clonality and mutualism are not statistically independent by the chi-square test,  $p < 0.001$ ).

#### DISCUSSION OF THE PATTERN

The above results are in agreement with the predictions of the model: the probability of development of a mutualism may be increased if the guest, or both the host and guest, are clonal organisms. The pattern of association is more striking for the symbionts, which is to be expected since the verbal model is also clearly stronger for clonal guests.

#### *"Exceptions" to the Predicted Pattern*

Exceptions to the pattern predicted are, of course, inevitable since the scale considered is so large. Moreover, and more importantly, the predictions of the model do not concern the specific advantages of associations, but merely how prior attributes (in particular, propagative options) of either prospective associate may change the probabilities that mutualism will evolve. Nevertheless, some classes of exceptions may give additional insight into the evolution of

**Table 12.2.** Summary of data in Appendix 12A.

NUMBER OF ORDERS OF INVERTEBRATES	WITH MUTUALISTIC SYMBIONTS	WITH NO MUTUALISTIC SYMBIONTS	TOTAL
With clonal members	22	58	80
With no clonal members	18	218	236
Total	40	276	316
Number of orders of invertebrates hosting mutualistic symbionts:			
With only clonal mutualistic symbionts			36
With both clonal and aclonal mutualistic symbionts			4
With only aclonal mutualistic symbionts			0
Total			40

mutualism. One type of exception includes the well-known and frequently studied crustaceans and fishes that are asexual symbionts of a variety of cnidarians (e.g., Mariscal 1970; Glynn 1976; Smith 1977). Advantages to the study of these partnerships include the large size of individual guests, which allows them to be easily manipulated and counted. Large guest size relative to host size may also be a key to this apparent exception. For guests much smaller than their hosts, sole control may be gained by clonal propagation within the host. However, crustaceans and fishes commonly approach the size of their hosts and thus may be able to control their hosts without clonal propagation. Indeed, crustacean mutualistic symbionts, with the exception of the crab *Trapezia* (Glynn 1976), live singly or in pairs with their cnidarian hosts.

Another class of exceptions of particular interest with respect to this model are the many asexual Insecta that harbor clonal symbionts. Many of these groups include members that are parthenogenetic. Price (1980) suggests that this is an adaptation to their parasitic life-style, which may in turn be dependent upon symbionts that aid them in using unusual foods. More directly relevant to the model presented here, some of these insects are also social. The Hymenoptera and Isoptera live in highly developed societies; and some Coleoptera, including ambrosia beetles, live in groups with subsocial organization (Wilson 1971). In these cases, sociality may favor evolution of mutualism by increasing the reliability of transmission of symbionts in ways very similar to those provided by clonal propagation (see above).

### *Limitations of Comparative Historical Analysis*

Attempts to gain an understanding of a historical process from currently observed patterns suffer from a common flaw: a correlation does not necessarily give any indication of the processes that generated it. Here I have taken the viewpoint that clonality and mutualism are correlated because clonality facilitates the evolution of mutualism, but an association between these characters could also have been generated by several other processes. Alternative explanations include: (1) taxa that are clonal and mutualistic may have higher rates of splitting; (2) particular taxonomic groups may be especially prone to the development of both clonality and mutualism; (3) one of these characters (clonality or mutualism) may represent an adaptation to the other; and (4) mutualism may facilitate the evolution of clonality.

Involvement in a mutualistic association is, unfortunately, a character that is not generally amenable to direct historical analysis. Historical analysis of mutualism is often stymied by the paucity of unambiguous morphological correlates of mutualism that fossilize and by the poor fossil record of many important groups, such as demosponges and ascidians. One case of mutualism involving two organisms that were, as far as is known, previously completely



naive with respect to symbiosis has been followed from its inception: bacteria infected amoebae in the lab and, after a period of parasitism, became required guests of their host (Jeon 1980). Unfortunately, but for obvious reasons, this is the only example for which the entire history of an association is known. Clonality may be more amenable to direct historical analysis in groups for which the record is adequate (see volumes edited by Boardman, Cheetham, and Oliver 1973 and by Larwood and Rosen 1979; also Coates and Jackson, this volume; Tiffney and Niklas, this volume), although complications can arise in the analysis of fossil material from clonal organisms that do not maintain connections with clonemates and from apparent clones that are actually the results of aggregation and not clonal propagation.

