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## Invertebrates in Endosymbiotic Associations<sup>1</sup>

MARY BETH SAFFO

*Institute of Marine Sciences, University of California, Santa Cruz, California 95064*

**SYNOPSIS.** Endosymbiosis is a phenomenon of central importance to the biology of many invertebrate animals. Parasitic, commensal and mutualistic endosymbioses are widely distributed among invertebrate taxa, and have arguably played a major role in the evolution of several invertebrate families, classes and phyla. Sometimes accounting for as much as 50% of invertebrate volume or biomass, endosymbionts can profoundly affect the ecology, physiology, development and behavior of invertebrate hosts. Endosymbiosis raises a number of questions that are worth the serious, sustained attention of a broad range of invertebrate biologists.

### INTRODUCTION

Barring the complexities of clonal invertebrates, we tend to think of an individual invertebrate animal as just that: an individual genome, a representative of a single taxon. But many invertebrate organisms are not merely individual genomes or single taxa; as hosts of persistent, intimately associated endosymbiotic communities, they can also be viewed as morphological, physiological or genetic chimeras of several taxa. With recent research, the pervasiveness and importance of symbiosis among invertebrates are beginning to be appreciated, but they have not yet been integrated into everyday teaching and research perspectives on general invertebrate biology. To stimulate such integration, a workshop, *The Impact of Symbiosis on Invertebrate Physiology, Ecology, and Evolution*, was sponsored by the Division of Invertebrate Zoology for the Centennial Meeting of the American Society of Zoologists.

### DISCUSSION

Symbiotic associations vary in their selective consequences, in their mode of transmission, and in their pervasiveness throughout invertebrate host populations. Endosymbiotic interactions can be harmful (parasitism) to host or endosymbiont; they

can also be mutually beneficial (mutualism), or have a beneficial effect on one partner, but a negligible effect (commensalism) on the other. Most commonly, the selective effect on the host or endosymbiont is either too poorly known, or too complex, to define in any of these three simple terms.

Endosymbionts can be intracellular or extracellular inhabitants, transmitted hereditarily (vertically) with their host, or non-hereditarily (horizontally), necessitating re-establishment of the symbiotic association each generation. Some endosymbionts (as in many parasites) infect only some members of a given invertebrate population. Others (as in many "mutualistic" or other endosymbioses which apparently benefit the host) are chronic symbionts (Saffo, 1991a), inhabiting 100% of the host population for a significant portion of the host's life history. Nevertheless, whatever the exact nature of symbiotic dynamics, endosymbionts can have profound effects on the biochemistry, physiology, morphology, behavior, population biology, ecology and evolution of invertebrate hosts. This impact can be demonstrated in a number of contexts:

- Symbiosis is taxonomically widespread among invertebrate animals, involving members of virtually every invertebrate class and phylum. No invertebrate taxon is entirely symbiont-free. At minimum, at least some percentage of individuals in every invertebrate species are hosts to parasites, commensalistic symbionts, or to pathogens.

Beyond the ubiquitous distribution of

<sup>1</sup> From the Workshop on *The Impact of Symbiosis on Invertebrate Physiology, Ecology, and Evolution* presented at the Centennial Meeting of the American Society of Zoologists, 27-30 December 1989, at Boston, Massachusetts.

parasites and pathogens, chronic endosymbioses (Table 1) are also broadly distributed throughout invertebrate phyla. Associations between invertebrates and autotrophic endosymbionts are among the most well-known chronic symbioses. For example, a wide range of fresh-water and marine invertebrate taxa from temperate and tropical latitudes are habitually associated with protistan or cyanobacterial photoautotrophs. Chemoautotrophic (especially sulfur-oxidizing) bacteria are chronic inhabitants of vestimentiferan and perviate pogonophorans; lucinids, thyasirids and other bivalves, and several species of nematodes, oligochaetes and turbellaria (Ott *et al.*, 1982; Cary *et al.*, 1988; Wood and Kelly, 1989).

