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The Ecology of Eating Systems

Eat or be Eaten: Anatomy of the Marine Food Chain

Overview

Trophic Levels

There is a phrase from everyday life: “big fish eat small fish.” There is much truth in this, but there are also exceptions from the simple idea of big eating small. Take the second biggest fish on earth, the basking shark. It is a plankton feeder and its diet consists mainly of copepods (*Calanus*). Copepods are phytoplankton eaters. The 11-m-long basking shark is thus placed relatively low in the food pyramid. Ecologists classify organisms in eating guilds. Primary producers like the phytoplankton by definition get the attribution to the first trophic level. Copepods, which range in size from 0.5 mm to 1 cm, feed on phytoplankton and are therefore classified in the second trophic level. At first glance, this does not seem to be the food to nourish a giant fish. However, this is not an isolated case. Take euphausians, which like copepods belong to the crustaceans, which reach sizes of 4–15 cm and are also suspension feeders. They are the favorite food choice for the biggest animal on earth, the baleen whales. And there is a good reason for this choice, apart from the fact that it is a protein- and lipid-rich food item. The biomass of one single species of this family, *Euphausia superba*, the Antarctic krill, has been estimated at 500 million tons at any given time. With that biomass it surpasses any other marine animal and even rivals the biomass of the dominant terrestrial animal, namely ants. If you specialize on this food, you have a readily prepared table. Again, despite their size, ecologists place baleen whales only in the trophic level three. This does not apply to other whales. Killer whales prey on mammals like the seal, which is already a predator placed at a higher trophic level. The food chain picture is even more complicated because differences in the attribution to trophic levels not only vary between animals belonging to the same family but also differ for different development stages of the same individual organism. The larvae of large predatory fishes start quite small, and during growth the animal works its way up the food chain until it reaches its final trophic level. As all these complicating factors blur the picture

of food chains, ecologists prefer frequently the term food webs to underscore the complex nature of feeding interaction in nature.

In the following, I have selected a number of reports from the recent research literature to illustrate these principles with a few examples from the ocean.

Algae and the Story of DMS

The Chemical Armor of the Primary Producer

It is useful to start the survey with a primary producer. We have met them several times in the book and to avoid repetition, I take now the alga *Emiliania huxleyi* to illustrate a new principle. Like other photosynthetic organisms, it does not like the idea of being eaten. However, it has many enemies that graze on it, one is the protozoan *Oxyrrhis marina*; ciliates and flagellates also belong to its predators. *Emiliania* uses a chemical that deters protozoan herbivores. It contains intracellularly about 100 mM DMSP. In full, DMSP reads dimethylsulphonio-propionate. If you decompose the name, it reveals a relatively simple structure. It is a carboxylic acid consisting of three carbon atoms and has at its other end a positively charged sulfur atom substituted with two methyl groups. One hundred millimolar is quite a substantial concentration stored in algae. The biosynthetic pathway was first deciphered for the green macroalga *Enteromorpha intestinalis* (Gage et al. 1997). It starts from methionine with a transamidation reaction, followed by reduction, methylation, and decarboxylation. Why do I tell you this? It means that the algae invest four enzymes into DMSP synthesis and allot substantial amounts of the sulfur-containing amino acid methionine for its production. Actually, the algae elaborate still another enzyme, DMSP lyase, but they keep this enzyme carefully in a different cellular compartment. Only when the algae are grazed, the enzyme comes in contact with its substrate and does what it was designed for. It cleaves DMSP into DMS (dimethylsulfide), acrylate, and a proton. Acrylate is moderately toxic. Why did algae not design a more toxic compound to deter protozoan grazers? We have seen that diatoms and dinoflagellates synthesize very potent toxins and teratogens. The answer is that the algae were obliged to compromise.

Multiple Purpose Substances

In view of the large amounts of DMSP synthesized, they could not allow to invest in a single purpose compound. DMSP is also a cellular osmolyte, a cryoprotectant, a biochemical methyl donor and, as recently proposed, an antioxidant. However, these arguments would in theory not stop the algae from producing small amounts of a more potent toxin.

Such multiple functions for a single compound are not rare. Marine ecologists know the dual function of diterpene alcohol synthesized by the phaeophyte *Dictyota*, which is a herbivore deterrent and an antifouling substance. Tetrodotoxin, the potent toxin from the puffer fish *Fugu*, also serves as a sex pheromone (Matsumura 1995). Despite this multipurpose design, DMSP works sufficiently

well as deterrent. Its ciliate and flagellate predators are unable to grow on high DMSP strains, while they grow well on low DMSP strains of *Emiliania*. *Oxyrrhis* grows on both strains, but make a strong feeding discrimination against the high DMSP strain when offered both strains (Wolfe et al. 1997).

Feeding Preferences

Phagotrophic protozoa are highly discerning feeders and use chemical cues, prey morphology, and motility to make their selection. Some ciliates even show an active postcapture prey rejection. The end result is that the grazing pressure shifts to other prey and the high DMSP producer profits from a reduced competition for nutrients. There is more than one ramification to the DMS release argument during zooplankton grazing on algae. In fact, the algae left untouched do not release significant amounts of DMS. However, when they are exposed to copepods, they release increasing amounts of DMS (Dacey and Wakeham 1986). The gut content of copepods and also of penguins contained large amounts of DMS. However, the copepods do not accumulate DMS in their body. When the animals were placed in algal-free water, DMS appeared soon in the water with the elimination of fecal pellets. If one considers further that zooplankton grazing usually matches phytoplankton production, thus keeping phytoplankton biomass at a steady state, one can estimate that 20% of the marine phytoplankton cells are ingested each day.

Meteorology of DMS

In view of the huge amounts of phytoplankton in the oceans, it is then no real surprise that meteorologists became interested in DMS. In fact, they calculated that DMS contributed annually about 10^{13} g of sulfur to the atmosphere. This contribution has enormous atmospheric consequences at the global level. Biogenic DMS is emitted from the ocean and oxidized in the atmosphere to acidic species like H_2SO_4 that form submicrometer aerosol particles. These particles act as cloud condensation nuclei and control then the albedo (reflectance) of clouds. Clouds play a crucial role in meteorology. The surface of the unfrozen ocean, which covers about 70% of our planet, is relatively dark and absorbs thus over 90% of the incident solar energy. The presence of clouds over the ocean decreases the amount of solar radiation reaching the sea surface. Since the transfer of solar radiation energy to the earth is the major driver of both atmospheric and ocean circulation, the role of clouds as radiation screens can thus not be overestimated. Since the solar radiation drives the growth of phytoplankton, it was even hypothesized that marine phytoplankton regulates the production of DMS as part of a global biological system to control the sunlight reaching the Earth. In fact, the observed linearity of the plot of DMS flux against daily solar radiation, underlines that such a feedback mechanism could well be at work (Bates et al. 1987). Variation in the optical properties of maritime clouds could decrease Earth's surface temperature by 1.3°C

(Charlson et al. 1987) and could thus have an important function to counter-balance global warming by emission of greenhouse gases.

Antioxidant?

Recently, it was demonstrated that DMSP and even more its degradation products DMS and its oxidized product DMSO are substantially more potent antioxidants than ascorbate and glutathione (Sunda et al. 2002). The true function of DMSP could thus be a protection system against hydroxyl radicals formed by solar UV light in photosynthetic organisms living in the upper ocean layer. A number of observations support this conclusion: the seasonal pattern of DMS production (high in the summer, low in the winter), the depth dependence (high at the surface, low in deeper layers), its close association with another antioxidants (carotenoids), its induction by known stressors of photosynthesis like CO₂ and iron limitation, and its increase with high Cu²⁺ and H₂O₂ concentrations. In this view, the deterrent function of DMSP becomes a side show; however, one that still has substantial zoological implications. Actually, these DMS effects go far beyond the primary consumer. DMS became even an important foraging cue for seabirds.

Foraging Cue for Seabirds

Many Procellariiform seabirds make their living flying over vast expanses of seemingly featureless ocean waters in search of food. In this family, you find the albatross, which uses its very developed visual sense to spot and exploit mixed-species feeding aggregates of seals, whales, and conspicuous seabirds. Its smaller relatives, the storm petrels, forage mainly during the night, which excludes visual cues for hunting. The secret of their success was a mystery, but an ability to hunt by smell was suspected from earlier data where petrels were attracted to sponges soaked in cod-liver oil (Grubb 1972). This is not a very likely scent at the ocean surface; therefore, zoologists set out to test other compounds. Petrels forage on Antarctic krill, which as suspension feeders live on phytoplankton. As DMS is released when phytoplankton is grazed, they reasoned that petrels should be attracted to DMS-scented oil slicks applied to the ocean surface. Indeed, a number of petrels showed a significant higher number of sightings over DMS slicks than over control slicks (Nevitt et al. 1995). It was an as strong foraging cue as cod-liver oil, the birds even showed conspicuous turning behavior when flying over DMS-loaded slicks. Petrels show a complex olfactory anatomy, which fits with a night hunting behavior guided by smell. The albatross did not care for the DMS-scented slicks. This observation is surprising since DMS is an ideal foraging cue if your preferred food item is krill. This compound is practically a biogenic aroma identifier for the presence of crustaceans grazing on phytoplankton. However, I was told that the Pacific black-winged albatross has a fantastic sense of smell and can be attracted from very large distances with fish oil (E. Framer, personal communication).

Albatross

The quest for food is not an easy business as can be demonstrated with the albatross (Figure 5.1). The wandering albatross spends 95% of its lifetime in the open ocean, with individual animals showing distinct preferences for specific foraging areas between breeding seasons. With remote sensing methods it could be shown that even a couple separated for over-wintering places as far away as Madagascar and the rim of the Antarctica (Weimerskirch and Wilson 2000). Visual foraging on the sea is not an easy business. Already, nineteenth-century zoologists knew from sailors that the albatross is always hungry demonstrating a certain inefficiency of its hunting technique. The birds regularly dip into water for food or rest. Although their electronically documented path resembles Brownian motion, a mathematical treatment showed that it obeyed a Lévy flight search pattern, a behavior also discussed for foraging ants and flies (Viswanathan et al. 1996). Unfortunately, the albatross spots very efficiently baited hooks from long-line fisheries and tens of thousands are annually killed while scavenging these baits.

Copepods and Krill

Vertical Migration

Interesting marine life histories also occur at the second trophic level. Major insights about the way of life of these organisms came from the documentation of their locomotion. Sophisticated electronics and a lot of mathematics were necessary to track world-traveling seabirds. High-tech equipment is also needed



FIGURE 5.1. The sooty albatross (*Phoebastria fuliginosa*) is a large seabird of the Diomedidae family, order Procellariiformes, which spends most of its lifetime in the air. Its foraging strategy is explored in the text.

for following the ways of 1-mm-sized zooplankton. Oceanographers placed a multibeam sonar at two coastal sides of the Red Sea (Genin et al. 2005). They could show that zooplankton dominated by copepods swam against the vertical currents at velocities of greater than 10 body lengths per second. In contrast, animals were passively drifting with horizontal currents. If copepods travel vertically, they must sense their depth position. Visual cues could be excluded, but copepods responded behaviorally to small pressure changes. Apparently they possess a “biological barostat.” The adaptive benefit of depth retention might be twofold: By swimming against the flow and forming aggregates, the copepods maintain their position in layers of high food concentration where their phytoplankton prey grows. Aggregation also enhances the probability to find a mate in an otherwise sparsely populated ocean. For the predators of copepods, their aggregation behavior is also important. The concentration of copepods is too small outside of these aggregation patches to make feeding on them profitable for such large predators as the basking shark. Invertebrate and vertebrate predators of copepods have thus learned to locate these patches of high prey concentrations.

Predation Risk

The risk of predation is all too evident for copepods. Therefore, it is not surprising that copepods developed countermeasures. One efficient strategy is to exploit the more abundant food resources in the upper strata of the water at night and to descend during the day to a depth where the light intensity is too low for planktivorous fish. A Polish biologist working in the Tatra Mountains found very nice confirmations for this diel vertical migration of copepods (Gliwicz 1986). Since the last glaciation, many mountain lakes lacked fish. In these lakes, no diel vertical migration of the copepod *Cyclops* was found, nor was this behavior apparent in lakes that did not show vertical food gradients. As an adult, *Cyclops* preys on rotifers, while the juvenile nauplia stages of *Cyclops* feed on phytoplankton. In contrast, the noon and midnight position of *Cyclops* differed markedly in lakes, where fish resided for thousands of years (40 vs. 20 m depth, respectively). Fish was introduced over the last decades in many of these lakes and, strikingly, either the copepods disappeared totally or they evolved a diel migration pattern over hundreds of generations. Interestingly, the degree of migration pattern varied according to the length of time since the introduction of the fish. However, this was not the only adaptation that evolved in copepods under predation pressure. In addition, their eggs developed resistance to digestion in the gut of predatory fish.

Diel Migration

For the sake of biological beauty, I have taken here an illustration from a freshwater environment, but diel migration as antipredation measure was also reported for the marine copepod *Calanus finmarchicus* in the North Sea. This animal is the favorite food for the herring (*Clupea harengus*). *C. finmarchicus* is fat-rich

and reaches a size of up to 8 mm. The herring is not a filter feeder, but picks each copepod individually. The herring lives also from other prey like larvae from annelids, small gastropods, and small fish. However, whenever possible the herring prefers *C. finmarchicus* as prey. Since the herring existed in huge amounts in the North Sea, the copepods also felt the predation pressure and developed in the marine environment a diel vertical migration pattern to avoid the risk of the visually hunting herring. In the 1970s, the herring population experienced a population collapse to a historical low before catch quotas were introduced that led to a recovery of the herring population in the 1980s. Interestingly, during the 1970s when *C. finmarchicus* was freed from the predation pressure by the herring, they partially lost their diel migration pattern (Hays 1995).

Population Dynamics

Copepods are probably the most numerous metazoans on earth. Their sheer number combined with their importance as a link in food chains makes them crucial elements in all food-web modeling. Small changes in the population structure can have substantial effects on the nutritional interaction in the ocean, ranging from the survival of pelagic fish to the biological pump into the deep sea. An important parameter in marine ecosystem modeling is the mortality rate of zooplankton. Surprisingly few data on zooplankton mortality have been collected. Important data were contributed by copepod counting in the Atlantic near Norway (Ohman and Hirche 2001). Late juvenile (copepodid stage 5) and adult female copepods appeared in late March, they originated from the overwintering population, which survived in deep water. They appear about 40 days before the phytoplankton bloom, the grazing rate is thus low and *C. finmarchicus* lived still largely from stored wax esters put aside for gonad maturation and oogenesis. They also started quickly with egg laying. The initial recruitment rate is high: Up to 60,000 eggs were produced per square meter of sea surface and day. However, eggs produced during the first 20 days of egg laying showed virtually no survival to the first larval stage (the nauplius). A second smaller peak of adult females was observed 10 days before the bloom, it was accompanied by a second peak in egg laying, but now the egg mortality was threefold lower.

Mortality

What is the reason for the high mortality during the first peak of egg production? Loss of eggs by water currents can only account for a quarter of the observed mortality. Diatoms and their toxic metabolites were not around. The male copepods were not short of sperm. The principle prey of copepods, ciliates, and phytoplankton were available. So where is a smoking gun? The most suspicious association was that the egg mortality rate declined in parallel with the decline in abundance of adult females. This observation solved the riddle: The explanation for the density-dependent egg mortality is egg cannibalism by con-specifics. Adult females and C5-stage juveniles ingested eggs with high clearance, particularly in the prebloom period.

Food-web Regulation

This loop introduces a self-limitation device into the population dynamics of copepods that is partially independent from limitation in food resources and independent of predation by animals from the next trophic level. These effects must now be incorporated into food-web models to ameliorate predictions. Predictions are difficult since the food-web interactions are very dynamic, especially in face of external systematic forcing factors like global warming. In the Northern hemisphere, biogeographical northward shifts probably forced by the current global warming trend were already documented in a number of terrestrial animals like butterflies, amphibians, and birds (e.g., Parmesan et al. 1999). Likewise, southward shifts for flies were seen in the Southern hemisphere. Such a trend with a 10° latitude shift for temperate copepods and a decrease in arctic copepods was documented in the Atlantic (Beaugrand et al. 2002). This observation has important consequences for predator fish like the cod that relies on an intact food web and which was anyway severely battered by over-fishing. If such an important trophic relay organism as copepods changes its geographical distribution, large-scale ecological changes in the ocean become likely.

Krill or Salp Years

A portrait of life in the second trophic level would be incomplete without some feeding information on krill in the Antarctic food web. Krill despite its small size is a relatively long-lived animal with a life span of more than 5 years (Figure 5.2). Surveys conducted near the Antarctic Peninsula showed large interannual abundance fluctuations between 1976 and 1996, with a significant trend to lower krill abundance in recent years. Marine biologists noted

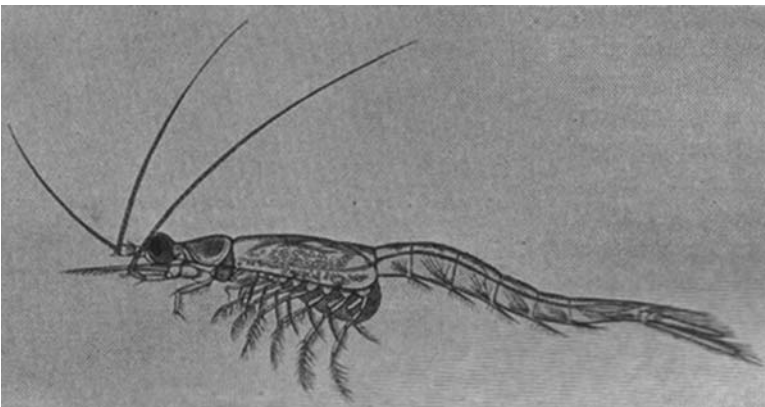


FIGURE 5.2. Krill denotes crustaceans belonging to the suborder Euphausiacea. *Euphausia superba* is—as the Latin name suggests—a crucial member for the marine food web, providing the food basis for many fishes, birds, and whales.

two interesting correlations. When krill populations were low, salp populations tended to be high. Winters with extensive sea ice cover favored krill and inhibited salp blooms. Salps are pelagic tunicates (Figure 5.3), which form together with the lancelets and the vertebrates the three subphyla of the Chordate phylum.

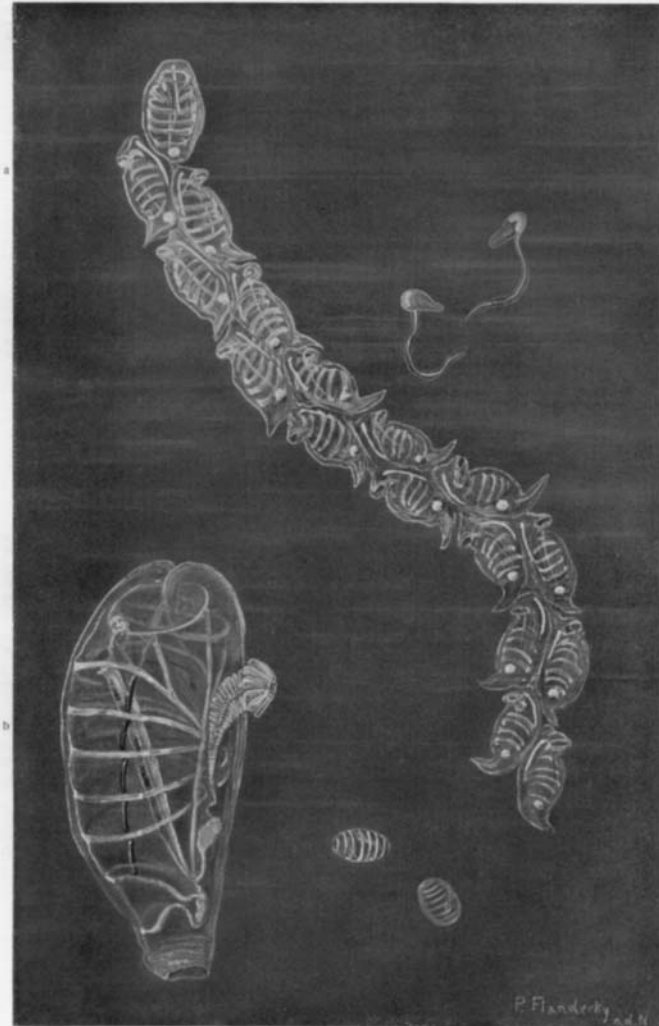


FIGURE 5.3. Salps, members of the class Thaliaceans, belong to the subphylum Tunicata. The two larger salps are *Salpa* and *Cyclosalpa* (bottom) and *Doliolum* (bottom right). The tailed animal is an appendicularian tunicate (*Oikopleura*). We deal with tunicates in food web regulations (krill vs. salp years) and with respect to tunicate feeding and its close affinity to vertebrates.

Salp Feeding

Salps are rather simple suspension feeders with an oral and atrial siphon at opposite ends of the body and a pharyngeal filtering basket for retaining plankton and organic detritus via various kinds of mucous nets. The linear water flow through the animal provides a means of “jet propulsion” supported by muscular action. Water enters a siphonal chamber, passes into the pharynx, which contains a groove called the endostyle. The bottom contains mucus-producing cells and a row of cilia. Iodine is also enriched from the water and added to the mucus (comparative anatomy links this organ to the later thyroid of vertebrates). The mucus sheets are rolled into cords, which pass into an esophagus, then a stomach equipped with a pyloric gland. Digestive enzymes are secreted into the stomach and an intestine passes the undigested material to the anus, which opens into the atrium near the exit siphon. Most are highly gelatinous and transparent and in contrast to krill not a good food source for higher trophic levels. Salps benefit from open-water conditions, while krill exploit ice algae that develop during the winter months under the ice cover.

Balancing Acts

During blooms, salps can ingest up to 20% of the primary phytoplankton production and can thus deprive krill of sufficient food to support their energy requirements, leading to poor reproductive success of krill (Loeb et al. 1997). Diminished krill production may already have caused a decline in the abundance of one of its vertebrate predators, the penguin *Pygoscelis adeliae*. Krill is one of the most important ecological links between the trophic levels of the primary producers and the vertebrate predators. The carbon from phytoplankton is lost with salp fecal pellets and transported to deeper waters. With autonomous underwater vehicles the relationship between krill and sea ice edges could be investigated. Krill is concentrated fivefold over the open ocean concentration in a narrow band between 1 and 13 km from the ice ridge (Brierley et al. 2002). This is a compromise position: The algal bloom is strongest directly at the ice edge, but receding under the ice offers protection from air-breathing predators. Predation and starvation were traditionally assumed to be the major causes of krill mortality imposing this risk-balancing act. However, data showed that parasitoid ciliates were also a cause of mass mortality of krill (Gomez et al. 2003). As frequently in biology, finding the right strategy is a difficult balancing act. Swarming confers benefits to krill since it improves the capture of motile prey, helps to find a mate and to escape a predator. However, on the dark side, it increases the risk of exposure to parasites.

Planktivorous Fish

Larval Fish

With these animals we do not yet climb up the trophic level, since they are found at the second (phytoplankton eater) or third level (zooplankton eater), but we reach fishes of substantial size or great economical importance. I have

chosen three research papers to illustrate this subject. With the first I touch a critical issue of fish ecology with economical relevance for fishery. Because of the prevailing fish reproduction strategy to spawn many eggs, which yield many small larval fish, most fish actually start as plankton feeders before they climb up the trophic level reserved for the adult forms. This is the case for the haddock (*Melanogrammus aeglefinus*, formerly *Gadus aeglefinus*, indicating that it is a cousin of the cod, *Gadus morhua*). The haddock is smaller than the cod, reaches commonly 50 cm length and 6 kg weight, and feeds as an adult mainly on mussels, crustaceans, annelidae, and echinoderms, while the adult cod is a predator of other fishes. The haddock is a commercially valuable fish, but it has suffered from overfishing in recent decades, such that haddock recruitment became a hot topic for fishery researchers.

Year Classes

A long-standing hypothesis in this field contends that the abundance of fish year-classes is determined by the food availability during the critical period of larval development. If food is abundant, one would expect that less larvae die from starvation and the quicker they grow, the earlier they reach larger size classes reducing the predation pressure on them. The relative timing between the spring bloom of phytoplankton and the time of fish spawning should set the pace. To be present before the phytoplankton bloom assures uncompleted access to an abundant food source. However, there is a risk when the spring bloom is delayed a greater proportion of the larvae will starve to death. Actually, the haddock larvae feed mainly on zooplankton, but since the zooplankton feed on phytoplankton, the easier-to-measure phytoplankton can be used as a sentinel. The prediction of the so-called Hjort–Cushing hypothesis is that precocious algal blooms will result in a larger survival index and thus later greater fish stocks. Canadian fishery scientists have surveyed the larvae, juveniles (up to 2-year-old fish), and adults since 1970 off Nova Scotia. The remote-sensing of the ocean color by satellites allowed now a test of the hypothesis. And indeed, 89% of the variance in larval survival could be accounted by the variation of the timing in the spring bloom (Platt et al. 2003). The reproductive success of haddock is thus controlled from bottom-up, it is food controlled. You have more juveniles because less larvae perish from lack of food.

Suspension Feeding in Fish

With the second research report we now turn to a physiological problem of suspension feeding in adult planktivorous fish from the *Clupea* family, comprising such common fish as the herring (Figure 5.4), the sardine, and the anchovy. The reported experiments were actually done with the shad, another member of this fish family. If you look into the mouth of these animals, you see at each side of the lower jaw four gill arches from which many gill rakers branch at a right angle resembling a miniature eel-basket. At the end of the oral cavity, you see the esophagus. The fish takes water up with the mouth



FIGURE 5.4. The herring (*Clupea harengus*), possibly the most abundant of fishes, is shown here in a large school. It eats plankton; and suspension feeding is discussed in the text. Its predator relationship with copepods and its prey relationship with tuna, seal, and sea lion is mentioned, including its echolocation avoidance reaction.

and expels the water again through the gills. However, it was not clear how the gill rakers function during suspension feeding. Two major hypotheses were proposed. In one version, the rakers function like a dead-end filter, they retain particles that are too large to pass the sieve. However, there are two problems with this hypothesis. A lot of food particles would become trapped on the gill rakers and clog the system unless a transport system would collect it from the gill rakers and transport it to the esophagus. The other problem is that these animals consume particles that range in size from $40\mu\text{m}$ to 1 mm. Many particles would be too small to be retained by the space gaps between the rakers. In the second version some animals solve these problems by a type of hydrosol filtration, they produce large amounts of mucus which traps the food particles (we have seen this above with the salps). Actually neither hypothesis was correct, food particles are caught in the cross-flow (Brainerd 2001). This is a process that is commonly used in the food industry when beverages like wine or beer have to be filtered from particular material to get a clear liquid. In cross-flow filtration, fluid flows parallel to the filter surface and particles become more concentrated as the filtrate (the liquid) leaves through the filter's pores (the gill system). Even if this system is industrially used, we still do not understand the underlying physical mechanisms. The researchers used first some mathematics to investigate the theoretical fluid dynamics by which they excluded the first two hypotheses and then they set out to prove the cross-filter hypothesis by using miniature fiber-optic endoscopes linked to high-tech cameras that they inserted into the oral cavity of the fish (Sanderson et al. 2001). With these medical instruments they measured impressive cross-flows

sweeping with a velocity of 55 cm/s across the raker's surface and more than 98% of the particles passed without any contact to the rakers directly into the esophagus.

Basking Shark

With a research report on the third planktivorous fish, I want to introduce a subject of behavioral biology. It deals with the second biggest fish, the basking shark *Cetorhinus maximus*, which reaches a size of up to 11 m. It illustrates a paradox that the biggest animals in the fish and the mammalian category feed mainly on plankton. Apparently, you do not need big prey if you want to grow to large size. What you need is only an efficient suspension filter, but here nature has come up with interesting solutions as we have just heard. However, time is also a problem. The most efficient filter is of no use if the animal forages in an area that does not offer food above a critical threshold. At the end of the day, the basking shark will starve when it has not ingested enough biomass by hunting in a dilute plankton suspension. To succeed, the basking shark must choose the richest, most profitable plankton patches. This is actually a general biological problem with which each mobile animal is confronted. The issue consists of several questions, which can be summarized under the following headings: choosing where to forage; choosing how long to stay; choosing what to eat; maximizing intake rate, while minimizing risk. There is a rich literature on this subject known under the term optimal foraging theory. However, the different animal groups are not homogeneously represented in this literature. While birds are favorite targets for animal observation by ethologists, much less literature exists on fish, which is explained by the obvious technical obstacles to observation. Environmental biologists tracked basking sharks visually from a boat, located their exact position, and took plankton samples (Sims and Quayle 1998). The sharks fed in areas where the dominant copepod *Calanus helgolandicus* was 2.5 times as numerous (1,500 organisms per cubic meter) and 50% longer (2 mm) than in areas where they did not feed. When they fed in rich areas, they showed an extensive zigzagging in their traveling, while in poor areas they swam in straight lines. The residence time in a given ocean patch was proportional to the density of the zooplankton. The movement between rich patches took them about 1–2 days where they traveled distances of 10 km. The sharks apparently knew where to feed: They followed fronts where warm water layers met cold layers and aligned their searching with temperature gradients and tidal flows. These are useful rules of thumb, which a marine biologist also would have chosen. The researchers speculated that the sharks sensed the weak electric fields induced from copepod muscle activity or DMS released from grazed phytoplankton. Apparently, the sharks were not alone in sensing these nutrient-rich fronts. The areas, where shark foraged, were also used by shoaling fish, including commercially important fish like the mackerel.

Sardine Versus Anchovy Years

In our survey, we touched several times on the impact of climate on food chains and a spectacular case is presented by two planktivorous fish species, both

of substantial economical importance to fishery industries, the sardine and the anchovy, both belong to the herring family (*Clupeidae*). Marine biologists have observed a sharp decline in sardine catches over the last 20 years off Peru, which were one of the richest fish grounds of the oceans. The harvest decreased from 4 million metric tons in the late 1980s to a bleak 40,000 tons in 2001. In view of the economical importance of fishery for Peru this was bad news, especially since the early 1970s a comparable crash in the harvest of anchovies was observed. At first glance this looks like the worldwide decline in fish resources we are currently experiencing as a likely consequence from overfishing. However, two observations did not fit with this diagnosis. One was that the decline of sardines in the 1990s was accompanied by a recovery of the anchovy, although not yet to the catches during the heydays of anchovy fishery in the 1960s. In the 1960s the sardines were not only low, they were practically nonexistent. This raised the hypothesis that we deal here with multidecade changes from a sardine to an anchovy regime (Chavez et al. 2003). The record of fish catches does not extend back beyond 1950 for Peru, so the fishery scientists looked for proxy measures.

On Guano and Haber-Bosch

They looked for the record of guano harvest, which goes back to 1900. There is a good reason for the preservation of this record, which justifies a digression. The German chemist Justus Liebig recognized in the 1840s the importance of fertilizers for agriculture, mainly of a usable nitrogen source for plant growth. Manure was not any longer sufficient as a fertilizer in agriculture to feed the growing world population. South America was during the nineteenth century the source of the most valued animal excretions for readily available nitrogen: guano, the droppings of seabirds, which formed large crusts on the rocks where the seabirds were resting. This business came down since the German physical chemist Fritz Haber convinced an engineer at the BASF chemical factory in the 1910s to reduce dinitrogen from the air with dihydrogen under great pressure and heat. The Haber–Bosch procedure became later actually the detonator of the population explosion during the twentieth century. However, guano remained sufficiently important for Peru that records of guano production were still kept. The Peruvian seabirds are mainly represented by a single species, the cormorant, which feeds nearly exclusively on anchovies. The guano record showed marked fluctuations, too.

El Niño

This observation called the meteorologists on the scene and they defined the anchovy regime by an Eastern Pacific cool phase and the sardine regime by an Eastern Pacific warm phase that varied over periods of about 50 years. The actual connections are more complicated because the El Niño events with shorter periods are disturbing this multidecade pattern. Overfishing and global warming due to anthropogenic CO₂ emission further influenced the analysis. However,

without a deeper understanding of these processes, we might be condemned to follow helplessly the coming and going of these important food reserves.

On Cod and Copepods

The collapse of the cod population is commonly attributed to overfishing, in ecological parlance top-down control. However, as is usual in biology, the causal connections are too complicated to be summarized under a single heading. Also bottom-up control contributed to the decline of the cod standing stock after 1980. Warming of the ocean also played here an important role. Survival of larval cod is of critical importance for the later size of the cod population. Survival of the larvae depends on three critical factors: the mean size of the prey, its seasonal timing, and its abundance. The female cod is a prodigious producer of eggs, up to 4 million eggs per animal were counted. Spawning time in the year differs depending on the geographical region. Once the larval fish is in the water, the race is on: The larvae will need appropriately sized prey commensurate with its own size and predator capacities. In the 1960s, the timing was optimal. The larval cod was ready for feeding on copepods between March and July and during this time period its favorite prey, *Calanus finmarchicus*, showed maximal abundance. In the 1970s, the prey showed a shift toward lower and later abundance, but this was not yet critical. Cod had had its hey-day, what fishery biologists speak of as the “gadoid outburst.” In the 1980s the situation changed suddenly. *C. finmarchicus* became rare in the North Sea. Of course, copepods did not disappear. There is always this “*horror vacui*” in nature; consequently, its position was taken up by *C. helgolandicus*. The latter grew to even higher concentrations in the sea, but there was a problem. It reached these higher titers only after August (Beaugrand et al. 2003). Ecologists diagnosed a mismatch between prey and predator with lethal consequences on the recruitment of young cod. Since warming caused this regime change in the North Sea, the problem became even more severe for the cod. Rising sea temperature means increase in metabolism and higher energetic costs, all with a thinner diet and unabated top-down mortality by fishing: small wonder that the cod population crashed.

Piscivorous Fish

Tuna

With the next chapter we stay with two other important commercial fish species, the tuna and the cod. I will summarize some recent research on their biology. In a later chapter, I will use the cod to illustrate problems of the sustainability of contemporary fishery. You will also recognize that I use here a journalistic trick. Both fish are herring eaters, we advance therefore in the food chain as the section title promised. You will therefore not be too much surprised to find in the next chapter the cod-eater, then the eater of the cod-eater, then with a slight ironic undertone the eater of the eater of the cod-eater.

*The Atlantic bluefin tuna (*Thunnus thynnus*) has fascinated humans from the beginning of written records. You can quote Aristotele and Strabo from Antiquity literature on the biology of the tuna. The reasons for this fascination are manifold. Humans are generally—a microbiologist would say naively—attracted by the sheer size of animals. Tuna are impressive in this respect: They grow to a length of 3 m and a weight of 680 kg. In many areas of the world, the tuna are prized for their flesh, in Japan a large tuna could command a price of \$100,000 per individual fish. One should therefore not be surprised that the stock biomass has dwindled to a mere 20% over the last 30 years. If you want to keep this valued fish on your menu card, a thorough knowledge on its feeding, migration, and spawning is necessary to rebuild the stocks.*

Endothermy

However, the tuna has characteristics that make this animal also attractive to biologists (Block et al. 2001, 2005). They are unique among teleosts (bony fish) for their endothermic capacity due to a special subcutaneous blood vessel system. They have thus high rates of heat production. Tuna use this heat to warm their eyes, which facilitates extremely rapid eye movements. The eyes are warmed in preference to other parts of the body and infrared imaging of shoals detects the glowing eyes. In their wide geographical distribution from the Mediterranean Sea over the Atlantic up to the north of Newfoundland to the Caribbean Sea, they experience water temperatures between 3 and 30 °C while maintaining a constant peritoneal temperature of 25 °C. The elevated body temperature of bluefin tuna increases their capacity for rapid migration by enhancing the power output of their muscles. The other side of the coin is that they have a large metabolic demand for food and oxygen. In the Caribbean spawning ground, the warm waters are favorable for the development of the eggs, but the adult animals reach their upper tolerance for heart function.

Migration

The two research papers that I have chosen could be entitled “A year in the life of a western tuna.” Actually the fish biologists tagged many tunas electronically and followed them over longer time periods. They documented impressive displacements both vertically and horizontally. In the vertical dimension they saw repetitive diving excursions for food, where the fishes got down to nearly 1000 m, but most of the time they spent in the upper 300 m of the ocean. Most western tuna, which had their spawning grounds in the Caribbean Sea, remained over the coastal shelf of the eastern US and Canada, but some reached out far into the Atlantic coming close to the Spanish coast. The eastern tuna which spawned in the Mediterranean Sea was a more daring character and traveled over the entire northern Atlantic. Apparently, the US/Canadian shelf and south of Iceland were the richest foraging areas, where both populations overlapped substantially. Rapid movements over thousands of kilometers (trans-Atlantic in 1–2 months) are common in tunas. Apparently, the metabolic costs for endothermic fish

swimming is low enough in comparison to the foraging and reproduction gain obtained from migratory behavior. However, no mixing of the two populations was observed at the level of the spawning grounds. Tuna smaller than 2 m in length did not enter the spawning area, indicating a late sexual maturation, which is a critical factor for the population biology of fishes. However, tuna grow quickly: fish larvae of few days of age weigh already 50 g, after a month they reach 100 g, while at 3 months they achieve already a weight of 1 kg. Quick growth assures rapid decrease of potential predators. Female tunas invest heavily in egg production, the ovaries increase in weight from 500 g to 6 kg within a month before spawning.

Cod Biology

Cod (*Gadus morhua*) is a smaller fish than bluefin tuna, but still of impressive size. It can reach up to 1.5 m length and 50 kg weight. It reaches 14, 27, 35, and 50 cm length after 1, 2, 3, and 4 years of age, respectively (Figure 5.5). Up to a length of 30 cm crustaceans dominate in stomach contents, then fish starts to appear in its prey and longer cod are nearly purely piscivorous. Spawning starts relatively late when the fish has reached 50 cm length and occurs then in yearly intervals. The cod is a bottom-dwelling predatory fish with populations in the northern Atlantic. Its southern limit was defined by New York and Bordeaux and to the north it reaches into the Arctic Sea. As for many other commercially important fish, relatively few data on the foraging behavior of cod is available, which will limit the management efforts of this severely depleted fish stock. Electronic tagging demonstrated striking behavioral differences between North Sea and Irish Sea cod (Righton et al. 2001). The latter was extremely

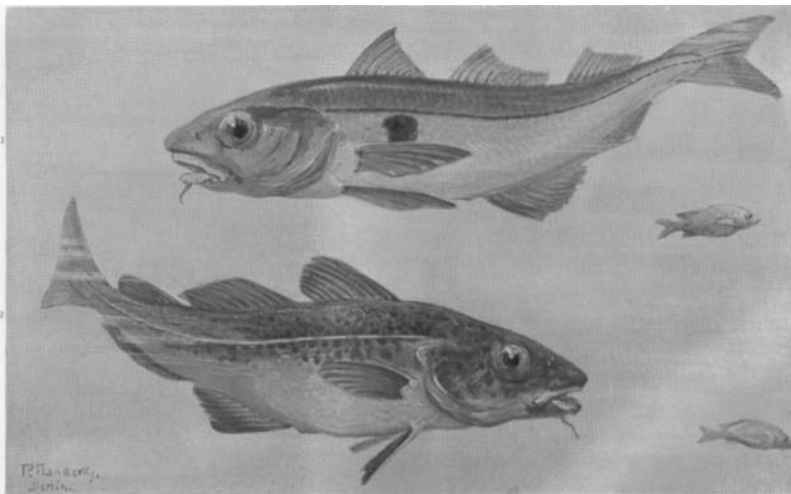


FIGURE 5.5. The cod (*Gadus morhua*, bottom) and the haddock (*Melanogrammus aeglefinus*), both belong to the family Gadidae.

active at all times, while the former was active during spring time, but stopped physical activity in June. In July they spent most of their time on the seafloor. In August and September they were active only during night and resumed an active life in October. During the summer months the North Sea cod moved less than 1 km in contrast to models that anticipated foraging activity over substantial geographical areas. In accordance with the behavioral differences, microsatellite markers revealed strong genetic differentiation between populations (Nielsen et al. 2001).

