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REVIEW ARTICLE

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Summary Here we review cases where initiation of morphogenesis, including the differentiation of specialized cells and tissues, has clearly evolved due to cyclical symbiont integration. For reasons of space, our examples are drawn chiefly from the plant, fungal and bacterial kingdoms. Partners live in symbioses and show unique morphological specializations that result when they directly and cyclically interact. We include here brief citations to relevant literature where plant, bacterial or fungal partners alternate independent with entirely integrated living. The independent, or at least physically unassociated stages, are correlated with the appearance of distinctive morphologies that can be traced to the simultaneous presence and strong interaction of the plant with individuals that represent different taxa.

Key words *Azolla* · *Geosiphon* · *Gunnera* · Symbiospecific morphology · Symbiont-induced tissue

Introduction

We argue that "symbiogenesis," an evolutionary concept, has been applied to the concept of evolutionary change less frequently than warranted. "Symbiosis" is simply organisms of different species living in close contact (i.e., the "differently named" beings living together of the 19th century German biologist Anton DeBary; [20]). Symbiogenesis, however, refers to the appearance of new physiologies, tissues, organs, and even new species of organisms as a direct consequence of symbiosis. Symbiogenesis, the term first introduced into the literature by Konstantin Sergeivich Mereschkovsky (1855–1921) is virtually equivalent to the independently derived concept of Ivan Emanuel Wallin (1883–1969): symbionticism or "microsymbiotic complexes." (The work of these authors is discussed in an historical context in [5] and [20].)

Techniques of ultrastructure, physiology and genetics coupled with light microscopic study of life history supply profound examples where new morphology is generated by identifiable symbiont interaction. We augment our own limited observations of plant-microbial interactions with examples drawn from the literature. Examples where morphogenetic novelty is cyclically generated by symbiogenetic association are listed in Table 1, and developmental sequences where such morphogenetic novelty has been documented by videomicroscopy are referenced. In all cases, each partner develops symbiospecific morphology not found in free-living forms, as we describe here for (I) cyanobacteria in bryophytes, fungi, ferns, cycads and angiosperms, (II) heterotrophic bacteria in dicotyledons, (III) fungi as symbionts, and (IV) symbiont-induced histogenesis (ant plants).

Table 1 Cyclical symbioses

Holobiont	Plant or fungal taxon	Cyclical biont
Anthoceros-cyanobacteria	Hornwort	*Nostoc*
Azolla-cyanobacteria	Fern	*Anabaena*
Cycad-cyanobacteria	Gymnosperm	*Nostoc*
Gunnera-cyanobacteria	Angiosperm	*Nostoc*
Geosiphon-cyanobacteria	Zygomycete	*Nostoc*
Lichen	Ascomycete	*Nostoc* /*Trebouxia*
Legume-proteobacteria	Angiosperm	*Rhizobium*
Dicotyledon-proteobacteria	Angiosperm	*Agrobacterium*
Plant-mycorrhizae	Plantae	*Glomus,* etc.
Myrmecophyte-ant	Angiosperm	*Azteca,* etc.

Cyanobacteria in plants

Plant-cyanobacterial symbioses have evolved in four major plant taxa (e.g., the bryophytes *Blasia* and *Anthoceros*, the fern *Azolla*, all cycads such as *Macrozamia* spp. and the angiosperm *Gunnera*). While specialized morphology develops in all these associations (e.g., leaf cavities in hornworts and *Azolla*, coralloid roots in cycads and stem glands in *Gunnera*), at least rudiments of these structures preexist in absence of the endosymbiont. Following infection, the symbiotic organs increase in size and complexity. A given one of these plant species may be symbiotically compatible with different strains of cyanobacteria, principally *Nostoc*. By contrast, legume root nodules are induced

by heterotrophic bacteria; their development requires a complex exchange of signals with the proper strain of *Rhizobium* or *Bradyrhizobium* [9].