In any case, the order in which a particular organism became clonal and also involved in a mutualistic association may be unclear. This, coupled with the ambiguities shrouding the phylogenies of many invertebrate groups, suggests that consideration of the association between clonality and mutualism from a viewpoint based on any or all of the four alternative explanations listed above would be appropriate. However, the widely scattered phylogenetic distribution (refer to appendix) of known mutualisms and the relatively small percentage of the total number of orders (40/315) known to harbor mutualistic symbionts suggest that the most likely of these are either that clonality is a common adaptation to mutualism or that clonality can facilitate the evolution of mutualism. Price (1980) has suggested that parthenogenesis is a common adaptation to the parasitic life-style. However, there appears to be no evidence against the view that clonal propagation by fragmentation or budding has arisen before mutualism in most invertebrate groups. This, combined with the observation that virtually all mutualistic clonal symbionts of invertebrate groups are from groups in which the normal free-living state is also clonal, suggests that the view taken in the model given here (i.e., that clonality can facilitate the development of mutualism) may be more generally appropriate.

#### *Correlated Characters That May Influence the Evolution of Mutualism*

A potentially more serious difficulty with this particular analysis is related to the tendency of clonal organisms to differ from asexual organisms in ways besides their ability to propagate asexually. Relative to asexual organisms, clonal organisms may have (depending upon the taxa) smaller unit size, larger genet size, higher regenerative powers, more flexible overall form, less sophisticated internal defense systems, and more heterogeneous distribution of genetic variation within populations (e.g., see other papers in this volume). Some of these attributes may be directly relevant to the evolution of mutualism.

Large genet size may predispose organisms for the role of host in a symbiotic association because a larger host may be less disrupted by a symbiont. A large

host may also be of greater value to its guests, and this may increase the selective value of decreased virulence of a symbiont and therefore the probability that mutualism will develop. Of the predominantly clonal phyla, genets of Porifera and Cnidaria, among which are included many hosts of mutualistic symbionts, tend to be larger than genets of Bryozoa or invertebrate Chordata, among which mutualism is relatively rare. Members of the sponge class Calcarea do not appear to participate in mutualisms as hosts, and individual calcareous sponges tend to be much smaller than individuals of the other sponge classes. However, this pattern may not only reflect a greater predisposition of large organisms to serve as hosts, but also a preference of investigators for studying larger organisms.

Flexible growth form and high regenerative powers, both related to meristic (modular) construction, and thus generally to clonality, may help a host tolerate an invader; and less sophisticated internal defense systems in the host may allow an invader to tolerate the host. Although these characters may therefore increase the probability that an organism will be able to become a host in a symbiosis, it is not clear that any of these would affect the probability that a symbiosis will develop into a mutualism.

Small unit size must help to predispose organisms to be symbionts, both mechanically and through more rapid generation time (e.g., Bonner 1965). All the mutualistic symbionts of 72 percent (29/40) of the orders that harbor helpful guests are unicellular algae, fungi, protozoa, and bacteria, and these organisms are also included among the mutualistic guests of 9 of the other host orders. Again, though, there is no clear reason why small size of a guest should increase the probability that a symbiosis will develop into a mutualism.

