Symbiosis and Parasitism

Introduction

Practically no living organism lives in isolation. With rare exceptions, to be alive is to live in companionships. This is a powerful reality because it affects practically all our considerations of biological phenomena, including evolution, ecology, and the functioning of individuals and species. The association between organisms encompasses a spectrum from beneficial and symbiotic to damaging and parasitic. Living in a relationship to other living beings defines health and disease. However, the boundaries are not always precise and definitions can be elusive because this is a shifting landscape set apart by the vast reactivity of all living things. For human beings for example, today’s benevolent companion may become tomorrow’s assailant. A person suffering from AIDS becomes the victim of infections by otherwise innocuous members of the body’s normal microbial biota. The balance between parasitism and symbiosis is therefore delicate and can be readily altered by genetic or induced changes in one of the partners.

The distinction between symbiosis and parasitism is therefore blurry. The two share common steps in the way the association is established: encounter, entry, and multiplication in the host. One notable distinction concerns when in the life of the host the relationship is established. Most infectious diseases are acquired during the life of the host, although a few can be inherited from the mother. Established symbioses, on the other hand, evolve over a period of time and tend to be passed on from generation to generation. Therefore, parasitic relationships are usually transmitted horizontally, symbioses vertically.

Symbiosis, a relationship that benefits both partners, is a pervasive force in evolution. As the result, organisms develop novel ways to occupy environmental niches, produce energy, acquire nutrients, or defend themselves from predation. Examples are all around us. Some are easily noticeable, such as the lichens, the fungus-algae partnership that adorns rocks and trees, or the root nodules of legumes by which bacteria supply plants with nitrogen. Other symbioses are not so readily visible. One would have to travel to the depth of the ocean to see communities of bacteria and worms that have combined into non-sun based biological communities in thermal vents. The effects of symbiosis are not always
obvious and are best revealed when the connection between the partners is severed. Thus, the function of the human intestinal bacteria becomes apparent when they are reduced in number by treatment with antibiotics. People so treated become susceptible to diarrheas caused by yeast, suggesting that, at a minimum, intestinal bacteria play a role in keeping out unwanted intruders.

Mitochondria, Chloroplasts, and the Origin of Eukaryotic Cells

The most pervasive and perhaps enduring symbiotic venture has been the acquisition of mitochondria by animals and plants and of chloroplasts by plants. These organelles were once microbes. The origin of these symbioses, which happened a billion or so of years ago, led to a momentous event, the development of the eukaryotic cell. It has taken some time to confirm that cell organelles have a microbial origin because today they hardly resemble their ancestors (Figure - EMs). Most convincing has been finding that the DNA of mitochondria has homologies to that of rickettsiae, the bacterial agents of typhus. Interestingly, to this date rickettsiae remain strict intracellular parasites, although they are a long way from becoming mitochondria. Likewise, the DNA of chloroplasts is similar to that of photosynthetic cyanobacteria.

In both mitochondria and chloroplasts, many of the genes of the original microbes were transferred to the nucleus and others have been lost. Thus, these organelles have become very reduced from their original free-living status and far from capable of independence existence. Mitochondrial genomes usually code for a few dozen proteins, the chloroplast genome often for ten times that many. Some of the mitochondrial genes are for this organelle’s main function, oxidative metabolism. Chloroplasts genomes, in keeping with this theme, contain genes for photosynthesis.