The relevant plant organs primarily grow by cell proliferation in response to cyanobacterial infection. The *Nostoc* or *Anabaena*, however, undergo more complex morphological changes in the partnership. First, short motile infective filaments called hormogonia form in response to a chemical signal from the plant (hormogonium initiation factor, HIF, documented in *Anthoceros*; [9]). DNA replication and phycobiliprotein synthesis ceases, and rapid septation occurs to form the hormogonial filaments [22]. Following infection, hormogonia dedifferentiate into nonmotile photosynthetic cells and nitrogen-fixing heterocysts. The heterocyst frequency of plant-associated *Nostoc* is far higher than necessary to support the fixed-N needs of the cyanobacteria (e.g. 40% in *Anthoceros* or mature *Azolla* compared to only 5–6% in free-living cyanobacteria). Some 45–90% of ammonium ion in both *Anthoceros* and *Azolla* is transferred to the plant [9]. Still, in contrast to plant-heterotroph symbioses, no gene transfer, bacteroid differentiation or expression of dual-partner gene products has been documented in plant-cyanobacterial consortia, suggesting that they are less well integrated and perhaps more recently evolved than, for example, the many legume-*Rhizobium* associations.

i. *Nostoc* in *Anthoceros*

Anthoceros punctatus colonizes nitrogen-poor acidic wetland habitats; the plant obtains its nitrogen from symbiotic *Nostoc* which infect preexisting cavities in the gametophyte thallus. The less conspicuous sporophyte plant is never infected by *Nostoc* [19]. The symbiosis has two distinct life history stages: first, formation of hormogonia, infection and dedifferentiation, and second, maturation into a functional association where heterocysts differentiate and release fixed nitrogen. The existence of two stages suggests that *Nostoc* are responding to chemical signals produced by *Anthoceros*, with different signals orchestrating specific steps in the sequential establishment of the symbiosis [9].

As infection progresses, *Nostoc* colonies in the *Anthoceros* tissue become more conspicuous. To the unaided eye, the leaf cavities that harbor *Nostoc* are bluish-black circular spots, evenly distributed along the margins of the ventral thallus. A transposon-induced mutant of *N. punctiforme*, approximately 50-fold more infective than wild type, induces proportionately more spots, symbiospecific morphological variation, on *Anthoceros* thalli.

ii. *Anabaena* in *Azolla*

Azolla is a heterosporous water fern, sometimes grouped with the Salviniaceae but accorded by most authors a single-genus family, the Azollaceae [7, 11]. The six widely distributed species include four New World (*Azolla caroliniana*, *Azolla filiculoides*, *Azolla mexicana* and *Azolla microphylla*) and two Eurasian representatives (*Azolla nilotica* and *Azolla pinnata*). The sporophytes, usually 1–3 cm in diameter, consist of multibranched, prostrate floating stems with deeply bilobed pinnae. The ventral lobe of each pinna is nonphotosynthetic and functions as a float. A cavity at the base of each dorsal lobe is densely populated with the filamentous heterocyst-forming cyanobacterium: *Anabaena azollae* (Fig. 1).

In contrast to other plant-cyanobacterial symbioses, *Azolla* hormogonium initiation factors (HIFs) are unknown. Instead, a colony of undifferentiated *Anabaena* is associated with each fern shoot apex; as the plant grows, blue-green filaments are partitioned off into each new leaf and entwine about specialized hair cells within the cavity. As the leaves mature, their cavities close. The symbiospecific morphology includes the fully enclosed, cyanobacteria-filled cavities and differentiation of the resident *Anabaena* into a higher proportion of nitrogen-fixing heterocysts relative to photosynthetic cells. Fixed atmospheric nitrogen is delivered to the plant as ammonium; pulse-chase isotope studies demonstrate that fixed nitrogen is transported from the mature leaf cavities to the apical meristem. The *Anabaena* receive fixed carbon as sucrose from the *Azolla* [12]. *Azolla*/*Anabaena* is economically important as green manure in rice paddies, and as fodder for pigs and waterfowl [13].

iii. *Nostoc* in *cycads*

Cycads are tropical and subtropical shrubs and trees. Common and widespread during the Mesozoic Era (225–66 mya), of the approximately 100 extant species, one-third harbor *Nostoc* or *Anabaena* spp. in the central root cortex. The negatively geotropic, cyanobiont-containing roots are termed "coralloid" because of their nodular appearance. Coralloid root cells are loosely organized to facilitate gas exchange; however, though they often grow above the soil surface, just as often they are underground. In contrast to *Azolla*-associated *Anabaena*, moreover, where light-dependent CO_2 fixation has been estimated at 85% of free-living levels, carbon fixation by *Nostoc* or *Anabaena* within cycads is undetectable [6]. Symbiospecific morphological changes are marked as small specialized root cortical cells that degenerate, leaving mucus-filled spaces that accommodate the cyanobacteria. Other cells of the root cortex differentiate into elongated, fingerlike shapes thought to facilitate nutrient exchange. The distinct cyanobacterial layer that forms between the inner and outer root cortical layers is symbiospecific tissue, recognizable by its oblong cells packed with *Nostoc*. We consider this to be an example of symbiont-induced histogenesis.

iv. *Nostoc* in *Gunnera*

Gunnera (monogeneric family Gunneraceae) is the only angiosperm known to form symbioses with cyanobacteria.