Characteristics typical of particular taxa may, however, encourage the transformation of symbioses involving them into mutualisms. Bacteria, for instance, produce a wild array of chemicals that allow them to aid in digestion of otherwise indigestible substances, produce light, and so on, for amenable host organisms. The evolution of such chemical diversity in bacteria, however, may be facilitated by their clonality, in conjunction with their extremely short generation times. The photosynthetic abilities of plants make them potentially good nutritional partners; and the nematocyst batteries of cnidarians and apparent toxicity of many sponges can serve to augment the defenses of a guest or host. Vermeij (1983) has suggested that the ability to defend against predators may predispose organisms to act as hosts. Before the guest and host are in a position to "bargain" with each other, however, they must have formed a consistent association, and these special characters may not increase the probability that an initial association will develop. Unusual chemical properties or especially effective defenses may actually decrease the probability that other organisms will be able to tolerate an intimate association with a creature so endowed.

Although characters that are commonly correlated with clonality, or that are special attributes of particular clonal groups, may therefore increase the probability that either an association develops between two species or that it becomes a mutualism, clonality may still play an important role in influencing the evolution of an interaction through both these stages. Determination of the relative importance of clonality per se versus other related or special characters to the observed association between clonality and mutualism will have to be based on detailed analysis of individual groups.

## SUMMARY

The consequences of clonality that may increase the probability that a new host-guest association lasts through the initial contact and first few generations, before any special adaptations to the association are made by the new partners, can be summarized briefly:

1. Clonality in the invader may increase its chances of success in the initial colonization of the host because it allows the single initial invader to build a population.
2. Clonality in the host may increase its physical tolerance of the invader.
3. Clonality in the invader, or in both the invader and host, can facilitate the continuity and spread of the association by increasing the probability that the invader can colonize a fresh host before the association is terminated by the deaths of the original associates. When both invader and host are clonal, they can proliferate in tandem.

A symbiotic association that involves clonal organisms as symbiont or as both symbiont and host may have a higher probability of developing into a mutually beneficial partnership because:

1. each host individual is more valuable to the symbiont, increasing the selective value of decreased symbiont virulence;
2. when symbionts within a host are all clonemates, selection for prudence in host use (decreased virulence of symbiont) is possible;
3. the apparently very effective competitive abilities of clonal symbionts may allow them to
  - a. gain and maintain control of their host, increasing its value and allowing selection for decreased symbiont virulence,
  - b. protect their hosts from harmful invaders, and
  - c. assure the host of the identity of its symbionts;
4. reinfection is greatly simplified, increasing the ensurance that
  - a. a host will consistently have symbionts,

- b. the symbiont population within a host will be sufficiently large for the host to benefit from it, and
- c. the control of the size of the symbiont population can rest with the host.

The predictions of this selective model were explored using the multicellular invertebrates as an example. Clonal guests are found in every order of hosts of mutualistic symbionts, and 28 percent of clonal orders host mutualistic symbionts, whereas only 8 percent of aclonal orders serve as hosts of beneficial partners. Thus the predictions of the model are matched. However, interpretation of such data with reference to a selective model is complicated by bias in the degree to which various groups of organisms have been studied, by a variety of ambiguities associated with any attempt to determine historical details from present correlations, and by characters common to clonal organisms or to specific clonal groups that may further predispose them to participating in mutualisms.

## APPENDIX 12A: CLONALITY AND MUTUALISM IN THE INVERTEBRATES

In the following list of invertebrate orders, names of phyla appear in SMALL CAPITALS, names of classes appear in *italic*, and names of orders and of subclasses and superorders that are not subdivided and that are counted as orders appear in roman type. Indication is given of groups that include members that are clonal (C), parthenogenetic (P), hosts of clonal mutualistic symbionts (HC), hosts of parthenogenetic symbionts (HP), and hosts of aclonal symbionts (HA). The groups of symbionts harbored include bacteria and cyanobacteria (B), rickettsia (R), fungi (F), unicellular algae (Z), protozoa (Pr), sponges (S), cnidarians (Cn), arthropods (A), and vertebrates (V). Numbers following names of phyla refer to references listed below.

