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REVIEW

Galls and tumor-like growths on marine macroalgae

Kirk E. Apt

Department of Biological Sciences, University of California, Santa Barbara, California 93106, USA

ABSTRACT: Galls and tumor-like growths can be found on numerous marine macroalgae. These growths are characterized by cell hyperplasia and hypertrophy producing an abnormal unorganized cell proliferation. Host tissues involved are typically differentiated and are induced to become meristematic after infection. These growths are associated with bacteria, algae, fungi, various animals, and other agents.

INTRODUCTION

Most of us are familiar with hyperplasia (galls) on terrestrial plants. Mani (1964), in his extensive treatise on plant galls, defined them as pathologically developed cells, tissues or organs of plants that have arisen mostly by hypertrophy (cell enlargement) and hyperplasia (cell proliferation) under the influence of parasitic organisms such as bacteria, fungi, and various animals (e.g. nematodes and insects). Additional information regarding the development and morphology of terrestrial plant galls can be found by consulting Mani (1964) and Meyer & Maresquelle (1983).

A number of analogous growths occur on marine macroalgae. These growths are associated with bacteria, fungi, other algae, nematodes, copepods, industrial pollutants, and unknown causes. Earlier literature was previously summarized by Trotter (1901), Merola (1956) and Tokida (1958). A general review on marine algal pathology can be found in Andrews (1976). Morphologically these growths are characterized by host cell hyperplasia and hypertrophy producing an abnormal callus-like unorganized cell proliferation. Typically, the host cells involved are initially differentiated and non-meristematic, but are induced to redifferentiate and become meristematic following infection. Cell growth and cell division are not coordinated as in normal development. As a result, the general development of the gall growths is a pronounced departure from the general morphogenetic restraints of the thallus.

Each of the major types of association will be summarized individually.

BACTERIA

As with the terrestrial flora (Riker et al. 1946) numerous seaweeds are apparently induced by bacteria to form galls (see Table 1). However, the nature of the interaction is poorly understood.

Work by Cantacuzene (1930) concerning the development of galls on species of the red algae *Chondrus, Cystoclonium* and the brown alga *Fucus* is one of the earlier and more thorough investigations. He described outgrowths which appeared on the base, stipe and lamina of infected thalli; these varied in size depending on their age and location. The largest growths appeared on the older portions of the host. Typically the growths were highly contorted in appearance with older portions of the gall senescing. Cantacuzene (1930) stated that primary tumors 'metasize', producing secondary growths in a linear pattern. Intervening tissues were hyperplastic and may or may not contain bacteria. Unlike crown gall of higher plants, bacteria were present in the secondary tumours and there is no evidence to date for a 'tumor-inducing

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Table 1. Galls and tumorous growths reported on marine macroalgae