Marine Highways

Impressive data obtained with echolocation are available for cod off Newfoundland (Rose 1993). Real cod highways were detected with fish shoals containing more than 10^8 individuals, amounting to 80% of the entire stock estimate in that region. The fish formed a large aggregate of mature animals organized around spawning columns of mature females at the center. Four- and five-year-olds accompanied the spawning core. The migrating cod aggregate was structured by fish size. At the front end were large scouts that led the shoal, the size of the cods decreased toward the rear guard. The aggregates followed a channel of 2–3 °C warm water undercutting a colder shelf water (<0 °C). During the spawning stop, which lasted 10 days, the fish density was 1 animal per cubic meter. When the migration started, a 20 km long column of fish moved forward and upward, keeping an interanimal distance of ten body lengths from the nearest neighbor, apparently maximizing the area swept for prey, while keeping visual contact to the next cods. An impressive echogram showed how cod scouts run into capelin (*Mallotus villosus*), which rouse in apparent panic in front of the hungry steamroller consisting of cod. The capelin searched the same areas for spawning, but one gets the impression that they passed by to serve the cods as fast food.

Piscivorous Mammals

Who eats the cod? Caught cod frequently carry scars from tentative unfriendly takeover, which the fish survived. There must be characters in the sea that do not shy away from this 1.5 m long and strong fish. Such attacks were recently documented for the Weddell seal, animals that weigh as adults 450 kg. If I look with my children at action movies on the TV, I have frequently the impression that you find better scripts in scientific journals than on the TV screen. To prove this point, take the science paper describing the hunting behavior of these marine mammals beneath the Antarctic fast ice (Davis et al. 1999).

The Weddell Seal

The scientists mounted video cameras on the back of the animals such that they could observe what happened just in front of the muzzle of the seal. Recall from a previous section in this chapter how krill explore the underside of the ice for

ice algae. This attracts other visitors that are interested in the krill like the small fish *Pagothenia borchgrevinki*. This fish knows that there are others out that have an open eye on them. When hunting for krill, it quickly seeks shelter in ice crevices. Now in the tradition of a good action film, the seal arrives on the scene. The small fish disappears into the crevice, where the seal cannot follow. Now the video documents a surprising behavior—the seals expels a blast of air through its nostrils for 1 s; the fish panics and immediately swims out of the crevice. In the next frame you see via the video camera directly into the eye of the fish, which tries to escape. The seal carried also electronic devices that allowed locating its position during its diving exercises. The scientists followed the hunt in 3D and saw how the seal stalked the large Antarctic cod without startling the fish. Not all attacks were successful, sometimes the cod struck back with a powerful tail thrust and escaped. Sometimes the seal displayed only curiosity, but no aggressive behavior during an encounter with a cod. However, on other days, the researchers observed seals eating cod on the ice. The video documented that the seal hunted under visual control. Some scientists suspected that seals use underwater sonar for hunting, but the electronically surveyed seals were not using calls during the predator–prey interactions. In the wild, blind but well-nourished seals were often described. Apparently, seals can hunt successfully without vision. Zoologists demonstrated that the seals use their whiskers to detect water movements. The spectral sensitivity was well tuned to the frequency range of fish-generated motion. Optical and acoustic cues in bait detection were excluded by placing eye caps and headphones on the animal—in that study handsome harbor seals were used (Dehnhardt et al. 1998, 2001). Seals in a zoo were trained to locate a miniature submarine. From these experiments the biologists calculated that seals detect with their whiskers water movements in the wake of fishes for several minutes. A herring swimming at a sustained speed of about 1 m/s leaves a hydrodynamic trail that remains detectable for the seal when the herring is 200 m away. As is usual in biology, one sense comes seldom alone. There is often a real arms race also at the level of senses between predators and preys. Therefore, one should not be surprised that some teleost fish have lateral line systems, which show hydrodynamic receptor properties that are one or two orders of magnitude more sensitive than the whiskers of seals.

Diving

The Weddell seal dived usually to depths of 100–350 m for 20 min duration, but exceptional dives to 740 m were also measured. Physiologists had a problem with these observations. Swimming is energetically expensive for mammals, resulting in transport costs that frequently exceeded those of fish by a factor of 10. They calculated that the Weddell seal would be unable to complete a 200-m-deep dive using aerobic metabolic pathways. It would have to rely on anaerobic metabolism leading to the accumulation of lactate, and the animal would require prolonged recovery periods. However, no lactate increases were measured even after deeper dives. What had happened? The video film was again revealing (Williams et al. 2000). Diving descents began with

up to 200 s of continuous stroking, followed by a prolonged period of gliding to maximal depth. The compression of the air space in the lungs decreased the volume of the animal without a change in mass, thus buoyancy decreases on descent and avoids the energetic cost associated with active stroking. These savings can thus be invested in a prolonged diving time.

Sea Lions

However, when offered a choice between a fish prey closer to the surface and one which necessitates deeper diving, many marine mammals prefer the easy prey even when they are capable of diving. This was the case for sea lions. Engineers used military spying instruments to locate predator and prey off Alaska (Thomas and Thorne 2001). Sea lions feed exclusively on herring schools when they swim at only 10–35 m depth during night. The sea lions lined up side by side with up to 50 individuals swimming along the edges of the school as if they were herding the herring (Thomas and Thorne 2001). The herring stocks are dwindling and food limitation is now the cause for the decline in sea lion populations. Alternative food sources are at hand: four times higher biomass of pollock (*Theragra*) is available in the waters, but the pollock does not figure on the menu card of the sea lion. One reason might be because the pollock swims day and night at 100 m depth. It is not clear why the sea lions do not change the prey since they are well capable of diving up to 250 m.

Killer Whales: Effect of a Top Predator Down the Food Chain

*Who eats the seal? The seal is not yet at the top of the food chain, it has still predators. The battle between seals and killer whales (*Orcinus orca*) is quite interesting since it is also a war of the senses, and I will tell it in one of the next chapters. Otherwise the gradual creeping up of the food chain becomes a bit dull. While it reflects a clear truth and is thus not just a textbook message, it oversimplifies the true ecological situation. Food chains are in reality often food webs. Apex predators often initiate forces that spiral down successive lower trophic levels and have sometimes even a surprising impact on the food base. Such a backfiring story of the killer whale will now be told to highlight the complexity of ecological interactions, this time a top-down control (Figure 5.6).*

Killer Whale

Some killer whales prey on harbor seals and sea lions, but these populations have collapsed in the Northern Pacific. The reason for the decline of the pinniped mammals is uncertain, but is probably a response to reduced abundance of their fish prey (Pacific herring) or forage fish stock changes (pollock). The reason for the changes is not very clear; increased fishery, increased ocean temperature, and depletion of baleen whales have all been proposed. If we move from the concept

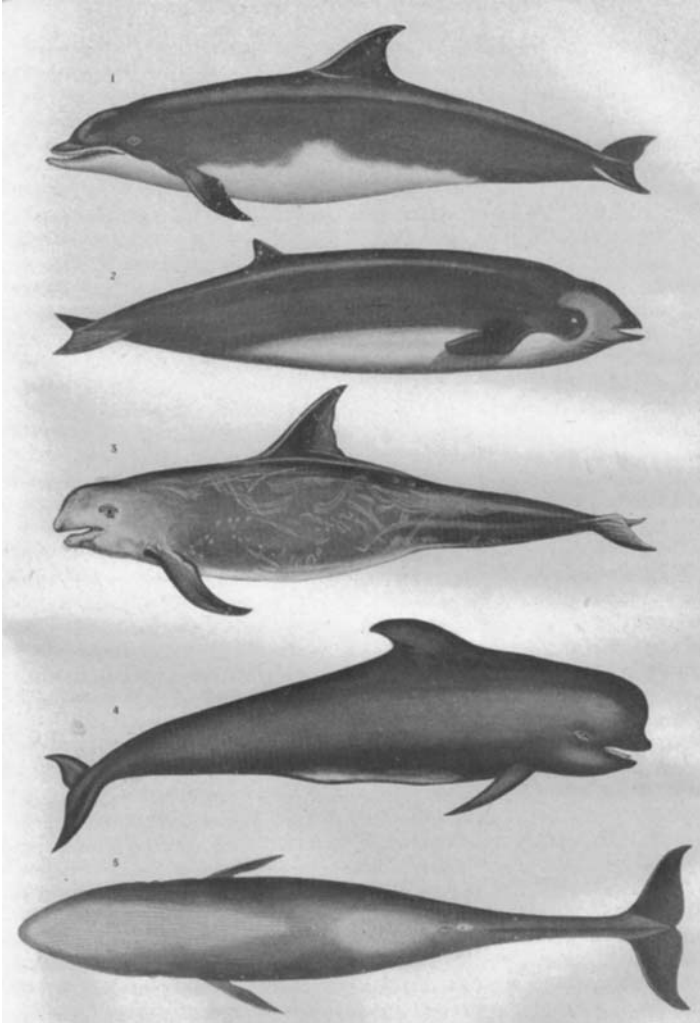


FIGURE 5.6. Cetacea are a group of aquatic mammals comprising whales, porpoises, and dolphins. The figure represents *Tursiops tursio* (1, a porpoise), *Ziphius cavirostris* (2), *Grampus griseus* (3, a dolphin), *Globicephala melas* (4), *Balaenoptera borealis* (5, a whale).

of food chains to food webs, the logical connection between the ecological elements will also increase in complexity. However, as in the following story, the food chain can still be followed back as a linear chain of arguments. So with decreasing prey abundance, the mammal-eating killer whales also face population reductions unless they find a replacement for their diet. In fact, killer whales profited from a human intervention, which offered them a new prey, the otter (*Enhydra lutris*).

The Otter

The otter (Figure 5.7) has a colorful history (Estes et al. 1998). Sea otters abounded at the rim of the Pacific until fur trade sent the animal to near extinction. More recently, the sea otter was put under protection and in the 1970s the otter population increased to near maximal densities in many regions, only to decline again in the 1990s. There is a lot of discussion whether infectious diseases have increased in the ocean as a consequence of maritime pollution (Harvell et al. 1999), but no stranded sea otter carcasses were observed. However, marine biologists observed in the 1990s the first attacks of killer whales on sea otters. If the killer whale wants to make a living on sea otters, on a purely energetic basis a single animal would have to consume 1,800 otters per year. Thus a relatively low number of killer whales that discovered this new food source could be at the basis of this tenfold decrease of the Pacific sea otter population. With this story we get into a fascinating scheme, linking an open ocean with a coastal ecosystem.

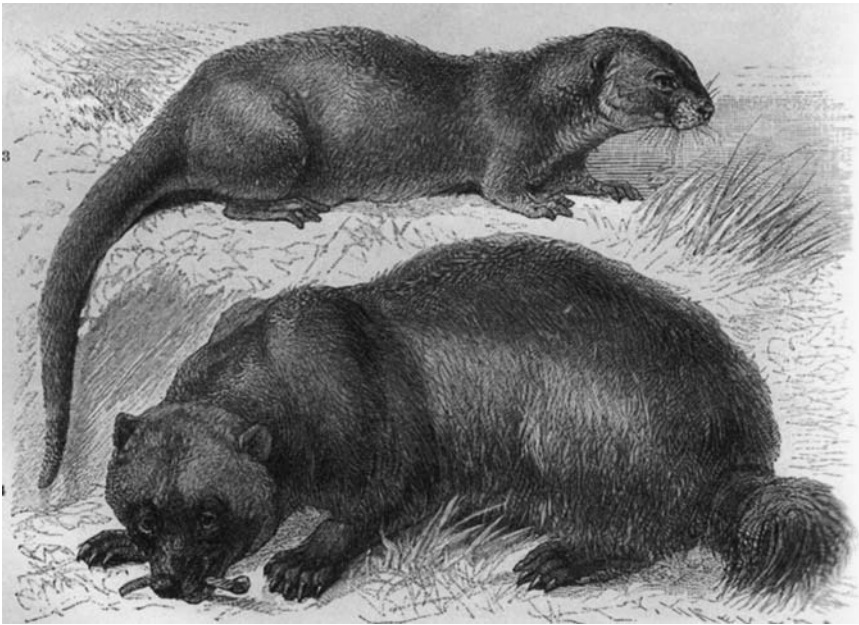


FIGURE 5.7. Otters are semiaquatic mammals of the weasel family (Mustelidae). The picture shows the common or river otter (*Lutra lutra*), which is a quick runner on land. The text deals with its cousin, the sea otter (*Enhydra lutris*), an exclusive marine otter living in the kelp beds from the North Pacific. It floats on the back with a stone on its chest and opens mollusks by smashing them on the stone. For comparison, the figure shows another Mustelidae: the wolverine (*Gulo gulo*). It is known for its voracity; therefore, it is also called glutton. It eats all kinds of prey and knows, except for man, no predators.

Sea Urchins and Kelp

Sea urchins are the principal prey of sea otters in the Aleutian islands. You have certainly seen these amusing pictures of otters swimming on the back with a flat stone on their breast on which sea urchins are butchered with the help of another stone. If we stay with our linear question “who eats whom?” then we get a simple answer. Sea urchins live on kelp. Kelp is a popular name for large seaweeds found in colder seas (Figure 5.8). Formally they belong to the order *Laminariales* of brown algae. Superficially they resemble higher plants with a root-, stem-, and leaf-like structure, but at a histological level it becomes clear that these are only analogous structures. The kelp *Nerocystis* carries the popular

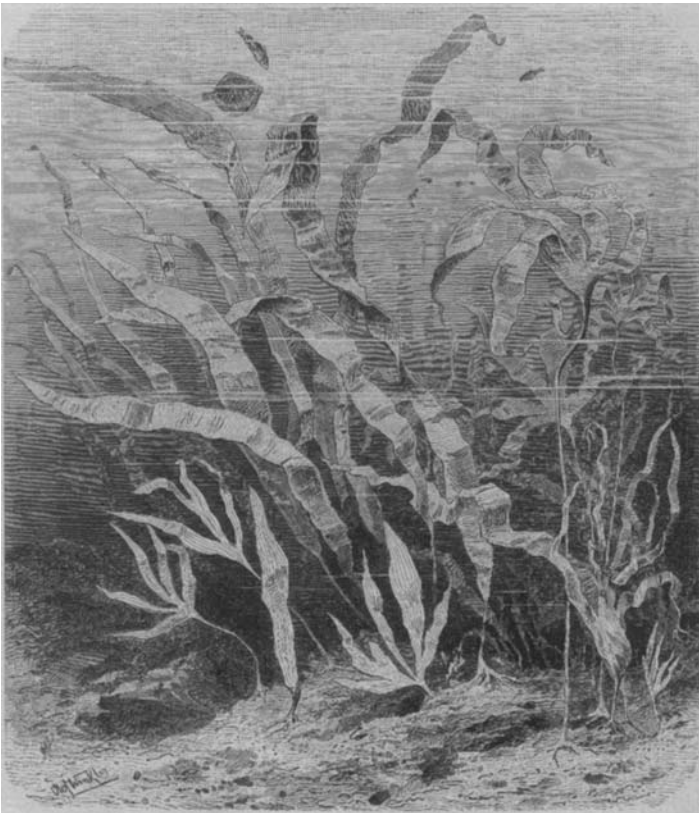
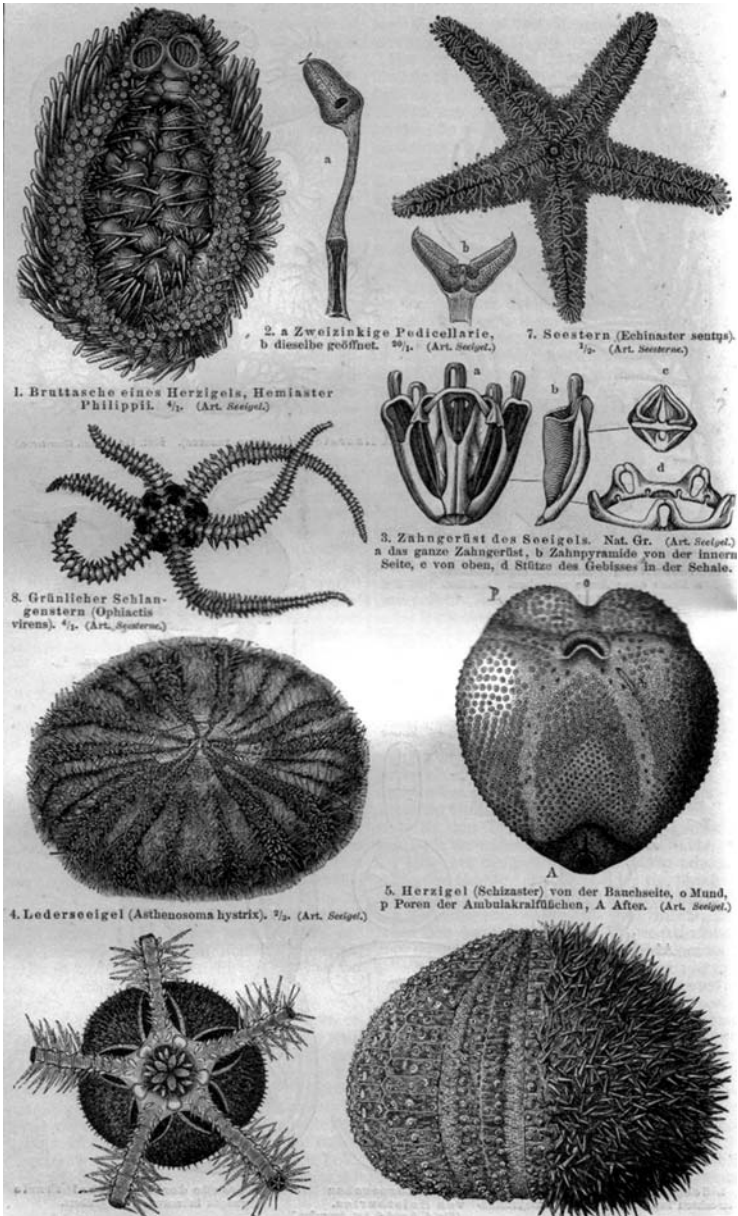


FIGURE 5.8. Kelp is the popular name for large seaweeds of the order *Laminariales*, class *Phaeophyceae* (brown algae). The picture shows several species from the North Sea including *Laminaria saccharina* and *Laminaria hyperborea*, which reach sizes of up to 3 m. Its largest member is *Macrocystis* with 65-m length. In the text we speak about *Nerocystis*, the “sea otter’s cabbage” and top-down control in a marine ecosystem.

name “sea otters cabbage.” The name for this up to 40 m long brown alga from the rapid tideways is of course a misnomer. The otter does not eat this cabbage. It searches only its prey there, namely the sea urchins which are herbivores of the kelp (Figure 5.9).



Putting all Actors Together

Causal relationships in ecology have a different structure than experiments in laboratory biology. However, the logical links in the killer whale case are very strong: In several islands of the Aleutian archipelago, the 1990s saw a parallel decrease in sea otter populations down to 10% of the 1970s levels. An inverse trend was seen in sea urchins; over the same time period they showed an eightfold increase in biomass. The kelp density, by contrast, decreased by a factor of 12. The kelp tissue loss due to herbivory was 1% in the 1970s and increased to nearly 50% in the 1990s. That the chain of events was actually set in motion by the killer whales was made likely by another observation: Areas that were inaccessible to killer whales for local geographical reasons showed no otter decline, while otters from nearby areas with open access to the ocean were severely affected. In the hindsight, you might argue that one could have predicted this chain reaction as early as the otter appeared on the diet of the killer whale. However, the first event could not be predicted since killer whales and otters coexisted side by side for a while without being involved in predator–prey relationships. Only when the orca’s favorite food item disappeared, the otters followed the seals and sea lions on the hunting list of killer whales.

The basic conclusion from this food web was recently confirmed by ecologists who surveyed the Californian kelp forest ecosystem over years to understand the importance of top-down, i.e., consumer-driven, versus the bottom-up, i.e., resource-driven, control of food webs. Coastal kelp forests receive large amounts of fertilizers via anthropogenic runoff. On the other hand, the abundances of large marine top-predators have been substantially reduced over the last decades. A multiyear satellite survey of primary productivity showed that the top-down control explained tenfold more of the variance in the abundance at the bottom trophic level of the kelp than the bottom-up nutrient supply (Halpern et al. 2006).

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FIGURE 5.9. Representative extant echinoderms. *Top row*: Sea urchin *Hemiaster* (1), which keeps its eggs in a brooding chamber. At the *right* the asteroid *Echinaster* (7), with the typical five-rayed symmetry. Between them are pedicellaria (2), pincer-like skeleton structures that have a controversial and not yet settled history of interpretation. Some stars use them to capture prey. *Next row*: The ophiuroids *Ophiactis virens* (8) and *Ophiothrix* (*bottom row, left*); at the *right*, Aristotle’s lantern, a complex masticatory apparatus lying just inside the mouth of sea urchins, with five protractible teeth (3). *Next row*: Two sea urchins (*Astenosoma* and *Schizaster*) seen from the ventral side showing the mouth as a central opening, A = anus. *Bottom right*: Sea urchin (*Echinus esculentus*, at the left side of this radial arranged animal, the characteristic spines were removed). The sea urchin is the actor in an oscillating marine food chain. They forage on large algae, but are eaten by otters, which fall prey to orcas. You will see how the effect of a top predator can spiral down in a food chain. You will also see Echinodermata as a surprising cousin of *Amphioxus*.

The Fall of the Whales

Humans as Top Predator

The chapter title is on purpose ambiguous. It refers first to the decline in the number of whales due to whaling. Herman Melville's wonderful novel on Moby Dick attracted literature fame to the business of whale hunting, which represented the economical basis for a number of coastal regions in the nineteenth century. Whale hunting is still practiced today for human food consumption. Before human intervention, baleen whales had not much to fear. Although they are situated as phytoplankton and krill eaters at a relatively low trophic level, only few predators have the courage to attack these giants of the sea. Only the killer whales were known to occasionally attack young baleen whale calves. All this changed when baleen whales became the target of the ultimate top predator of our planet. Hunting has thus dramatically reduced all baleen whale populations. Protection measures have led to a recovery of the reduced populations, but to what level? Since we have no reliable statistics of whale numbers before the start of the hunting, it is difficult to estimate the carrying capacity of the oceans for whales. This has practical consequences when, for example, the International Whaling Commission states that catches should not be allowed on stocks below 54% of their estimated carrying capacity. The level of neutral genetic variations increases with population size. This allows suggesting historical population sizes from the observation of genetic diversity in baleen whales. Taken at face value, the genetic data indicate that the current population levels of baleen whales are only a fraction of the past numbers (down perhaps by a factor of between 6 and 20; Roman and Palumbi 2003). This subject has received sufficient media coverage, not to be repeated in this book.

The Death of the Whale

Actually, the story I want to retell starts quite recently with the submarine Alvin in 1987. The researchers crossed by chance the 21-m long skeleton of a blue whale. They found bacteria and worms living on the whale's bones that were previously only known from hydrothermal vents (Haag 2005). All whales die sometime and as they have no natural predators of ecological importance, their carcasses fall to the floor of the sea. Mortality is in fact relatively high in female whales during migration. They are stressed by the birth process, and they accompany the newborns that are sometimes hunted by killer whales. However, the killer whales carry their name with justification since they do eat only few organs of the baleen calves and leave the rest to the sea. A whale carcass is a nutritional feast to the nutritionally desert of the seafloor. Sharks, hagfish, and lobsters prey on the soft tissue for many months. Then the falls feed worms and crustaceans. When anaerobic bacteria start with their work, they create a sulfide-rich environment, which prepares the niche for the invasion of further worms, clams, and mussels. Even when all

soft tissue has disappeared, the fat-rich bone marrow of the whale bones will feed a specialized community, which will still live from the whale for up to a century.

Life Histories Between the Land and the Sea

On the Value of Case Reports

Medical research journals publish in addition to controlled clinical trials and large epidemiological surveys also the case reports of interesting medical observations in an individual patient. As an example, I remember a report of a patient that suffered transient paralysis when eating bananas. This fruit is rich in potassium and the patient showed a defect in the absorption of dietary potassium, which led to a short-term benign disturbance of the Na^+/K^+ gradient over the excitable muscle membrane. In this way a single patient might lead to the identification of interesting metabolic mutation and thus contribute new insights into human physiology. In the following, I will report on a series of animal case reports that each touch a nutritional life history of an animal living at the interface between the sea and the land. They are hopefully as entertaining as instructive in our quest for food survey and guide us to the ecology of land animals, which will be the subject of the next section.

The Shrinking Reptile

Some reptiles are special with respect to growth. For example, the Nile crocodile shows an open growth: It grows in length as long as it lives. You can thus actually tell the relative age of these crocodiles by measuring their length. Despite this precedence, it came as a surprise when zoologists learned that reptiles could also reversibly shrink as a response to food shortage (Wikelski and Thom 2000). The animal in question is a marine iguana from Galapagos (Figure 5.10). This long-lived (about 35 cm long) reptile feeds on green and red algae growing in the submerged intertidal zone. During periodic El Niño events the sea surface temperature around Galapagos can increase from 18 to 32 °C due to the disruption of cold nutrient-rich ocean current upwelling. Green and red algae disappear during this regime and are replaced by brown algae that the iguanas find difficult to digest. Until the arrival of the next La Niña conditions, which furthers again the growth of their favorite food, up to 90% of the iguanas can die of starvation. A few animals found an answer: They shrank in size by as much as 20% of the body size between successive years. The degree of shrinkage was positively correlated with the survival of the individual animal. The explanation is easy: As in many grazers, smaller animals are frequently more efficient feeders than larger individuals. The 20% shrinkage cannot be explained by a decrease in cartilage and connective tissue alone, it must also involve bone absorption. Females showed a greater shrinkage than males, probably because they suffer

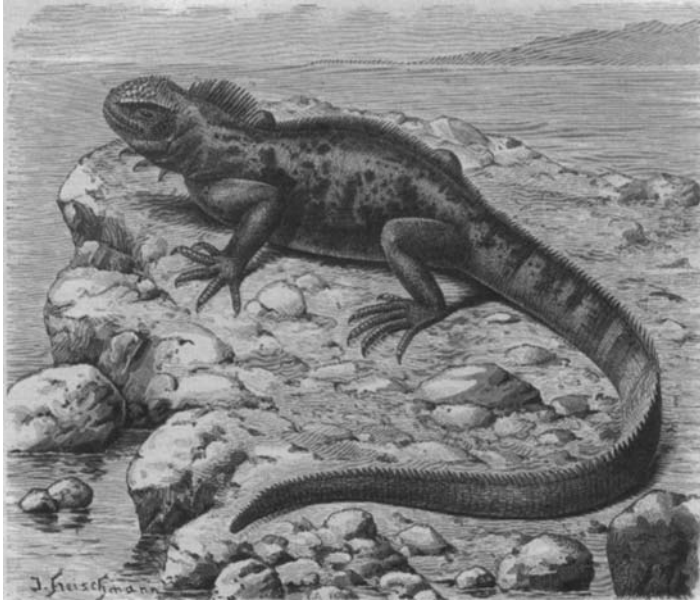


FIGURE 5.10. Galapagos is a world of its own. The picture shows the reptile *Amblyrhynchus cristatus*, which belongs to family Iguanidae, order Squamata. The book tells the story how this reptile shrinks in body size in times of food shortage.

from the extra energy expenses due to egg-laying. It is striking that this strategy, well known from bacteria under starvation, is so little used in starving animals since it is apparently possible in a large vertebrate.

The Fasting Father Penguin

King penguin partners alternate in staying with their egg in the 54-day incubation period between laying and hatching (Gauthier-Clerc et al. 2000; Figure 5.11). They feed only when at sea and must fast when ashore. The nonincubating partner forages at sea, but has to travel up to 500 km away from the colony to satisfy its food needs. Return to the incubating partner is thus somewhat unpredictable. During the early parts of the incubation period, both parents come back only with a few pebbles in the stomach (as in many birds the stones functionally replace the lack of teeth in the beak). Males try to replace the female near hatching time. The male penguins apparently have an internal clock: They return with about 200 g of fish remains and squid parts in their stomach 20 days before hatching, but increase the stomach content up to 1 kg in a narrow window around the calculated hatching time. During the final male egg incubation period, the males lose 160 g body weight per day. This amounts over a 3-week period to 20% of their initial body weight. If the female does not return at time and the young



FIGURE 5.11. The king penguin (*Aptenodytes patagonicus*) is presented in the book as a caring father to the hungry chick.

hatches, the male starts to feed the chick from its stomach contents. Notably, the regurgitated food shows the same preservation state as the initial stomach filling. The father penguin has not touched the stored food whose energy content covers the energy need of the hatched chick for 10 days, thus providing a buffer against delayed return of the female partner. In contrast, males returning 10 days after hatching come with empty stomach. If the female deserted the egg, the males also returned with empty stomach, they can thus overrule their internal clock.

Growth Limitations for Seabird Colonies

British ornithologists observed that smaller kittiwake colonies tended to grow proportionally faster than larger colonies. A model known as Ashmole's population regulation hypothesis was developed setting an upper limit to the colony growth. According to this model, adult birds forage close to the colony and cause a depletion of local fish prey. Birds from larger colonies therefore have to travel longer to find the same amount of food for their chicks as birds from smaller colonies. The tenets of this hypothesis were tested for the gannet (*Morus bassanus*, Figure 5.12; Lewis et al. 2001). The extensive observation of birds in Britain over nearly a century documented an expansion in size of gannet colonies. Satellite tracking verified that the foraging range is closely related with foraging trip duration. The researchers found a significant



FIGURE 5.12. The gannet (*Morus bassanus*) of the family Sulidae, order Pelecaniformes, is the largest seabird in the northern Atlantic.

correlation between trip duration and colony size. In a densely populated colony with 40,000 occupied sites, the average trip duration was 21 h. This corresponds to an excursion of about 150 km. Birds from smaller colonies had to travel only 50 km to land the same amount of catches. They have to work less hard and achieve thus a better breeding success. The researchers measured that the growth of gannet colonies was density dependent, reaching stagnancy when approaching a limiting upper size. Intraspecific food competition became the limiting factor for further growth. Paradoxically, seabird colonies have only a small influence on local total fish mortality. The seeming paradox was resolved when it became clear that pelagic fish prey of gannets showed an escape response when attacked by gannets. Gannets hunt by plunge diving. In the vicinity of the colonies, fish escaped predation simply by swimming vertically downward.

Diet Shifts in the Great Skua

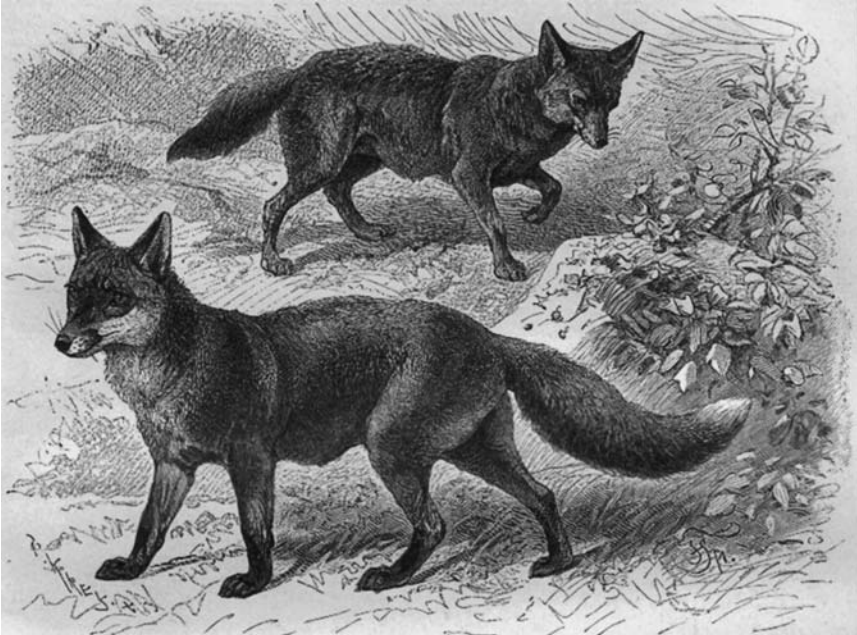
Fishery produces a large quantity of waste, being offal or the catch of undersized fish without commercial value. This results annually in the discarding of about 30 million tons of fish. A whole population of seabirds feeds extensively on discards and in the past times many of their populations have substantially increased. The current decline of fish stocks, changes in catching techniques, and recovery programs have led in the North Sea to a substantial decline in discarded undersized whittings (*Merlangius merlangus*). The changed discard availability had important effects on the scavenging seabird population consisting of fulmars, gannets, several gulls, and the great skuas (Figure 5.13; Votier et al. 2004). The latter is a top predator in the marine food web of the North Sea. This sizable bird reaches more than half a meter in length and is a restless warrior governed by a nearly insatiable hunger. The bird requires 2,500 kJ/day. The declining fish discards resulted in a shift to alternative prey like the small, shoaling sandeel, a lipid-rich fish. However, the sandeel population also fluctuates in availability and forced the great skua to still other prey and this is notably also other seabirds. In Shetland the skua ate about a third of the adult population of the kittiwakes. It was calculated that with a modest 5% contribution of birds to the diet of the skua, this means that a single colony of 5,000 skuas on the island Foula consumes about 800 kg of birds per breeding season. Prey remains indicate that skuas forage on adult birds between April and mid-July. From mid-July eggs and fledglings from fulmars and puffins are their preferred bird prey. The fish discard decline resulted thus in a substantial pressure on the North Sea bird population and the predation by the skua became a substantial component of the annual mortality of the seabird populations. Only further ecological observation will show whether the skua will drive some seabirds into a population collapse or whether it changes again its diet to avoid its own population collapse due to dwindling food resources.



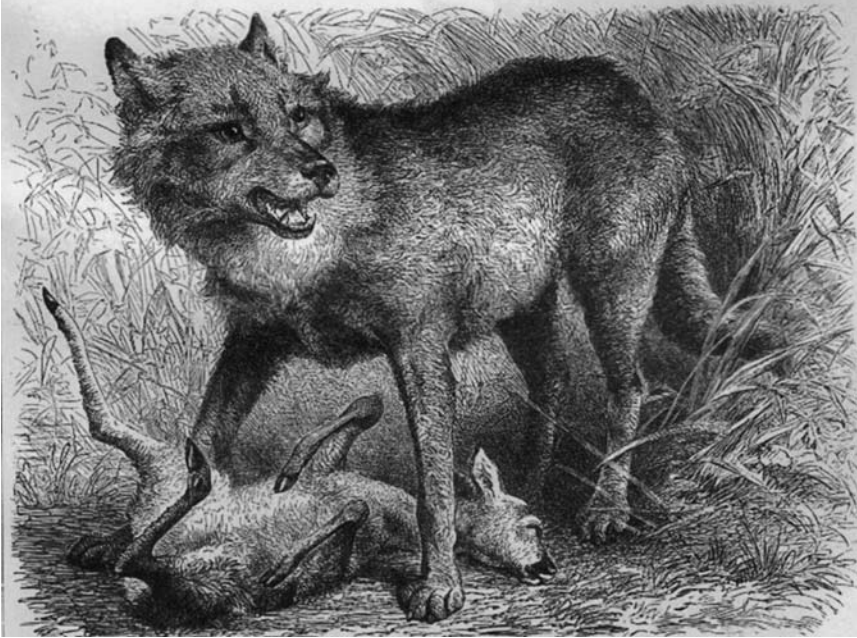
FIGURE 5.13. Skua (*Catharacta skua*), family Stercorariidae, order Charadriiformes, is an agile predatory bird that forces other birds to disgorge food. When its fish food basis dwindles, it does not shy away to prey on other seabirds as recounted in one of the life stories from the border of the sea.

The Fox and the Gull – Complex Webs of Interaction

The title reads like a fable from Aesop, but this life history was recently told in a scientific journal (Croll et al. 2005). The facts are easily recalled and are seemingly logic. The theoretical implications are, however, important and deal with cascading trophic interactions. Trophic cascades are defined by top-down control of community structure by top predators. These cascading effects can completely restructure an entire food web. The theoretical treatment of food webs is mathematically rather demanding. It is thus gratifying that its basic principles can be illustrated with a simple example. The scene is the Aleutian archipelago. The fur trade in the late nineteenth century led to a collapse of top mammalian predators around the Bering Sea. To revive the fur business, the Arctic fox (*Alopex lagopus*) was introduced on some islands where they had an astonishing domino effect. The islands on which foxes were introduced showed a striking transformation from grassland to a maritime tundra ecosystem: The more productive grasses and sedges were replaced by the less productive forbs and shrubs. What caused this change of ecosystem to a nutrient-impoverished regime? Apparently, the introduction of a top predator (Figure 5.14) caused effects that spiraled down to the level of the primary producers. Cascading



1. Fuchs (*Canis Vulpes*), $\frac{1}{12}$. (Art. *Fuchs*.) — Oben: 2. Schakal (*Canis aureus*), $\frac{1}{12}$. (Art. *Schakal*.)



trophic interactions were set in motion. The archipelago carried 29 species of seabirds representing a population that exceeded 10 million individuals. On fox-infested islands this bird fauna was severely reduced. Due to their large number the birds were important linkers between the ocean and the terrestrial ecosystem. The birds foraged on the sea and extracted food from the ocean. This food was digested and resulted in the excretion of nitrogen-rich guano on the bird's resting places on the island. The seabirds exported thus nitrogen and phosphorus from the sea onto the land thereby subsidizing the terrestrial ecosystem with ocean-derived nutrients. On fox-infested islands the breeding seabird density decreased by almost 100-fold and the annual guano input decreased in parallel from 360 to 6 g m^{-2} , thus reducing the soil fertility. Controlled fertilization experiments on fox-infested islands resulted in the shift back from the tundra to grassland proving the nutrient link for the regime change.

Nutritional Ecology

Trophic Cascades Across Ecosystems

Ecologists have described a number of systems where predation can result in strong effects through a food web. If a member of the food chain shows a change from the aquatic to terrestrial life style, one can get astonishing effects across ecosystems. This was recently shown for dragonflies (Figure 5.15). Dragonflies and damselflies belong to the insect order Odonata. Both larvae and adults are active predators. Larvae consume various invertebrates from their aquatic niche, while adults capture other flying insects. They possess chewing mouthparts with massive mandibles. The labium is modified into a prehensile organ. US zoologists looked into a site in Florida dotted with small ponds (Knight et al. 2005). Four naturally contained fish, four lacked fish, and they observed that fish facilitated plant reproduction near the pond. What happened? Actually, the juvenile forms of dragonflies are submitted to predation by fish. When there are no fishes in the pond, more and larger sizes of dragonfly larvae can develop. This gives rise to more dragonflies around the fish pond. The adults are active flyers, which avoid fish-containing ponds for oviposition since their success in reproduction here will be lower. This increased concentration of dragonflies



FIGURE 5.14. The red fox (*Vulpes vulpes*) (*center*) belongs to the dog family (Canidae) like the jackal and the wolf. The fox from the Old World eats mice, rabbits, birds, eggs, and fruits. A lot of folklore surrounds this animal, not the least the fox is the hero in a great verse epos "Reinecke Fuchs" from Goethe. The jackal (*Canis aureus*, at the *top*) is in contrast known to folklore for its cowardice. Its eating habits probably earned it this reputation: the jackal lives from small mammals, carrion, and plant material. It follows lions and finishes the leftovers of their prey. The wolf (*Canis lupus*) (*bottom*) is the largest feral animal of the dog family. This social animal lives and hunts in packs. Its preferred prey is deer, moose, and caribou, but it also attacks mice, rabbits, and birds.