### PORIFERA (1,14,21,42)

#### *Calcarea*

Clathrinida	C
Leucettida	C
Leucosoleniida	C
Sycettida	C
Pharetronida	C
Sphinctozoidia	C

#### *Hexactinellida*

Amphidiscosida	
Reticulosida	
Hexactinosida	
Lychniscosida	
Lyssacosida	C

<i>Demospongiae</i>				Zoanthidea	C HC Z
Dendroceratida	C	HC	B,Cn	Antipatharia	C
Dictyoceratida	C	HC	B,Cn	Ceriantharia	
Verongiida	C	HC	B,Cn		
Haplosclerida	C	HC	Cn,Z		
Poecilosclerida	C	HC	Cn,Z		
Halichondrida	C			CTENOPHORA (16)	
Homosclerophorida	C	HC	B	<i>Tentaculata</i>	
Choristida	C			Cydippida	
Spirophorida	C			Lobata	
Hadromerida	C	HC	Cn,Z	Cestida	
Axinellida	C	HC	Cn	Platyctenea	C
Agelasida	C	HC	Cn	<i>Nuda</i>	
Lithistida	C			Beroida	
<i>Sclerospongiae</i>					
Ceratoporellida	C				
Stromatoporoida	C			PLATYHELMINTHES (17,39)	
Tabulospongida	C			<i>Turbellaria</i>	
Merliida	C			Acoela	HC Z
Cnidaria (7,11,16,23,35,37,39,45)				Rhabdozoa	C HC Z
<i>Hydrozoa</i>				Alleocoela	
Trachymedusae	C			Tricladida	C
Limnomedusae	C			Polycladida	
Narcomedusae	C			<i>Trematoda</i>	
Anthomedusae	C	HC	Z	Monogenea	
Leptomedusae	C			Aspidobothrea	
Pteromedusae	C			Digenea	
Chondrophora	C	HC	Z	<i>Cestoda</i>	
Siphonophora	C			Amphilinidea	
Milleporina	C	HC	Z	Gyrocotylidea	
Stylasterina	C			Tetraphyllidea	
<i>Schizophzoa</i>				Lecanicephaloidea	
Coronatae	C			Proteocephaloidea	
Semaeostomae	C			Diphyllidea	
Rhizostomae	C	HC	Z	Trypanorhyncha	
Stauromedusae	C			Pseudophyllidea	C
<i>Cubozoa</i>				Nippotaeniidea	
<i>Anthozoa</i>				Taenioidea	C
Stolonifera	C			Aporidea	
Telestacea	C				
Alcyonacea	C	HC	Z	NEMERTINEA (10)	
Gorgonacea	C	HC	Z	<i>Anopla</i>	
Pennatulacea				Paleonemertini	
Coenothecalia	C			Heteronemertini	C
Actiniaria	C	HC	Z	<i>Enopla</i>	
		HA	A,V	Hoploneimertini	
Scleractinia	C	HC	Z,S	Bdellonemertini	
		HA	A		