Habit may be succulent creeping ground cover (e.g. *Gunnera monoica* from New Zealand) or polystelous giant herbs (e.g. South American *Gunnera manicata*, the "poor man's umbrella"). High and continuous water supply requirements restrict *Gunnera* to boggy, acidic habitats which are often low in combined nitrogen. Such environments selected symbiotic associations of *Gunnera* with *Nostoc*. Coevolution has led to symbiotic plant organs (glands), where multicellular papillae, first visible in cotyledon stage seedlings, occur in hemispherical concentric arrangements paired at each node (Fig. 2D). The mature stem in cross-section reveals a more irregular array of *Nostoc* colonies, one for each vascular cylinder of the polystelous architecture (Fig. 2C).

Infection by *Nostoc* hormogonia occurs via copious carbohydrate- and HIF-rich mucus produced by the glands. Interpapillary channels permit entry of hormogonia into a gland, following which *Gunnera* cell walls in proximity to *Nostoc* dissolve. The details of this symbiospecific morphological change are unknown. Hormogonia penetrate the plant cells, though not their membranes. Between cell wall and membrane, they soon dedifferentiate into less elongate, larger nonmotile photosynthetic cells. Other bacteria and fungi accompany hormogonia into the channels, yet only *Nostoc* enter the plant cells. A mechanism of cyanobiont recognition by the plant must therefore be inferred. New cell walls soon form, enclosing tightly packed *Nostoc* filaments; the proportion of nitrogen-fixing heterocysts relative to nonmotile photosynthetic cells increases. *Nostoc* filaments proliferating within the *Gunnera* cells fail to stimulate hostile plant responses such as systemic acquired resistance or phytoalexins. The form of fixed nitrogen, which in *Azolla* and bryophytes is ammonium ion, is not yet identified in *Gunnera* (or in cycads, [2]).

In *G. manicata*, we observed young seedlings well populated with *Nostoc* while still attached to the viviparous compound spike (Fig. 2B). Hormogonia from the soil may be transmitted to the spike via specialized involucral bracts, usually coated with mucus. These bracts (Fig. 2A), varying in color from bright pink to nearly black, are a slimy plant tissue that provides community support for a number of protists, bacteria and even nematodes. The bracts, considered stipules by some observers [K. Searcy, personal communication], are present in the giant herbs (e.g., *Gunnera magellanica*) but absent in the ground cover species (e.g., *G. monoica*). Inasmuch as the bracts also subtend petioles in the mature plant, they may aid in transmission of *Nostoc* to newly formed steles.