FIGURE 5.15. Dragonflies around a pond. The picture shows various species of Brazilian dragonflies (top to bottom: *Chalcopteryx*, *Hataerina*, *Euthore*, *Thore*), family Libellulidae, order Odonata.

around fish-free ponds leads to a decrease in their favorite prey—bees, followed by moths and flies. Bees play an important role as pollinators for plants that grow at the border of these ponds like St John’s wart (*Hypericum*). This plant has evolved traits to attract bees as pollinators. However, near fish-free ponds bees are rare and flies have to take up this role, but they are apparently less efficient (Figure 5.16). The consequence is clear: The plants become pollen limited and less seeds are produced. This is not just the effect of lower numbers



FIGURE 5.16. Insects as pollinators. The figure mainly shows flies (Diptera), on the top of flowers *Dioctria*, *Helophilus*, two species of *Volucella*, at the bottom left a Hymenoptera, *Bombus*, a bumblebee. The figure illustrates the prey of dragonfly.

of bees. Pollinators perceive the risk and avoid foraging near dragonflies, they hastily rush from flower to flower and search a quieter place. Animals which change from aquatic to terrestrial ecosystems are not rare; actually an important class of vertebrates carry a name that reflects their split loyalty—Amphibia. Salamanders are similarly predators in both ecosystems.

The War of the Senses: The Example of Echolocation

Killer Whale Versus Harbor Seal

With the killer whales (*Orcinus orca*) we got to a top predator of the ocean. One of its preys is the harbor seal (*Phoca vitulina*) and it needs all its senses to stay alive. In one of the previous chapter, we heard how its bigger cousin was using its whiskers to detect the herring prey. Now the seal needs its ears to detect and interpret the underwater calls of killer whales. Not all killer whales are dangerous for seals. The resident killer whales live in large stable groups and feed exclusively on fish. However, in the waters there are also transient killer whales that live in small groups and feed only on marine mammals. The piscivorous whales emit echolocation clicks in the quest for their prey, and they have in addition a rich repertoire of vocal dialects for communication. Harbor seals have a good underwater hearing and the calls of the fish-eating whales can be heard over great distance. It would be a waste of energy if seals would respond to the calls of all killer whales with an escape response, i.e., leaving the sea surface where the seal is well visible and an easy target to echolocating predators. Therefore, it is not surprising that seals do not care about the calls of the resident whales. To be on the safer side they make the investment to “learn” all local dialects of the resident whales, which is no small memory task (Deecke et al. 2002). The mammal-hunting whales, in contrast, are usually silent, but when they give a call, the seals immediately start with the escape reaction. Probably, this explains why the mammal-hunting whales vocalize less frequently than the fish-eating whales. Then the marine biologists did an interesting experiment. They recorded the calls of fish-eating killer whales living in Alaska, which “spoke” a different dialect, and displayed these sounds to the British Columbia seals. What would they do? Actually, they interpreted the intrinsically harmless Alaska orca calls as danger and showed an escape reaction. Apparently, they did not recognize a specific dangerous killer call, they treated any calls as potentially dangerous except those they learned to associate with harmless neighbors. Only by selective habituation the seals learned what not to fear, a conservative but safe strategy.

Ultrasound Detection and Escape Reaction:

From the Herring to the Butterfly

Echolocation is also a hunting strategy used by dolphins. Most fish species do not hear the ultrasonic clicks used by the predator. Cods and clupeid fish like the herring or shad show an escape response. Do they actually hear ultrasound? Zoologists established audiograms for shads by training them to reduce their heartbeat when they detected a sound. They confirmed the sensitivity of shads to ultrasound signals (Mann et al. 1997). In addition, clupeids show a unique ear structure: A pair of thin air-filled tubes project from the swim bladder and terminate in air chambers that are connected with the utricles of the inner ear.

Cetaceans like the dolphin and the killer whale are not the only users of echolocation. The same hunting tool evolved in bats. Also its prey had to evolve counterstrategies to stay alive. Take Lepidopteran as example. One straightforward strategy is to avoid the bat. As bats are hunting at night, a simple strategy is to be active during daytime. This is the option of butterflies (Figure 5.17), the diurnal Lepidopteran. They rely on a well-developed visual system for predator detection and communication. The first makes them difficult to hunt as you remember from your childhood days and the second makes them beautiful animals. The butterfly was thus “invented” by the bat. Lepidopteran which are active at night are called moths (Figure 5.18). Due to the predation pressure by echolocating bats, moths have evolved five times ultrasound hearing. Escape under the sunlight seems to be a late development of Lepidopteran. Interestingly, *Hedyloidea*, the living ancestor of modern-day butterflies, which forages still in the night possess ultrasound hearing. At the basis of their wings, they have ultrasound hearing ears showing a tympanic membrane connected to an ear canal. When they are caught in an ultrasound wave package, they initiate with very short latency of 40 ms—an elaborate flight manoeuvre. They increase the flight speed fourfold and make steep dives or climbs mixed with unpredictable loops and spirals (Yack and Fullard 2000).

Parallels and Differences in Echolocation

It is remarkable how a basic problem, namely lack of visibility of the prey to the predator, led to a similar solution. Bats do not see the moth because they hunt at night and dolphins do not see the fish because of the low penetration of light in their marine environment. The very different physical medium, air and water, did not prevent the convergent evolution of very comparable echolocation systems. In detail, there are of course many differences between both echolocation systems. For example, both animals solve differently the problem how to avoid being deafened by their own ultrasound cries when they get very near to the prey. When approaching the prey, fewer echos are lost to the medium, thus the sound becomes louder. In dolphins, the amplitude of the sonar they emitted decreased by 6 dB every time the distance was halved. Thus the echo does not increase in strength. In contrast, bats keep the amplitude of their sonar signals constant, but they can decrease the sensitivity of the hearing process as they get nearer to the prey. The different strategies are dictated by different anatomies in the middle ear. The local muscles are stiffer in the ear of the dolphins than in the bats thereby precluding a down regulation of the hearing sensitivity (Tromans 2003; Au and Benoit-Bird 2003).

Background for the Bat

Other observations, namely those with bats, concur with a food differentiation in coexisting predator species. First, I will provide a short historical note on this fascinating foraging technique. The discovery that bats could “see” with their ears was made by L. Spallanzini more than 200 years ago (Figure 5.19). It was heavily



FIGURE 5.17. Because of their day-flying habits and bright colors, butterflies (superfamily Papilionoidea) are very visible to humans. The figure shows several common examples of European butterflies (from top: *Lycaena*, *Gonepteryx*, *Vanessa atalanta*, *Vanessa io*, *Lycaena arion*). However, the vast majority of the Lepidopteran diversity comes with night-flying and dull-colored moths. Biologists think that the evolution of butterflies is a response to the predation pressure by night-hunting bats.

rejected by G. Cuvier, but after repeating Spallanzini's experiments D. Griffin confirmed the interpretation in 1940. He also coined the term echolocation to describe the phenomenon of how bats use the echoes of the calls they produced to locate objects in their path (Fenton and Ratcliffe 2004). Fossil evidence supported



FIGURE 5.18. The nighttime brethren of butterflies, represented by common European moths, is shown. The three larger animals belong to the order Sphingidae, Heterocera (*Sphinx convolvuli* (top), *Sphinx neri* (center), *Sphinx ligustri* (bottom)). Some moths have developed ultrasound hearing and escape reactions.

the hypothesis that the oldest known bats had already evolved this technique nearly 50 million years ago (Novacek 1985). Echolocating bats can be divided into guilds according to their preferred habitat and foraging behavior. There are “hawks” and “gleaners,” “trawlers” and vegetarians within echolocating bats.

Let’s start with the trawlers. Five species of the European bat *Myotis* (Figure 5.20) were investigated for their foraging technique. They all screen prey in the aerial edge space near vegetation. This could lead to potential competition

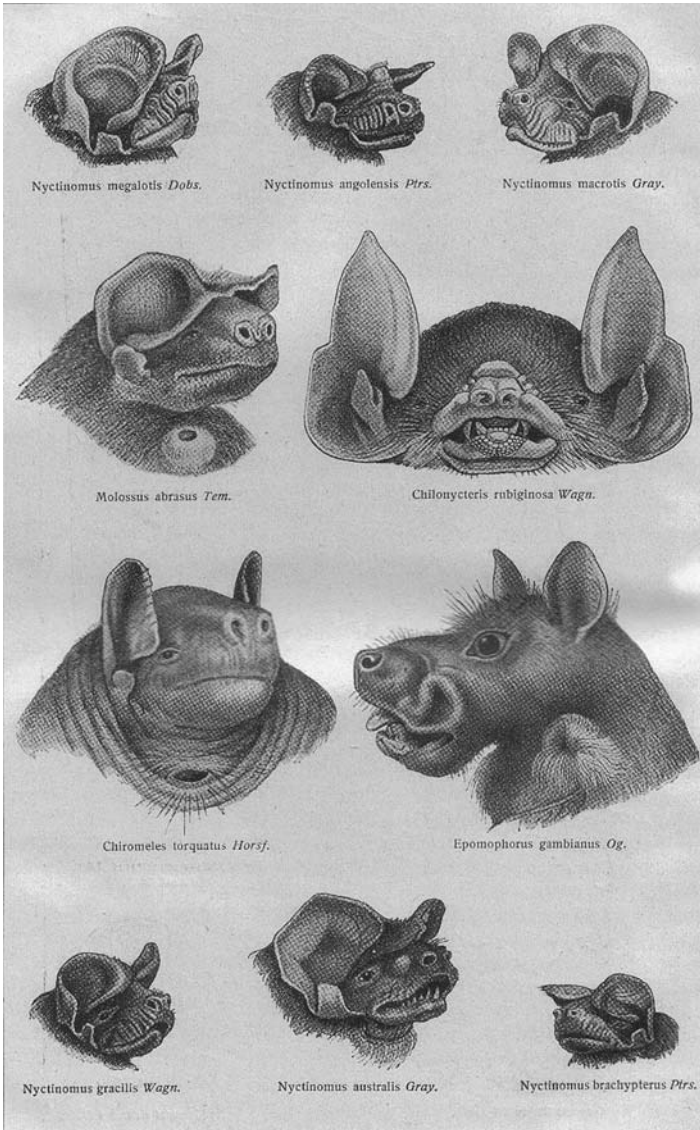


FIGURE 5.19. Portraits of different bats (Chiroptera) showing that in many of them the acoustic orientation dominates over the visual or olfactory senses.

between these animals; however, differences in the echolocation signals contribute to within-guild niche differentiation. These bats catch flying insects and spiders walking close to vegetation. This creates a problem for the bats: How can they differentiate the prey against the background? Experience with mealworms on a clutter screen, which mimicked the vegetation noise, showed that they could not see the prey when sitting on the screen. The prey became



FIGURE 5.20. Brown bat (*Myotis myotis*), a common Chiroptera with worldwide distribution—next to man it could be the most widespread of land mammals. Its echolocation-based foraging covers strategies of hawks, gleaners, or trawlers as discussed in the text.

visible only when removed several centimeters away from the screen. The interesting observation was that the five species differed in their capability to locate the prey according to the distance (Siemers and Schnitzler 2004). Within a 5 cm distance between prey and screen only *Myotis nattereri* showed a 100% capture success rate; the four other species needed a successively greater distance for successful hunting. Visual, olfactory, and passive acoustic cues were excluded for the capture success as well as wing morphology. The difference was in the quality of the echolocating systems. All five bats chose an oblique flight path when approaching the screen. However, the sonar differed substantially: The best performing bat at low distance showed the highest start frequency in the sonar, which then swept also the broadest frequency band from 135 to 16 kHz. Expressed as wavelength it covers 3–22 mm, this is just the size range of arthropods they prey and leave background clutter. In other words, *M. nattereri* illuminates the sonar scene with more “light.” It is thus possible that these five bat species are not competing at all for a common food source, but each specialized to an invisible food layer at different distances from the background vegetation.

Bats Structuring the Food Space

Bats are fascinating animals for zoologists. Take the large-eared horseshoe bat (*Rhinolophus philippinensis*), a rare but interesting species from the Wallacea region (southeast Asia to northwest Australia, named after A. Russel Wallace the co-discoverer of the evolution theory, who did important field work in that

region). This species comes in three morphs: a large, an intermediate, and a small form, where the extremes differ by a factor of two in weight. Each size class was associated with different echolocation call frequencies: the large called at 27 kHz, the small at 53 kHz. The intermediate was also for this property between the extremes (Kingston and Rossiter 2004). The physical consequences are immediately clear: Animals with low frequency calls emit longer wavelengths, which reflect poorly from small prey. Thus for them, prey below 13 mm wing lengths should be difficult to detect. However, as is usual in biology, there is a trade-off: Low frequency calls are less subject to environmental attenuation and allows thus a larger detection range. The large morph samples thus a five times larger volume for large prey compared to the small morph. The latter “sees” nine times as much small insects than the large morph, but its “visual field” range is smaller. The size difference might reflect a secondary adaptation. If you catch bigger prey, you need also a bigger mouth. The impact of this differentiation goes actually further. The bat’s sonar is used not only in the quest for food, but also in intraspecific communication, namely mate recognition. The large and the small morphs are functionally deaf to each other’s calls. The intermediate form can hear the large and the small morph, but it is unable to establish a reciprocal relationship between either of them. In this way, reproductive isolation can be established in sympatric populations (i.e., those living in the same geographical area without physical barriers).

Bats as Pollinators

*You can illustrate many basic biological principles with bats. Blood sucking vampire bats provided fascinating examples for R. Dawkins book The Selfish Gene, where you can deal with the problems of mutual help, cheating, and altruism in mammals. I will use here another aspect of bat’s echolocation system. Actually, not all prey dislikes the idea of a visit by a bat. Some like and even need bats and found forms to attract them. This sounds pretty paradox, but is easily understood when realizing that some bats are pollinators. Several hundred species of neotropical plants are pollinated by glossophagine bats. Remember the disrespect for scientific terms, this reads as “tongue-eating” bats. The tit-for-tat is clear; the bat gets nectar as its food and serves as a distributing system of the pollen for the plant. It is one of the great ironies of natural selection that we find the flowers of plants esthetical while they evolved to be attractive for insect pollinators. We and insects see flowers in different wavelengths due to the distinct wavelength of the two eye systems. Bats do not see the flowers when they are foraging during the night, they literally hear them. Plants don’t cry, but the bat-pollinated neotropical vine *Mucuna holtonii* evolved a flower structure that functions like a cat’s eye on your bike in the optical range. The flower is of the more complicated type of Papilionaceae (e.g., the pea). The inflorescences hang down several meters from the canopy and are located at the edge of the rain forest. When the pollen is mature, the flower lifts its upper petal, which signals a virgin willing to give 100 μ l nectar on the first visit and an explosion of pollen*

on the back of the bat when it presses its snout into the flower. The remarkable observation is that the immature flower is a poor echo reflector, but with the top petal lifted the plant becomes a good reflector and thus very “visible” to the bat (von Helversen and von Helversen 1999). In fact, in the first night bats visited 88% of virgin flowers with the lifted petal. When the researchers cut the top petal, this frequency fell to 21%. To prove that they had only touched the sonar reflector and not other cues (e.g., olfactory signals), they let the flower intact, but put some cotton wool into the top petal reflector. The rate of the bat visits fell to 17% and the reflectance of the flower was only marginally higher than that of the closed flower. *With the latter example we come to a new level of complexity in the sensory structuring of the food space. The senses of the predator are answered by a sensory response of the prey, in this case of a consenting prey. In case of unfriendly takeover, the war of the senses is declared in the “eat and be eaten” scenario.*

Listening Bats

Echolocation is a formidable tool for insectivorous bats, but it cannot serve all purposes. It is well adapted to aerial hawking, i.e., the location and capture of airborne prey. The prey stays clear against a void background. The prey can avoid this dangerous position when hiding in bushes. Bats cannot detect the prey against the reflecting leaves, especially when the prey remains immobile. In such echo-cluttering environments, bats must change their foraging strategy. They change for substrate gleaning. They switch off echolocation and listen instead for prey-generated sounds to locate the insect (Arlettaz et al. 2001). Some prey has to call, for example, frogs that must attract a mating partner. The bat *Trachops cirrhosus* uses these acoustic cues to capture calling frogs. Its performance is poor when the frog is not calling. But if the frog is vocalizing, the bat can distinguish a palatable species from a poisonous one, or a small species from one that is too large to be captured or eaten (Tuttle and Ryan 1981).

Antipredation Strategies

Sleep: The Problem of Putting Senses to Rest

Survival depends heavily on the sharpness of your senses. However, nobody can be on the alert all the time. Higher animals need, like us, a fair dose of sleep. However, the shut down of the senses exposes the animal to substantial danger. Birds have overcome the problem of sleeping in risky situations by developing the ability to sleep with one eye open and one hemisphere of the brain awake. The investigated ducks showed a group-edge effect. Individuals, which are exposed at the edge, kept that eye open that faced the outside of the group. The waking hemisphere was capable of quick predator detection and the ducks initiated escape behavior with a latency of only 0.16 s (Rattenborg et al. 1999).

Alarm Calls

Since predation is the major cause of mortality for most animal species, one should not be surprised that many species have evolved alarm signals that warn conspecifics about imminent danger. Recent studies with *Poecile atricapilla*, a small North American songbird, revealed one of the most subtle alarm systems in animals. Chickadees (Figure 5.21) form groups of eight birds that communicate socially by vocalization. The calls encode information about food, social identity, and also predators. Closer acoustic inspections of the alarm calls demonstrated a sophistication, which ornithologists would not have believed before this study (Templeton et al. 2005). The researchers knew that chickadees distinguished aerial (raptors) from terrestrial (snake, ferret) predators. The bird produce a sound described as a “chick” syllable and one known as “dee” notes. The D-notes differed significantly across the predators and the researchers got a linear relationship when they plotted the number of D-notes against the wingspan of the predator. This is an important information for the potential prey: Birds with large wingspan are less maneuverable, eating few songbirds, while smaller predators are well adapted to hunting songbirds, which thus compose a major part of their diets. The question is, whether the birds were aware of that information in the calls. Playback experiments showed that they modified well their behavior according to the degree of danger. This was not necessarily a flight reaction, mobbing calls recruited other chickadees to harass a predator.

Semantic combinations of two basic calling sounds are now described in *Cercopithecus* monkeys (Arnold and Zuberbuhler 2006). Males call frequently during morning foraging and when seeking sleeping places in the evening. One call warns the group from an approaching terrestrial predator like the leopard (*Panthera pardus*). The group reacts with flight into the canopy. The second call is given when a male had spotted another predator, the crowned eagle (*Stephanoaetus coronatus*). The group does not move into the canopy because this would only increase the predation risk. Psychologists detected now a simple semantic: Combinations of the two calls in series induced a lateral movement in the group. Thus a surprising complex behavior can be induced by using combinations of just two calls.

Flocking

Many vertebrates build large groups of animals, be it shoals of fish, swarms of birds, or herds of grazing mammals. The individual animal experiences a greater protection when hidden in a large group where the predator has difficulties to single out an individual prey than when outside of the group where a predator can easily concentrate on an individual prey. This strategy is widely distributed and also found in invertebrates (e.g., juvenile locusts, Figure 5.22; and migration column of flies, Figure 5.23). The flightless Mormon crickets (*Anabrus simplex*) form enormous migration columns up to 16 km long and several kilometers wide that consist of millions of individuals marching over the countryside, devastating

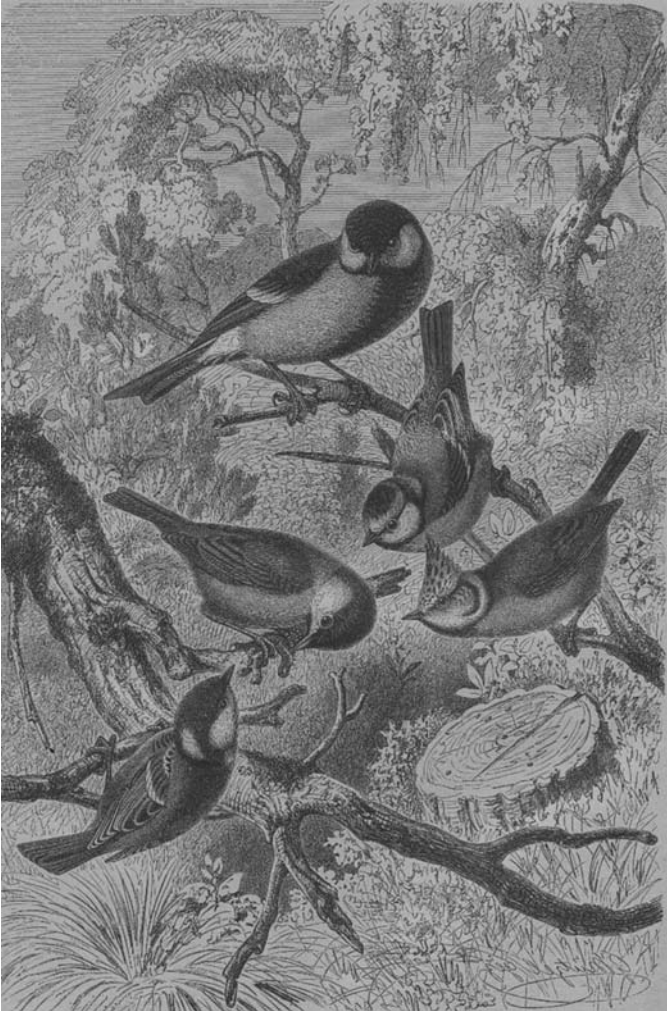


FIGURE 5.21. Various species of chickadees are shown. From *top to bottom*: *Parus major*, *Parus caeruleus*, *Parus palustris* (left) and *Parus cristatus* (right), *Parus ater*. Their alarm called as antipredation strategy is discussed in the book.

all agricultural areas that they cross. It is commonly anticipated that a number of benefits are linked to this flocking. They range from earlier detection of predators, predator confusion by the sheer mass of prey, and if the predator should nevertheless decide to attack, the individual risk is well diluted and the predator arrives to saturation before the counts of the prey is measurably affected. This phenomenon is known as the selfish-herd effect. Agronomists have measured this protection by marking individuals with lightweight radiotransmitters fixed on the back of the crickets (Sword et al. 2005). Half of the marked crickets were

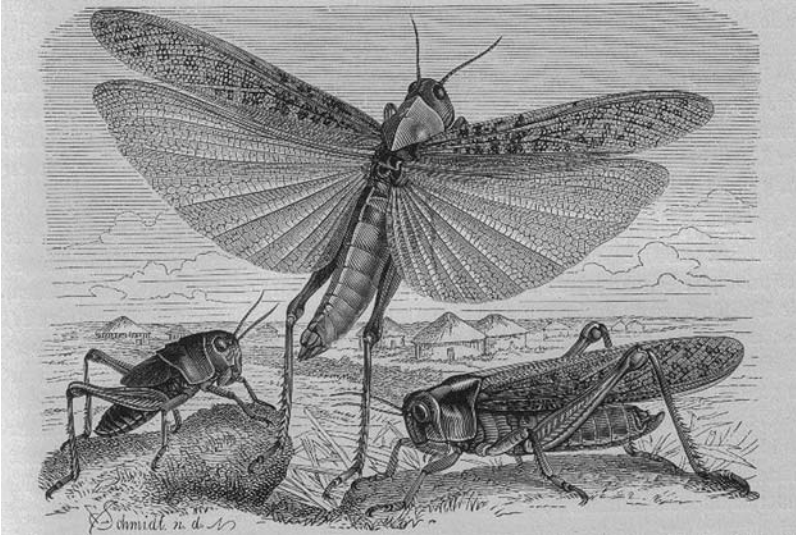


FIGURE 5.22. Locusts (here the European form *Locusta migratoria*, grasshopper family Acrididae) are known from Biblical times as plagues to humankind. Locusts are also part of the diet from hunter-gatherers.

put back into the marching column, the other half was placed outside of the band. Two days later the radiotransmitters were relocated: All column marchers were alive, while the displaced crickets suffered 50% mortality mainly from rodents and birds.

The desert locust *Schistocera gregaria* is from Biblical time known for its catastrophic effects on human society in economic terms. The animal exists in two forms: a harmless nonband-forming solitary form and an actively aggregating band-forming gregarious form. The solitary phase is the normal state of the species and the gregarious migratory phase is a physiological response to unfavorable environmental conditions or overcrowding. The two stages differ in metabolic state, oxygen consumption, and irritability. An understanding of this transition is crucial to the pest control of mobile swarming insects. Before the adult locusts develop flight, juvenile wingless locusts form like crickets kilometer-long marching bands. Control measures depend on the predictability of the marching direction. Ecological zoologists used a model from physicists and treated the animals as self-propelled particles that adjusted its speed and direction in response to near neighbors (Buhl et al. 2006). They tracked locusts in a video-controlled running arena and varied locust density. The time during which the locusts were aligned increased with increasing density and above a density of more than 70 locusts per square meter, spontaneous changes in direction did not any longer occur. They observed that inactive locusts did not affect the behavior of moving locust and that solitary locusts increased their activity levels within hours when exposed to crowding. The scientists suspected



FIGURE 5.23. *Sciara militaris* from the family Mycetophilidae, order Diptera, is a “midge” that owes its name to a behavior shown by its larvae. The larvae eat fungi and decaying plant materials in forests. Like the crickets described in section “Antipredation Strategies,” they form large flocks that march through forests from central Europe, interpreted in the seventeenth century as a harbinger of war (with high predictive value in the times of the Thirty Years’ War). In German they are called “Heerwurm,” army crowd. The animals probably do not search for food, but they do search for favorable places to transform into pupae.

that marching bands allow a sensitive tracking of weak food gradients in the environment that cannot be sensed by individual locusts.

More on Crickets: A Story of Cannibalism

Joining a large mass of conspecifics is, however, also linked with risks since the migration is apparently forced by starvation. These insects selectively feed on high-protein food sources like seed heads and pods, flowers, carrion, and mammal feces, even soil soaked with cattle urine, suggesting that they suffer from nitrogen and salt deprivation. Protein but not carbohydrate satiation inhibited the tendency to march (Simpson et al. 2006). When crickets could satisfy their protein needs on day 1, they decreased their protein intake and increased their carbohydrate intake on day 2. The starved crickets preferred 0.25 M NaCl strongly over water and they selected food in the path of the marching band according to the protein content. The protein and salt deprivation was so strong that they ingested their own shed exoskeleton after molting. Actually, the richest source of the lacking protein and salts were conspecifics. Some protein-deprived insects

consumed another cricket in a single meal. Protein or salt prefeeding reduced that cannibalistic tendency. Actually, the marching is largely imposed by this threat of cannibalism. Consumption of dead animals started within 20 seconds, while experimentally immobilized crickets, which were still able to defend themselves by kicking the attacker with their hindlimbs, largely survived. Cutting one and then two hindlimbs increased the cannibalism rate. Moving in a migratory band is thus a choice of the lesser of two evils, cannibalism over predation threat.

Crickets: A Story of Parasite, Prey, and Predators

Crickets suffer not only from predators, but also from parasites. A gut parasite of crickets is the Gordian worm (*Paragordius*; Ponton et al. 2006). To achieve mating in water, the worm has to convince the cricket to commit suicide in water, which the cricket duly executes. The worm then leaves the gut via the anus of the cricket. In the water, the adult worms are free-living organisms, where they mate as a knotted mass of individuals—hence the name. Few parasites have a predator, but parasites easily fall as victims to predators of their hosts. Some parasites manipulate the behavior of their host such that they avoid zones of predation (or search them actively if their parasites need to reach a different host). During its suicidal action the cricket is active at the water surface and attracts the attention of aquatic predators like fish or frogs. Does it try to get on land? Or does the worm need the next host and the swimming behavior of the cricket is just another trick of the parasite? Such cases are well known in parasitology. The Gordian worm (Figure 5.24) does not need a vertebrate as the next host. Actually, if it would not escape from the attack of the predator, it would be lost together with the cricket. The worm achieves just this escape feat with high efficiency. Minutes after the capture of the cricket prey, the worm escapes from the mouth of the frog or the gill of the trout. Selection has apparently found a solution for the worm's dilemma.

Mimicry

Mimicry comes in many forms and has caused a lot of theoretical discussion since the times of Darwin. Biologists generally distinguish two forms of mimicry. Batesian mimicry is cheating: A prey species uses the look of an inedible species and profits from the protection conferred by the signal evolved by the species warning its predator. In Müllerian mimicry, two species are both unpalatable to a predator and share the cost of teaching a naïve predator their unpleasant nature. However, the teacher pays the lesson with its life and only its conspecifics and the species using the same signals will profit from the deterrence in this educated predator. A recent work with domestic chicks suggested that when the two Müllerian prey species use, for example, two different chemical deterrents, they will heighten the attention level of the predator. When encountering two aversive chemicals, where the predator suspected only one, it will induce a greater caution in the predator (Ruxton and Speed 2005). There are many interesting stories around mimicry—for this book I have chosen two fascinating examples.

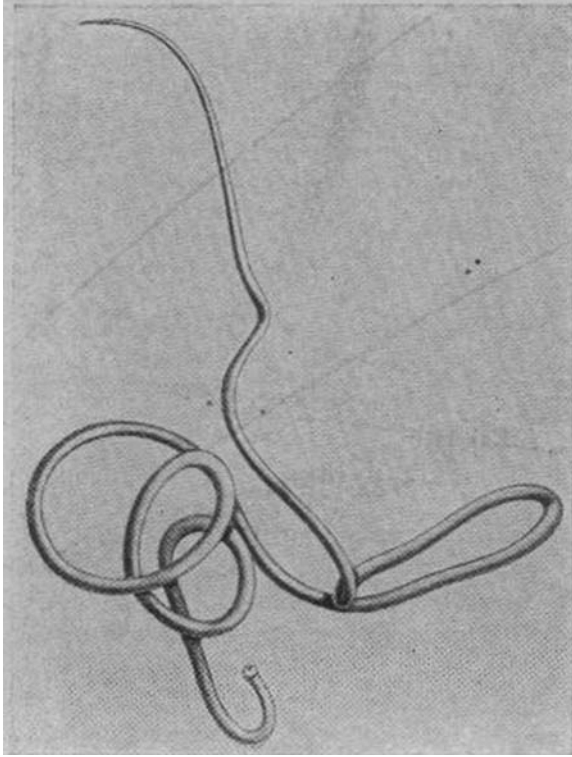


FIGURE 5.24. Gordian worms belong to the class Nematomorpha of the phylum Aschelminthes. The young animals of this roundworm live as parasites in insects, while the adult is free living in water.

Cleaner Fish

The first example is from the reef. The story has a first chapter, where the model of the mimetic is presented. The model is the cleaner fish *Labroides*, which picks from the client fish *Hemigymnus* parasitic isopods (Grutter 1999). The isopods infest the client fish during both day and night, while the cleaner fish eats its daily meal of 1,200 parasites only during the day. The client fish cycles thus with respect to parasite load between morning highs and sunset lows. Overall, the presence of cleaner fish results after a 12-h period in a more than fourfold lower parasite count for the client fish. The latter benefits from the cleaner and will leave it unscarred because the cleaning is of mutual benefit for both animals. The story has a second chapter, where the mimetic is presented: the bluestriped fangblenny *Plagiotremus*, which mimics the juvenile cleaner fish. This disguise allows it to approach and ambush other fish tearing away tissue and scales with its large canines (Cote and Cheney 2005). What makes the story special is the third chapter. *Plagiotremus* can change its color at will. Within minutes of a transfer experiment, it changes into a form that easily blends into shoaling fish

swimming just above the reef. This does not mean that *Plagiotremus* has changed the character. It conceals only in the fish shoals and will mount attacks from the shoal on unsuspect passing fish.

Poisonous Frogs

The second story about mimicry is from the Amazonian part of Ecuador. It deals with Batesian mimicry, i.e., the resemblance of an edible mimic with a toxic model. A nontoxic prey animal thus has to deceive its predator by imitating a toxic animal. US zoologists investigated a theoretically interesting scene with four actors (Darst and Cummings 2006). The first two are poisonous frogs: *Epipedobates bilinguis* and *Epipedobates parvulus*, both with a brightly colored back. However, skin extracts injected into mice demonstrated that *E. parvulus* is more toxic than *E. bilinguis*. The third actor is *Allobates zaparo*, the edible mimic. The fourth actors are avian predators, more about them later. The mimic is dimorphic: In Northern Ecuador, *A. zaparo* mimics the there dominant *E. bilinguis*, in Southern Ecuador it resembles the dominant *E. parvulus*. So far, so good—but what happens in the transition zone where both toxic species overlap? Will the edible frog mimic a polymorphic phenotype or one intermediate between both toxic models or resemble the more prevalent or the more toxic species? In fact, the zoologists were taken by surprise—against their expectation *A. zaparo* mimics the less toxic *E. bilinguis*. To understand this choice we need now the fourth partner in this play, the predator. However, this was a frustrating hunt in the field, even the preparation of plasticine frog models provided no biting marks that could identify the predator. Therefore, the rest of the story unfolded in the Texas garden of one of the zoologists with chicken trained on frog prey. As expected, the lesson with the more poisonous frog was learned quicker and led to generalized avoidance. The lesson with the less poisonous frog, however, was restricted to *E. bilinguis* and its specific mimic. Now it becomes clear why the mimic in the overlap zone mimics counterintuitively the less toxic model. Thereby it reaps the take home messages of the generalized and the specialized lessons from the chick predator and enjoys near complete protection.

Predator–Prey Cycles: From Chaos in the Food Web to Infectious Diseases

It is a major task of ecologists to develop an understanding for the patterns of predator–prey abundance in nature. The first impression when opening an ecology textbook is that of complexity. You find cases where the predator population remains at a rather constant level while its prey shows marked fluctuation in abundance (e.g., tawny owls vs. wood mice and bank voles on the prey side). You find a herbivore population that tracks the abundance of its plant prey, while the plant varies according to other forces than herbivory (e.g., cinnabar moth larvae and ragwort plants). Finally, there are cases where predator and

prey populations are linked together by coupled oscillations in abundance (e.g., lynx and snowshoe hare; examples from Begon's *Ecology*; Blackwell Science 1996). If you read these textbooks, you will see a tendency toward abundance cycles and at the same time you will realize that the mathematical treatment of the predator–prey relationship dominates the discussion. Due to the many factors acting simultaneously on organisms in their environment, the trend for cycles is not so apparent in real populations. Ecologists have therefore increasingly turned to laboratory simulations of predator–prey interactions. In the following, I have chosen a few papers with some recent research results, which document current trends in the predator–prey discussion.

Ciliates and Bacteria in a Chemostat

Even in such simplified systems the outcome of predator–prey interaction can be highly variable (Becks et al. 2005). The ecologists used a simple predator, the ciliate *Tetrahymena*, which had two prey bacteria at its reach, one is the rod-shaped *Pedobacter*, the other the coccus *Brevundimonas*. The ciliate can live on either of the two bacteria as food source, but it prefers the rod on the coccus by a factor of four. In the absence of both bacteria, *Tetrahymena* did not survive the experiment. In the absence of the predator, the rods always outcompeted the cocci documenting their greater fitness in this system. The rules of the game seem pretty clear now. If you are a British, you might find this system worth a bet, but I would recommend that you start with small amounts of money—even this simple system might surprise you. The researchers conducted this three-partner mesocosmos in a chemostat where fresh nutrients for the mesocosm was provided and waste was removed according to a dilution rate determined by the experimentalist. The first run was done with the highest dilution rate $D = 0.9$ per day, i.e., 90% of the medium is exchanged per day. The less competitive coccus is out-diluted within 5 days and the system is reduced to two partners, both the ciliate and the rod bacterium are maintained at high and constant level. The next run was at $D = 0.75$: After 5 days, all three protagonists persisted at constant level with a fixed ratio (rod > coccus). Then the ecologists reduced the dilution to $D = 0.45$ and the system changed its behavior completely. After 10 days you get highly regular abundance oscillations maintained over indefinite time periods. The ciliate and its preferred rod bacterium showed a shift of one-half cycle in their abundance curves, one peaks in the trough of the other. The coccus cycles with lower amplitudes. When you find the system surprising with respect to its variability, you should keep part of your surprise for the final change. The ecologists set D marginally higher, namely to $D = 0.5$. Four replica experiments now showed distinct and aperiodic oscillations, what ecologists call a “deterministic chaos.” Theoretical biologists had made many predictions about chaotic behavior in nature, but the surprise was that this chaos can now be studied experimentally in an extremely simple, but real biological system. Microbiologists believe that deterministic chaos is a characteristic of tiny fragmented populations that occur on soil grains or on detritus particles in the pelagic zone of the open ocean.

Rotifer and Algae: Rapid Evolution Affects the Cycles

US researchers studied a predator–prey system with organisms of a higher morphological complexity. Complexity is relative: Rotifers are tiny metazoa—most are less than 1mm long (Figures 5.25 and 5.26). They belong to a group of animals called Blastocoelomata, referring to the retention of an embryonic feature, the blastocoel body cavity, into adulthood. Despite their small size, the body organization is complex and they are divided into head, trunk, and foot. The anterior part bears a ciliary organ, the corona that rotates in the active animal like wheels, hence the English name “wheel animalcules.” The pharynx is modified as a mastax, a grinding apparatus with jaws adapted to crushing, grinding, grasping, or sucking. They feed on other small animals and algae. The mastax leads into the esophagus and from there into a thick-walled stomach. Salivary and gastric glands add digestive enzymes to the ingested food. Digestion is extracellular in the stomach where nutrients are also absorbed. The intestine is short and fuses with the “kidneys” to a cloaca. In the experiment I want report, scientists fed the planktonic rotifer *Brachionus* with the unicellular asexual green algae *Chlorella*. As in the preceding experiment, the two organisms were held in a flow-through chemostat. The researchers expected well-behaved cycles as predicted by the conventional predator–prey model. However, what they saw were far longer cycles. Disturbingly, they observed extended periods where algal biomass was high, but rotifer densities remained low. This period was followed by increased rotifer growth, but algal density remained nearly constant (Yoshida et al. 2003). In the classical model, peaks in predator abundance follow peaks of prey by a shift of one-quarter of the cycle. What had happened? The algae evolved under the grazing pressure of the rotifer to a heritably smaller form of lower food value. As the algal population was grazed down by the rotifer, these clones increased to dominance. The rotifer population could not efficiently feed on these clones and consequently crashed. When that happens, the larger algae, which are better in nutrient uptake, outcompeted the smaller clones and rose in prevalence. When they again reached a high density, the rotifers could once again grow out. To test their interpretation the scientists used only a single clone of algae in the next experiment and they obtained the classical cycle with a quarter-cycle delay in predator abundance. This system has important lessons for biologists. One take-home lesson is what was called the “life-dinner” dichotomy. The selection pressure on the prey is greater than on the predator because the former loses in this race its life, the latter only a dinner. The other lesson is that the selection forces are fluctuating: Depending on the presence or absence of the rotifer predator, the algae will experience distinct selective pulls. What might be a selective advantage now, might become a disadvantage a few days later. No optimal organism can develop because selection pulls into one direction only to push back moments later. As an end result, fluctuating selective forces favors genetic diversity in the prey species. However, even if it is only for a dinner, predators can also evolve rapidly, but for fun let’s explore the strategies of predators in a different biological system.



FIGURE 5.25. Rotifers, also called Wheel Animalcules, were formerly attributed to the “worm” phylum Aschelminthes, then to an own phylum, which was again contested. The figure shows on top *Melicerta*; bottom left *Noteus*, bottom right *Floscularia*.