Most of the genes for oxidative metabolism are not carried in the mitochondria but are nuclear and their protein products must be transported across the cytoplasm to the mitochondria. Although few in number, mitochondria-encoded proteins must be especially important because of the have conserved through the ages to a greater extent than the nuclear ones. This does not mean that mitochondrial genes are unchangeable. There are several congenital diseases that have been attributed to mutations in the mitochondrial genome. In fact, the mutation rate in mitochondria is quite high, possibly due to the lack of a proofreading function in their DNA replication machinery. However, the medical importance of such mutations is relatively small because most of these mutations take place in somatic cells and are not inherited. Plus, there are many mitochondria in one cell and a mutation in one may not have a large genetic effect. Mitochondrial genetics is colored by the fact that these organelles are inherited from the mother only - those of the sperm cells are degraded after fertilization. Therefore, inheritance of mitochondrial genes is not Mendelian but maternal.
These organelles reveal their microbial origin in various ways: their protein synthesis has a bacterial signature (they start the process with formylated methionine rather than with methionine as in eukaryotes), their ribosomes resemble those of bacteria (they are smaller than eukaryotic ones) and, like the ribosomes of bacteria, they are sensitive to antimicrobial antibiotics. Mitochondria also have circular chromosomes and no histones.

Mitochondria and chloroplasts are not the only ex-microbes to inhabit eukaryotic cells. Certain protists, such as the parasites that cause malaria, have structures called APICOPLASTS (Figure). These organelles are essential and their host cannot survive without them. They contain only enough DNA to encode for about 35 genes. This DNA is related to that of chloroplasts although apicoplasts reside in non-photosynthetic organisms. Apicoplasts then have functions different than photosynthesis, including the synthesis of fatty acids and the repair, replication, and transcription of their DNA. Apicoplasts seem to be the result of an ancient event whereby a eukaryotic ancestor acquired a chloroplast but converted it from a photosynthetic factory to one involved in other biochemical activities.

The topic of DNA-containing organelles has further surprises. Certain parasites, e.g., the trypanosomes that cause sleeping sickness or Chagas disease, tell an Alice-in-Wonderland-like story. These organisms have a unique DNA-containing organelle called the KINETOPLAST, which is a highly specialized mitochondrion located at the base of the cilium (also known as undulipodium) (Figure). Each cell contains a single kinetoplast. Kinetoplasts contain a mesh of interwoven DNA circles resembling the chain mall of medieval armor (Figure). The circles occur in two sizes: maxi and mini. Maxicircles are fewer in number – 20-50 per kinetoplast - as opposed by around 10,000 minicircles. Maxicircles resemble mitochondria because the proteins they encode are involved in energy production. Minicircle DNAs are much smaller (0.5-1.5 kilobases vs. 20-35 kilobases for the maxicircles) and are heterogeneous in sequence. The DNAs of the minicircles are not known to encode for proteins. Instead, the RNA they make, called guide RNA, is involved in editing of the regular messenger RNA. The origin of kinetoplasts is under investigation and some researchers favor a microbial endosymbiotic origin for these structures as well.

Two- or More-sided Relationships

Nitrogen-fixing Bacteria and the Legumes

Nitrogen gas is the most abundant element in our atmosphere but it is inert and cannot be directly used by living organisms for making their many nitrogen-containing compounds, such as amino acids, purines or pyrimidines. To be biologically available, nitrogen has to be reduced to ammonia, a form in which it can enter biosynthetic pathways. This process, the reduction of the molecule dinitrogen to an utilisable form, is called NITROGEN FIXATION.
IS TO NITROGEN AS PHOTOTROPHY AND LITHOTROPHY ARE TO CARBON. As in the case of carbon, not all organisms can reduce nitrogen and depend on those that do.

Most of nitrogen fixation in the environment is carried out by bacteria, some living free, others in association with plants. The biochemistry of nitrogen fixation is described in Chapter xx. Here, we deal only with nitrogen-fixing bacteria that are symbiotic with plants. This symbiosis is most readily demonstrable in legumes such as peas, alfalfa, and beans. When a legume is pulled up from the ground, the roots appear to be decorated with small granules, typically 1 mm in diameter, the so-called ROOT NODULES (Figure). Looking at a squashed or sectioned root nodule reveals that they are filled with bacteria-like bodies.

