Symbiosis and parasitism

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Living organisms are permanently closely associated with each other. Their interactions can be classified according to the level of association of the organisms involved, the duration of these interactions and their beneficial (or not) impact on both partners. All intermediate situations exist, forming a true continuum from free organisms that need other organisms to feed themselves to parasites which life cycle is entirely based on specific hosts. Symbiosis and parasitism illustrate -beyond the extreme diversity of situations- that interactions are in all cases essential to partners' lives, and are often at the origin of the emergence of new properties for the systems thus constituted. This is the case, for example, of microbiota associated with each of the living organisms. But it is also the case for organisms modified by parasites that infect them and even disturb the behaviour of infected hosts compared to healthy individuals.

1. Some definitions

The network of interactions and interdependencies that exists between billions of organisms within the biosphere{ind-text}A living space where all the Earth's ecosystems are located, corresponding to the thin layer of the atmosphere, hydrosphere and lithosphere where life is present. This dynamic living space is maintained by an energy supply (mainly due to the sun) and the metabolism of living organisms in interaction with their environment. {end-tooltip}; a level of organization that is founder of the concept of **biodiversity** (read What is biodiversity?). These interactions are most often of mutual benefit and their role in the physiology and adaptation of organisms to the environment is essential. For example, many animals cannot digest without the help of bacteria in their digestive tract, most plants can only use the soil with fungi colonizing their roots, which they feed in return [1].

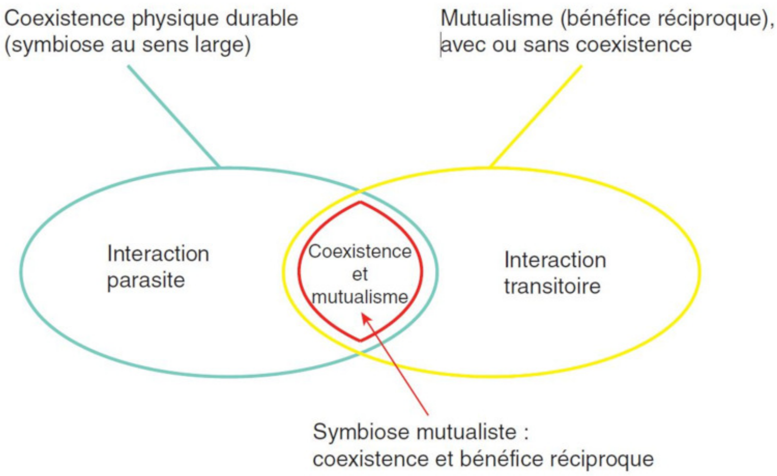

Figure 1. Relationship between symbiosis and mutualism. [Source: From Lefèvre et al.; see ref. [2].

But this is not always the case: interactions between two organisms can be classified according to their beneficial, harmful or neutral effect for both partners. Thus, one can distinguish interactions that are beneficial for one partner and harmful for the other (predation, parasitism), beneficial for one and neutral for the other (commensalism) and mutually beneficial interactions (mutualism). In addition, all intermediate situations exist, in a true continuum of interaction types (Figure 1) [2]. They can also be classified according to their instantaneous (predation) or sustainable nature (parasitism, mutualism, etc.), as well as according to the degree of association between the partners [2]. Etymologically, the term symbiosis refers to "the common life of organisms of distinct species". This broad definition refers to a sustainable coexistence, involving all or part of the life cycle of the two organisms, regardless of the exchanges between them. A more restrictive definition reserves the term symbiosis for sustainable and mutualist coexistence (see red part in Figure 1).