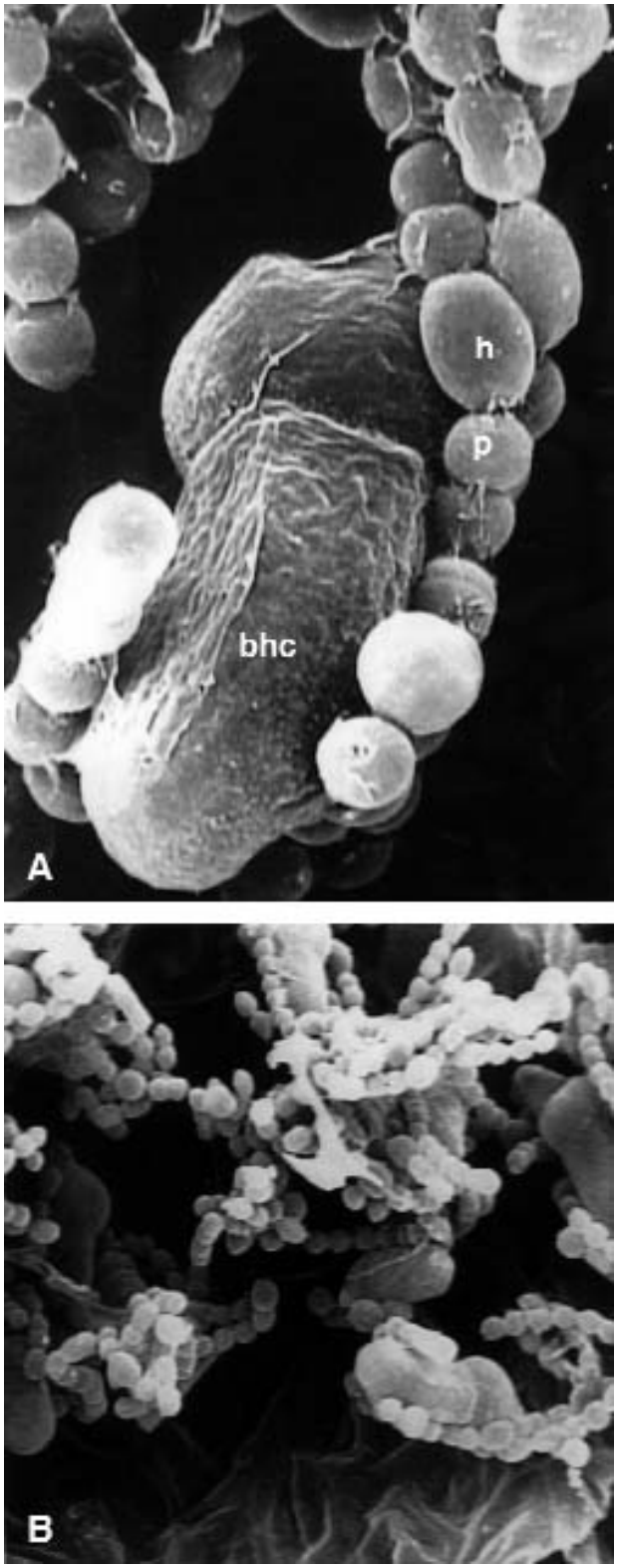

Fig. 1 *Anabaena* cyanobiont in *Azolla*. (A) Branched hair cell (bhc), a specialized internal trichome with transfer cell ultrastructure. Photosynthetic cells (p) and heterocysts (h) of *Anabaena* maintain close contact with the bhc, facilitating nutrient exchange. SEM, 2000×. (B) Specialized epidermis within *Azolla* leaf cavity showing multiple *Anabaena* filaments associated with branched hair cells. SEM, 500×

Cyanobacteria in fungi

i. *Nostoc* in *Geosiphon*

Geosiphon pyriforme, originally identified as an alga and assigned to genus *Botrydium*, is now known to be a green zygomycete. First discovered on the banks of the River Salze

