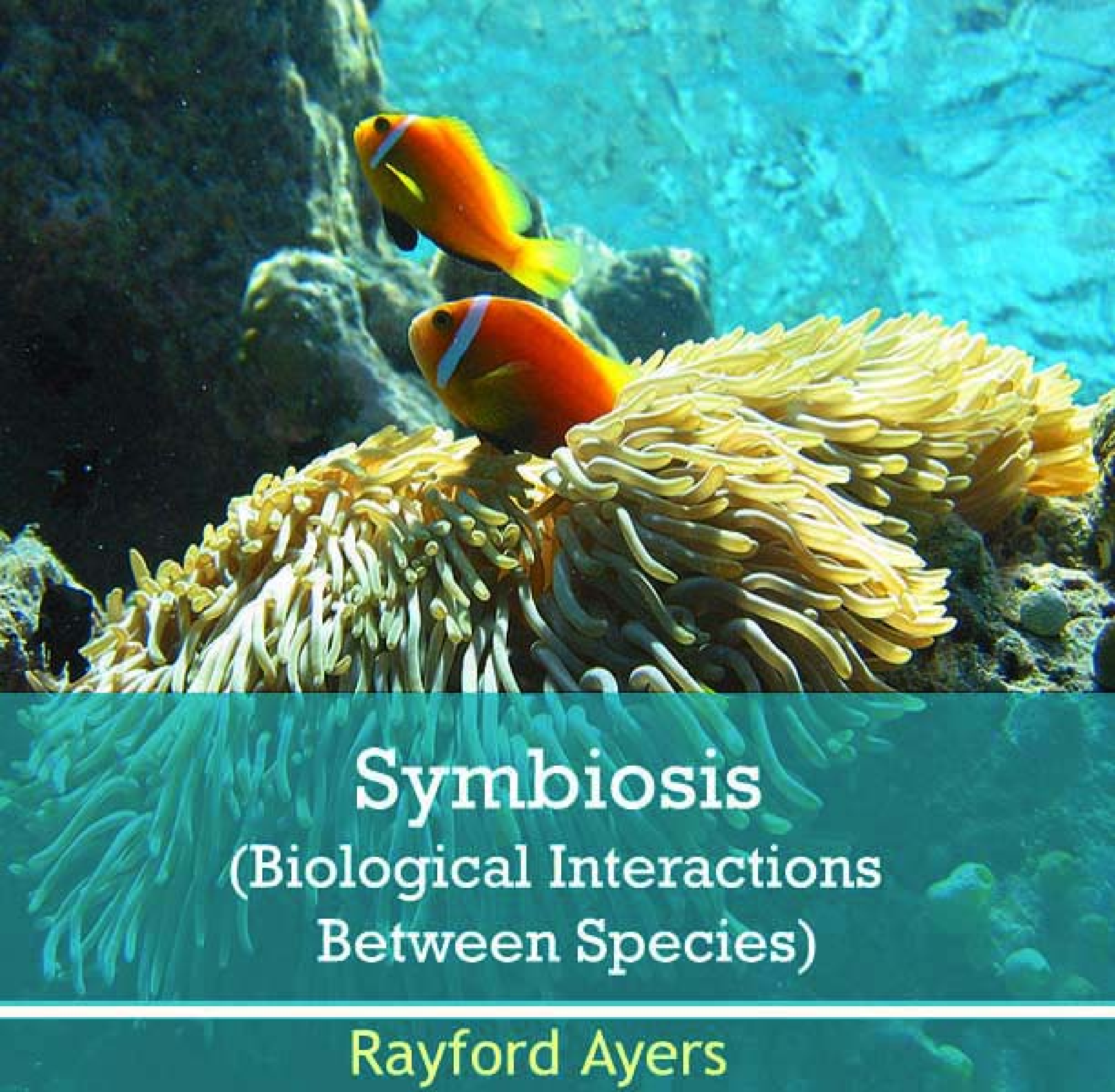

Symbiosis
(Biological Interactions Between Species)

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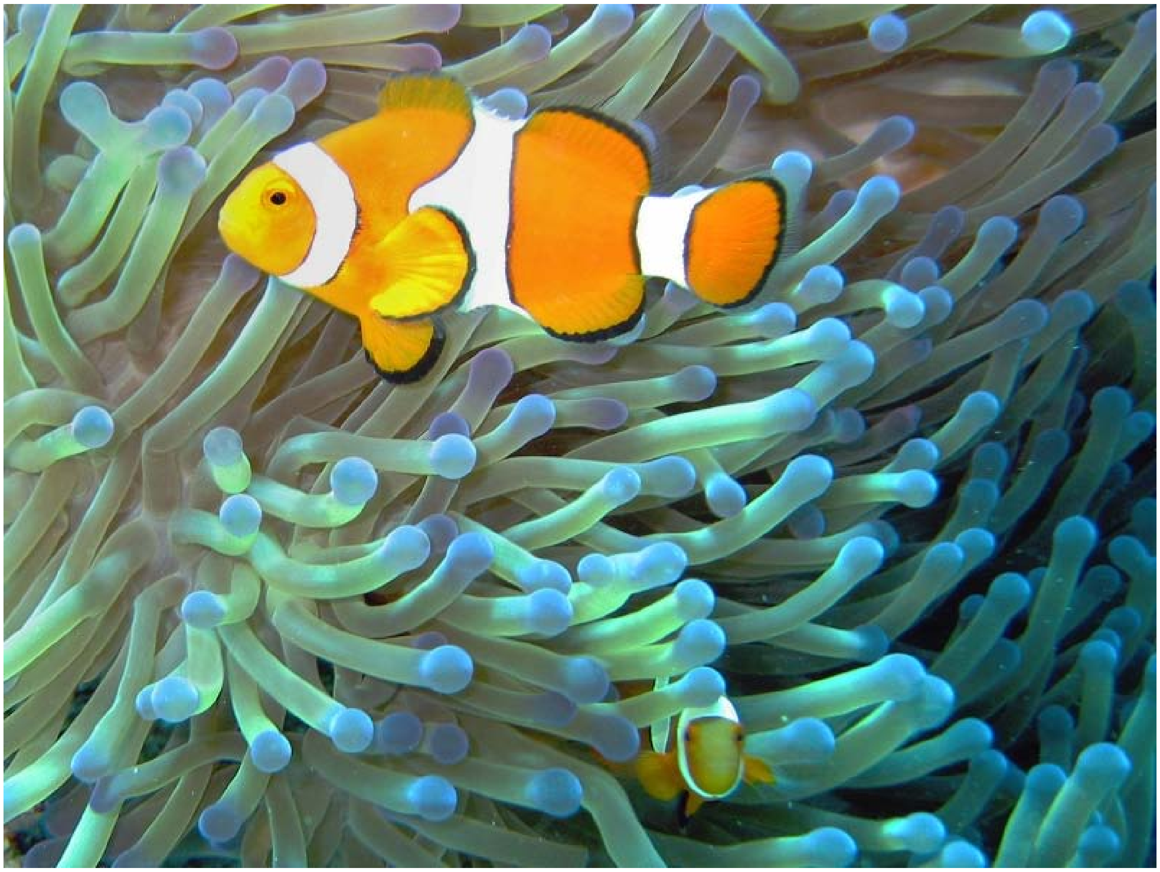
Symbiosis



In a symbiotic mutualism, the clownfish feeds on small invertebrates which otherwise potentially could harm the sea anemone, and the fecal matter from the clownfish provides nutrients to the sea anemone. The clownfish is additionally protected from predators by the anemone's stinging cells, to which the clownfish is immune.

Symbiosis is close and often long-term interactions between different biological species. In 1877 Bennett used the word symbiosis (which previously had been used of people living together in community) to describe the mutualistic relationship in lichens. In 1879 by the German mycologist Heinrich Anton de Bary, defined it as "the living together of unlike organisms."

The definition of symbiosis is in flux, and the term has been applied to a wide range of biological interactions. The symbiotic relationship may be categorized as mutualistic, commensal, or parasitic in nature.

Some symbiotic relationships are obligate, meaning that both symbionts entirely depend on each other for survival. For example, many lichens consist of fungal and photosynthetic symbionts that cannot live on their own. Others are facultative, meaning that they can but do not have to live with the other organism.

Symbiotic relationships include those associations in which one organism lives on another (ectosymbiosis, such as mistletoe), or where one partner lives inside the other (endosymbiosis, such as lactobacilli and other bacteria in humans or zooxanthelles in corals).

Physical interaction

Alder tree root nodule

Endosymbiosis is any symbiotic relationship in which one symbiont lives within the tissues of the other, either in the intracellular space or extracellularly. Examples are rhizobia, nitrogen-fixing bacteria that live in root nodules on legume roots; actinomycete nitrogen-fixing bacteria called *Frankia*, which live in alder tree root nodules; single-celled algae inside reef-building corals; and bacterial endosymbionts that provide essential nutrients to about 10%–15% of insects.

Ectosymbiosis, also referred to as *exosymbiosis*, is any symbiotic relationship in which the symbiont lives on the body surface of the host, including the inner surface of the digestive tract or the ducts of exocrine glands. Examples of this include ectoparasites such as lice, commensal ectosymbionts such as the barnacles that attach themselves to the jaw of baleen whales, and mutualist ectosymbionts such as cleaner fish.

Mutualism

Hermit crab, *Calcinus laevimanus*, with sea anemone.

Mutualism is any relationship between individuals of different species where both individuals derive a benefit. Generally, only lifelong interactions involving close physical and biochemical contact can properly be considered symbiotic. Mutualistic relationships may be either obligate for both species, obligate for one but facultative for the other, or facultative for both. Many biologists restrict the definition of symbiosis to close mutualist relationships.

A large percentage of herbivores have mutualistic gut fauna that help them digest plant matter, which is more difficult to digest than animal prey. Coral reefs are the result of mutualisms between coral organisms and various types of algae that live inside them. Most land plants and land ecosystems rely on mutualisms between the plants, which fix carbon from the air, and mycorrhyzal fungi, which help in extracting minerals from the ground.

An example of mutual symbiosis is the relationship between the ocellaris clownfish that dwell among the tentacles of Ritteri sea anemones. The territorial fish protects the anemone from anemone-eating fish, and in turn the stinging tentacles of the anemone protect the clownfish from its predators. A special mucus on the clownfish protects it from the stinging tentacles.

Another example is the goby fish, which sometimes lives together with a shrimp. The shrimp digs and cleans up a burrow in the sand in which both the shrimp and the goby fish live. The shrimp is almost blind, leaving it vulnerable to predators when above ground. In case of danger the goby fish touches the shrimp with its tail to warn it. When that happens both the shrimp and goby fish quickly retract into the burrow.

One of the most spectacular examples of obligate mutualism is between the siboglinid tube worms and symbiotic bacteria that live at hydrothermal vents and cold seeps. The worm has no digestive tract and is wholly reliant on its internal symbionts for nutrition. The bacteria oxidize either hydrogen sulfide or methane which the host supplies to them. These worms were discovered in the late 1980s at the hydrothermal vents near the Galapagos Islands and have since been found at deep-sea hydrothermal vents and cold seeps in all of the world's oceans.

There are also many types of tropical and sub-tropical ants that have evolved very complex relationships with certain tree species.

Commensalism

Phoretic mites on a fly (*Pseudolynchia canariensis*).

Commensalism describes a relationship between two living organisms where one benefits and the other is not significantly harmed or helped. It is derived from the English word commensal used of human social interaction. The word derives from the medieval Latin word, formed from *com-* and *mensa*, meaning "sharing a table".

Commensal relationships may involve one organism using another for transportation (phoresy) or for housing (inquilinism), or it may also involve one organism using something another created, after its death (metabiosis). Examples of metabiosis are hermit crabs using gastropod shells to protect their bodies and spiders building their webs on plants.

Parasitism

Flea bites on a human is an example of parasitism (the flea as parasite to the human host in this case).

A parasitic relationship is one in which one member of the association benefits while the other is harmed. Parasitic symbioses take many forms, from endoparasites that live within the host's body to ectoparasites that live on its surface. In addition, parasites may be necrotrophic, which is to say they kill their host, or biotrophic, meaning they rely on their host's surviving. Biotrophic parasitism is an extremely successful mode of life. Depending on the definition used, as many as half of all animals have at least one parasitic phase in their life cycles, and it is also frequent in plants and fungi. Moreover, almost all free-living animals are host to one or more parasite taxa. An example of a biotrophic relationship would be a tick feeding on the blood of its host.

Amensalism

Amensalism is the type of symbiotic relationship that exists where one species is inhibited or completely obliterated and one is unaffected. This type of symbiosis is relatively uncommon in rudimentary reference texts, but is omnipresent in the natural world. An example is a sapling growing under the shadow of a mature tree. The mature tree can begin to rob the sapling of necessary sunlight and, if the mature tree is very large, it can take up rainwater and deplete soil nutrients. Throughout the process the mature tree is unaffected. Indeed, if the sapling dies, the mature tree gains nutrients from the decaying sapling. Note that these nutrients become available because of the sapling's decomposition, rather than from the living sapling, which would be a case of parasitism.

Symbiosis and evolution

Leafhoppers protected by an army of meat ants

While historically, symbiosis has received less attention than other interactions such as predation or competition, it is increasingly recognised as an important selective force behind evolution, with many species having a long history of interdependent co-evolution. In fact, the evolution of all eukaryotes (plants, animals, fungi, and protists) is believed under the endosymbiotic theory to have resulted from a symbiosis between various sorts of bacteria.

Vascular Plants

Up to 80% of vascular plants worldwide form symbiotic relationships with fungi, for example, in arbuscular mycorrhiza.

Symbiogenesis

The biologist Lynn Margulis, famous for her work on endosymbiosis, contends that symbiosis is a major driving force behind evolution. She considers Darwin's notion of evolution, driven by competition, as incomplete and claims that evolution is strongly based on co-operation, interaction, and mutual dependence among organisms. According to Margulis and Dorion Sagan, "Life did not take over the globe by combat, but by networking."

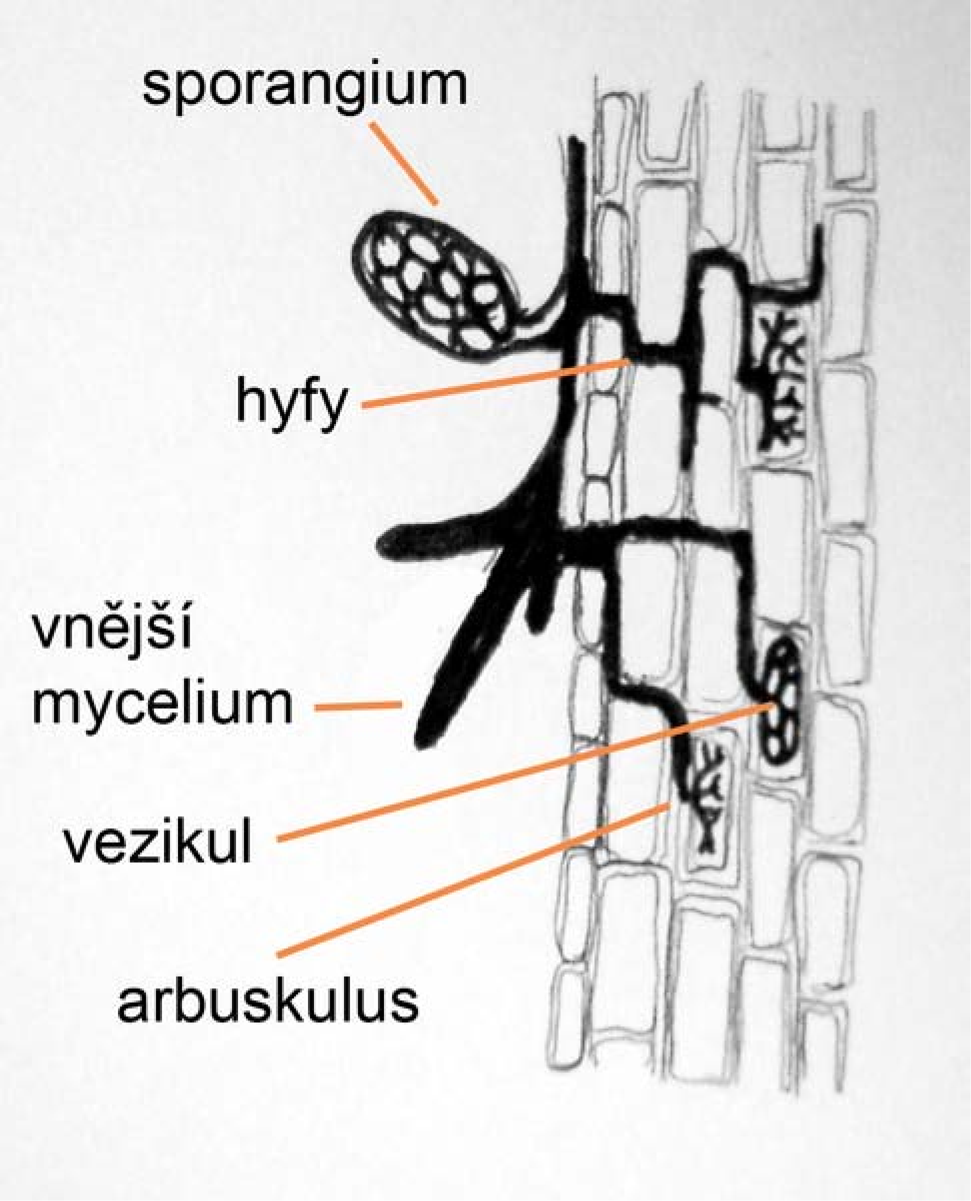
Co-evolution

Symbiosis played a major role in the co-evolution of flowering plants and the animals that pollinate them. Many plants that are pollinated by insects, bats, or birds have highly specialized flowers modified to promote pollination by a specific pollinator that is also correspondingly adapted. The first flowering plants in the fossil record had relatively simple flowers. Adaptive speciation quickly gave rise to many diverse groups of plants, and, at the same time, corresponding speciation occurred in certain insect groups. Some groups of plants developed nectar and large sticky pollen, while insects evolved more specialized morphologies to access and collect these rich food sources. In some taxa of plants and insects the relationship has become dependent, where the plant species can only be pollinated by one species of insect.

Chapter 2

Mutualism (Biology)

Hummingbird Hawkmoth drinking from *Dianthus*. Pollination is a classic example of mutualism.



Arbuscular mycorrhiza

Mutualism is the way two organisms biologically interact where each individual derives a fitness benefit (i.e. increased reproductive output). Similar interactions within a species are known as co-operation. It can be contrasted with interspecific competition, in which each species experiences *reduced* fitness, and exploitation, or parasitism, in which one species benefits at the *expense* of the other. Mutualism and symbiosis are sometimes used as if they are synonymous, but this is strictly incorrect: symbiosis is a broad category, defined to include relationships which are mutualistic, parasitic or commensal. Mutualism is only one *type*.

A well known example of mutualism is the relationship between ungulates (such as cows) and bacteria within their intestines. The ungulates benefit from the cellulase produced by the bacteria, which facilitates digestion; the bacteria benefit from having a stable supply of nutrients in the host environment.

Mutualism plays a key part in ecology. For example, mutualistic interactions are vital for terrestrial ecosystem function as more than 48% of land plants rely on mycorrhizal relationships with fungi to provide them with inorganic compounds and trace elements.

In addition, mutualism is thought to have driven the evolution of much of the biological diversity we see, such as flower forms (important for pollination mutualisms) and co-evolution between groups of species. However mutualism has historically received less attention than other interactions such as predation and parasitism.

Measuring the exact fitness benefit to the individuals is not always straightforward, particularly when the individuals can receive benefits from a range of species, for example most plant-pollinator mutualisms. It is therefore common to categorise mutualisms according to the closeness of the association, using terms such as obligate versus facultative. Defining "closeness," however, is also problematic. It can refer to mutual dependency (the species cannot live without one another) or the biological intimacy of the relationship in relation to physical closeness (e.g. one species living within the tissues of the other species).

Types of relationships

Mutualistic transversals can be thought of as a form of "biological barter" in which species trade resources (for example carbohydrates or inorganic compounds) or services such as gamete, offspring dispersal, or protection from predators.

Resource-resource relationships

Resource-resource interactions, in which one type of resource is traded for a different resource, are probably the most common form of mutualism; for example mycorrhizal associations between plant roots and fungi, with the plant providing carbohydrates to the fungus in return for primarily phosphate but also nitrogenous compounds. Other examples include rhizobia bacteria which fix nitrogen for leguminous plants (family Fabaceae) in return for energy-containing carbohydrates.

Service-resource relationships

The Red-billed Oxpecker eats ticks on the impala's coat

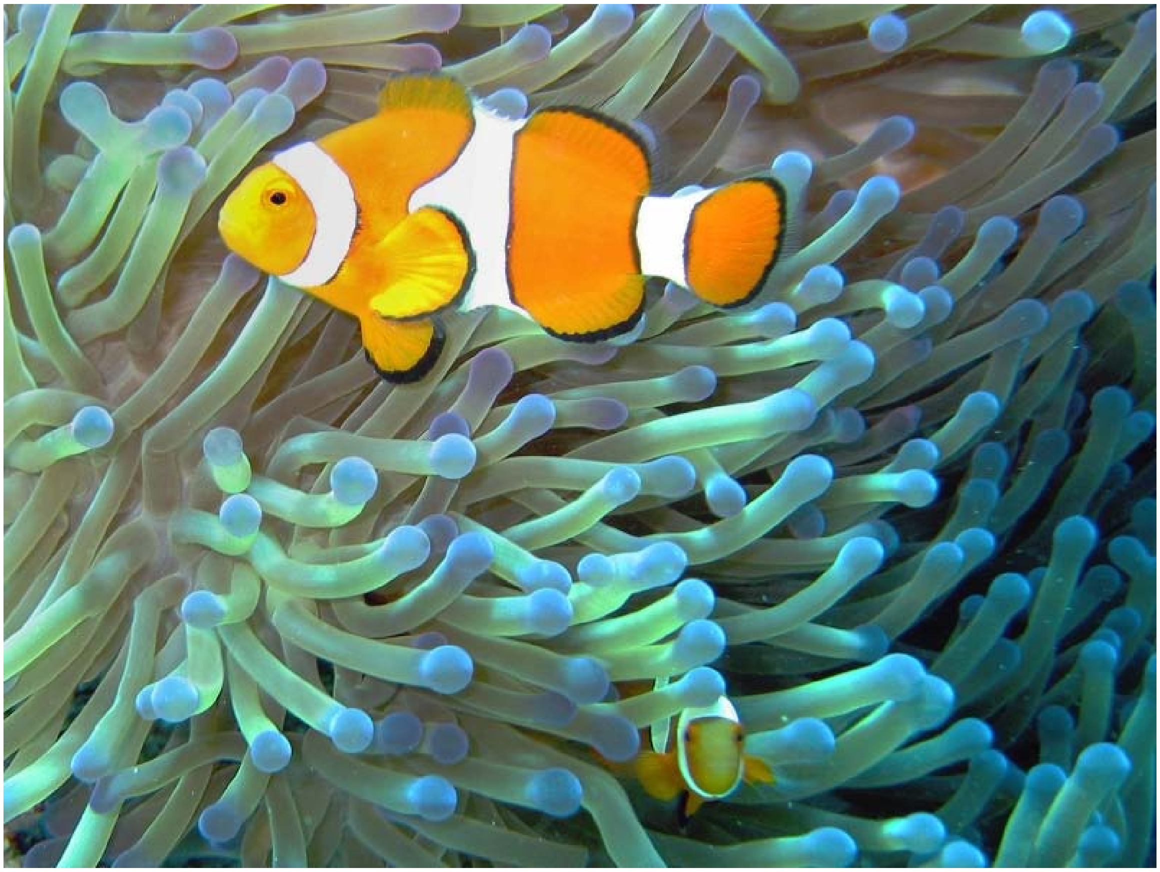
Service-resource relationships are also common.

Pollination in which nectar or pollen (food resources) are traded for pollen dispersal (a service) or ant protection of aphids, where the aphids trade sugar-rich honeydew (a by-product of their mode of feeding on plant sap) in return for defense against predators such as ladybird beetles.

Phagophiles feed (resource) on ectoparasites, thereby providing anti-pest service.

Zoochory is an example where animals disperse the seeds of plants. This is similar to pollination in that the plant produces food resources (for example, fleshy fruit, overabundance of seeds) for animals that disperse the seeds (service).

Service-service relationships



An example of mutual symbiosis is the relationship between Ocellaris clownfish that dwell among the tentacles of Ritteri sea anemones.

Strict service-service interactions are very rare, for reasons that are far from clear. One example is the relationship between sea anemones and anemonefish in the family Pomacentridae: the anemones provide the fish with protection from predators (which cannot tolerate the stings of the anemone's tentacles) and the fish defend the anemones against butterflyfish (family Chaetodontidae) which eat anemones. However, in common with many mutualisms, there is more than one aspect to it: in the anemonefish-anemone mutualism, waste ammonia from the fish feed the symbiotic algae that are found in the anemone's tentacles. Therefore what appears to be a service-service mutualism in fact has a service-resource component. A second example is that of the relationship between some ants in the genus *Pseudomyrmex* and trees in the genus *Acacia*, such as the Whistling Thorn and Bullhorn Acacia. The ants nest inside the plant's thorns. In exchange for shelter, the ants protect acacias from attack by herbivores (which they frequently eat, introducing a resource component to this service-service relationship) and competition from other plants by trimming back vegetation that would shade the acacia. In addition, another service-resource component is present, as the ants regularly feed on lipid-rich food-bodies called Beltian bodies that are on the *Acacia* plant.

In the Neotropics, the ant, *Myrmelachista schumanni* makes its nest in special cavities in *Duroia hirsute*. Plants in the vicinity which belong to other species are killed with formic acid. This selective gardening can be so aggressive that small areas of the rainforest are dominated by *Duroia hirsute*. These peculiar patches are known by local people as "devil's gardens".