2. Mutualist symbiosis

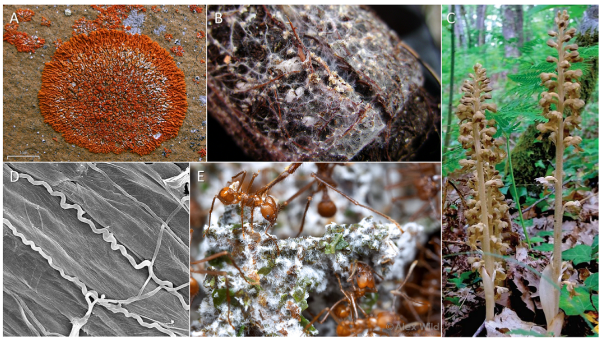

Figure 2. Examples of mutualist symbiosis involving fungi. A, Symbiosis between a green algae and an ascomycete fungus in the lichen Xanthoria elegans [Source: © Jason Hollinger @Mushroom Observer (CC BY-SA 3.0) via Creative Commons]; B, Mycelium (white) of ectomycorhizian fungus associated with the (brown) roots of Picea glauca [© André-Ph. D. Picard (CC BY-SA 3.0) via Wikimedia Commons]; C, Neottia nidus-avis, a non-chlorophyllous plant, exploits the carbon of mycorrhizal fungi and therefore of other plants [Source: © Marc-André Selosse]; D, Neotyphodium coenophialum, an endosymbiotic fungus living in tall fescue (Festuca arundinacea) that it protects from herbivores by secreting an alkaloid toxic for herbivores. [http://betterknowamicrobe.tumblr.com/post/75909408589/neotyphodium-coenophialum]; E. Growing mushrooms from a colony of cephalotic Atta cephalots, microscopic fungi form a white mold that grows on leaf pieces brought by ants. [Source: © Alex Wild/alexanderwild.com, with permission].

The benefits of symbiosis are often trophic{ind-text}Adjective related to the nutrition of an individual, a living tissue. Refers to the relationships between species (predator-prey relationships in particular), the cycles and flows of energy and nutrients within ecosystems between producers, consumers and decomposers. The basic level of this network is that of autotrophic primary production, above this level, each link in a food chain corresponds to a trophic level.{end-tooltip}, when one of the partners accesses a resource of which the other is deprived, or which is limiting it [2]. Many symbiosis thus involve autotrophic organisms{ind-text}Organism that produce organic matter from the reduction of inorganic matter and an external energy source: light (photoautotrophic organism) or chemical reactions (chemoautotrophic organism).{end-tooltip} : in lichens{ind-text}Organisms resulting from a symbiosis between a fungus and an alga. Algae synthesizes organic matter from carbon dioxide (CO_2) in the air and solar radiation (photosynthesis). In return, the fungus removes from the environment the water and mineral salts essential for licenical symbiosis {end-tooltip} (Figure 2A) or mycorrhizae{ind-text}A symbiotic association between the roots of plants and soil fungi. They affect more than 95% of terrestrial plants. They give plants better access to soil nutrients and help them better resist environmental stresses. {end-tooltip} (Figure 2B), a photosynthetic partner -algae or plant respectively- feeds a fungus that in turn exploits water and mineral salts from the environment for itself and its partner. Heterotrophic{ind-text}Qualifies organisms (animals, fungi, some plants, prokaryotes) unable to synthesize their components themselves from simple mineral molecules (CO_2...) and which therefore use sources of exogenous organic matter initially produced by autotrophic organisms.{end-tooltip} organisms also establish trophic links. For example, bird's-nest orchid (*Neottia nidus-avis*, Figure 2C) or pinesap (*Monotropa hypopitys*) are non-chlorophyllous plants that reverse the usual mycorrhizal relationship by exploiting the carbon of their mycorrhizal fungi, thus, indirectly, that of other neighboring plants related to these fungi [3]. Similarly, several groups of colonial insects, ants and termites, have established symbiosis with fungi that they feed in their nests by collecting plant biomass outside the nest (Figure 2D). These insects consume part of the fungus mycelium, which they can digest, while they are unable to digest plant biomass (lignin in particular).

Figure 3. Some symbiotic organisms of a coral reef. A, Clown fish Amphiprion ocellaris in a sea anemone [Source: © Nick Hobgood (CC BY-SA 3.0) via Wikimedia Commons]; B, Symbiotic shrimp Periclimenes yucatanicus in an anemone [Source: © Ilyes Lazlo (CC BY 2.0) via Wikimedia Commons]; C, Zooxantelle of the symbiotic Symbiodinium type of coral [Source: © Penn State/Flickr (CC BY-NC 2.0)]; D, Pygmy seahorse Hippocampus satomiae attached to coral [Source: © John Sear (CC BY 3.0) via Wikicommons]