ACANTHOCEPHALA (18)		<i>Gymnolaemata</i>	
Archiacanthocephala		Ctenostomata	C
Palaeacanthocephala		Cheilostomata	C HC Cn
Eoacanthocephala		<i>Stenolaemata</i>	
		Cyclostomata	C
		<i>Phylactolaemata</i>	C
ROTIFERA (18)		BRACHIOPODA (34)	
Seisonacea		<i>Inarticulata</i>	
Bdelloidea	P	Lingulida	
Monogononta	P	Acrotretida	
GASTROTRICHA (18)		<i>Articulata</i>	
Macrodasyoidea		Strophomenida	
Chaetonotoidea	P	Rhynchonellida	
		Terebratulida	
KINORHYNCHA (18)		SIPUNCULIDA (19,32)	C
NEMATODA (18)		MOLLUSCA (3,5,12,24,25,26,38,40)	
Enoploidea		<i>Monoplacophora</i>	
Dorylaimoidea	P	<i>Aplacophora</i>	
Chromadoroidea		Neomenioidea	
Trichiuroidea		Chaetodermatoidea	
Rhabditoidea	P	<i>Polyplacophora</i>	
Mermithoidea	P	<i>Gastropoda</i>	
Araeolaimoidea		Archaeogastropoda	
Monhysteroidea		Mesogastropoda	
Desmoscolecoidae		Neogastropoda	
Rhabdiasoidea	P	Entomotaeniata	
Oxyuroidea		Parasita	
Ascaroidea		Cephalaspidea	
Strongyloidea		Acochlidoidea	
Dracunculoidea		Philinioglossoidea	
Filarioidea		Thecosomata	
Spiruroidea		Basommatophora	
Dioctophymoidea		Stylommatophora	
NEMATOMORPHA (18)		Sacoglossa	(HA)
Gordioidea		Anaspidea	
Nectonematoidea		Gymnosomata	
ENTOPROCTA (25)	C	Notaspidea	
		Nudibranchia	HC Z
		Soleolifera	
PRIAPULIDA (25)	C	<i>Bivalvia</i>	
		Nuculoida	
PHORONIDA (19)	C	Solemyoidea	
		Arcoidea	
BRYOZOA (29,36)		Mytiloidea	

Pterioida	HC S	TARDIGRADA (25)	P
Unionoidea	HC Z		
Trigonioida			
Veneroidea	HC Z,S,Cn	ARTHROPODA (4,13,27,30,31,33,41,43,44)	
Myoidea	HC B	<i>Merostomata</i>	
Pholadomyoidea		Xiphosura	
<i>Scaphopoda</i>		<i>Pycnogonida</i>	
<i>Cephalopoda</i>		<i>Arachnida</i>	
Nautiloidea		Palpigradida	
Sepioidea		Uropygida	
Teuthoidea	HC B	Amblypigida	
Octopoda		Ricinuleida	
		Scorpionida	
ECHIURA (25)		Pseudoscorpionida	
		Solpugida	
		Araneae	
		Opiliones	
		Acarina	P HC R
ANNELIDA (9,25)		<i>Cephalocarida</i>	
<i>Polychaeta</i>		<i>Branchiura</i>	
Orbiniida		<i>Mystacocarida</i>	
Ctenodrilida		<i>Branchiopoda</i>	
Psammodrillida		Notostraca	P
Cossurida		Conchostraca	P
Spionida	C	Cladocera	P
Capitellida		Anostraca	P
Opheliida		<i>Ostracoda</i>	
Phyllodocida	C	Palaeocopida	
Amphinomida		Podocopida	
Spintherida		Myocopida	
Eunicida		<i>Copepoda</i>	
Sternaspida		Calanoida	
Oweniida		Harpacticoida	
Flabelligerida		Cyclopoida	
Fauveliopsida		Notodelphoida	
Terebellida		Monstrilloida	
Sabellida	C	Caligoida	
<i>Oligochaeta</i>		Lernaeopodoida	
Lumbriculida	C	<i>Cirripedia</i>	
Haplotaxida	C	Thoracica	
<i>Branchiobdellida</i>		Acrothoracica	
<i>Hirudinea</i>		Ascothoracica	
Acanthobdellida		Rhizocephala	
Rhynchobdellida		<i>Malacostraca</i>	
Gnathobdellida	HC B	Leptostraca	
Pharyngobdellida		Anaspidacea	
ONYCHOPHORA (25)		Bathynellacea	
		Stygocaridacea	
PENTASTOMA (25)		Thermosbaenacea	