In some of these relationships, the cost of the ant’s protection can be quite expensive. *Cordia* sp. trees in the Amazonian rainforest have a kind of partnership with *Allomerus* sp. ants, which make their nests in modified leaves. To increase the amount of living space available, the ants will destroy the tree’s flower buds. The flowers die and leaves develop instead, provisioning the ants with more dwellings. Another type of *Allomerus* sp. ant lives with the *Hirtella* sp. tree in the same forests, but in this relationship the tree has turned the tables on the greedy ants. When the tree is ready to produce flowers, the ant abodes on certain branches begin to wither and shrink, forcing the occupants to flee, leaving the tree’s flowers to develop free from ant attack.

Humans and mutualism

Dogs and sheep were among the first animals to be domesticated.

Humans also engage in mutualisms with other species, including their gut flora (without which they would not be able to digest food efficiently) and domesticated animals such as horses, which provide transportation in return for food and shelter. In traditional agriculture, many plants will function mutualistically as companion plants, providing each other with shelter, soil fertility and the repelling of pests. For example, beans may grow up cornstalks as a trellis, while fixing nitrogen in the soil for the corn, as exploited in the Three Sisters gardening technique.

Mathematical theory

In 1989, David Hamilton Wright developed a mathematical explanation for mutualism using the Lotka–Volterra equation. Wright modified the Lotka-Volterra equations by adding a new term, $\beta M/K$, to represent a mutualistic relationship.

The mutalistic relationship is quantified by:

$dN/dt = r_1 N(1 - N/K1 + \beta_{12} M/K_1)$

$dM/dt = r_2 M (1 - M/K2 + \beta_{21} N/K_2)$

where,

- N and M = the population density
- r = intrinsic growth rate of the population
- K = carrying capacity of its local environmental setting.
- β = coefficient converting encounters with one species to new units of the other

Mutualism is essentially the logistic growth equation + mutualistic interaction. The mutualistic interaction term represents the increase in population growth of species one as a result of the presence of greater numbers of species two, and vice versa. Wright also considered the concept of saturation, which means that with higher densities, there are decreasing benefits of further increases of the mutualist population. Without saturation, species' densities would increase indefinitely. Because that isn't possible due to environmental constraints and carrying capacity, a model that includes saturation would be more accurate. Wright's mathematical theory is based on the premise of a simple two-species mutualism model in which the benefits of mutualism become saturated due to limits posed by handling time. Wright defines handling time as the time needed to process a food item, from the initial interaction to the start of a search for new food items and assumes that processing of food and searching for food are mutually exclusive. Mutualists that display foraging behavior are exposed to the restrictions on handling time. Mutualism can be associated with symbiosis

Type II functional response

In 1959, C. S. Holling performed his classic disc experiment that assumed the following: that (1), the number of food items captured is proportional to the allotted searching time; and (2), that there is a variable of handling time that exists separately from the notion of search time. He then developed an equation for the Type II functional response, which showed that the feeding rate is equivalent to

$ax/(1 + axT_H)$.

where,

- a = the instantaneous discovery rate
- x = food item density
- T_H = handling time

The equation that incorporates Type II functional response and mutualism is:

$dN/dt = N [r(1-cN) + \beta M(X+M)]$

where,

- N and M = density of the two mutualists
- r = intrinsic rate of increase of N
- c = coefficient measuring negative intraspecific interaction
- $X = 1/a\ T_H$
- $\beta = b/\ T_H$
- a = instantaneous discovery rate
- b = coefficient converting encounters with M to new units of N

Rearranged: $dN/dt = N[r(1-cN) + baM/(1+aT_HM)]$

These two graphs show the isoclines of mutualistic relationships. Presence of the mutualist has a positive effect on the recipient population at low densities of mutualists but at high densities, saturation takes place, and further increases in mutualist populations have little effect. Arrows indicate the stability or instability of equilibrium points.

Graph A illustrates a facultative mutualism in which both species derive benefits from each other, but do not depend on the existence of the other for survival.

Graph B demonstrates an obligate mutualism in which both species are interdependent on each other in a way that one species cannot survive without the other. Once the population of one species drops below the first equilibrium point, both populations will go extinct.

The model presented above is most effectively applied to free-living species that encounter a number of individuals of the mutualist part in the course of their existences. Of note, as Wright points out, is that models of biological mutualism tend to be similar qualitatively, in that the featured isoclines generally have a positive decreasing slope, and by and large similar isocline diagrams. Mutualistic interactions are best visualized as positively sloped isoclines, which can be explained by the fact that the saturation of benefits accorded to mutualism or restrictions posed by outside factors contribute to a decreasing slope.

Chapter 3

Commensalism

The cattle egret, *Bubulcus ibis*, is a classic example of commensalism. It forages in fields among cattle and horses, feeding on insects stirred up by the grazing animals. The egret benefits from this relationship, while the livestock are typically unaffected by it.

In ecology, **commensalism** is a class of relationship between two organisms where one organism benefits but the other is neutral (there is no harm or benefit). There are three other types of association: mutualism (where both organisms benefit), competition (where both organisms are harmed), and parasitism (one organism benefits and the other one is harmed).

Commensalism derives from the English word *commensal*, meaning "sharing of food" in human social interaction, which in turn derives from the Latin *cum mensa*, meaning "sharing a table". Originally, the term was used to describe the use of waste food by second animals, like the carcass eaters that follow hunting animals, but wait until they have finished their meal.

Examples of commensal relationships

Commensalism is harder to demonstrate than parasitism and mutualism, for it is easier to show a single instance whereby the host is affected, than it is to prove or disprove that possibility. Often, a detailed investigation will show that the host indeed has become affected by the relationship.

Cattle egrets and livestock

An example of commensalism: cattle egrets foraging in fields among cattle or other livestock. As cattle, horses, and other livestock graze on the field, they cause movements that stir up various insects. As the insects are stirred up, the cattle egrets following the livestock catch and feed upon them. The egrets benefit from this relationship because the livestock have helped them find their meals, while the livestock are typically unaffected by it.

Tigers and golden jackals

In India, lone golden jackals expelled from their pack have been known to form commensal relationships with tigers. These solitary jackals, known as *kol-bahl*, will attach themselves to a particular tiger, trailing it at a safe distance in order to feed on the big cat's kills. A *kol-bahl* will even alert a tiger to a kill with a loud *pheal* (thereby straying into mutualism). Tigers have been known to tolerate these jackals: one report describes how a jackal confidently walked in and out between three tigers walking together a few feet away from each other. Tigers will however kill jackals on occasion: the now extinct tigers of the Amu Darya region were known to eat jackals frequently.

Other examples

Another example of commensalism: birds following army ant raids on a forest floor. As the army ant colony travels on the forest floor, they stir up various flying insect species. As the insects flee from the army ants, the birds following the ants catch the fleeing insects. In this way, the army ants and the birds are in a commensal relationship because the birds benefit while the army ants are unaffected.

Orchids and mosses are plants that can have a commensal relationship with trees. The plants grow on the trunks or branches of trees. They get the light they need as well as nutrients that run down along the tree. As long as these plants do not grow too heavy, the tree is not affected.

Barnacles

Barnacles, a type of arthropod in the subphylum Crustacea

Barnacles are highly sedentary crustaceans that must attach themselves permanently to a hard substrate, such as rocks, shells, whales, or anything else on which they can gain a foothold. When they attach to the shell of a scallop, for instance, barnacles benefit by having a place to stay, leaving the scallop presumably unaffected.

Arguments

Whether the relationship between humans and some types of our gut flora is commensal or mutualistic is still unanswered.

Some biologists argue that any close interaction between two organisms is unlikely to be completely neutral for either party, and that relationships identified as commensal are likely mutualistic or parasitic in a subtle way that has not been detected. For example, epiphytes are "nutritional pirates" that may intercept substantial amounts of that would otherwise go to the host plant. Large numbers of epiphytes can also cause tree limbs to break or shade the host plant and reduce its rate of photosynthesis. Similarly, the phoretic mites may hinder their host by making flight more difficult, which may affect its aerial hunting ability or cause it to expend extra energy while carrying these passengers.

Types

Phoretic mites on a fly (*Pseudolynchia canariensis*)

Like all ecological interactions, commensalisms vary in strength and duration from intimate, long-lived symbioses to brief, weak interactions through intermediaries.

Phoresy

> One animal attaching to another for transportation only. This concerns mainly arthropods, examples of which are mites on insects (such as beetles, flies, or bees), pseudoscorpions on mammals or beetles, and millipedes on birds. Phoresy can be either obligate or facultative (induced by environmental conditions).

Inquilinism

> Using a second organism for housing. Examples are epiphytic plants (such as many orchids) that grow on trees, or birds that live in holes in trees.

Metabiosis

> A more indirect dependency, in which one organism creates or prepares a suitable environment for a second. Examples include maggots, which feast and develop on corpses, and hermit crabs, which use gastropod shells to protect their bodies.

Chapter 4

Parasitism

Brood parasitism is a form of parasitism

Parasitism is a type of symbiotic relationship between organisms of different species where one organism, the **parasite**, benefits at the expense of the other, the host. Traditionally **parasite** referred to organisms with lifestages that went beyond one host (e.g. Taenia solium), which are now called macroparasites (typically protozoa and helminths). Parasites can now also refer to microparasites, which are typically smaller, such as viruses and bacteria and can be directly transmitted between hosts of one species.

Unlike predators, parasites are generally much smaller than their host, although both are special cases of consumer-resource interactions. Parasite show a high degree of specialization for their mode of life, and reproduce at a faster rate than their hosts. Classic examples of parasitism include interactions between vertebrate hosts and diverse animals such as tapeworms, flukes, the *Plasmodium* species, and fleas. Parasitism is differentiated from parasitoidism, a relationship in which the host is normally killed by the parasite and which occurs in some species of moth, butterfly, ant, fly and other insects.

The harm and benefit in parasitic interactions concern the biological fitness of the organisms involved. Parasites reduce host fitness in many ways, ranging from general or specialized pathology (such as parasitic castration), impairment of secondary sex characteristics, to the modification of host behaviour. Parasites increase their fitness by exploiting hosts for resources necessary for the parasite's survival: (i.e. food, water, heat, habitat, and dispersal).

Although the concept of parasitism applies unambiguously to many cases in nature, it is best considered part of a continuum of types of interactions between species, rather than an exclusive category. Particular interactions between species may satisfy some but not all parts of the definition. In many cases, it is difficult to demonstrate that the host is harmed. In others, there may be no apparent specialization on the part of the parasite, or the interaction between the organisms may be short-lived. In medicine, only eukaryotic organisms are considered parasites, with the exclusion of bacteria and viruses. Some branches of biology, however, regard members of these groups as parasitic.

Etymology

First attested in English 1539, the word *parasite* comes from the Medieval French *parasite*, from the Latin *parasitus*, the latinisation of the Greek παράσιτος (*parasitos*), "one who eats at the table of another" and that from παρά (*para*), "beside, by" + σῖτος (*sitos*), "wheat". Coined in English 1611, the word *parasitism* comes from the Greek παρά (*para*) + σιτισμός (*sitismos*) "feeding, fattening".

Types of parasitism

Parasites are classified based on their interactions with their hosts and on their life cycles.

Parasites that live on the surface of the host are called **ectoparasites** (e.g. some mites) and those that live inside the host are called **endoparasites** (including all parasitic worms). Endoparasites can exist in one of two forms: intercellular (inhabiting spaces in the host’s body) or intracellular (inhabiting cells in the host’s body). Intracellular parasites, such as bacteria or viruses, tend to rely on a third organism which is generally known as the carrier or vector. The vector does the job of transmitting them to the host. An example of this interaction is the transmission of malaria, caused by a protozoan of the genus *Plasmodium*, to humans by the bite of an anopheline mosquito.

An *epiparasite* is one that feeds on another parasite. This relationship is also sometimes referred to as *hyperparasitism* which may be exemplified by a protozoan (the hyperparasite) living in the digestive tract of a flea living on a dog.

Social parasites take advantage of interactions between members of social organisms such as ants or termites. In *kleptoparasitism*, parasites appropriate food gathered by the host. An example is the brood parasitism practiced by many species of cuckoo and cowbird, which do not build nests of their own but rather deposit their eggs in nests of other species and abandon them there. The host behaves as a "babysitter" as they raise the young as their own. If the host removes the cuckoo's eggs, some cuckoos will return and attack the nest to compel host birds to remain subject to this parasitism. The cowbird’s parasitism does not necessarily harm its host’s brood; however, the cuckoo may remove one or more host eggs to avoid detection, and furthermore the young cuckoo may heave the host’s eggs and nestlings from the nest.

Parasitism can take the form of isolated *cheating* or *exploitation* among more generalized mutualistic interactions. For example, broad classes of plants and fungi exchange carbon and nutrients in common mutualistic mycorrhizal relationships; however, some plant species known as myco-heterotrophs "cheat" by taking carbon from a fungus rather than donating it.

Parasitoids are organisms whose larval development occurs inside or on the surface of another organism, resulting in the death of the host. This means that the interaction between the parasitoid and the host is fundamentally different from that of a true parasite and shares some of the characteristics of predation.

An adelpho-parasite is a parasite in which the host species is closely related to the parasite, often being a member of the same family or genus. An example of this is the citrus blackfly parasitoid, *Encarsia perplexa*, unmated females of which may lay haploid eggs in the fully developed larvae of their own species. These result in the production of male offspring. The marine worm *Bonellia viridis* has a similar reproductive strategy, although the larvae are planktonic.

Evolutionary aspects

Biotrophic parasitism is a common mode of life that has arisen independently many times in the course of evolution. Depending on the definition used, as many as half of all animals have at least one parasitic phase in their life cycles, and it is also frequent in plants and fungi. Moreover, almost all free-living animals are host to one or more parasite taxa.

Restoration of a *Tyrannosaurus* with parasite infections. A 2009 study showed that holes in the skulls of several specimens might have been caused by *Trichomonas*-like parasites

Parasites evolve in response to defense mechanisms of their hosts. Examples of host defenses include the toxins produced by plants to deter parasitic fungi and bacteria, the complex vertebrate immune system, which can target parasites through contact with bodily fluids, and behavioral defenses. An example of the latter is the avoidance by sheep of open pastures during spring, when roundworm eggs accumulated over the previous year hatch en masse. As a result of these and other host defenses, some parasites evolve adaptations that are specific to a particular host taxon and specialize to the point where they infect only a single species. Such narrow host specificity can be costly over evolutionary time, however, if the host species becomes extinct. Thus, many parasites are capable of infecting a variety of host species that are more or less closely related, with varying success.

Host defenses also evolve in response to attacks by parasites. Theoretically, parasites may have an advantage in this evolutionary arms race because of their more rapid generation time. Hosts reproduce less quickly than parasites, and therefore have fewer chances to adapt than their parasites do over a given span of time.

In some cases, a parasite species may coevolve with its host taxa. In theory, long-term coevolution should lead to a relatively stable relationship tending to commensalism or mutualism, in that it is in the evolutionary interest of the parasite that its host thrives. A parasite may evolve to become less harmful for its host or a host may evolve to cope with the unavoidable presence of a parasite to the point that the parasite's absence causes the host harm. For example, although animals infected with parasitic worms are often clearly harmed, and therefore parasitized, such infections may also reduce the prevalence and effects of autoimmune disorders in animal hosts, including humans.

The presumption of a shared evolutionary history between parasites and hosts can sometimes elucidate how host taxa are related. For instance, there has been dispute about whether flamingos are more closely related to the storks and their allies, or to ducks, geese and their relatives. The fact that flamingos share parasites with ducks and geese is evidence these groups may be more closely related to each other than either is to storks.

Parasitism is part of one explanation for the evolution of secondary sex characteristics seen in breeding males throughout the animal world, such as the plumage of male peacocks and manes of male lions. According to this theory, female hosts select males for breeding based on such characteristics because they indicate resistance to parasites and other disease.

Co-speciation

In rare cases, a parasite may even undergo co-speciation with its host. One particularly remarkable example of co-speciation exists between the simian foamy virus (SFV) and its primate hosts. In one study, the phylogenies of SFV polymerase and the mitochondrial cytochrome oxidase subunit II from African and Asian primates were compared. Surprisingly, the phylogenetic trees were very congruent in branching order and divergence times. Thus, the simian foamy viruses may have co-speciated with Old World primates for at least 30 million years.

Ecology

Quantitative ecology

When considering the distribution of a single parasite species, one finds that they exhibit an aggregated distribution among host individuals, which means that most hosts harbour few parasites, while a few hosts carry the vast majority of parasite individuals. This poses considerable problems for students of parasite ecology: the use of parametric statistics should be avoided. Log-transformation of data before the application of parametric test, or the use of non-parametric statistics is recommended by several authors. However, these give rise to further problems. Therefore, modern day quantitative parasitology is based on more advanced biostatistical methods.

Diversity ecology

Hosts represent discrete habitat patches that can be occupied by parasites. A hierarchical set of terminology has come into use to describe parasite assemblages at different host scales.

Infrapopulation	All the parasites of one species in a single individual host.
Metapopulation	All the parasites of one species in a host population.
Infracommunity	All the parasites of all species in a single individual host.
Component community	All the parasites of all species in a host population.
Compound community	All the parasites of all species in all host species in an ecosystem.

The diversity ecology of parasites differs markedly from that of free-living organisms. For free-living organisms, diversity ecology features many strong conceptual frameworks including Robert MacArthur and E. O. Wilson's theory of island biogeography, Jared Diamond's assembly rules and, more recently, null models such as Stephen Hubbell's unified neutral theory of biodiversity and biogeography. Frameworks are not so well-developed for parasites and in many ways they do not fit the free-living models. For example, island biogeography is predicated on fixed spatial relationships between habitat patches ("sinks"), usually with reference to a mainland ("source"). Parasites inhabit hosts, which represent mobile habitat patches with dynamic spatial relationships. There is no true "mainland" other than the sum of hosts (host population), so parasite component communities in host populations are metacommunities.

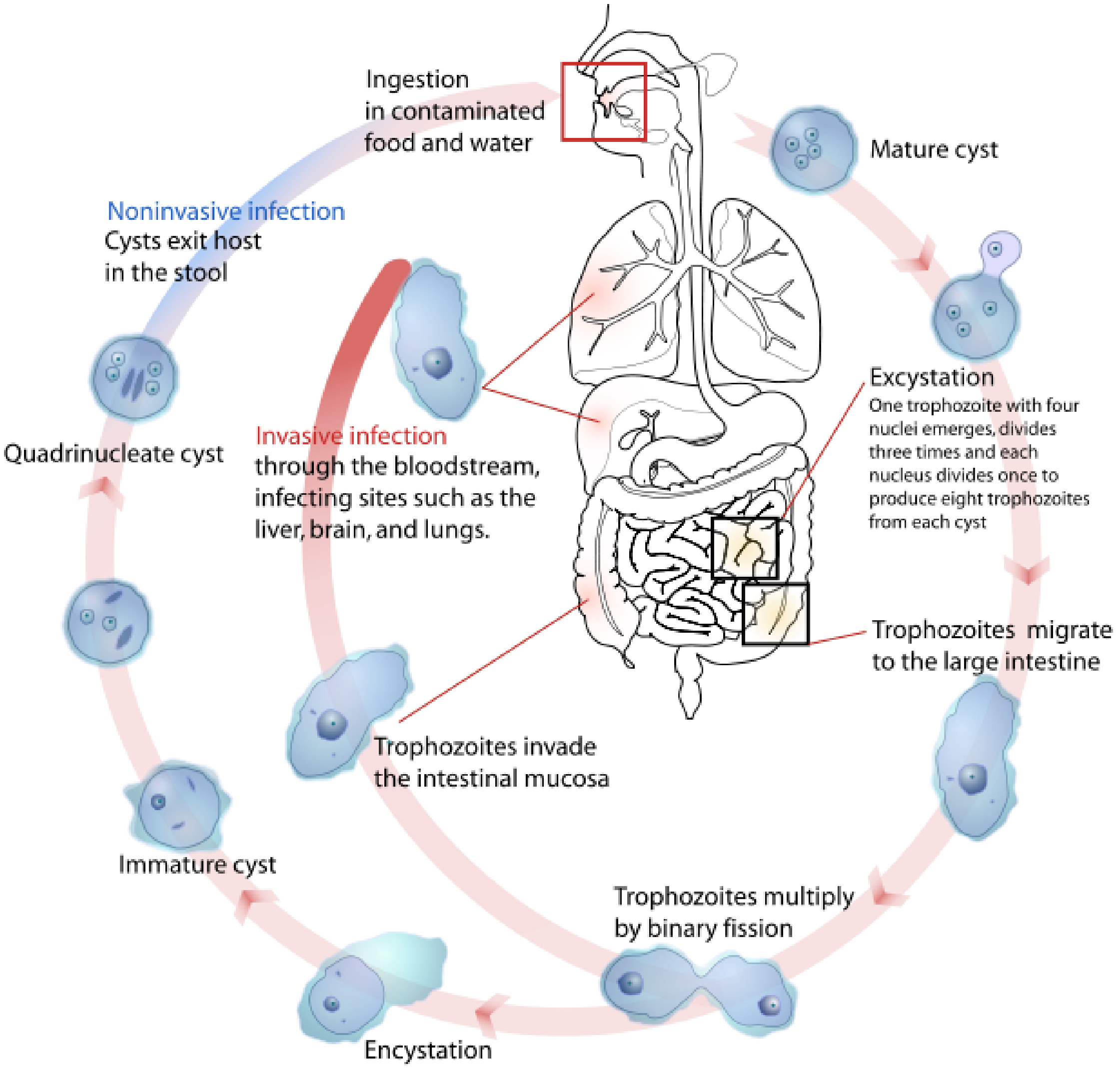
Nonetheless, different types of parasite assemblages have been recognised in host individuals and populations, and many of the patterns observed for free-living organisms are also pervasive among parasite assemblages. The most prominent of these is the interactive-isolationist continuum. This proposes that parasite assemblages occur along a cline from interactive communities, where niches are saturated and interspecific competition is high, to isolationist communities, where there are many vacant niches and interspecific interaction is not as important as stochastic factors in providing structure to the community. Whether this is so, or whether community patterns simply reflect the sum of underlying species distributions (no real "structure" to the community), has not yet been established.

Adaptation

Parasites infect hosts that exist within their same geographical area (sympatric) more effectively. This phenomenon supports the "Red Queen hypothesis - which states that interactions between species (such as host and parasites) lead to constant natural selection for adaptation and counter adaptation." The parasites track the locally common host phenotypes, therefore the parasites are less infective to allopatric (from different geographical region) hosts.

Experiments published in 2000 discuss the analysis of two different snail populations from two different sources- Lake Ianthe and Lake Poerua in New Zealand. The populations were exposed to two pure parasites (digenetic trematode) taken from the same lakes. In the experiment, the snails were infected by their sympatric parasites, allopatric parasites and mixed sources of parasites. The results suggest that the parasites were more highly effective in infecting their sympatric snails than their allopatric snails. Though the allopatric snails were still infected by the parasites, the infectivity was much less when compared to the sympatric snails. Hence, the parasites were found to have adapted to infecting local populations of snails.

Transmission



Life cycle of *Entamoeba histolytica*, an anaerobic parasitic protozoan.

Parasites inhabit living organisms and therefore face problems that free-living organisms do not. Hosts, the only habitats in which parasites can survive, actively try to avoid, repel, and destroy parasites. Parasites employ numerous strategies for getting from one host to another, a process sometimes referred to as parasite *transmission* or *colonization*.

Some endoparasites infect their host by penetrating its external surface, while others must be ingested. Once inside the host, adult endoparasites need to shed offspring into the external environment in order to infect other hosts. Many adult endoparasites reside in the host's gastrointestinal tract, where offspring can be shed along with host excreta. Adult stages of tapeworms, thorny-headed worms and most flukes use this method.

Among protozoan endoparasites, such as the malarial parasites and trypanosomes, infective stages in the host's blood are transported to new hosts by biting-insects, or vectors.

Larval stages of endoparasites often infect sites in the host other than the blood or gastrointestinal tract. In many such cases, larval endoparasites require their host to be consumed by the next host in the parasite's life cycle in order to survive and reproduce. Alternatively, larval endoparasites may shed free-living transmission stages that migrate through the host's tissue into the external environment, where they actively search for or await ingestion by other hosts. The foregoing strategies are used, variously, by larval stages of tapeworms, thorny-headed worms, flukes and parasitic roundworms.

Some ectoparasites, such as monogenean worms, rely on direct contact between hosts. Ectoparasitic arthropods may rely on host-host contact (e.g. many lice), shed eggs that survive off the host (e.g. fleas), or wait in the external environment for an encounter with a host (e.g. ticks). Some aquatic leeches locate hosts by sensing movement and only attach when certain temperature and chemical cues are present.

Some parasites modify host behaviour to make transmission to other hosts more likely. For example, in California salt marshes the fluke *Euhaplorchis californiensis* reduces the ability of its killifish host to avoid predators. This parasite matures in egrets, which are more likely to feed on infected killifish than on uninfected fish. Another example is the protozoan *Toxoplasma gondii*, a parasite that matures in cats but can be carried by many other mammals. Uninfected rats avoid cat odours, but rats infected with *T. gondii* are drawn to this scent, a change which may increase transmission to feline hosts.

Roles in ecosystems

Modifying the behaviour of infected hosts to make transmission to other hosts more likely is one way parasites can affect the structure of ecosystems. For example, in the case of *Euhaplorchis californiensis* (discussed above) it is plausible that the abundance of local predator and prey species would be different if this parasite were absent from the system.

Although parasites are often omitted in depictions of food webs, they usually occupy the top position. Parasites can function like keystone species, reducing the dominance of superior competitors and allowing competing species to co-exist.