Many more invertebrate taxa contain chronic heterotrophic endosymbionts, most of which have received little study. Several species of bioluminescent sepioloid squid (Wei and Young, 1989; Mcfall-Ngai and Ruby, 1989) harbor luminescent bacteria, as do *Pyrosoma* (Leisman *et al.*, 1980) and some insect pathogenic nematodes (Nealson, 1991). In the above symbioses, at least one effect of the endosymbionts (bioluminescence) is obvious, although the ecological significance of the luminescence is not always clear. Less is understood about other heterotrophic endosymbionts. For instance, although dicyemid "mesozoans" colonize the kidneys of 100% of the populations of temperate and boreal octopods, the metabolic and ecological impact of the symbiosis is not known (Hochberg, 1983). Heterotrophic bacteria are found in placozoa (Grell, 1981), demosponges and sclerosponges (Vacelet, 1975; Bergquist, 1978); in leeches and earthworms (Buchner, 1965); in the cytoplasm of *Nephromyces*, a protistan endosymbiont of molgulid ascidians (Saffo, 1990, 1991a); in shipworms and terrestrial prosobranchs (*Pomatias elegans*: Buchner, 1965); and in species of echinoids, brittle stars and asteroids (De Ridder *et al.*, 1985; Walker and Lesser, 1989; Bosch, 1992). Mollicutes (mycoplasmas) and walled bacteria have been reported from larval and adult bryozoans (Lutaud, 1969; Woollacott, 1981; Zimmer and Woollacott, 1983; Boyle *et al.*, 1987). Ten percent of all insect species

(Douglas, 1989; Ishikawa, 1989), as well as some arachnids (*e.g.*, ticks and mites), harbor non-pathological bacterial endosymbionts, either as extracellular intestinal symbionts (as in termites and cockroaches), or as intracellular inhabitants of "mycetomes" or other organs (as in grain weevils, aphids, sucking lice, and cockroaches). Only in shipworms (Waterbury *et al.*, 1983), luminescent symbioses and herbivorous insects have the metabolic activities of heterotrophic symbiotic prokaryotes been clearly demonstrated.

- Especially among chronic endosymbioses, a significant percentage of "invertebrate" biomass can be microbial symbiont biomass. A typical termite gut, for instance, contains as many as  $10^7$  protozoan cells and  $10^9$ - $10^{10}$  bacterial cells (Smith and Douglas, 1987), accounting for 33-50% of total termite weight (Whitfield, 1979). Similarly, bacterial symbionts make up 37.5% of the uncontracted mesohyl volume of the demosponge *Verongia*, equal to, or slightly exceeding, the volume of host cells (Vacelet, 1975; Bergquist, 1978). In larvae of the grain weevil *Sitophilus oryzae*, there are 1 to 3 million endosymbiotic bacteria, comparable to the total number of host cells (Nardon and Grenier, 1991). Parasitic symbionts (*e.g.*, rhizocephalan symbionts in crabs, acanthocephalan symbionts in pill bugs) can also take up a significant percentage of host volume (Moore, 1984a, b; Schmidt and Roberts, 1989).

- Endosymbiosis has played a major role in the evolution of several invertebrate taxa. The ubiquitous distribution of endosymbionts among several groups of invertebrates suggests that chronic symbionts have been intimately involved in the evolution and radiation of a number of invertebrate genera, families and orders (lucinid bivalves, molgulid ascidians, hermatypic scleractinian corals: Saffo, 1991a, b), classes (Hirudinea: Buchner, 1965) and even phyla (Pogonophora: Vetter, 1991). Endosymbionts can affect the evolution of their hosts directly, by coevolution or cospeciation with their hosts, or indirectly, by their impact on host metabolism and ecology.

Many invertebrates are themselves symbionts. Several orders and classes, especially

among flatworms, nematodes, and annelids, consist exclusively of endo- or ecto-parasites, and some phyla (orthonectids, dicyemids and acanthocephalans) contain only endosymbiotic species. Several other orders and classes (e.g., polychaetes, isopods, copepods, cirripedes), include many parasitic or commensalistic members. These organisms show striking morphological, developmental and physiological adaptations to endosymbiotic life.

Endosymbiont-induced speciation has been demonstrated, thus far, in about a dozen species of arthropods (Thompson, 1987; Nardon and Grenier, 1991). Pathologic or nonpathologic symbionts can effect host speciation either through reproductive isolation of individuals with differing (or absent) endosymbiotic communities, or through divergent selection of host populations which differ in symbiont composition or in dynamics of host-symbiont interactions (Thompson, 1987; Saffo, 1991b).

- Invertebrate endosymbioses can have major ecological impact, both on the habitat range and inter-species relationships of the invertebrate hosts themselves, and on the ecosystems of which they are a part.