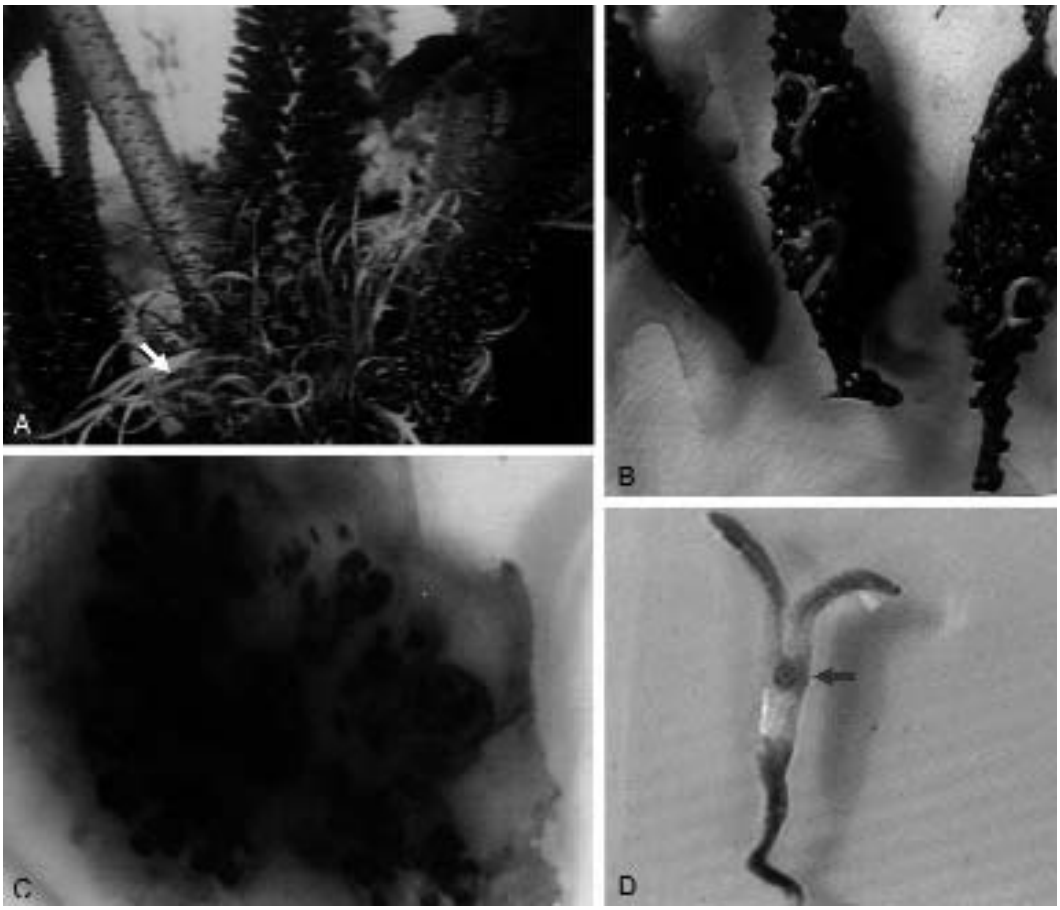

Fig. 2 *Nostoc* cyanobiont in *Gunnera*. (A) Mature *Gunnera* plant with involucral bracts (arrow) subtending petioles and inflorescence. (B) Viviparous compound infructescence (spike) with attached seedlings. (C) Stem cross-section, diameter 3 cm, showing random array of *Nostoc* inclusions. (D) *Gunnera* 2 cm seedling showing one of two symbiospecific glands (arrow)

in Nordhausen, Germany, and seldom reported elsewhere, its distinctive 0.5 mm blue-black ovoid bladders (the symbiospecific organs) emerge in moist habitats between thalli of *Anthoceros* and other bryophytes. When *Nostoc* hormogonia encounter hyphae of *Geosiphon*, the fungal wall dissolves and the hyphal tip engulfs one or more cyanobacterial cells. Fungal cytoplasm then flows into the hyphal tip and lipid vacuoles form. Elevated turgor pressure helps to expand the young bladder. Inside the bladder, *Nostoc* cells divide and heterocysts differentiate. Gold-lectin staining has revealed chitinous fungal wall surrounding each *Nostoc* cell, a symbiosome remarkably like those of V–A mycorrhizal associations involving *Glomus* spp. Within the bladder, heterocyst frequency increases as other *Nostoc* cells become pale, indicating degradation of phycobilins. Bladders take approximately one week to mature, after which no further *Nostoc* cell division occurs; after about two weeks, bladder senescence ensues and cyanobionts begin to die. Under stress conditions such as low temperature and desiccation, *Geosiphon* forms spherical propagules approximately 0.25 mm in diameter. On rewetting, a new hyphal network emerges from such spores; young bladders develop only if potentially infective *Nostoc* hormogonia are present, and the strange life history stages repeat.

Geosiphon hyphal networks are often intertwined with rhizoids of *Anthoceros* and other bryophytes, with which they may exchange nutrients as mycorrhizae. HIF from the bryophytes facilitates differentiation of new hormogonia. The signal, if any, that attracts *Nostoc* to its fungal partner is unidentified. Our description is based on the magnificent videotape of Mollenhauer [10].

ii. Cyanobacterial lichens

Lichens are symbiotic consortia of ascomycetes with green algae or cyanobacteria. They are famous colonizers of extreme habitats, such as Antarctica and the Siberian tundra, where they are basic to the food chain and economically important as reindeer fodder. Of the 14,370 species of lichen recognized by Poelt [14], 61% harbor unicellular green algae (8698 lichen species; genus *Trebouxia* is the most common algal photobiont). Some 4478 lichen species form associations with the filamentous chlorophyte, *Trentepohlia*, and 8% (1194 species) contain N_2-fixing *Nostoc* cyanobacteria. Of this latter group, some species simultaneously harbor both green algae and cyanobacteria, and others only cyanobacteria. Lichens are often the first colonists of newly exposed rocky areas. Cyanobacterial

lichens are of particular importance in this regard, since during succession they contribute fixed nitrogen to the nascent topsoil.

Although the fungal partner determines the overall form of the lichen, reassociation experiments show that a given fungus produces quite different morphologies correlated with different algal or cyanobacterial associates [16]. Lichenized *Nostoc* undergo morphologic as well as metabolic changes: in addition to heterocyst differentiation and N_2-fixation, they have thicker gelatinous sheaths, smaller cells, cyanophycin granules (copolymers of aspartic acid and glutamine residues), and fewer heterocysts. *Nostoc* cells when components of lichens contain more polyglucoside granules than when free-living. In lichens involving both green algae and cyanobacteria, *Nostoc* often dwell within gall-like structures called cephalodia. Heterocyst differentiation within cephalodia is 10–30%, compared to 4% when *Nostoc* are the primary symbionts [15]. Cyanobiont cell wall changes have also been noted including an outer cell wall consisting of 2–3 nm thick interwoven ribbons [1]. The symbiospecific morphology is unmistakable in these cases since the lichenized *Nostoc* can be grown facultatively by itself or with green algae as an internal control.