Many parasites require multiple hosts of different species to complete their life cycles and rely on predator-prey or other stable ecological interactions to get from one host to another. In this sense, the parasites in an ecosystem reflect the "health" of that system.

Chapter 5

Ant

Ants
Temporal range: 130–0 Ma
Cretaceous - Recent

Meat eater ant feeding on honey

Scientific classification

Kingdom: Animalia
Phylum: Arthropoda
Class: Insecta
Hymenoptera
Suborder: Apocrita
Superfamily: Vespoidea
Formicidae
Latreille, 1809

Subfamilies

- Aenictogitoninae
- Agroecomyrmecinae
- Amblyoponinae (incl. "Apomyrminae")
- Aneuretinae
- Cerapachyinae
- Dolichoderinae
- Ecitoninae (incl. "Dorylinae" and "Aenictinae")
- Ectatomminae
- Formicinae
- Heteroponerinae
- Leptanillinae
- Leptanilloidinae
- Martialinae
- Myrmeciinae (incl. "Nothomyrmeciinae")
- Myrmicinae
- Paraponerinae
- Ponerinae
- Proceratiinae
- Pseudomyrmecinae

Ants are social insects of the family **Formicidae** along with the related wasps and bees, belong to the order Hymenoptera. Ants evolved from wasp-like ancestors in the mid-Cretaceous period between 110 and 130 million years ago and diversified after the rise of flowering plants. More than 12,500 out of an estimated total of 22,000 species have been classified. They are easily identified by their elbowed antennae and a distinctive node-like structure that forms a slender waist.

Ants form colonies that range in size from a few dozen predatory individuals living in small natural cavities to highly organised colonies which may occupy large territories and consist of millions of individuals. These larger colonies consist mostly of sterile wingless females forming castes of "workers", "soldiers", or other specialised groups. Nearly all ant colonies also have some fertile males called "drones" and one or more fertile females called "queens". The colonies are sometimes described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.

Ants have colonised almost every landmass on Earth. The only places lacking indigenous ants are Antarctica and a few remote or inhospitable islands. Ants thrive in most ecosystems, and may form 15–25% of the terrestrial animal biomass. Their success in so many environments has been attributed to their social organisation and their ability to modify habitats, tap resources, and defend themselves. Their long co-evolution with other species has led to mimetic, commensal, parasitic, and mutualistic relationships.

Ant societies have division of labour, communication between individuals, and an ability to solve complex problems. These parallels with human societies have long been an inspiration and subject of study.

Many human cultures make use of ants in cuisine, medication and rituals. Some species are valued in their role as biological pest control agents. However, their ability to exploit resources brings ants into conflict with humans, as they can damage crops and invade buildings. Some species, such as the red imported fire ant, are regarded as invasive species, establishing themselves in areas where they are accidentally introduced.

Etymology

The word *ant* is derived from *ante* of Middle English which is derived from *æmette* of Old English and is related to the Old High German *āmeiza*, hence the modern German *Ameise*. All of these words come from West Germanic **amaitjo*, and the original meaning of the word was "the biter" (from Proto-Germanic **ai-*, "off, away" + **mait-* "cut"). The family name *Formicidae* is derived from the Latin *formīca* ("ant") from which the words in other Romance languages such as the Portuguese *formiga*, Italian *formica*, Spanish *hormiga*, Romanian *furnică* and French *fourmi* are derived. It has been hypothetized that a Proto-Indo-European word *morwi- was used, cf. Sanskrit vamrah, Latin formīca, Greek myrmex, Old Church Slavonic mraviji, Old Irish moirb, Old Norse maurr.

Taxonomy and evolution

Ants fossilised in Baltic amber.

The family Formicidae belongs to the order Hymenoptera, which also includes sawflies, bees and wasps. Ants evolved from a lineage within the vespoid wasps. Phylogenetic analysis suggests that ants arose in the mid-Cretaceous period about 110 to 130 million years ago. After the rise of flowering plants about 100 million years ago they diversified and assumed ecological dominance around 60 million years ago. In 1966, E. O. Wilson and his colleagues identified the fossil remains of an ant (*Sphecomyrma freyi*) that lived in the Cretaceous period. The specimen, trapped in amber dating back to more than 80 million years ago, has features of both ants and wasps. *Sphecomyrma* was probably a ground forager but some suggest on the basis of groups such as the Leptanillinae and Martialinae that primitive ants were likely to have been predators underneath the surface of the soil.

During the Cretaceous period, a few species of primitive ants ranged widely on the Laurasian super-continent (the northern hemisphere). They were scarce in comparison to other insects, representing about 1% of the insect population. Ants became dominant after adaptive radiation at the beginning of the Tertiary period. By the Oligocene and Miocene ants had come to represent 20-40% of all insects found in major fossil deposits. Of the species that lived in the Eocene epoch, approximately one in ten genera survive to the present. Genera surviving today comprise 56% of the genera in Baltic amber fossils (early Oligocene), and 92% of the genera in Dominican amber fossils (apparently early Miocene).

Termites, though sometimes called *white ants*, are not ants and belong to the order Isoptera. Termites are actually more closely related to cockroaches and mantids. Termites are eusocial but differ greatly in the genetics of reproduction. The similar social structure is attributed to convergent evolution. Velvet ants look like large ants, but are wingless female wasps.

Distribution and diversity

Region	Number of species
Neotropics	2162
Nearctic	580
Europe	180
Africa	2500
Asia	2080
Melanesia	275
Australia	985
Polynesia	42

Ants are found on all continents except Antarctica, and only a few large islands such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species. Ants occupy a wide range of ecological niches, and are able to exploit a wide range of food resources either as direct or indirect herbivores, predators and scavengers. Most species are omnivorous generalists but a few are specialist feeders. Their ecological dominance may be measured by their biomass, and estimates in different environments suggest that they contribute 15-20% (on average and nearly 25% in the tropics) of the total terrestrial animal biomass, which exceeds that of the vertebrates.

Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in), and vary in colour. Most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 12,000 species are currently known (with upper estimates of about 22,000), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants. Online databases of ant species, including AntBase and the Hymenoptera Name Server, help to keep track of the known and newly described species. The relative ease with which ants can be sampled and studied in ecosystems has made them useful as indicator species in biodiversity studies.

Morphology

Ants are distinct in their morphology from other insects in having elbowed antennae, metapleural glands, and a strong constriction of their second abdominal segment into a node-like petiole. The head, mesosoma and metasoma or gaster are the three distinct body segments. The petiole forms a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole can be formed by one or two nodes (the second alone, or the second and third abdominal segments).

Bull ant showing the powerful mandibles and the relatively large compound eyes that provide excellent vision.

Like other insects, ants have an exoskeleton, an external covering that provides a protective casing around the body and a point of attachment for muscles, in contrast to the internal skeletons of humans and other vertebrates. Insects do not have lungs; oxygen and other gases like carbon dioxide pass through their exoskeleton through tiny valves called spiracles. Insects also lack closed blood vessels; instead, they have a long, thin, perforated tube along the top of the body (called the "dorsal aorta") that functions like a heart, and pumps haemolymph towards the head, thus driving the circulation of the internal fluids. The nervous system consists of a ventral nerve cord that runs the length of the body, with several ganglia and branches along the way reaching into the extremities of the appendages.

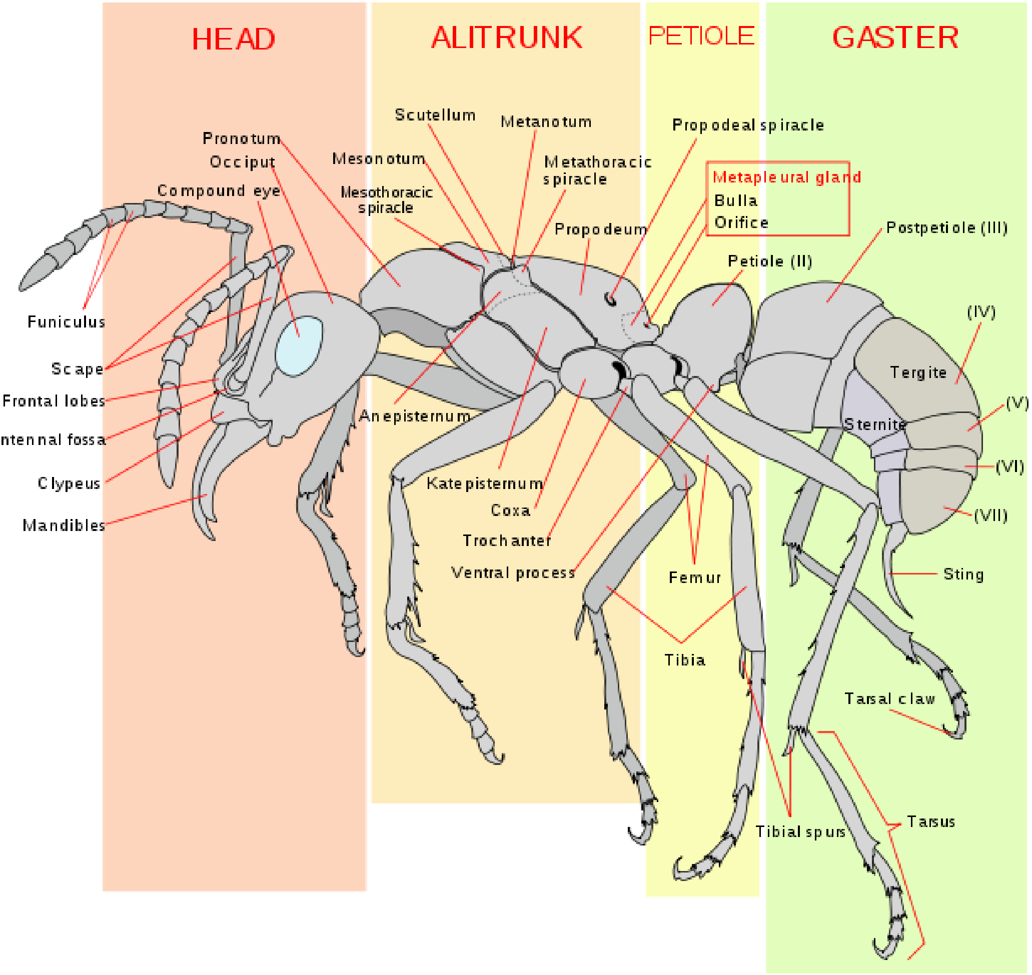


Diagram of a worker ant (*Pachycondyla verenae*).

An ant's head contains many sensory organs. Like most insects, ants have compound eyes made from numerous tiny lenses attached together. Ants' eyes are good for acute movement detection but do not give a high resolution. They also have three small ocelli (simple eyes) on the top of the head that detect light levels and polarization. Compared to vertebrates, most ants have poor-to-mediocre eyesight and a few subterranean species are completely blind. Some ants such as Australia's bulldog ant, however, have exceptional vision. Two antennae ("feelers") are attached to the head; these organs detect chemicals, air currents and vibrations; they are also used to transmit and receive signals through touch. The head has two strong jaws, the mandibles, used to carry food, manipulate objects, construct nests, and for defence. In some species a small pocket (infrabuccal chamber) inside the mouth stores food, so it can be passed to other ants or their larvae.

All six legs are attached to the mesosoma ("thorax"). A hooked claw at the end of each leg helps ants to climb and hang onto surfaces. Most queens and male ants have wings; queens shed the wings after the nuptial flight, leaving visible stubs, a distinguishing feature of queens. However, wingless queens (ergatoids) and males occur in a few species.

The metasoma (the "abdomen") of the ant houses important internal organs, including those of the reproductive, respiratory (tracheae) and excretory systems. Workers of many species have their egg-laying structures modified into stings that are used for subduing prey and defending their nests.

Polymorphism

Seven Leafcutter ant workers of various castes (left) and two Queens (right).

In the colonies of a few ant species, there are physical castes—workers in distinct size-classes, called minor, median, and major workers. Often the larger ants have disproportionately larger heads, and correspondingly stronger mandibles. Such individuals are sometimes called "soldier" ants because their stronger mandibles make them more effective in fighting, although they are still workers and their "duties" typically do not vary greatly from the minor or median workers. In a few species the median workers are absent, creating a sharp divide between the minors and majors. Weaver ants, for example, have a distinct bimodal size distribution. Some other species show continuous variation in the size of workers. The smallest and largest workers in *Pheidologeton diversus* show nearly a 500-fold difference in their dry-weights. Workers cannot mate; however, because of the haplodiploid sex-determination system in ants, workers of a number of species can lay unfertilised eggs that become fully fertile haploid males. The role of workers may change with their age and in some species, such as honeypot ants, young workers are fed until their gasters are distended, and act as living food storage vessels. These food storage workers are called *repletes*. This polymorphism in morphology and behaviour of workers was initially thought to be determined by environmental factors such as nutrition and hormones which led to different developmental paths; however, genetic differences between worker castes have been noted in *Acromyrmex* sp. These polymorphisms are caused by relatively small genetic changes; differences in a single gene of *Solenopsis invicta* can decide whether the colony will have single or multiple queens. The Australian jack jumper ant (*Myrmecia pilosula*) has only a single pair of chromosomes (males have just one chromosome as they are haploid), the lowest number known for any animal, making it an interesting subject for studies in the genetics and developmental biology of social insects.

Development and reproduction

Meat eater ant nest during swarming.

The life of an ant starts from an egg. If the egg is fertilised, the progeny will be female (diploid); if not, it will be male (haploid). Ants develop by complete metamorphosis with the larval stages passing through a pupal stage before emerging as an adult. The larva is largely immobile and is fed and cared for by workers. Food is given to the larvae by trophallaxis, a process in which an ant regurgitates liquid food held in its crop. This is also how adults share food, stored in the "social stomach", among themselves. Larvae may also be provided with solid food such as trophic eggs, pieces of prey and seeds brought back by foraging workers and may even be transported directly to captured prey in some species. The larvae grow through a series of moults and enter the pupal stage. The pupa has the appendages free and not fused to the body as in a butterfly pupa. The differentiation into queens and workers (which are both female), and different castes of workers (when they exist), is influenced in some species by the nutrition the larvae obtain. Genetic influences and the control of gene expression by the developmental environment are complex and the determination of caste continues to be a subject of research. The developmental environment Larvae and pupae need to be kept at fairly constant temperatures to ensure proper development, and so are often moved around the various brood chambers within the colony.

A new worker spends the first few days of its adult life caring for the queen and young. It then graduates to digging and other nest work, and later to defending the nest and foraging. These changes are sometimes fairly sudden, and define what are called temporal castes. An explanation for the sequence is suggested by the high casualties involved in foraging, making it an acceptable risk only for ants that are older and are likely to die soon of natural causes.

Fertilised meat eater ant queen beginning to dig a new colony.

Most ant species have a system in which only the queen and breeding females have the ability to mate. Contrary to popular belief, some ant nests have multiple queens while others can exist without queens. Workers with the ability to reproduce are called "gamergates" and colonies that lack queens are then called gamergate colonies; colonies with queens are said to be queen-right. The winged male ants, called drones, emerge from pupae along with the breeding females (although some species, like army ants, have wingless queens), and do nothing in life except eat and mate. Most ants are univoltine, producing a new generation each year. During the species specific breeding period, new reproductives, winged males and females leave the colony in what is called a nuptial flight. Typically, the males take flight before the females. Males then use visual cues to find a common mating ground, for example, a landmark such as a pine tree to which other males in the area converge. Males secrete a mating pheromone that females follow. Females of some species mate with just one male, but in some others they may mate with anywhere from one to ten or more different males. Mated females then seek a suitable place to begin a colony. There, they break off their wings and begin to lay and care for eggs. The females store the sperm they obtain during their nuptial flight to selectively fertilise future eggs. The first workers to hatch are weak and smaller than later workers, but they begin to serve the colony immediately. They enlarge the nest, forage for food and care for the other eggs. This is how new colonies start in most species. Species that have multiple queens may have a queen leaving the nest along with some workers to found a colony at a new site, a process akin to swarming in honeybees.

Ants mating.

A wide range of reproductive strategies have been noted in ant species. Females of many species are known to be capable of reproducing asexually through thelytokous parthenogenesis and one species, *Mycocepurus smithii* is known to be all-female.

Ant colonies can be long-lived. The queens can live for up to 30 years, and workers live from 1 to 3 years. Males, however, are more transitory, and survive only a few weeks. Ant queens are estimated to live 100 times longer than solitary insects of a similar size.

Ants are active all year long in the tropics but, in cooler regions, survive the winter in a state of dormancy or inactivity. The forms of inactivity are varied and some temperate species have larvae going into the inactive state (diapause), while in others, the adults alone pass the winter in a state of reduced activity.

Behaviour and ecology

Communication

Weaver ants collaborating to dismember a red ant (the two at the extremities are pulling the red ant, while the middle one cuts the red ant until it snaps).

Ants communicate with each other using pheromones. These chemical signals are more developed in ants than in other hymenopteran groups. Like other insects, ants perceive smells with their long, thin and mobile antennae. The paired antennae provide information about the direction and intensity of scents. Since most ants live on the ground, they use the soil surface to leave pheromone trails that can be followed by other ants. In species that forage in groups, a forager that finds food marks a trail on the way back to the colony; this trail is followed by other ants, these ants then reinforce the trail when they head back with food to the colony. When the food source is exhausted, no new trails are marked by returning ants and the scent slowly dissipates. This behaviour helps ants deal with changes in their environment. For instance, when an established path to a food source is blocked by an obstacle, the foragers leave the path to explore new routes. If an ant is successful, it leaves a new trail marking the shortest route on its return. Successful trails are followed by more ants, reinforcing better routes and gradually finding the best path.

Ants use pheromones for more than just making trails. A crushed ant emits an alarm pheromone that sends nearby ants into an attack frenzy and attracts more ants from further away. Several ant species even use "propaganda pheromones" to confuse enemy ants and make them fight among themselves. Pheromones are produced by a wide range of structures including Dufour's glands, poison glands and glands on the hindgut, pygidium, rectum, sternum and hind tibia. Pheromones are also exchanged mixed with food and passed by trophallaxis, transferring information within the colony. This allows other ants to detect what task group (*e.g.*, foraging or nest maintenance) other colony members belong to. In ant species with queen castes, workers begin to raise new queens in the colony when the dominant queen stops producing a specific pheromone.

Some ants produce sounds by stridulation, using the gaster segments and their mandibles. Sounds may be used to communicate with colony members or with other species.

Defence

A *Plectroctena sp* attacks another of its kind to protect its territory.

Ants attack and defend themselves by biting and, in many species, by stinging, often injecting or spraying chemicals like formic acid. Bullet ants (*Paraponera*), located in Central and South America, are considered to have the most painful sting of any insect, although it is usually not fatal to humans. This sting is given the highest rating on the Schmidt Sting Pain Index. The sting of Jack jumper ants can be fatal, and an antivenom has been developed. Fire ants, *Solenopsis* spp., are unique in having a poison sac containing piperidine alkaloids. Their stings are painful and can be dangerous to hypersensitive people.

A weaver ant in fighting position, mandibles wide open.

Trap-jaw ants of the genus *Odontomachus* are equipped with mandibles called trap-jaws, which snap shut faster than any other predatory appendages within the animal kingdom. One study of *Odontomachus bauri* recorded peak speeds of between 126 and 230 km/h (78 - 143 mph), with the jaws closing within 130 microseconds on average. The ants were also observed to use their jaws as a catapult to eject intruders or fling themselves backwards to escape a threat. Before the strike, the ant opens its mandibles extremely widely and locks them in this position by an internal mechanism. Energy is stored in a thick band of muscle and explosively released when triggered by the stimulation of sensory hairs on the inside of the mandibles. The mandibles also permit slow and fine movements for other tasks. Trap-jaws are also seen in the following genera: *Anochetus*, *Orectognathus*, and *Strumigenys*, plus some members of the Dacetini tribe, which are viewed as examples of convergent evolution. A Malaysian species of ant in the *Camponotus cylindricus* group has enlarged mandibular glands that extend into their gaster. When disturbed, workers rupture the membrane of the gaster, causing a burst of secretions containing acetophenones and other chemicals that immobilise small insect attackers. The worker subsequently dies. Suicidal defences by workers are also noted in a Brazilian ant *Forelius pusillus* where a small group of ants leaves the security of the nest after sealing the entrance from the outside each evening.

Ant mound holes prevent water from entering the nest during rain.

In addition to defence against predators, ants need to protect their colonies from pathogens. Some worker ants maintain the hygiene of the colony and their activities include undertaking or *necrophory*, the disposal of dead nest-mates. Oleic acid has been identified as the compound released from dead ants that triggers necrophoric behaviour in *Atta mexicana* while workers of *Linepithema humile* react to the absence of characteristic chemicals (dolichodial and iridomyrmecin) present on the cuticle of their living nestmates.

Nests may be protected from physical threats such as flooding and over-heating by elaborate nest architecture. Workers of *Cataulacus muticus*, an arboreal species that lives in plant hollows, respond to flooding by drinking water inside the nest, and excreting it outside. *Camponotus anderseni* which nests in the cavities of wood in mangrove habitats deals with submergence under water by switching to anaerobic respiration.

Learning

Many animals can learn behaviours by imitation but ants may be the only group apart from mammals where interactive teaching has been observed. A knowledgeable forager of *Temnothorax albipennis* leads a naive nest-mate to newly discovered food by the process of tandem running. The follower obtains knowledge through its leading tutor. Both leader and follower are acutely sensitive to the progress of their partner with the leader slowing down when the follower lags, and speeding up when the follower gets too close.

Controlled experiments with colonies of *Cerapachys biroi* suggest that individuals may choose nest roles based on their previous experience. An entire generation of identical workers was divided into two groups whose outcome in food foraging was controlled. One group was continually rewarded with prey, while it was made certain that the other failed. As a result, members of the successful group intensified their foraging attempts while the unsuccessful group ventured out less and less. A month later, the successful foragers continued in their role while the others moved to specialise in brood care.

Nest construction

Leaf nest of weaver ants, Pamalican, Philippines.

Complex nests are built by many ants, but other species are nomadic and do not build permanent structures. Ants may form subterranean nests or build them on trees. These nests can be found in the ground, under stones or logs, inside logs, hollow stems or even acorns. The materials used for construction include soil and plant matter, and ants carefully select their nest sites; *Temnothorax albipennis* will avoid sites with dead ants, as these may indicate the presence of pests or disease. They are quick to abandon established nests at the first sign of threats.

The army ants of South America and the driver ants of Africa do not build permanent nests, but instead alternate between nomadism and stages where the workers form a temporary nest (bivouac) from their own bodies, by holding each other together.

Weaver ant (*Oecophylla* spp.) workers build nests in trees by attaching leaves together, first pulling them together with bridges of workers and then inducing their larvae to produce silk as they are moved along the leaf edges. Similar forms of nest construction are seen in some species of *Polyrhachis*.

Food cultivation

Myrmecocystus, honeypot ants, store food to prevent colony famine.

Most ants are generalist predators, scavengers and indirect herbivores, but a few have evolved specialised ways of obtaining nutrition. Leafcutter ants (*Atta* and *Acromyrmex*) feed exclusively on a fungus that grows only within their colonies. They continually collect leaves which are taken to the colony, cut into tiny pieces and placed in fungal gardens. Workers specialise in tasks according to their sizes. The largest ants cut stalks, smaller workers chew the leaves and the smallest tend the fungus. Leafcutter ants are sensitive enough to recognise the reaction of the fungus to different plant material, apparently detecting chemical signals from the fungus. If a particular type of leaf is toxic to the fungus the colony will no longer collect it. The ants feed on structures produced by the fungi called *gongylidia*. Symbiotic bacteria on the exterior surface of the ants produce antibiotics that kill bacteria that may harm the fungi.

Navigation

Foraging ants travel distances of up to 200 metres (700 ft) from their nest and usually find their way back using scent trails. Some ants forage at night. Day foraging ants in hot and arid regions face death by desiccation, so the ability to find the shortest route back to the nest reduces that risk. Diurnal desert ants (*Cataglyphis fortis*) use visual landmarks in combination with other cues to navigate. In the absence of visual landmarks, the closely related Sahara desert ant (*Cataglyphis bicolor*) navigates by keeping track of direction as well as distance travelled, like an internal pedometer that counts how many steps they take in each direction. They integrate this information to find the shortest route back to their nest. Several species of ants are able to use the Earth's magnetic field. Ants' compound eyes have specialised cells that detect polarised light from the Sun, which is used to determine direction. These polarization detectors are sensitive in the ultraviolet region of the light spectrum. In some army ant species, a group of foragers that get separated from the main column can sometimes turn back on themselves and form a circular ant mill. The workers may then run around continuously until they die of exhaustion.

Locomotion

Worker ants do not have wings and reproductive females lose their wings after their mating flights in order to begin their colonies. Therefore, unlike their wasp ancestors, most ants travel by walking. Some species are capable of leaping. For example, Jerdon's jumping ant (*Harpegnathos saltator*) is able to jump by synchronising the action of its mid and hind pairs of legs. There are several species of gliding ant including *Cephalotes atratus*; this may be a common trait among most arboreal ants. Ants with this ability are able to control the direction of their descent while falling.

Other species of ants can form chains to bridge gaps over water, underground, or through spaces in vegetation. Some species also form floating rafts that help them survive floods. These rafts may also have a role in allowing ants to colonise islands. *Polyrhachis sokolova*, a species of ant found in Australian mangrove swamps, can swim and live in underwater nests. Since they lack gills, they breathe in trapped pockets of air in the submerged nests.

Cooperation and competition

Meat-eater ants feeding on a cicada. Social ants cooperate and collectively gather food.

Not all ants have the same kind of societies. The Australian bulldog ants are among the biggest and most basal of ants. Like virtually all ants they are eusocial, but their social behaviour is poorly developed compared to other species. Each individual hunts alone, using its large eyes instead of its chemical senses to find prey.