Root nodules are nitrogen-fixing factories. They require that a symbiotic relationship between the bacteria and the plant become established. Both partners contribute to nodule formation and both partners undergo crucial changes in the process. What are the steps in this association? The bacteria involved in nodule formation are soil dwelling members of the genus Rhizobium and related ones. Different species of bacteria are quite specific for their hosts, one for mustard plants, another for alfalfa, etc.

The process of nodule formation begins with the plant roots excreting compounds (flavonoids) that are sensed by the bacteria nearby. As the result, the bacteria are induced to express genes involved in nodulation (nod). The products of several nod genes work together to make NODULATION FACTORS, substances that signal to the plant to initiate nodule formation. Nodulation factors are fatty acids plus chitin-like compound and are very powerful. When applied at concentrations as low as $10^{-9}$ M, they can induce nodule formation even in the absence of the bacteria. Interestingly, the nod genes are carried on plasmids. The specificity of association between bacterial strains and certain plants is due to the genes on the plasmids and is altered when the plasmids are transferred to new bacterial hosts.

Nodule formation requires that the bacteria penetrate through the root hairs of the plant. The invasion process is unique in its details and represents a specialized form of bacterial penetration into a host. The first step is the binding of the bacteria to the root hairs, which requires the recognition between a ligand on the bacterial surface and a receptor on the host cell surface. Binding usually takes place at the tip of the root hairs, where the bacteria cause localized hydrolysis of the tough plant cell wall. This allows the organisms to invade the root hair cells. Soon, this leads to a morphological change in the hair roots, which now curl up to look like a shepherd’s crook (Figure of nodule formation). The internalized bacteria reside in intracellular vacuoles, much like certain animal pathogens that survive in vacuoles of phagocytes. Nodule formation requires that the bacteria move inwards, towards the root center. This is a difficult trip because the bacteria have to negotiate their way along tough cellulose-encased plant cells. Travel is facilitated by the plant forming a tube
(called INFECTIOUS THREAD) that stretches from the root hair to the root’s interior. The bacteria travel along this tube. When they arrive at a deep location, they exit the infectious thread and begin to proliferate. The plant cells responds to bacterial stimuli by rapidly proliferating into a tumor-like structure, the nodule. This host response to the bacteria requires a delicate balance because plants have defense mechanisms that would otherwise destroy the invading bacteria. Rhizobia and their relatives make capsules and, being Gram negative, possess lipopolysaccharides. Both these constituents are required for bacterial survival because mutants lacking them are destroyed after invasion.

Having arrived at their ultimate place of business, the bacteria differentiate into nitrogen fixation workshops. They become branched and swollen and are now called BACTEROIDS, (Figure). Before being able to fix nitrogen, the bacteria must address a last problem: nitrogen fixation is a highly anaerobic process but the plant roots are aerobic. Bacteroids produce an anaerobic environment by synthesizing a form of hemoglobin called leghemoglobin that absorbs the oxygen. Bacteroids are incapable of growth and are totally depended on the plant for nutrients. Thus, for their side of the bargain, bacteroids receive from the host organic acids that provide energy and the reducing power need for nitrogen fixation. In return, they provide assailable nitrogen to the host in the form of ammonia. This symbiotic relationship requires that both partners undergo profound biochemical and structural adaptations.

The Rumen and its Microbes

Animals cannot digest cellulose and some other plant polysaccharides directly, which is a major inconvenience for herbivores. Depending solely on plant material and not being able to use these polymers would be wasteful and inefficient. However, microbes in symbiotic relationship with plant-eating animals degrade these compounds and transform them into digestible products. This kind of symbiosis does not require major modification by the microbes, unlike nodule formation of legumes, but it does depend on the host providing a large chamber for the biochemical transformations to take place. There are two general ways to do this: Cattle, goats, and deer have such a chamber in front of their stomach called the RUMEN, which is why the animals ruminants. Non-ruminants such as horses, rabbits, and elephants, microbes carry out cellulose digestion in an extra-large large intestine.