Spelaeogriphacea				Mantodea		
Mysidacea				Blattaria		HC B,Pr
Cumacea				Isoptera		HC B,Pr
Tanaidacea				Ephemera		
Isopoda				Odonata		
Amphipoda				Thysanura		
Euphausiacea				Microcoryphia		
Decapoda		HC,HA	S,Cn,V	Entotrophi		
Stomatopoda						
<i>Pauropoda</i>						
<i>Diplopoda</i>				ECHINODERMATA (8,25,28)		
Pselaphognatha				<i>Crinoidea</i>		
Oniscomorpha				Articulata		
Limacomorpha				<i>Asteroidea</i>		
Colobognatha				Zorocallida		
Polydesmoidea				Phanerozonida		C
AscospERMOMORPHA				Spinulosida		C
Juliformia				Forcipulatida		
<i>Chilopoda</i>				Platyasterida		
Scolopendromorpha				Euclasterida		
Lithobiomorpha				<i>Holothuroidea</i>		
ScutigermORPHA				Aspidochirotida		C
Geophilomorpha				Elasipodida		
<i>Symphyla</i>				Dendrochirotida		C
<i>Insecta</i>				Dactylochirotida		
Lepidoptera				Molpadiida		
Zeugloptera				Apodida		
Trichoptera				<i>Echinoidea</i>		
Diptera		HC	R,B,F	Cidaroida		
Mecoptera				Diadematoidea		
Siphonaptera				Diadematoida		
Hymenoptera		P	HC,HP R,B,A,F	Lepidocentroida		
Neuroptera				Holectypoida		
Raphidiodea				Clypeasteroida		
Megaloptera				Holasteroida		
Coleoptera		P	HC B,F	Nucleolitoida		
Strepsiptera				Cassiduloida		
Hemiptera		P	HC B,F	Spatanguloida		
Thysanoptera		P		<i>Ophiuroidea</i>		
Phthiraptera			HC B	Ophiurac		C
Corrodentia				Euryalae		C
Zoraptera						
Plecoptera						
Embiaria				CHAETOGNATHA (19)		
Grylloblattodea						
Phasmatodea				POGONOPHORA (6,20)		
Orthoptera				<i>Obturata</i>		HC B
Dermaptera				<i>Perviatia</i>		
Diploglossata						



HEMICHORDATA (19)		<i>Larvacea</i>		
<i>Enteropneusta</i>	C	Copelata		
<i>Pterobranchia</i>		<i>Asciacea</i>		
Rhabdopleurida	C	Enterogona	C	HC B
Cephalodiscida	C	Pleurogona	C	
<i>Planctosphaeroidea</i>		<i>Thaliacea</i>		
		Pyrosomida	C	
		Doliolida	C	
CHORDATA (2,15,22)		Salpida	C	HC B

*References:* 1, Bergquist 1978; 2, Berrill 1950; 3, Bloom 1975; 4, Brooks 1963; 5, Buck 1978; 6, Cavanaugh et al. 1981; 7, Dunn 1981; 8, Emson and Wilkie 1980; 9, Fauchald 1977; 10, Gibson 1972; 11, Glynn 1976; 12, Greene 1974; 13, Harada 1969; 14, Hartman 1980; 15, Herring 1978; 16, Hyman 1940; 17, Hyman 1951a; 18, Hyman 1951b; 19, Hyman 1959; 20, Jones 1981; 21, Levi and Porte 1962; 22, Lewin 1981; 23, Mariscal 1970; 24, McLaughlin and Zahl 1966; 25, Meglitsch 1972; 26, Moore 1969; 27, Moore and Teichert 1969; 28, Nichols 1967; 29, Osman and Haugness 1981; 30, Price 1980; 31, C.L. Remington, pers. com., 1982; 32, Rice 1975; 33, Ross 1971; 34, Rudwick 1970; 35, Russell 1953; 36, Ryland 1970; 37, Smith 1977; 38, D.W. Taylor and Sohl 1962; 39, Trench 1979; 40, Vance 1978; 41, Waterman and Chace 1960; 42, West 1976; 43, Wood 1977; 44, Wright 1973; 45, Wulff and Buss 1979.

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