Algal species and inducing agent	Presumed cause	Source
Bacteria		
Ahnfeltia plicata	Not isolated	Chemin 1937
Bonnemaisonia asparagoides	Not isolated	Chemin 1937
Ceramium rubrum	Not isolated	Chemin 1932
Chantransia spp. (= *Acrochaetum* spp.)	Not isolated	Brand 1897, Starmarch 1930
Chondrus crispus	Not isolated	Schmitz, 1892, Cantacuzene 1930
Curdiea laciniata	Not isolated	Schmitz 1892
Cystoclonium purpureum	Not isolated	Schmitz 1892, Chemin 1937
Delesseria sanguinea	Not isolated	Schmitz 1892
Dumontia filiformis	Not isolated	Schmitz 1892
Fucus lutarius (= *F. vesiculosus*)	Not isolated	Lami 1946
Fucus platycarpus (= *F. spiralis*)	Not isolated	Lami 1946
Gigartina teedii	Not isolated	Schmitz 1892, Tsekos 1982
Grateloupia filicina	Not isolated	Schmitz 1892
Rhodymenia palmata (= *Palmaria palmata*)	Not isolated	Schmitz 1892
Plocamium coccineum (= *P. cartilagineum*)	Not isolated	Chemin 1937
Polyneuropsis stolonifera	Not isolated	McBride et al. 1974
Prionitis decipiens	Not isolated	Schmitz 1892
Prionitis lanceolata	Not isolated	Schmitz 1892, McBride et al. 1974, Apt 1985
Pterocladia capillacea	Not isolated	Felicini & Perrone 1972
Saccorhiza bulbosa	Isolated (?)	Cantacuzene 1928a, 1928b, 1930
Schizymenia dubyi	Not isolated	Lami 1946
Fungi		
Cystoseira balearica	*Haloguignardia*	Kohlmeyer & Demoulin 1981
Cystoseira osmundacea	*Haloguignardia*	Estee 1913, Kohlmeyer & Kohlmeyer 1979, Apt 1988b
Cystophora retroflexa	*Massarina*	Kohlmeyer & Kohlmeyer 1979
Cystophora subfarcinata	*Massarina*	Kohlmeyer & Kohlmeyer 1979
Halidrys dioica	*Haloguignardia*	Estee 1913, Kohlmeyer & Kohlmeyer 1979
Sargassum daemelii	*Haloguignardia*	Cribb & Cribb 1956, Kohlmeyer & Kohlmeyer 1979
S. decipiens	*Haloguignardia*	Cribb & Cribb 1956, Kohlmeyer & Kohlmeyer 1979
S. fallax	*Haloguignardia*	Cribb & Cribb 1956, Kohlmeyer & Kohlmeyer 1979
S. fluitans	*Haloguignardia*	Kohlmeyer & Kohlmeyer 1979
S. globulariaefolium	*Haloguignardia*	Cribb & Cribb 1956, Kohlmeyer & Kohlmeyer 1979
S. natans	*Haloguignardia*	Kohlmeyer & Kohlmeyer 1979
S. sinclairii	*Haloguignardia*	Cribb & Cribb 1956, Kohlmeyer & Kohlmeyer 1979, Kohlmeyer & Demoulin 1981
S. undulatum	*Haloguignardia*	Kohlmeyer & Demoulin 1981
Algae		
Cystoseira ericoides	*Herponema*	Sauvageau 1892
Cystoseira opuntioides	*Streblonemaopsis*	Valiante 1883, Feldmann 1937
Laminaria flexicaulis (= *L. digitata*)	*Ectocarpus*	Dangeard 1931
Laminaria japonica	*Streblonema*	Apt 1988a
Laminaria saccharina	*Streblonema*	Andrews 1977, Apt 1988a
Macrocystis integrifolia	*Streblonema*	Andrews 1977, Apt 1988a
Nereocystis luetkeana	*Streblonema*	Andrews 1977, Apt 1988a
Animals		
Ascophyllum nodosum	Nematode	Barton 1892, deMan 1892
Chondrus crispus	Nematode	deMan 1892, Barton 1901
Desmarestia aculeata	Nematode	Barton 1892, deMan 1892
Fucus vesiculosus	Nematode	Coles 1958
Furcellaria fastigiata (= *F. lumbricalis*)	Nematode	deMan 1892, Barton 1901
Rhodymenia palmata (= *Palmaria palmata*)	Copepod	Barton 1891, Brady 1894, Harding 1954
Vaucheria spp.	Rodifer	Trotter 1901, Merola 1956
Other		
Ceramium spp.	Unknown	Dixon 1960
Fucus serratus	Unknown	Brucker 1958, Künzenbach & Brucker 1960
Gracilaria confervoides	Unknown	Merola 1952, Chemin 1937
Gracilaria epihippisora	Unknown	Apt 1984
Gracilaria verrucosa	Unknown	Tripodi & Beth 1976
Porphyra tenera	Pollution	Ishio et al. 1971, 1972a, b, c, Watanabe & Kato 1972

principle'. (For a review of higher plant tumor systems, see Gelvin 1984.)

The galls as described by Cantancuzene (1930) were proliferations of inner (medullary) tissue containing bacteria in the intercellular spaces. The bacteria were isolated and partially characterized but they were not classified, nor were there indications as to the purity of the isolates. Galls were induced by inoculating healthy algae with the isolated bacterial cultures or homogenized galls. Apparently similar organisms were present in each of the host species studied and Cantacuzene (1930) concluded that they were the pathogenic agent, based on their strict association with gall growths, the damaging action they caused on the host, their affinity for specific tissues and their induction of galls on thalli inoculated artificially.