Cellulose and other indigestible polymers are degraded in steps. The first step is the thorough grinding of plant material into small pieces and herbivores have teeth with flat apposing surfaces that are well suited to this task. To improve further on this, ruminants chew the cud, meaning that they regurgitate previously eaten food and re-chew it in order to reduce to even smaller bits. This permits these animals to eat rapidly and to process the food further at their leisure, away from predators.

The well-chewed plant particles now enter the rumen, a large segmented chamber that contains about 15 gallons of liquid in cattle. Here diverse groups of
CELLULOYLTIC MICROBES degrade cellulose into sugars. Other bacteria then ferment the sugars to yield VOLATILE FATTY ACIDS, such as acetic, propionic, and butyric. The rumen is highly anaerobic, which is why sugars cannot be oxidized entirely to carbon dioxide via respiration, leading to the accumulation of fermentation products. Ruminants absorb the fatty acids through the epithelium of the rumen and use them for their metabolic needs (unlike non-ruminants, who use glucose). The pH of the rumen does not drop perceptibly with acid production because ruminants secrete prodigious amounts of well-buffered saliva, 25 gallons and more a day per cow. A large amount of fatty acids is made, which accounts for the high efficiency of cattle in milk and meat production and the worldwide distribution of ruminant species. The microbes in the rumen, however, provide carbon sources only. How do ruminants obtain their nitrogen? The answer is, from the rumen microbes themselves. Once the rumen content is emptied into the stomach, the microbial cells are killed by the acid and are then degraded by digestive enzymes. Many of the bacteria are broken down by a cell-wall-degrading lysozyme that, uniquely in ruminants and befitting its site of action, is acid resistant. There is little, then that ruminants do use from their feed.

In non-ruminant herbivores, cellulose degradation takes place in the large intestine. Here, the microbes are not recycled as efficiently as in the rumen but are passed into the feces, which accounts for the fact that many of these animals, e.g., rabbits and rats, are coprophagic, that is, they eat their highly nutritional feces.

The rumen contains a large culture of different kinds of bacteria, protozoa, and fungi that are constantly being renewed. A cow could therefore be called a walking continuous culture device. The rumen microbes include a highly diverse group of organisms. Bacteria are by far the most numerous (as many as \(10^{10}\) per ml) and include over 200 species. Protozoa make up almost half the total microbial load by weight but, being larger, are present in smaller numbers. Although protozoa are also involved in cellulose degradation, they also prey on the bacteria and may have a negative influence on the overall fermentation, a still controversial point.

The biochemical transformation of cellulose to fatty acids and carbon dioxide requires the workings of a FOOD CHAIN, starting with cellulose degradation and ending with the fermentation of sugars. The final process, making volatile fatty acids results in the production of large amounts of hydrogen. If hydrogen were to accumulate under the highly anaerobic conditions of the rumen, it would inhibit further fermentation. Here’s why: the formation of acetate from pyruvate is energetically unfavorable and would not take place appreciably unless the concentration of products of the reaction is decreased. Removing one of the products, hydrogen, then allows a thermodynamically unfavorable reaction to proceed. How is hydrogen removed from the rumen? The biota of the rumen includes some METHANOGENS, archaeal species that can use hydrogen and carbon dioxide to make methane. Being quite insoluble, methane becomes a gas that can be expelled by eructation. This can be demonstrated by carefully holding a lit match away from a belching cow and seeing a small flame appearing. Removing
hydrogen allows fermentation to proceed efficiently. The removal of hydrogen by the methanogens results in the synthesis of more microbial cells, which increases available protein to the ruminant.

The rumen and its microbes represent a particularly intricate set of relationships both between host symbionts and among the symbiotic microbes themselves. This can be expected because utilizing the complexity of the food eaten by ruminants requires such a large number of biochemical activities that they could not be contained in a single species. No wonder the microbes of the rumen are highly varied and specialized.