Daphnia and Algae: Resource Management via Reproduction

Daphnia are still further up on the complexity scale of the animal reign: They belong to a mainly freshwater order of the Crustacea, the Cladocerans or “water fleas.” These 0.5–3-mm-long animals have a carapace that encloses the trunk, which is fused from the thorax and abdomen. Under the carapace is the brood chamber for the eggs. The trunk carries the phyllopodous appendages, which serve in locomotion and in creating currents to get food into the mouth. The

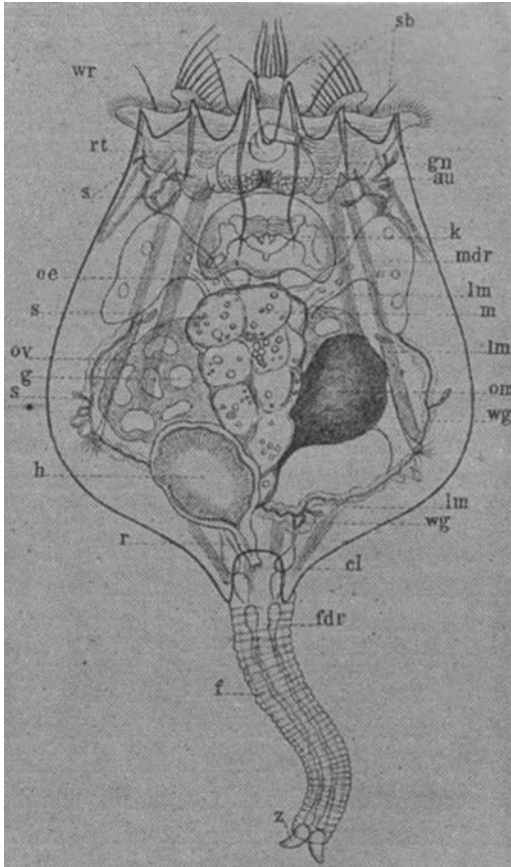


FIGURE 5.26. Section through the rotifer *Brochionus*. Between the ciliary organ (wr: rotating wheels) at the top of the animal you find the mouth, which leads via a buccal tube into a masticating pharynx (k). Between the pharynx (k) and the large stomach (m), salivary and gastric glands (mdr) inject digestive enzymes into the gut. The stomach leads into a short intestine (r) ending with a cloaca (cl) located at the transition to the foot (f).

benthic forms of water fleas scrape organic material from sediment particles; the planktonic species are suspension feeders. The digestive tract is a simple tubing, an esophagus leads into a midgut, that crosses the entire body. This tube is filled with a food string. A digestive cecum is an appendix to the esophagus.

Coming back to mathematical ecology, models predict that in predator-prey cycles the abundance amplitudes will be greatly enhanced by enriching the food source of the prey. However, this enrichment effect was not observed in these *Daphnia*-algae experiments. One explanation for this contradictory behavior could be in analogy to the rotifer-algae situation—the emergence of inedible algae that competed successfully with the edible algae in rich environments

and reduced thereby the effective prey-carrying capacity of the system. Indeed, when inedible algae were removed from the system, fluctuations in the daphnia biomass exceeded a factor of five (McCauley et al. 1999). However, some experiments continued to show only small amplitudes. What had happened that created two different situations? There must be alternative attractors that dampened the cycle, other factors than prey characteristics. McCauley and colleagues found the key: *Daphnia* are parthenogenic (they reproduce without sex) and these eggs quickly hatch into juveniles. However, *Daphnia* can have sex and this produces energy-intensive resting eggs (ephippia) that drop to the bottom and do not contribute to population growth. Ehippia are a response to dwindling food resources, their production prevents the over-exploitation of the prey and leads thus to small abundance amplitudes. The researchers replaced in their experiments the ehippia-producing females with asexually reproducing females and—as a nice confirmation of their predictions—they obtained especially high amplitude population cycles. We see here a life history feature of the predator that uncouples consumer dynamics from food supply. Many other organisms respond to food scarcity by shutting off reproduction (e.g., secondary amenorrhoea in humans). Natural populations of zooplankton like *Daphnia* are rich in genotypic diversity. Coexisting genotypes frequently show strong fitness differences in the laboratory, yet they are maintained in nature. This phenomenon has been called the “paradox of the plankton.” Competition theory offers a solution for this paradox. This theory states that relative fitness is not a constant between genotypes, but a function of the resource abundance, i.e., it is density dependent. To test this hypothesis, Canadian researchers either maintained the algal prey at constant level or induced low or high prey amplitudes. To these systems they added a mixture of *Daphnia* genotypes. Yet, under all externally driven environments, the same genotype became dominant (Nelson et al. 2005). It was a deterministic system. Where was the density dependence? In contrast, when the *Daphnia*–algae dynamics was internally generated by their coupled interaction, selection between the genotypes was reduced. What was now the equalizer of the chances between different *Daphnia* genotypes? Internally generated cycles began with a burst of *Daphnia* fecundity, followed 2 weeks later by a burst of small juveniles, followed later by a burst in large juveniles. However, most juveniles died from starvation during the prey-decline phase before entering the adult stage. The authors concluded that this stage-specific mortality reduced the fitness differences between the genotypes. Survivorship of over-wintering diapause eggs became thus more important for maintaining genotypic diversity in *Daphnia*.

Bacterial Predator and Human Prey: Syphilis

Scientific journals tend to group their research articles according to subjects, but adjacent articles normally do not come in any logical connection. Thus the above *Daphnia* article was followed in the scientific journal *Nature* by an article on syphilis in the USA. However, when I turned the pages I was struck by the similarity of the curves and the scientific approaches used in both articles. When taking a second look on both articles, I realized that the similarities go

beyond superficial analogies. Both processes display aspects of predator–prey dynamics. The predator–prey pair is somewhat unusual for ecologists, but the phenomenon can be treated with the same rules of mathematical ecology, even if physicians use the term epidemiology for this form of ecology. Who is the predator? It is a spirochaete bacterium called the “great imposter” by clinicians and *Treponema pallidum* by microbiologists (Figure 5.27). It is diagnosed in darkfield microscopy by its corkscrew appearance and it shares this morphology with cousin spirochaetes like those causing relapsing fever and Lyme disease. *Although not proven by microbiological evidence, historians of medicine believe in their majority that syphilis was imported from the New World by the sailors traveling with Christopher Columbus. When coming back to Spain, they transmitted the new disease, which then caused a pandemic known at the time as the Great Pox to distinguish it from the Small Pox. It quickly moved through Europe in this period of political unrest mainly transmitted by soldiers during the movement of armies through the old continent. Its way can be followed by its names: Spanish, French, and English disease. Its first medical descriptions and its sexual mode of transmission were described in plain English in the Breviary of Helthe in 1547 and in fine Latin hexameters in 1530 by an Italian Renaissance physician. In this poem, Syphilis is a shepherd that angered the god Apollon, who took revenge by giving him this new disease (Grenfell and Bjornstad 2005).* Syphilis remained a major sexually transmitted disease throughout the twentieth century, and the British epidemiologists took advantage

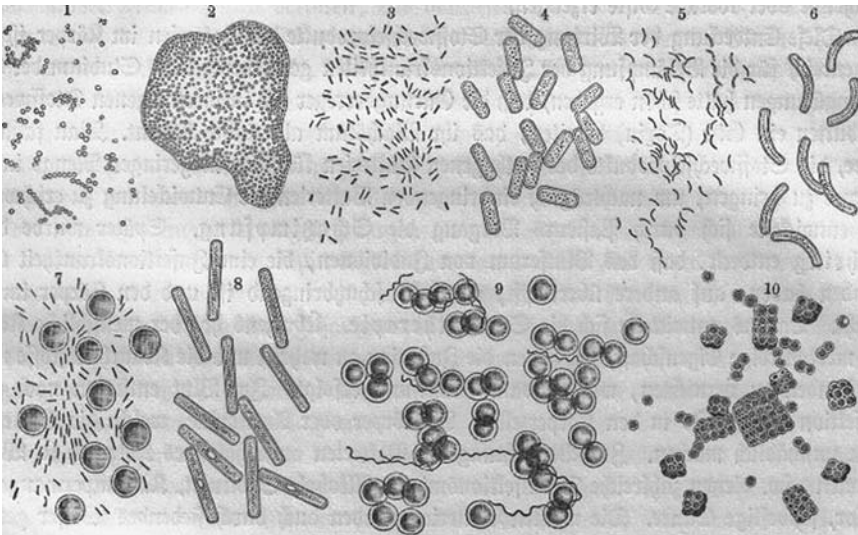


FIGURE 5.27. Bacteria as seen by late nineteenth-century microbiologists: 1, 2 *Bacillus* species isolated and in association; 3, 4 *Acetobacter*; 5, 6 *Vibrio cholerae*; 7, 8 *Bacillus anthracis* in low and high magnification, respectively; 9 *Treponema pallidum* (with erythrocytes for size comparison); and 10 *Sarcina*.

of the US documentation on this notifiable disease to address central questions not only of medical epidemiology but also of population ecology (Grassly et al. 2005). They asked for the role of exogenous environmental factors and density-dependent endogenous biological factors that drove this epidemic. Their numerical basis was a 60-year nationwide documentation of a predator–prey relationship that could make ecologists jealous. In fact, the epidemic pattern of syphilis in the USA has been explained by social and behavioral changes: a high in World War II due to troop movements, another high in the 1970s due to sexual revolution and gay liberation, followed by a 1980s poverty high, and a 1990s decline due to safer sex practices in the wake of the AIDS epidemic. The London epidemiologists did not buy this hypothesis and stated that syphilis is an unusually clear example of unforced, endogenous disease incidence with an 8–11-year periodicity, which is predicted by the infection dynamics and immunity development. They used the simple SIRS model with “susceptible,” “infected,” “recovered (immune)” states followed by the loss of immunity and return to the susceptible state. By anticipating a reproductive number of $R_0 = 3$ (newly infected cases per index case), the SIRS model predicts very well the period and the amplitude of the epidemic for the USA. The authors provided evidence for increased synchrony of syphilis oscillations across cities over time, pointing to networks between cities, connected by travel and sexual contact. The critical test was made with another sexually transmitted bacterial disease, gonorrhea, caused by *Neisseria gonorrhoea*. This disease is frequently transmitted with syphilis and should therefore show a similar dynamics, but it differs from syphilis by the fact that the *Neisseria* pathogen camouflages itself with different arrays of surface proteins, thereby preventing the development of immunity. In these diseases the simpler SIS model applies because no *R* state (recovered = immune) exists. Fittingly, no periodicity in the disease behavior was detected in the US data set.

Viral Predator and Human Prey: Measles

If we extend our predator–prey model to include ourself as food prey, many other would-be predators come into focus. I will here mention only one viral predator. In a later section of this book, I will provide some further examples where we become the food of such types of predators. The viral predator that I want to mention here is measles. From a historical viewpoint it is fitting to mention measles directly after syphilis. When the shipmates of Columbus first sailed from Europe to the New World they carried a blind passenger in their ships which might be the key to the startling question of historians as to how so few Spaniards could conquer so belligerous and numerically superior Indian warriors like the azteques. The answer is most likely not the superior European gun power or determination, but the introduction of a new virus into a totally susceptible nonimmune population that had never met this virus. Measles is highly communicable. A single index case can infect up to 15–18 secondary cases and measles is dangerous. It can cause pneumonia, blindness, and can even lead to death. British epidemiologists analyzed measles epidemics

in England and they used for their study advanced methods of time-series analysis (Grenfell et al. 2001). Measles epidemics showed seasonal cycles and long-term biennial epidemics, not unlike those we had seen in predator–prey interactions in ecology. The latter cycling became less evident after the introduction of vaccination in 1968. They analyzed the spatio-temporal epidemic pattern with great resolution and got striking results. There was a clear wave of infection moving out of London with a wave speed of 5 km per week. The wave could be followed for up to 30 km out of London. Similar waves spread from large population centers around Manchester–Liverpool to the surrounding hinterland to capture distant small towns. After the epidemic, the recovered individuals become immune to reinfection and are lost from the susceptible pool. In small towns, the infection goes extinct because the concentration of the remaining and replenished (newborns) susceptible subjects became too small. Epidemiologists estimate 300,000 people necessary for measles maintenance. Smaller towns have to wait for a spark from larger population centers to restart an epidemic. In big cities the population concentration is high enough to maintain measles in the population. After a deterministic threshold of susceptible subjects has again been built up, a new epidemic can start.

*One could add a number of reflections to infectious diseases as a predator–prey phenomenon. Also microbial predators need a certain prey population size not to go extinct. Some human viral infections might therefore not predate the neolithic revolution. A well-poised predator–prey system will avoid overexploitation (death) of the prey because otherwise the predator might go extinct. Presumably old human infections will thus not do much harm to its prey (e.g., chickenpox, retroviruses). Highly virulent viral infections are likely intruders into the human population coming from other animal species as trans-species infections (AIDS, SARS, Spanish flu, more on that later). Even very virulent infections show a trend for attenuation. Take the Black Death caused by *Yersinia pestis*. You can isolate this bacterium from patients in India, but it does not make headlines any longer. Several factors have contributed to this low profile for *Y. pestis*. Certainly, the blood group composition in the European population seems to reflect the selection for more resistant prey genotypes (remember the inedible algae). Antibiotics are also particularly efficient against *Y. pestis*. However, microbiologists would argue that the bacterium has attenuated its virulence and there is some evidence for this hypothesis. In fact, ecology and epidemiology do not only have some formally similar topics, Darwinian thinking might matter in medical research. Actually, the term of Darwinian medicine is already used in the biological research literature.*

Toxic Predator–Prey Arms Races

On Snake's Venom

Many animals have developed venom systems either to their defense against predation or as a tool of predation. We sometimes get into this biological battle line and make painful, occasionally lethal experiences. This experience has

shaped our cultural heritage, the most obvious case being the snake which is made responsible for the original sin in the Bible. I regret the shortsighted view of the creationist with respect to the Biblical record, who pulls biologists against the record of the Genesis report. This is a pity because it has—as I alluded at another place in this book—more than one grain of truth. I mentioned the nearly evolutionary report of what Biblical scholars refer to as the P author, who composed in the fifth century BC an attractive cosmogony borrowed from Babylonian mythology. As a scientist, I frequently admire the insight of the authors of the Book of Genesis. Here I will pay my reference to the J author, who wrote in the tenth century BC his more human story of the creation of the paradise from wasteland and the story of Eve and the snake. We see here how animals have taken the role of scapegoats (in fact goats), the very name reminding us how people from the Ancient Near East have used animals to transfer their feeling of sin and guilt to animals. This is certainly an interesting subject to explore for psychologists. However, the Biblical report has also an interesting message for biologists—the snake is punished for its temptation (and what temptation for scientists: knowledge; in this sense, scientists are the most faithful children of Eve. The National Institutes of Health carry the snake in their logo. It might be interesting to look back whether this choice was only taken in the Greek tradition linking the snake to the medical profession by the pharmaceutical activities of snake venom or whether it is also a hidden tribute to the Hebrew snake *Najash*, the legged Biblical snake). The snake's punishment is the loss of the limbs; the Biblical author thus sees snakes as relatives of four-legged reptiles like lizards. Not enough with that the snake is condemned to eat earth and there is eternal fight between the children of Eve and the snakes because of their poisonous bite (Figure 5.28). I would like to quote two recent research papers which come marvelously close to the insight of the J author of the book of Genesis. Argentine paleontologists found now a mid-Cretaceous snake fossil with a sacrum supporting a nonsutured pelvic girdle consisting of separate pubis, ileum, and ischium bones and robust hindlimbs. Cranial and vertebral bones show an adaptation to subterranean life. The authors speculated on a surface-dwelling terrestrial species that occasionally used tunnels to hunt burrowing prey. The fossil animal got the speaking name *Najash rionegrina* to honor the Hebrew account and the Argentine finding place. *Najash* is a more basal snake than the other known legged snakes, which carry the funny species names *Pachyrhachis problematicus* (Caldwell and Lee 1997), which possessed hind limb, but no fore limbs, and *Haasiophis terrasanctus*. The latter are marine species from marine limestone at the border of the Tethys sea—intriguingly near Jerusalem—suggesting a marine origin of the snakes, which is now dispelled by the terrestrial *Najash*. With that new fossil the origin of snakes from Cretaceous marine lizards like mosasaurus is rejected and the pendulum is back to the previous link to fossorial lizard ancestors. *The Bible wins over the Greek goddess Tethys, wife of the god of the oceans Okeanos. Perhaps the NIH should think on a legged snake for its logo?*

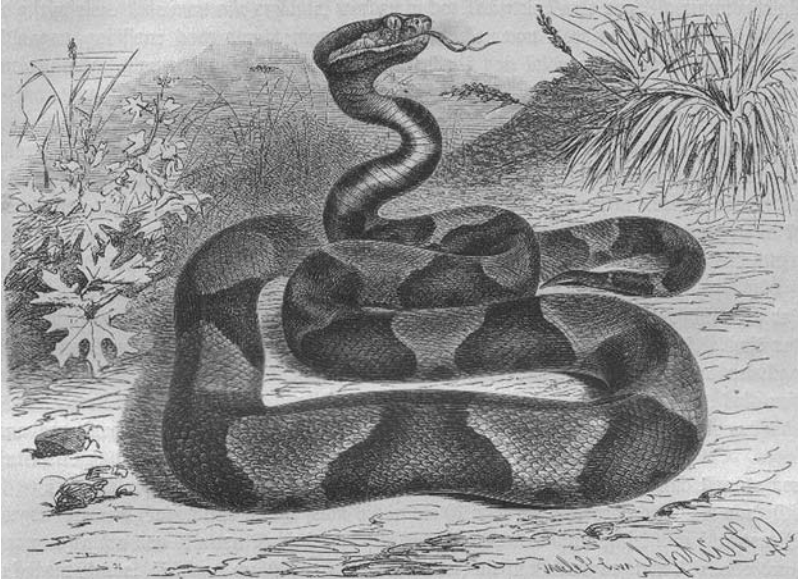


FIGURE 5.28. The copperhead snake from North America (*Ancistrodon contortrix*) belonging to the viper family is shown in defense position. Its poisonous bite kills rodents within few minutes.

Also the old venomous ancestry of snakes was now confirmed by a large research consortium (Fry et al. 2006). It observed venom not only in advanced snakes, but also in evolutionary relatives like Iguania, Varanidae (e.g., Komodo Dragon), Anguillidae, and Helodermatidae lizards (e.g., Gila Monster; Figure 5.29). In fact, the rapid swelling, dizziness, and shooting pain of the bite of the Komodo Dragon is now attributed to bioactive secretions and not bacterial infections as was previously believed. The comparative investigation of the venoms and the anatomical support suggested that venomous functions arose once in the evolution of squamata reptiles at about 200 million years ago. A group of nine toxin types are shared between all these animals, e.g., crotonamine is found both in the rattlesnake and the Bearded Dragon. These nine toxins have well-characterized activities that induce hypolocomotion, hypotension, hypothermia, intestinal cramping, paralysis of muscle, bloodclotting disorder, and a marked increased sensitivity to pain. The venomous lizards added later on in evolution only a few new toxins, while the advanced snakes complemented this initial toxin tool set by an impressive array of further toxins. The toxins are stored as liquid venoms in glands associated with the upper jaw in snakes and in the lower jaw in lizards. From the gland a duct leads to a grooved tooth. The evolution of venom is now considered a key innovation driving the ecological diversification in advanced snakes. Beyond this classical snake–venom connection, the venom story has many players and ramifications. I have selected a few recent toxic stories to illustrate the field.

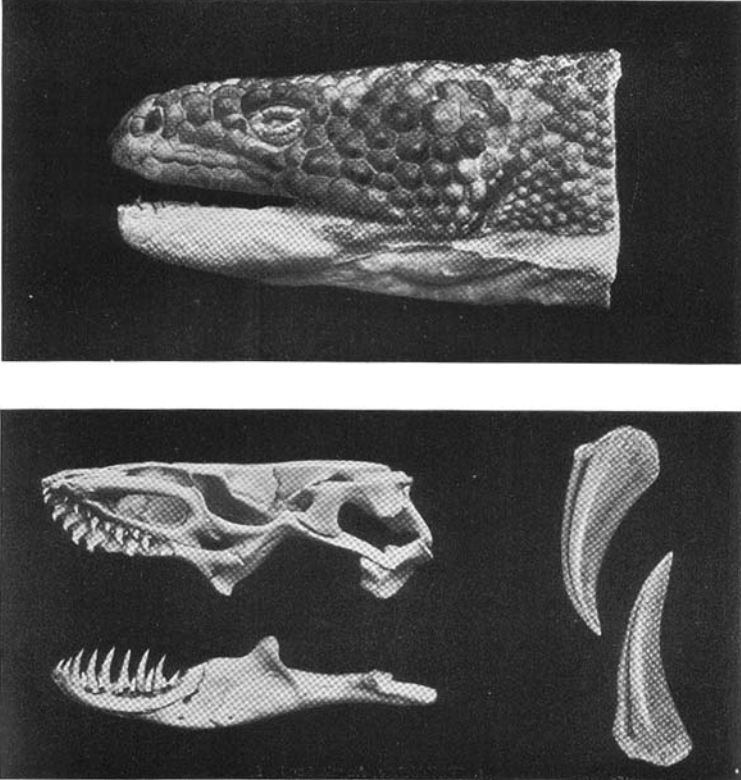


FIGURE 5.29. The Gila monster carrying the ominous scientific names *Heloderma suspectum* and *Heloderma horridum* are venomous lizards from the family Helodermatidae, order Squamata. They feed on small mammals, birds, and eggs. The Gila monster has a strong bite, which is easily understood when looking at the skull of the animal. It shows well-developed teeth especially in the lower jaw. The teeth have grooves that conduct the venom from venom glands in the lower jaw into the prey.

Getting Used to Toxins: The Clam Case

Filter feeders like bivalves (Figure 5.30) are especially exposed to toxin-producing phytoplankton like diatoms (domoic acid) and dinoflagellates (saxitoxin). By their nutritional way of life bivalves are also passive carriers of viruses like hepatitis A virus or norovirus. Shellfish surveillance is thus an important public health measure to prevent paralytic shellfish poisoning or the transmission of food-borne viral infections. Bivalves are not targets for the human viruses, which arrive to them via fecal contamination of oyster banks, but how do bivalves escape from the action of saxitoxin? Saxitoxin is an inhibitor of the neuronal Na^+ channel. Marine biologists first thought that bivalves are not susceptible to saxitoxin. This is, however, not the case. They then discovered large differences in the capacity of different bivalves to accumulate saxitoxin or

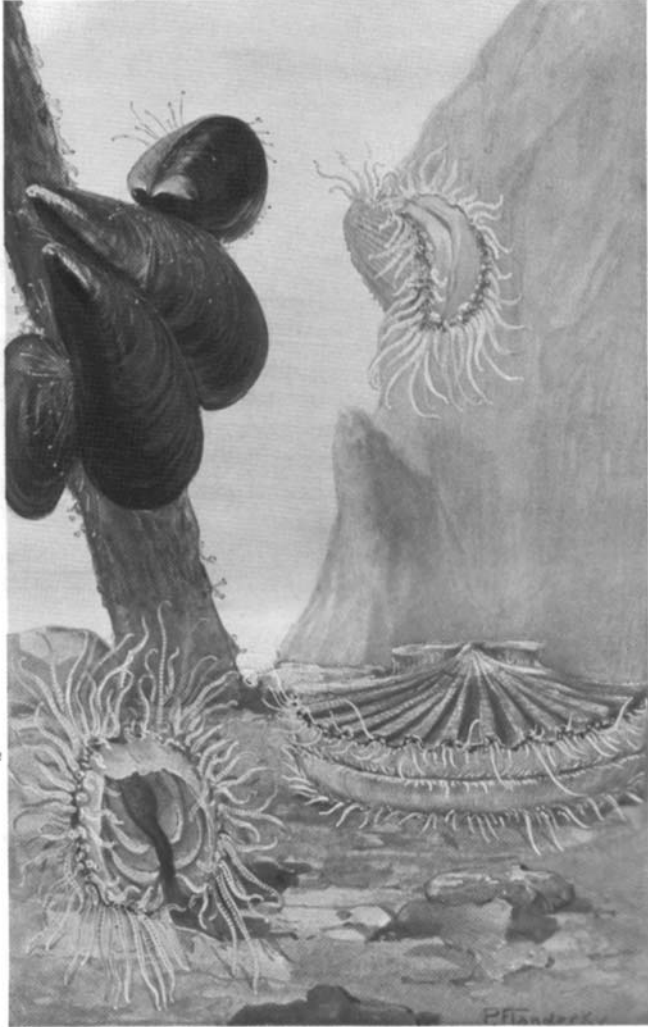


FIGURE 5.30. Clams are important suspension feeders. The figure shows the mussels *Mytilus edulis* (1), *Lima hians* (2, top swimming), and *Pecten jacobaeus* (3, its shell was used for drinking by pilgrims and as decorates in many mediaeval churches) all from the Filibranchia suborder in the bivalve class (phylum Mollusca). The blue mussel (1) is raised in Europe as food since the thirteenth century.

tetrodotoxin in vivo. Notably, this capacity correlated with in vitro differences in the sensitivity of isolated nerves to these toxins. *Mya arenaria*, a commercially important clam of North America showed a striking geographical distribution with respect to this toxin tolerance. Mollusks from the western and eastern coast of Nova Scotia differed in toxin tolerance; the western population was exposed

to regular toxic blooms and was consequently more resistant. This looks like evidence for an evolutionary arms race between predator and prey. Most eastern clams were unable to re-burrow and to retract the siphon after toxin exposure, putting them at higher risk of mortality due to drying and predation. Not so the western races. Explanted cerebrovisceral nerve trunks of the former clams experienced a full block of action potential at 30- μ M saxitoxin, while those from the latter were not inhibited by tenfold higher concentrations. The western clams accumulated high toxin levels in the viscera. When the researchers sequenced the voltage-gated Na^+ channels from both populations, they found a single nucleotide change that correlated with the *in vivo* resistance of clams to the toxin (Bricelj et al. 2005).

The Sodium Channel

Here we need a short backup on the structure of this membrane protein. The Na^+ channel is a multiprotein complex, but the essential part is its about 1,800 aa-long α -subunit. It contains four homologous domains (I–IV), each containing six transmembrane helices (h1–h6). The voltage sensor h4 shifts depending on the polarization state of the membrane toward the outside of the cell membrane and pulls thereby h6, the activation gate opens and allows thus the inflow of sodium ions. To confer selectivity to the ion transport you have as a guardian a “pore region” formed by the protein segment between h5 and h6. The membrane channel rests open only for a moment and the channel is then inactivated via a ball-and-chain mechanism by the inactivation gate, which is formed by a loop connecting domains III and IV.

The resistant clams had an aspartic instead of a glutamic acid in the “pore region” of domain II. The pore regions of the Na^+ channel are conserved over a wide range of animals, from flatworms to mammals. To prove the link, the researchers introduced the mutation into the rat channel protein and they observed a dramatic decrease in saxitoxin and tetrodotoxin resistance.

Pharmacologists knew about differences between cardiac and brain Na^+ channels with respect to sensitivity toward tetrodotoxin. They localized the difference to a critical amino acid (Tyr 374) in the “pore region,” this time in domain I. Electrophysiological work with mutant proteins confirmed that the primary determinant of high tetrodotoxin and saxitoxin sensitivity is a critical aromatic residue (Satin et al. 1992).

A Parallel Case: The Garter Snake Versus the Newt

Biologists frequently despair when they are confronted with a sheer endless variation of life strategies and get a gratifying feeling when nature uses and reuses the same basic principles in its manifold emanations. Actually, if you look behind the surface of the organisms and into their inner biochemistry, you don't have to look very far to see the common principle. However, here we have an absolute analogous situation of a toxic predator–prey interaction in two pairs

that are evolutionarily widely separated. On one side you have the dinoflagellate–bivalve pair and on the other side you have an amphibian–snake pair. The garter snake (*Thamnophis sirtalis*; Figure 5.31) is among the commonest serpents of North America. It is small, usually not more than 60 cm, and quite harmless. It won't bite you, but may try to deter you by discharging a foul secretion from an anal gland. They live chiefly on insects, earthworms, and amphibians. On this diet they can be quite gregarious especially before breeding and hibernating. Its prey is the Californian newt *Taricha granulosa* (Figure 5.32), this 10–20-cm-long animal belongs to the Salamandridae family. It has a similar diet as the garter snake: earthworms, snails, and slugs. Unfortunately, it is also on the menu plan of bigger predators and newts are an easy prey to snakes. When the newt is attacked, it does not hide, but erects its head and tail to show a warning color. If the predator now bites, the punishment will be severe. The newt secretes the neurotoxin tetrodotoxin from skin warts, and virtually all snakes die of muscular paralysis if they mistakenly eat a newt. With one exception: Garter snakes dine readily on newts because they have evolved a remarkable resistance against this toxin. Nevertheless, directly after a newt meal their crawling speed is temporarily reduced (Huey and Moody 2002). Now a fascinating evolutionary playing ground is offered for biologists. If garter snakes developed resistance against tetrodotoxin, an untapped food source is opened, unchallenged by competitors. The newt should be doomed. However, if you look on a geographical map of garter snake distribution, the animals vary nearly by a factor of thousand with respect to tetrodotoxin resistance (Geffeney et al. 2005). If you look for a molecular correlation of resistance, you again get amino acid replacements in the neuronal

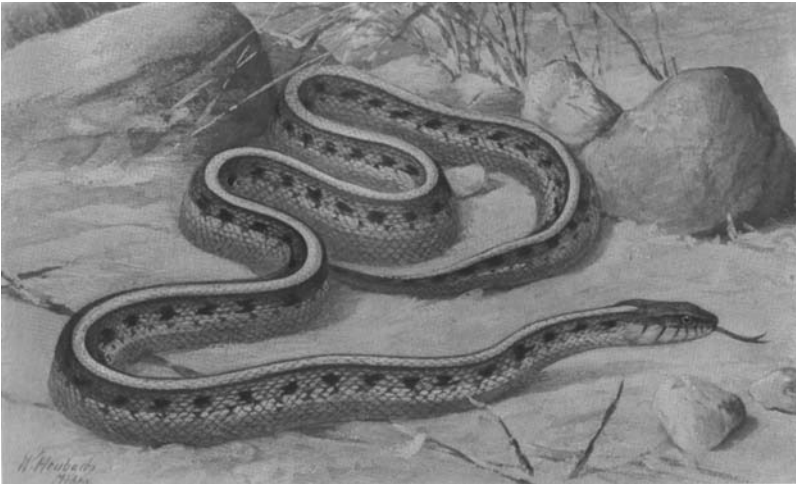


FIGURE 5.31. The garter snake (*Thamnophis sirtalis*) is North America's most widely distributed reptile. This harmless snake for humans (you risk being threatened by a foul discharge from the anus) is involved in a toxic predator–prey cycle with a poisonous Californian newt.

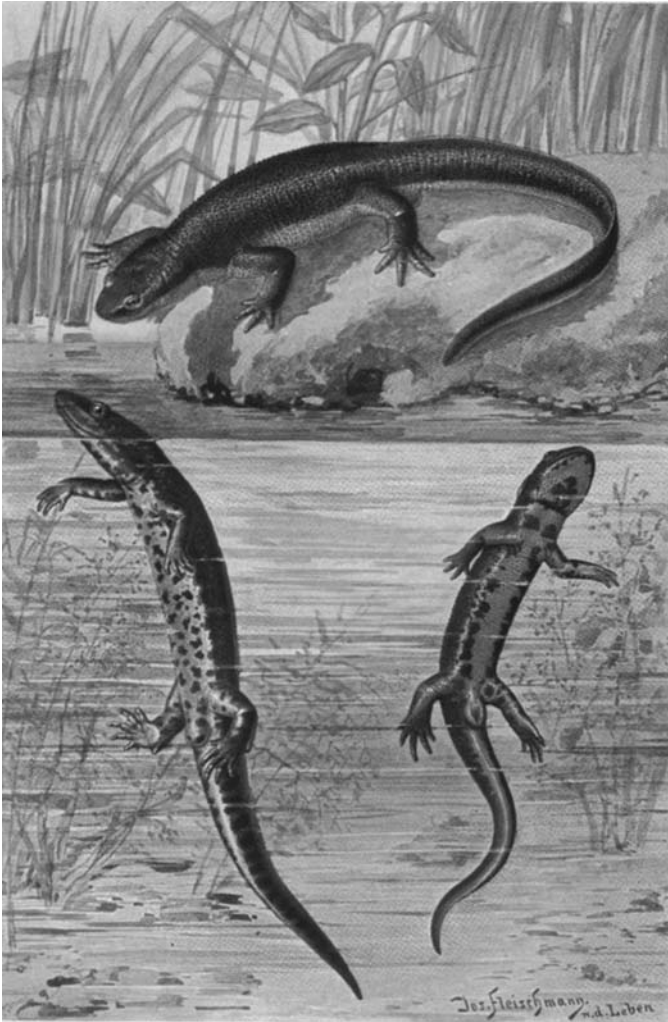


FIGURE 5.32. A Californian newt (*Taricha granulosa*) secretes from its skin a potent neurotoxin, tetrodotoxin, to deter its predator the garter snake, resulting in a chemical arms' race in a prey–predator relationship. The newt at the top is *T. granulosa*, the species at the bottom are *Molge rusconi* (left) and *Molge pyrrhogastra* (right).

Na⁺ channel, this time in the pore region of domain IV. In fact, the molecular data demonstrate that the resistance has evolved at least twice and independently. The investigating biologists were interested in the details of the mechanism to reconstruct a case story for evolutionary interaction. Indeed, the effect of the toxin on the intracellular action potential correlated with the population differences. This was true not only between the populations, but held even for the variation within a given population (Geffeney et al. 2002). Again, the transfer of the

mutation into a toxin-sensitive Na^+ channel conferred toxin resistance. Why all this diligence around this observation? In fact, the researchers were interested in tying a point mutation to an ecological relevant physiological phenotype, which can explain much of the evolutionary interplay between the predator and the prey.

Extensions of the Principle

Why do garter snakes vary in tetrodotoxin sensitivity. One key to the understanding is that snakes living outside of the geographical distribution range of the poisonous newt do not show this mutation. Then why are not all garter snakes highly tetrodotoxin-resistant when they live together with the newt? Here, you apparently have an evolutionary trade-off. The mutation comes with a price. Resistant garter snakes show a slower maximal crawling speed than sensitive snakes. If you introduce a third trophic level, let's say a predator of garter snakes, the reduced speed might result in higher losses due to inefficient flight reaction. Not all details are clear yet in this system, sound ecological data on the third trophic level are, for example, lacking. Nevertheless, we have here a fascinating case of analogous chemical warfare between predator-prey pairs separated by wide evolutionary distances. And this is not the only case where animals use tetrodotoxin in self-defense: Fugu pufferfish, Atelopus frogs, blue-ringed octopus, and Phallusia tunicates all use this poison to deter predators. Apparently, also in the ecological context, nature reuses successful solutions to general problems. However, not all animals are likewise successful with this strategy. Fugu became a delicacy in Japanese restaurants without humans developing toxin resistance. The gourmand relies in this case on an anatomical certificate for the chef to remove safely the gall bladder such that his clients escape from deadly food poisoning.

Herbivory

At first glance you might be surprised to see a section on herbivory directly after sections on antipredation strategies and predator-prey interactions. However, if the basic principles of these interactions apply to so unusual pairs as viruses and humans, it would be surprising if the relationships between herbivores and plants were not governed by similar principles. In fact, herbivory is a difficult life style and it needs a lot of education by evolution to make a living from vegetable material. I want to demonstrate this point by three chapters. The first explores the evolutionary origin of land plants and why herbivory took so long to develop in the history of terrestrial life. The second chapter shows what we can do with carbohydrates as omnivores—not too much in fact. The third introduces the surprising observation that even such well-known herbivores like the cow can on its own not do much with plant material. It needs a lot of small helpers to deal with cellulose. Finally you will learn how plants strike back against herbivores.

Terra Firma—Bacteria and Plants Conquer the Land

Problems at Land

Why did life set out to conquer the land? Is the “*horror vacui*,” the fear of the void the guiding principle in biology? Life was born in the ocean because it offered what life needed most, namely water. The land in contrast is often characterized by dryness. Small wonder that life filled first all opportunities offered by the world’s oceans, which cover anyway the biggest share of the earth’s surface. In the beginning there were other problems, too. Without an ozone shield there were killing conditions at the land’s surface—the genetic material of endeavoring organisms would quickly have been destroyed by the intensive ultraviolet radiation. Sufficient amounts of oxygen in the atmosphere might thus also have been a basic requirement for life on land.

Microbial Crusts: Cyanobacteria Again?

The earliest terrestrial communities were probably microbial crusts and mats venturing the land already in the Precambrian and leaving as witness organic traces in paleosols. Good candidates were cyanobacteria living in the intertidal zones. They had already learned to cope with changes from wet to dry conditions and had experienced great fluctuations in salt conditions. Why again cyanobacteria? We encounter them in our survey again and again. Are these cells for all seasons? Probably. I will illustrate their remarkable ecological qualities by one recent publication. Hot and cold deserts support only sparse plant growth because of the surface dessication that they suffer in these environments. In these regions, important primary producers are cyanobacteria. Microbiologists observed a possible key to their success. When they looked at the barren desert soil, nothing betrayed the presence of photosynthetic organisms. Then they wetted the surface with water and observed a greening of the soil, which occurred within half an hour (Garcia-Pichel and Pringault 2001). What had happened? Filamentous cyanobacteria of the *Oscillatoria* genus maintained a population at a depth of about 2 mm below the soil. In the presence of water, the bacteria showed a hydrotactic (water-seeking) reaction. When the soil subsequently dried out again, the cyanobacteria retreated again into the soil. The movements were perfectly reversible. Only high light intensity could prevent the active movement of cyanobacteria to the soil surface. Inhibitors of ATP generation also inhibited the movement. These sturdy cells are thus good candidates for the first pioneers of the continent.

Lichens

After the bacteria, the eukaryotes prepared the assault on the land. Fungi had been on the land at least since the Silurian and some paleobiologists believe that they derive from red seaweeds. Possibly they lost the race with the precursors of the land plants and specialized as saprophytes that lived from sending hyphae into the decaying corpses of the early plants to extract the nutrients. Fungi also

discovered the new life style to team up with living photosynthetic cyanobacteria and green algae to form what we call lichens (Figure 5.33). Lichen crusts are still nowadays the outposts of life in the alpine regions. It is well possible that lichen crusts formed the second wave toward the land. Lichen-like symbiosis has a very ancient fossil record. Again, it is the Doushantuo Formation from southern China that provides interesting specimens (Yuan et al. 2005). Filamentous hyphae, which branch dichotomously and carry spore-like terminal structures and loops, surround what looks like cyanobacteria sheathed in a hyaline envelope. The coccoidal cyanobacterial thalli show no evidence of host reaction to the filaments excluding mycoparasitism. The association appears specific since nearby thalli from red algae show no filament association. Since these fossils are dated to 600 million years ago, fungi had in shallow marine environments already evolved symbiotic partnerships before the evolution of vascular plants. Today about one-fifth of all known extant fungal species form obligate symbiotic associations with green algae, cyanobacteria, or with both photosynthetic organisms. The molecular phylogeny analysis of rRNA sequences from 52 species of Ascomycota representing 18 orders revealed that lichens evolved earlier than previously believed and support the interpretation of the fossils (Lutzoni et al. 2001). Only the basal groups comprising organisms like *Candida albicans*, *Saccharomyces cerevisiae*, and *Morchella esculenta* are primary nonlichenized Ascomycota. The acquisition of lichenization followed quickly in one or up to three events. All other nonlichenized Ascomycota are secondary losses. Global weathering of rocks is heavily influenced by lichens as pioneer community since the Devonian.

The first colonists faced a harsh physical environment. Lichens, often associated with bryophytic plants, form still today a biological crust in many

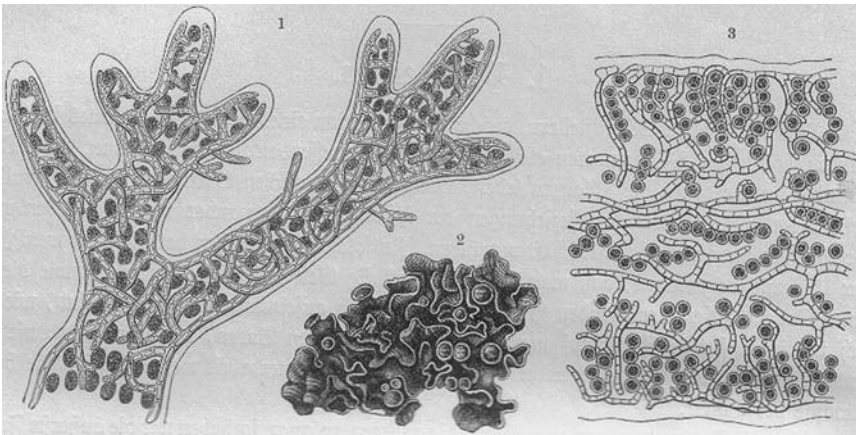


FIGURE 5.33. Lichens are a consortium of algae and fungal hyphae as demonstrated here by microscopical observation of *Epebe kernerii* (1) and *Collema pulposa* (3, $\times 450$). *Collema* in original size in (2).

harsh terrestrial conditions. Molecular clock estimates support a scenario according to which the major lineages of fungi were present 1 billion years ago and land plants appeared by 700 million years ago, such that a colonization of the land can be anticipated by 600 million years ago despite the lack of a clear fossil evidence (Heckman et al. 2001).