McBride et al. (1974) studied the cytology of red algal galls and concluded that *Lobocolax deformans* Howe, originally described as a distinct parasitic red algal species, was a proliferation of host tissue of *Prionitis lanceolata* induced by bacterial infection. The appearance and structure of the tumors were much the same as those described by Cantacuzene (1930). Affected cells were smaller and less regular than adjacent medullary cells. At the ultrastructural level, small proplastids containing few thylakoids replaced the well-developed plastids, and nucleic acid areas of the chloroplasts were more conspicuous. Cell wall structure and certain cytoplasmic membrane systems were also altered. The bacteria were rods of 1×2 µm and appeared as typical prokaryotes. Tsekos (1982) examined bacteria-associated galls on *Gigartina teedii* and found results similar to those of McBride et al. (1974).

Recent infection studies (Apt 1985) on bacteria-associated growths on *Prionitis lanceolata* (Fig. 1) have shown that gall growths can be induced on healthy uninfected hosts by application of homogenized gall tissue. Development of hyperplasia only occurs if the causative agent comes into contact with internal medullary cells through a wound site. These internal cells begin unorganized cell divisions forming a callus-like cell mass which displaces and disrupts the surrounding normal cells. The adjacent cortical cells do not participate in gall formation. The causative agent has been found to be of bacterial size, but the specific bacterium responsible for these growths has not been identified.

ALGAE

Several examples of galls produced by algae (see Table 1) on species of brown algae are known. Sauvageau (1892) described a gall on *Cystoseira ericoides* caused by the brown alga *Herponema valiantei*. Valiante (1883) reported *Streblonemopsis irritans* as causing nodular galls on *Cystoseira opuntioides*. *Ectocarpus deformans* was considered the cause of gall growths on *Laminaria digitata* (Dangeard 1931).

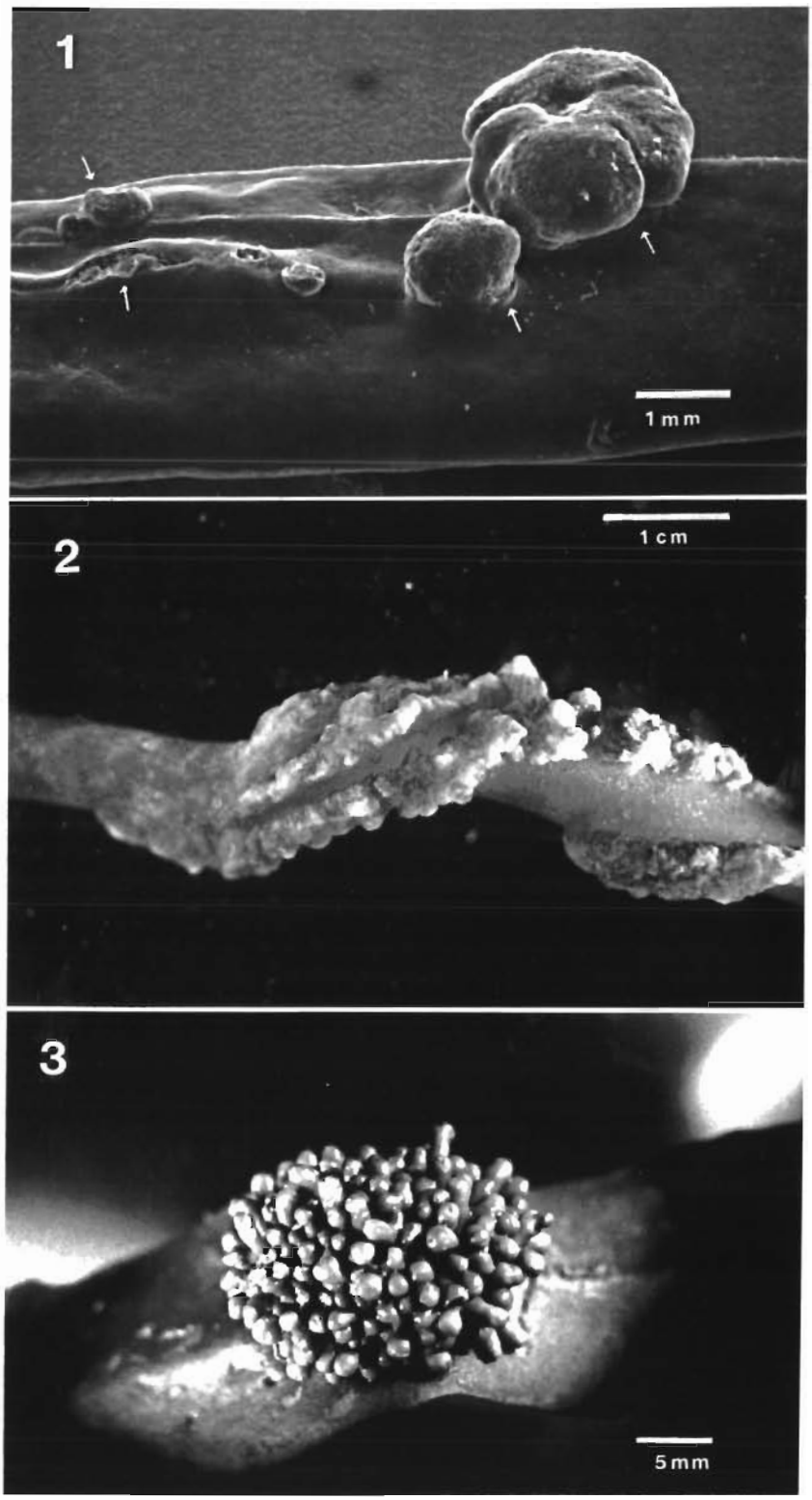
Galls found on the stipes of *Nereocystis, Laminaria* and *Macrocystis* (Fig. 2) were invariably associated with a filamentous and endophytic *Streblonema*-like brown alga (Andrews 1977). These growths were quite large compared to the thickness of stipes bearing them. In general, they appeared as round wart-like tumours or as highly convoluted elongated ridges (up to 20 cm long).

