REVIEW

# Chemical defense and evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods

## D. John Faulkner[1] and Michael T. Ghiselin[2]

[1]Scripps Institution of Oceanography, La Jolla, California 92093, USA
[2]California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA

ABSTRACT: In the evolution of dorid nudibranchs and some other opisthobranch gastropods loss of the shell is correlated with the presence of defense mechanisms based upon chemicals derived from food. The chemicals are present as the result of adaptations, not by accident. Chemical defenses were preadaptive, enabling the animals to dispense with the shell. They have been gradually elaborated and made more effective, occasionally leading to de novo synthesis, independent of diet. Food dependencies have constrained the adaptive radiation of opisthobranchs, and this may reflect relationships to predators as well as prey. For the opisthobranchs considered here, distastefulness is often combined with conspicuousness (aposematic coloration): since these animals do not occur in family groups, the aposematic coloration must have evolved without kin-selection.

## INTRODUCTION

In the gastropod subclass Opisthobranchia there has been a general trend toward loss of the shell, with many lineages evolving from snails into sea-slugs. The loss of the shell has been compensated for by various adaptations, including autotomy and camouflage (for reviews see T. E. Thompson, 1960a, b; Edmunds, 1966, 1974; Stasek, 1967; Harris, 1971; Ros, 1976). In the eolid nudibranchs, stinging capsules from the coelenterates in the diet are used defensively. Certain sea hares (order Anaspidea) and sacoglossans (order Sacoglossa) contain repugnant chemicals obtained from the plants they eat. The orders Cephalaspidea and Notaspidea also have chemical defense mechanisms, some of which are based upon materials derived from food. Chemical defense in the two orders of pteropods has yet to be investigated. Certain herbivorous marine pulmonates, close relatives of opisthobranchs, are known to have chemical defenses (Ireland and Faulkner, 1978).

It is the dorid nudibranchs, however, which have received the most attention from chemists. Recent studies have shown that many dorids contain secondary metabolites obtained from sponges in the diet and use these chemicals to deter potential predators. Although not all dorids eat sponges, those that do display some significant evolutionary patterns. In particular, the establishment of a chemical defense mechanism appears to have rendered the physical protection afforded by the shell obsolete, leading to its loss. Subsequently the new defense mechanism has served as a major constraint upon the evolution of the group, especially with respect to feeding habits and adaptive radiation. The present review supports this theory both for dorid nudibranchs, and for certain other opisthobranchs.

## REVIEW OF LITERATURE AND DISCUSSION

Sponges are primitive invertebrates that frequently contain biologically-active chemicals (Minale, 1978). Although sponges are all filter-feeders, they nonetheless possess such a wide variety of secondary metabolites that it does not seem likely that these substances

are of exogenous origin. Indeed Tymiak and Rinehart (1981) have demonstrated the biosynthesis of brominated secondary metabolites in *Aplysina fistularis*. Similar brominated metabolites were found to be localized in the spherulous cells of A. *fistularis* (J. E. Thompson et al., in press) and the rates of exudation of these metabolites were measured (Walker, 1982). Moreover, sponges lacking spicules invariably contain appreciable quantities of secondary metabolites, implying that those metabolites have a defensive role (e. g. Walker et al., 1980). Studies of temperate sponges revealed that sponges containing secondary metabolites rarely had predators and were frequently free of epiphytes. J. E. Thompson (pers. comm.) observed a negative correlation between the degree of fouling of marine sponges and the presence of compounds having antimicrobial activity. A substantial number of sponges are toxic to animals, including crustaceans and fish (Green, 1977; Bakus, 1981). It is, therefore, reasonable to believe that the ability to produce secondary metabolites has better enabled sponges to inhibit predation and overcome competition.

The taxonomic distribution of defense mechanisms in sponges suggests that the early adaptive radiation of the group involved elaboration and development of the skeleton as the primary defense mechanism. The available data suggest that the secondary metabolites are most prevalent in 'advanced' sponges, especially those with reduced spiculose skeletons, though this needs to be documented with a better taxonomic sample and more sophisticated phylogenetic techniques. Evolution nonetheless seems to have featured a shift away from spicules as a primary defense mechanism, with secondary metabolites as an auxiliary defense mechanism taking on increasing importance, allowing the skeleton to be reduced. As discussed below, a parallel replacement of skeletal defense by chemical defense may also have occurred during the evolution of dorid predators of sponges.