The First Land Animals

These authors also proposed that resistant biological crusts already contained the first animal land colonizers quoting Tardigrades as likely candidates. In zoology textbooks, the Phylum Tardigrada is quoted together with the Phylum Onychophora as distant relatives of Arthropods. In fact, Onychophoran (“velvet worms”) resemble caterpillars superficially: The animal shows an inconspicuous head with two antennae and a mouth where circular lips surround a pair of jaws. The body is lined by about 20 pairs of sac-like legs. In fact, many zoologists regard Onychophorans as potential missing link between the Phyla Arthropods and Annelids. Even more exciting from an evolutionary point of view is the interpretation that the Cambrian fossil *Hallucigenia* (*nomen est omen*, a really bizarre spiny creature) is an onychophorian with pairs of elongated legs and pairs of dorsal spines. Likewise, *Aysheaia* from the Cambrian Burgess Shale is a probable onychophoran. These currently exclusively terrestrial animals have thus a prominent family tree. Today they occupy a niche shared with centipedes and are carnivores that prey on small invertebrates. Their feeding strategy relies on slime glands that discharge up to 30 cm of adhesive glue that entangles the prey. The velvet worm then injects the salivary gland contents into the victim, which is then digested extracorporally. The predigested food is then sucked up with the mouth. Fossil evidence suggests that a terrestrial invasion took place in the Ordovician (500 million years ago).

Tardigrades are somewhat more structured and their funny morphology earned them the trivial name “water bears,” displaying an eight-legged miniature body in the submillimeter size range with a “smiling” head. Their weapon is an oral stylet, which is pierced into plant or animal cells for sucking the cell sap. Some tardigrades feed on bacteria, algae, and decaying plant material, carnivorous predators of small invertebrates are also known. The mouth opens into a buccal tube, which leads into a muscular pharynx that allows some form of mastication. A small esophagus opens into a large midgut, where digestion and nutrient absorption takes place. Strangely, defecation and molting is synchronized in some species. The association of tardigrades with moss is notorious, a spectacular case being a revival of a tardigrade from a 100-year-old desiccated moss museum specimen. Other characteristics make tardigrades likely candidates for early animal land colonizers. Tardigrades have fossils going back to the Lower Cambrian, are still today associated with early terrestrial colonizers like lichens, mosses, and liverworts, and show metabolic characteristics that allow them to resist physical hardship. During unfavorable environmental conditions tardigrades adopt as cysts a state of dormancy (“anabiosis”) with greatly

reduced metabolic activity or in the so-called tun stage even a state of cryptobiosis without detectable metabolic activity. This state allows tardigrades to survive extreme temperatures ranging from +140 to -270°C, extreme dryness, and toxic chemicals like absolute alcohol. Such hardy animals could reasonably accompany photosynthetic organisms in the conquest of the land.

The Next Waves

Lichens as second wave to the land were probably quickly followed by mats of algae and then plants of a moss-like organization (Shear 1991). Notably, nearly all land plants have associations with fungi in their roots, called arbuscular mycorrhizae. In view of their beneficial effect on plant growth and survival via their contribution to nutrient acquisition by the plant, this symbiosis is ecologically important for most vascular plants. The fungal symbionts belong to one order, namely the Glomales in the Zymogomycota division of fungi, one of the four major branches of fungi (Figures 5.34–5.37). Fungi diverged at least 1 Ga ago probably before the divergence of the metaphyta and metazoa lineages in the Eukarya. Molecular clock analysis identified the onset of the diversification in the Glomales at 460 Ma ago in the Ordovician (Simon et al. 1993). This molecular date was later confirmed by a 460 Ma fossil find of hyphae and spores of Glomales fungi from the Ordovician (Redecker et al. 2000). The famous Devonian Rhynie Chert plant fossils like *Aglaphyton*, *Asteroxylon*, and *Rhynia* contain structures resembling vesicles and spores from extant Glomales fungi, demonstrating that latest at 365 Ma ago the arbuscular mycorrhizae was established. Here fungi played again a critical role as helpers for the conquest of the land.

Liverworts, hornworts, and mosses (Figure 5.38) are documented in the fossils from the Ordovician. A number of adaptations are necessary for plants living on land. Conducting strands, cuticles, stomata, and dryness-resistant spores had to develop. Early Devonian plants from the famous Scottish Rhynie Chert like *Cooksonia*, long regarded as the earliest vascular plant, still lacked conducting strands despite its 4 cm height. Phylogenetic studies favor a single origin of land plants from charophycean green algae (Figure 5.39). However, *Cooksonia* demonstrates that not all main adaptations to life on land were made in one phase. In the Devonian, plants with tracheids and cuticles were documented. This line led to quite sizable land plants, which were of 1 m diameter and several meters high, the largest land organisms of their time (*Prototaxites*). Tracheids are tubular cells, which are dead when they are functional. To prevent a collapse, their cell walls are strengthened by thick spirals or rings of bands containing lignin. Cuticles appeared first in enigmatic plants called nematophytes. These structures also represent chemical inventions, namely the biosynthesis of lignin and suberin. This is until today a very resistant material with respect to digestion and biodegradation. Since terrestrial plants are not treated in this book with the place they deserve, I offer a figure panorama on the major groups of land plants that shaped the planet Earth to at least visually compensate for this defect (Figures 5.40–5.63).

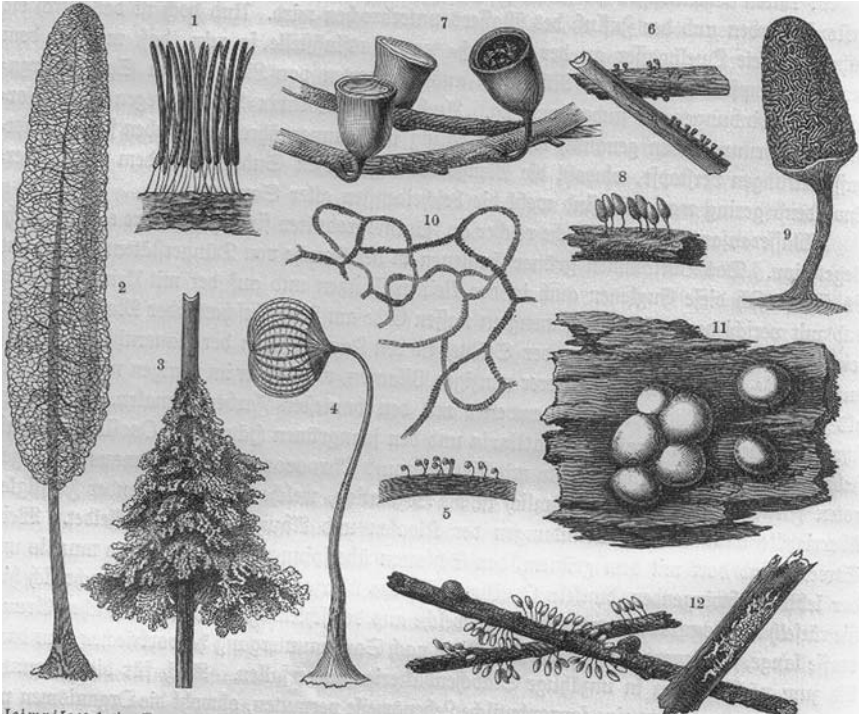


FIGURE 5.34. Mycophyta I: Phycomycetes. This is a primitive group of fungi that still plays around with different forms of sexuality and cell-wall chemistry (cellulose vs. chitin). The thallus (plant body of lower organisms) consists of siphonal tubes lacking septation. The order Oomycetales is here represented with *Achlya prolifera* (1) and *Saprolegnia lactea* (6) in the process of release of zoospores (2–4 and 6, 7). Chytridiales live as parasites and saprophytes on water plants and water insects, or are as demonstrated by *Polyphagus euglenae* even carnivorous where a single mycelium can contain up to 50 protists in different digestion states. *Rhizophyidium* lives on pollen from higher plants. Saprolegiaceae live as saprophytes on decaying plants and insects in the water, occasionally also as parasites on fish).

Lignin Synthesis and Degradation

Biosynthesis of Lignin

What is so special about lignin synthesis that makes it so resistant to chemical attack? The start of the pathway to lignin is quite conventional: It starts with the aromatic amino acid phenylalanine. The precious amino group is recovered, remember that photosynthetic organisms are nearly pathological carbon-fixing machines, but they have problems with nitrogen. Therefore, in the final product of the structural tissue of plants you have a lot of carbon, but nearly no nitrogen, which creates problems for herbivorous animals. The phenyl ring undergoes one to three hydroxylation reactions, which determines the chemical identity of the

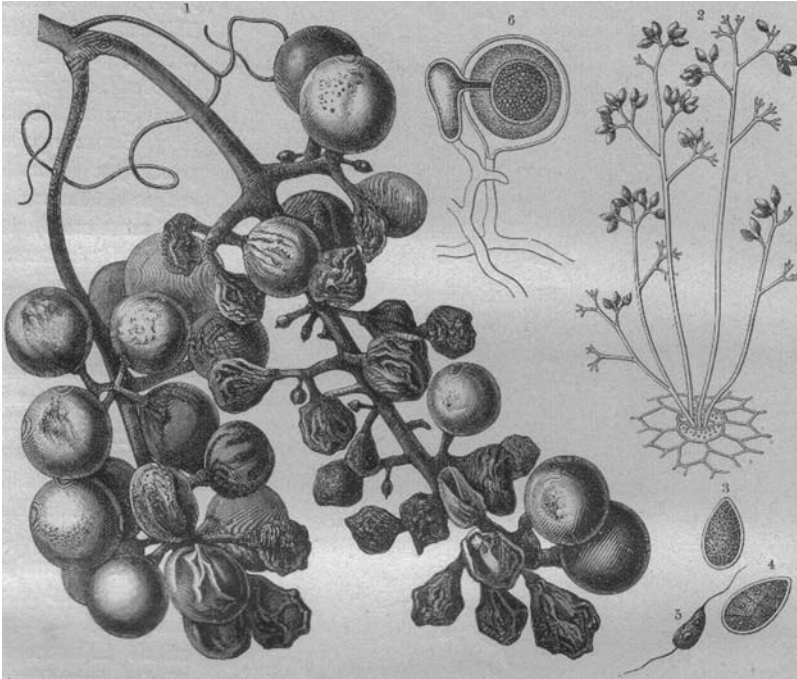


FIGURE 5.35. Mycophyta II: Peronosporaceae are another family of the Oomycetales, order of the Phycmycetes. Most live as parasites on higher land plants and cause substantial economical damage on potato (*Phytophthora infestans*), tobacco (*Peronospora tabacina*), or vine (*Plasmopara viticola*). The latter represented in the figure causes a characteristic drying of the grapes (1). The fungus lives in the leaves and its sporangia reach the outside via stomata, a gas exchange organ (2). It releases spores, which differentiate into zoospores (3–5) that infect new leaves by entering again via stomata. If untreated, up to 20% of the wine harvest might be lost to fungal infections, as much as by animal damage.

starting material for lignin and lignan synthesis. According to plants that produce a lot of them, these natural products are called coumaryl, coniferyl, or sinapyl; the carboxyl group of the exphenylalanine is subsequently reduced to an alcohol group. Nothing is special so far. The first complications are introduced when the plant cells synthesize lignans, which are dimers and oligomers formed from primary coniferyl alcohol. It uses for this reaction probably laccase, an enzyme that creates aromatic alcohol radicals with the help of oxygen, but the data are not yet very clear.

A Purposeful Anarchic Synthesis?

Radicals can be created at the eighth position (in the C3 side chain) or at the fourth and fifth positions (the meta and para positions in the phenyl ring). As any of the unpaired radical electrons can combine, a number of chemical bonds can be formed with a single starting compound. In lignans the process is still steered by a

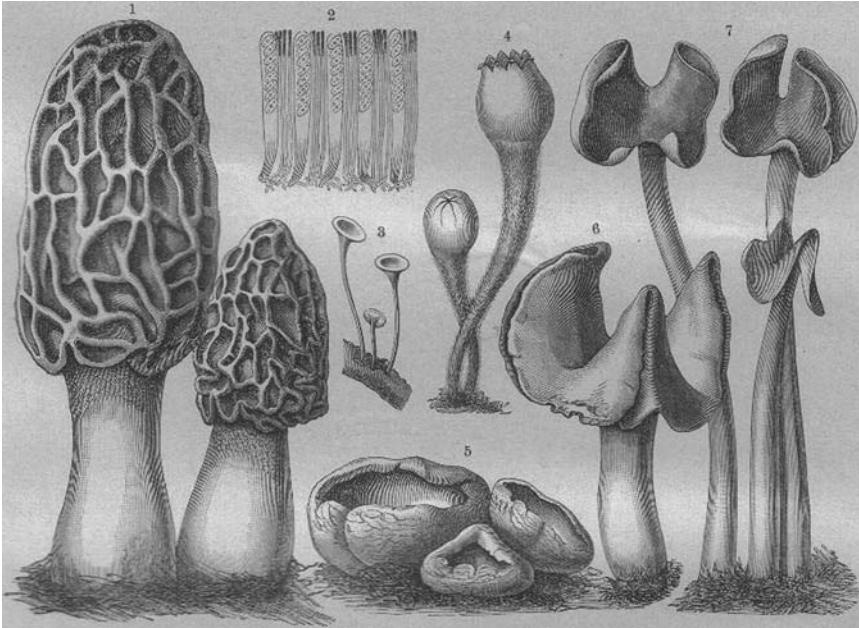


FIGURE 5.36. Mycophyta III: Ascomycetes. Another large group of fungi are the ascomycetes, which get their name from the ascus, a tubular sporangium in which eight spores are created by meiotic division (2). Most of them are terrestrial organisms that live as saprophytes. A few of the ascomycetes represent what the layman associates with mushrooms as the culinary appreciated *Morchella esculenta* (1). The picture represents a collection of specimen from the Discomycetidae: *Helotium* (3), *Anthopeziza* (4), *Peziza* (5), *Helvella infula* (6) and *Helvella fistulosa* (7). These fungi are saprophytes of the forest ground where they live on decaying wood. However, the ascomycetes are a divers group and also include organisms like the yeast *Saccharomyces*, the molds *Aspergillus*, and the plant parasite *Claviceps*, which we will encounter at different places of this book.

“dirigent protein” that yields preferentially 8-8’ intermediates. In lignin the matter gets more complicated. The name lignin is derived from the Latin word lignum, which means wood. This is a very appropriate name since wood contains 20 to 30% lignin. After cellulose, lignin is the most abundant organic material of all vascular plant tissues. Lignin is a macromolecular meshwork starting with the three above-mentioned aromatic alcohols. The process is not that anarchic as initially proposed by biochemists. We know now that the tracheid cell still controls this process. Coumaryl alcohols are mainly deposited in the middle lamella between the approximately rectangular cells. Coniferyl alcohols, in contrast, go toward the walls that grow telescope like into the interior of the tracheid cell. Peroxidases working with H_2O_2 as cosubstrate mediate one-electron oxidations leading to radicals that start to polymerize the monomer. The following reactions were initially believed to be nonenzymatically free-radical coupling reactions. *In this chemical view, the second most common compound in the terrestrial ecosystem is not formed under enzymatic*



FIGURE 5.37. Mycophyta IV: Basidiomycetes. The common denominator of this large and diverse group of fungi is the basidium, the organ that bears sexually reproduced bodies called basidiospores (7). The picture shows a panorama of Holobasidiomycetidae: *Clavaria* (1), *Daedalea* (2), *Marasmius* (3, 4), *Craterellus* (5), *Amanita phalloides* (6), *Hydnum* (8), and *Polyporus* (9). These fungi have inspired human imagination as an appreciated source of food that could be mixed up with deadly poisonous fungi. The hallucinogenic specimen played a role in many old religious rites. Fungi provide antibiotics and medical and nonmedical drugs and they were used as tinder (*Fomes fomentarius*) for fire making in the neolithic. However, basidiomycetes also contain in the Phragmobasidiomycetidae group important plant pathogens like the rusts (Uredinales) and smuts (Ustilaginales).

control. This is at the same time astonishing and cute. Astonishing because it leaves such a central cellular process uncontrolled; cute because the anarchic polymerization makes this big macromolecule nearly unassailable to would-be herbivores. As you will see below, this trick worked extremely well during the first

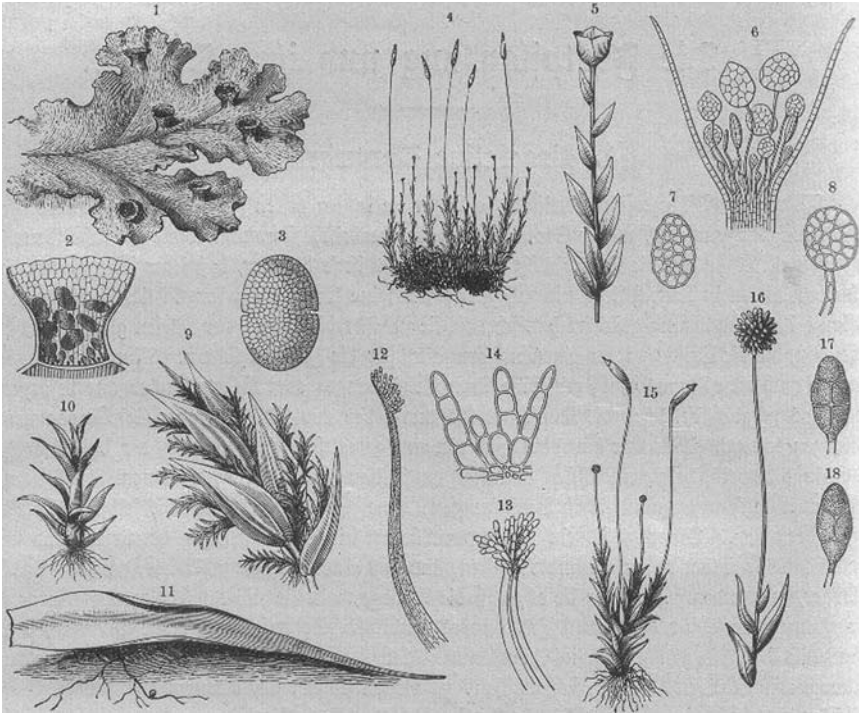


FIGURE 5.38. Bryophyta. Mosses are shown with a representative of the class Hepatica (1–3, *Marchantia polymorpha*) and the class Musci (4–8 *Tetraphis pellucida*) 9, *Leucodon*; 12, *Syrrhopodon*; 15–18, *Aulacomnion*.

100 millions years after the conquest of the land by plants. Herbivory was not an issue. Was it the nonenzymatic growth of lignin that made it so resistant to enzymes of evolving herbivores? Later on, biochemists recognized that the process was not that undirected as initially thought. Some bonds formed with much higher frequency: For example, the 8-O-4' bond represents 50% of all bonds. The synthesis of lignin is still an active research field at the moment as is the degradation of lignin.

Designed Imperfectness in Nature?

In view of its biosynthesis, we should not be surprised that lignin is one of the few natural polymers that can only be degraded with the help of molecular oxygen. Bacteria had their problem with this compound. Small wonder that the earliest land animals were not much more successful in attacking lignin. Under anoxic conditions bacteria could only grab some O-methyl groups from the polymer, but they could not crack the backbone of this formidable macromolecule. The savior was fungi, which were lurking in the zone between the sea and the land and were waiting for their chance. Still the decay of organic plant material in the soil is the job of fungi, which outnumber bacteria in that environment in both biomass and numbers. I said savior with hindsight. Evolution cannot work with perfect

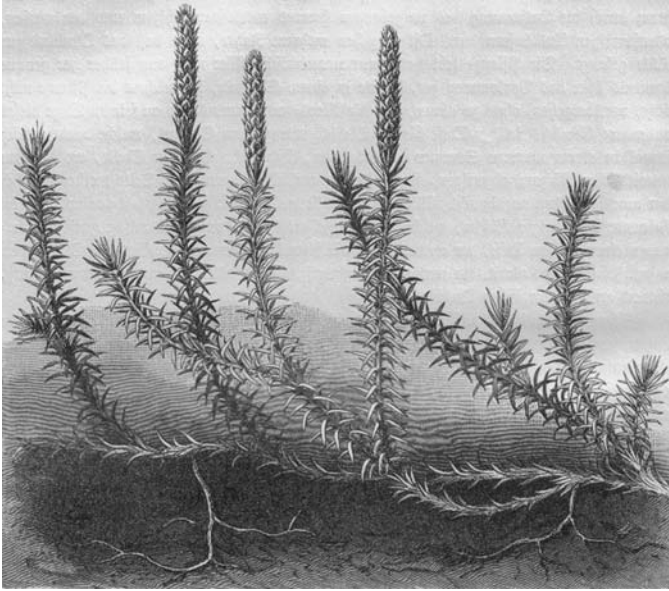


FIGURE 5.40. Pteridophyta I: extant Lycopsidea. The club moss (*Lycopodium clavatum*) belongs, with the spike mosses (*Selaginella*) and quillworts (*Isoetes*), to the Lycopsidea class of the Pteridophyta (fern-like plants). They are spore-bearing vascular plants that range from fossil trees to ground-creeping organisms like the depicted species. Protolopodendraceae like *Drepanophycus*, which closely resembles the depicted living representative of this group, are known from the Lower Devonian and are thus the oldest land plants of Central Europe.

is as usual a complicated trade-off. Elements of recalcitrance are still visible in our world.

Lignin Degradation

Lignocellulose is still today only very slowly and incompletely degraded in soil giving rise to humic acids. *There is also an element of truce: Lignolysis is mainly the job of filamentous white-rot fungi as the basidiomycete Phanerochaeta chrysosporium. The curious trivial name refers to the fact that it degrades the brown lignin in wood to gain access to the readily metabolized white cellulose and hemicellulose. Also this fungus cannot support cell growth with an exclusive lignin feed. Where is the truce? White-rot fungi are saprophytes that live from dead plant material; only few are pathogens of living plants (e.g., Armillaria mellea). The solution evolution found is well poised: Lignocellulose is the perfect armor as long as the plant needs protection during life. Once dead, the contract has expired and the fungi get the green light to degrade the plant material to the direct benefit of the fungus, but also to the benefit of the next generation of plants. Ask this from a packaging engineer in the food industry. A bottle that is*

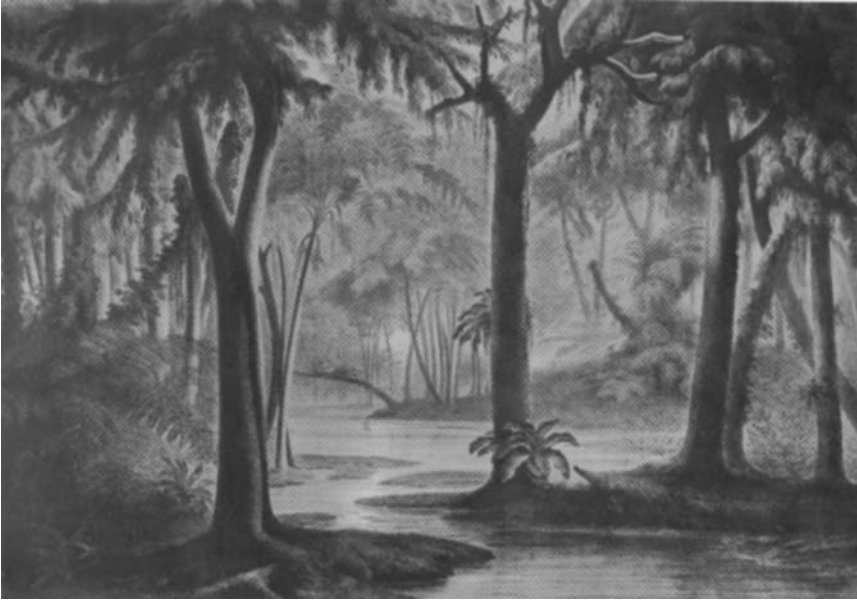


FIGURE 5.41. Pteridophyta II: extinct Lycopsidea. An artistic impression of a forest of up to 40-m high *Lepidodendrales* trees from the Carboniferous; these trees contributed substantially to coal formation. The burial of the photosynthetically produced organic carbon prevented its reoxidation with atmospheric oxygen in respiration, resulting in a net oxygen increase in the atmosphere due to unbalanced water splitting in photosynthesis. *Lepidodendron* is an extinct relative of the club moss (*Lycopsidea*).

extremely stable when filled with milk or orange juice quickly decomposes into biodegradable compounds when emptied. He would have a hard time to design a solution.

Fungi are well adapted to their degradation job: They possess hyphae that allow fungi to grow into the decaying plant material. This strategy allows release of a true battery of compounds on the spot where it is needed: Numerous enzymes like lignin peroxidase and manganese peroxidase receive H_2O_2 from glyoxal oxidation, metals like manganese and molecular oxygen. The degradation creates, like the synthesis, cation radicals from lignin that then undergo a variety of nonenzymatic degradation reactions. It is curious that a macromolecule that was created via radical reactions is also degraded by radical reactions. However, as the synthesis of lignin has not yet been elucidated in detail, there are still major gaps in our understanding of lignin degradation. For example, lignocellulose is too tight a molecule to allow access to enzymes, at least in sound wood. To what extent are nonenzymatic radical reactions initiated first to make a breach into the substrate, thus allowing access to the enzyme later? *Is the well-known Fenton reaction ($Fe^{2+} + H_2O_2 \rightarrow Fe^{3+} + OH + OH^-$) part of it, creating the highly reactive hydroxyl radical for the pioneer reactions? Our uncertainty about the biochemical details of both the synthesis and the degradation of lignin and its*

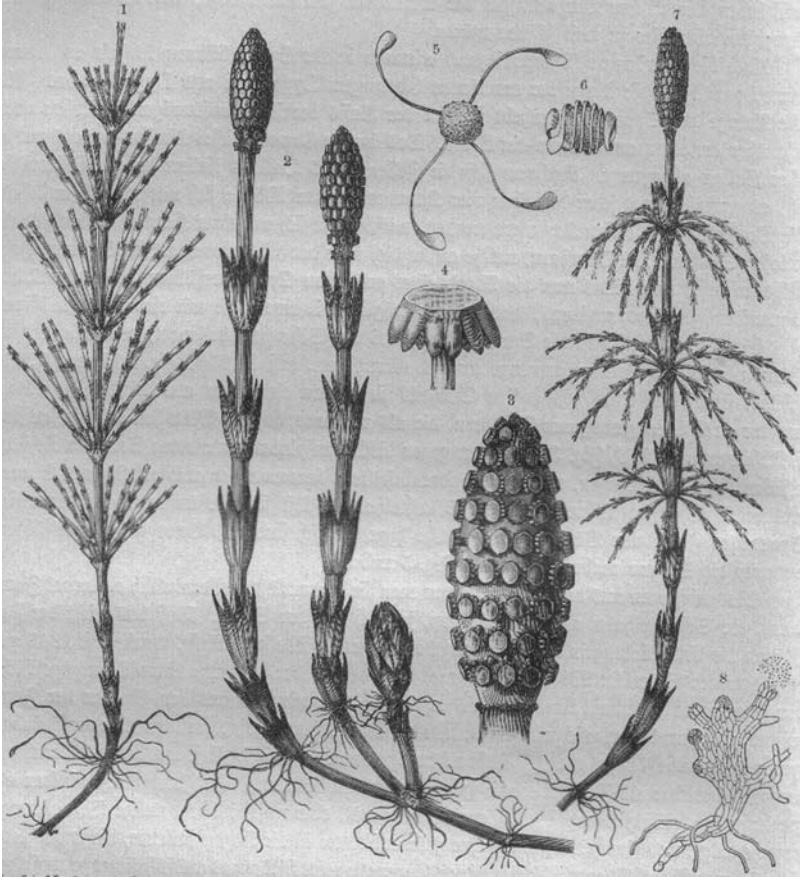


FIGURE 5.42. Pteridophyta III: extant Sphenopsida. The common horsetail *Equisetum arvense* (1 the summer form; 2 in spring time) grows in meadows and along stream banks where it is fairly abundant, while the wood horsetail (*Equisetum sylvaticum*, 7) grows in cool moist woods. 3, 4 (amplified) sporangium carrier; 5, 6 spores; 8 prothallium. This genus with about 30 species is the only survivor of the class Sphenopsida from the Pteridophyta.

proven resistance in the biosphere is a vivid demonstration of the evolutionary "success" of the lignin design in the plant world.

Taking to the Air: Early Insects

Devonian Insects: Hard Time on Plants

In the Ordovician, there is little evidence for animal life on land. Poorly preserved millipedes and coprolites is all what we have. The Rhynie cherts of the Devonian provide the oldest remains of insects with well-preserved mandibles (Engel and

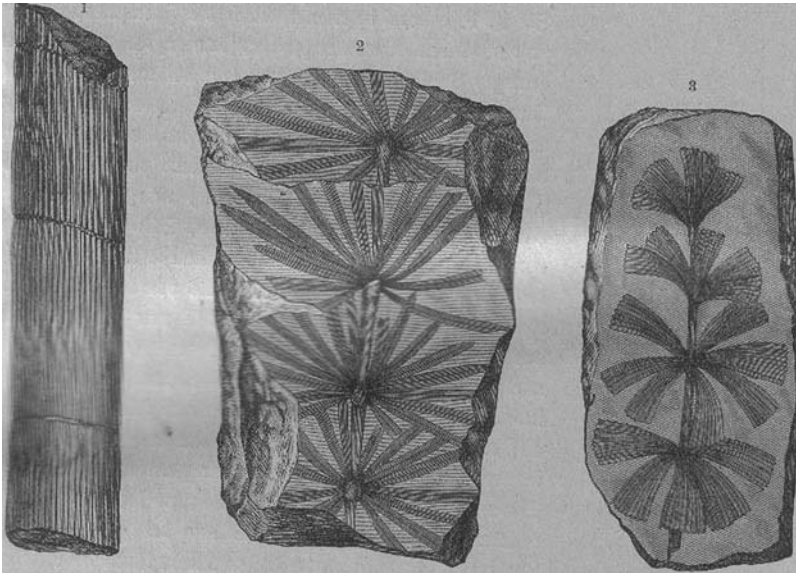


FIGURE 5.43. Pteridophyta IV: extinct Sphenopsida. Fossil Sphenopsida are in this picture represented with two fossils from the order Equisetales, namely with a stem from *Archaeocalamites* from the Lower Carboniferous (1) and a stem with leaves from *Calamites* (2), another important coal-forming plant of the Carboniferous. At the right is a stem with leaves from *Sphenophyllum*, which belongs to the only other order of the Sphenopsida.

Grimaldi 2004). *Rhyniognatha hirsti* was clearly a chewing insect, but it is unclear whether its diet was spores and pollen, leaf and stem tissue, or other animals. The authors of this article take great pain to suggest from indirect evidence that this beast was a winged insect. Part of the excitement is certainly a Guinness book of records entry. If their interpretation is correct, then insect flight would have preceded that of pterosaurs, birds and bats by full 90, 170, and 270 million years, which are not small time spans. This hypothesis would at the same time challenge and concur with current models. The challenge is presented by the fact that insect wings are powered by thorax muscles, which are among the highest oxygen consumers we know in the animal kingdom. These high-metabolic costs need a good food source and an atmosphere rich in oxygen. However, the Devonian sported only about 15% oxygen, less than the current atmosphere. On the food side the early land animals formed a strange guild. Herbivores were rare and if present only active as microherbivores. The early arthropods had no answer to lignin. In addition plants lack excretion organs. Toxic waste products are therefore frequently stored in cell walls. The plant material was thus not only hard to digest, it was even poisonous. Those vegetative parts of plants that could be attacked were of low nutritional value. They lacked and still lack today sodium and aromatic amino acids. The early arthropods had



FIGURE 5.44. Pteridophyta V: Calamites. An artistic impression of a Carboniferous swamp with Calamites trees (class Sphenopsida, depicted at the *left*), which could reach 30 m in height, and true ferns of the class Filicopsida at the *right*; both plants are members of the Pteridophyta.

to wait until fungi and bacteria had made their attack on plant litter; the animals could only form the second wave of attack.

Detrivores and Taking to the Air

Most of the animals were detrivores (Figure 5.64) and many were predators. In fact, this has remained a characteristic of soil ecosystems until the present. Mites living on saprophytic fungi and collembolans are found in the lower layers of the soil food web. In the upper ranks, one finds today nematode-feeding mites and predaceous mites feeding on the latter (Neutel et al. 2002). When bacteria and fungi had done their job, the plant material was sufficiently detoxified and the nutritional value of the explant material was enhanced. True herbivory was not yet an option and this remained so for a while. Even in the Carboniferous fossil, evidence for insects chewing on living plant parts is weak (Figure 5.65). For example, paleobotanists looked for bite marks on leaves from *Neuropteris*: Only 4% showed evidence for chewing (Shear 1991). When looking today at trees during spring, some biologists will argue that this is still a respectable rate. However, evolution is a tough teacher (or “need makes inventors”). Spores, ovules, and seeds contain less toxin and they are nutritionally a much richer food source than the vegetative plant parts. It is only logical that the early insects specialized on this food source. However, there was a problem: The plants started to grow in the Devonian. Tracheophytes became shrubby plants ~1 m

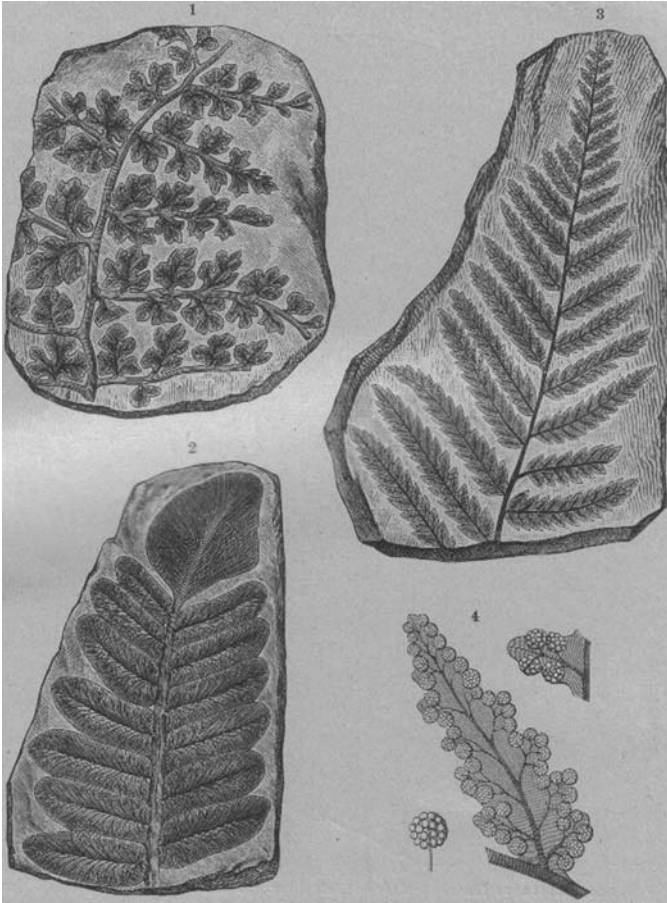


FIGURE 5.45. Pteridophyta VI: Filicopsida. Four fossil representatives from Filicopsida ferns of the Carboniferous: *Sphenopteris* (1), *Neuropteris* (2), *Pecopteris* (3), and *Oligocarpia* (4), which resemble some living ferns.

tall. In the Carboniferous, the trend for arborescence was in full swing and plants were of sizable height. As the reproductive organs were passively lifted with the size increase, insect flight became a necessity. Now you understand why the discoverers of *Rhyniognatha* argue for a winged insect—it would just come in time to keep pace with the size evolution of plants. This is in evolutionary terms a healthy argument since other races can also be read from the fossil record. The predator–prey fight also took a new gear. Plant prey grew larger to avoid predation, but the insect predator participated in this size arms race, too. In some way, the competition got out of control and the largest insects that ever lived on the planet had evolved in the Carboniferous: *Meganeuron* with a wingspan that exceeded 60 cm. The winged insects of the Carboniferous had specialized mouthparts that allowed, for example, *Homaloneura* to tear apart the soft cones

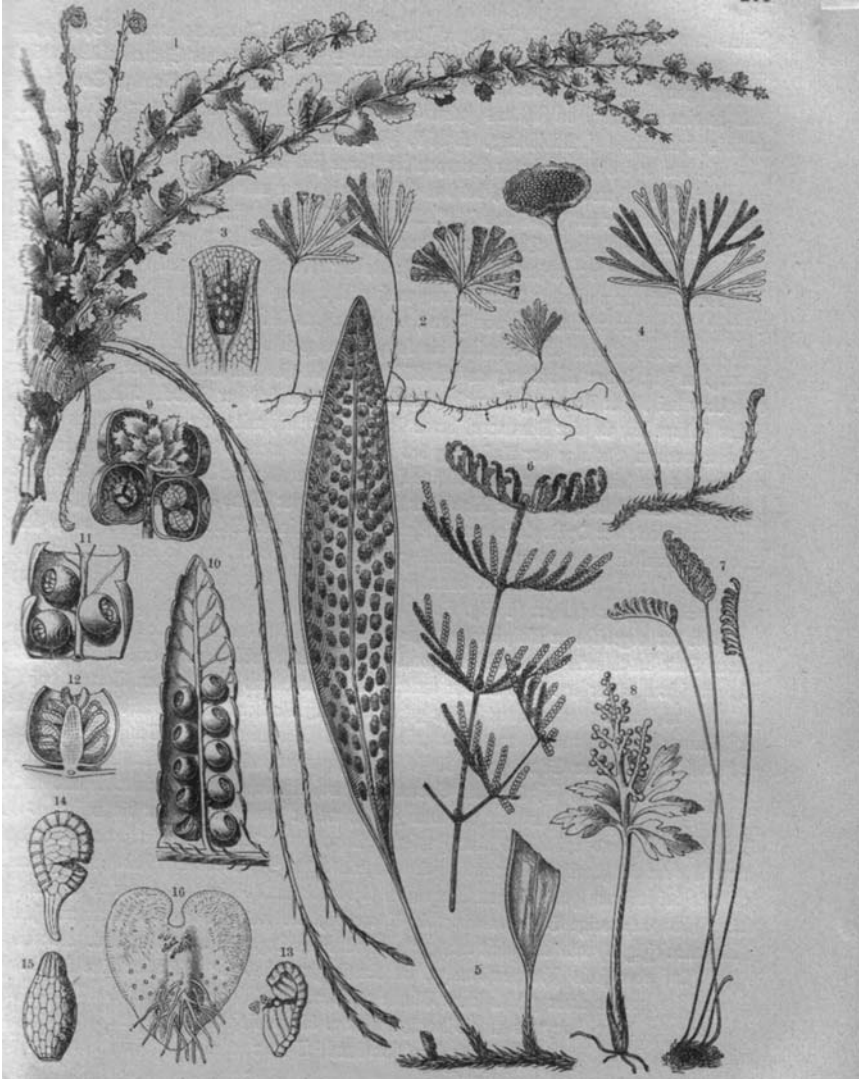


FIGURE 5.46. Pteridophyta VII: Filicopsida. The figure compiles different forms of extant ferns showing the widely distinct leaf forms: (1 *Nephrolepis* (1), *Trichomanes* (2–3), *Rhipidopteris* (4), *Polypodium* (5), *Gleichenia* (6), *Schizaea* (7), *Botrychium* (8), *Cyathea* (10) and the sporangia (spore-producing organs) from *Gleichenia* (9), *Cyathea* (10–13), *Polypodium* (14), and *Schizaea* (15). 16 shows a prothallium, the gametophyte of ferns.

of *Cordaites* trees. Others pierced ovules or fed by sucking with stylet-like mouthparts. Still others specialized on spores as demonstrated by fossils where the gut of the insects is entirely filled with spores. However, in the Carboniferous a long-term mutualistic insect–plant relationship started: pollination by insects

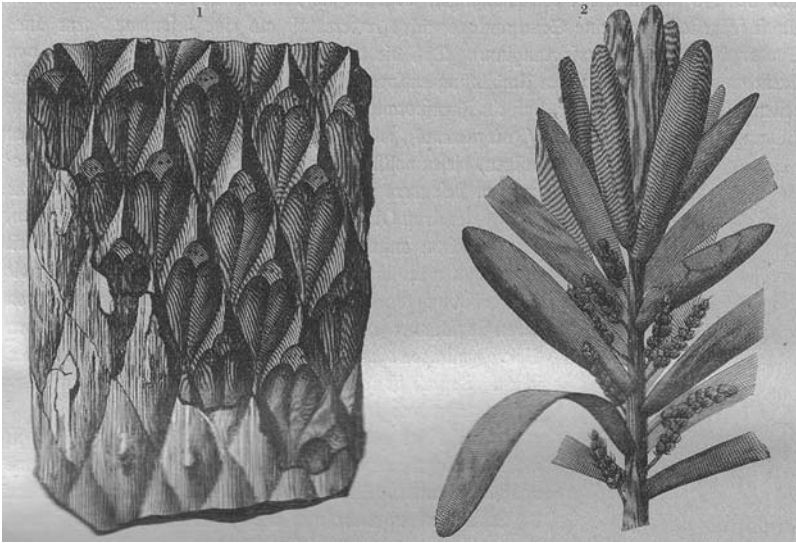


FIGURE 5.47. Conifers I. Cordaitales are perhaps the best-characterized order on the way to spermatophyta. They derive from Progymnospermae in the Devonian, flourished with 30-m tall trees in the genus *Cordaites* in the Carboniferous, but became extinct in the Late Permian. In the popular cordaite–conifer hypothesis they gave rise through the intermediate of the primitive conifer family Lebachiaceae to the Coniferophytinae. The figure shows a stem with leaves and inflorescences from *Cordaites laevis*.