Heterotrophic bacteria in plants

i. *Rhizobium* in root nodules

Because they have enjoyed extensive study at the genetic, metabolic, morphological and paleobotanical levels, legume root nodules provide our best example of symbiospecific morphogenesis. The primary source of combined nitrogen to the world's biota is the well known nitrogen-fixing symbiosis between *Rhizobium* or *Bradyrhizobium* spp. and members of the angiosperm family Fabaceae. Fast growing *Rhizobium* species are usually named for the plant crop, e.g. *Rhizobium phaseoli* in bean, *Rhizobium meliloti* in alfalfa and *Rhizobium trifolii* in clover. Slower growing *Bradyrhizobium*, usually associated with tropical legumes, is of similar economic importance in cultivation of soybeans and lupines.

The first visible sign of plant–*Rhizobium* interaction is root hair curling. This indicates that biochemical crosstalk has passed between the plant and the bacterium, and that the *Rhizobium* are of the appropriate host-specific strain. Bacteria first infect this "shepherd's crook" structure, the result of root hair curling, following which they move into the cortex down a tube of plant tissue, mostly cell wall material, called the infection thread. Root cortical cells are induced to divide; macroscopic nodules form (Fig. 3A), within which bacteria divide and produce special polysaccharides. Ultimately, bacteria cease dividing and are engulfed by plant cell membrane. They differentiate as bacteroids: these wall-less, nondividing cells with bacterial genetic organization are the agents of nitrogen fixation (Fig. 3B). A number of bacterial mutations interrupt steps in this interaction, e.g. *hac* mutants block root hair curling; *nop* (nodule-persistence) mutants give rise to prematurely senescent root nodules. These and other mutants allow detailed study of the metabolic sequence of nodulation.

The highly integrated nature of the legume-*Rhizobium* symbiosis is best documented by the presence of the symbiosis-specific protein: the oxygen carrier molecule leghemoglobin. This oxygen-carrying pigment imparts a reddish color to nodules in cross-section. Leghemoglobin functions to remove oxygen from the vicinity of the bacteroids and their oxygen-sensitive nitrogenase. The apoprotein is encoded by the plant, while *Rhizobium* encodes enzymes for synthesis of the heme moiety. Proper timing, transport and recognition of host and symbiont gene products are absolute requirements for the functional holoenzyme. A small fraction of nodules (5–10%), termed "incompetent," illustrate the importance of the oxygen carrier. White in cross-section and lacking leghemoglobin, the nodules are totally incompetent to fix nitrogen.

ii. *Agrobacterium* in dicotyledons

A Gram-negative alpha-proteobacterial relative of *Rhizobium*, *Agrobacterium*, makes its living by interkingdom gene transfer. Three species are recognized: *Agrobacterium tumefaciens*, the crown gall organism, best known for its utility in plant genetic engineering; *Agrobacterium rhizogenes*, which causes hairy root disease, and the avirulent strain *Agrobacterium radiobacter*.

Agrobacterium moves down a wound-induced plant hormonal gradient to enter tissues; it then inserts plasmid-derived *vir* genes into the cells. The transformed plant cells dedifferentiate into the symbiospecific callus known as the crown gall tumor. Such tumor cells grow indefinitely in tissue culture. Biochemical analysis reveals tumors to be associated with unusual compounds collectively called opines, specialized amino acids important for bacterial growth but not normally found in any plant. The enzymes for opine synthesis are encoded by the *Agrobacterium* Ti plasmid—the transgenic vector. Plant hormone levels are altered in tumor callus, extracts of which can support growth of nontumorous callus without exogenous hormones.