Endosymbiotic{ind-text}Characterizes a symbiotic association where one of the organisms, called the endosymbiont, is present within the cells of its host. {end-tooltip} bacteria are very common in insects, and complement their often specialized nutrition [5]. For example, sap-sucking hemiptera suffer from a deficiency of essential amino acids, compensated by endosymbiotic bacteria that synthesize them. Symbiosis can protect against environmental stresses, especially when one partner lives inside the other. In mycorrhizae, the fungus is often protected in the root (where it stores its reserves, in the case of some endomycorrhizae), but it can also protect the root when it forms a sleeve around the root (ectomycorrhizae). A fungus of the genus *Neotyphodium* (Figure 2E) lives in symbiosis within the tall fescue *(Festuca arundinacea*) and protects it from herbivores by secreting alkaloids that are toxic to insects and mammals. This fungus spreads from generation to generation by colonizing the seeds [4]. Protection is sometimes the only benefit obtained, as in the cleaning symbiosis of coral ecosystems, where one small animal (fish or shrimp) cleans the skin and/or cavities of the other, eliminating debris and small parasites (Figure 3). However, some anemones in these reefs grow faster, have a greater chance of survival and have a higher density of Zooxanthellae (unicellular symbiotic algae living within sea anemones) when they are visited by fish. This increase in anemone performance is the result of a transfer of nutrients from fish to anemone, which uses the fish's urine as a source of nitrogen and phosphate [5]. These observations show that clownfish contribute to feeding the sea anemone and that their symbiotic algae benefit from this supply [6].

Other benefits depend on the ability of one of the partners to move (pollination by bees, seed dispersal by ants or birds). On the balance sheet, similarly functioning associations have been set up several times during the **evolution**. Such convergences are illustrated by the diversity of insects cultivating fungi (ants, termites, beetles) and eukaryotes{ind-text}Unicellular or multicellular organisms whose cells have a nucleus and organelles (endoplasmic reticulum, Golgi apparatus, various plasters, mitochondria, etc.) delimited by membranes. Eukaryotes are, together with bacteria and archaea, one of the three groups of living organisms. {end-tooltip} that harbour photosynthetic algae in their cells (such as the appearance of chloroplasts{ind-text}Organites of the cytoplasm of photosynthetic eukaryotic cells (plants, algae). As a site of photosynthesis, chloroplasts produce O_2 oxygen and play an essential role in the carbon cycle: they use light energy to fix CO_2 and synthesize organic matter. They are thus responsible for the autotrophy of plants. Chloroplasts are the result of the endosymbiosis of a photosynthetic prokaryote (cyanobacterium type) in a eukaryotic cell, about 1.5 billion years ago.{end-tooltip} in the **eukaryotic cell**) (see Symbiosis and evolution). All the organizations have had the opportunity to contract, during their evolution, one or more mutualist symbiosis(s). This is particularly true for large multicellular organisms, which constitute an ecosystem for microscopic organisms. The **rhizosphere** (the soil surrounding the root of plants) or the digestive tract of animals are thus major microbial niches, populated by thousands of species for each individual host, some of whose occupants are favourable to the host. As a result, each organism has a procession of symbiotes, especially developed in multicellular organisms.

3. Emerging symbiosis properties

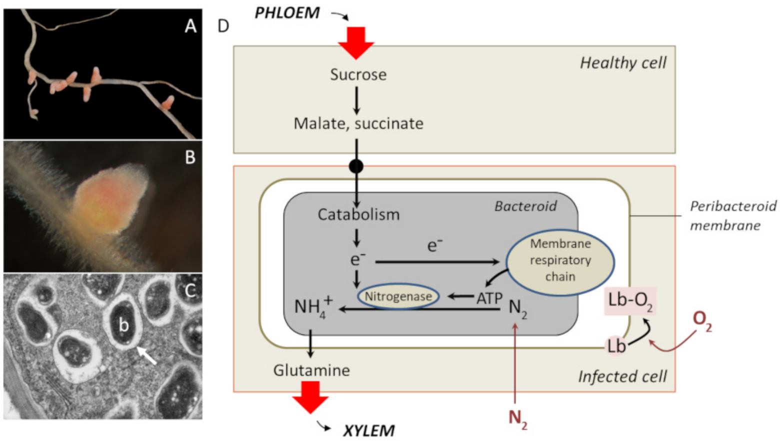

Figure 4. Legume nodules. A, Nodosities due to Sinorhizobium meliloti bacteria on a Medicago root (note the pink color, due to an oxygen-carrying protein, leghemoglobin, Lb); B, View of a section of a nodosity due to Sinorhizobium meliloti bacteria on a Medicago root ; C, Transmission electron microscopy showing symbiotic bacteroids (b) (Bradyrhyzobium japonicum) in soybean root nodules, surrounded by an endocytosis membrane (white arrow); D, Nodosities metabolism, bacteroids ensure nitrogen fixation through a controlled supply of oxygen and carbonaceous substrates from the plant. A & B: [Source: © Ninjatacoshell (CC BY-SA 3.0) via Wikimedia Commons]. C: [Source: © Louisa Howard - Dartmouth Electron Microscope Facility, via Wikimedia Commons].