It should be emphasized that most chemical investigations of dorid nudibranchs were concerned with the isolation and description of new molecules, which were usually obtained in quantities insufficient for tests of their repugnatorial effects. Therefore, most feeding inhibition assays have been performed on material derived from the dietary sources, which often were difficult to locate. However, a convincing case for dorids deriving their chemical defenses from sponges can be made by bringing together the results of several recent studies.

The natural products chemistry of dorid nudibranchs has recently been reviewed in detail (J. E. Thompson et al., 1982; Schulte and Scheuer, 1982). Metabolites originally obtained from sponges have been found in many nudibranchs, although the relevant sponges were not always found in the same geographical area as the nudibranchs. The digestive glands of *Anisodoris nobilis* contained the cardioactive metabolite 1-methylisoguanisine (Fuhrman et al., 1981) that was independently identified from an Australian sponge *Tedania digitata* (Quinn et al, 1980). The metabolites of *Cadlina luteomarginata* (Hellou et al, 1982; J. E. Thompson et al., 1982), *C. limbaughorum*, and *C. flavomaculata* were traced to the sponges *Axinella* sp., *Dysidea amblia*, *Euryspongia* sp., and *Leiosella idia*. Three specimens of *Chromodoris maridadilus* and 1 specimen of *Hypselodoris godeffroyana* found feeding on *Dysidea fragilis* contained the same furanosesquiterpenes as the sponge (Schulte et al., 1980). The same furanosesquiterpenes were isolated from *Hypselodoris ghiselini* and *H. californiensis* collected from the Gulf of California, while *H. californiensis* and *H. porterae* from San Diego accumulated metabolites from *Euryspongia* sp. and *Dydisea amblia* (Hochlowski et al, 1982). The acetylenes found in *Peltodoris atromaculata* were from the sponge *Petrosia ficiformis* (Castiello et al, 1980) while the isonitriles from *Phillidia varicosa* were also isolated from a Hawaiian sponge *Hymeniacidon* sp. (Hagadone et al., 1979). The chlorinated acetylenes from *Diaulula sandiegensis* were present in the crude extract of a sponge (probably *Haliclona* sp.) collected many years prior to the research on *Diaulula* but the sponge has never been collected since (Walker and Faulkner, 1981). There are also examples of compounds isolated from nudibranchs that are so closely related to known sponge metabolites that the chemist feels confident in proposing an undiscovered sponge source (Hochlowski et al, 1983a, b). For example, the major metabolite of *C. marislae* is related to a metabolite of the sponge *Pleraplysilla spinifera* by a simple rearrangement that slowly occurred when the sample was stored at room temperature (Hochlowski and Faulkner, 1981).

Nudibranchs may also obtain pigments from sponges in the diet; retention of these pigments can be considered as a passive chemical defense mechanism. *Rostanga pulchra* lives exclusively on red sponges and incorporates the carotenoid pigments from the sponge so that it is effectively camouflaged when on its preferred food source (Anderson, 1971). The notaspidean *Tylodina fungina* is always found on sponges of the genus *Aplysina*; although the external color of these sponges varies from yellow to purple or black, the interior of the sponge has a bright yellow pigment that is accumulated by *Tylodina*. Thus *Tylodina* may be camouflaged on *Aplysina* species that are always yellow yet obvious on the darker *Aplysina* species. An even more striking example of food-derived cryptic coloration was observed in the opisthobranch *Aplysia*

*parvula.* Small specimens of *A. parvula* were pink when found on a pink alga *(Asparagopsis taxiformis).* As they grew they migrated to a green-colored alga *(Laurencia johnstonii)* where they gradually became dark green. Such dietary camouflage, which is not uncommon in marine invertebrates, might be interpreted as an *accidental* consequence of the pigment being present in food. This conjecture seems all the more reasonable when it is realized that the animals are already protected by diet-derived chemical defense mechanisms. At least the camouflage is less important than one might suppose. On the other hand, crypsis based upon the deposition of pigments in a way that causes the animals to match their substrate in great detail cannot be explained in this way.