Some species (such as *Tetramorium caespitum*) attack and take over neighbouring ant colonies. Others are less expansionist but just as aggressive; they invade colonies to steal eggs or larvae, which they either eat or raise as workers/slaves. Extreme specialists among these slave-raiding ants, such as the Amazon ants, are incapable of feeding themselves and need captured workers to survive. Captured workers of the enslaved species *Temnothorax* have evolved a counter strategy, destroying just the female pupae of the slave-making *Protomognathus americanus*, but sparing the males (who don't take part in slave-raiding as adults).

A worker *Harpegnathos saltator* (a jumping ant) engaged in battle with a rival colony's queen.

Ants identify kin and nestmates through their scent, which comes from hydrocarbon-laced secretions that coat their exoskeletons. If an ant is separated from its original colony, it will eventually lose the colony scent. Any ant that enters a colony without a matching scent will be attacked.

Parasitic ant species enter the colonies of host ants and establish themselves as social parasites; species like *Strumigenys xenos* are entirely parasitic and do not have workers, but instead rely on the food gathered by their *Strumigenys perplexa* hosts. This form of parasitism is seen across many ant genera, but the parasitic ant is usually a species that is closely related to its host. A variety of methods are employed to enter the nest of the host ant. A parasitic queen can enter the host nest before the first brood has hatched, establishing herself prior to development of a colony scent. Other species use pheromones to confuse the host ants or to trick them into carrying the parasitic queen into the nest. Some simply fight their way into the nest.

A conflict between the sexes of a species is seen in some species of ants with the reproductives apparently competing to produce offspring that are as closely related to them as possible. The most extreme form involves the production of clonal offspring. An extreme of sexual conflict is seen in *Wasmannia auropunctata*, where the queens produce diploid daughters by thelytokous parthenogenesis and males produce clones by a process where a diploid egg loses its maternal contribution to produce haploid males that are clones of the father.

Relationships with other organisms

The spider *Myrmarachne plataleoides* (here a female) mimics weaver ants to avoid predators.

Ants form symbiotic associations with a range of species, including other ant species, other insects, plants, and fungi. They are preyed on by many animals and even certain fungi. Some arthropod species spend part of their lives within ant nests, either preying on ants, their larvae and eggs, consuming the ants' food stores, or avoiding predators. These inquilines can bear a close resemblance to ants. The nature of this ant mimicry (myrmecomorphy) varies, with some cases involving Batesian mimicry, where the mimic reduces the risk of predation. Others show Wasmannian mimicry, a form of mimicry seen only in inquilines.

An ant collects honeydew from an aphid.

Aphids and other hemipteran insects secrete a sweet liquid called honeydew when they feed on plant sap. The sugars in honeydew are a high-energy food source, which many ant species collect. In some cases the aphids secrete the honeydew in response to the ants' tapping them with their antennae. The ants in turn keep predators away and will move the aphids between feeding locations. On migrating to a new area, many colonies will take the aphids with them, to ensure a continued supply of honeydew. Ants also tend mealybugs to harvest their honeydew. Mealybugs can become a serious pest of pineapples if ants are present to protect mealybugs from their natural enemies.

Myrmecophilous (ant-loving) caterpillars of the family Lycaenidae (e.g., blues, coppers, or hairstreaks) are herded by the ants, led to feeding areas in the daytime, and brought inside the ants' nest at night. The caterpillars have a gland which secretes honeydew when the ants massage them. Some caterpillars produce vibrations and sounds that are perceived by the ants. Other caterpillars have evolved from ant-loving to ant-eating: these myrmecophagous caterpillars secrete a pheromone that makes the ants act as if the caterpillar is one of their own larvae. The caterpillar is then taken into the ants' nest where it feeds on the ant larvae.

An ant transporting an aphid.

Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus in the *Leucoagaricus* or *Leucocoprinus* genera of the Agaricaceae family. In this ant-fungus mutualism, both species depend on each other for survival. The ant *Allomerus decemarticulatus* has evolved a three-way association with the host plant *Hirtella physophora* (Chrysobalanaceae), and a sticky fungus which is used to trap their insect prey.

Lemon ants make devil's gardens by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees (*Duroia hirsuta*). This modification of the forest provides the ants with more nesting sites inside the stems of the *Duroia* trees. Some trees have extrafloral nectaries that provide food for ants, which in turn protect the plant from herbivorous insects. Species like the bullhorn acacia (*Acacia cornigera*) in Central America have hollow thorns that house colonies of stinging ants (*Pseudomyrmex ferruginea*) that defend the tree against insects, browsing mammals, and epiphytic vines. Isotopic labelling studies suggest that plants also obtain nitrogen from the ants. In return, the ants obtain food from protein and lipid rich Beltian bodies. Another example of this type of ectosymbiosis comes from the *Macaranga* tree, which has stems adapted to house colonies of *Crematogaster* ants.

Many tropical tree species have seeds that are dispersed by ants. Seed dispersal by ants or myrmecochory is widespread and new estimates suggest that nearly 9% of all plant species may have such ant associations. Some plants in fire-prone grassland systems are particularly dependent on ants for their survival and dispersal as the seeds are transported to safety below the ground. Many ant-dispersed seeds have special external structures, elaiosomes, that are sought after by ants as food. A convergence, possibly a form of mimicry, is seen in the eggs of stick insects. They have an edible elaiosome-like structure and are taken into the ant nest where the young hatch.

A Meat ant tending a common leafhopper nymph.

Most ants are predatory and some prey on and obtain food from other social insects including other ants. Some species specialise in preying on termites (*Megaponera* and *Termitopone*) while a few Cerapachyinae prey on other ants. Some termites, including *Nasutitermes corniger*, form associations with certain ant species to keep away other predatory ant species. The tropical wasp *Mischocyttarus drewseni* coats the pedicel of its nest with an ant-repellant chemical. It is suggested that many tropical wasps may build their nests in trees and cover them to protect themselves from ants. Stingless bees (*Trigona* and *Melipona*) use chemical defences against ants. Army ants forage in a wide roving column attacking any animals in that path that are unable to escape. *Eciton burchellii* is the swarming ant most commonly attended by "ant-following" birds such as antbirds and woodcreepers.

Flies in the Old World genus *Bengalia* (Calliphoridae) prey on ants and are kleptoparasites, snatching prey or brood from the mandibles of adult ants. Wingless and legless females of the Malaysian phorid fly (*Vestigipoda myrmolarvoidea*) live in the nests of ants of the genus *Aenictus* and are cared for by the ants.

Fungi in the genera *Cordyceps* and *Ophiocordyceps* infect ants, causing them to climb up plants and sink their mandibles into plant tissue. The fungus kills the ant, grows on its remains, and produces a fruiting body. It appears that the fungus alters the behaviour of the ant to help disperse its spores in a microhabitat that best suits the fungus. Strepsipteran parasites also manipulate their ant host to climb grass stems, to help the parasite find mates. A nematode (*Myrmeconema neotropicum*) that infects canopy ants (*Cephalotes atratus*) causes the black coloured gasters of workers to turn red. The parasite also alters the behaviour of the ant, and makes them carry their gasters high. The conspicuous red gasters are mistaken by birds for ripe fruits such as *Hyeronima alchorneoides* and eaten. The droppings of the bird are collected by other ants and fed to their young leading to the further spread of the nematode.

Spiders sometimes feed on ants.

South American poison dart frogs in the genus *Dendrobates* feed mainly on ants, and the toxins in their skin may come from the ants. Several South American antbirds follow army ants to feed on the insects that are flushed from cover by the foraging ants. This behaviour was once considered mutualistic, but later studies show that it is instead kleptoparasitic, with the birds stealing prey. Birds indulge in a peculiar behaviour called anting that is as yet not fully understood. Here birds rest on ant nests, or pick and drop ants onto their wings and feathers; this may remove ectoparasites. Anteaters, pangolins and several marsupial species in Australia have special adaptations for living on a diet of ants. These adaptations include long, sticky tongues to capture ants and strong claws to break into ant nests. Brown bears (*Ursus arctos*) have been found to feed on ants, and about 12%, 16%, and 4% of their faecal volume in spring, summer, and autumn, respectively, is composed of ants.

In science and technology

Myrmecologists study ants in the laboratory and in their natural conditions. Their complex and variable social structures have made ants ideal model organisms. Ultraviolet vision was first discovered in ants by Sir John Lubbock in 1881. Studies on ants have tested hypotheses in ecology, sociobiology and have been particularly important in examining the predictions of theories of kin selection and evolutionarily stable strategies. Ant colonies can be studied by rearing or temporarily maintaining them in formicaria, specially constructed glass framed enclosures. Individuals may be tracked for study by marking them with colours.

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems. This area of biomimetics has led to studies of ant locomotion, search engines that make use of "foraging trails", fault-tolerant storage and networking algorithms.

Chapter 6

Anthroposystem and Cleaner Fish

Anthroposystem

The term **anthroposystem** is used to describe the anthropological analogue to the ecosystem. In other words, the anthroposystem model serves to compare the flow of materials through human systems to those in naturally occurring systems. As defined by Santos, an anthroposystem is "the orderly combination or arrangement of physical and biological environments for the purpose of maintaining human civilization...built by man to sustain his kind." The anthroposystem is intimately linked to economic and ecological systems as well.

Both the anthroposystem and ecosystem can be divided into three groups: producers, consumers, and recyclers. In the ecosystem, the producers or autotrophs consist of plants and some bacteria capable of producing their own food via photosynthesis or chemical synthesis, the consumers consist of animals that obtain energy from grazing and/or by feeding on other animals and the recyclers consist of decomposers such as fungi and bacteria.

In the anthroposystem, the producers consist of the energy production through fossil fuels, manufacturing with non-fuel minerals and growing food; the consumers consist of humans and domestic animals and the recyclers consist of the decomposing or recycling activities (i.e. waste water treatment, metal and solid waste recycling).

The ecosystem is sustainable whereas the anthroposystem is not. The ecosystem is a closed loop in which nearly everything is recycled whereas the anthroposystem is an open loop where very little is recycled. In contrast to the ecosystem, the anthroposystem's producers and consumers are significantly more spatially displaced than those in the ecosystem and thus, more energy is required to transfer matter to a producer or recycler. Currently, a large majority of this energy comes from non-renewable fossil fuels.

Additionally, recycling is a naturally occurring component of the ecosystem, and is responsible for much of the resources used by the system. Under the anthroposystem model, however, recycling does not naturally occur. Outside input is relied on for material and energy supplies, and recycling systems that do exist are artificially created. The process of improving the flow of energy, such that waste can be reused as input resources, is known as industrial ecology.

A matrix can be used to describe the anthropological network of producers, consumers and recyclers and the movement of materials between each.

However, the matrix model of the anthroposystem - based on a model for the ecosystem - fails in acknowledging the physical redistribution of mobilized matter. In developing the anthroposystem model, there is a trade-off between simplicity and completeness. A simple representative model can be created involving only producers, consumers, and recyclers, but this is an open, incomplete system. More components and analogues (such as a matrix that encompasses the producers, consumers and recyclers) can be added to the system to make a more complete model, but the model loses simplicity in the process. Though the anthroposystem concept is flawed in this manner, it is a very good starting point for analyzing human activities and their effects on the environment.

When viewing the Earth as one large anthroposystem, we are essentially eliminating the uncertainty in material flow. All goods (i.e. fossil fuels) will still exist in the system but in a new form (i.e. pollutants). Therefore, the Laws of Conservation of Matter and Conservation of Energy can be applied to analyze how material flow will impact the environment.

Cleaner fish

The cleaner wrasses *Labroides dimidiatus* removing dead skin and external parasites from the grouper *Epinephelus tukula*.

Cleaner fish are fishes that provide a service to other fish species by removing dead skin and ectoparasites. This is an example of mutualism, an ecological interaction that benefits both parties involved. A wide variety of fishes have been observed to display cleaning behaviors including wrasses, cichlids, catfish, and gobies, as well as by a number of different species of cleaner shrimp. There is also at least one predatory mimic, the sabre-toothed blenny, that mimics cleaner fish but in fact feeds on healthy scales and mucous.

Diversity of cleaner fish

Marine fishes

White-spotted puffer being cleaned by a bluestreak cleaner wrasse

The best known cleaner fish are the cleaner wrasses of the genus *Labroides* found on coral reefs in the Indian Ocean and Pacific Ocean. These small fish maintain so-called cleaning stations where other fish, known as hosts, will congregate and perform specific movements to attract the attention of the cleaner fish. Remarkably, these small cleaner fish will safely clean large predatory fish that would otherwise eat small fish such as these. Cleaner wrasses appear to get almost all their nutrition through this cleaning service, and when maintained in aquaria rarely survive for long because they cannot obtain enough to eat.

Caribbean cleaning goby *Elacatinus evelynae*

Cleaning behaviors have been observed in a number of other fish groups. Neon gobies of the genera *Gobiosoma* and *Elacatinus* provide a cleaning service similar to the cleaner wrasses, though this time on reefs in the Western Atlantic, providing a good example of convergent evolution. Unlike the cleaner wrasses, they also eat a variety of small animals as well being cleaner fish, and generally do well in aquaria. However, the Caribbean cleaning goby (*Elacatinus evelynae*) will gladly eat scales and mucus from the host when the ectoparasites it normally feeds on are scarce, making the relationship somewhat less than mutually beneficial. The symbiosis does not break down because the abundance of these parasites varies significantly seasonally and spacially, and the overall benefit to the larger fish outweighs any cheating on the part of the smaller.

Brackish water fishes

An interesting example of a cleaning symbiosis has been observed between two brackish water cichlids of the genus *Etroplus* from South Asia. The small species *Etroplus maculatus* is the cleaner fish, and the much larger *Etroplus suratensis* is the host that receives the cleaning service.

Freshwater fishes

Cleaning is notably less common in freshwater habitats than in marine habitats. One of the few examples of cleaning is juvenile Striped Raphael catfish cleaning the piscivorous *Hoplias* cf. *malabaricus*.

Mimicry

The sabre-toothed blenny *Aspidontus taeniatus* is a blenny that mimics the ritualised dance the cleaner wrasse makes when passing fish swim by. Instead of providing a useful cleaning service, however, it bites off pieces of healthy skin and scales from the host before darting away to safety.

Chapter 7

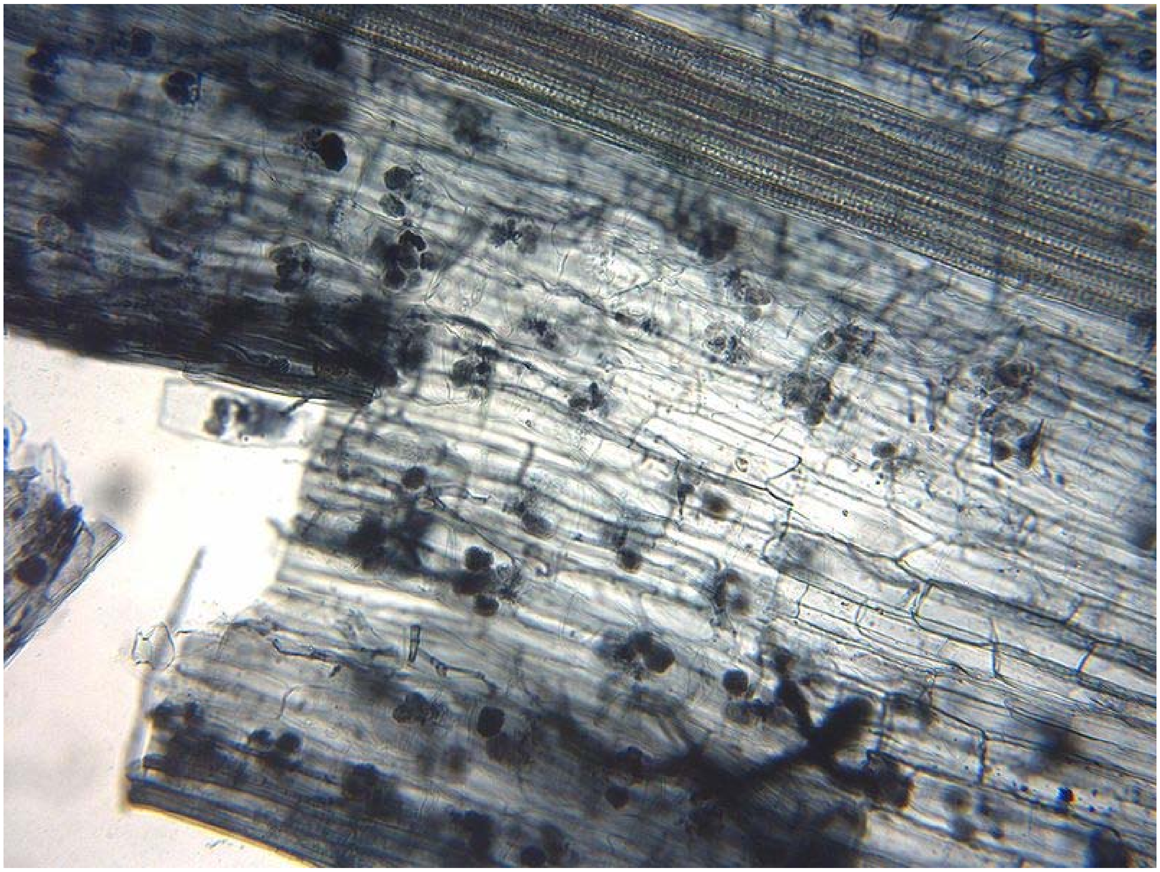
Arbuscular Mycorrhiza

An **arbuscular mycorrhiza** (plural **mycorrhizae** or **mycorrhizas**, aka *AM Fungi*) is a type of mycorrhiza in which the fungus penetrates the cortical cells of the roots of a vascular plant.

Arbuscular mycorrhizae (AMs) are characterized by the formation of unique structures such as arbuscules and vesicles by fungi of the phylum Glomeromycota (AM fungi). AM fungi (AMF) help plants to capture nutrients such as phosphorus and micronutrients from the soil. It is believed that the development of the arbuscular mycorrhizal symbiosis played a crucial role in the initial colonisation of land by plants and in the evolution of the vascular plants.

It has been said that it is quicker to list the plants that do not form mycorrhizae than those that do. This symbiosis is a highly evolved mutualistic relationship found between fungi and plants, the most prevalent plant symbiosis known, and AM is found in 80% of vascular plant families of today.

The tremendous advances in research on mycorrhizal physiology and ecology over the past 40 years have led to a greater understanding of the multiple roles of AMF in the ecosystem. This knowledge is applicable to human endeavors of ecosystem management, ecosystem restoration, and agriculture.



Flax root cortical cells containing paired arbuscules

Evolution of mycorrhizal symbiosis

Paleobiology

Both paleobiological and molecular evidence indicate that AM is an ancient symbiosis that originated at least 460 million years ago. AM symbiosis is ubiquitous among land plants, which suggests that mycorrhizae were present in the early ancestors of extant land plants. This positive association with plants may have facilitated the development of land plants.

The Rhynie chert of the lower Devonian has yielded fossils of the earliest land plants in which AM fungi have been observed. The fossilized plants containing mycorrhizal fungi were preserved in silica.

The Early Devonian saw the development of terrestrial flora. Plants of the Rhynie chert from the Lower Devonian (400 m.yrs ago) were found to contain structures resembling vesicles and spores of present *Glomus* species. Colonized fossil roots have been observed in *Aglaophyton major* and *Rhynia*, which are ancient plants possessing characteristics of vascular plants and bryophytes with primitive protostelic rhizomes.

Intraradical mycelium was observed in root intracellular spaces, and arbuscules were observed in the layer thin wall cells similar to palisade parenchyma. The fossil arbuscules appear very similar to those of existing AMF. The cells containing arbuscules have thickened walls, which are also observed in extant colonized cells.

Mycorrhizae from the Miocene exhibit a vesicular morphology closely resembling that of present *Glomerales*. The need for further evolution may have been lost due to the readily available food source provided by the plant host. However, it can be argued that the efficacy of signaling process is likely to have evolved, which could not be easily detected in the fossil record. A finetuning of the signaling processes would improve coordination and nutrient exchange between symbionts while increasing the fitness of both the fungi and the plant symbionts.

The nature of the relationship between plants and the ancestors of arbuscular mycorrhizal fungi is contentious. Two hypotheses are:

- Mycorrhizal symbiosis evolved from a parasitic interaction that developed in to a mutually beneficial relationship.
- Mycorrhizal fungi developed from saprobic fungi that became endosymbiotic.

Both saprotrophs and biotrophs were found in the Rhynie Chert, but there is little evidence to support either hypothesis.

There is some fossil evidence that suggests that the parasitic fungi did not kill the host cells immediately upon invasion, although a response to the invasion was observed in the host cells. This response may have evolved into the chemical signaling processes required for symbiosis.

In both cases, the symbiotic plant-fungi interaction is thought to have evolved from a relationship in which the fungi was taking nutrients from the plant into a symbiotic relationship where the plant and fungi exchange nutrients.

Molecular Evidence

Increased interest in mycorrhizal symbiosis and the rapid development of sophisticated molecular techniques has led to the rapid development of genetic evidence. Wang et al.performed an intensive investigation of three widely occurring plant genes that encode for a signal transduction cascade vital for communication with order Glomales fungal partners (DMI1, DMI3, IPD3). Sequences of these three genes were obtained from all major clades of modern land plants (including liverworts, the most basal group), and the maximum probability phylogeny of the three genes was in complete agreement with the current land plant phylogenies. These findings imply that the mycorrhizal genes must have been present in the common ancestor of land plants, and that these genes must have been vertically inherited since the colonization of land by plants.

Physiology

Presymbiosis

The development of AM fungi prior to root colonization, known as presymbiosis, consists of three stages: spore germination, hyphal growth, host recognition and appressorium formation.

Spores of the AM fungi are thick-walled multi-nucleate resting structures. The germination of the spore does not depend on the plant, as spores have been germinated under experimental conditions in the absence of plants both *in vitro* and in soil. However, the rate of germination can be increased by host root exudates. AM fungal spores germinate given suitable conditions of the soil matrix, temperature, carbon dioxide concentration, pH, and phosphorus concentration.

The growth of AM hyphae through the soil is controlled by host root exudates and the soil phosphorus concentration.

Low-phosphorus concentrations in the soil increase hyphal growth and branching as well as induce plant exudation of compounds that control hyphal branching intensity.

The branching of AM fungal hyphae grown in phosphorus media of 1 mM is significantly reduced, but the length of the germ tube and total hyphal growth were not affected. A concentration of 10 mM phosphorus inhibited both hyphal growth and branching. This phosphorus concentration occurs in natural soil conditions and could thus contribute to reduced mycorrhizal colonization.

Root exudates from AMF host plants grown in a liquid medium with and without phosphorus have been shown to effect hyphal growth. Pre-germinated surface-sterilized spores of *Gigaspora magarita* were grown in host plant exudates. The fungi grow in the exudates from roots starved of phosphorus had increased hyphal growth and produced tertiary branches compared to those grown in exudates from plants given adequate phosphorus. When the growth-promoting root exudates were added in low concentration, the AM fungi produced scattered long branches. As the concentration of exudates was increased, the fungi produced more tightly clustered branches. At the highest-concentration arbuscules, the AMF structures of phosphorus exchange were formed.

This chemotaxic fungal response to the host plants exudates is thought to increase the efficacy of host root colonization in low-phosphorus soils. It is an adaptation for fungi to efficiently explore the soil in search of a suitable plant host.

Further evidence that AM fungi exhibit host-specific chemotaxis: Spores of *Glomus mosseae* were separated from the roots of a host plant, nonhost plants, and dead host plant by a membrane permeable only to hyphae. In the treatment with the host plant, the fungi crossed the membrane and always emerged within 800 µm of the root. Whereas in the treatments with nonhost plants and dead plants, the hyphae did not cross the membrane to reach the roots. This demonstrates that arbuscular mycorrhizal fungi have chemotaxic abilities that enable hyphal growth toward the roots of a potential host plant.

Molecular techniques have been used to further understand the signaling pathways that occur between arbuscular mycorrhizae and the plant roots. In the presence of exudates from potential host plant roots, the AM undergoes physiological changes that allow it to colonize its host. AM fungal genes required for the respiration of spore carbon compounds are triggered and turned on by host plant root exudates. In experiments, there was an increase in the transcription rate of 10 genes half-hour after exposure and an even greater rate after 1 hour. A morphological growth response was observed 4 hours after exposure. The genes were isolated and found to be involved in mitochondrial activity and enzyme production. The fungal respiration rate was measured by O_2 consumption rate and increased by 30% 3 hours after exposure to root exudates. This indicates that AMF spore mitochondrial activity is positively stimulated by host plant root exudates. This may be part of a fungal regulatory mechanism that conserves spore energy for efficient growth and the hyphal branching upon receiving signals from a potential host plant.

When arbuscular mycorrhizal fungal hyphae encounter the root of a host plant, an apressorium (an infection structure) is formed on the root epidermis. The apressorium is the structure from which the hyphae can penetrate into the host's parenchyma cortex. The formation of apressoria does not require chemical signals from the plant. AM fungi could form apressoria on the cell walls of "ghost" cells in which the protoplast had been removed to eliminate signaling between the fungi and the plant host. However, the hyphae did not further penetrate the cells and grow in toward the root cortex, which indicates that signaling between symbionts is required for further growth once appresoria are formed.

Symbiosis

Once inside the parenchyma, the fungi forms highly branched structures for nutrient exchange with the plant called "arbuscules". These are the distinguishing structures of arbuscular mycorrhizal fungus. Arbuscules are the sites of exchange for phosphorus, carbon, water, and other nutrients. There are two forms: *Paris* type is characterized by the growth of hyphae from one cell to the next; and *Arum* type is characterized by the growth of hyphae in the space between plant cells. The choice between *Paris* type and *Arum* type is primarily determined by the host plant family, although some families or species are capable of either type.