Filaments of *Streblonema* sp. have been isolated from hyperplasia on *Nereocystis luetkeana* and characterized in culture (Apt 1988a). When inoculated on juvenile thalli of the brown algal kelps *Laminaria japonica, Nereocystis luetkeana* and *Macrocystis integrifolia*, filaments of *Streblonema* sp. induced identical growths to those found in nature. Hyperplasia originates from the internal cells of the epidermal meristematic zone. These cells are induced to divide in a highly irregular and unorganized manner, producing a structure that is a distinct departure from normal morphogenesis. These growths are unusual because the organism which causes cell proliferations belongs taxonomically to the same phylum as the host.

FUNGI

Fungal infections associated with galls are caused by species of *Haloguignardia* and *Massarina*, which infect a number of phaeophycean species (see Table 1). These galls (Fig. 3) take the form of subglobose, ellipsoidal or elongated outgrowths which are more or less prominent protuberances containing ascocarps and spermogonia. Algal genera attacked by *Haloguignardia* spp. are *Cytoseira, Halidrys* and *Sargassum*. *Massarina cystophorae* forms galls on the genus *Cystophora*.

The tissue of *Cystoseira osmundacea* undergoes pronounced developmental changes (Apt 1988b) when in association with the fungus *Haloguignardia irritans*. Non-meristematic differentiated cortical cells are induced to dedifferentiate and begin dividing in a random manner forming a callus-like tissue. As the infection continues this tissue is induced to redifferentiate into a structure composed of tightly packed club-shaped projections. This structure is unique to the association and has no counterpart in normal morphology. Each projection contains a single fungal reproductive conceptacle (ascocarp or spermogonium). Algal host tissue completely surrounds the fungal reproductive structures and appears to function as a protective layer replacing the need for a thick ascocarp or sper-



Figs. 1 to 3. Galls on marine macroalgae. Fig. 1. Scanning electron micrograph of *Prionitis lanceolata* with bacteria-associated galls (arrows). Gall tissue has split the cortical tissue and emerged from the internal medullary region. Infection was conducted in the laboratory. Fig. 2. Stipe of *Nereocystis luetkeana* infected with *Steblonema*. Convoluted gall tissue spirals down the stipe. Non-infected tissue retains smooth surface. Fig. 3. Frond of *Cystoseira osmundacea* with *Haloguignardia*-associated gall. Gall is composed of numerous tightly packed club-shaped projections

mogonial wall. The association of fungus with *C. osmundacea* is not a simple matter of the fungus developing inside the alga; algal morphology is significantly altered in the association to the apparent advantage of the fungus.