With respect to demonstrating the adaptive significance of the chemicals in question, however, we need to face up to some serious methodological difficulties. Such authors as Gould and Lewontin (1979) have cast aspersions upon the 'adaptationist program' in general, and with some justification. Nonetheless, it would be rash to go to the opposite extreme, and deny adaptation where it really exists. We must admit that it is possible that a substance derived from food might be present incidentally and afford no protection. On the other hand, the gratuitous assumption that metabolites of terrestrial plants were merely fortuitous byproducts without ecological significance had pernicious consequences. We need to apply sophisticated canons of evidence to avoid both kinds of excess (Süffert, 1932; Ghiselin, 1969, 1974, 1983). Our reasoning is that in an adapted system the biology of the organism is so structured and coordinated as to maximize the hypothesized effect. In this case the materials derived from food will be (1) selectively retained, with the most effective portions accumulating, the less effective discarded or catabolized; (2) distributed in the body so as to maximize the effect; (3) mobilized at the appropriate time, e. g. secreted actively when and only when a predator attacks; (4) effective against predators. The hypothesis should be consistent with evolutionary theory as well. There should be a general tendency for the prey to resist damage; often the predator is given an opportunity to taste the prey, or eat only part of it, then reject it. Except in the case of protecting a relative (kin-selection – see below) a lethal attack by a predator has no selective advantage, as it removes the prey's genes from the gene pool. Evolutionary systematics is also useful: a given scenario will often predict a certain pattern of distribution of chemicals in the phylogenetic tree of a taxon. Such evidence is particularly useful when we want to know whether we are dealing with a preadaptation or a postadaptation. For instance, finding that slugs with chemical defenses are related to snails already equipped with the chemi-

cal defense indicates that the shell was lost after the chemical defense had evolved. To use such evidence, however, requires that one know the phylogeny of the group. The traditional classification systems do not always reflect the phylogenetic relationships within the group. However, the phylogeny of the opisthobranchs is now sufficiently well understood (Ghiselin, 1966; Gosliner, 1981) to justify the evolutionary interpretations here presented.

That aforementioned utilization of sponge metabolites for defense was confirmed by showing that the nudibranchs localize selected sponge metabolites in body parts other than the digestive system and that these compounds are capable of acting as feeding inhibitors. The evidence that dorid nudibranchs store selected sponge metabolites is based upon (1) observations of the difference in metabolite content in samples collected from different places, and (2) comparisons of the metabolites from the nudibranch to those of the sponge from which the nudibranch was collected. Since different sponges can be available to nudibranchs in 2 locations, it is not surprising that *Cadlina luteomarginata* from British Columbia (Helou et al., 1982) contained an array of chemicals different from that of specimens collected at La Jolla, California (J. E. Thompson et al., 1982), with only 1 sponge metabolite in common. Chemical analysis of the sponges eaten by *C. luteomarginata* from La Jolla, as determined by feeding observations and analysis of sponge spicules from the gut, revealed that the metabolites of interest came from only a few of all the sponge species consumed. Furthermore, *C. flavomaculata* found on *Spongia idia* contained only 1 of 5 major sponge metabolites while the same species of nudibranch found on *Dysidea amblia* contained only 1 of 3 major sponge metabolites. Similarly, *Phyllidia varicosa* contained only 1 of 2 similar metabolites from *Hymeniacidon* sp. (Schulte and Scheuer, 1982). That dorid nudibranch metabolites are obtained from dietary sources seems to be the general rule, the only known exception being *Dendrodoris limbata,* which is capable of *de novo* synthesis of polygodial (Cimino et al., 1982).