Further to the addition of partners' capacities, mutualistic symbiosis expresses certain properties that separate partners do not have. First, at the morphological level, symbiosis creates structures that do not exist outside the association: this is the case of nodules (Figure 4A and B), organs induced by bacterial colonization whose anatomy differs from the roots (frequent absence of terminal meristem, vessels conducting peripheral sap, etc.). The structure of bacteria is also modified by living in the cell: loss of flagella, wall and increased size (as in nodules, Figure 4C). This modified morphology is called "**bacteroids**" due to small proteins injected into the bacteria by the plant.

Other emergences are functional. In the example of nodules (Figure 4D), the bacteroid uses energy obtained from its respiration to reduce -thanks to the nitrogenase{ind-text}Enzyme complex specific to certain prokaryotes that catalyzes the complete sequence of reactions during which the reduction of dinitrogen N_2 leads to the formation of ammonia NH_3. This reaction is accompanied by hydrogenation. {end-tooltip}- the atmospheric nitrogen N_2 to ammonium NH_3, which serves as a source of nitrogen for the plant (and bacteroid). Conversely, the plant provides carbon and oxygen supply. Oxygen is required for respiration, but nitrogenase is inactivated by oxygen: this contradiction explains why a free rhizobium{ind-text} Aerobic soil bacterium that can create symbiosis with legumes. These bacteria are found in nodules where they will fix and reduce atmospheric nitrogen, which can then be assimilated by the plant. In exchange plants provide carbonaceous substrates to bacteria. {end-tooltip} in the soil is unable to fix nitrogen. On the other hand, in the nodosity, oxygen does not diffuse freely, but is captured by a protein of the host cell, **leghaemoglobin** [7]**.** Located around the bacteroid, leghaemoglobin protects the nitrogenase from the inactivating effects of the oxygen and provides an oxygen reserve for bacteria respiration. Nitrogen fixation can therefore only be achieved within in the nodosity.

Many other functional traits are induced by symbiosis, such as some protective effects that rely on the induction of partner defences, tolerated by the symbiont but harmful to pathogens. Mycorrhizal fungi, for example, induce the accumulation of protective tannins at the root level, which are responsible for inducing an increased level of defence and reactivity throughout the plant, including the aerial parts. Thus, the mycorrhized plant reacts faster and more strongly to an herbivore or parasite than a non-mycorrhized control plant. In lichens, algae induce the fungus to synthesize secondary metabolites that have a protective role against strong light and herbivores.

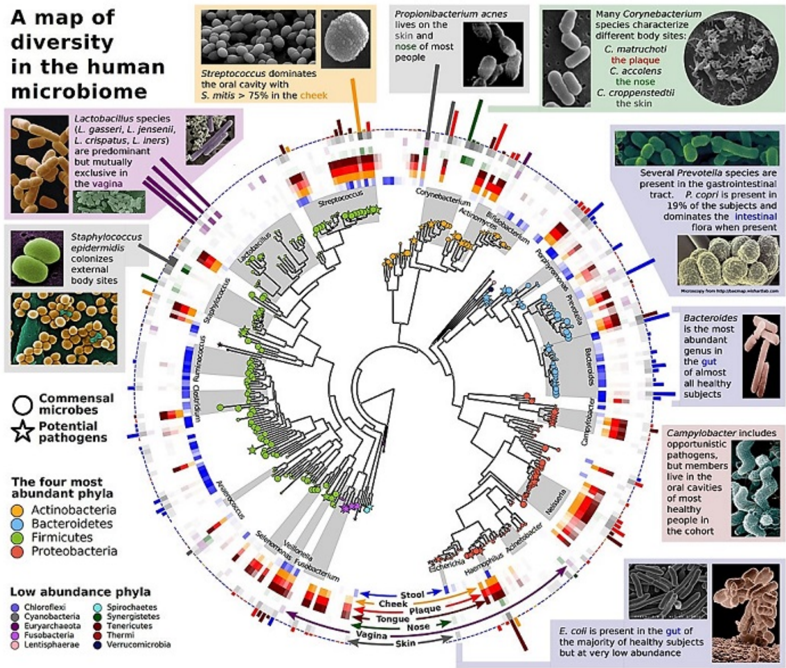

Figure 5. Representation of the diversity of the human microbiome. In the centre is the phylogenetic tree representing the species of the microbiota. On the periphery, representation of specific microbiota (gut, stomach, mouth, vagina, etc.). [Source: Scheme reproduced from Morgan et al (2013); See ref. [9].]