**Feeding Via A Murderous Partnership – Bacteria and Nematodes**

In some instances two organisms gang up in order to kill a third one. Nematodes - small roundworms about 1 mm long - are abundant in soils and varied in their feeding habits. One of them, *Caenorhabditis elegans*, has acquired prominence as a model system for the study of differentiation and other major biological phenomena. Some nematodes live on a diet of plants, others on fungi or bacteria. One kind of nematodes feed by burrowing into the caterpillars of certain insects. As the result of this invasion, the caterpillars are killed; the nematodes reproduce and eventually leave the caterpillar’s carcass. The worms do not feed or reproduce in the soil, thus they must parasitize insects in order to survive. The worms cannot carry this life cycle alone but require the help of certain bacteria in a symbiotic relationship. Without the bacteria, the nematodes would be destroyed by the insects. What the bacteria do is kill the insect host and disable its defense mechanisms.

Inside the nematodes, the bacteria are contained in their host’s digestive system. When the worm penetrates a caterpillar, the bacteria exit the worm and produce toxins that kill the insect. One of these toxins is known to cause apoptosis in the insect’s gut epithelial cells, leading to loss of turgor. The caterpillars now look floppy and the toxin is called Mcf (“makes caterpillar floppy”). The bacteria secrete hydrolases that break down the insect’s tissues, which provides a rich soup of nutrients needed by the worms. Once they have fed, the worms can mate and reproduce. After two weeks or so, the nematodes exit what is left of the caterpillar’s body, but not before picking up their symbiotic bacteria. The process may last as long as two weeks. How come the carcass of the caterpillar has not putrefied during that period? This calls into play another fiendish-sounding maneuver by the bacteria – they make powerful antibiotics that kill other kinds of bacteria. The dead caterpillar, therefore, becomes a sepulchral chamber that contains the reproducing nematodes and one kind of bacteria mainly, the worm’s symbionts.
This conspiracy to commit murder constitutes a true symbiotic relationship between worms and bacteria because neither partner subsists in the soil alone. Even though the bacteria involved can grow on ordinary laboratory media, they have not been found free in the soil. The worms, then, provide the bacteria with shelter and transportation, the bacteria make food available to the worms.

An aside: some of the bacteria (*Photorhabdus luminescens* and others) involved in this symbiosis are bioluminescent. It is not know why they emit light, although it has been speculated that this may serve to attract the worms to them. Some of these bacteria can also cause wound infection in people. In the darkness of the trenches of World War 1, the infected tissues were actually seen to glow. Experienced physicians took this to be a good omen because luminous wounds were likely to heal fast. Was this due to the production of antibiotics by the bacteria, which could keep out more powerful invaders? Given the better lighting in modern hospitals, this diagnosis is likely to be missed.

**Leaf-cutting Ants, Fungi, and Bacteria**

In tropical and subtropical America, from Argentina to the southern United States, there are ants that subsist solely on the fungi they grow. These ants make huge underground nests, to which they bring pieces of leaves, flowers, and other organic materials to construct elaborate fungus gardens. In cross-section, the fungus gardens can be seen as whitish, irregular masses that almost fill the large cavity of the nest. To grow these gardens, various agricultural chores are divided among members of the different castes. The larger workers gather sections of leaves, often half an inch across, and carry them in long and fast-moving processions to their nest. The ants effortlessly carry a burden that to a human would be as heavy and awkward to carry as a large plywood panel. Given this industrious dedication to gathering leaves, it is not surprising that early observers thought that the leaves themselves were the food for the ants. It took considerable investigation to find out that the plant material only serves as a growth medium for the real foodstuff, the fungi.