In his discussion of defensive adaptations among opisthobranchs T. E. Thompson (1960a) observed that 'skin glands have been found whose position and function can only be explained satisfactorily as defensive. They are always present in addition to the usual mucous glands associated with ciliated epithelia.' In dorid nudibranchs he found non-mucous skin glands to be abundant in the dorsum. We now believe that these glands are the source to chemicals contained in the defensive secretions although no satisfactory analysis of excised glands has yet been reported. The fact that most secondary metabolites from dorids can be extracted by a relatively short immersion of the intact

animal in a suitable solvent suggests that the metabolites are contained in the skin glands. This inference was further corroborated by 2 studies that found feeding inhibitors in the dorsum but not in the gut, foot, or head parts (Cimino et al., 1982; J. E. Thompson et al., 1982) and one study (Hagadone et al., 1979) that found the active principle in a mucous secretion. It is not absolutely necessary for all dorid nudibranchs to store defensive chemicals in the dorsum, provided that there is a mechanism for mobilizing chemicals stored in alternative locations such as the digestive gland.

Early studies on interactions between nudibranchs and possible predators relied either upon behavioral reactions to entire organisms or crude bioassays. Remarkably few of the compounds found in dorids have been tested for feeding inhibition by quantitative assays. However, all those compounds tested quantitatively thus far have shown positive feeding inhibition toward fish at 100 µg mg$^{-1}$ of food pellet, and most were active at 10 µg mg$^{-1}$ pellet (Hellou et al., 1982; Thompson et al., 1982). Comparison of the chemicals found in different dorid nudibranchs reveals that the majority belong to two chemical classes, isonitriles and furans. Both groups of compounds are represented among the feeding inhibitors.

In accordance with modern evolutionary theory, the loss of the shell can be explicated in economic terms. There is a tradeoff, with a savings in the cost of producing and transporting a shell on the one hand, and an increased risk of predation on the other. The relative advantage of shell loss will be increased if it is inexpensive to provide an alternative means of protection. The spicules in the integument of many dorid nudibranchs are, in effect, a secondary, internal shell, and perhaps not much of a saving. On the other hand, the use of chemicals from food allows 'free' protection though only in the cost of production, not the cost of storage and mobilization. There is a sort of economic threshold here as well. In order to feed upon sponges it is necessary to develop the wherewithal to deal with their spicules and toxins. The toxins are then available for other use. It is noteworthy that certain gastropods which feed upon acidic tunicates secrete sulfuric acid in their dermal repugnatorial glands. Here, a combination of labor may reduce fixed costs (Ghiselin, 1978). It should be emphasized that defensive adaptations in general do not prevent predation altogether but only mitigate it. Fish do eat even distasteful nudibranchs, but probably only if preferred food is not available, and then usually only after the nudibranch has been attacked a number of times to exhaust the supply of defensive chemicals (Thompson, 1960a). Animals have an array of defense mechanisms, but these are not equally effective against all kinds of predators and each of them will have its costs. A general purpose

defense mechanism is cheaper, but can be breached by specialists. This may set up a selection pressure either to strengthen the defense, to supplement it, or both. To calculate the relative advantages under such constraints would be a very difficult problem. Hence the evolutionary discussion to follow oversimplifies matters somewhat.

We believe that there was a cause and effect relationship between loss of the shell and the gain of chemical defense mechanisms. Two hypotheses need to be considered. Chemical defense could have been (1) a postadaptation, evolving after the shell was lost, or (2) a preadaptation, which allowed the animals to survive without a shell. We much prefer the second alternative, although it is clear that chemical defenses were elaborated gradually, as the shell was being lost. It seems biologically implausible for an animal to dispense with a protection so effective as a shell without a substitute defense. One would have to hypothesize such unrealistic conditions as a peculiar environment with no effectual predators, or circumstances under which the advantage of shell loss overrode the risk of getting eaten. It seems unlikely, for instance, that the ancestral dorid was a 'top predator'.

Whatever the merits of such theoretical considerations, the preadaptation hypothesis fits the empirical data. As suggested above, the shell is an effective defense, but not a perfect one, among molluscs in general. Auxiliary defense mechanisms, including behavioral, anatomical, and chemical ones, are present in forms with a well-developed shell. In a group of cephalaspideans that includes the Actaeonidae and Hydatinidae, the shell ranges from well-developed to considerably reduced. The animals burrow and also secrete repugnatorial substances (Rudman, 1972a, b). They feed upon cirratulid polychaetes, a group in which chemical defense has been shown to reduce predation by fishes (Yoshiyama and Darling, 1982). In *Philine*, a cephalaspidean with a reduced shell, protection is afforded by burrowing and by secretion of acidic mucus (T. E. Thompson, 1960b). The more primitive Sacoglossa retain a somewhat reduced shell, but one that still affords a certain measure of protection. These already possess a defense mechanism based upon chemicals derived from green algae of the genus *Caulerpa*, upon which they feed (Doty and Aguilar-Santos, 1970; Lewis, 1970). They also have other auxiliary defense mechanisms, including camouflage and autotomy (Stamm, 1968; Warmke and Almodóvar, 1972; Poorman and Poorman, 1977). For the nudibranchs, especially dorid nudibranchs, we do not have such good evidence, because intermediate forms are not known. However, the nudibranchs probably arose at least biphyletically from the Notaspidea, many of which have shells. A fairly well developed shell is