Overall, the phenotype{ind-text}All the observable characteristics of an individual. {end-tooltip} of the organism therefore also results from its symbionts, either by adding their capacities or because they modify it. The phenotype is therefore more than what the genome encodes. Symbionts and their genes are part of what Dawkins [8] calls an "extended phenotype", that is, the set of elements recruited into the environment that modify the phenotype of a species. In humans, for example, the digestive tract contains a large number of bacterial species (Figure 5): **metagenomic** analysis applied to our intestine has shown that it contains nearly 100,000 billion microorganisms, ten times more than our own cells! This is called the **microbiota** (see Human microbiotas: allies for our health).

The gut microbiota{ind-text}All microorganisms (bacteria, yeasts, fungi, viruses) living in a specific environment (called microbiome) in a host (animal or plant). An important example is the set of microorganisms living in the intestine or intestinal microbiota, formerly called "intestinal flora".{end-tooltip} is essential for the proper functioning of its human host, not only in terms of digestion or vitamin production, of course, but also for metabolism, immunity... or the nervous system. The imbalances in the intestinal flora are now suspected of being at the origin of a series of pathologies: obesity, diabetes, cardiovascular diseases, allergies, inflammatory diseases, even autism [2],[7]. The human microbiota is not limited to the digestive tract: international metagenomic programs have identified genes from a large number of symbiotic microorganisms living in the mouth, nose, vagina or on the skin (Figure 5).

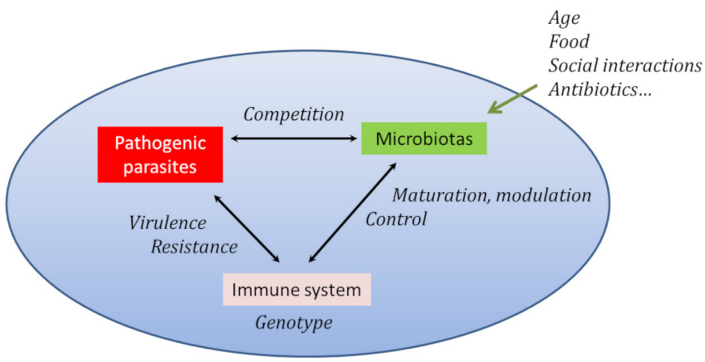

Figure 6. Microbial modulation of interactions between a host and its parasites/pathogens. The action of the host genotype (represented by the blue ellipse) and all environmental factors that affect the composition of the microbiota will affect the interaction between the host and its parasites/pathogens, particularly through the immune system. [Source: Adapted from Gross et al. [See ref. 10]]

The microbiota is able to modulate the interactions between a host and its parasites/pathogens (Figure 6). The action of the microbiota can be direct (competition) or indirect through its action on the establishment, maturation and functioning of the immune system. We know, by studying mice raised in an axenic{end-text} Caracterise a culture (of prokaryotic or eukaryotic cells, tissues, living organisms) free of all saprophytic or pathogenic germs. {end-tooltip} environment, that the development of the nervous system and even the behaviour are partly influenced by it!

It has therefore been proposed that the unit relevant for biology or evolution should be less the organism than the symbiotic procession: we speak of holobionte{ind-text}means the biological unit composed of the host (plant or animal) and all its microorganisms.{end-tooltip} to name this entity more relevant to the importance of biotic interactions [11].

4. Parasitism, an evolutionary success story

If one of the partners in the symbiosis discovers how to use the other effectively, it becomes a parasite. There is indeed a continuum between symbiosis and parasitism [5]. The parasite exploits resources provided by another unrelated individual, the host, to the detriment of the latter. Parasitism is a long-lasting interaction with a host, unlike predation, where the interaction lasts only as long as the time of capture and digestion. However, from an evolutionary point of view, it can be said that predation is only an extreme form of parasitism. There are parasites that slowly kill their host. This is the case of plant parasitic fungi (Mildew, Armillaries, Hoof fungus, etc...) that complete their life cycle on dead tissues. When a cheetah grabs an antelope, there is an exchange of energy and only energy. In host parasite systems where the host survives (referred to as biotrophic parasitism), the duration of the interaction is quite different: the two organisms then live together, often one in the other, sometimes cell in cell or even genome within genome. The genetic information of each partner is expressed side by side and durably in a tiny portion of space [11].