Only about 20% of the relatively large (appr. 200 kb) Ti plasmid is transferred into the plant. The t-DNA, responsible for the actual transfer, and the *vir* genes which encode the enzymes for tumorogenesis and opine synthesis, enter susceptible plant cells. Site-directed mutagenesis studies show that certain plasmid mutations (*tms*, or "shooter") produce shoots instead of callus. Others (*tmr*, or "rooter") produce roots. Either mutant phenotype can be rescued back to callus by addition of auxin or cytokinin to the tissue culture [17]. *Agrobacterium* has so profoundly coevolved with its dicot hosts that its plasmid encodes enzymes for plant hormone synthesis. A variant of the Ti plasmid has been used to engineer tobacco plants transgenic for BT (*Bacillus thuringensis*) toxin, which kills the pestilential *Manduca* moth larva. Even the firefly luciferase enzyme has been inserted into the dicot genome via

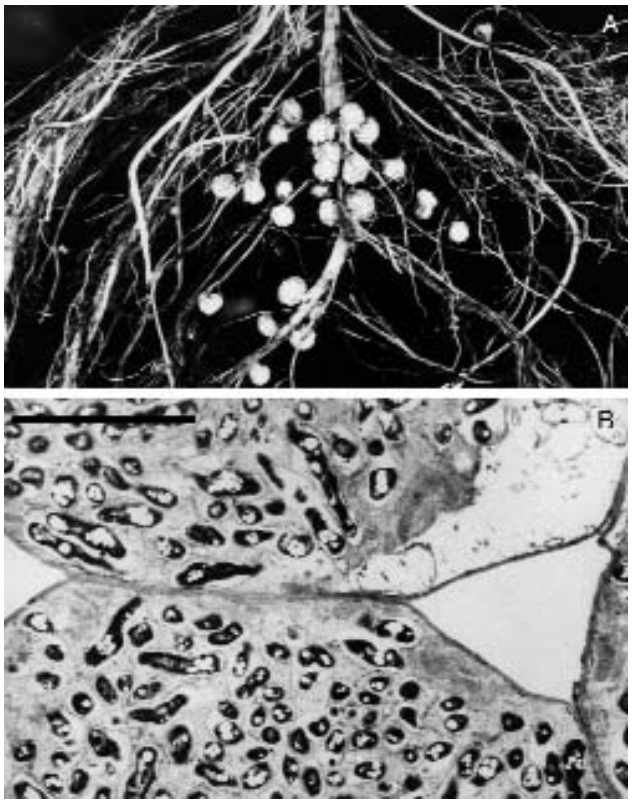

Fig. 3 *Rhizobium* in roots of soybean (*Glycine max*). (A) Well-nodulated roots in a mature plant. (B) Three root nodule cells replete with bacteroids (differentiated *Rhizobium* incapable of division). Bar = 100 μm

Agrobacterium. When supplied with the luciferin substrate through the roots, the transgenic plants glow! This example shows that gross symbiospecific morphological change can be induced by a partner contribution far below the level of resolution even with the electron microscope: a 40 kb piece of bacterial DNA.

Fungi as symbionts

i. Chlorophyte lichens

More common than cyanolichens but unable to fix atmospheric nitrogen, chlorophyte lichens share their cousins' tolerance of extreme environmental conditions. Lichens have been collected within 5° of the South Pole. Such remarkable tolerance to cold and UV radiation is attributed by some authors to lichens' rapid drying ability. Lichens in the field often contain as little as 2% water by weight; under such circumstances, photosynthesis ceases and the lichen enters the cryptobiotic state of "suspended animation." Dryness renders it impervious to cold, while the photosynthetic pigments of the dormant algal partner are protected from light-bleaching by the surrounding fungal tissue.

Reassociation experiments have shown marked morphologic and metabolic changes in the chlorophyte lichen relative to axenic culture. Lichen-forming ascomycetes are virtually never collected in a free-living state. In laboratory axenic cultures, however, they form small circumscribed plaques which require

Fig. 4 Rubiaceous myrmecophytes. (A) *Hydnophytum formicarium* bisected. This greenhouse specimen has never seen an ant. (B) *Myrmecodia solomonensis*, an epiphytic ant plant. (C) *H. formicarium* crown epidermis showing entry pores. (D) *H. formicarium* interior. In the field, the chambers may be colonized by a wide variety of insects including ants; this in contrast to the usual ant plant propensity for species-specific associations

complex growth media including many different carbohydrates. *Trebouxia* by contrast grows much more vigorously in lab culture than in the lichen. Lichen-associated *Trebouxia* cells are usually penetrated by fungal haustoria or appresoria (hyphal structures specialized for penetration and absorption). The alga produces large quantities of certain sugar alcohols such as D-sorbitol and D-ribitol only when growing within the lichen. These findings suggest that lichens are better described as states of controlled "parasitism" in which the fungal partner exploits the "imprisoned" photobiont, rather than as "mutualistic partnerships" [1]. Bits of mycelium encasing one or more algal cells (soredia) are released from the thallus. These propagules, dispersed by wind or rain to colonize new sites, are excellent examples of symbiospecific morphological innovation.