present in *Tylodina*, animals that eat sponges and contain sponge metabolites, but have poorly developed chemical defenses. *Tylodina* is commonly cryptic upon sponges, but sometimes occurs on sponges with contrasting colors, a fact which shows that in nature such protection need not involve a close fit. The animals tend to be restricted to the most favorable habitat, where food is abundant and predation reduced, but this is only a tendency. Occasional opisthobranch specimens have been collected where the usual food is lacking, and been found not to contain metabolites that elsewhere provide protection (Faulkner and Ireland, 1977). Another spongivorous notaspidean is *Berthellina* (see Marbach and Tsurnamal, 1973). It has not been tested for any dietary metabolites, but it is known to have repugnatorial acidic mucus. A shell is present, but much reduced. The animals are noctural and live under stones.

All these facts point to an early, preadaptive evolution of chemical defense. In becoming spongivores, the dorids have had to overcome both the spicules and the defensive chemicals that have protected sponges from other potential predators. At first the harmful sponge metabolites were probably excreted along with the spicules. The development of an efficient mechanism for the separation of harmful metabolites from those to be catabolized may have led to the modification of the digestive gland for storage, as in the anaspidean *Aplysia californica* (Stallard and Faulkner, 1974). The dorids subsequently evolved a variety of glands providing for effective mobilization and delivery. All these changes facilitated loss of the shell. Yet another stage in the evolution of chemical defense seems apparent in a few dorids and other opisthobranchs. A slug with a food-derived defensive chemical is dependent upon its food source. The ability to synthesize its own feeding inhibitor would have obvious advantages. Among dorids this is known only in *Dendrodoris limbata* (Cimino et al., 1982), which belongs to the specialized suborder Porostomata. As another porostome, *Phyllidia*, derives its metabolites from food (Hagadone et al., 1979) synthetic capacity has evolved within the group. *De novo* synthesis has also evolved within the Sacoglossa, again in more modified representatives of the group (Ireland and Scheuer, 1979).

Chemical defense may also have played an important role in the adaptive radiation of the group. Ghiselin (1966), in basing a phylogenetic tree on the structure of the reproductive system of opisthobranchs, pointed out that the various lineages had diversified in feeding habits. Different groups eat different kinds of food – often hard to utilize except by specialists. Exploiting diverse food sources and deriving a variety of defensive materials from them suggests that both feeding opportunity and predator resistance have

influenced nudibranch diversification. Such differences extend to all taxonomic levels. Sympatric sponge-feeding dorids, notably four species of *Hypselodoris* (Hochlowski et al., 1981) eat different species of sponges and utilize different chemicals. A similar pattern obtains in the anaspidean genus *Aplysia* (Faulkner and Ireland, 1977). The extent of specialization and degree of overlap remain to be investigated, but the significance of such findings for niche theory should nonetheless be apparent. Investigations of such matters (e. g. Nybakken and Eastman, 1977) tend to take it for granted that one and only one 'limiting resource' is being 'partitioned', and that the resource in question is food. But are we dealing here with a diversification of diet, means of avoiding predators, or both?

It is also noteworthy that chemical defense may relate to the global pattern of diversity. Bakus (1974) and Green (1977) (see also Bakus and Green, 1974) have argued that there are geographical gradients in toxicity among sponges and holothurians, with increase into the tropics. Vermeij (1978) documents a large number of geographical and ecological trends in the strength of the shell and other defensive features in molluscs and other animals. Bertsch and Johnson (1982) assert that the sponge-feeding dorids predominate in tropical faunas, while those that feed upon bryozoans and other animals form a larger proportion in temperate ones. Such trends are very poorly understood, however, and even the factual basis upon which they are grounded remains debatable.