ANIMALS

Relatively little is known about gall-inducing animals on seaweeds (see Table 1). Nematodes described by Barton (1892) were associated with small, round galls on the brown algae *Ascophyllum* and *Desmarestia*. DeMan (1892), who examined Barton's specimens, described the nematode which is now known as *Halenchus fucicola*. Coles (1958) reported this species and *Halenchus dumnonicus* found in galls on the brown alga *Fucus vesiculosus*. Barton (1891, 1901) discovered nematodes in galls on the red algae *Palmaria, Furcellaria,* and *Chondrus*. However, a copepod was apparently responsible for the symptoms on *Palmaria* and whether nematodes were the causal agents in the latter 2 cases was not established. It is also not clear from the descriptions provided by the above-mentioned authors just how much, if any, cell proliferation had taken place or if any internal structural modifications were evident.

CARCINOGENIC COMPOUNDS

There is little information about the effects of carcinogenic compounds on marine algae and most of what is known has been derived from short-term experiments. Certain polycyclic aromatic hydrocarbons stimulate abnormal growth and may be oncogenic. At low concentrations these compounds induced increased cell growth in red algal sporelings (Boney & Corner 1962, Boney 1974). Tumor-like structures developed on fronds of the red alga *Porphyra tenera* when these were placed in contact with mud from polluted waters that was subsequently shown to contain 2-chloranthraquinone and reduced dibenzanthrone (Ishio et al. 1971, 1972a, b, c, Watanabe & Kato 1972). Similar growths appeared on *P. tenera* exposed in the laboratory for several weeks to these purified compounds at concentrations of less than 1 ppm. It is not known how if at all these cells differ biochemically or genetically from their untreated counterparts.

OTHERS

There are no confirmed reports of tumor-like growths caused by viral or genetic abnormalities on marine algae. One possible viral case is the growths found on the red alga *Gracilaria epihippisora* by Apt (1984). They were not associated with exogenous microorganisms, but were associated with virus-like particles (VLP) present within the cytoplasm (Apt unpubl.). However, these VLP's have not been shown to be the cause of the abnormal growths. These growths are derived from epidermal meristematic cells which have apparently lost their ability to differentiate, and divide randomly producing a callus-like mass. This cell mass, when excised, continues to proliferate as an undifferentiated tissue mass. Along with morphology these growths have a distinct cell wall composition and ultrastructure.

Tripodi & Beth (1976) described 'caterpillar-like' bodies within abnormal growths on the red alga *Gracilaria verrucosa*. These unusual bodies were found only within the cells of the swellings and were absent from cells of normal tissue. It is not clear what relationship, if any, these bodies have with inducing abnormal growths.

Künzenbach & Brucker (1960) attempted to infect 44 different marine green, brown and red algae with the bacterium *Agrobacterium tumefaciens,* which causes tumors on higher plants. No detectable changes in differentiation or morphology were observed.

CONCLUSIONS

Observations on algal galls have been made for ca 100 yr. The majority of these reports have dealt with the gross morphology. The growths are apparently common on a variety of algae (Dixon 1973), but are rarely reported or examined in detail. In only one case has the infecting organism been isolated, identified and demonstrated to be the causative agent. There is no information available on the biochemical or genetic interactions between pathogen and host.

One significant similarity between the different gall types is that, in every case examined in detail, cell proliferations originate from specific areas. The bacteria-associated galls on *Prionitis* originate only from internal medullary tissue; other tissues are not affected. Another similarity is that the growths are typically composed of a single cell type, forming a homogeneous unorganized tissue. Notable exceptions are the growths associated with the fungus *Haloguignardia*. These growths are composed of several specific tissues.

The study of higher plant systems has shown that pathogenic microorganisms and the growth regulatory substances they produce play an important role in gall formation. It is likely that microorganisms associated with algal galls and the substances they produce are also important in the induction of cell division in gall formation on marine macroalgae. The nature of the

interaction between gall inducer and host should provide valuable information on general development and processes coordinating cell growth and division in marine algae.

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