(Figures 5.66–5.68). The evidence is, however, indirect. The fern-seed pollen became so large that wind pollination became an unlikely option.

Insect Diversification in the Age of Angiosperms

Ants have a good fossil record: The oldest amber fossils are 100 million years old and come from the Early Cretaceous. However, these ambers contain both crown and stem groups of ants suggesting that the origin of ants substantially predates this time period. A large-scale molecular phylogeny of ants from nearly all 20 described subfamilies pointed to a shared common ancestor living 170 million years ago in the Middle Jurassic (Moreau et al. 2006). The authors asked the question why ants were so slow to diversify. Ants were rare in the Cretaceous and their march to ecological dominance began only in the Eocene 90 million years ago. They linked the dramatic diversification of ants to the rise of angiosperm-dominated forests. They suggested that the litter of angiosperm forests is more diverse than that of gymnosperm forests, providing more habitats. Ants could then exploit different food sources using predatory to a scavenger lifestyles. Still other ants lived on carbohydrate-rich honeydew secretions excreted through the anus of angiosperm sap-sucking insects like homoptera (aphids). These “trophobionts” receive for their nutritious excretions protection from predators

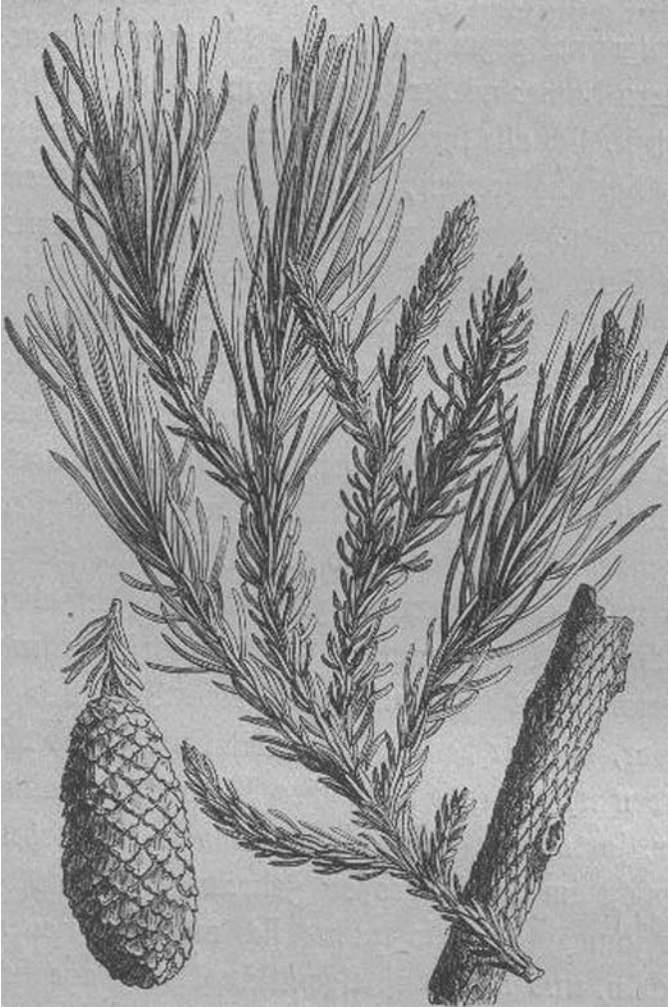


FIGURE 5.48. Conifers II: The evolutionary history of conifers began in the Carboniferous where descendants from the Cordaitales evolved what was lumped for convenience in the family Voltziaceae, here represented by *Voltzia heterophylla* from the Lower Triassic. They formed forests in the Triassic and Jurassic, but then became extinct. They gave rise to the Pinidae (pines), but not the Taxidae (yews).

and parasitoids by the tending ants. In addition, a third of tropical woody dicots produce extrafloral nectar or lipid-rich pearl bodies to attract ants that defend in turn “their” ant plants against herbivorous insects. Still other ants are “leaf foragers” to feed their fungal gardens, while folivory (leaf eating as herbivores) has not evolved in ants. Some ant species glean food from the leaf lamina eating adherent fungal hyphae and spores. A recent analysis of food nitrogen sources



FIGURE 5.49. Conifers III: The order Pinales remained competitive against angiosperms in the cold climate of high altitudes and the Northern hemisphere, where they represent the dominant tree flora. The figure shows *Picea cembra*, typically growing at the limits of forests in high altitudes of the Alps, but also of Siberia.

in ants from tropical rainforest canopies revealed that plant-resource losses to insects greatly exceeded the previous estimates of 0.8 tons/ha/year. Already, the smaller former estimates were threefold greater than losses due to vertebrate herbivory (Davidson et al. 2003).

Ants were not the only insects that showed a radiation with the evolution of angiosperms. This was recently also demonstrated for Chrysomelidae or “leaf beetles” (Wilf et al. 2000; Figure 5.69). These animals lack a body-fossil

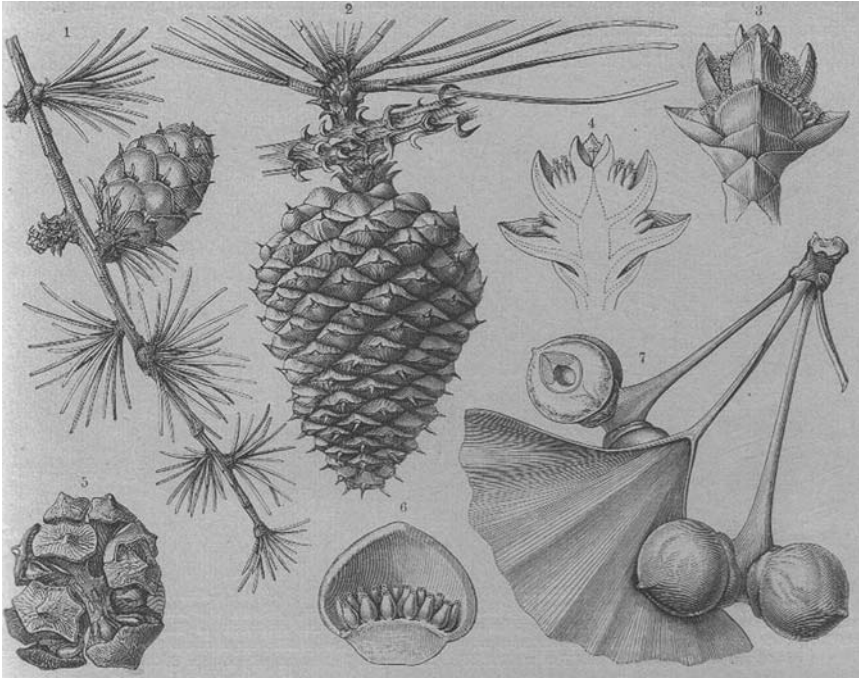


FIGURE 5.50. Conifers IV: Twigs with needles and ripe cones from the larch (*Larix europea*, 1), the pine (*Pinus serotina*, 2) and young (3, 4 cross section, 6 detail) and old (5) cones from *Cupressus sempervirens*. *Ginkgo biloba* (7) here shown with a leaf and immature seeds also belongs to the conifers, but forms a distinct class of mainly extinct plants (Ginkgoatae) from the class Pinatae.

record, but their feeding attack on rolled juvenile leaves of ginger and heliconias (moncot order Zingiberales) in the understories of Neotropical forests lead to so characteristic damage trails on the plants that their identification on fossil plants is diagnostic for the leaf beetles. The Zingiberales contain many compounds like tannins, phenols, alkaloids, and terpenes that are of potential defensive use against insect herbivores. Heliconia, a basal member of the Zingiberales group, harbors a high diversity of leaf beetles. At the same time, they conspicuously lack these defensive compounds. The fossil record of Zingiberales shows feeding attacks by leaf beetles near the time of the first appearance of the hosts for these leaf beetles in the Cretaceous. Insects and angiosperms showed thus a coupled diversification to numerical dominance in the animal and plant world such that their trophic association is a dominant feature of the evolving terrestrial ecosystems. Over half of all beetles are herbivorous and they fared well with this food source. Actually, when the British biologist Haldane was asked by a group of theologians what one can conclude as to the nature of the Creator from the study of His creation, he quipped, “An inordinate fondness for beetles” (Farell 1998). In fact, the insect order Coleoptera exceeds with respect to species

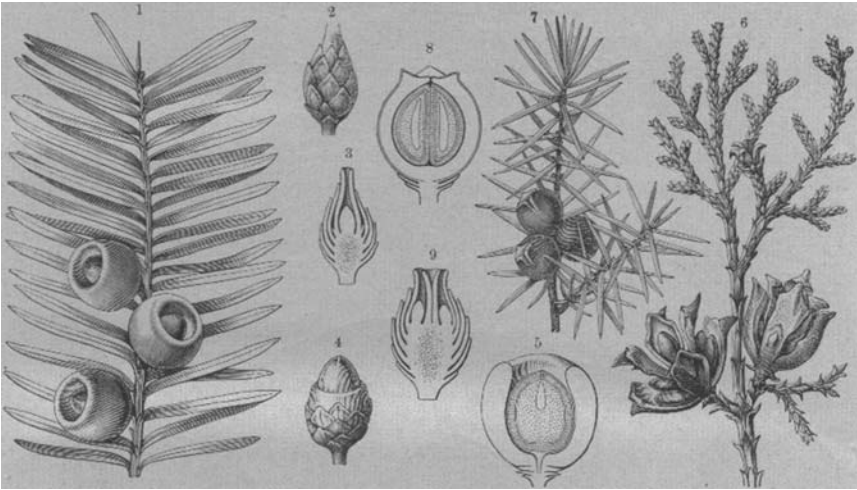


FIGURE 5.51. Conifers V: This figure shows further members of the cypress family, namely the oriental arborvitae (*Thuja orientalis*) with narrow, scale-like leaves pressed against the branchlets (6) and the juniper (*Juniperus communis*), which carries a cone encased in a fleshy fruit (7, 8 cross section). The yew here depicted with *Taxus baccata* (1) belongs to a distinct subclass of the conifers (Taxidae) shows small female reproductive organs (2, 3), which form a cone (4) that is surrounded by a fleshy, red, cup-shaped aril (5). These are the only nontoxic parts of the plant in line with the function of fruits as a nutritional incentive for animals to disperse the enclosed seeds.

richness any other animal or plant group. The earliest beetles in the Permian were saprophages (eaters of dead organisms). Feeding on plants arose 50 million years later in the Triassic, but most of the beetles were still saprophages. At this time, angiosperms were nonexistent and the terrestrial plant world was represented by Bryophytes, Pteridophytes, Ginkgoales, Gnetales, Coniferales, Cycadales, and Bennettitales (Figures 5.40–5.57). Interestingly, the phylogenetic

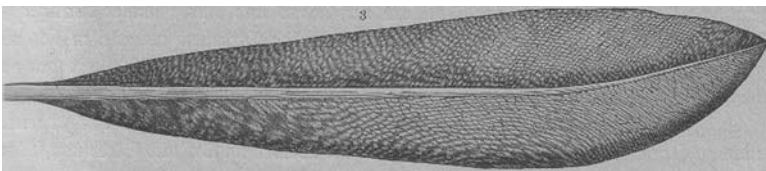


FIGURE 5.52. Cycadophytina I: Pteridospermae. Charles Darwin described the origin of angiosperms as “an abominable mystery” and it still remains so today. In older hypotheses the angiosperms (Magnoliophytina) and the Cycadophytina derive from the Progymnospermae via Pteridospermae (seed ferns), which flourished in the Carboniferous and Permian of the Palaeozoic, but died out in the Mesozoic. A rather modern-looking leaf with mesh-like venation is shown here for the seed fern *Glossopteris indica*, a characteristic fossil of the Gondwana flora.

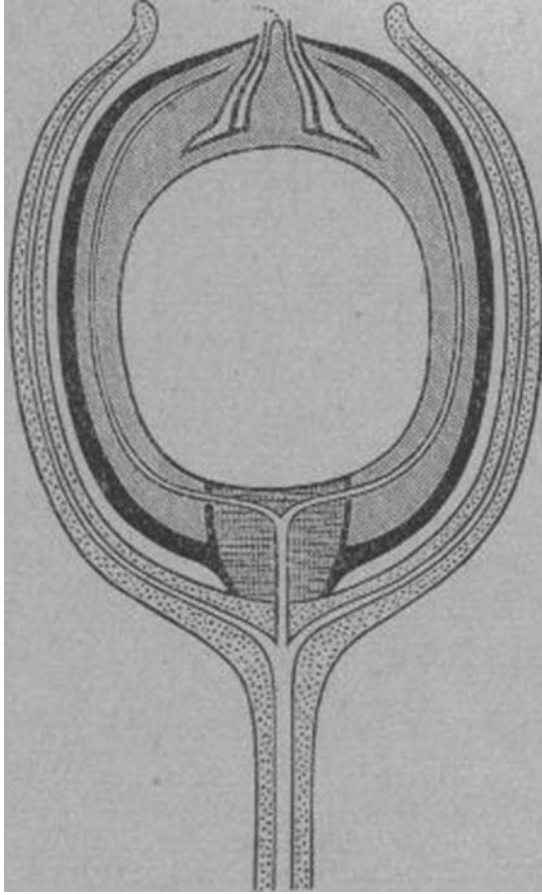


FIGURE 5.53. Cycadophytina II: Pteridospermae. One of the characteristics that permitted exploitation of the land was retention of the embryo within the maternal tissue. This trend culminated in the development of the seeds. The embryo is not only retained within the parent gametophyte, but the gametophyte in turn is encased in and protected by tissue from the sporophyte that produced it. Thus every seed includes tissues of three generations: the sporophyte plant, the microscopic gametophyte, and the second-generation sporophyte plant, which is the embryo. This development started with the seed ferns in the Devonian and the three tissues are reconstructed in the picture for the seed fern *Lyginodendron* from the Carboniferous.

tree of the phytophagous beetles shows as most basal branches conifer- and cycad-feeding beetle lineages. The larvae of these basal beetles feed on nutrient-rich reproductive structures, which apparently preceded foliage feeding (Farell 1998). When angiosperms arose, leaf mining and seed and root feeding evolved in beetles consistent with the plant-beetle coevolutionary model of Ehrlich and Raven.

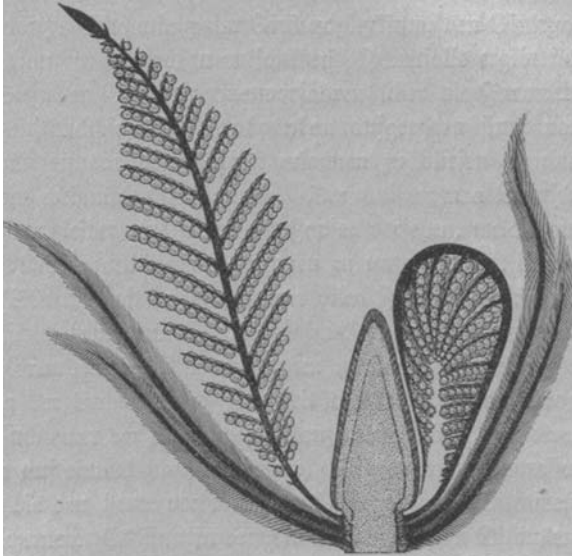


FIGURE 5.54. Cycadophytina III: Bennettitatae are an extinct class of plants that dominated with cycads the Middle Mesozoic times, which is also called the “Age of Cycads.” The rise and fall of Bennettitatae paralleled that of the dinosaurs. In certain bennettites, reproductive organs were observed that resemble conspicuously “flowers” with a central cone-like female reproductive organ surrounded by whisks of male reproductive organs (*left bent, right extended*) in a ring-like arrangement surrounded by perianth-like leaves. Despite that strikingly similar structure, they are not related to the flowers of angiosperms. When the angiosperms rose to dominance in the Cretaceous, the Bennettitales lost the race and became quickly extinct leaving perhaps the Gnetatae.

Early Herbivorous Vertebrates

Pelycosaur as First Vertebrate Herbivores

The follow-up of the tetrapod story, which we retold in one of the preceding chapters was hampered by Romer’s Gap, a 30 million years period after *Ichtyostega*, which nearly lacked tetrapod fossils. This gap was in 2002 filled with a beautiful fossil named *Pederpes* (Clack 2002). Paleontologists are held to justify their name, this name is rather tricky since it can be read in two reading frames and in both it makes sense. One message the name conveys is *pes*, Latin for foot. It shows a modern foot with five digits in contrast to the earlier amphibians, which showed seven or eight digits. Also this animal does not look like an herbivore. The first proposal of potential herbivores is made by tetrapods in the transition from the Carboniferous to the Permian with edaphosaurs from the reptilian lineage and diadectids from the amphibians. Only later in the Permian unequivocal evidence for adaptations to feeding on vegetation was documented for pelycosaur. Thus only relatively late animals found an access to the lush vegetation surrounding them. Until then this food source was, for

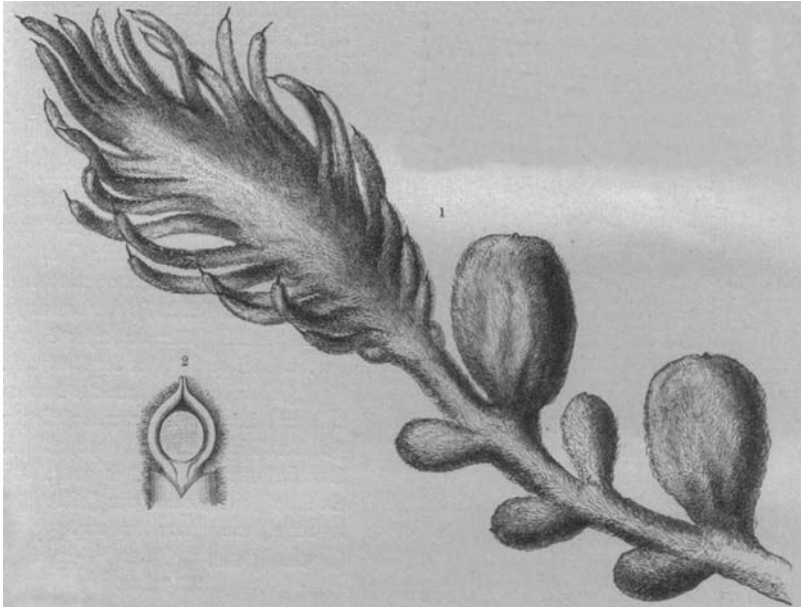


FIGURE 5.55. Cycadophytina IV: *Cycas*. Cycadatae are another branch that derived in parallel to the Bennettitatae from Pteridospermae. In the depicted *Cycas revoluta* the ovules develop on megasporophylls, which remain brown, but otherwise clearly resemble leaves. The ovules (the “buds” at the stem of the leaf in 1, 2 shows a cross section) are not surrounded by further tissue, *Cycas* is thus like the conifers a gymnosperm. The wind-borne pollen develops on other plants in cone-like microstroboli. Notably, at the time of pollination each ovule exudates a mucilaginous droplet and the pollen releases 0.3-mm large multiflagellate sperms, the largest in the plant and animal kingdoms. The plant thus recalls in its male reproductive behavior still its origin in the water, but has done the necessary adaptation to the conquest of the land.

vertebrates, untapped and became available only through the intermediate of fungi and bacteria. Animal detritivores funneled the primary productivity of plants into higher trophic levels. A very intensive life took place at the ground level where organic carbon was intensively traded. Gigantic myriapods testify the heat of the battle for food in the litter.

Lessons from Cretaceous Gut Contents: Titanosaurus Dined on Grass

Not all beasts of Zallinger’s mural paintings in the Peabody museum of the Yale University are carnivores, there are also peaceful, although sometimes gigantic herbivores among them. They dine on conifers, cycas, and ferns. Early flowering plants, but no grass, are depicted. This is somewhat astonishing since grass provides today staple foods for much of humankind and its domesticated animals. Until last year there was actually not much reason for painters to change the

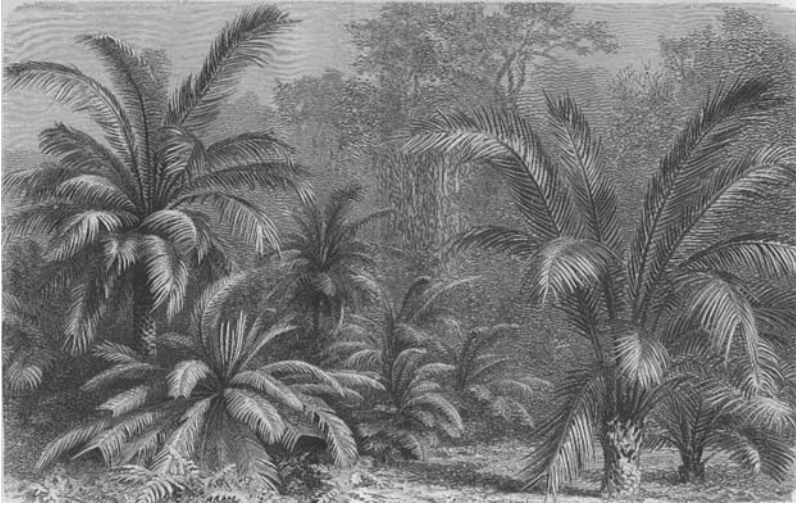


FIGURE 5.56. Cycadophytina V: *Cycas*. Today Cycadatae are represented only with a few living fossils, some of them resembling superficially palm trees.

picture since the fossil record of grasses (*Poaceae* or *Gramineae*) reached only back to 56 million years ago, the beginning of the Cenozoic and thus well after the demise of the dinosaurs. The dental features of the most prominent terrestrial plant eaters of the Late Cretaceous, titanosaurs, did not display specializations for grass eating, like grinding cheek teeth. Mammals show this specialization with hypsodont (high crowned) teeth in the Miocene. Actually, these teeth are necessary to digest such abrasive material like grass. The abrasiveness is a low-tech invention of grass against herbivory. Grass impregnates its structure with silica—this invention was apparently made by angiosperms 65 million years ago when they experienced a considerable herbivory pressure from herd forming dinosaurs. Phytoliths (“plant stones”), as these silica remains are called, are found today in basal angiosperms, monocots, and dicots as counterattack against insect and vertebrate herbivores. They induced an arms race leading to the modification of animal mouthparts to cope with these plant defenses. These phytoliths take very bizarre forms, they can be bilobate, cross-shaped, saddle-shaped and they are characteristic for the plant group (Piperno and Sues 2005). The exciting new finds are now coproliths associated with titanosaur skeletal remains that show phytoliths (Prasad et al. 2005). Phytoliths were found before in their fossilized dung and testified conifers and cycads in their diet in addition to bacterial colonies, fungal spores, and algal remains. Now unequivocal phytoliths of basal *Poaceae* were added to the list, which prolong the fossil record of grasses into the Late Cretaceous. They weren’t prominent parts of the diet of these sauropods, but grasses extend thus definitively farther into the past than was thought before. In light of the new findings, another observation becomes clearer. A previously enigmatic gondwanatherian (in plain English:



FIGURE 5.57. Cycadophytina VI: Gnetatae. *Welwitschia mirabilis* is a surviving member of the plant order Gnetales, which probably derived from the extinct Bennettitales and which share at the same time some floral characteristics with angiosperms. A single species exists in the Kalahari desert. It is anchored by a deep taproot in the ground and sports only two several-meters-long leaves growing from the basis. The plant in the foreground shows flowers carried on cones that grow in a ring covering the basis of the two leaves.

a mammal from the continent Gondwana) with highly hypsodont teeth is the early answer of mammals to the problem of making a living from grazing grass in the Cretaceous. When in this coevolutionary arms race grass used more and more silica for enforcing its structures, it started to monopolize the bioavailable silica to the detriment of other organisms that used silica for their casing like sponges. Sponges lost this battle with grass for the silica resource and the arrival of grasses broke the prominent role of sponges in the geological record.

A Bite of Plant Material by an Omnivore Like us

In the following, I will illustrate what we as omnivorous mammals can do with plant material, not that much in fact. You might have wondered why we cannot survive on leaves and grass like caterpillars and cows; in the end, we are called omnivores and have to deal with many different forms of foodstuff. Starving human populations have tried to eat many plant materials growing around them—to no avail. It turned out to be nondigestible, unyielding, even antinutritional or frankly toxic. Our digestion capacity is limited to relatively simple sugar compounds. For more complex sugar macromolecules, we have only learned to attack a relatively small number of bonds, notably those of the plant storage polysaccharide starch. For the somewhat more complex polysaccharides, we get some help from colonic bacteria. Next we will see that even professional herbivores like cattle need the assistance of microorganisms to come to grips with plant polysaccharides. As animals learned to deal with plants, plants had to

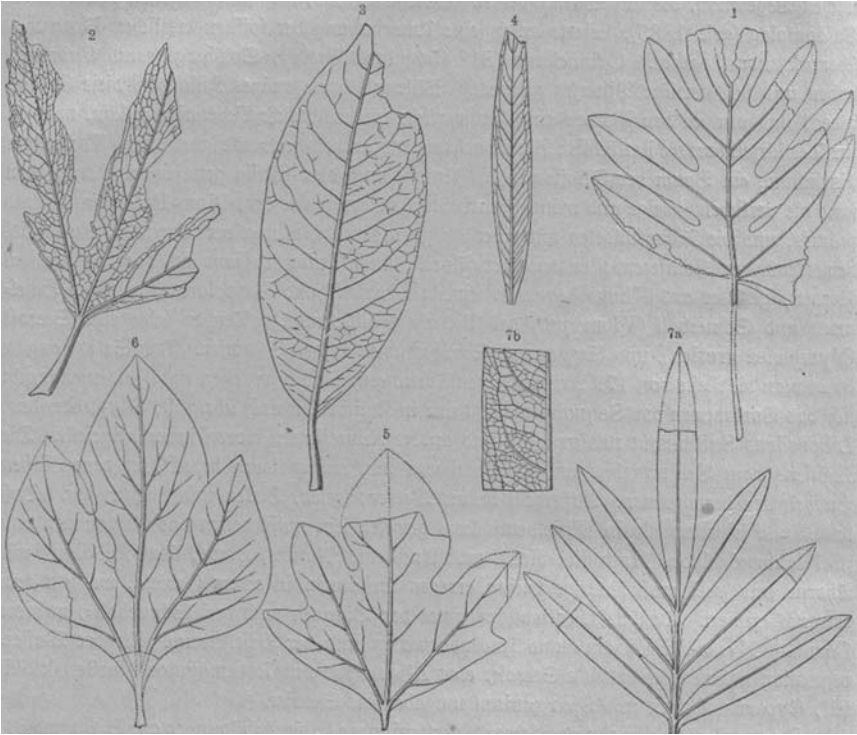


FIGURE 5.58. Angiosperms I: fossil leaves. The fossil record of angiosperms starts with the Cretaceous and presents already an astonishing differentiation with *Artocarpus* (1) (Hamamelididae) from Greenland and *Araliaephyllum* (5), and *Aceriphyllum* (6) from the Cretaceous Potomac formation. The Magnolia-like angiosperms are commonly believed to represent the oldest forms of angiosperms here represented with a leaf from the Lower Cretaceous in Portugal (3). The other leaves are attributed to *Aralia* (2), *Salix* (4) and *Sapindopsis* (7, 7b magnified).

design new strategies to thwart feeding attacks on them, which is the subject of the last two chapters in the herbivory context.

On Teeth and Enzymes

There is a great difference between carbohydrate and, for example, lipid digestion. While normal adults absorb about 95% of the dietary lipids, only part of the dietary carbohydrate is digestible. There are two reasons for this difference. One is size: Lipids come as only moderately sized molecules, while carbohydrates can be very large. The carbohydrates from the cell walls of plant material in our diet are molecules of enormous molecular weight and they are frequently part of tough plant tissues. In fact cellulose, the carbohydrate making up a substantial part of the cell wall of plants, was designed by evolution to confer mechanical strengths to plants. Tough or not, Nature has also endowed us with

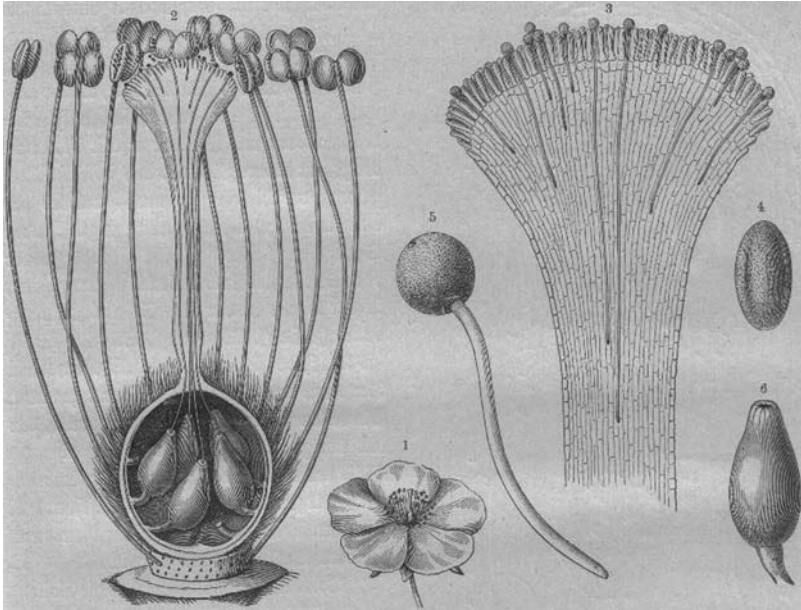


FIGURE 5.59. Angiosperms II: The flower. The most important distinguishing feature separating angiosperms (flowering plants) from gymnosperms is not the possession of flowers, but the fact that the ovules from angiosperms are enclosed in a carpel. The Greek words recall this fact: gymnosperms “marry nakedly,” while angiosperms “marry under the blanket.” The conditions are illustrated for the flower of *Helianthemum marifolium* (1). The flower is enlarged in (2) with petals and sepals removed to better visualize the many stamens separated into the anthers on a long filament, which produce the male gametophyte, the pollen (4). The stamens surround the single pistil, consisting of the stigma (enlarged in 3), which is connected via a style to the five ovules (enlarged in 6) encased in the carpel (ovary). When the pollen gets wetted on the stigma, it develops a tube (5) and grows down the style to reach the ovule, the female gametophyte, for fertilization.

tools to handle rough food. The toothed jaws of vertebrates can do wonders with many robust food materials—look how carnivores are cracking bones. However, digestion is more than just chewing food down to pieces that you can swallow. In that sense you can also eat straw. But you will not extract much energy from straw because we lack the digestive enzymes that can cut down the plant cell walls to their constituting monomers. At the enzymatic level, cellulose is a very sturdy material: It is glucose linked by β -1,4 bonds. We simply do not have enzymes able to attack this seemingly simple bond and such enzymes are indeed relatively rare in nature. Cows that make a living from eating cellulose rely for this digestive property on microbes in their rumen (more on that later). The reason is evolutionarily quite clear. Not only did plants need mechanical strength, but because they had to build this strength with biological material, they also had to resist attack by herbivores. It is thus not surprising that we have a lot of nondigestible

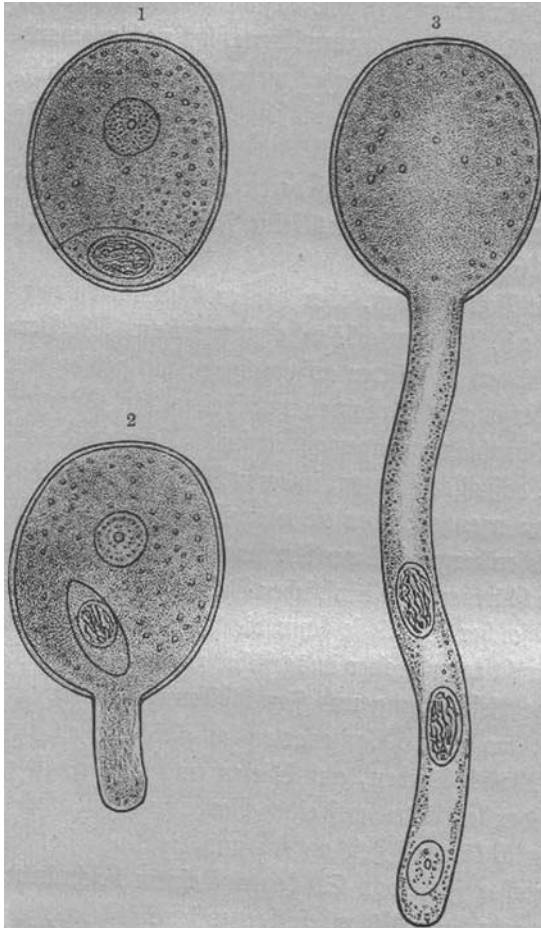


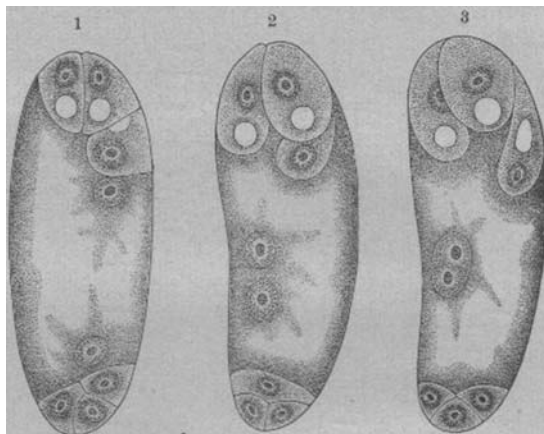
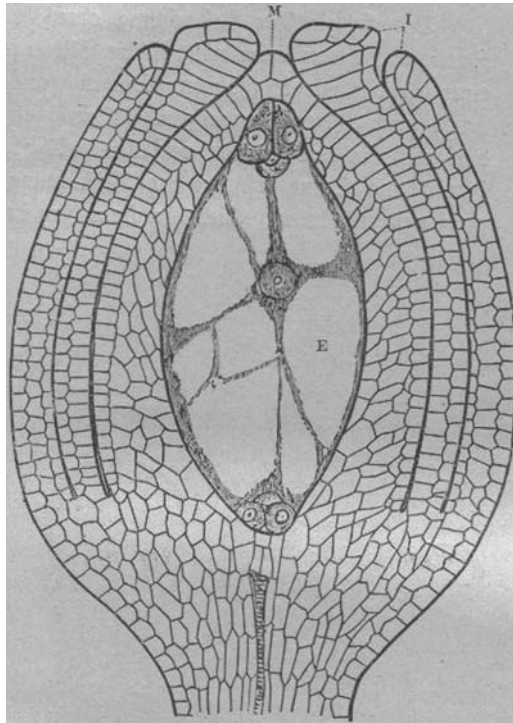
FIGURE 5.60. Angiosperms III: The male gametophyte. The pollen grain separates into two cells, the generative spindle-shaped cell and the vegetative tube cell with a round nucleus (1). The generative cell divides in the tube into the two sperm nuclei to prepare the characteristic double fertilization of angiosperms (2). At the tip of the tube is the nucleus of the vegetative cell (3).

carbohydrates, collectively called fiber, in our diet. There are substantial cultural and economical differences with the fiber content in the human diet. People from industrialized countries consume substantial amounts of so-called “refined” sugar in their diet and only small amounts of fiber. Lack of fiber in the Western diet has been linked to diseases that are more prevalent in industrial than in developing countries, like colon carcinoma and vascular diseases. Actually, part of the nondigestible carbohydrates becomes food to bacteria that grow in great number in our colon. Pectins, gums, and mucilages are digested by colonic

bacteria. In contrast, cellulose and hemicellulose are only degraded to a small extent and lignin not at all and they are excreted unaltered with the feces.

Starch Digestion in Humans

Approximately 45–60% of the digestible carbohydrates in a European diet are in the form of starch, the storage form of glucose in plants. Amylose,



the nonbranched type of starch, consists of glucose residues in α -1,4 linkage. Amylopectin, the branched form of starch, has about one α -1,6 linkage per thirty α -1,4 linkages. These chemical linkages between glucose residues are much easier to crack than those in cellulose. Their digestion starts already in the mouth with the α -amylase secreted with saliva. Chewing starch in the mouth quickly gives you a sweet taste because of the release of oligosaccharides. However, the digestion of starch in the mouth is incomplete and the salivary α -amylase is inactivated in the stomach acidity. Starch digestion is resumed in the duodenum with a pancreatic α -amylase, which is 94% identical in its amino acid sequence to the salivary enzyme. This enzyme completes starch digestion in the lumen of the small intestine. Completes is perhaps too great a word: α -Amylase is an endoenzyme that cleaves internal, but not terminal α -1,4 linkages, nor does it cut α -1,6 linkages or α -1,4 linkages adjacent to α -1,6 linkages. The end result of starch digestion is therefore the disaccharide maltose, the trisaccharide maltotriose, and the limit dextrins around the branching points. The starch digestion is in fact finished by “membrane digestion” on the epithelia of the small intestine. These cells have a particular ultrastructure, they ride on the basal lamina which separates them from the lamina propria containing blood capillaries. The epithelial cell rises as a columnar structure ending in a brush border of so-called microvilli that enormously increases their absorptive surface. The glycocalyx covers the tips of the microvilli and consist



FIGURE 5.61. Angiosperms IV: The female gametophyte. (a): cut through the ovary, the central ovule is covered by two layers of integuments. The development of the female gametophyte starts with a single nucleus in the embryo sac cell. It forms a tetrad of four megaspores as a result of meiosis. Then a complicatedly orchestrated nuclear dance sets in (*right*). Three megaspores degenerate, one divides into the typical eight-nucleate, seven-celled female gametophyte (“embryo sac”). At the *top* near the microphyle (M) you see the synergid cells and slightly below the egg cell. The central cell shows two nuclei and opposite to the microphyle are the antipodal cells. As the pollen tube discharges its content into the female gametophyte, one sperm nucleus fuses with the egg nucleus forming the next-generation sporophyte, the new plant. The other pollen sperm nucleus fuses with the two polar nuclei in the central cell thus forming a triploid primary endosperm nucleus. This nucleus then divides further forming the endosperm tissue, which becomes filled with stored food like starches, oils, and proteins, which are recruited from the parental plant. The embryo grows thus from the food supplied by the parent as a form of accepted parasite. You can see that also angiosperms have their triumph of the egg story, where nutrition of the next generation became one crucial asset for the evolutionary success underlining again the close connection between food and sex. In legumes the embryo consumes the endosperm during its development, resulting in mature seeds with massive embryos and no sperm. A recent report on *Amborella trichopoda* shows a variant to the standard scheme of the nuclear divisions by displaying an extra synergid (Friedman 2006). As *Amborella* is the sole member of the most ancient extant angiosperm lineage, the variation testifies to an extensive experimentation phase during the early evolution of angiosperms, which occurred within a time span of 15 million years at about 130 million years ago.