Finally, the opisthobranchs may provide some critical evidence relevant to the question of the evolutionary origin of aposematic coloration and related topics. The theory of kin-selection as developed by R. A. Fisher, W. D. Hamilton and others provides an attractive way to explain how distasteful or poisonous animals might have become conspicuously colored, in spite of the most conspicuous organisms being killed. The distasteful animals would live in family groups. The predator would eat one and thereafter would leave the remaining siblings alone; thus genes of common descent would survive. This is, at least superficially, a very plausible hypothesis. But is it the correct explanation? It definitely cannot be valid for the opisthobranchs, which, with rare exceptions, do not live in family groups, but rather hatch out of egg masses as free-swimming larvae. We mention this matter because, as Ghiselin (1974), Järvi et al. (1981), and others have pointed out, kin-selection has often been invoked uncritically, as if it were a necessary condition for aposematic coloration, 'altruism', the neuter castes of social insects and other phenomena. To invoke kin-selection only where the necessary social conditions do obtain, begs the question of the extent to which more orthodox modes of selection will explain the facts. An

untested hypothesis is then treated as if it were a premise not to be questioned. A legitimate solution to such problems will have to involve comparative studies of groups with differing social structures, and marine invertebrates present some excellent opportunities. Evolutionary ecology has been biased through over-emphasis upon birds and insects. A greater variety of data could only benefit the science. For instance, Gittleman and Harvey (1980) invoke kin-selection in a paper entitled 'Why are distasteful prey not cryptic?' As a general rule, opisthobranchs are *both* distasteful and cryptic. Some, however, including a substantial number of dorid nudibranchs are quite conspicuous, whether on or off their usual substrate. Again, our materials can be used to test and develop theories. Marine ecologists need not merely follow the lead of terrestrial ecologists, whose data may be inadequate and whose hypotheses may be false.

## LITERATURE CITED

Anderson, E. S. (1971). The association of the nudibranch *Rostanga pulchra* MacFarland, 1905, with the sponges *Ophlitaspongia pennata*, *Esperiopsis originalis*, and *Plocamia karykina*. Doctoral thesis, University of California, Santa Cruz

Bakus, G. J. (1974). Toxicity in holothurians: a geographical pattern. Biotropica 6: 229–236

Bakus, G. J. (1981). Chemical defense mechanisms on the Great Barrier Reef, Australia. Science, N. Y. 211: 497–499

Bakus, G. J., Green, G. (1974). Toxicity in sponges and holothurians: a geographical pattern. Science, N. Y. 185: 951–953

Bertsch, H., Johnson, S. (1982). Comparative opisthobranch (Mollusca: Gastropoda) zoogeography, with emphasis on the Pacific Basin (Hawaii and California): faunal composition, provincial affinities, and subtital density. Ciencias Marinas (Mex.) 8: 125–153

Castiello, D., Cimino, G., De Rosa, S., De Stefano, S., Sodano, G. (1980). High molecular weight polyacetylenes from the nudibranch *Peltodoris atromaculata* and the sponge *Petrosia ficiformis*. Tetrahedron Lett. 21: 5047–5050

Cimino, G., De Rosa, S., De Stefano, S., Sodano, G. (1982). The chemical defense of four Mediterranean nudibranchs. Comp. Biochem. Physiol. (B) 73: 471–474

Doty, M. S. and Aguilar-Santos, G. (1970). Transfer of toxic algal substances in marine food chains. Pacif. Sci. 24: 351–355

Edmunds, M. (1966). Protective mechanisms in the Eolidacea (Mollusca Nudibranchia). J. Linn. Soc. (Zoology) 46: 25–71

Edmunds, M. (1974). Defence in animals: a survey of antipredator defences. Longman, Harlow, Essex

Faulkner, D. J., Ireland, C. (1977). The chemistry of some opisthobranchs. In: Faulkner, D. J., Fenical, W. H. (ed.) Marine natural products chemistry. Plenum Press, New York, p. 23–34