Many invertebrate hosts of chronic endosymbioses, such as termites, cockroaches, scleractinian corals, and molgulid ascidians are abundant or globally distributed taxa, conspicuously present in terrestrial or marine ecosystems. For these and other symbiotic invertebrates, the physiological contributions of chronic endosymbionts can allow exploitation of profoundly new niches. Symbioses with autotrophic symbionts have allowed species from at least 7 phyla (Table 1) to lead partially or exclusively autotrophic lives, where some of them, such as scleractinian corals, Pogonophora, and lucinid bivalves, play significant or even key roles in tropical reefs, sulfur-rich habitats and other marine communities. The metabolic contributions of cellulases, amino acids, B vitamins, sterols, and nitrogen fixation or nitrogen recycling by intracellular bacteria and microbial intestinal symbionts have allowed insects, bivalves and others to exploit specialized, nutritionally limited plant diets such as wood, phloem, and grain. All blood-sucking invertebrates, including

sucking lice, leeches and ticks, are obligately associated with bacterial endosymbionts.

- Beyond the contributions of symbionts to host nutrition per se, both parasitic and mutualistic endosymbioses can have profound effects on many other aspects of the biology of invertebrate hosts. In several mutualistic endosymbioses, some of these effects can be interpreted nevertheless as general consequences of symbiont contributions to host nutrition, underscoring the impact of endosymbiont metabolism in many such symbioses. In bacterial-grain weevil symbioses, for instance, aposymbiotic populations of the hosts, *Sitophilus oryzae* and *S. zeamais* (Nardon and Grenier, 1991) cannot fly. Further, the development time of aposymbiotic weevils is lengthened, and their fertility reduced, compared to their symbiotic counterparts. All these effects are plausibly linked to the contributions of vitamins and amino acids and enhancement of mitochondrial enzyme activity by the bacterial symbionts of *Sitophilus*.

Other effects of symbiont infection suggest biochemical interactions that are not tied to nutrient exchange between symbiont and host. In rhizocephalan-parasitized crustaceans, for instance, the alteration of secondary sexual characteristics of hosts, and reduction or elimination of host reproduction by parasites result from hormonal interactions between parasite and host. In several insects and mites, bacterial or protozoan symbionts can alter sex ratios of host populations, usually through selective mortality of male embryos or juveniles (Huger *et al.*, 1985).

Parasites can also dramatically alter host behavior, especially that of invertebrate intermediate hosts. Acanthocephalan infestation of arthropods (Moore, 1984a, b) can reverse typical host responses to light (in infected amphipods and cockroaches), humidity, shelter and background color (infected pill bugs). Individuals of the gastropod *Ilyanassa obtusata* parasitized by the trematode *Gynaecotyla adunca* crawl higher up into the intertidal zone than either unparasitized individuals, or individuals parasitized by other species (Curtis, 1987); *G. adunca* and other trematode species

TABLE 1. Chronic endosymbioses among invertebrates.

Host phylum	Class	Example	Symbiont	Symb. locale	Symbiont activity*	Reference
Placozoa		<i>Trichoplax adhaerens</i>	bacteria	fiber cells: cisternae of E.R.	?	Grell, 1981; Grell and Benwitz, 1981
Sponges	Demospongiae	<i>Cliona</i>	<i>Symbiodinium</i>		photoautotroph	Smith and Douglas, 1987
	Demospongiae	<i>Spongilla verongia</i> , <i>Ceratoporella</i>	<i>Chlorella</i> heterotrophic bacteria	mesohyl	photoautotroph ?some facultative anaerobes	Bergquist, 1978 Vacelet, 1975; Santavy <i>et al.</i> , 1990
	Demospongiae and Calcarea	about 38 genera	cyanobacteria	mesohyl	photoautotroph + (?) nitrogen fixation	Wilkinson, 1983; Smith and Douglas, 1987
Cnidaria	hydrozoa	<i>Chlorohydra</i>	<i>Chlorella</i>	gastrodermal cells	photoautotroph	Smith and Douglas, 1987
	hydrozoa	<i>Veella</i> , <i>Millepora</i>	dinoflagellates	gastrodermal cells	photoautotroph	Smith and Douglas, 1987
	scyphozoa	<i>Mastigias</i> , <i>Cassiopeia</i>	dinoflagellates	gastrodermal cells	photoautotroph	Smith and Douglas, 1987
	anthozoa	scleractinian corals	dinoflagellates	gastrodermal cells	photoautotroph	Smith and Douglas, 1987
Platyhelminthes	turbellaria	acoels	prasinophytes, dinoflagellates, diatoms	host vacuoles near body wall	photoautotroph	Smith and Douglas, 1987
		<i>Paracatenula</i> spp.	bacteria		chemoautotroph	Ott <i>et al.</i> , 1982
		neorhabdocoels	<i>Chlorella</i>	mesenchyme	photoautotroph	Douglas, 1987
		<i>Astomonema jeneri</i>	bacteria	gut rudiment	chemoautotroph	Ott <i>et al.</i> , 1982
Nematoda		<i>Xenorhabdus</i> spp.	luminescent bacteria	intestine/vesicles	entomopathogenesis of host	Nealson, 1991
	hirudinea	<i>Placobdella</i> , ichthyobdellids	bacteria	esophageal ceca	suppl. nut.	Buchner, 1965
		<i>Hirudo medicinalis</i>	1. <i>Pseudomonas</i> 2. bacteria	1. intestinal lumen 2. urinary bladder	1. blood feeder: suppl. nut. 2. ?	Buchner, 1965
	oligochaetes	<i>Phalodrilus leukodermata</i> lumbricids	bacteria	nephridial ampulla	chemoautotroph	Giere, 1981; Felbeck <i>et al.</i> , 1983
			bacteria	trophosome	chemoautotroph	Buchner, 1965
Pogonophora	perviate and vestimentifera		sulfur-oxidizing bacteria		chemoautotroph	Smith and Douglas, 1987