The host plant exerts a control over the intercellular hyphal proliferation and arbuscule formation. There is a decondensation of the plant's chromatin, which indicates increased transcription of the plant's DNA in arbuscule-containing cells. Major modifications are required in the plant host cell to accommodate the arbuscules. The vacuoles shrink and other cellular organelles proliferate. The plant cell cytoskeleton is reorganized around the arbuscules.

There are two other types of hyphae that originate from the colonized host plant root. Once colonization has occurred, short-lived runner hyphae grow from the plant root into the soil. These are the hyphae that take up phosphorus and micronutrients, which are conferred to the plant. AM fungal hyphae have a high surface-to-volume ratio, making their absorptive ability greater than that of plant roots. AMF hyphae are also finer than roots and can enter into pores of the soil that are inaccessible to roots. The third type of AMF hyphae grows from the roots and colonizes other host plant roots. The three types of hyphae are morphologically distinct.

Nutrient uptake and exchange

AMF are obligate symbionts. They have limited saprobic ability and are dependent on the plant for their carbon nutrition. AM fungi take up the products of the plant host's photosynthesis as hexoses.

The transfer of carbon from the plant to the fungi may occur through the arbuscules or intraradical hyphae. Secondary synthesis from the hexoses by AM occurs in the intraradical mycelium. Inside the mycelium, hexose is converted to trehalose and glycogen. Trehalose and glycogen are carbon storage forms that can be rapidly synthesized and degraded and may buffer the intracellular sugar concentrations. The intraradical hexose enters the oxidative pentose phosphate pathway, which produces pentose for nucleic acids.

Lipid biosynthesis also occurs in the intraradical mycelium. Lipids are then stored or exported to extraradical hyphae where they may be stored or metabolized. The breakdown of lipids into hexoses, known as **gluconeogenesis**, occurs in the extraradical mycelium. Approximately 25% of the carbon translocated from the plant to the fungi is stored in the extraradical hyphae. Up to 20% of the host plant's photosynthate carbon may be transferred to the AM fungi. This represents a considerable carbon investment in mycorrhizal network by the host plant and contribution to the below-ground organic carbon pool.

An increase in the carbon supplied by the plant to the AM fungi increases the uptake of phosphorus and the transfer of phosphorus from fungi to plant (Bücking & Shachar-Hill 2005). Phosphorus uptake and transfer is also lowered when the photosynthate supplied to the fungi is decreased. Species of AMF differ in their abilities to supply the plant with phosphorus. In some cases, arbuscular mycorrhizae are poor symbionts, providing little phosphorus while taking relatively high amounts of carbon.

The benefit of mycorrhizae to plants is mainly attributed to increased uptake of nutrients, especially phosphorus. This increase in uptake may be due to increase surface area of soil contact, increased movement of nutrients into mycorrhizae, a modification of the root environment, and increased storage. Mycorrhizae can be much more efficient than plant roots at taking up phosphorus. Phosphorus travels to the root or via diffusion and hyphae reduce the distance required for diffusion, thus increasing uptake. The rate of inflow of phosphorus into mycorrhizae can be up to six times that of the root hairs. In some cases, the role of phosphorus uptake can be completely taken over by the mycorrhizal network, and all of the plant’s phosphorus may be of hyphal origin.

The available phosphorus concentration in the root zone can be increased by mycorrhizal activity. Mycorrhizae lower the rhizosphere pH due to selective uptake of NH_4^+ (ammonium-ions) and release of H^+ ions. Decreased soil pH increases the solubility of phosphorus precipitates. The hyphal uptake of NH_4^+ also increases the flow of nitrogen to the plant as NH_4^+ is adsorbed to the soil's inner surfaces and must be taken up by diffusion.

Ecology

Habitat

Arbuscular mycorrhizal fungi are most frequent in plants growing on mineral soils. The populations of AM fungi is greatest in plant communities with high diversity such as tropical rainforests and temperate grasslands where they have many potential host plants and can take advantage of their ability to colonize a broad host range. There is a lower incidence of mycorrhizal colonization in very arid or nutrient-rich soils. Mycorrhizas have been observed in aquatic habitats; however, waterlogged soils have been shown to decrease colonization in some species.

Host range and specificity

The specificity, host range, and degree of colonization of mycorrhizal fungi are difficult to analyze in the field due to the complexity of interactions between the fungi within a root and within the system. There is no clear evidence to suggest that arbuscular mycorrhizal fungi exhibit specificity for colonization of potential AM host plant species as do fungal pathogens for their host plants. This may be due to the opposite selective pressure involved.

In parasitic relations, the host plant benefits from mutations that prevent colonization, whereas, in a symbiotic relationship, the plant benefits from mutation that allow for colonization by AMF. However, plant species differ in the extent and dependence on colonization by certain AM fungi, and some plants may be facultative mycotrophs, while others may be obligate mycotrophs.

The ability of the same AM fungi to colonize many species of plants has ecological implications. Plants of different species can be linked underground to a common mycelial network. One plant may provide the photosynthate carbon for the establishment of the mycelial network that another plant of a different species can utilize for mineral uptake. This implies that arbuscular mycorrhizae are able to balance below-ground intra–and interspecific plant interactions.

Rhizosphere ecology

The rhizosphere is the soil zone in the immediate vicinity of a root system.

Arbuscular mycorrhizal symbiosis affects the community and diversity of other organisms in the soil. This can be directly seen by the release of exudates, or indirectly by a change in the plant species and plant exudates type and amount.

Mycorrhizae diversity has been shown to increase plant species diversity as the potential number of associations increases. Dominant arbuscular mycorrhizal fungi can prevent the invasion of non-mycorrhizal plants on land where they have established symbiosis and promote their mycorrhizal host.

Recent research has shown that AM fungi release an unidentified diffusional factor, known as the **myc factor**, which activates the nodulation factor's inducible gene MtEnod11. This is the same gene involved in establishing symbiosis with the nitrogen fixing, rhizobial bacteria (Kosuta *et al.* 2003). When rhizobium bacteria are present in the soil, mycorrhizal colonization is increased due to an increase in the concentration of chemical signals involved in the establishment of symbiosis (Xie *et al.* 2003). Molecules similar to Nod factors were isolated from AM fungi and were shown to induce MtEnod11, lateral root formation and enhance mycorrhization. Effective mycorrhizal colonization can also increase the nodulations and symbiotic nitrogen fixation in mycorrhizal legumes.

The extent of arbuscular mycorrhizal colonization and species affects the bacterial population in the rhizosphere. Bacterial species differ in their abilities to compete for carbon compound root exudates. A change in the amount or composition of root exudates and fungal exudates due to the existing AM mycorrhizal colonization determines the diversity and abundance of the bacterial community in the rhizosphere.

The influence of AM fungi on plant root and shoot growth may also have indirect effect on the rhizosphere bacteria. AMF contributes a substantial amount of carbon to the rhizosphere through the growth and degeneration of the hyphal network. There is also evidence to suggest that AM fungi may play an important role on mediating the plant species' specific effect on the bacterial composition of the rhizosphere.

Phytoremediation

The use of arbuscular mycorrhizal fungi in ecological restoration projects has been shown to enable host plant establishment on degraded soil and improve soil quality and health (phytoremediation).

Disturbance of native plant communities in desertification-threatened areas is often followed by degradation of physical and biological soil properties, soil structure, nutrient availability, and organic matter.

When restoring disturbed land, it is essential to replace not only the above ground vegetation but also the biological and physical soil properties.

A relatively new approach to restoring land and protecting against desertification is to inoculate the soil with arbuscular mycorrhizal fungi with the reintroduction of vegetation. A long-term study demonstrated that a significantly greater long-term improvement in soils' quality parameters was attained when the soil was inoculated with a mixture of indigenous arbuscular mycorrhizal fungi species compared to the noninoculated soil and soil inoculated with a single exotic species of AM fungi (Figure 2). The benefits observed were an increased plant growth and soil nitrogen content, higher soil organic matter content, and soil aggregation. The improvements were attributed to the higher legume nodulation in the presence of AMF, better water infiltration, and soil aeration due to soil aggregation.

Inoculation with native AM fungi increased plant uptake of phosphorus, improving plant growth and health. The results support the use of AM fungi as a biological tool in the restoration of biotopes to self-sustaining ecosystems.

Agriculture

Many modern agronomic practices are disruptive to mycorrhizal symbiosis. There is great potential for low-input agriculture to manage the system in a way that promotes mycorrhizal symbiosis.

Conventional agriculture practices, such as tillage, heavy fertilizers and fungicides, poor crop rotations, and selection for plants that survive these conditions, hinder the ability of plants to form symbiosis with arbuscular mycorrhizal fungi.

Most agricultural crops can perform better and are more productive when well-colonized by AM fungi. AM symbiosis increases the phosphorus and micronutrient uptake and growth of their plant host (George *et al.* 1992).

Management of AM fungi is especially important for organic and low-input agriculture systems where soil phosphorus is, in general, low, although all agroecosystems can benefit by promoting arbuscular mycorrhizae establishment.

Some crops that are poor at seeking out nutrients in the soil are very dependent on AM fungi for phosphorus uptake. For example flax, which has poor chemotaxic ability, is highly dependent on AM-mediated phosphorus uptake at low and intermediate soil phosphorus concentrations (Thingstrup *et al.* 1998).

Proper management of AMF in the agroecosystems can improve the quality of the soil and the productivity of the land. Agricultural practices such as reduced tillage, low phosphorus fertilizer usage, and perennialized cropping systems promote functional mycorrhizal symbiosis.

Tillage

Tillage reduces the inoculation potential of the soil and the efficacy of mycorrhizaes by disrupting the extraradical hyphal network (Miller *et al.* 1995, McGonigle & Miller 1999, Mozafar *et al.* 2000).

By breaking apart the soil macro structure, the hyphal network is rendered non-infective (Miller *et al.* 1995, McGonigle & Miller 1999). The disruption of the hyphal network decreases the absorptive abilities of the mycorrhizae because the surface area spanned by the hyphae is greatly reduced. This, in turn, lowers the phosphorus input to the plants that are connected to the hyphal network (Figure 3, McGonigle & Miller 1999).

In reduced-tillage system, heavy phosphorus fertilizer input may not be required as compared to heavy-tillage systems. This is due to the increase in mycorrhizal network, which allows mycorrhizae to provide the plant with sufficient phosphorus (Miller *et al.* 1995).

Phosphorus fertilizer

The benefits of AMF are greatest in systems where inputs are low. Heavy usage of phosphorus fertilizer can inhibit mycorrhizal colonization and growth.

As the soil's phosphorus levels available to the plants increases, the amount of phosphorus also increases in the plant's tissues, and carbon drain on the plant by the AM fungi symbiosis become non-beneficial to the plant (Grant 2005).

A decrease in mycorrhizal colonization due to high soil-phosphorus levels can lead to plant deficiencies in other micronutrients that have mycorrhizal-mediated uptake such as copper (Timmer & Leyden 1980).

Perennialized cropping systems

Cover crops are grown in the fall, winter, and spring, covering the soil during periods when it would commonly be left without a cover of growing plants.

Mycorrhizal cover crops can be used to improve the mycorrhizal inoculum potential and hyphal network (Kabir and Koide 2000, Boswell *et al.*1998, Sorensen et al. 2005).

Since AM fungi are biotrophic, they are dependent on plants for the growth of their hyphal networks. Growing a cover crop extends the time for AM growth into the autumn, winter, and spring. Promotion of hyphal growth creates a more extensive hyphal network. The mycorrhizal colonization increase found in cover crops systems may be largely attributed to an increase in the extraradical hyphal network that can colonize the roots of the new crop (Boswell *et al.* 1998). The extraradical mycelia are able to survive the winter, providing rapid spring colonization and early season symbiosis (McGonigle and Miller 1999). This early symbiosis allows plants to tap into the well-established hyphal network and be supplied with adequate phosphorus nutrition during early growth, which greatly improves the crop yield.

Soil quality

Restoration of native AM fungi increases the success of ecological restoration project and the rapidity of soil recovery. There is evidence to suggest that this enhancement of soil aggregate stability is due to the production of a soil protein known as glomalin.

Glomalin-related soil proteins (GRSP) have been identified using a monoclonal antibody (Mab32B11) raised against crushed AMF spores. It is defined by its extraction conditions and reaction with the antibody Mab32B11.

There is other circumstantial evidence to show that glomalin is of AM fungal origin. When AM fungi are eliminated from soil through incubation of soil without host plants, the concentration of GRSP declines. A similar decline in GRSP has also been observed in incubated soils from forested, afforested, and agricultural land and grasslands treated with fungicide.

Glomalin is hypothesized to improve soil aggregate water stability and decrease soil erosion. A strong correlation has been found between GRSP and soil aggregate water stability in a wide variety of soils where organic material is the main binding agent, although the mechanism is not known. The protein glomalin has not yet been isolated and described, and the link between glomalin, GRSP, and arbuscular mycorrhizal fungi is not yet clear.

Chapter 8

Clownfish

Clownfish

Ocellaris clownfish, *Amphiprion ocellaris*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Order:	Perciformes
Family:	Pomacentridae
Subfamily:	**Amphiprioninae**

Genera

Amphiprion Bloch & Schneider, 1801
Premnas Cuvier, 1816

Clownfish or **anemonefish** are fishes from the subfamily **Amphiprioninae** in the family Pomacentridae. About twenty-nine species are recognized, one in the genus *Premnas*, while the remaining are in the genus *Amphiprion*. In the wild they all form symbiotic mutualisms with sea anemones. Depending on species, clownfish are overall yellow, orange, reddish or blackish, and many show white bars or patches. The largest can reach a length of 18 centimetres (7.1 in), while some barely can reach 10 centimetres (3.9 in).

Ecology and habitat

Clownfish are native to warmer waters of the Indian and Pacific oceans, including the Great Barrier Reef and the Red Sea. While most species have restricted distributions, others are widespread. They are generally highly host specific, and especially the genera *Heteractis* and *Stichodactyla*, and the species *Entacmaea quadricolor* are frequent partners.

Clownfish live at the bottom of the sea in sheltered reefs or in shallow lagoons, usually in pairs They are found in northwest Australia, southeast Asia, Japan and the Indo-Malaysian region. There are no clownfish in the Caribbean. Scientific name: Amphiprion species Country: Worldwide tropical

Continent: Oceania, Asia, Africa, South America, Central and North America

Diet: Algae, crustaceans, molluscs

Food & feeding: Omnivore

Habitats: Ocean

Conservation status: Not Threatened

Relatives: Thread-fin damselfish

Diet

The clownfish feeds on small invertebrates which otherwise potentially could harm the sea anemone, and the fecal matter from the clownfish provides nutrients to the sea anemone. Clownfish are omnivorous: in the wild they eat live food such as algae, plankton, mollusks, and crustacea; in captivity they can survive on live food, fish flakes, and fish pellets. Algae accounts for around 20 to 25 percent of its diet in the wild (and should also account for its amount of algae diet in captivity as well). The diet of the clownfish also consists of copepods, mysids, isopods, zooplankton and undigested food from their host anemones.

Special Characteristics

Clownfish and certain damselfish are the only species of fishes that can avoid the potent poison of a sea anemone. There are several theories about how this is accomplished:

- The mucus coating of the fish may be based on sugars rather than proteins. This would mean that anemones fail to recognize the fish as a potential food source and do not fire their nematocysts, or sting organelles.

- The coevolution of certain species of clownfish with specific anemone host species and may have acquired an immunity to the nematocysts and toxins of their host anemone. Experimentation has shown that *Amphiprion percula* may develop resistance to the toxin from *Heteractis magnifica*, but it is not totally protected, since it was shown experimentally to die when its skin, devoid of mucus, was exposed to the nematocysts of its host.

A pair of pink anemonefish (*Amphiprion perideraion*) in their anemone home.

In a group of clownfish, there is a strict hierarchy of dominance. The largest and most aggressive female is found at the top. Only two clownfish, a male and a female, in a group reproduce through external fertilization. The clownfish are hermaphrodites, meaning that they develop into males first, and when they mature, they become females. Also, as mentioned earlier, more than one clownfish is able to live in a sea anemone. If the female clownfish is removed from the group, such as by death, one of the largest and most dominant males would become a female. The rest of the remaining males will move up a rank on the hierarchy.

Life of a clown fish

Clownfish lay eggs on any flat surface close to their host anemones. In the wild, clownfish spawn around the time of the full moon and the male parent guards them until they hatch about 6 to 10 days later, typically 2 hours after dusk.

Depending on the species, clownfish can lay hundreds or thousands of eggs. Clownfish were the first type of marine ornamental fish to be successfully bred in captivity on a large scale. It is one of a handful of marine ornamentals whose complete life cycle has been closed in captivity. Members of some clownfish species, such as the maroon clownfish, become aggressive in captivity; others, like the false percula clownfish, can be kept successfully with other individuals of the same species.

In captivity, the clownfish can live from 3 to 5 years. In the wild, they live 6 to 10 years.

Symbiosis and Mutualism

Symbiosis describes the special relationship between clownfish and sea anemones. It has been suggested that the activity of the clownfish results in greater water circulation around the sea anemone. In addition to providing food for the clownfish, the sea anemone also provides safety due to its poison. The Clown Fish is dependent on the Sea Anemone for its daily bread. After the Anemone paralyzes and eats a fish, the Clown fish will polish off the remaining uneaten bits and pieces. In return, the Clown Fish helps to keep the Anemone free of dead tentacles by eating these. The Clown Fish also helps the Anemone get food by using its bright coloration to lure unsuspecting fish into the vicinity of the Anemone. This symbiotic relationship with the Anemone makes the Clown Fish one of the most curious creatures living in water.

In the aquarium

A clownfish swimming.

Clownfish are now reared in captivity by a handful of marine ornamental farms in the USA. Clownfish were the first species of Saltwater fish to successfully be Tank-raised. Tank-raised fish are a better choice for aquarist, because wild-caught fish are more likely to die soon after purchasing them due to the stress of capture and shipping. Also, tank-bred fish are usually more disease resistant and in general are less affected by stress when introduced to the aquarium. Captive bred clownfishes may not have the same instinctual behavior to live in an anemone. They may have to be coaxed into finding the anemone by the home aquarist. Even then, there is no guarantee that the anemone will host the clownfish.

When a sea anemone is not available in an aquarium, the clownfish may settle in some varieties of soft corals, or large polyp stony corals. If the fish settles in a coral, it could agitate the fish's skin, and, in some cases, may kill the coral. Once an anemone or coral has been adopted, the clownfish will defend it. As there is less pressure to forage for food in an aquarium, it is common for clownfish to remain within 2-4 inches of their host for an entire lifetime.

A clownfish swimming around an anemone.

Taxonomy

- Genus *Amphiprion*:
    - *Amphiprion akallopisos* – Skunk clownfish
    - *Amphiprion akindynos* – Barrier Reef Anemonefish
    - *Amphiprion allardi* – Twobar anemonefish
    - *Amphiprion bicinctus* – Twoband anemonefish
    - *Amphiprion chagosensis* – Chagos anemonefish
    - *Amphiprion chrysogaster* – Mauritian anemonefish
    - *Amphiprion chrysopterus* – Orange-fin anemonefish
    - *Amphiprion clarkii* – Yellowtail clownfish
    - *Amphiprion ephippium* – Saddle anemonefish
    - *Amphiprion frenatus* – Tomato clownfish
    - *Amphiprion fuscocaudatus* – Seychelles anemonefish
    - *Amphiprion latezonatus* – Wide-band Anemonefish
    - *Amphiprion latifasciatus* – Madagascar anemonefish
    - *Amphiprion leucokranos* – Whitebonnet anemonefish
    - *Amphiprion mccullochi* – Whitesnout anemonefish
    - *Amphiprion melanopus* – Fire clownfish
    - *Amphiprion nigripes* – Maldive anemonefish
    - *Amphiprion ocellaris* – Clown anemonefish
    - *Amphiprion omanensis* – Oman anemonefish
    - *Amphiprion percula* – Orange clownfish
    - *Amphiprion perideraion* – Pink skunk clownfish
    - *Amphiprion polymnus* – Saddleback clownfish
    - *Amphiprion rubacinctus* – Red Anemonefish
    - *Amphiprion sandaracinos* – Yellow clownfish
    - *Amphiprion sebae* – Sebae anemonefish
    - *Amphiprion thiellei* – Thielle's anemonefish

    - *Amphiprion tricinctus* – Three-band anemonefish
- Genus *Premnas*:
    - *Premnas biaculeatus* – Maroon clownfish

Sebae anemonefish kika

Allard's clownfish (*Amphiprion allardi*).

Maldive anemonefish (*Amphiprion nigripes*). It is sometimes called the Black-finned anemonefish due to its black pelvic and anal fins.

Pink skunk clownfish (*Amphiprion perideraion*).

Saddleback clownfish (*Amphiprion polymnus*) off Sulawesi, Indonesia.

Yellow clownfish (*Amphiprion sandaracinos*) and sea anemone off Sulawesi, Indonesia.

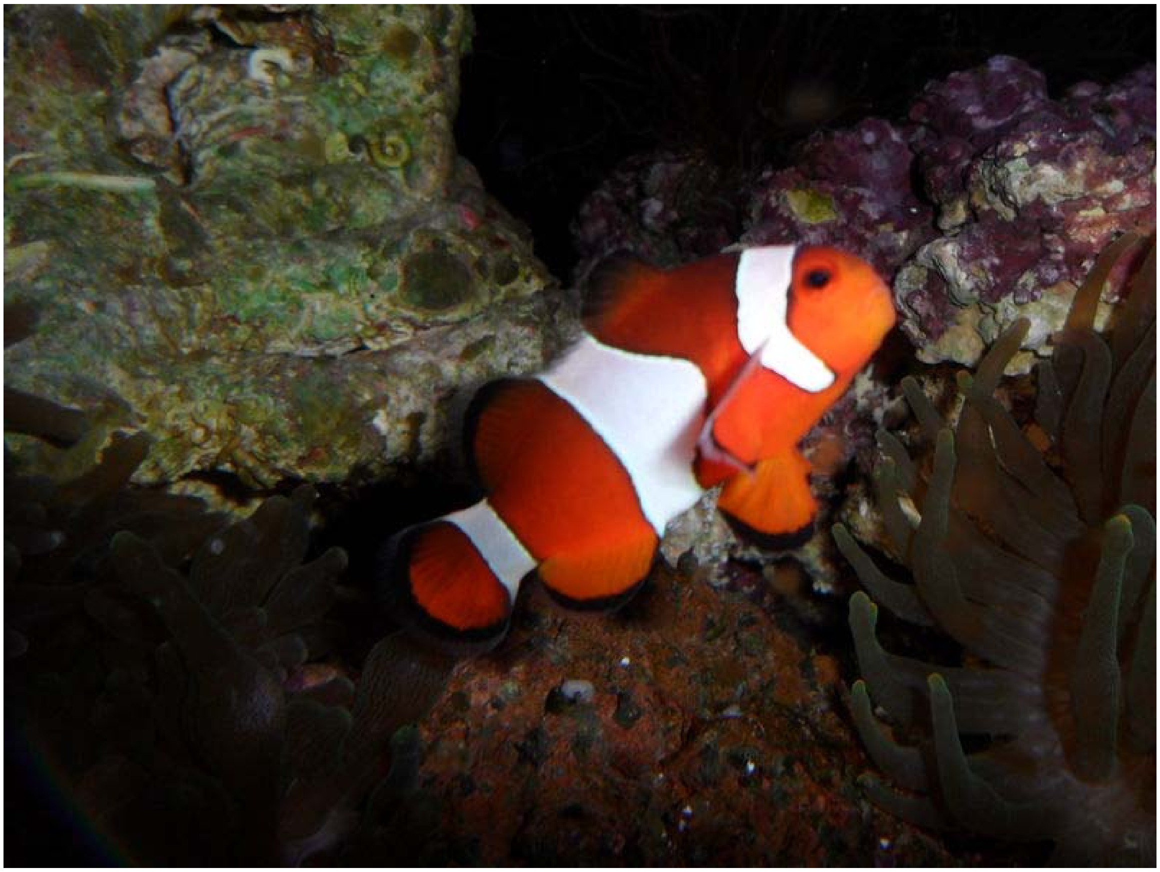
Yellowtail clownfish (*Amphiprion clarkii*) with sea anemone.

Orange-fin anemonefish (*Amphiprion chrysopterus*) is one of the few anemonefish with a white tail.

Twoband anemonefish (*Amphiprion bicinctus*). It is, as suggested by its alternative common name Red Sea clownfish, almost entirely restricted to the Red Sea.

Clown anemonefish (*Amphiprion ocellaris*) occurs in a 'normal' orange and a melanistic blackish variant. The exact taxonomic status of the latter is unclear.

Fire clownfish (*Amphiprion melanopus*) and sea anemone at the Great Barrier Reef.



Clownfish in typical coral reef environment

Maroon clownfish (*Premnas biaculeatus*), here with a tang, is the only member of the genus *Premnas*, and the largest species of clownfish.

Clownfish are initially male; the most dominant fish in a group becomes female.

Chapter 9

Ecosystem

Coral reefs are an example of a marine ecosystem.

Rainforests often have a great deal of biodiversity with many plant and animal species. This is the Gambia River in Senegal's Niokolo-Koba National Park.

An **ecosystem** is a biological environment consisting of all the organisms living in a particular area, as well as all the nonliving, physical components of the environment with which the organisms interact, such as air, soil, water and sunlight. It is all the organisms in a given area, along with the nonliving (abiotic) factors with which they interact; a biological community and its physical environment.

Overview

The entire array of organisms inhabiting a particular ecosystem is called a community. In a typical ecosystem, plants and other photosynthetic organisms are the producers that provide the food. Ecosystems can be permanent or temporary. Ecosystems usually form a number of food webs.