Fuhrman, F. A., Fuhrman, G. J., Kim, Y H., Pavelka, L. A., Mosher, H. S. (1981). Doridosine: a new hypotensive N-methylpurine riboside from the nudibranch *Anisodoris nobilis*. Science, N. Y 207:193–195

Ghiselin, M. T. (1966). Reproductive function and the phylogeny of opisthobranch gastropods. Malacologia 3: 327–378

Ghiselin, M. T. (1969). The triumph of the Darwinian method. University of California Press, Berkeley

Ghiselin, M. T. (1974). The economy of nature and the evolution of sex. University of California Press, Berkeley

Ghiselin, M. T (1978). The economy of the body. Am. Econ. Rev. 68: 233–237

Ghiselin, M. T (1983). Evolutionary aspects of marine invertebrate reproduction. In: Giese, A. C., Pearse, J. S. (ed.) Reproduction of marine invertebrates, Vol. 9. Academic Press, New York, in press

Gittleman, J. L., Harvey, P. H. (1980). Why are distasteful prey not cryptic? Nature, Lond. 286: 149–150

Gosliner, T. M. (1981). Origins and relationships of primitive members of the Opisthobranchia (Mullusca: Gastropoda). Biol. J. Linn. Soc. 16: 197–225

Gould, S. J., Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. London (B) 205: 581–598

Green, G. (1977). Ecology of toxicity in marine sponges. Mar. Biol. 40: 207–215

Hagadone, M. R., Burreson, B. J., Scheuer, P. J., Finer, J. S., Clardy, J. (1979). Defense allomones of the nudibranch *Phyllidia varicosa* Lamarck 1801. Helv. chim. Acta 62: 2484–2494

Harris, L. G. (1971). Nudibranch associations as symbioses. In: Cheng, T. C. (ed.) Aspects of the biology of symbiosis. University Park Press, Baltimore, p. 77–90

Hellou, J., Andersen, R. J., Thompson, J. E. (1982). Terpenoids from the dorid nudibranch *Cadlina luteomarginata*. Tetrahedron 38: 1875–1879

Hochlowski, J. E., Faulkner, D. J. (1981). Chemical constituents of *Chromodoris marislae*. Tetrahedron Lett. 22: 271–274

Hochlowski, J. E., Walker, R. P., Ireland, C., Faulkner, D. J. (1982). Metabolites of four nudibranchs of the genus *Hypselodoris*. J. org. Chem. 47: 88–91

Hochlowski, J. E., Faulkner, D. J., Matsumoto, G. K., Clardy, J. (1983a). Norrisolide, a novel diterpene from the dorid nudibranch *Chromodoris norrisi*. J. org. Chem. 48: 1141–1142

Hochlowski, J. E., Faulkner, D. J., Bass, L. S., Clardy, J. (1983b). Metabolites of the dorid nudibranch *Chromodoris sedna*. J. org. Chem. 48: 1738–1741

Ireland, C., Faulkner, D. J. (1978). The defensive secretion of the opisthobranch mollusc *Onchidella binneyi*. Bioorgan. Chem. 7: 125–131

Ireland, C., Scheuer, P. J. (1979). Photosynthetic marine mollusks: In vivo $^{14}$C incorporation into metabolites of the sacoglossan *Placobranchus ocellatus*. Science, N. Y. 205: 922–923

Järvi, T., Sillén-Tullberg, B., Wiklund, C. (1981). Individual kin selection for aposematic coloration: a reply to Harvey and Paxton. Oikos 37: 393–395

Lewein, R. A. (1970). Toxin secretion and tail autonomy by irritated *Oxynoe panamensis* (Opisthobranchiata; Sacoglossa). Pacif. Sci. 24: 356–358

Marbach, A., Tsurnamal, M. (1973). On the biology of *Berthellina citrina* (Gastropoda: Opisthobranchia) and its defensive acid secretion. Mar. Biol. 21: 331–339

Minale, L. (1978). Terpenoids from marine sponges. In: Scheuer, P. J. (ed.) Marine natural products: chemical and biological perspectives, Vol. I. Academic Press, New York, p. 175–240