TABLE 1. Continued.

Host phylum	Class	Example	Symbiont	Symb. locale	Symbiont activity*	Reference
Mollusca	gastropods	sacoglossans, nudibranchs	(chloropalists)	gut or digestive diverticula	(photoautotroph)	Smith and Douglas, 1987
		terrestrial prosobranchs	bacteria	"concrement gland"	urate recycling?	Buchner, 1965
	bivalves	lucinids, thyasirids, <i>Calyplogena</i> <i>Tridacna</i>	bacteria	gills	chemoautotroph, methanotroph	Wood and Kelly, 1989
cephalopods	shipworms	temperate/boreal octopods <i>Euprymna scolopes</i>	dinoflagellates	siphonal tissue	photoautotroph	Smith and Douglas, 1987
			bacteria	gills	cellulase, nitrogen fixation	Waterbury <i>et al.</i> , 1983
	Echiura	Bonnellia	dicyemids	renal sac	?	Hochberg, 1983
			bacteria	epithelial light organ	bioluminescence	Wei and Young, 1989; McFall-Ngai and Montgomery, 1990
Bryozoa	<i>Watersipora</i>	1. cyanobacteria 2. heterotrophic bacteria	mollicutes (mycoplasmas)	visceral coelom	1. N fixation? 2. ?	Smith and Douglas, 1987
			bacteria	pallial sinus (larvae); funicular bodies (adults)	?	Zimmer and Woolacott, 1983; Boyle <i>et al.</i> , 1987
			bacteria	intestinal cecum	?	Lutaud, 1969; Woolacott, 1981
Echinodermata	echinoids	<i>Echinocardium</i>	bacteria	extracellular, subcuticular region	sediment processing?	De Ridder <i>et al.</i> , 1985
	asteroids	<i>Luidia</i>	bacteria	near gut	?	Bosch, 1992
Chordata (urochordates)	ophiuroids	<i>Amphipholis squamata</i>	bacteria	burseae and developing embryos	embryo growth and development?	Walker and Lesser, 1989
	ascidiacea	tropical didemnids	cyanobacteria (including prochlorophytes)	atrial cavity	photoautotrophy and N fixation	Smith and Douglas, 1987

TABLE 1. Continued.

Host phylum	Class	Example	Symbiont	Symb. locale	Symbiont activity*	Reference	
Arthropoda (partial list)	thaliacea	molgulids	<i>Nephromyces</i> (with intracellular bacteria)	renal sac	urate catabolism	Saffo, 1990, 1991a	
	arachnida	<i>Pyrosoma</i>	bacteria	intracellular	bioluminescence	Leisman <i>et al.</i> , 1980	
		gamasid mites ( <i>Liponyssus</i> )	bacteria	mycetocytes near intestine	blood feeders: suppl. nut.	Buchner, 1965	
		ixodids and argasids	rickettsiae	Malpighian tubules, ovaries	blood feeders: suppl. nut.	Buchner, 1965; Hayes and Burgdorfer, 1989	
	insecta	<i>Cryptoceros</i>	protozoa	protozoa	hindgut	cellulase	Smith and Douglas, 1987
		<i>Periplaneta americana</i>	bacteria	bacteria	1. hindgut 2. fat body	1. cellulase, suppl. nut. 2. urate recycling?	Smith and Douglas, 1987
		scale insects	bacteria	bacteria	mycetocytes	xylem and phloem feeders: suppl. nut.	Tremblay, 1989
		aphids <i>e.g.</i> , <i>Euscelis</i>	bacteria	bacteria	mycetome	B vitamins, sterols	Douglas, 1989
		bed bugs ( <i>e.g.</i> , <i>Cimex</i> )	bacteria	bacteria	midgut	blood feeders: suppl. nut.	Douglas, 1989
		sucking lice, <i>e.g.</i> , <i>Pediculus humanus</i>	bacteria	bacteria	mycetocytes near midgut wall	blood feeders: B vitamins	Douglas, 1989
		tephritid fruit flies	bacteria	bacteria	midgut cecum (larva); esophageal pouch and hindgut (adults)	suppl. nut.?	Buchner, 1965; Smith and Douglas, 1987; Gassner, 1989
		<i>Culex</i> , <i>Aedes</i>	<i>Wolbachia</i>	<i>Wolbachia</i>	egg, germ cells	?	Gassner, 1989
		<i>Drosophila</i> spp.	mycoplasmas, spiroplasmas, rickettsias, viruses	mycoplasmas, spiroplasmas, rickettsias, viruses	various tissues, hemolymph	?	Thompson, 1987; Gassner, 1989
		screwworm <i>Cochliomyia hominivorax</i>	bacteria ( <i>Providencia rettgeri</i> )	bacteria ( <i>Providencia rettgeri</i> )		?	Gassner, 1989
		tsetse flies ( <i>Glossina</i> )	bacteria	bacteria	midgut	blood feeders: B vitamins	Douglas, 1989
crane fly larvae		bacteria	bacteria	hindgut	cellulase	Smith and Douglas, 1987	