Ecosystems are functional units consisting of living things in a given area, non-living chemical and physical factors of their environment, linked together through nutrient cycle and energy flow.

1. Natural
    1. Terrestrial ecosystem
    2. Aquatic ecosystem
        1. Lentic, the ecosystem of a lake, pond or swamp.
        2. Lotic, the ecosystem of a river, stream or spring.

2. Artificial, ecosystems created by humans.

Central to the ecosystem concept is the idea that living organisms interact with every other element in their local environment. Eugene Odum, a founder of ecology, stated: "Any unit that includes all of the organisms (ie: the "community") in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (i.e.: exchange of materials between living and nonliving parts) within the system is an ecosystem."

Etymology

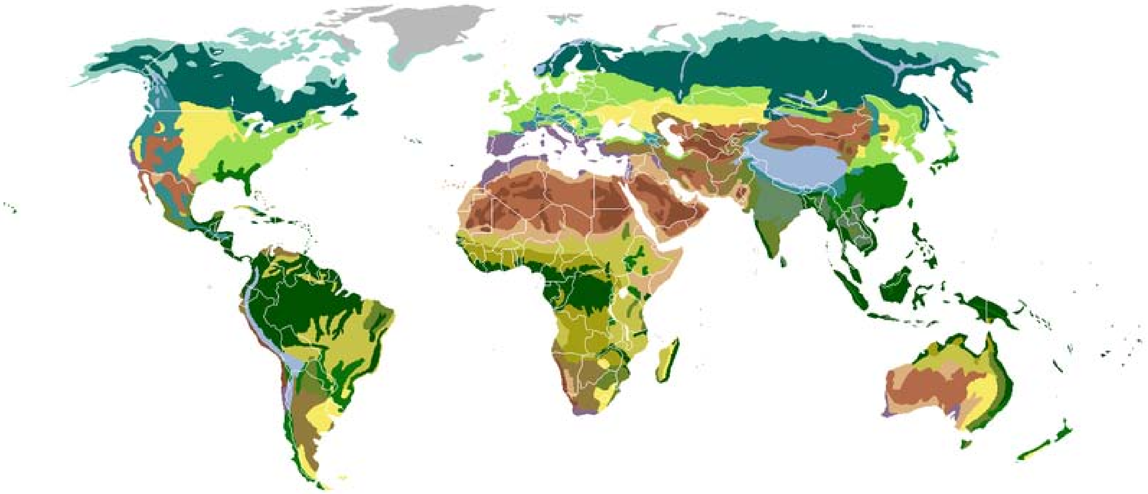
The term ecosystem was coined in 1930 by Roy Clapham to mean the combined physical and biological components of an environment. British ecologist Arthur Tansley later refined the term, describing it as "The whole system, … including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment". Tansley regarded ecosystems not simply as natural units, but as mental isolates. Tansley later defined the spatial extent of ecosystems using the term ecotope.

Examples of ecosystems

- agro-ecosystems
- Agroecosystem
- Aquatic ecosystem
- Chaparral
- Coral reef
- Desert
- Forest
- Greater Yellowstone Ecosystem
- Human ecosystem
- Large marine ecosystem
- Littoral zone
- Lotic
- Marine ecosystem
- Pond Ecosystem
- Prairie
- Rainforest
- Riparian zone
- Savanna
- Steppe
- Subsurface Lithoautotrophic Microbial Ecosystem
- Taiga
- Tundra
- Urban ecosystem

A freshwater ecosystem in Gran Canaria, an island of the Canary Islands.

Biomes



Map of Terrestrial biomes classified by vegetation.

Biomes are a classification of globally similar areas, including ecosystems, such as ecological communities of plants and animals, soil organisms and climatic conditions. Biomes are in part defined based on factors such as plant structures (such as trees, shrubs and grasses), leaf types (such as broadleaf and needleleaf), plant spacing (forest, woodland, savanna) and climate. Unlike ecozones, biomes are not defined by genetic, taxonomic or historical similarities. Biomes are often identified with particular patterns of ecological succession and climax vegetation.

A fundamental classification of biomes is:

1. Terrestrial (land) biomes.
2. Freshwater biomes.
3. Marine biomes.

Classification

Summer field in Belgium (Hamois). The blue flower is Centaurea cyanus and the red one a Papaver rhoeas.

The High Peaks Wilderness Area in the 6,000,000-acre (2,400,000 ha) Adirondack Park is an example of a diverse ecosystem.

Flora of Baja California Desert, Cataviña region, Mexico.

Ecosystems have become particularly important politically, since the Convention on Biological Diversity (CBD) - ratified by 192 countries - defines "the protection of ecosystems, natural habitats and the maintenance of viable populations of species in natural surroundings" as a commitment of ratifying countries. This has created the political necessity to spatially identify ecosystems and somehow distinguish among them. The CBD defines an "ecosystem" as a "dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit".

With the need of protecting ecosystems, the political need arose to describe and identify them efficiently. Vreugdenhil et al. argued that this could be achieved most effectively by using a physiognomic-ecological classification system, as ecosystems are easily recognizable in the field as well as on satellite images. They argued that the structure and seasonality of the associated vegetation, or flora, complemented with ecological data (such as elevation, humidity, and drainage), are each determining modifiers that separate partially distinct sets of species. This is true not only for plant species, but also for species of animals, fungi and bacteria. The degree of ecosystem distinction is subject to the physiognomic modifiers that can be identified on an image and/or in the field. Where necessary, specific fauna elements can be added, such as seasonal concentrations of animals and the distribution of coral reefs.

Several physiognomic-ecological classification systems are available:

- Physiognomic-Ecological Classification of Plant Formations of the Earth: a system based on the 1974 work of Mueller-Dombois and Heinz Ellenberg, and developed by UNESCO. This classificatie "describes the above-ground or underwater vegetation structures and cover as observed in the field, described as plant life forms. This classification is fundamentally a species-independent physiognomic, hierarchical vegetation classification system which also takes into account ecological factors such as climate, elevation, human influences such as grazing, hydric regimes and survival strategies such as seasonality. The system was expanded with a basic classification for open water formations".
- Land Cover Classification System (LCCS), developed by the Food and Agriculture Organization (FAO).
- Forest-Range Environmental Study Ecosystems (FRES) developed by the United States Forest Service for use in the United States.

Several aquatic classification systems are available, and an effort is being made by the United States Geological Survey (USGS) and the Inter-American Biodiversity Information Network (IABIN) to design a complete ecosystem classification system that will cover both terrestrial and aquatic ecosystems.

From a philosophy of science perspective, ecosystems are not discrete units of nature that simply can be identified using the most "correct" type of classification approach. In agreement with the definition by Tansley ("mental isolates"), any attempt to delineate or classify ecosystems should be explicit about the observer/analyst input in the classification including its normative rationale.

Two Giant Sequoias, Sequoia National Park. Note the large fire scar at the base of the right-hand tree; fires do not kill the trees but do remove competing thin-barked species, and aid Giant Sequoia regeneration.

Ecosystem services

Ecosystem services are “fundamental life-support services upon which human civilization depends,”[i] and can be direct or indirect. Examples of direct ecosystem services are: pollination, wood and erosion prevention. Indirect services could be considered climate moderation, nutrient cycles and detoxifying natural substances.

The services and goods an ecosystem provides are often undervalued as many of them are without market value. Broad examples include:

- regulating (climate, floods, nutrient balance, water filtration)
- provisioning (food, medicine, fur)
- cultural (science, spiritual, ceremonial, recreation, aesthetic)
- supporting (nutrient cycling, photosynthesis, soil formation).

Ecosystem legal rights

Ecuador's new constitution of 2008 is the first in the world to recognize legally enforceable Rights of Nature, or ecosystem rights.

The borough of Tamaqua, Pennsylvania passed a law giving ecosystems legal rights. The ordinance establishes that the municipal government or any Tamaqua resident can file a lawsuit on behalf of the local ecosystem. Other townships, such as Rush, followed suit and passed their own laws.

This is part of a growing body of legal opinion proposing 'wild law'. Wild law, a term coined by Cormac Cullinan (a lawyer based in South Africa), would cover birds and animals, rivers and deserts.

Function and biodiversity

Savanna at Ngorongoro Conservation Area, Tanzania.

The side of a tide pool showing sea stars (*Dermasterias*), sea anemones (*Anthopleura*) and sea sponges in Santa Cruz, California.

From an anthropocentric point of view, some people perceive ecosystems as production units that produce goods and services, such as wood by forest ecosystems and grass for cattle by natural grasslands. Meat from wild animals, often referred to as bush meat in Africa, has proven to be extremely successful under well-controlled management schemes in South Africa and Kenya. Much less successful has been the discovery and commercialization of substances of wild organism for pharmaceutical purposes. Services derived from ecosystems are referred to as ecosystem services. They may include

1. facilitating the enjoyment of nature, which may generate many forms of income and employment in the tourism sector, often referred to as eco-tourisms,
2. water retention, thus facilitating a more evenly distributed release of water,
3. soil protection, open-air laboratory for scientific research, etc.

A greater degree of species or biological diversity - commonly referred to as Biodiversity - of an ecosystem may contribute to greater resilience of an ecosystem, because there are more species present at a location to respond to change and thus "absorb" or reduce its effects. “Some theories predict that biodiversity will promote ecosystem integrity in changing climates, because high diversity ensures that functional groups will retain at least one species able to tolerate altered condition." This reduces the effect before the ecosystem's structure is fundamentally changed to a different state. One hypothesis about this is the Rivet Poper Hypothesis. According to Paul and Anne Ehrlich “the diversity of life is something like the rivets on an airplane. Each species plays a small but significant role in the working of the whole, and the loss of any rivet weakens the plane by a small but measurable amount. Pop too many rivets and the plane will crash that is, some vital function will collapse." They are saying if too many species die out then some sort of vital function of the ecosystem such as a food web would collapse causing the ecosystem to fail. When thinking about species as rivets the smaller species would actually be the larger rivet though because of their importance to the ecosystem. Without the smaller species the ecosystem there to produce, the rest would not survive.This is not universally the case and there is no proven relationship between the species diversity of an ecosystem and its ability to provide goods and services on a sustainable level: Humid tropical forests produce very few goods and direct services and are extremely vulnerable to change, while many temperate forests readily grow back to their previous state of development within a lifetime after felling or a forest fire. Some grasslands have been sustainably exploited for thousands of years (Mongolia, Africa, European peat and mooreland communities).

The study of ecosystems

Forest on San Juan Island

Ecosystem dynamics

Loch Lomond in Scotland forms a relatively isolated ecosystem. The fish community of this lake has remained unchanged over a very long period of time.

Introduction of new elements, whether biotic or abiotic, into an ecosystem tend to have a disruptive effect. In some cases, this can lead to ecological collapse or "trophic cascading" and the death of many species within the ecosystem. Under this deterministic vision, the abstract notion of ecological health attempts to measure the robustness and recovery capacity for an ecosystem; i.e. how far the ecosystem is away from its steady state.

Often, however, ecosystems have the ability to rebound from a disruptive agent. The difference between collapse or a gentle rebound is determined by two factors—the toxicity of the introduced element and the resiliency of the original ecosystem.

Ecosystems are primarily governed by stochastic (chance) events, the reactions these events provoke on non-living materials and the responses by organisms to the conditions surrounding them. Thus, an ecosystem results from the sum of individual responses of organisms to stimuli from elements in the environment.The presence or absence of populations merely depends on reproductive and dispersal success, and population levels fluctuate in response to stochastic events. As the number of species in an ecosystem is higher, the number of stimuli is also higher. Since the beginning of life organisms have survived continuous change through natural selection of successful feeding, reproductive and dispersal behavior. Through natural selection the planet's species have continuously adapted to change through variation in their biological composition and distribution. Mathematically it can be demonstrated that greater numbers of different interacting factors tend to dampen fluctuations in each of the individual factors.

Spiny forest at Ifaty, Madagascar, featuring various Adansonia (baobab) species, Alluaudia procera (Madagascar ocotillo) and other vegetation.

Given the great diversity among organisms on earth, most ecosystems only changed very gradually, as some species would disappear while others would move in. Locally, sub-populations continuously go extinct, to be replaced later through dispersal of other sub-populations. Stochastists do recognize that certain intrinsic regulating mechanisms occur in nature. Feedback and response mechanisms at the species level regulate population levels, most notably through territorial behaviour. Andrewatha and Birch suggest that territorial behaviour tends to keep populations at levels where food supply is not a limiting factor. Hence, stochastists see territorial behaviour as a regulatory mechanism at the species level but not at the ecosystem level. Thus, in their vision, ecosystems are not regulated by feedback and response mechanisms from the ecosystem itself and there is no such thing as a balance of nature.

If ecosystems are governed primarily by stochastic processes, through which its subsequent state would be determined by both predictable and random actions, they may be more resilient to sudden change than each species individually. In the absence of a balance of nature, the species composition of ecosystems would undergo shifts that would depend on the nature of the change, but entire ecological collapse would probably be infrequent events.

Arctic tundra on Wrangel Island, Russia.

The theoretical ecologist Robert Ulanowicz has used information theory tools to describe the structure of ecosystems, emphasizing mutual information (correlations) in studied systems. Drawing on this methodology and prior observations of complex ecosystems, Ulanowicz depicts approaches to determining the stress levels on ecosystems and predicting system reactions to defined types of alteration in their settings (such as increased or reduced energy flow, and eutrophication.

In addition, Eric Sanderson has developed the Muir web, based on experience on the Mannahatta project. This graphical schematic shows how different species are connected to each other, not only regarding their position in the food chain, but also regarding other services, i.e. provisioning of shelter,

Ecosystem ecology

Ecosystem ecology is the integrated study of biotic and abiotic components of ecosystems and their interactions within an ecosystem framework. This science examines how ecosystems work and relates this to their components such as chemicals, bedrock, soil, plants, and animals. Ecosystem ecology examines physical and biological structure and examines how these ecosystem characteristics interact.

Chapter 10

Endosymbiont

An **endosymbiont** is any organism that lives within the body or cells of another organism, i.e. forming an **endosymbiosis**. Examples are nitrogen-fixing bacteria (called rhizobia) which live in root nodules on legume roots, single-celled algae inside reef-building corals, and bacterial endosymbionts that provide essential nutrients to about 10%–15% of insects. Many instances of endosymbiosis are obligate- that is, either the endosymbiont or the host cannot survive without the other, such as the gutless marine worms of the genus *Riftia*, which get nutrition from their endosymbiotic bacteria. The most common examples of obligate endosymbiosis are mitochondria and chloroplasts. Some human parasites, e.g. : *Wucherichia bancrofti* and *Mansonella perstans* thrive in their hosts because of an obligate endosymbiosis with *Wolbachi spp.*. They can both be eliminated from their host by treatments that target this bacterium. However, not all endosymbioses are obligate. Also, some endosymbioses can be harmful to either of the organisms involved.

It is generally agreed that certain organelles of the eukaryotic cell, especially mitochondria and plastids such as chloroplasts, originated as bacterial endosymbionts. This theory is called the endosymbiotic theory, and was first articulated by the Russian botanist Konstantin Mereschkowski in 1905.

Endosymbiosis theory and mitochondria and chloroplasts

The endosymbiosis theory attempts to explain the origins of organelles such as mitochondria and chloroplasts in eukaryotic cells. The theory proposes that chloroplasts and mitochondria evolved from certain types of bacteria that eukaryotic cells engulfed through endophagocytosis. These cells and the bacteria trapped inside them entered a symbiotic relationship, a close association between different types of organisms over an extended time. However, more specifically, the relationship was endosymbiotic, meaning that one of the organisms (the bacteria) lived within the other (the eukaryotic cells).

According to endosymbiosis theory, an anaerobic cell probably ingested an aerobic bacterium but failed to digest it. The aerobic bacterium flourished within the cell because the cell's cytoplasm was abundant in half-digested food molecules. The bacterium digested these molecules with oxygen and gained great amounts of energy. Because the bacterium had so much energy, it probably leaked some of it as Adenosine triphosphate into the cell's cytoplasm. This benefited the anaerobic cell because it enabled it to digest food aerobically. Eventually, the aerobic bacterium could no longer live independently from the cell, and it therefore became a mitochondrion. The origin of the chloroplast is very similar to that of the mitochondrion. A cell must have captured a photosynthetic cyanobacterium and failed to digest it. The cyanobacterium thrived in the cell and eventually evolved into the first chloroplast. Other eukaryotic organelles may have also evolved through endosymbiosis; it has been proposed that cilia, flagella, centrioles, and microtubules may have originated from a symbiosis between a Spirochaete bacterium and an early eukaryotic cell, but this is not widely accepted among biologists.

There are several examples of evidence that support endosymbiosis theory. Mitochondria and chloroplasts contain their own small supply of DNA, which may be remnants of the genome the organelles had when they were independent aerobic bacteria. The single most convincing evidence of the descent of organelles from bacteria is the position of mitochondria and plastid DNA sequences in phylogenetic trees of bacteria. Mitochondria have sequences that clearly indicate origin from a group of bacteria called the alpha-Proteobacteria. Plastids have DNA sequences that indicate origin from the cyanobacteria (blue-green algae). In addition, there are organisms alive today, called living intermediates, that are in a similar endosymbiotic condition to the prokaryotic cells and the aerobic bacteria. Living intermediates show that the evolution proposed by the endosymbiont theory is possible. For example, the giant amoeba *Pelomyxa* lacks mitochondria but has aerobic bacteria that carry out a similar role. A variety of corals, clams, snails, and one species of *Paramecium* permanently host algae in their cells. Many of the insect endosymbionts have been shown to have ancient associations with their hosts, involving strictly vertical inheritance. In addition, these insect symbionts have similar patterns of genome evolution to those found in true organelles: genome reduction, rapid rates of gene evolution, and bias in nucleotide base composition favoring adenine and thymine, at the expense of guanine and cytosine.

Further evidence of endosymbiosis are the prokaryotic ribosomes found within chloroplasts and mitochondria as well as the double-membrane enclosing them. It used to be widely assumed that the inner membrane is the original membrane of the once independent prokaryote, while the outer one is the food vacuole (phagosomal membrane) it was enclosed in initially. However, this view neglects the fact that i) both modern cyanobacteria and alpha-proteobacteria are Gram negative bacteria, which are surrounded by double membranes; ii) the outer membranes of the endosymbiotic organelles (chloroplasts and mitochondria) are very similar to those of these bacteria in their lipid and protein compositions. Accumulating biochemical data strongly suggest that the double membrane enclosing chloroplasts and mitochondria derived from those of the ancestral bacteria, and the phagosomal membrane disappeared during organelle evolution. Triple or quadruple membranes are found among certain algae, probably resulting from repeated endosymbiosis (although little else was retained of the engulfed cell).

These modern organisms with endosymbiotic relationships with aerobic bacteria have verified the endosymbiotic theory, which explains the origin of mitochondria and chloroplasts from bacteria. Researchers in molecular and evolutionary biology no longer question this theory, although some of the details, such as the mechanisms for loss of genes from organelles to host nuclear genomes, are still being worked out.

Bacterial endosymbionts in marine invertebrates

Extracellular endosymbionts are also represented in all four extant classes of Echinodermata (Crinoidea, Ophiuroidea, Echinoidea, and Holothuroidea). Little is known of the nature of the association (mode of infection, transmission, metabolic requirements, etc.) but phylogenetic analysis indicates that these symbionts belong to the alpha group of the class Proteobacteria, relating them to *Rhizobium* and *Thiobacillus*. Other studies indicate that these subcuticular bacteria may be both abundant within their hosts and widely distributed among the Echinoderms in general.

Some marine oligochaeta (e.g. Olavius or Inanidrillus) have obligate extracellular endosymbionts that fill the entire body of their host. These marine worms are nutritionally dependent on their symbiotic chemoautotrophic bacteria lacking any digestive or excretory system (no gut, mouth or nephridia).

Symbiodinium *dinoflagellate endosymbionts in marine metazoa and protists*

Dinoflagellate endosymbionts of the genus *Symbiodinium*, commonly known as zooxanthellae, are found in corals, mollusks (esp. giant clams, the *Tridacna*), sponges, and foraminifera. These endosymbionts drive the amazing formation of coral reefs by capturing sunlight and providing their hosts with energy for carbonate deposition.

Previously thought to be a single species, molecular phylogenetic evidence over the past couple decades has shown there to be great diversity in *Symbiodinium*. In some cases there is specificity between host and *Symbiodinium* clade. More often, however, there is an ecological distribution of *Symbiodinium*, the symbionts switching between hosts with apparent ease. When reefs become environmentally stressed, this distribution of symbionts is related to the observed pattern of coral bleaching and recovery. Thus the distribution of *Symbiodinium* on coral reefs and its role in coral bleaching presents one of the most complex and interesting current problems in reef ecology.

Endosymbionts in protists

Mixotricha paradoxa is a protozoan that lacks mitochondria, however, spherical bacteria live inside the cell and serve the function of the mitochondria. *Mixotricha* also has three other species of symbionts that live on the surface of the cell.

Paramecium bursaria, a species of ciliate, has a mutualistic symbiotic relationship with green alga called Zoochlorella. The algae live inside the cell, in the cytoplasm.

Bacterial endosymbionts in insects

Scientists classify insect endosymbionts in two broad categories, 'Primary' and 'Secondary'. Primary endosymbionts (sometimes referred to as P-endosymbionts) have been associated with their insect hosts for many millions of years (from 10 to several hundred million years in some cases), they form obligate associations (see below), and display cospeciation with their insect hosts. Secondary endosymbionts exhibit a more recently developed association, are sometimes horizontally transferred between hosts, live in the hemolymph of the insects, and are not obligate.

Among primary endosymbionts of insects, the best studied are the pea aphid (*Acyrthosiphon pisum*) and its endosymbiont *Buchnera sp.* APS, the tsetse fly *Glossina morsitans morsitans* and its endosymbiont *Wigglesworthia glossinidia brevipalpis* and the endosymbiotic protists in lower termites. As with endosymbiosis in other insects, the symbiosis is obligate in that neither the bacteria nor the insect is viable without the other. Scientists have been unable to cultivate the bacteria in lab conditions outside of the insect. With special nutritionally-enhanced diets, the insects can survive, but are unhealthy, and at best survive only a few generations.

In some insect groups, these endosymbionts live in specialized insect cells called bacteriocytes (also called *mycetocytes*), and are maternally-transmitted, i.e. the mother transmits her endosymbionts to her offspring. In some cases, the bacteria are transmitted in the egg, as in *Buchnera*; in others like *Wigglesworthia*, they are transmitted via milk to the developing insect embryo. In termites, the endosymbionts reside within the hindguts and are transmitted through trophallaxis among colony members.

The primary endosymbionts are thought to help the host either by providing nutrients that the host cannot obtain itself, or by metabolizing insect waste products into safer forms. For example, the putative primary role of *Buchnera* is to synthesize essential amino acids that the aphid cannot acquire from its natural diet of plant sap. Similarly, the primary role of *Wigglesworthia* is probably to synthesize vitamins that the tsetse fly does not get from the blood that it eats. In lower termites, the endosymbiotic protists play a major role in the digestion of lignocellulosic materials which constitutes a bulk of the termites' diet.

Bacteria benefit from the reduced exposure to predators and competition from other bacterial species, the ample supply of nutrients and relative environmental stability inside the host.

Genome sequencing reveals that obligate bacterial endosymbionts of insects have among the smallest of known bacterial genomes and have lost many genes that are commonly found in closely related bacteria. Several theories have been put forth to explain the loss of genes. Presumably some of these genes are not needed in the environment of the host insect cell. A complementary theory suggests that the relatively small numbers of bacteria inside each insect decrease the efficiency of natural selection in 'purging' deleterious mutations and small mutations from the population, resulting in a loss of genes over many millions of years. Research in which a parallel phylogeny of bacteria and insects was inferred supports the belief that the primary endosymbionts are transferred only vertically (i.e. from the mother), and not horizontally (i.e. by escaping the host and entering a new host).

Attacking obligate bacterial endosymbionts may present a way to control their insect hosts, many of which are pests or carriers of human disease. For example aphids are crop pests and the tsetse fly carries the organism *Trypanosoma brucei* that causes African sleeping sickness. Other motivations for their study is to understand symbiosis, and to understand how bacteria with severely depleted genomes are able to survive, thus improving our knowledge of genetics and molecular biology.

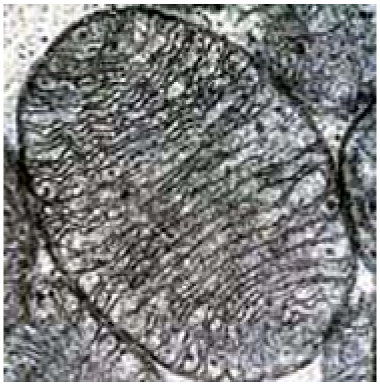
Less is known about secondary endosymbionts. The pea aphid (*Acyrthosiphon pisum*) is known to contain at least three secondary endosymbionts, *Hamiltonella defensa*, *Regiella insecticola*, and *Serratia symbiotica*. *H. defensa* aids in defending the insect from parasitoids. *Sodalis glossinidius* is a secondary endosymbiont tsetse flies that lives inter- and intracellularly in various host tissues, including the midgut and hemolymph. Phylogenetic studies have not indicated a correlation between evolution of *Sodalis* and tsetse. Unlike tsetse's P-symbiont *Wigglesworthia*, though, *Sodalis* has been cultured *in vitro*.

Viral endosymbionts and endogenous retrovirus

During pregnancy in viviparous mammals, endogenous retrovirii (ERVs) are activated and produced in high quantities during the implantation of the embryo. On one hand they act as immunodepressors, and protect the embryo from the immune system of the mother and on the other hand viral fusion proteins cause the formation of the placental syncytium in order to limit the exchange of migratory cells between the developing embryo and the body of the mother, where an epithelium won't do because certain blood cells are specialized to be able to insert themselves between adjacent epithelial cells. The ERV is a virus similar to HIV (the virus causing AIDS in humans). The immunodepressive action was the initial normal behavior of the virus, similar to HIV. The fusion proteins was a way to spread the infection to other cells by simply merging them with the infected one (similar to HIV). It is believed that the ancestors of modern vivipary mammals evolved after an accidental infection of an ancestor with this virus, that permitted the fetus to survive the immune system of the mother.