Nybakken, J., Eastman, J. (1977). Food preference, food availability and resource partitioning in *Triopha maculata* and *Triopha carpenteri* (Opisthobranchia: Nudibranchia). Veliger 19: 279–289

Poorman, L. H., Poorman, F. L. (1977). Four opisthobranchs living on marine algae from west Mexico. Nautilus 91: 62–66

Quinn, R. J., Gregson, R. P., Cook, A. F., Bartlett, R. T. (1980). Isolation and synthesis of 1-methylisoguanosine, a potent pharmacologically active constituent from the marine sponge *Tedania digitata*. Tetrahedron Lett. 21: 567–568

Ros, J. (1976). Sistemas de defensa en los opistobranquios. Oecología Aquática 2: 41–77

Rudman, W. B. (1972a). Studies on the primitive opisthobranch genera *Bullina* Férussac and *Micormelo* Pilsbury. Zool. J. Linn. Soc. 51: 105–119

Rudman, W. B. (1972b). The anatomy of the opisthobranch genus *Hydatina* an the functioning of the mantle cavity and alimentary canal. Zool. J. Linn. Soc. 51: 121–139

Schulte, G. R., Scheuer, P. J. (1982). Defensive allomones of some marine molluscs. Tetrahedron 38: 1857–1863

Schulte, G. R., Scheuer, P. J., McConnell, O. J. (1980). Two furanosesquiterpene marine metabolites with antifeedant properties. Helv. chim. Acta 63: 2159–2167

Stallard, M. O., Faulkner, D. J. (1974). Chemical constituents of the digestive gland of the sea hare *Aplysina californica*. I. Importance of diet. Comp. Biochem. Physiol. (B) 49: 25–36

Stamm, R. A. (1962). Zur Abwehr von Raubfeinden durch *Lobiger serradifalci* (Calcara), 1840, und *Oxynoe olivacea* Rafinesque, 1819 (Gastropoda, Opisthobranchia). Revue Suisse Zool. 75: 661–665

Stasek, C. R. (1967). Autotomy in the Mollusca. Occ. Pap. Calif. Acad. Sci. 61: 1–44

Süffert, F. (1932). Phänomene visueller Anpassung. Z. Morph. Tiere 26: 147–316

Thompson, J. E., Barrow, K. D., Faulkner, D. J. Localization of two brominated metabolites, aerothionin and homoaerothionin, in spherulous cells of a marine demosponge, *Aplysina fistularis*. Acta Zool., in press

Thompson, J. E., Walker, R. P., Wratten, S. J., Faulkner, D. J. (1982). A chemical defense mechanism for the nudibranch *Cadlina luteomarginata*. Tetrahedron 38: 1865–1873

Thompson, T. E. (1960a). Defensive adaptations in opisthobranchs. J. mar. biol. Ass. U. K. 39: 123–134

Thompson, T. E. (1960b). Defensive acid-secretion in marine gastropods. J. mar. biol. Ass. U. K. 39: 115–112

Thymiak, A. A., Rinehart, K. L. Jr. (1981). Biosynthesis of dibromotyrosine-derived antimicrobial compounds by the marine sponge *Aplysina fistularis* (= *Verongia aurea*). J. Am. chem. Soc. 103: 6763–6765

Vermeij, G. J. (1978). Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge

Walker, R. P. (1982). The chemical ecology of some sponges and nudibranchs from San Diego. Doctoral thesis, University of California, San Diego

Walker, R. P., Faulkner, D. J. (1981). Chlorinated acetylenes from the nudibranch *Diaulula sandiegensis*. J. org. Chem. 46: 1475–1478

Walker, R. P., Thompson, J. E., Faulkner, D. J. (1980). Sesterterpenes from *Spongia idia*. J. org. Chem. 45: 4976–4979

Warmke, G. L., Almodóvar, L. R. (1972). Observations on the life cycle and regeneration in *Oxynoe antillarum* Mörch, an ascoglossan opisthobranch from the Caribbean. Bull. mar. Sci. 22: 67–74

Yoshiyama, R. M., Darling, J. D. S. (1982). Grazing by the intertidal fish *Anoplarchus purpurescens* upon a distasteful polychaete worm. Environ. Biol. Fish. 7: 39–45