Some species of leaf-cutting ants leave trails of denuded earth between their nest and the source of vegetation. These clear trails can reach astonishing dimensions, over six hundred feet in length and twelve inches in width. The amount of coming and going is remarkable, often resulting in traffic jams where the outbound and inbound individuals must literally climb on top of one another (a technique that has yet to be developed for the cars on California freeways). At the nest, the larger workers carry out an elaborate composting operation. The leafy pieces are cut into smaller sizes, licked thoroughly, and mixed with fecal material. Using their mandibles, legs, and antennae, the ants then knead them into tiny juicy balls. This pulpy material is carefully deposited at the edge of the garden and jabbed into place. It is then “seeded” with the mycelium from the older sections of the garden. The garden rapidly becomes permeated with new filaments. The fungal surface consists of aggregates of hyphal tips that end in roundish bodies.
Leaf-cutting antshave received very bad press because of the damage they cause to vegetation and the threat they constitute to cultivated crops, such as coffee and cacao. They are, in fact, the dominant herbivores in the American tropics. In Brazil, the saúva, the local name for these ants, inspired an old saying: “Either Brazil gets rid of the saúva, or the saúva gets rid of Brazil.” In partial defense of the ants, it should be mentioned that they do not completely defoliate the plants on which they feed. In addition, the spent litter from the fungus gardens, still rich in organic matter, is returned to the environment where it serves as plant fertilizer. Typically, this material is carried up the trunk of a tree or over vines and allowed to drop to the ground. The ants of one nest have been observed to carry the waste to a smooth rock and allow it to tumble down the slope.

The relationship appears to be remarkably old, dating perhaps to fifty million years. When the more specialized groups of ants selected a given fungus as a favorite crop, they remained with it for eons. Comparing the ribosomal RNA of different species of ants and their fungi, researchers learned that once the symbiotic relationship was established, the two partners remained true to each other over the eons.

There is more to this story. How come only the desired fungi growing the fungus gardens? There are other fungi that can grow on such a substrate but only one kind predominates – a monoculture. The answer is that these ants carry on their body a bacterium of the genus Streptomyces that makes antibiotics that inhibit a common fungal invader. This then is a three-way symbiosis between ants, fungi, and bacteria. Note that the ants made use of antibiotics agents some 50 million years earlier than humans.

**One-sided Relationships**

The range of interactions ranges from beneficial symbioses to deleterious forms of parasitism. The chapters on pathogenesis deal with the latter in their classical manifestations. There are, however, other nuances in the interaction between living organisms, some of which quite startling. For example, the behavior of animals and plants may be altered significantly by their interaction with microbes. A few examples of such manipulations will do better than definitions.

**Reckless Rats and Fatal Attraction**

Rats infected with a parasite lose their fear of cats. This suicidal change from the normal behavior is due the infection by the protozoan Toxoplasma gondii. This may make little sense for the rat but it does make sense for the parasite.
Understanding why requires knowing about the life cycle of *T. gondii*. Both rats and other rodents and cats are involved, with people being incidental hosts. In the cat’s intestine, the protozoan reproduces and eventually makes tough environmental forms called **oocysts** that are eliminated through the feces. Oocysts survive in the soil for long times where they may be picked up orally by rodents. Once in the rat, the agents reproduce and induce a strong immune response. To withstand it, *T. gondii* make resistant forms that remain dormant in the rat’s tissue and usually cause no further damage. Similar events take place when people ingest *T. gondii* oocysts. This would seem to be a dead end of the parasite. However, when an infected rat happens to be eaten by a cat, the parasites reproduce in the cat’s intestine and are eventually shed in the feces to start the cycle anew. Thus, the capture and ingestion of rodents by cats is an essential aspect of the parasite’s life cycle.

Using outdoor pens, researchers compared the reaction of normal and infected rats to cats’ urine. Normal rats, not surprisingly, were highly averse to the cats’ scent, as if knowing what is good for them. Infected rats, on the other hand, appeared to have lost this inhibition. In fact, they even seemed to be attracted to their nemesis’ scent. Such behavior would hardly be to the rats’ advantage, but it certainly helps the parasites complete their life cycle. The significance of this finding had not been confirmed in field studies, but the implications remain intriguing.