Chapter 11

Endosymbiotic Theory



Electron micrograph of a mitochondrion showing its mitochondrial matrix and membranes

The **endosymbiotic theory** concerns the mitochondria, plastids (e.g. chloroplasts), and possibly other organelles of eukaryotic cells. According to this theory, certain organelles originated as free-living bacteria that were taken inside another cell as endosymbionts. Mitochondria developed from proteobacteria (in particular, Rickettsiales or close relatives) and chloroplasts from cyanobacteria.

History

The endosymbiotic (from the Greek: endo- meaning inside and -symbiosis meaning cohabiting) theory was first articulated by the Russian botanist Konstantin Mereschkowski in 1905. Mereschkowski was familiar with work by botanist Andreas Schimper, who had observed in 1883 that the division of chloroplasts in green plants closely resembled that of free-living cyanobacteria, and who had himself tentatively proposed (in a footnote) that green plants had arisen from a symbiotic union of two organisms. Ivan Wallin extended the idea of an endosymbiotic origin to mitochondria in the 1920s. These theories were initially dismissed or ignored. More detailed electron microscopic comparisons between cyanobacteria and chloroplasts (for example studies by Hans Ris), combined with the discovery that plastids and mitochondria contain their own DNA (which by that stage was recognized to be the hereditary material of organisms) led to a resurrection of the idea in the 1960s.

The endosymbiotic theory was advanced and substantiated with microbiological evidence by Lynn Margulis in a 1967 paper, *The Origin of Mitosing Eukaryotic Cells.* In her 1981 work *Symbiosis in Cell Evolution* she argued that eukaryotic cells originated as communities of interacting entities, including endosymbiotic spirochaetes that developed into eukaryotic flagella and cilia. This last idea has not received much acceptance, because flagella lack DNA and do not show ultrastructural similarities to bacteria or archaea. According to Margulis and Dorion Sagan, "Life did not take over the globe by combat, but by networking" (i.e., by cooperation). The possibility that peroxisomes may have an endosymbiotic origin has also been considered, although they lack DNA. Christian de Duve proposed that they may have been the first endosymbionts, allowing cells to withstand growing amounts of free molecular oxygen in the Earth's atmosphere. However, it now appears that they may be formed *de novo*, contradicting the idea that they have a symbiotic origin.

It is believed that over millennia these endosymbionts transferred some of their own DNA to the host cell's nucleus during the evolutionary transition from a symbiotic community to an instituted eukaryotic cell (called "serial endosymbiosis"). This hypothesis is thought to be possible because it is known today from scientific observation that transfer of DNA occurs between bacteria species, even if they are not closely related. Bacteria can take up DNA from their surroundings and have a limited ability to incorporate it into their own genome.

Evidence

Evidence that mitochondria and plastids arose from bacteria is as follows:

- New mitochondria and plastids are formed only through a process similar to binary fission. In some algae, such as *Euglena*, the plastids can be destroyed by certain chemicals or prolonged absence of light without otherwise affecting the cell. In such a case, the plastids will not regenerate.
- They are surrounded by two or more membranes, and the innermost of these shows differences in composition from the other membranes of the cell. They are composed of a peptidoglycan cell wall characteristic of a bacterial cell.
- Both mitochondria and plastids contain DNA that is different from that of the cell nucleus and that is similar to that of bacteria (in being circular in shape and in its size).
- DNA sequence analysis and phylogenetic estimates suggest that nuclear DNA contains genes that probably came from plastids.
- These organelles' ribosomes are like those found in bacteria (70S).
- Proteins of organelle origin, like those of bacteria, use N-formylmethionine as the initiating amino acid.
- Much of the internal structure and biochemistry of plastids, for instance the presence of thylakoids and particular chlorophylls, is very similar to that of

cyanobacteria. Phylogenetic estimates constructed with bacteria, plastids, and eukaryotic genomes also suggest that plastids are most closely related to cyanobacteria.
- Mitochondria have several enzymes and transport systems similar to those of bacteria.
- Some proteins encoded in the nucleus are transported to the organelle, and both mitochondria and plastids have small genomes compared to bacteria. This is consistent with an increased dependence on the eukaryotic host after forming an endosymbiosis. Most genes on the organellar genomes have been lost or moved to the nucleus. Most genes needed for mitochondrial and plastid function are located in the nucleus. Many originate from the bacterial endosymbiont.
- Plastids are present in very different groups of protists, some of which are closely related to forms lacking plastids. This suggests that if chloroplasts originated *de novo*, they did so multiple times, in which case their close similarity to each other is difficult to explain.
- Many of these protists contain "primary" plastids that have not yet been acquired from other plastid-containing eukaryotes.
- Among eukaryotes that acquired their plastids directly from bacteria (known as Primoplantae), the glaucophyte algae have chloroplasts that strongly resemble cyanobacteria. In particular, they have a peptidoglycan cell wall between the two membranes.
- Mitochondria and plastids are similar in size to bacteria.

Secondary endosymbiosis

Primary endosymbiosis involves the engulfment of a bacterium by another free living organism. Secondary endosymbiosis occurs when the product of primary endosymbiosis is itself engulfed and retained by another free living eukaryote. Secondary endosymbiosis has occurred several times and has given rise to extremely diverse groups of algae and other eukaryotes. Some organisms can take opportunistic advantage of a similar process, where they engulf an alga and use the products of its photosynthesis, but once the prey item dies (or is lost) the host returns to a free living state. Obligate secondary endosymbionts become dependent on their organelles and are unable to survive in their absence. RedToL, the Red Algal Tree of Life Initiative funded by the National Science Foundation highlights the role red algae or Rhodophyta played in the evolution of our planet through secondary endosymbiosis.

One possible secondary endosymbiosis in process has been observed by Okamoto & Inouye (2005). The heterotrophic protist *Hatena* behaves like a predator until it ingests a green alga, which loses its flagella and cytoskeleton, while *Hatena*, now a host, switches to photosynthetic nutrition, gains the ability to move towards light and loses its feeding apparatus.

The process of secondary endosymbiosis left its evolutionary signature within the unique topography of plastid membranes. Secondary plastids are surrounded by three (in euglenophytes and some dinoflagellates) or four membranes (in haptophytes, heterokonts, cryptophytes, and chlorarachniophytes). The two additional membranes are thought to correspond to the plasma membrane of the engulfed alga and the phagosomal membrane of the host cell. The endosymbiotic acquisition of a eukaryote cell is represented in the cryptophytes; where the remnant nucleus of the red algal symbiont (the nucleomorph) is present between the two inner and two outer plastid membranes.

Despite the diversity of organisms containing plastids, the morphology, biochemistry, genomic organisation, and molecular phylogeny of plastid RNAs and proteins suggest a single origin of all extant plastids – although this theory is still debated.

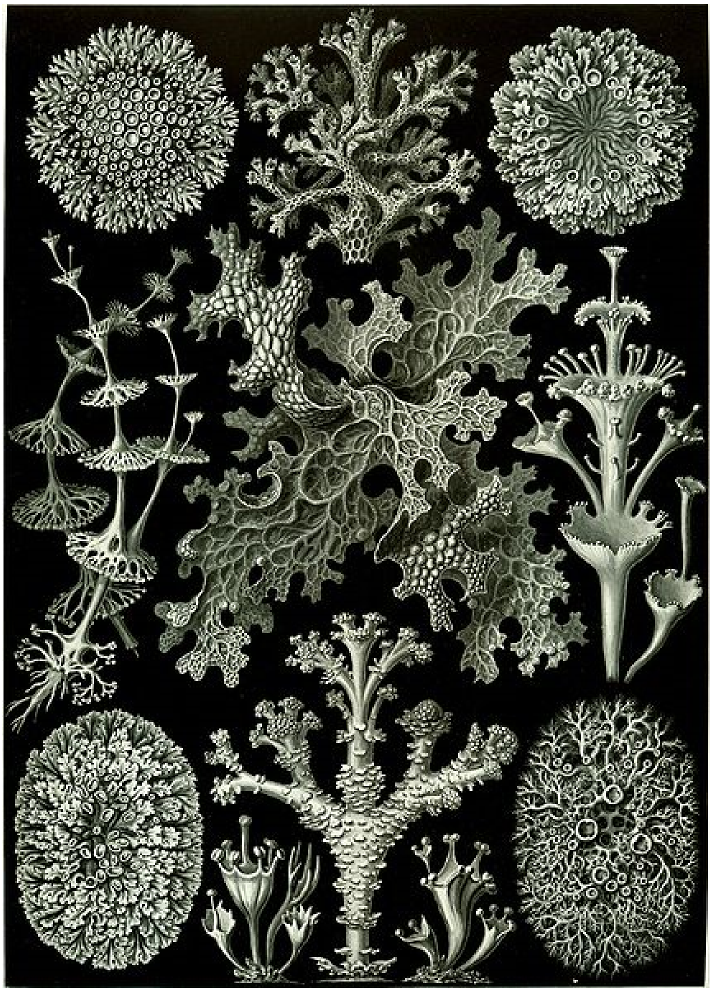
Problems

- Neither mitochondria nor plastids can survive in oxygen or outside the cell, having lost many essential genes required for survival. The standard counterargument points to the large timespan that the mitochondria/plastids have co-existed with their hosts. In this view, genes and systems that were no longer necessary were simply deleted, or in many cases, transferred into the host genome instead. (In fact these transfers constitute an important way for the host cell to regulate plastid or mitochondrial activity.) For example, most plastids are not able to produce respiratory proteins necessary for respiration. Like any living cell, plastids would die if energy is not provided to them by respiration.
- A large cell, especially one equipped for phagocytosis, has vast energetic requirements, which cannot be achieved without the internalisation of energy production (due to the decrease in the surface area to volume ratio as size increases). This implies that, for the cell to gain mitochondria, it could not have been a eukaryote, and must have been a bacterium. This in turn implies that the emergence of the eukaryotes and the formation of mitochondria were achieved simultaneously. This may be explained by possibly a very close symbiotic relationship between two types of bacteria which eventually led to gene exchange and engulfing of the mitochondria precursors through partial fusion or engulfing by the host bacteria.
- Genetic analysis of small eukaryotes that lack mitochondria shows that they all still retain genes for mitochondrial proteins. This implies that all these eukaryotes once had mitochondria. This objection can be answered if, as suggested above, the origin of the eukaryotes coincided with the formation of mitochondria. Alternatively, we may postulate extinction of all other descendants of a mitochondrion-free ancestral eukaryote, perhaps due to competition from the symbiotic clade, or oxygen poisoning as levels continued to rise.

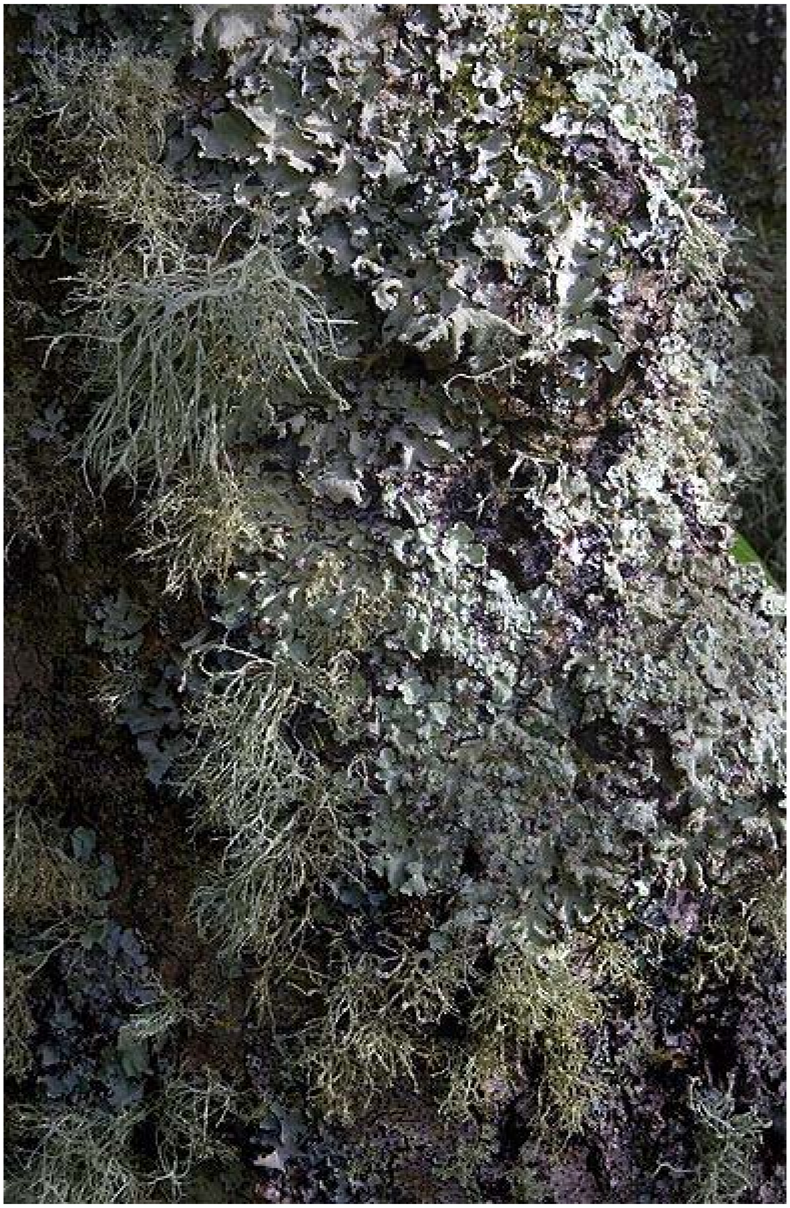
These last two problems are accounted for in the Hydrogen hypothesis.

Chapter 12

Lichen



"Lichenes" from Ernst Haeckel's *Artforms of Nature*, 1904



Lichen-covered tree: Grey, leafy *Parmotrema perlatum* on upper half of trunk; yellowy-green *Flavoparmelia caperata* on middle and lower half and running up the extreme right side; and the fruticose *Ramalina farinacea*. Tresco, Isles of Scilly, UK

Lichens are composite organisms consisting of a symbiotic association of a fungus (the mycobiont) with a photosynthetic partner (the photobiont or phycobiont), usually either a green alga (commonly *Trebouxia*) or cyanobacterium (commonly *Nostoc*). The morphology, physiology and biochemistry of lichens are very different from those of the isolated fungus and alga in culture. Lichens occur in some of the most extreme environments on Earth—arctic tundra, hot deserts, rocky coasts, and toxic slag heaps. However, they are also abundant as epiphytes on leaves and branches in rain forests and temperate woodland, on bare rock, including walls and gravestones, and on exposed soil surfaces (e.g. *Collema*) in otherwise mesic habitats. Lichens are widespread and may be long-lived; however, many are also vulnerable to environmental disturbance, and may be useful to scientists in assessing the effects of air pollution, ozone depletion, and metal contamination. Lichens have also been used in making dyes and perfumes, as well as in traditional medicines.

Overview

The body (thallus) of most lichens is quite different from those of either the fungus or alga growing separately, and may strikingly resemble simple plants in form and growth. The fungus surrounds the algal cells, often enclosing them within complex fungal tissues unique to lichen associations. In many species the fungus penetrates the algal cell wall, forming penetration pegs or haustoria similar to those produced by pathogenic fungi. Lichens are poikilohydric, capable of surviving extremely low levels of water content. However, the re-configuration of membranes following a period of dehydration requires several minutes at least. During this period a “soup” of metabolites from both the mycobiont and phycobiont leaks into the extracellar spaces. This is readily available to both bionts to take up essential metabolic products ensuring a near perfect level of mutualism. Other epiphytic organisms may also benefit from this nutrient rich leachate. This phenomenon also points to a possible explanation of lichen evolution from its original phycobiont and mycobiont components with its subsequent migration from an aquatic environment to dry land.

The algal or cyanobacterial cells are photosynthetic, and as in plants they reduce atmospheric carbon dioxide into organic carbon sugars to feed both symbionts. Both partners gain water and mineral nutrients mainly from the atmosphere, through rain and dust. The fungal partner protects the alga by retaining water, serving as a larger capture area for mineral nutrients and, in some cases, provides minerals obtained from the substrate. If a cyanobacterium is present, as a primary partner or another symbiont in addition to green alga as in certain tripartite lichens, they can fix atmospheric nitrogen, complementing the activities of the green alga.

Algal and fungal components of some lichens have been cultured separately under laboratory conditions, but in the natural environment of a lichen, neither can grow and reproduce without a symbiotic partner. Indeed, although strains of cyanobacteria found in various cyanolichens are often closely related to one another, they differ from the most closely related free-living strains. The lichen association is a close symbiosis: It extends the ecological range of both partners and is obligatory for their growth and reproduction in natural environments. Propagules (diaspores) typically contain cells from both partners, although the fungal components of so-called "fringe species" rely instead on algal cells dispersed by the “core species.”

Lichen associations may be considered as examples of mutualism, commensalism or even parasitism, depending on the species. Cyanobacteria in laboratory settings can grow faster when they are alone rather than when they are part of a lichen. The same, however, might be said of isolated skin cells growing in laboratory culture, which grow more quickly than similar cells that are integrated into a functional tissue. However, from the work of Coxson mutualism would appear to best summarise our current knowledge.

History

Simon Schwendener proposed the dual theory of lichens in 1867.

Although lichens had been recognized as organisms for quite some time, it was not until 1867, when Swiss botanist Simon Schwendener proposed his dual theory of lichens, that the true nature of the lichen association began to emerge. Schwendener's hypothesis, which at the time lacked experimental evidence, arose from his extensive analysis of the anatomy and development in lichens, algae, and fungi using a light microscope. Many of the leading lichenologists at the time, such as James Crombie and Nylander, rejected Schwendener's hypothesis because the common consensus was that all living organisms were autonomous. Other prominent biologists, such as Heinrich Anton de Bary, Albert Bernhard Frank, and Hermann Hellriegel were not so quick to reject Schwendener's ideas and the concept soon spread into other areas of study, such as microbial, plant, animal and human pathogens. When the complex relationships between pathogenic microorganisms and their hosts were finally identified—refuting the idea of holistic organisms—Schwendener's hypothesis began to gain popularity. Further experimental proof of the dual nature of lichens was obtained when Eugen Thomas published his results in 1939 on the first successful re-synthesis experiment.

Symbionts

Living as a symbiont in a lichen appears to be a very successful way for a fungus to derive essential nutrients, as about 20% of all fungal species have acquired this mode of life. The largest number of lichenized fungi occur in the Ascomycota, with about 40% of species forming such an association. Some of these lichenized fungi occur in orders with nonlichenized fungi that live as saprotrophs or plant parasites (for example, the Leotiales, Dothideales, and Pezizales). Other lichen fungi occur in only five orders in which all members are engaged in this habit (Orders Graphidales, Gyalectales, Peltigerales, Pertusariales, and Teleoschistales). Lichenized and nonlichenized fungi can even be found in the same genus or species. Overall, about 98% of lichens have an ascomycetous mycobiont . Next to the Ascomycota, the largest number of lichenized fungi occur in the unassigned fungi imperfecti. Comparatively few Basidiomycetes are lichenized, but these include agarics, such as species of *Lichenomphalia*, clavarioid fungi, such as species of *Multiclavula*, and corticioid fungi, such as species of *Dictyonema*.

The autotrophic symbionts occurring in lichens are simple, photosynthetic organisms commonly and traditionally known as algae. These symbionts include both prokaryotic and eukaryotic organisms. Approximately 100 species of photosynthetic partners from 40 genera and five distinct classes (prokaryotic: Cyanphyceae; eukaryotic: Tribophyceae, Phaephyceae, Chlorophyceae, and Pleurostrophyceae) have been found to associate with the lichen-forming fungi. The prokaryotes belong to the Cyanobacteria, whose representatives are often called bluegreen algae. The bluegreen algae occur as symbionts in about 8% of the known lichens. The most commonly occurring genus is *Nostoc*. The majority of the lichens contain eukaryotic autotrophs belonging to the Chlorophyta (green algae) or to the Xanthophyta (yellow-green algae). About 90% of all known lichens have a green algae as a symbiont, and among these, *Trebouxia* is the most common genus, occurring in about 40% of all lichens. The second most commonly represented green algae genus is *Trentepohlia*. Overall, about 100 species are known to occur as autotrophs in lichens. All the algae are probably able to exist independently in nature as well as in the lichen.

A particular fungus species and algal species are not necessarily always associated together in a lichen. One fungus, for example, can form lichens with a variety of different algae. The thalli produced by a given fungal symbiont with its differing partners will be similar, and the secondary metabolites identical, indicating that the fungus has the dominant role in determining the morphology of the lichen. Further, the same algal species can occur in association with different fungal partners. Lichens are known in which there is one fungus associated with two or even three algal species. Rarely, the reverse can occur, and two or more fungal species can interact to form the same lichen.

Both the lichen and the fungus partner bear the same scientific name, and the lichens are being integrated into the classification schemes for fungi. The alga bears its own scientific name, which bears no relationship to that of the lichen or fungi.

Morphology and structure

Crustose lichens on a wall

Some lichens have the aspect of leaves (foliose lichens); others cover the substrate like a crust (crustose lichens) (*illustration, right*), others such as the genus *Ramalina* adopt shrubby forms (fruticose lichens), and there are gelatinous lichens such as the genus *Collema*.

Although the form of a lichen is determined by the genetic material of the fungal partner, association with a photobiont is required for the development of that form. When grown in the laboratory in the absence of its photobiont, a lichen fungus develops as an undifferentiated mass of hyphae. If combined with its photobiont under appropriate conditions, its characteristic form emerges, in the process called morphogenesis (Brodo, Sharnoff & Sharnoff, 2001). In a few remarkable cases, a single lichen fungus can develop into two very different lichen forms when associating with either a green algal or a cyanobacterial symbiont. Quite naturally, these alternative forms were at first considered to be different species, until they were first found growing in a conjoined manner.

There is evidence to suggest that the lichen symbiosis is parasitic or commensalistic, rather than mutualistic (Ahmadjian 1993). However, this now needs to be re-examined in light of Coxon's work. The photosynthetic partner can exist in nature independently of the fungal partner, but not vice versa. Furthermore, photobiont cells are routinely destroyed in the course of nutrient exchange. The association is able to continue because reproduction of the photobiont cells matches the rate at which they are destroyed. (ibid.)

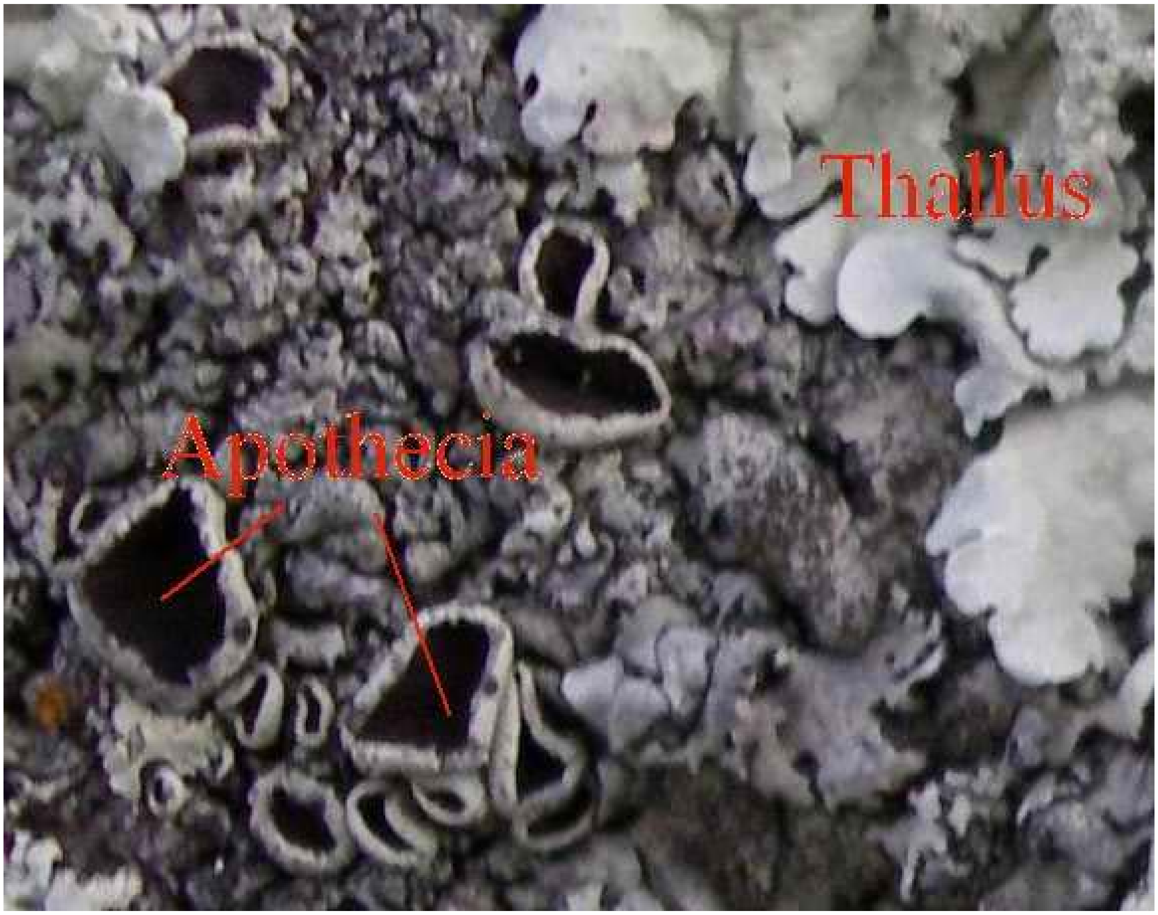
Under magnification, a section through a typical foliose lichen thallus reveals four layers of interlaced fungal filaments. The uppermost layer is formed by densely agglutinated fungal hyphae building a protective outer layer called the cortex, which can reach several hundred µm in thickness. This cortex may be further topped by an epicortex 0.6-1µm thick in some Parmeliaceae, which may be with or without pores, and is secreted by cells—it is not itself cellular. In lichens that include both green algal and cyanobacterial symbionts, the cyanobacteria may be held on the upper or lower surface in small pustules called cephalodia. Beneath the upper cortex is an algal layer composed of algal cells embedded in rather densely interwoven fungal hyphae. Each cell or group of cells of the photobiont is usually individually wrapped by hyphae, and in some cases penetrated by an haustorium. Beneath this algal layer is a third layer of loosely interwoven fungal hyphae without algal cells. This layer is called the medulla. Beneath the medulla, the bottom surface resembles the upper surface and is called the lower cortex, again consisting of densely packed fungal hyphae. The lower cortex often bears rootlike fungal structures known as rhizines, which serve to attach the thallus to the substrate on which it grows. Lichens also sometimes contain structures made from fungal metabolites, for example crustose lichens sometimes have a polysaccharide layer in the cortex. Although each lichen thallus generally appears homogeneous, some evidence seems to suggest that the fungal component may consist of more than one genetic individual of that species. This seems to also be true of the photobiont species involved.