All living beings are affected by parasitism as hosts or parasites (Figure 7). Among the known species, 30% of the approximately 2 million eukaryotic species are thought to be parasites [12]. The best known parasito-fauna{ind-text}All the parasitic fauna of an organism. {end-tooltip} is that of man. It consists of 179 species of parasites, 35 of which appear to be specific to *Homo sapiens* [13]. This image can be increased by hyperparasitism (parasite's parasites), a widespread phenomenon in parasitic arthropods and parasitoids{ind-text}An organism that develops on or in a "host" organism in a two-phase process: it is first biotrophic and then predatory, leading to the final death of the host.{end-tooltip} [14]. Recent estimates suggest that the world of **viruses**, which parasitize cells by diverting their functioning to the production of new viral particles, has been profoundly underestimated. They are present in all ecosystems and would constitute the most abundant and diversified genetic entities in living organisms [15].

For evolutionists{ind-text}Partisans of evolutionism, who believe that species evolve over time,{end-tooltip}, host-parasite models raise countless questions about parasitism itself, the evolutionary dynamics of their interactions, and the evolutionary consequences on host species. The role played by parasites on the world of free species is indeed enormous. The success of the parasitic lifestyle has never been denied throughout the evolutionary process because a host offers, to any organism that knows how to exploit it, not only habitat and food but also an effective means of dispersal. While in the past, research has focused on the direct effects of pathogens on the fertility and survival of their hosts, current research illustrates consequences on such diverse traits as behaviour, selection processes and life history, to name but a few.

Figure 7. Some examples showing the diversity of parasitic organisms and their host. A, Cymothoa exigua, parasitic crustacean, it attaches itself to the base of the tongue of a fish, here a marbled one (Lithognathus mormyrus) [Source: © Marco Vinci (CC BY-SA 3.0) via Wikimedia Commons]; B, Egg bags of the parasitic copepod Acanthochondria cornuta on the lid of a fish (Platichthys flesus), the length of the bags is about 4 mm, [Source: © Hans Hillewaert, via Wikimedia Commons]; C, Engraving made by Delorieux (1831) [see ref. 16] representing a tapeworm (Taenia solis); D. Tropical ant (Cephalotes atratus) infected by a parasitic nematode [Source: © Steve Yanoviak/University of Arkansas via Wikimedia Commons]; E, Rotifer parasitizing a volvox colony [Source: © Michel Delarue, BioMedia-UPMC]; F, Chinese silkworm pest Tussah (Antheraea pernyi) colonized by Cordyceps militaris [Source: © Zheng et al. ref. 17]; G, Scatophagus of manure (Scathophaga stercoraria) colonized by the parasitic fungus Entomophthora muscae [Source: © Hans Hillewaert via Wikimedia Commons]; H, Anonconotus orthopter parasitized by a nematomorphic vertex [Source: © Roger de La Grandière].

As for any living organism, the biological traits of parasites are subjected to selection pressures exerted by their environment. Body size in the adult stage is by far the most important trait, since it can determine the value of other key traits (longevity or fertility). But parasites are likely to adjust their development if growth conditions (host feeding, intraspecific{ind-text}Term that describes the relationships that are established between individuals belonging to the same species.{end-tooltip} and interspecific{ind-text}Term that describes the relationships that are established between individuals belonging to different species.{end-tooltip} competition) are not optimal. In addition, the maximum size of a pest remains limited by the space available on or within the host (Figure 7). Finally, there is generally a sexual dimorphism{ind-text}Set of morphological differences more or less marked between male and female individuals of the same species.{end-tooltip} in the adult size of parasites: females are often much larger than males.

5. Parasitic cycles

The parasite cycle is the result of the transformations undergone by a parasite during its lifetime to ensure its reproduction, in the various ecological niches it occupies: host(s), external environment. While many parasite species have simple cycles, exploiting a single host species, others successively exploit several host species: this allows seasonal relays, or to multiply infectious forms, because the success rate of host colonization is often low. The complexity of the cycles has appeared several times independently during the evolution. Among the most complex records, we can mention the case of the trematode *Halipegus ovocaudatus* whose cycle includes 4 obligatory hosts: a mollusc, a crustacean copepod, a dragonfly larva and a frog. In addition to these extreme situations, complex cycles with two or three hosts are found, particularly in helminths{ind-text} Generic term that includes various types of worms that are generally parasitic: roundworms (nematodes), thorny trunk worms (acanthocephalus - "thorny-headed" worms) and flatworms (plathelminths : these are codes and trematodes). {end-tooltip} or rust (pathogenic fungi). In addition to the complexity of simple cycles, there are also complex cycles during the evolution of secondary simplifications.