**The Urge to Climb**

Certain ants that live on the forest floor show drastic changes in their behavior when infected by fungi. The invading fungi develop slowly enough for the infected ants to stay alive and active for some time but to be altered in their deportment: they acquire the urge to climb up the stalks of vegetation and trees. When they have reached a certain height, they impale themselves with their mandibles and remain perched aloft for the rest of their life and thereafter. Other insect groups, grasshoppers, locusts, aphids, and flies, also exhibit this so-called “summit disease.” The fungi then grow and develop fruiting bodies filled with spores (**Figure**). The spores can now be dispersed from on high, possibly to be carried over great distances.

The reason given for the ants’ urge to climb depends on one’s tolerance for teleology. “Because it’s there” won’t do, but claiming that the fungus makes the insect climb for its own benefit is also seen with suspicion by some researchers. Clearly, remaining on the forest floor decreases the chances for aerial spore dispersal. However, getting off the forest floor means that infected insects are exposed to sunlight, therefore warming up to temperatures deleterious to the fungi. In the words of the entomologist R.A. Humber, “this is a behavior quite analogous to your heading for a warm bed and constant supply of chicken soup when feeling sick.” In addition, the infected insect may climb for altruistic reasons, namely to avoid infecting other members of its colony. Indeed, certain other insects exhibit the opposite behavior when infected by fungi. When infected by
fungi, larvae of certain butterflies and moths crawl into inaccessible spaces such as crevices or beneath tree bark, as if to get away from their kin. Such fungi must develop long stalks on their fruiting body to be able to spread their spores. Whatever the reason, the interplay of signals between the fungus and the insects seems extraordinary. Is there a mechanism that keeps the fungus from growing until the insect reaches a certain distance above the ground? What makes the insects develop the urge to climb up a tree? Who gains and who loses?

**How Locusts Swarm**

Swarms of locust, well known since Biblical times, consist of prodigious numbers of individuals. The damage they can cause is huge. In a 1948 episode in Ethiopia, the insects destroyed enough cereals to feed one million people for a year. Biological and chemical control measure have cut the damage but have not eliminated it, thus there is considerable interest in further research on locusts.

Locusts have two phases, a sluggish solitary one and a gregarious one capable of aggregating and swarming. The switch is triggered by a number of factors: “gregarization” and eventual swarm formation involve chemical communication between the insects via pheromones. In very small concentrations, pheromones are “smelled” by most insects to induce many essential functions such as mating. Such compounds are also required for some of the steps in gregarization. One may think that such pheromones are just “locust talk,” but it turns out that some of the signals are made by the bacteria. These pheromones are phenolic compounds manufactured by a species of bacteria that inhabit the digestive tract of these insects. How has this been determined? Axenic (bacteria free) locusts that were reared in a sterile environment from surface-sterilized eggs did not produce the pheromones. The introduction of bacteria normally found in the locusts’ gut reestablished the production of these compounds. Thus, the bacteria are needed for the change in the locusts’ behavior from solitary to swarming forms.

**When Is a Flower Not a Flower?**

For tweaking the host into making a new and elaborate structure, the prize goes to a rust fungus, *Puccinia monoica*. This species infects wild plants of the mustard family and induces them to develop dense clusters of leaves at the tips of stems. These rosettes of leaves look like the petals of a real flower, all the more so because they become covered with fungal growth (Figure). The surface becomes sticky and sweet smelling. These pseudoflowers, as they are called, are of a beautiful yellow color, different from that of the normal flowers of this plant but similar to those of other plants that grow in the same area. Insects arrive, with pollen on their agenda, and poke around the pseudoflower, collecting fungal spores instead of the desired pollen. And off they go, spreading spores to other plants. As seen in the
photograph, the impersonation is nearly faultless and at a distance has fooled even professional botanists.