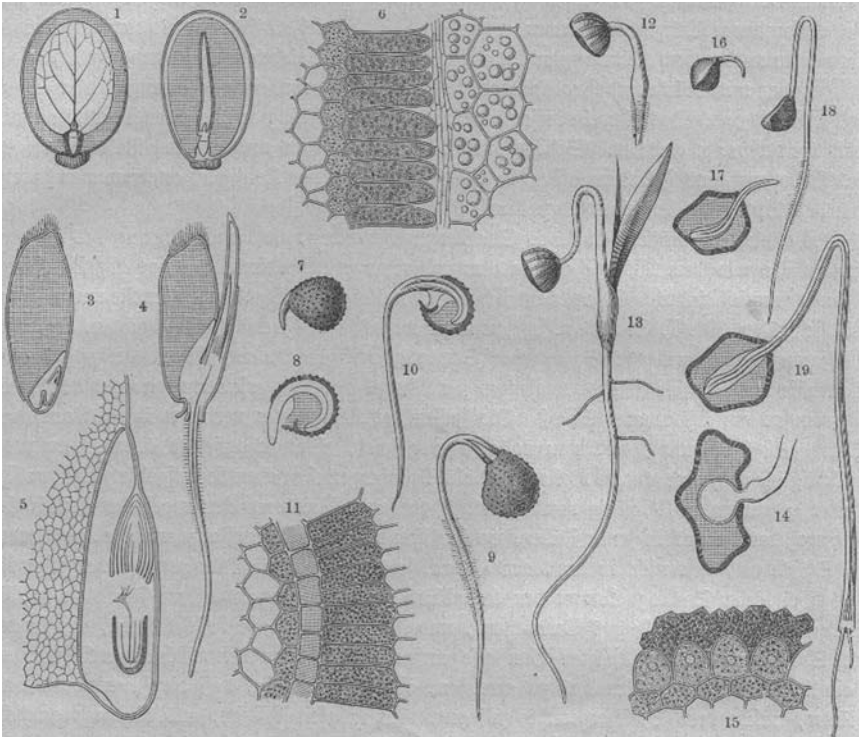


FIGURE 5.62. Angiosperms V: The seeds. The embryo (white) sits commonly within the endosperm (fine gray granulation) as shown for the *Ricinus* seed with cross sections (1, 2) along different planes, *Agrostemma* (7–11), *Tradescantia* (12–15) or the onion *Allium cepa* (16–19). The embryo of *Agrostemma githago* curls around the endosperm, while the embryo of the wheat (*Triticum vulgare*) sits apposed at one side of the large mass of the starchy endosperm (3). The bulk of the embryo consists of the fleshy body, the scutellum, which lies in contact with the endosperm (4) and serves as the digestive and absorptive structure during germination (5, 6 show the absorptive cell layer of the scutellum in contact with the starch grain-filled endosperm cells). The food reserves in the endosperm powers the outgrowth of the stem and the leaves on one side and the root on the other side (4) and ensures nutrition before leaves and root become functional and can feed the new plant. The grains of grasses also feed now directly and indirectly a large part of the world population.

of a network of glycoproteins and membrane-bound digestive enzymes. One of them is sucrase–isomaltase. Limit dextrin is digested by isomaltase subunit to maltose and maltotriose. A second membrane-bound enzyme is glucoamylase, it cleaves maltose and maltotriose into the glucose monomers.

Disaccharides

The rest of the digestible carbohydrates in our diet consist of sucrose (table sugar, a disaccharide consisting of a glucose and fructose) and lactose. Sucrose

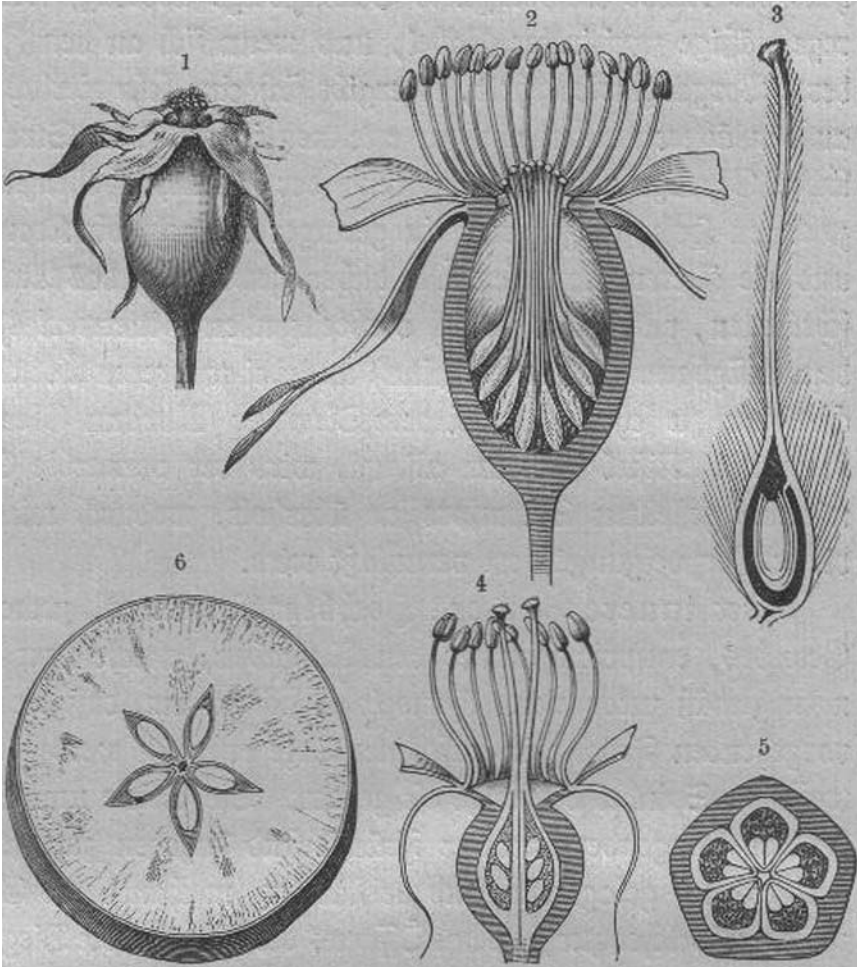


FIGURE 5.63. Angiosperms VI: The fruits. The seed is the reproductive body of angiosperms and gymnosperms, consisting of the undeveloped plant (embryo), the stored food (endosperm) and a protective coat (testa). Seeds provide man with his most important foods (e.g. wheat, maize, rice; beans, peas, peanuts, soybeans, nuts). Many plants surround their seeds by an additional nutritious layer of different anatomical origin (e.g. olive, banana, avocado, apple, orange, date palm) forming a fruit. Most fruits develop from a single pistil. However, most pronounced in roses, additional flower parts like the stem axis and floral tubes participate in fruit formation, resulting in an accessory fruit here represented by the rose (*Rosa*, 1–3) and the apple (*Malus sylvestris*, 4–6). The fruit is an organ of dispersal for the sperm attracting animals that eat the fruit, but cannot digest the protected seed, which they excrete and disperse with their feces. This function was initially fulfilled by reptiles, but was later largely taken over by the evolving mammals (here mainly primates, including man, rodents, and bats) and birds. According to the senses of the dispersing animals, fruits attract with intense colors (birds) or scents (mammals). Also invertebrates like ants play a prominent role in the dispersal of some plants via seeds and fruits.



FIGURE 5.64. Detrivores have an important function in the ecosystem and this lifestyle is widely distributed in insects. The figure shows carrion beetles (*Necrophorus vespillo*) which bury the dead mouse within minutes. They belong to the family Siphidae, order Coleoptera.

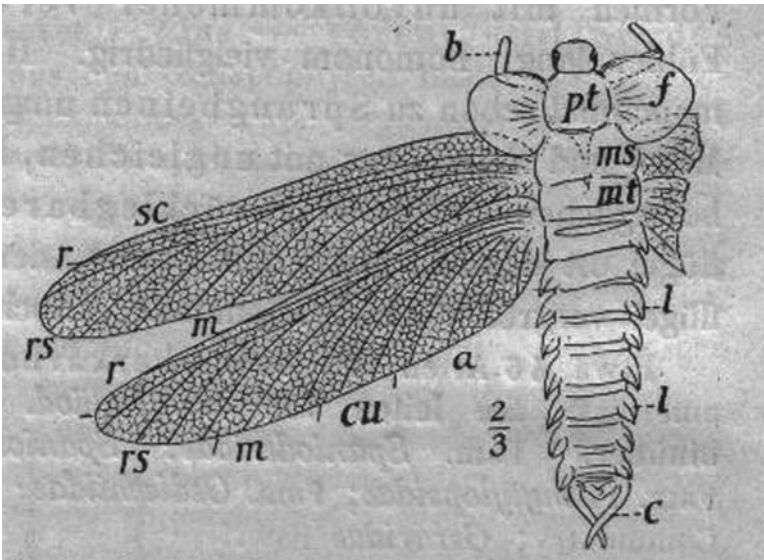


FIGURE 5.65. Paleodictyoptera- early flying insects are here represented by *Stenodictya* from the Carboniferous: pt: prothorax; f: paranotal lobe; forewing and hindwing (sc subcosta, r radius, rs sector radii, m medialis, cu cubitus) ms: mesothorax, mt: metathorax, l: abdomen, c: cerci. The paranotal lobe gave rise to wings in a hypothesis formulated by Müller in 1873. Currently the appendage hypothesis is more popular, which sees wing evolution starting from legs (Kukalova-Peck hypothesis 1983).

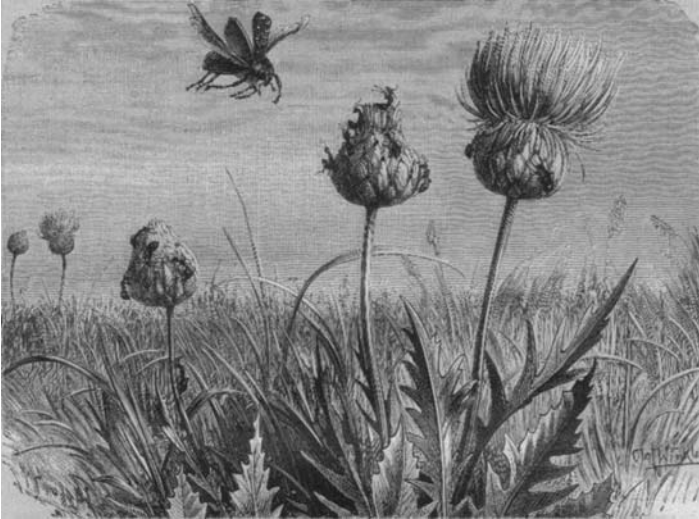


FIGURE 5.66. Pollination I. Pollination is the transfer of pollen grains from the stamen to the ovule-bearing organs. Pollination is another fascinating cross road between sex and food. Pollination by insects probably occurred in primitive seed plants. As flowering plants evolved in the Mesozoic, the first pollinators were probably beetles that had specialized on the reproductive organs from primitive plants. Beetles became pollen eaters, and pollination a chance event with spared pollen. Some visits of beetles can have devastating effects on the developing flower, like that of the beetle *Oxythyrea funesta* on the plant *Serratula lycopofolia*. The plant develops nectaria outside of the flower, which attracts the ant *Formica exsecta*, which in turn defends this food source against the landing of the beetle and spare the flower an unwelcome visit of a beetle. The figure alludes to the story of early insect herbivory on reproductive organs of primitive plants.

is the major transport form of sugar between the different plant tissues, while lactose is the sugar transferred with the milk to the breast-fed mammalian young. These two disaccharides make up about 30–40% of the digestible carbohydrates in our diet. The remaining digestible carbohydrates are the monosaccharides fructose and glucose, representing 5–10% of the total carbohydrates. Sucrose is split into its monomers glucose and fructose by the sucrase subunit of the sucrase–isomaltase membrane protein. Lactose is cleaved into its monosaccharides glucose and galactose by the membrane enzyme lactase. Uptake, not hydrolysis, is the rate-limiting step for sugar digestion except for lactase, which is a slow enzyme. The peak oligosaccharide activity is found in the proximal jejunum, much less is located in the duodenum and the ileum, none in the colon. As we have seen lactase activity is developmentally regulated, lactase is also more susceptible to enterocyte damage. Acute



FIGURE 5.67. Pollination II. Probably in a next step other flowers began to exploit primitive gall-forming insects for pollination. The figure tells two fascinating stories in this field. In the *left* you can see the *Yucca filamentosa* visited by the moth *Pronuba yuccasella*. This moth takes more than a mouthful of pollen during a visit (center of the figure), which is carried to the next flower. The moth does not eat the pollen, but discharges it on the pistil and at the same time deposits its eggs into the flower. Equally remarkable is the story of the fig (*Ficus pumila*) at the *right* side. Short-styled female flowers are found next to a leaf (*top right*). They are penetrated by the fig wasp (*Blastophaga grossorum*) (11), which deposit the egg that develops into a gall (10, with numerous small galls). The progeny insect leaves the gall (15) and gets over powdered with pollen when leaving the flower. During a visit to the next flower, the fig wasp deposits the pollen.

childhood diarrhea leads to temporary loss of lactase activity, which led in the past to the recommendation to withhold milk during a bout of diarrhea. Sucrose overfeeding can increase sucrose expression, this cannot be done with lactose on lactase.

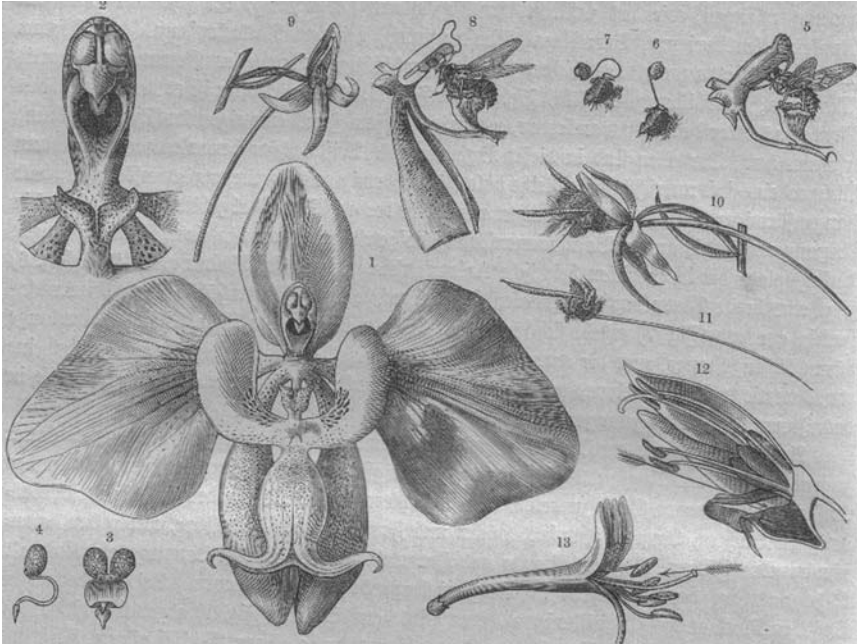


FIGURE 5.68. Pollination III. In more advanced flowers, nectar replaced pollen as reward for the pollinator. Flowers also developed guidance for the pollinator in the form of landing platforms. Intensive odor and bright color advertise the nectar to the pollinator. An impressive insect–flower coevolution took place and insects evolved sophisticated sucking mouthparts to forage on nectar. The picture shows such a seat for pollinating flies (5,8) in an attractive flower *Phalaenopsis schilleriana* (1).

Transporters: Sugar–Sodium Copackers

Now the carbohydrates are in the form of monosaccharides and ready for transport across the plasma membrane of the intestinal epithelia. The SGLT1 transporter takes charge of glucose and galactose, GLUT5 cares for fructose. Both show 12 membrane-spanning helices, but SGLT1 has a higher molecular weight. SGLT1 has two structural requirements for its substrate: it must be a hexose in D configuration able to build the pyranose ring. This applies to glucose and galactose as dietary digestion products, but not to L-glucose (a product of carbohydrate digestion by some bacteria that produce mixtures of D- and L-glucose) nor to fructose, which builds as a ketose the furanose ring.

SGLT1 is a cotransporter. As the name implicates, it transports glucose together with another compound, in the case of SGLT1 a sodium ion. Cotransporters come in two types: symporter and antiporter, depending on the

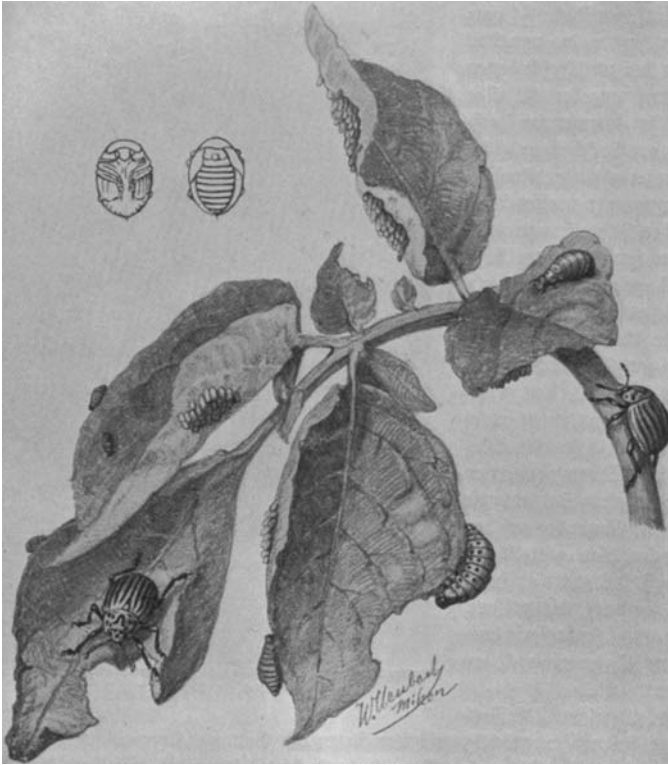


FIGURE 5.69. The Colorado potato beetle (*Leptinotarsa decemlineata*) belongs to the very species-rich family of Chrysomelidae (leaf beetle) of the order Coleoptera. It originally fed on buffalo bur (*Solanum rostratum*) in the Rocky Mountains, but with the westward moving farmers, who introduced potato (*Solanum tuberosum*), the beetle changed in the 1880s to a new host plant. Ten years later it was reported on the US east coast and arrived further ten years later in continental Europe. The picture shows egg masses, larvae, and adult beetles and on the *top left* a pupa.

transport direction of the two compounds. SGLT1 is a symporter: Sodium and glucose both travel from the lumen of the intestine into the epithelial cell. From an energetic viewpoint, SGLT1 is an interesting protein since it transports glucose against a concentration gradient. Remarkably, it can do this uphill transportation of glucose without using ATP. In fact, it derives the energy for the transport against the diffusion gradient by the cotransport of Na^+ , which goes downhill. Glucose absorption is driven by the Na^+ electrochemical gradient. This gradient has two components: The tenfold higher Na^+ concentration outside when compared to the inside of the epithelial cell and the inside negative voltage across the apical cell membrane (-60 mV). Both driving forces can be multiplied: The chemical gradient “buys” a tenfold gradient, the electric gradient

another tenfold glucose gradient allowing SGLT to achieve a 100-fold glucose concentration gradient across the membrane. However, this might not be enough since organisms might want to concentrate glucose even more, e.g., during urine production. Here the body recovers glucose from the primary urine filtrate. Avoiding the loss of useful calories is also an aspect of the quest for food. How is this achieved? The kidney SGLT form carries two Na^+ ions with each glucose molecule. As the concentration gradient enters the transport equation in squared form, glucose can now be concentrated 10,000-fold. This is the same underlying thermodynamic logic as we have seen before when the energy contained in the hydrolysis of a single ATP is not sufficient to allow an endergonic reaction to proceed. You simply couple the desired reaction to the hydrolysis of two or three ATPs.

Of course, there is a problem with SGLT-mediated glucose import: If Na^+ is constantly cotransported into the cell, you will lose the Na^+ concentration gradient across the apical intestinal membrane and thus the driving force for the transport. Hence, you have to drive intracellular Na^+ out again. This job is done by a primary active transport—the Na–K pump. This Na–K pump is energized by ATP hydrolysis and exchanges 3Na^+ (outward) against 2K^+ (inward). Now comes an important point. This Na–K pump is only localized in the basolateral membrane of the intestinal epithelial cell. By placing different transporters at the apical and basolateral membranes, epithelia can achieve direct transport of solutes across the epithelial layer, both in the absorption and in the secretion mode. In the intestinal cell, Na^+ is thus transported from the intestinal lumen across the epithelial cell into the interstitial space and from there into the blood. Glucose and fructose follow the same way. As glucose is concentrated in the intestinal cell, its export from the cell into the interstitial space can be done by facilitated diffusion. Consequently, this transport is mediated by GLUT2 located in the basolateral membrane.

Fructose

Fructose is transported into the intestinal epithelial cell across the apical (luminal) surface via the GLUT5 transporter. GLUT5 is an example for a uniporter-catalyzed transport. Helices 7, 8, and 11 contain aa that can form hydrogen bonds with the hydroxyl groups of the hexose. They are thought to form the alternatively inward and outward facing hexose-binding sites in the interior of the protein. Binding of the substrate to the outward-facing binding site triggers a conformational change in the uniporter, moving the bound hexose through the protein such that it is now bound to the inward-facing binding site. The sugar is then released to the inside of the cell. Finally, the transporter undergoes the reverse transformational change, inactivating the inward-facing hexose-binding site and regenerating the outward-facing site. The uniporter mediates facilitated diffusion, it only transports the fructose downhill of the concentration gradient.

Traffic Control

Accumulation of hexoses does not occur inside the cell since the intestinal epithelial cells contain the full complement of glycolytic enzymes and part of the absorbed hexoses is metabolized to lactate. Lactate diffuses into the blood and will be resynthesized to glucose in the liver cell via gluconeogenesis. Glucose concentration is maintained at 5 mM in the blood. This assures a sufficient concentration gradient for glucose import into the cells of the mammalian body, which express GLUT1. However, under conditions of starvation the blood glucose levels fall and in glucose-synthesizing liver cells the uniporter then transports glucose out of the cell. This is a useful reaction since it can now replenish the decreased blood glucose level by the liver cell that synthesizes glucose from lipid or protein degradation, which becomes visible as a loss of body fat and muscles.

A Bioreactor Fueled by Grass

Cellulase in Animals

Cellulose is one of the most abundant organic compound in the biosphere, it was estimated that the astronomical quantity of 10^{15} kg of cellulose is synthesized and degraded on earth each year. Cellulose is a nonbranched chain of glucose residues linked in β -1,4 linkages. We are surrounded by a major carbon and energy source, but cannot use it because we do not have the enzyme cleaving the β -1,4 linkages between the glucose residues in cellulose. *At first glance, this seems to be a terrible mistake of stepmother Nature that cries for remediation to ban hunger forever from human memory. However, we should think twice about that question: Evolution had long time periods to tinker with different solutions. There might be something really odd with cellulose that we do not possess a cellulase enzyme in our intestine.* Notably, we know of only two animals that express a cellulose-digesting enzyme: termites (Figure 5.70) and crayfish. Termites are well known for their capacity to digest what appears even more unpalatable than grass, namely wood. However, in both animals it is still unclear whether their cellulase contributes really to their nutrition.

The Consequence of the β -1,4 Glycosidic Bond

So what is the underlying problem in cellulose digestion that makes famines possible in human history? The answer is really trivial: It is the geometry of the glycosidic bond between the glucose residues in cellulose. More precisely, it is the difference between the α - and β -1,4 glycosidic bond between the glucose residues in starch/glycogen and cellulose, respectively. In both configurations, an oxygen atom links the C1 carbon from one glucose to the C4 carbon of the next glucose, hence a 1,4 bond. The α or β designation means that the hydroxyl group attached to the C1 carbon is below or above the plane of the six-member

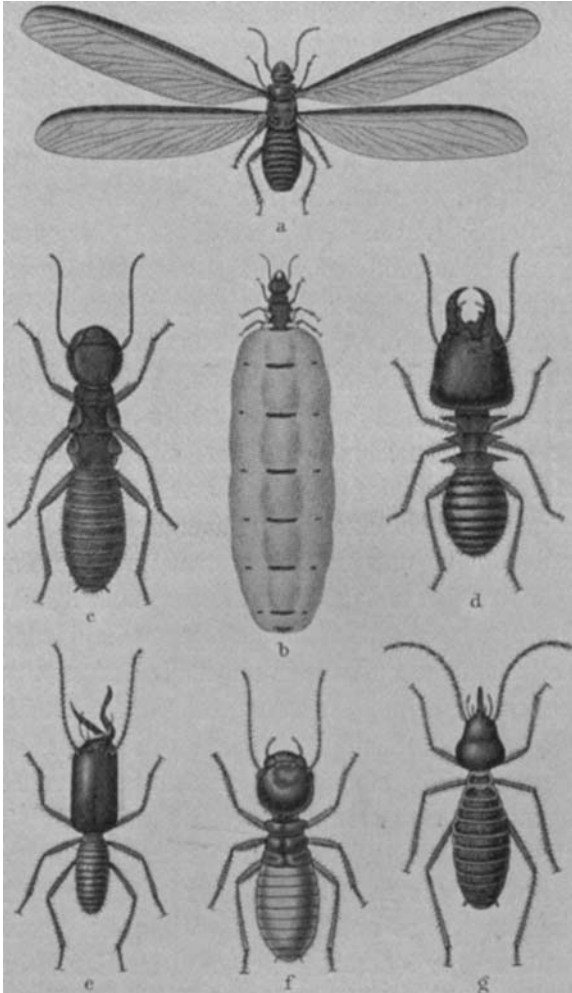


FIGURE 5.70. Termites: social insects of the order Isoptera. a young female from *Termes spinosius*; b queen from *T. gilvus*; c king from *Hodotermes ochraceus*; d–g soldiers from different species; f worker. Termites are mentioned in the book as one of the few truly cellulose-digesting animals.

pyranose ring of glucose. This difference has dramatic consequences. In the β -1,4 bond each glucose residue is related to the next one by a rotation of 180° and the oxygen in the pyranose ring of one glucose is hydrogen bonded to the 3-OH group of the adjacent glucose. The β configuration thus allows cellulose to form long straight chains, chains can align to fibers that are again linked by hydrogen bonds. This parallel alignment makes the fibrils rigid and insoluble and confers a substantial tensile strength to them—ideal for a polymer that has

to fulfill a structural role. The α -1,4 bond, in contrast, forces the starch and glycogen-type glucose polymer into a hollow helix conformation. The structure is water-soluble and solubility is still further favored by the side chains. In fact, this is what you would expect for a storage molecule. In times of need, the animal or plant cell should have an easy access for enzymes to peel off glucose residues from this store of glucose. This is what we are doing already in our mouth: We produce the starch-digesting enzyme α -amylase in great quantities in our saliva. You can actually sense the result, if you keep a starch source in your mouth, it will soon develop a sweet taste. Nothing like this happens when you masticate grass.

Cellulolytic Bacteria

Actually, a mammalian herbivore that can extract energy from eating straw still lacks the capacity to digest cellulose. However, herbivores like ruminants teamed up with organisms that have learned to digest cellulose. The ability to digest cellulose is widely distributed among many genera in the domain of Eubacteria (but strangely absent in Archaea) and in the fungal groups of Eukarya. However, the system must have evolved relatively late, i.e., after the appearance of algae and land plants, since cellulose is only very rarely produced outside of this realm (a few bacteria, e.g., *Azetobacter*, within animals tunicates, a primitive chordata). Within eubacteria cellulolytic capacities developed in aerobic bacteria (*Actinomycetales* is a prominent order), as well as in anaerobic bacteria (e.g., *Clostridia* order). Physiologically, these bacteria fit into distinct environments: The anaerobic Gram-positive bacteria like *Ruminococcus* are found—as the name suggest—in a specialized fermentation chamber of the alimentary tract of ruminants where they start the digestion of cellulose (for a review see Krause et al. 2003). In contrast, the aerobic Gram-positive bacteria like *Cellulomonas* and the gliding bacterium *Cytophaga* are found in soil where their task is the degradation of plant litter falling on the ground. If one looks at the enzymatic systems elaborated by cellulolytic microbes, the complexity of the enzymatic task becomes immediately evident (for a review see Lynd et al. 2002). Microorganisms that use “noncomplexed” cellulase systems impress us by the sheer amount of different enzymes. This system has been studied intensively in the fungus *Trichoderma* used in industrial processing of cellulose. It displays five endoglucanases, two exoglucanases, and two β -glucosidases. Attack on cellulose starts with endoglucanases, enzymes that cut in the middle of the cellulose chain. However, they cannot attack the tightly aligned so-called crystalline parts of the cellulose complexes, they gain access to cellulose in the amorphous regions of the cellulose fibrils, regions of imperfect alignment of the cellulose chains. Why this organism has five different endoglucanases is not clear. Part of the answer may be that the laboratory experiments were conducted with purified cellulose while cellulose in nature frequently comes in association with hemicelluloses.

Hemicellulose and *Trichoderma*

Hemicellulose accompanies cellulose particularly in secondary cell walls and represents the second most important source of carbohydrates in nature. The backbone of hemicellulose (xyloglucan) is glucose in β -1,4 linkage. Actually, the core structure of cellulose and hemicellulose are identical although only cellulose is made at the plasma membrane. Hemicellulose is decorated with xylose and some other sugars. Hemicelluloses are only slightly branched and more easily degraded than cellulose in part because they do not form microcrystalline structures. When the endoglucanase EGI from the fungus *Trichoderma* shows a broad substrate specificity including a xylanase activity, it will assure the physical access to cellulose. The endoglucanase cuts increase the amorphous character of these regions, some chains peel off from the fibril and then become targets to exoglucanases, enzymes that digest cellulose from the ends in a processive way. *Trichoderma* has two of this kind: CBHI, which attacks cellulose from the reducing end (i.e., showing a free aldehyde group), and CBHII, which starts digestion from the nonreducing end (showing the hydroxyl group) of the cellulose chain cut by the endoglucanase. CBHI contains four surface loops that give rise to a tunnel with a length of 50 Å, the cellulose chain gets into this tunnel and processive cleavage of cellulose occurs. Also the 3D structure of two endoglucanases was resolved. Interestingly, it showed a surface groove and not a tunnel for cellulose binding and cleavage, probably reflecting the difficulty to get primary access to the intact cellulose chain even in the amorphous region. The 3D structure of the exoglucanase revealed that cellobiose (two linked glucose residues) is the major hydrolytic product as the cellulose chain passes through the tunnel (Divne et al. 1994, Rouvinen et al. 1990). Only very small amounts of cellodextrins (3–4 glucose residues) or of glucose monomers are released at the beginning of the reaction. Therefore, two β -glucosidases are still necessary to complete the digestion. Interestingly, these two enzymes are cell bound to keep the diffusion path of the released glucose small, which favors the absorption of glucose by the *Trichoderma* cell and discourages stealing of the glucose by organisms living in the same environment. However, the exoglucanases reduce the degree of polymerization in cellulose only very slowly. The fungus tries to compensate it by producing more of these enzymes, 80% of the total cellulases are these two exoglucanases. *Trichoderma* strains used in industrial cellulose degradation produce 0.33 g of cellulase protein per gram of utilizable carbohydrate (Lynd et al. 2002).

Cellulosome

Cellulose digestion is apparently a tedious business—this is also true for cellulolytic bacteria, which generally show slow growth on cellulose. This is apparently the price to pay for living on an assured carbon source. The price is paid in the form of a very specialized digestion apparatus built by many cellulolytic bacteria. They developed a real machine, a cellulosome, for cellulose

digestion, which is very costly to construct. Cellulolytic bacteria are metabolic specialists; they are unable to use proteins or lipids as energy sources for their growth. No wonder that they are outcompeted by bacteria, which can use these alternative food sources. It thus appears logical that these so-called “complexed” cellulase systems are typically found in anaerobic environments like the rumen of herbivores where they live in consortia with high concentrations of other microorganisms. Stealing of your processed food product is under these conditions a big problem. The solution is to do all next to your cell wall; you organize a coordinated enzyme activity in a Henry Ford-like way, this time, however, as a disassembly line. Electron microscopy showed that cellulosomes are compact fist-like protuberances on the cell wall that open when attaching to cellulose. A *Clostridium* cellulosome has been studied in some detail (Lamed et al. 1994). It contains a large concatalytic scaffolding protein, CipA. On one side it is anchored to the cell wall via a type II dockerin/cohesin, on the other side an association of type I cohesins/dockerins link it to more than 20 different catalytic modules, including nine distinct endoglucanases, four exoglucanases, and five hemicellulases. The high efficiency of this megazyme has been attributed to the appropriate combination and spacing of enzymatic activities that can remove physical hindrances of other polysaccharides found in plant-derived crude cellulose. Some cellulosomes reach a molecular weight exceeding 10 MDa, but not all cellulosomes are so complex. We understand now that a significant metabolic effort has to be devoted to its synthesis. The justification for this effort is the high caloric value and natural abundance of cellulose in nature—a cellulolytic microbe is unlikely to starve in any habitat that carries plant life. The major cellulose degrading microbes in the rumen, *Ruminococcus albus* and *Fibrobacter succinogens*, have developed further adaptations like a glycocalyx envelope consisting of glycoproteins. This structure has multiple functions: It mediates attachment to the cellulose, protects against grazing by ciliates and bacteriophage attack in the rumen, and assures that not too many degradation products are lost by cross-feeding of nonadherent cellulolytic and noncellulolytic bacteria. The oligosaccharides are taken up and fermented via the Embden-Meyerhof pathway.

Ruminants: A Bit of Microbiology and Physiology

The digestive system of all mammalian herbivores shows specific adaptations to the fermentation of plant material, e.g., a large cecum (a postgastric fermentation chamber distal from the small intestine) and an increased large intestine. Ruminants went one step further by developing a huge dilatation of the esophagus, the rumen, and a restructuring of the stomach. A 500 kg bovine has a rumen containing 70 L of liquid. The feed consisted classically of grass, hay, and straw, but is today supplemented. In the traditional regime, the dry material is roughly half hemicellulose and half cellulose, 3% are lignins and <1% protein and lipids. The rumen receives in addition to the fodder daily about 60 L of saliva, which is buffered with bicarbonate. The turnover time differs for liquids and solids, but does not exceed 55 h for solids. This is sufficiently long

for bacteria to proceed with cellulose degradation. Populations whose generation times are longer than the turnover time would simply be washed out of the system without leading to fermentation products. The rumen is the fermentation chamber of the cow. It contains a large number of microbes, both in absolute numbers (10^{10} – 10^{11} bacteria, 10^4 – 10^6 ciliates, 10^2 – 10^4 fungi per gram) and in species composition. More than 200 prokaryotic species were identified, the population is diverse (remarkably, no single species makes more than 3% of the total community), but stable. There are cellulose-, hemicellulose-, starch-, and lactate-degrading bacteria, succinate-decarboxylating bacteria, and methanogenic archaea. Pyruvate produced in the Embden-Meyerhof pathway is then transformed into succinate (via net fixation of CO_2 by PEP carboxykinase), which is then decarboxylated to propionate. Decarboxylation of pyruvate leads also to acetate and in a side reaction to butyrate. These volatile fatty acids are partly taken up by the rumen mucosa and their absorption is finished in the omasum part of the stomach. The cow thus feeds on these fatty acids and not really on plant polysaccharides. The amount of fatty acids absorbed are substantial: These are daily about 3.7 kg acetate, 1.1 kg propionate, and 0.7 kg butyrate. They enter the bloodstream and are further oxidized by the host; they cover about 40% of the energy needs of the cow.

The reticulum part of the stomach sieves out the fibrous part of the rumen outflow, which is then regurgitated into the mouth for renewed chewing. The liquid part of the rumen is pumped into the omasum. The liquid contains now many ciliates and bacteria from the rumen fermentation chamber. These fermenting microorganisms become themselves food when the liquid flows then into the abomasum, which corresponds physiologically to a true stomach. Pepsin and HCl are secreted and digest the microorganisms and protists providing a nitrogen source for the cow. Lysozyme is secreted by the abomasum to assist in the digestion of the bacterial biomass produced in the rumen. Actually, 400 g of bacterial and 300 g of protist cells are added daily to the bovine diet. This is important since the feed is low in nitrogen. However, there is a dilemma: The microbes need first a nitrogen source to grow in the rumen. The bovine invented an elegant nitrogen supply. Urea is synthesized in the liver of mammals during amino acid degradation. Urea is in most mammals excreted with the urine as a waste product. Not so in ruminants: The urea produced in the liver reenters the alimentary tract via the saliva (ureohepatic cycle). Urea is decomposed in the rumen into ammonium ions, the preferred nitrogen source of bacteria, and CO_2 .

Biotechnology Meets Complexity

In view of the economical importance of bovines as a source of milk, meat, and leather (wool in the case of sheep), substantial efforts were made to improve the fiber digestion in ruminants and thus animal productivity. This is a bold approach in view of the complexity of a symbiotic system linking the metabolism of a mammalian host and such a complex microbiota in the rumen. Genetically modified bacteria were developed under the assumption

that the rumen microbiota does not produce the correct mixture of enzymes to maximize plant cell-wall degradation. This approach met technical difficulties; *Ruminococcus* and *Fibrobacter*, the most fibrolytic rumen bacteria, could not be genetically transformed. The introduction of a xylanase into *Butyrovibrio fibrisolvens* improved fiber digestibility in vitro, but the recombinant strains could not compete with *Ruminococcus* and did not persist in the rumen beyond 15 days. Collectively, all these attempts of introducing “ameliorated” strains failed, the inoculated microorganism usually disappeared from the rumen. This observation is an important lesson for the genetic engineer: Microbes do not exist in ecosystems of their own, but reproduce and persist as members of complex microbial communities. These communities generally show complex networks of metabolic cooperation between different microbes that cannot yet be simulated in the laboratory. An example is the transfer of cellodextrins from cellulolytic bacteria to noncellulolytic carbohydrate fermenting bacteria, which in turn produce ammonia and branched-chain fatty acids, which are consumed by the cellulolytic bacteria. We have here a simple case of cross-feeding. The relationships between microbes in the rumen are in reality even more complicated. Many bacteria produce inhibitors of other bacteria, they kill by secreting bacteriocins; bacteriophages were isolated from the rumen and ciliates feed on bacteria.

Plant Defense Against Herbivory

Cattle

Terrestrial plants have a problem: They are rooted into the ground. If a herbivore approaches, they cannot run away. This immobility of plants is so deeply rooted in our consciousness that moving woods sent terror waves to Macbeth (or a more welcome horror to the spectator of the *Lord of the Rings* movie). Plants cannot mount a fancy defense posture, but this does not mean that plants are defenseless against herbivorous predators. Plants have evolved many means to make them a difficult food source. Some defense measures are easily seen, e.g., thorns and spines (Figure 5.71). You feel pity for the hungry mouths of those mammals, which take a bite from them. Other plants look quite palatable, but they are carefully avoided by grazing cattle. If you hike across mountain pastures in the Alps, you will not miss *Veratrum album*, a 1 m high Liliaceae. Cattle eat it only once and the experience of the vertigo caused by its poison will deter them to repeat this unpleasant food experience. But there are many plants that do not sport spines and are not poisonous. How do they defend themselves against the many herbivores?