TABLE 1. Continued.

Host phylum	Class	Example	Symbiont	Symb. locale	Symbiont activity*	Reference
		anobid and cer- ambycid beetles	yeasts	midgut caeca	cellulase	Douglas, 1989; Nardon and Grenier, 1989
		curculionid bee- tles: e.g., <i>Apion</i>	bacteria	Malpighian tu- bules	cellulase, suppl. nut.	Douglas, 1989
		curculionid bee- tles: e.g., <i>Sitoph- ilus oryzae</i>	bacteria	mycetocytes	B vitamins, amino acids, sterols	Nardon and Gre- nier, 1989, 1991
		termites	protozoa and bac- teria	hindgut	cellulase, N fixa- tion, N recycling	Breznak, 1984
		carpenter ants	bacteria	midgut	suppl. nut.	Douglas, 1989

\* N = nitrogen; suppl. nutr. = supplemental nutrition.

influence, both positively and negatively (depending on the species), the response of nonbreeding *I. obsoleta* to carrion (Curtis, 1985). As Moore (1984b) noted, field observations of invertebrate behavior need to take into account that some observed behaviors "may have been 'rigged' " by the presence of endoparasites.

In some cases (e.g., the symbiotic light organs of sepiolid squid, colonized by *Vibrio fischeri*: McFall-Ngai and Ruby, 1991) the development of symbiont-containing invertebrate organs is affected by the presence or absence of symbionts. In others, the absence of chronic symbionts may affect not only the development of the symbiotic organ, but larger developmental patterns: Schwemmler (1989) has asserted, though not without controversy (Douglas, 1989), that aposymbiotic leafhoppers do not develop abdomens. In addition, the function and evolution of several other invertebrate structures (e.g., mycetocyte tissues of other insects, the renal sac of molgulid ascidians, the trophosome of pogonophorans) are closely tied to the chronic presence of microbial symbionts in such tissues.

Given such data, it is clear that symbiotic invertebrates are not marginal exotica, but rather a significant phenomenon of invertebrate biology worthy of the serious, sustained attention of a broad range of researchers. From this perspective, workshop participants have exploited novel experimental approaches and less familiar invertebrate systems to provoke fresh views on several symbiotic questions:

- (Mark Patterson) How is the metabolic economy of endosymbionts affected by their lack of direct communication with the outside environment? How does the architecture of the host-environment interface affect nutrient and oxygen flux in the endosymbiont?

- (Wayne Sousa) What factors determine the diversity and density of symbiotic communities within an invertebrate host? What role do interspecific interactions, such as competition, play in structuring communities of endoparasites?

- (Michael M. Martin) How do mutualistic endosymbioses evolve? How does

mutualism and endosymbiosis affect patterns of speciation in symbiotic partners?

The following articles document the participants' perspectives on these questions, drawn from their studies of symbiotic invertebrates in marine and terrestrial habitats. While focused on particular cases of symbiotic interactions—biomechanical aspects of algal-cnidarian symbiosis, the community ecology of trematode parasites in marine gastropod hosts, and the evolution of insect-fungus symbioses—we hope that the questions raised by the workshop will play a broader role in helping restructure our general perspectives both on symbiosis and on invertebrate biology.

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