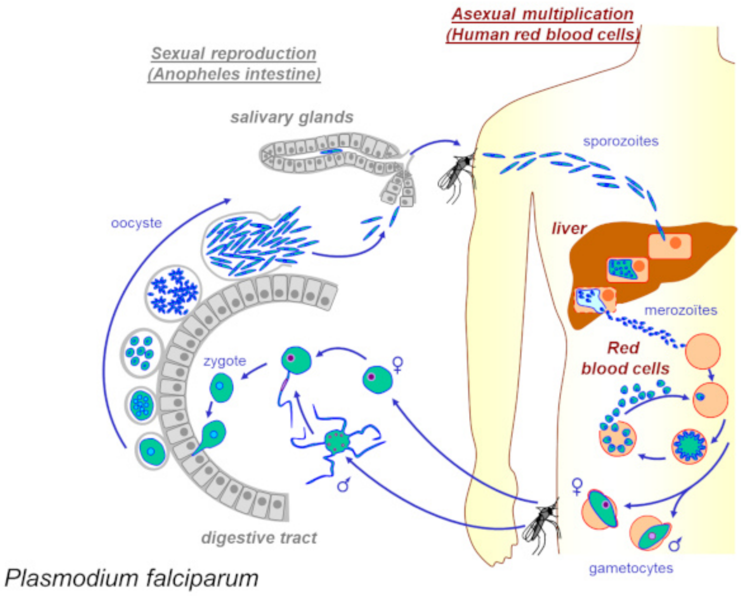

Figure 8. Parasitic cycle of Plasmodium falciparum, causal agent of Malaria. The plasmodium cycle (cf. focus) has two phases in humans (in liver and blood) and in mosquitoes (in the intestine and salivary glands); [Source: scheme by © Eric Maréchal].

Figure 8 describes the example of a parasitic cycle with two hosts, the causative agent of Malaria, *Plasmodium falciparum* which successively infects an Anopheles mosquito and humans (see Focus Plasmodium falciparum). During its life cycle, *Plasmodium* presents extremely varied forms. After being introduced into humans via an infected mosquito bite, *Plasmodium* migrates very rapidly into liver cells via the bloodstream and multiplies intensely without causing symptoms. In some cases, the parasite may persist in the liver in a latent form, causing recurrences of malaria attacks years after the first infection. Then, the thousands of parasites formed leave the liver cells and colonize the red blood cells where they multiply, then destroy the infected cells before infecting new ones. By biting a sick person, an *Anopheles* mosquito ingests male and female forms of *Plasmodium* present in the blood. The parasites reproduce in the insect's digestive tract, and then pass through its salivary glands, from where they can infect other people at a future bite.

When infected with plasmodium, mosquitoes change their behaviour: they become more active, more aggressive and bite more people, thus increasing their probability of transmission [2]. These changes seem to be synchronized with the development of the parasite (e.g. decrease in mosquito bite rate when the parasite is immature, and increase when the parasite has reached the transmissible stage). Once in the vertebrate host, these same parasites seem to be able to modify the odours of the hosts to make them more attractive to mosquito vectors. This change in host behaviour after infection is a characteristic example of parasitic manipulation [2].

6. Parasitic manipulations

Some parasites are capable of significantly modifying the physiology, morphology or behaviour of their host with the consequence of increasing their probability of transmission. This host exploitation strategy is now described in many host parasite systems phylogenetically{ind-text}Adverb describing the result of an analysis of the relationship relationships between distant living things.{end-tooltip} distant. Phenotypic {end-text} Characterize a trait or character of a living organism (anatomical, physiological, molecular or behavioural aspects), which can be analyzed.{end-tooltip} changes in infected hosts are generally considered an illustration of the extended phenotype concept [18]. These phenotypic changes actually correspond to the expression of the parasite's genes and the effect of the corresponding proteins on the host's phenotype. According to this idea, these induced modifications are adaptive for the parasite and not for the host.

Figure 9. Some examples of the diversity of parasitic manipulations. A, Ladybird caring for the larvae of the wasp Dinocampus coccinellae [Source: © BeatWalkerCH (CC BY-SA 3.0) via Wikimedia Commons]; B, Brazilian Forest Ant parasitized by the fungus Ophiocordyceps camponoti-rufipedis [Source: © David Hughes, Penn State University] ; C, Carterpillar from the butterfly Thyrinteina leucocerae caring for the pupae of the Glyptapantel wasp [Source: © José Lino-Neto (CC BY 2.5) via Wikimedia Commons]; D, Leucochloridium paradoxum infecting the snail Succinea putris [Source: © Studyblue Vancouver Island University]; E, Crustacean Sacculina carcini parasitizing crab Liocarcinus holsatus [Source: © Hans Hillewaert via Wikimedia Commons].