ii. Mycorrhizae

Associated with the roots of most vascular plants are mycorrhizae, fungal networks known for their enhancement of plants' nutrient uptake from the soil. The fungal symbionts occupy one of two broad categories, ecto- and endomycorrhizae, depending on whether the mycelium penetrates the root cortical cells. Mycorrhizal associations in bryophytes, especially liverworts, can be found in almost all habitats except where the soil is especially moist or nutrient-rich. Mycorrhizae are probably the most abundant symbioses in the world.

Four general types are recognized, depending on the topology of the association and/or the plant taxa involved: Ectomycorrhizae do not deeply penetrate the root cortex, but form the so-called Hartig net, a mycelium that sheaths the root and penetrates the apoplast (cellular interstices) 1–2 cell layers into the cortex. Ectomycorrhizal fungi associate with plant species of many families including Pinaceae (conifers), Betulaceae (birches and poplars) and Fagaceae (oaks and beeches). Three categories of endomycorrhizae are recognized. By far the most common, V–A (vesicular/arbuscular) mycorrhizae, with their characteristic intracellular vesicles, arbuscules and coils, infect representatives of all major plant groups. The last two categories, ericalean and orchid mycorrhizae, have morphologies peculiar to the plant taxa they infect. Ericalean mycorrhizae are remarkable for the large number of root penetration points; in some cases, every cell contains a fungal coil and has a hyphal connection with the rhizosphere. Monotropoid (a subgroup of ericalean) and orchid mycorrhizae supply carbohydrate to their plant hosts even in the seedling stage [21].

Symbiont-induced histogenesis: "ant plants"

Myrmecophytes (Fig. 4), or plants which harbor ant colonies, are common in the tropics. Typified by the "ant acacias," the syndrome is not confined to acacias or even legumes, but appears in many different genera and families. Myrmecophytism by definition involves production of hollow structures by the plant, which are inhabited by ants of a given species or colony. "Extreme" myrmecophytes develop highly specialized nutritious tissue that forms conspicuous meristic organs harvested by the ants. Classic examples of this form of symbiont-induced morphology occur in the "scrub" trees of the tropical American forests. Each *Pourouma* and *Cecropia* spp. individual develops 1–2 mm red or yellow polyps that form dense mats of "hair" at the base of the petioles. These symbio-organs, called "Müllerian bodies," contain oil, protein and (remarkably) glycogen [18]. *Azteca* ants, the usual inhabitants of the trees, harvest and carry away the easily detached Müllerian bodies. "Beltian bodies," that develop at the leaflet tips of *Acacia* spp., are similarly harvested by the resident *Pseudomyrmex* ants. Tiny, transparent glands rich in lipids and sugars (*Perldrüsen*), generously distributed over the plant epidermis and exploited by resident ant colonies as their main food source, are found in representatives of many plant families [23].

Janzen [4] and others have proven by ant removal experiments that myrmecophytes are protected from herbivory by their resident ants. Analysis of species distribution within the genus *Acacia* showed that ant-enticing organs such as Beltian bodies are restricted to African acacias [3]. Beltian symbiont-induced organs are conspicuously absent in the many Australian members of the genus, where selection pressures from large herbivores are markedly reduced. The conclusion by inference is that Beltian bodies coevolved in plants specifically in response to selection pressure from herbivores and corresponding protective ant behaviors.

The few examples we cite here illustrate the ubiquity of combinatorial modes of evolutionary innovation. Ancient symbioses gave rise to the eukaryotic condition itself, enabling cells bearing mitochondria (former alpha-proteobacteria) to thrive in an oxygen-poisoned atmosphere [8]. Extant symbioses likewise combine the developmental potential of two or more genomes. Selection pressures on the associates lead them to interact strongly and eventually to exploit niches where extreme environmental conditions or lack of nutrients defy all other life. K. S. Merezhkovsky and I. E. Wallin, respectively the earliest symbiogeneticist and symbionticist, pioneered a more comprehensive theory of speciation than that in neo-Darwinian currency: accretions of single-gene mutations in a given nucleus are strongly enhanced by the remarkable competitive advantages of holobionts. Cyclical morphogenesis, induced by symbiogenesis, is an underestimated mode of evolutionary innovation requiring closer scrutiny.

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