Growth form

Lichens are informally classified by growth form into:

- crustose (paint-like, flat), e.g., *Caloplaca flavescens*
- filamentous (hair-like), e.g., *Ephebe lanata*
- foliose (leafy), e.g., *Hypogymnia physodes*
- fruticose (branched), e.g., *Cladonia evansii*, *C. subtenuis*, and *Usnea australis*
- leprose (powdery), e.g., *Lepraria incana*
- squamulose (consisting of small scale-like structures, lacking a lower cortex), e.g., *Normandina pulchella*
- gelatinous lichens, in which the cyanobacteria produce a polysaccharide that absorbs and retains water.

Reproduction and dispersal



Thalli and apothecia on a foliose lichen

Xanthoparmelia sp.

Many lichens reproduce asexually, either by vegetative reproduction or through the dispersal of diaspores containing algal and fungal cells. *Soredia* (singular soredium) are small groups of algal cells surrounded by fungal filaments that form in structures called *soralia*, from which the soredia can be dispersed by wind. Another form of diaspore are *isidia*, elongated outgrowths from the thallus that break off for mechanical dispersal. Fruticose lichens in particular can easily fragment. Due to the relative lack of differentiation in the thallus, the line between diaspore formation and vegetative reproduction is often blurred. Many lichens break up into fragments when they dry, dispersing themselves by wind action, to resume growth when moisture returns.

Many lichen fungi appear to reproduce sexually in a manner typical of fungi, producing spores that are presumably the result of sexual fusion and meiosis. Following dispersal, such fungal spores must meet with a compatible algal partner before a functional lichen can form. This may be a common form of reproduction in basidiolichens, which form fruitbodies resembling their nonlichenized relatives. Among the ascolichens, spores are produced in spore-producing bodies, the three most common spore body types are the **apothecia**, **perithecia** and the **pycnidia**.

For reproduction, lichen possess isidia, soredia, and undergo simple fragmentation. These structures are also composed of a fungal hyphae wrapped around cyanobacteria. (Eichorn, Evert, and Raven, 2005) While the reproductive structures are all composed of the same components (Mycobiont and Photobiont) they are each unique in other ways. Isidia are small outgrowths on the exterior of the lichen. Soredia are powdery propagules that are released from the top of the thallus. In order to establish the lichen, the soredia propagules must contain both the photobiont and the mycobiont

Growth and longevity

Lichenometry

Lichenometry is a technique used to determine the age of exposed rock surfaces based on the size of lichen thalli. Introduced by Beschel in the 1950s, the technique has found many applications.

Ecology

Lichens must compete with plants for access to sunlight, but because of their small size and slow growth, they thrive in places where higher plants have difficulty growing. Lichens are often the first to settle in places lacking soil, constituting the sole vegetation in some extreme environments such as those found at high mountain elevations and at high latitudes. Some survive in the tough conditions of deserts, and others on frozen soil of the Arctic regions.

A major ecophysiological advantage of lichens is that they are poikilohydric (*poikilo*- variable, *hydric*- relating to water), meaning that though they have little control over the status of their hydration, they can tolerate irregular and extended periods of severe desiccation. Like some mosses, liverworts, ferns, and a few "resurrection plants", upon desiccation, lichens enter a metabolic suspension or stasis (known as cryptobiosis) in which the cells of the lichen symbionts are dehydrated to a degree that halts most biochemical activity. In this cryptobiotic state, lichens can survive wider extremes of temperature, radiation and drought in the harsh environments they often inhabit.

Lichens do not have roots and do not need to tap continuous reservoirs of water like most higher plants, thus they can grow in locations impossible for most plants, such as bare rock, sterile soil or sand, and various artificial structures such as walls, roofs and monuments. Many lichens also grow as epiphytes (*epi*- on the surface, *phyte*- plant) on plants, particularly on the trunks and branches of trees. When growing on plants, lichens are not parasites; they do not consume any part of the plant nor poison it. Some ground-dwelling lichens, such as members of the subgenus *Cladina* (reindeer lichens), however, produce chemicals which leach into the soil and inhibit the germination of plant seeds and growth of young plants. Stability (that is, longevity) of their substrate is a major factor of lichen habitats. Most lichens grow on stable rock surfaces or the bark of old trees, but many others grow on soil and sand. In these latter cases, lichens are often an important part of soil stabilization; indeed, in some desert ecosystems, vascular (higher) plant seeds cannot become established except in places where lichen crusts stabilize the sand and help retain water.

Pine forest with lichen ground-cover

The European Space Agency has discovered that lichens can survive unprotected in space. In an experiment led by Leopoldo Sancho from the Complutense University of Madrid, two species of lichen—*Rhizocarpon geographicum* and *Xanthoria elegans*—were sealed in a capsule and launched on a Russian Soyuz rocket on 31 May 2005. Once in orbit the capsules were opened and the lichens were directly exposed to the vacuum of space with its widely fluctuating temperatures and cosmic radiation. After 15 days the lichens were brought back to earth and were found to be in full health with no discernible damage from their time in orbit.

When growing on mineral surfaces, some lichens slowly decompose their substrate by chemically degrading and physically disrupting the minerals, contributing to the process of weathering by which rocks are gradually turned into soil. While this contribution to weathering is usually benign, it can cause problems for artificial stone structures. For example, there is an ongoing lichen growth problem on Mount Rushmore National Memorial that requires the employment of mountain-climbing conservators to clean the monument.

Lichens may be eaten by some animals, such as reindeer, living in arctic regions. The larvae of a number of Lepidoptera species feed exclusively on lichens. These include Common Footman and Marbled Beauty. However, lichens are very low in protein and high in carbohydrates, making them unsuitable for some animals. Lichens are also used by the Northern Flying Squirrel for nesting, food, and a water source during winter.

Air pollution

Some lichens, like *Lobaria pulmonaria*, are sensitive to air pollution.

Lichens are exposed to air pollutants at all times and, without any deciduous parts, they are unable to avoid the accumulation of pollutants. Also, by lacking stomata and a cuticle, aerosols and gases may be absorbed over the entire thallus surface from which they may readily diffuse to the photobiont layer. Because lichens do not possess roots, their primary source of most elements is the air, and therefore elemental levels in lichens often reflect the accumulated composition of ambient air. The processes by which atmospheric deposition occurs include fog and dew, gaseous absorption, and dry deposition. Consequently, many environmental studies with lichens emphasize their feasibility as effective biomonitors of atmospheric quality.

Not all lichens are equally sensitive to air pollutants, so different lichen species show different levels of sensitivity to specific atmospheric pollutants. The sensitivity of a lichen to air pollution is directly related to the energy needs of the mycobiont, so that the stronger the dependency of the mycobiont on the photobiont, the more sensitive the lichen is to air pollution. Upon exposure to air pollution, the photobiont may use metabolic energy for repair of cellular structures that would otherwise be used for maintenance of photosynthetic activity, therefore leaving less metabolic energy available for the mycobiont. The alteration of the balance between the photobiont and mycobiont can lead to the breakdown of the symbiotic association. Therefore, lichen decline may result not only from the accumulation of toxic substances, but also from altered nutrient supplies that favor one symbiont over the other.

Evolution and paleontology

The evolution of lichens and the phylum Ascomycota is complex and not well understood, but because there are fifteen different classes of Ascomycetes, scientists generally believe that different lichens have evolved independently from one another through analogous evolution. Lichenized fungi have continued to evolve, developing differently than those that do not form lichens.

Lichenization is an ancient nutritional strategy for fungi. The extreme habitats that lichens inhabit are not ordinarily conducive to producing fossils. the oldest fossil lichens in which both symbiotic partners have been recovered date to the Early Devonian Rhynie chert, about 400 million years old. The slightly older fossil *Spongiophyton* has also been interpreted as a lichen on morphological and isotopic grounds, although the isotopic basis is decidedly shaky. It has been suggested—although not yet proven—that the even older fossil *Nematothallus* was a lichen.

It has also been claimed that Ediacaran fossils were lichens; although this claim was met with scepticism and has since been retracted by its author. Lichen-like fossils consist of coccoid cells and thin filaments, preserved in marine phosphorite of the Doushantuo Formation in southern China. These fossils are thought to be 551 to 635 million years old (belonging to the Neoproterozoic era). Discovery of these fossils suggest that fungi developed symbiotic partnerships with photoautotrophs long before the evolution of vascular plants. *Winfrenatia*, an early zygomycetous lichen symbiosis that may have involved controlled parasitism, is an impression found in Scotland, belonging to the early Devonian times. There are also several examples of fossilized lichens embedded in amber. The fossilized *Anzia* is found in pieces of amber in northern Europe and dates back approximately 40 million years. Fossilized *Lobaria* comes from Trinity County in northern California, USA and dates back to the early to middle Miocene.

In 1995, Gargas and colleagues proposed that there were at least five independent origins of lichenization; three in the basidiomycetes and at least two in the Ascomycetes. However, Lutzoni et al. (2000) indicate that lichenization probably evolved earlier and was followed by multiple independent losses. Some non-lichen-forming fungi may have secondarily lost the ability to form a lichen association. As a result, lichenization has been viewed as a highly successful nutritional strategy.

Lichens were a component of the early terrestrial ecosystems, and the estimated age of the oldest terrestrial lichen fossil is 400 Ma;;; Recent (2009) studies suggest that the ancestral ecological state of the Ascomycota was saprobism, and that independent lichenization events have occurred multiple times.

Taxonomy and classification

Lichens are named based on the fungal component, which plays the primary role in determining the lichen's form. The fungus typically comprises the majority of a lichen's bulk, though in filamentous and gelatinous lichens this is not always the case. The lichen fungus is typically a member of the Ascomycota—rarely a member of the Basidiomycota, and then termed **basidiolichens** to differentiate them from the more common **ascolichens**. Formerly, some lichen taxonomists placed lichens in their own division, the **Mycophycophyta**, but this practice is no longer accepted because the components belong to separate lineages. Neither the ascolichens nor the basidiolichens form monophyletic lineages in their respective fungal phyla, but they do form several major solely or primarily lichen-forming groups within each phylum. Even more unusual than basidiolichens is the fungus *Geosiphon pyriforme*, a member of the Glomeromycota that is unique in that it encloses a cyanobacterial symbiont inside its cells. *Geosiphon* is not usually considered to be a lichen, and its peculiar symbiosis was not recognized for many years. The genus is more closely allied to endomycorrhizal genera.

Economic uses

Iwatake (*Umbilicaria esculenta*) gathering at Kumano in Kishū, by Hiroshige II

Food

Lichens are eaten by many different cultures across the world. Although some lichens are only eaten in times of famine, others are a staple food or even a delicacy. Two obstacles are often encountered when eating lichens: lichen polysaccharides are generally indigestible to humans, and lichens usually contain mildly toxic secondary compounds that should be removed before eating. Very few lichens are poisonous, but those high in vulpinic acid or usnic acid are toxic. Most poisonous lichens are yellow.

In the past Iceland moss (*Cetraria islandica*) was an important human food in northern Europe, and was cooked as a bread, porridge, pudding, soup, or salad. Wila (*Bryoria fremontii*) was an important food in parts of North America, where it was usually pitcooked. Northern peoples in North America and Siberia traditionally eat the partially digested reindeer lichen (*Cladina* spp.) after they remove it from the rumen of caribou or reindeer that have been killed. Rock tripe (*Umbilicaria* spp. and *Lasalia* spp.) is a lichen that has frequently been used as an emergency food in North America, and one species, *Umbilicaria esculenta*, is used in a variety of traditional Korean and Japanese foods.

Other Uses

Many lichens produce secondary compounds, including pigments that reduce harmful amounts of sunlight and powerful toxins that reduce herbivory or kill bacteria. These compounds are very useful for lichen identification, and have had economic importance as dyes such as cudbear or primitive antibiotics.

There are reports dating almost 2000 years of lichens being used to extract purple and red colors. Of great historical and commercial significance are lichens belonging to the family Roccellaceae, commonly called orchella weed or orchil. Orcein and other lichen dyes have largely been replaced by synthetic versions. The pH indicator litmus is a dye extracted from the lichen genus *Rocella tinctoria* by boiling.

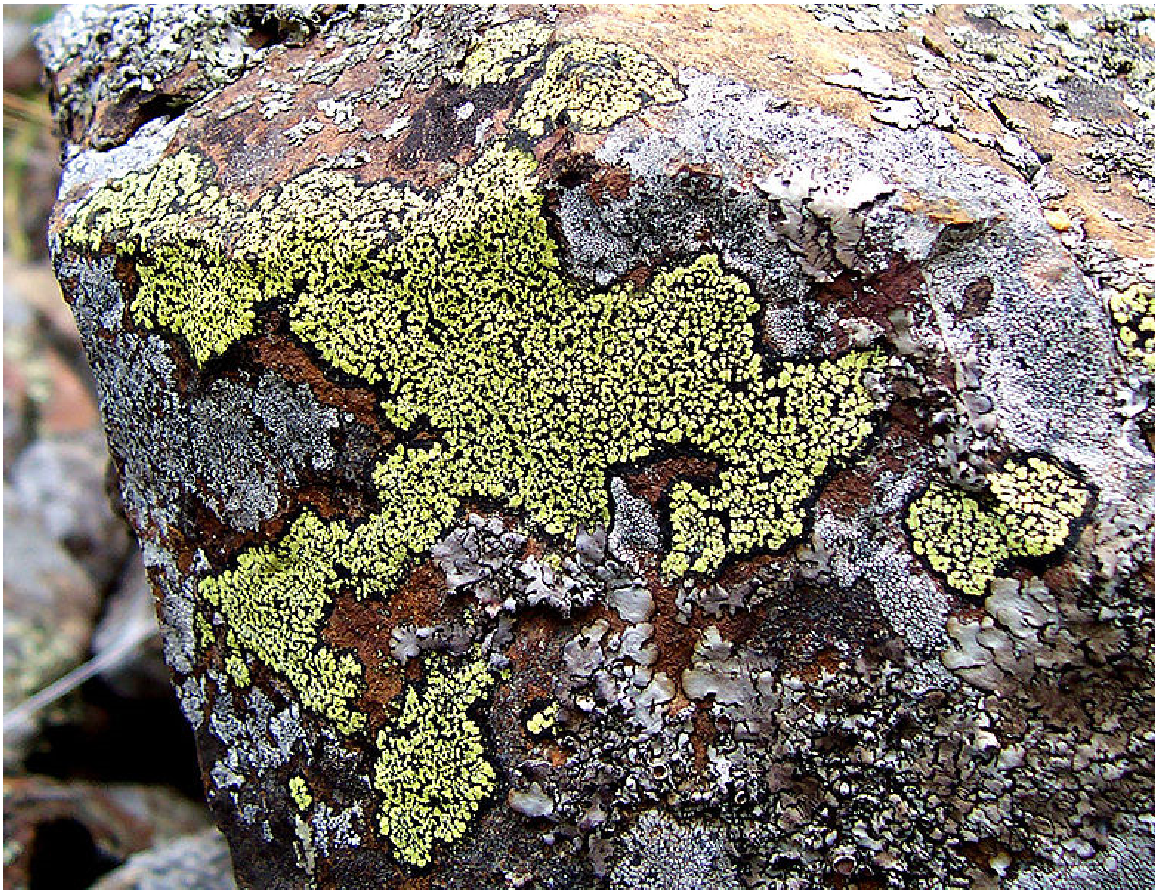
Extracts from many *Usnea* species were used to treat wounds in Russia in the mid-twentieth century.

The substance olivetol is found to be naturally present in certain species of lichens. This is a property it shares with the cannabis plant, which internally produces the related substance olivetolic acid (before using it to biosynthesise tetrahydrocannabinol (THC)).

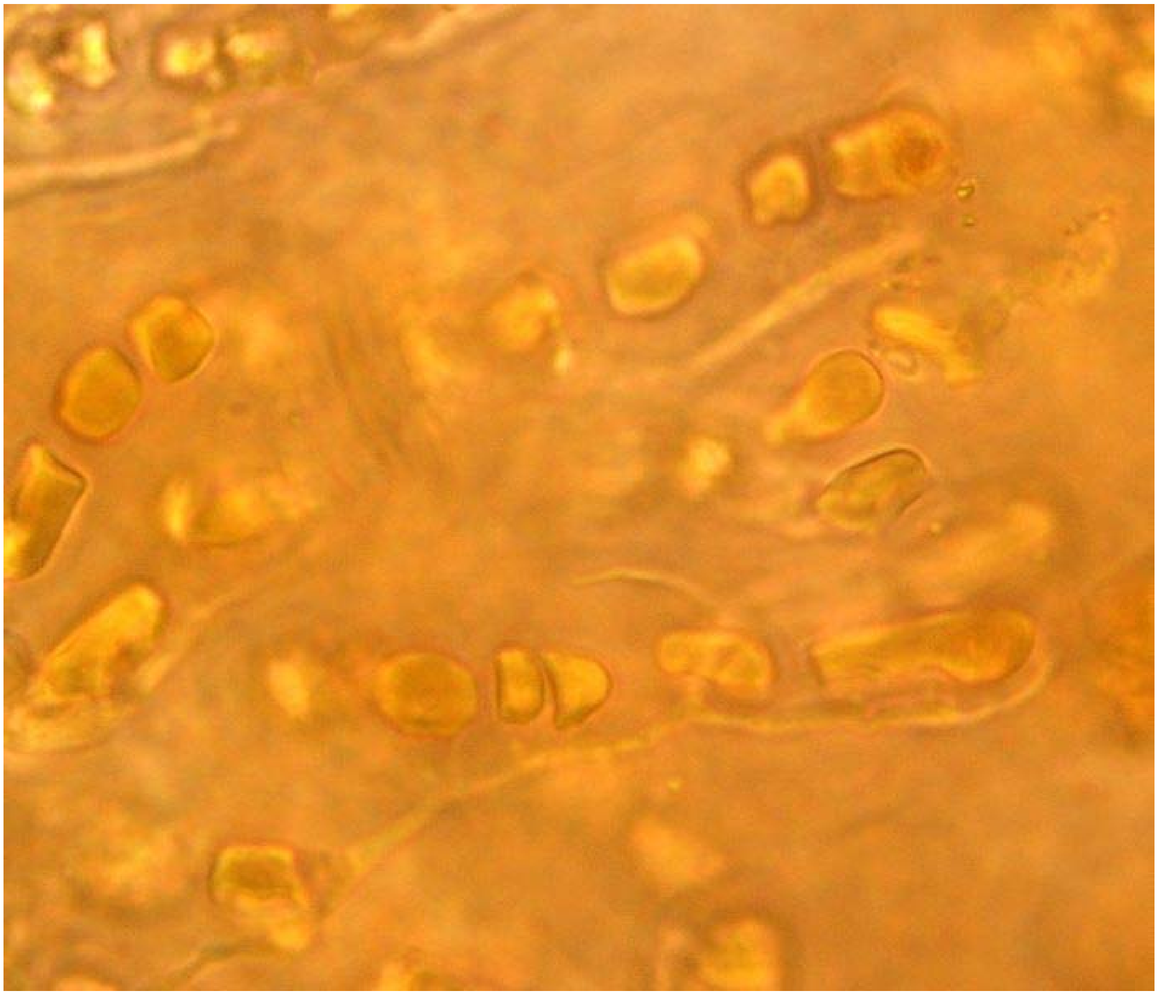
Lichen is used in model railroading and other modeling hobbies as a material for making trees and shrubs.

Xanthoparmelia cf. *lavicola,* a foliose lichen, on basalt.

Usnea australis, a fruticose form, growing on a tree branch



Map lichen (*Rhizocarpon geographicum*) on rock



The cyanobacterium *Hyella caespitosa* with fungal hyphae in the lichen *Pyrenocollema halodytes*

Physcia millegrana (a foliose lichen), with an unlichenized polypore fungus (bottom right), on a fallen log.

Reindeer moss (*Cladonia rangiferina*)

Hypogymnia cf. *tubulosa* with *Bryoria* sp. and *Tuckermannopsis* sp. in the Canadian Rockies

Crustose lichens on limestone in Alta Murgia-Southern Italy

Cladonia cf. *cristatella,* a lichen commonly referred to as 'British Soldiers'. Notice the red tips.

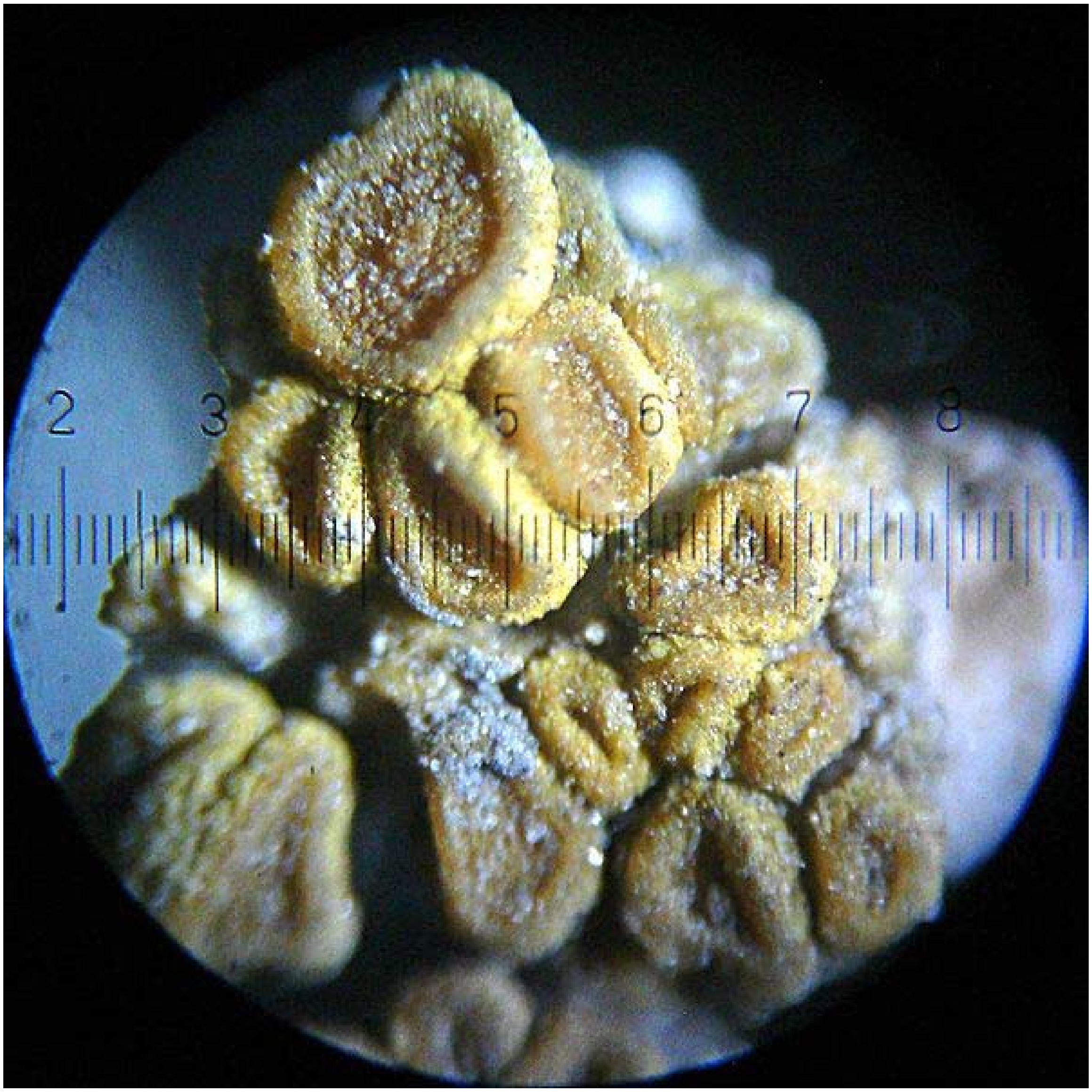
Foliose lichens on rock growing outward and dying in the center. These lichens are at least several decades old.

Letharia sp. with *Bryoria* sp. on pine branches near Blackpine Lake, Washington

Xanthoria sp. lichen on volcanic rock in Craters of the Moon National Monument (Idaho, USA)

Lecanora cf. *muralis* lichen on the banks of the Bega canal in Timisoara

Caloplaca marina, a marine lichen



Microscopic view of lichen growing on a piece of concrete dust.