Figure 9 presents some examples of the diversity of parasitic manipulation. The parasite will often manipulate the host to take care of its offspring. Thus, after the larvae of the parasitic wasp *Dinocampus coccinellae* emerged from the abdomen of the parasitized ladybird, then transformed into a cocoon, the ladybird will take care of it and protect the cocoon until the wasp emerges (Figure 9A). The *Glyptapanteles* wasp lays eggs inside the caterpillar of the butterfly *Thyrinteina leucocerae*, which will change its behaviour after the eggs hatch and transform them into pupae: it stops feeding, becomes immobile, and protects the pupae from predators until they hatch (Figure 9C). Some manipulations are even more extreme. By invading an ant in the Brazilian forest, the fungus *Ophiocordyceps camponoti-rufipedis* (Figure 9B) manipulates its behaviour by taking control of its "brain", leading the ant to climb to the top of a plant where conditions (light, humidity) are favourable to the fungus' development. Once the ant is firmly attached to the stem, the fungus kills it and grows slowly: the spores produced are then easily dispersed. A somewhat similar strategy is being implemented for the snail *Succinea putris* infected with the parasite *Leucochloridium paradoxum*. The latter is housed in the snail's antennas, which will take on the appearance and movements of a worm, becoming a prey that is all the more noticeable for birds as the snail's behaviour is also modified because it tends to leave the protection of vegetation. The life cycle of the parasite continues in the bird whose droppings allow the spread of parasite eggs (Figure 9E). Sacculin *(Sacculina carcini*), a small crab parasite crustacean, colonizes its host, alters its hormonal balance and prevents it from reproducing, its only function being to feed the parasite (Figure 9F). After the sacculin has been fertilized, the crab will take care of the parasite's eggs as if they were its own..

Some parasite manipulations lead the host to suicidal behaviour. A well described case is that of non-segmented nematomorphs{ind-text}Worms with cylindrical bodies, extremely long and thin (on average from 0.5 to 2.5 mm in diameter for 10 to 70 cm in length). Also called Gordian worms because of the impression they give of making complicated knots with their bodies.{end-tooltip} worms, whose adult form lives in water and looks like a kind of thread. The host is usually a terrestrial insect, such as a grasshopper (Figure 7H) that hosts the larval form. The adult worm must return to the aquatic environment to reproduce. To do this, it manipulates the host's behaviour, forcing it to jump into the water. Thanks to this final drowning, he can then return to the environment in which he completes his life cycle. However, this type of suicidal can be beneficial to noninfected animals of the same species, as it reduces the risk of contamination. This is the case of the ant parasitized by *Ophiocordyceps* (Figure 9B), which is then recognized as such and rejected from the anthill by its congeners.

In a few cases concerning plants, the determinism of handling is a little better known. It reveals a surprisingly convergent mechanism in pathogenic fungi and bacteria, but also in plant-parasitic nematodes{in-text}Round, non-segmented worms. Some lead a "free" life (in soil, water, etc.). Others have a parasitic life, within fungal, plant or animal organisms.{end-tooltip}. They cause root deformations where they take shelter and feed, called galls. The genomes of these organisms encode a multitude of small secreted proteins (or peptides), which modify the functioning of other host proteins. We talk about effectors: some penetrate the host cells, and reorganize the metabolism or alter the defense reactions... Sometimes they act at the level of the cell nucleus and are responsible for changes in gene expression. It is likely that these mechanisms also play a role in other types of parasitism: they are even found in mycorrhizal fungi. This suggests that secreted peptides could contribute to the changes observed in mutualist symbiosis - again highlighting the existence of similarities in mechanisms between mutualist and parasitic symbiosis.

Beyond the spectacular and fascinating nature of parasitic manipulation, some of the pathogens involved are responsible for many crop losses, but also for serious diseases, including vector-borne diseases such as malaria mentioned above, dengue{ind-text}Mosquito-borne viral infection in tropical and subtropical regions around the world. Causes a flu-like syndrome that can progress to life-threatening complications. There is no specific treatment for dengue fever, {end-tooltip}, trypanosomiasis{ind-text}Infections caused by trypanosome parasites, {end-tooltip} or leishmaniasis{ind-text}Parasitic diseases causing very disabling or even fatal skin or visceral diseases if not treated. They are caused by various parasites of the genus Leishmania, transmitted by the bite of insects commonly known as sandflies.{end-tooltip}, and thus represent major public health problems [19].

References and notes

Cover photo: © Jenny Huang from Taipeh (CC BY 2.0) via Wikimedia Commons.

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