Ants

Actually, vertebrate herbivores are not the greatest threat to plants. If you take the tropical rainforest as richest manifestation of terrestrial plant life on earth, its ecologically dominant animals are ants. In fact, ants constitute about 20–40%

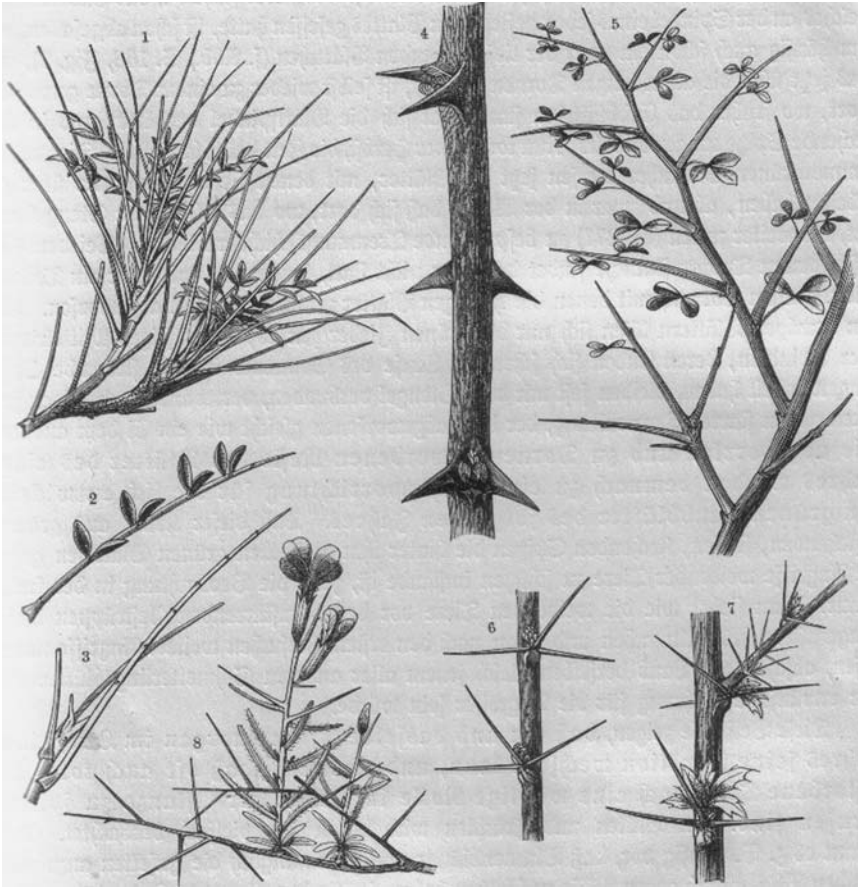


FIGURE 5.71. Plant weapons in defense mission are shown for the Fabaceae shrub *Astragalus tragacantha* (1–3) and the Fabaceae tree *Robinia pseudoacacia* (4). The figure displays also the defense structures against herbivores developed by *Cytisus spinosus* (5), *Berberis vulgaris* (6, 7) and *Vella spinosa* (8).

of the arthropod biomass in the rainforest canopies. This dominance of ants is for an ecologist surprising and is referred to in the literature as Tobin's paradox (Hunt 2003). The greatest animal biomass in a terrestrial ecosystem must be herbivores, situated at the second level of the trophic pyramid. The reason is based on sound principles of thermodynamics: Each transition from one to the next trophic level (primary producer–herbivore–carnivore) is paid by substantial reduction of cumulative biomass in the next higher trophic level because the rule of the thumb is that 10 g of food from the lower trophic level gives not more than 1 g of body mass in the next higher trophic level. However, ants do not feed (directly) on leaf tissue. The solution to this conundrum of the cryptic herbivores will be given in the next chapter.

Aphids

Plants are under assault by an armada of invertebrate herbivores. I will just mention three feeding guilds. There are the leaf-chewing insects like caterpillars and sap-sucking insects like aphids (Figure 5.72). Finally, there are nematodes and insects that attack from below the ground targeting the roots. The caterpillars, beetles, and locusts have a rather simple strategy: they have very efficient mouthpieces for chewing, they are very hungry and numerous, and at least at one stage in their life cycle airborne and thus very mobile. Potato beetles may defoliate an entire crop covering several acres within a day and locusts are known from Biblical times as a plague. Some pests actually grow with the victim: The European corn borer larvae attack the leaves of the young maize plants, while the mature animal becomes the dreaded stalk borer pest of adult maize.

In contrast, sap-sucking insects like aphids, leafhoppers, and thrips cause only minimal direct tissue damage because they have evolved a fine stylet with which they locate, penetrate, and drain sap from the phloem sieve cells of the plant's vascular system. This feeding stylet of aphids is such an efficient locator of the sieve elements that it represents still today the favorite needle of plant physiologists who want to sample the phloem fluid. For the plant this exploitation means a substantial loss of photosynthate, which is transported via the phloem from the sites of production to the sites of consumption. Heavy infestation can thus severely reduce the growth of the affected plant.

Nematodes

Nematodes are a major threat to plant roots. Also nematodes have evolved a sophisticated feeding stylet, which penetrates the cell wall of the root cell and contacts the plasma membrane of the cell without pushing through it. The nematode releases glandular secretions into the root cell, which increases their metabolic activity substantially. The cyst nematodes dissolve the plant cell walls and syncytial feeding structures consisting of up to 200 plant cells are formed. The root-knot nematodes induce aberrant series of mitosis without cell division resulting in giant cells. The nematode becomes sessile when it has found the feeding position and elaborates feeding tubes in the cytoplasm that connect to the end of the stylet. Strangely, the nematode builds a new feeding tube for each meal. The giant root cell becomes thus littered with hundreds of feeding tubes in its cytoplasm.

Fungi

All this sounds not very rosy. Not to mention that aphids are an excellent vector for the transmission of viral diseases. Also many fungi are lurking on or near the plant. The concept that fungi are saprophytes, meaning that they feed on dead organisms, can unfortunately not be generalized. Actually, fungi have a long history for predation of living photosynthetic cells. Fungal attack on the alga *Palaeonitella* was documented in a 400-million-year-old fossil (Taylor et al. 1992). That this fossil is a case for parasitism is revealed by distinct hypertrophism of internodal cells of the alga, which represents still today the host



FIGURE 5.72. Aphids in different developmental stages sucking on a stem of a plant are tended by ants interested in the honeydew excretion of the aphids. The ants will defend the aphids against the attack from *Aphidius* wasps.

response of two living species of the alga *Chara* to fungal attack. The host-parasite relationship between plants/algae and fungi has thus a very long evolutionary history (Figure 5.73). Interestingly, this fossil comes from the famous Rhynie Chert in Scotland, which yielded also the first undeniable higher land plants with *Rhynia* known to those visitors of natural history museums who also explore the botanical departments.

The Rules of the Game

Of course, plants are not passive spectators of these attacks—otherwise evolution would have wiped them out from the planet. Actually, a few plants living under nitrogen-poor conditions became active carnivores to cover their nutritional needs as predators of animals (Figures 5.74–5.76). However, here we want to explore diverse defence modes of plants. Research over the last years has provided us some fascinating insights into this silent war between herbivores and plants. In view of the immobile nature of plants, there is as expected a lot of chemical warfare. As is usual in the big game of evolution, all tricks are allowed and plants have mustered chemicals that range from fragrance to antinutrients, from pain killers to poisons. But beware, the same lack of rules apply for your enemy. The outcome is as usual an antagonistic coevolution. Those organisms that lost the race are only found in the annals of paleontology. There are many entries in this Book of Life and Death. Only a very small fraction of life forms that existed once on earth still have living descendents. Most organisms had their time and were then discarded because they turned out not to be sufficiently adaptable to changing environments or the pressure of competitors and predators. Evolutionary biologists adopted a nice image for this everlasting evolutionary fight—the Red Queen. This is not a peculiar tropical ant queen, but a figure from Lewis Carroll’s “Through the Looking Glass,” in which Alice and the Red Queen have to run faster and faster only to stay at the same place relative to one another.

Antinutrients

Let’s start with an antinutrient. The plant might not be able to stop the chewing of the insect, but leaves or roots frequently contain protease inhibitors. Soybean trypsin inhibitor is likewise known to biochemists and nutritionists. The evolutionary purpose is clear: These plant peptides inhibit serine, cysteine, and aspartyl proteinases in the insect gut and interfere negatively with the proteolysis of the ingested food. Less amino acid is released and the growth and sometimes even the life of the herbivore is at risk. How efficient this system is becomes apparent when you compare the hornworm *Manduca*, a major pest of crops, grown on the wild-type tomato plant or the mutant *defenseless*, which is defective in the synthesis of the proteinase inhibitor as part of the systemic wound response (Howe et al. 1996). Compared to its growth on the mutant plant, you get only hornworm dwarfs on the wild-type tomato.

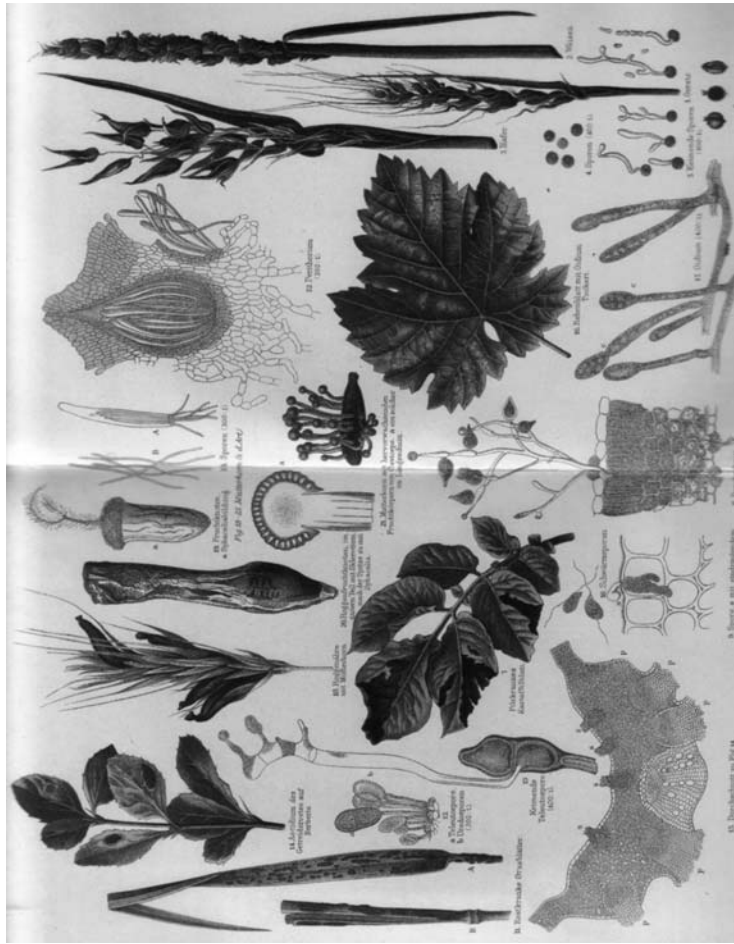


FIGURE 5.73. Fungal infections of cultivated plants: barley (1), wheat (2; the spores of various smuts are shown in 4–6), oat (3), rye (18; *Claviceps* fungus in different stages, 19–23, at the top is a perithecium, 22, the fruiting body of *Claviceps* that contains the ascospores), vine (16, and its fungus *Oidium*, 17) and potato (7, cut through the leaf, 8, and spores 9, 10). Rust is also found on grass (11, teleutospores of grass and cereal rust 12, 13) and shrubs like barberry (14; cut through the rust-infected barberry, 15).

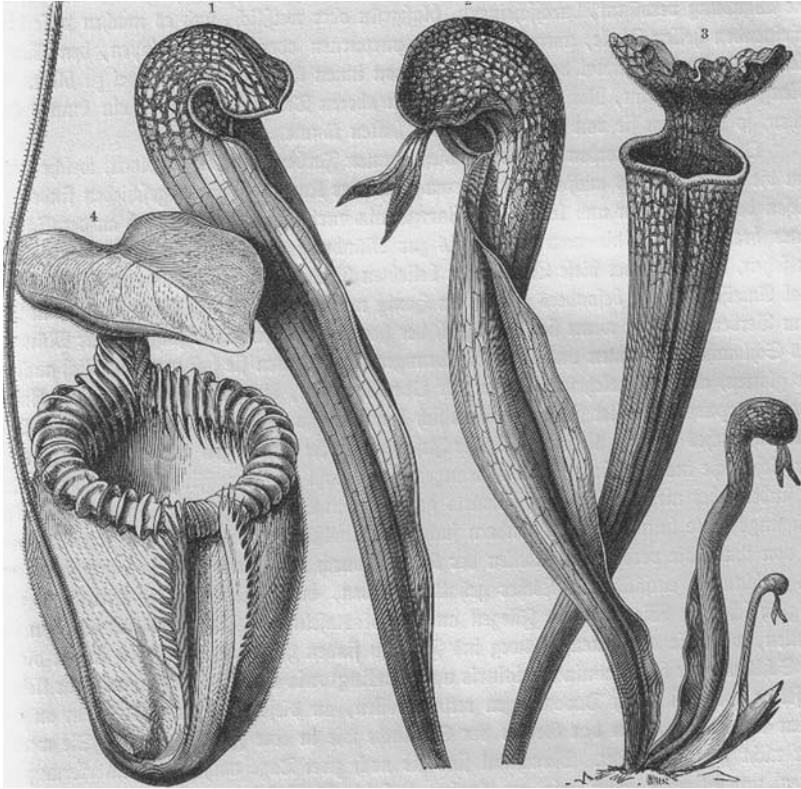


FIGURE 5.74. Plant weapons in attack mode I. The figure shows two species of Sarraceniales that trap insects in urn-like leaves containing a digestive fluid (1 *Sarracenia variolaris*, 3 *Sarracenia laciniata*). These plants are true honey traps, where nectaria guide the insects down a gliding slope. At the end of the season, an 8-cm-high layer of insects is found in the 30-cm urns. The fun of biology is that one fly carrying the telling name *Sarcophaga sarraceniae* has learned to survive in this trap and can thus make a living for their larvae on the carcasses of the entrapped insects. *Darlingtonia californica* (2), the cobra plant, follows the same strategy as does *Nepenthes villosa*. The latter has gone even a step farther by developing a very active digestion system at the bottom of the modified leaf: thousands of digestive glands per cm^2 secrete enzymes and acids. A structure analogous to an animal stomach has developed in plants. To make the analogy complete, teeth-like structures surround the entrance of the urn. The nitrogen-containing end products of digestion are absorbed by the plant through the walls of the pitcher.

Chemical Warfare

Plants produce a number of secondary metabolites that protect them against unfriendly takeover. Saponins like the steroidal glycoalkaloid avenacin belong to this class. As the name indicates, it is produced by oat plants (*Avena*), which become via this chemical defense very resistant against the fungal pathogen *Gaeumannomyces graminis*, which affects wheat and barley, but never oat.

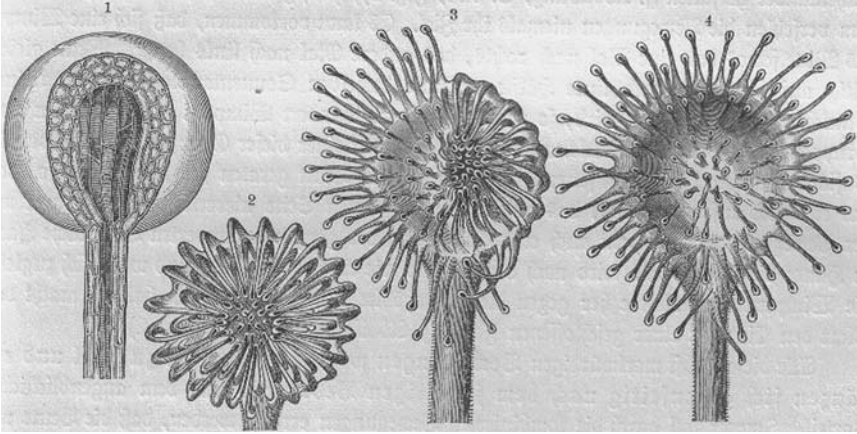


FIGURE 5.75. Plant weapons in attack mode II. The plant order Nepentales shows active insect predators. *Drosera* has numerous stalked glands (1) that secrete a clear sticky fluid. Many tentacles sit on the leaves of this plant (4), which progressively bend around an insect that landed on its leaves. The folding occurs on a time scale of minutes to hours (2, 3).

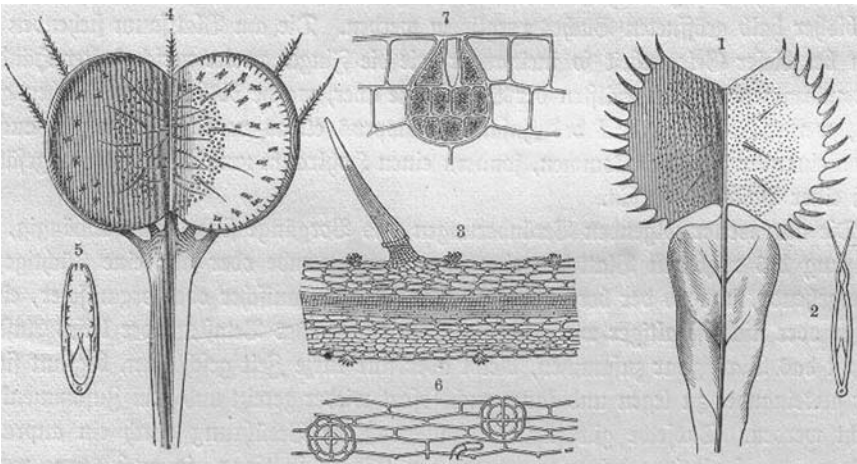


FIGURE 5.76. Plant weapons in attack mode III. Even quicker is *Dionaea*, another member of the Nepentales order, commonly known as Venus fly trap, which works like a mouse trap. The plant is shown open in 1 depicting the spine-like teeth at the margin of the leaf and sensitive hairs in the trap (enlarged 3). When an insect touches these hairs the trap snaps (2 shows a cut through the closed trap). *Aldrovandia* (4, 5) is another genus of this plant order that preys on insects. Inserts 6 and 7 show gland cells. The closing of the trap is a very fast process and was recently reinvestigated with contemporary methodology (Forterre 2005).

This barrier is overcome by a fungal variety, which elaborates the detoxifying enzyme avenacinase. This enzyme removes the terminal glucose molecule from the saponin making it nontoxic. A number of other plants produce glucosinolates, sulfur-containing glucosides, that are as such nontoxic. They become biologically active only in response to tissue damage by the chewing insect. The enzyme myrosinase is released from its compartment and removes the glucose, which renders the compound unstable, leading to the release of toxic nitriles and thiocyanates. Cyanogenic glucosides are derived from tyrosine and can release hydrogen cyanide when the cell is disrupted. Again some insects, e.g., the butterfly *Heliconius*, can strike back and evolved enzymes that can deal with cyanogenic glucosides. The butterfly replaces the nitrile group by a thiol and preempts thus the release of cyanide and at the same time recovers a valuable nitrogen into the insect's own metabolism (Engler et al. 2000). The deterrent effect is better when it meets an unprepared herbivore like the flea beetle *Phylotreta*. As a specialist crucifer-feeder, it has never met cyanogenic glucosides since they are not produced by crucifers. Researchers have now transferred the biosynthetic pathway of one of these compounds, dhurrin, from its native host *Sorghum* to the model plant and crucifer *Arabidopsis*. The plant accepted this diversion of tyrosine into this new pathway and deterred the flea beetle larvae, only few animals started a leaf mine and many of them died. This type of research opens new possibilities for pest control in crop plants (Tattersall et al. 2001).

Salicylate and Jasmonate

Now to the pain killer salicylate, which is a member of the signal transduction pathway leading to resistance in plants. Systematic acquired resistance allows the plant to mount a robust, active, and broad spectrum defense throughout its whole body in response to a highly localized attack by a microbial pathogen. Necrosis induced by viral, fungal, or bacterial attack increases locally the concentration of salicylate. This leads to the activation of an as yet undefined phloem-mobile signal, which increases in distal parts of the plant the salicylate concentration and also that of volatile methyl-salicylate, which can signal to more distant sites. Other forms of attack induce different signals. For example, chewing insects and mechanical wounds induce the synthesis of jasmonate, a derivative of the membrane lipid linolenic acid. Its synthesis is mediated by a series of enzymes that are activated by the tissue damage. Jasmonate belongs to another signal cascade in which a gas (ethylene), a small peptide, proteolytically derived from prosystemin, electrical signals, and a volatile methyl jasmonate are involved. The salicylate and jasmonate pathways activate different sets of plant defense genes, but there is substantial communication between both pathways. Amplification of the signals leads to the synthesis of toxic compounds (allelochemicals). On the other hand, herbivores increased their production of enzymes that detoxify these allelochemicals, their counterdefense system includes cytochrome P450, a microsomal enzyme system that we use for the transformation of pharmaceutical drugs.

The Reaction of the Insect Herbivore

For the herbivore there is a dangerous window between the encounter of the toxin and the induction of the detoxifying enzymes. The corn earworm *Helicoverpa zea* has found a solution. It intercepts the plant signal molecules jasmonate and salicylate. Both induce in the midgut and the fat body of the chewing insect the synthesis of cytochrome P450. When the plant lashes allelochemicals at the insect, its detoxifying system is already in place. Its ability to eavesdrop on plant defense signals protects the herbivore (Li et al. 2002). Not enough with that, *Helicoverpa's* saliva contains glucose oxidase as its principal enzyme, which counteracts the production of the toxic nicotine induced in tobacco plants by caterpillar feeding (Musser et al. 2002). The importance of jasmonate signaling was demonstrated by an antimessenger RNA approach to silence lipoxygenase, the first enzyme on the pathway to jasmonate. The hornworm *Manduca* gained weight faster on the silenced plant than on the wild type. The herbivore resistance could be restored by treating the silenced plant with jasmonate. Also the leafhopper *Empoasca* preferred the silenced plant over the wild type and caused much greater damage (Kessler et al. 2004). Jasmonate is not the only product of the linolenic acid oxidation pathway. Also volatile aldehydes are produced that play a major role in forming the aroma of many fruits and flowers. In fact, methyl jasmonate is known to the perfume industry as fragrant components of the essential oils of jasmine. Hydroperoxide lyase is such an enzyme leading to fragrant aldehydes with antimicrobial properties. Silencing of this enzyme in transgenic potato plants led to a twofold fecundity increase in sap-sucking aphids (Vancanneyt et al. 2001).

It is astonishing to realize that plant compounds which inspire poets to love songs like the fragrant of flowers should have so mundane biological functions as wound healing and herbivore defense. In the following chapter, we will realize that poets are not the only beings on earth that are attracted by volatiles from plants, poets share this property with such uninspiring animals as parasitoid wasps and entomophagic nematodes. However, the story is worth telling since it shows how ingenious plants can be in their defense against herbivores. Since plants cannot flee, they use volatile chemicals to cry for help. And they are heard or, better, sniffed.

The Enemy of My Enemy is My Friend

Parasitoids

Before discussing the role of plant volatiles in herbivore defense, we must first get acquainted with a group of insects that are liked by ecologists despite their rather rude life style. Parasitoids are insects, usually flies or wasps, whose immature stages feed on their hosts' bodies, usually other insects, and ultimately kill the host. The basis of their peculiar feeding mode is the egg-laying behavior of the adult female. They lay their eggs into other insects (Figure 5.77). The larval parasitoids develop inside the host individual, which is usually also a



FIGURE 5.77. An *Aphidius* wasp, a parasitoid wasp named after its victim, the aphid. The wasp belongs to the Hymenoptera, the aphid to the Homoptera order of insects. Aphids are plant sap-sucking insects that cause substantial damage to plants, not the least as transmitter of viral diseases.

preadult organism. Initially, the parasitoid does not cause much harm to its host. But then it starts to eat the host from the inside and normally kills it when the host goes into the pupal stage. What looks like a normal host pupa gives birth to a parasitoid instead of the host. You have certainly already seen these wasps with their egg-laying apparatus looking like a super-long sting (Figure 5.78, compare with another food prey specialization in Figure 5.79). You might find that this is a rather crude way of quest for food, but you might not expect them to represent about 10% of all species on earth. However, this figure should not surprise you since it reflects the great number of insect species, most of them are attacked by a parasitoid.

Finding the Victim

Now comes a problem: The parasitoid wasp does not eat the host, it uses it just as a cradle for its eggs. It needs to search its victims and foster mothers just for egg laying and this might not be an easy task with cryptic and evasive hosts. The problem is compounded by the selectivity of parasitoids for their host. Consumers are classified by ecologists as either monophagous (feeding on a single prey), oligophagous (having few preys) or polyphagous (having many prey types); the former are also called specialists while the latter is a generalist. While true predators generally have relatively broad diets, parasitoids are generally specialized, frequently even monophagous. How do they solve the problem of finding the appropriate host? The wasp uses chemical cues to locate the victims. It rubs the feces of the victim with its antennae for several minutes as if it has to memorize the odor and the animal shows subsequently host-seeking flight responses to these chemical attractants in a wind channel. Behavioral studies showed that the parasitoid wasp *Microplitis* uses two types of learned information for seeking the host. One is a nonvolatile contact chemical from the host and the other is a volatile chemical. Since researchers could teach the wasps to recognize vanilla odor, scientists suspected already nearly 20 years ago that the volatiles might be plant derived (de Moraes et al. 1998). This preference for perfumes should not surprise since adult parasitic wasps need nectar or some

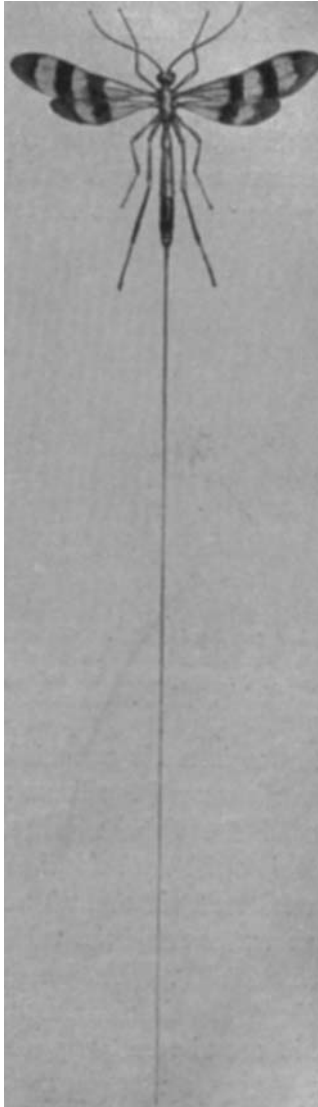


FIGURE 5.78. A parasitoid wasp (*Rhammura filicauda*) from Africa sporting an extremely long ovipositor. Parasitoids deposit their eggs into other animals in which the young develop by eating up the host from the inside. This is a widely distributed group of animals, which has split into many species due to host-specialization. As parasitoids can also attack other parasitoids, Russian doll parasitism is known in this group.

other fragrant food source. Entomologists trained parasitoids to associate odors with food sources when feeding them on sucrose solutions and offering simultaneously vanilla or chocolate smell. If taste and smell sensation were temporally separated, no training effect was achieved. Females could also learn to associate

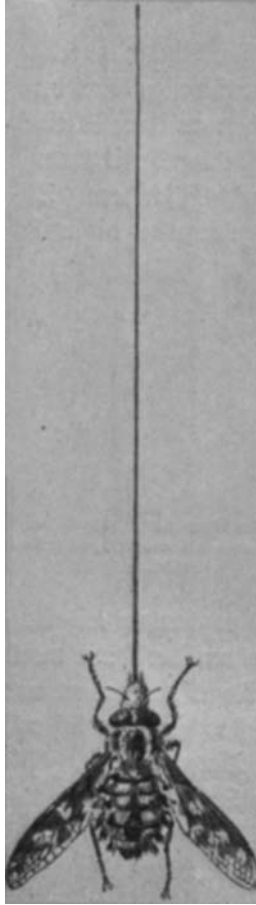


FIGURE 5.79. The evolutionary flexibility of the insect body plan is demonstrated with *Megistorrhynchus longirostris*, order Nemestrinae, from South Africa, showing an extraordinary long mouth part. Nemestrinae are relatives of Tabanidae, which are fierceful bloodsuckers. Tabanidae that attack animals with a thick skin develop large mouthparts, but the shown species uses its mouth part for nectar foraging. An even more exciting case is the hawkmoth (*Xanthopan morgani*) with a 22-cm long proboscis pollinating the orchid *Angraecum sesquipedale* with an extremely deep nectarium. Charles Darwin and Alfred Russel Wallace predicted the insect knowing only the plant 40 years before the insect was actually discovered.

their hosts for egg-laying with odors. They were also able to learn both odor associations, e.g., vanilla-to-hosts and chocolate-to-food. Interestingly, hungry females followed the odor they associated with food, while well-fed females followed the odor they learned together with the host (Lewis and Tumlinson 1988). When they are foraging for food or seeking a host, female parasitoids constantly monitor their environment with their olfactory system.

Terpenoids

The following data were published by scientists from the US Department of Agriculture and one could therefore suspect that they had a hindsight with their research (Turlings et al. 1990). They let larvae from the beet armyworm *Spodoptera exigua* chew on maize seedlings in a glass gas collector. The insect-infested, but not mechanically injured plants released a set of volatiles, mostly terpenoids. Terpenoids is a historical name derived from the German word for turpentine and refers to a vast class of chemicals that are formally (but not biochemically) derived from the condensation of isoprene (unsaturated isopentane) subunits. Chromatographic analysis revealed 11 terpenoids, with bergamotene as the most prominent compound. These volatiles attracted the parasitoid *Cotesia* in two-choice flight tunnel tests. Also synthetic terpenoids attracted the wasps. Interestingly, mechanically injured leaves on which the oral secretions of the beet armyworm were applied also became a source of volatiles that showed a comparable terpenoid composition and behavioral attraction for its specific parasitoid wasp.

Volicitins

The US entomologists then took a deeper look into the oral secretions of the caterpillar and identified a low molecular weight compound as the sole active principle and named it volicitin (i.e., volatile inciting). This new name hides a well-known class of compounds; volicitin is a linolenic acid product that is coupled to glutamine. In plants, the synthesis and release of volatiles seem to be under the control of jasmonic acid, which is also produced from linolenic acid via the octadecanoid signaling pathway. Volicitin could thus be a chance inducer of the plant defense system. But why should the caterpillar synthesize a compound that elicits plant chemicals directed against itself? It is most probable that volicitins are emulsifying agents necessary for membrane disruption—they resemble amphipathic detergents. Or does the plant here intercept a compound of the insect as an advance warning system? Volicitin activity is not diet related and also produced by caterpillars reared on an artificial diet, speaking in favor of an intrinsic insect function for this compound. Lewis and Tumlinson from USDA continued with their research and explored the next aspect of this fascinating system now consisting of three trophic levels: the plant, the herbivore, and the parasitoid. Sensing terpenoids is not enough for a busy parasitoid, to be an efficient olfactory signal the volatiles should contain chemical information on the attacking herbivore that can be read by the parasitoid.

Chemical Attraction

To test this possibility, they tested the volatiles released by tobacco, cotton, and maize in response to two closely related herbivores, *Heliothis virescens* (tobacco budworm) and *Helicoverpa zea* (maize earworm). In field trials, the

tobacco budworm-specific parasitoid wasp *Cardiochiles nigriceps* distinguished the odor emanating from the tobacco plants infested by its host (De Moraes et al. 1998). The nonhost-induced volatiles were hardly more attractive to the wasp than undamaged control plants. The budworm-infested plants remained attractive even when the leaves plus the budworms were removed—the signal comes from the plant and not the victim for oviposition. The wasp could also distinguish its victim when it infested cotton. This is a remarkable result: It means that the wasp can distinguish between host and nonhost infestations on phylogenetically distant plants that produce varying chemical blends. As a host-specific parasitoid, it locates its polyphageous host over a range of different habitats. In the past, insect physiologists have anticipated behavioral responses to be relatively hard-wired. The parasitoids convinced them that learning and context-dependent analysis of chemical cues confer substantial behavioral plasticity to wasps.

The next question is whether this seemingly efficient chemical attraction of wasps via the jasmonate pathway results also in an increased parasitism of the herbivore. This question is not trivial since the caterpillar comes under double attack. The jasmonate response attracts the wasp to its victim, but it induces also allelochemicals in the plant that reduce the growth of the herbivore, which could negatively affect the reproduction success of the wasp. The net result of both processes was a twofold increase in parasite level in the herbivores (Thaler 1999). The volatiles released by the plant did not only reduce the growth rate and attracted parasitoids, it also attracted general predators that emptied the eggs and discouraged the oviposition rate of the herbivore. As a consequence, a tobacco plant confronted with three different leaf-feeding herbivores could reduce the number of herbivores by more than 90% when releasing volatiles (Kessler and Baldwin 2001). Elicitors of plant resistance may thus become useful in agriculture.

Rootworm Generalization

It is always important in biology to ask whether the reported observation represents an interesting case that adds just a new thread to the huge carpet of natural phenomena or a new general principle. Recent data obtained in maize confirm that we deal here with a new principle. The scene is now below the ground and this is now an interesting case of how far volatiles can carry a message within the soil as compared to the air. The herbivore is in this case Western corn rootworm *Diabrotica virgifera*, a voracious coleopteran pest that threatens maize production in central Europe. The beetle larvae feed on the roots of maize and a Swiss–German group of scientists asked the question whether the attacked plant releases a signal molecule that can attract a predator of the beetle larvae. The answer to their question came from experiments with a six-armed olfactometer (essentially a star-type arrangement of pots with plants connected via tubing to a central pot, all filled with soil) that allowed the researchers to give an organism that feeds on rootworms the choice between healthy and rootworm-infected maize plants. In addition, field trials were conducted (Rasmann et al. 2005). The plants released a compound that they identified as

caryophyllene, this compound traveled rapidly through the sand and qualifies as an exceptionally suitable below ground signal. In addition, caryophyllene- either produced naturally or added to mechanically injured roots- attracted a predator of the rootworm, the entomopathogenic nematode *Heterorhabditis megidis*. The predators rushed to their prey at a velocity of 250 body lengths per day. Plants that released the below ground volatile showed 43% infected larvae compared to only 8% for a commercial US maize variety that did not produce caryophyllene. The commercial maize variety had apparently lost this signal chemical during the breeding program since the ancestor of modern maize, teosinte, still produced caryophyllene.

Herbivores: Patterns of Predation

Carnivores as Protectors Against Mammalian Grazers

Plants have developed a number of strategies to discourage mammalian herbivores. However, the best protectors of plants are probably still carnivorous mammals (Figures 5.80, 5.81). A 40-year study of mammalian herbivores in the Serengeti provided important insights into these predator-prey relationships, which poise the exploitation of the grassland by herbivores (Sinclair et al. 2003).

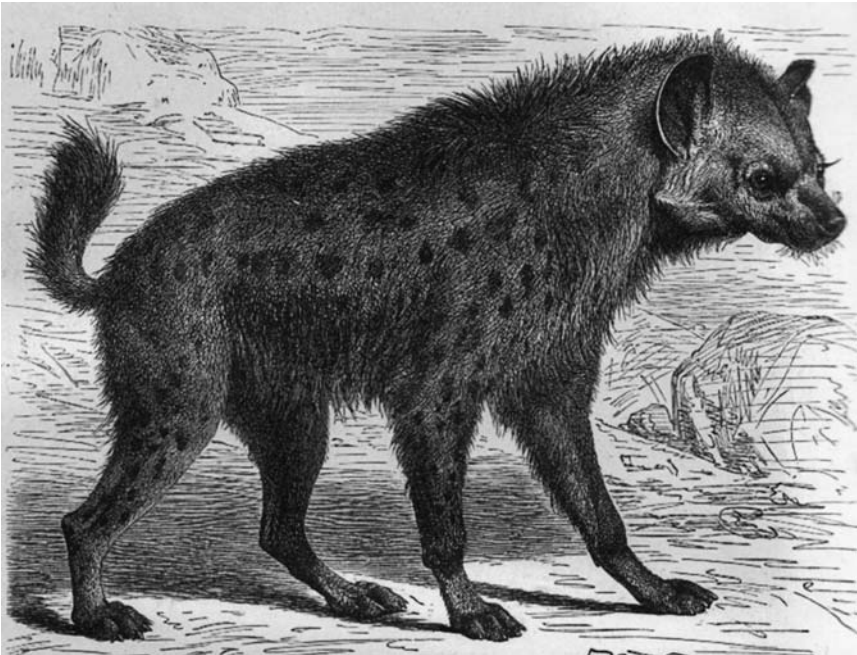


FIGURE 5.80. The spotted hyena (*Crocuta crocuta*) is a dog-like carnivore that depends for its food on the rest of the meals from more powerful carnivores; it also takes carrion and small animals.



FIGURE 5.81. Tapirs (*Tapirus*) are represented with four species of the family Tapiridae, order Perissodactyla. They live in the tropical forests in Malaysia and the New World. They eat plants, mainly leaves of trees, but they like also fallen fruits, especially the *Spondias* plum. They also eat soil to satisfy their salt needs. Their main enemies are the tiger in Asia, and the jaguar in America (*Leo onca*), the largest New World member of the cat family (Felidae). The jaguar is a solitary predator that preys on deer, tapirs, and capybaras.

This ecological study is a fascinating number game. The Serengeti is composed of open grassland and savannah. This ecosystem supports 28 species of ungulates and 10 species of carnivores that prey on the herbivores. Each predator specializes on a different prey: The lion preferentially attacks the large prey like wildebeest (*Connochaetes taurinus*) (Figure 5.82) and the zebra in the 170–250 kg weight range, which corresponds to its own weight of 150 kg. Lion can attack larger prey, but buffalo and giraffe comprise only 10% of its diet. However, still 40% of the lion's prey is lighter than 50 kg. The diet niche of the smaller carnivores (hyena, wild dog: upper limit 250 kg, leopard, cheetah: upper limit 100 kg) is nested within the prey range of the larger carnivores. The consequence is that if you are getting smaller as a prey, you have increasingly more enemies. Small prey like the Thomson's gazelle is confronted with an uncomfortable predator: prey ratio of 1:3. Small wonder that all recorded causes of death in this herbivore weight range is by predation. This rate falls with the weight of the herbivore: It is only 23 and 5% for buffalo and giraffe, respectively. The giant herbivores like the elephant (Figure 5.83), hippopotamus, and rhinoceros almost never suffer predation. Their mortality is mainly caused by food limitation. The threshold from a top-down control (predation) to a bottom-up (food) control is at 150 kg herbivore size. In the undisturbed situation, the Serengeti carries 1.1 predators per square kilometer (lions contribute 0.2 and hyenas 0.5 to this figure). The density of the Thomson gazelle is three animals per square



FIGURE 5.82. The wildebeest (*Connochaetes taurinus*), family Bovidae, order Artiodactyla, is a large mammalian grazer. Its impact on plants is kept in check by carnivores.



FIGURE 5.83. The African elephant (*Loxodonta africana*) is one of the two surviving species of the family Elephantidae, order Proboscidea. An adult African elephant weighs up to 7,500 kg and eats 300 kg of solid food per day. The food consists of grass, branches, and the fruits of various palm trees. The animal is too great for predation by any carnivore and its mortality is therefore only determined by shortage of food and water.

kilometer. In a natural experiment, the majority of the large predators was removed in part of the Serengeti. All herbivores below 60 kg weight were thus relieved from predation pressure. As expected, an increase in prey density was observed; the Thomson gazelle, for example, rose to 18 animals per square kilometer. When the predators immigrated from neighboring areas into the void niche the prey density quickly returned to the initial levels. Large herbivores like the giraffe were not predation limited; in fact, their density fell in the predator-free areas.