6
Eating Cultures

Choosing Food

To Eat or Not to Eat

We are omnivores. As the name indicates, we eat various foodstuffs. Other animals have opted for more restricted diets. Carnivores eat only meat in the large sense; herbivores eat plant material; detrivores eat decomposing organic material; many other "-vores" exist. Within each category, there are still substantial differences. Some animals are not very selective in a given food category, whereas others are specialized—in extreme cases, to a single food item. This has the advantage that you can optimize your search strategy and physiology to a single food item. This can of course sometimes be a risky decision when your food item gets under pressure. The panda and the koala are doomed should something happen to the bamboo or the eucalyptus tree, respectively. In contrast, if you were an anteater, one would guess that you are on the safer side in view of the fact how many ants populate the world. Living from a single organism has further inherent risks. Much prey does not like the idea to be eaten and plants frequently deploy chemical weapons to discourage herbivores. You might then be well advised to vary your food: By mixing different toxins, you can push each below a critical level. Other questions emerge: Does the target organism really offer all ingredients you need? Take a grazing cattle. The body composition of the cow differs substantially from that of grass. Will grass satisfy all nutrient requirements of a mammal? We have seen in the previous chapter that ruminants in a certain respect do not eat grass. For ecologists and ethologists, the "who eats whom?" is a central question, and many theoretical thinking went into this field. The optimal foraging theory, the marginal value theorem, the scalar expectancy theory, and Charnov's optimal diet model are important theoretical concepts in the field. Some achieve even mathematical descriptions of predator–prey relationships. Instead of presenting you equations, I will illustrate you general problems with examples. They are easier to grasp, hopefully entertaining, and they suffice to define the problem.

The Moose and Its Sodium Problem

My first example is the moose (*Alces alces*) (Figure 6.1), a herbivore of the northern hemisphere. G. E. Belovsky has developed some instructive concepts for the moose feeding on the shores of the Lake Superior (quoted from C. Barnard Animal Behaviour, Pearson 2004). Plants and animals have distinct physiologies. *It was said that our blood, which bathes all our body cells, still reflects in a certain respect the salty environment of the ocean*. We need salts like NaCl to maintain the ion concentration gradients across membranes that contribute to the electrical potential necessary for nerve and muscle activities. *Plants do not have nerves and muscles, and consequently, they do not really care about* Na^+ *ions*. If you are eating plants (moose browse the leaves of deciduous trees), you get nutritious food, but the leaves will be deficient in sodium ions. So foraging exclusively on leaves will not be an option for the moose, and if only for its sodium needs, the moose has to vary its food intake. If you have observed moose in nature, you will remember them standing in water. Moose crop aquatic plants in shallow lakes. The reason is simple: Aquatic plants are richer in sodium than terrestrial plants. With this strategy, the sodium problem has been settled, but not all problems have been solved. Aquatic plants contain less food energy than terrestrial plants. So you might propose that moose will have to eat more aquatic plants to get both energy and salt. But there is another constraint: the rumen capacity.

FIGURE 6.1. The moose (*Alces alces*) is the largest member of the deer family (Cervidae, order Artiodactyla).

Economical Decisions in Biology

Stated simply: Any animal has the gut it needs. It makes no sense to invest in a gut that is oversized for your needs. This would only be a waste of resources. As a first approximation, you can start with the idea that all organs are maintained to their needs. When the need does not persist any longer, the body economizes immediately on these investments. A classical example is domesticated animals. Under such conditions, the rancher puts them in an enclosure and mounts the guard against predators. Sharp senses then become a luxury function, and consequently the senses come quickly down in domesticated animals, when compared with their wild cousins. To address the problem with the moose, G. E. Belovsky developed an optimization approach known as linear programming. A rumen that provides the daily energy needs based on leave food is too small and the animal would quickly become deficient in salt. A rumen that satisfies the caloric need on the basis of aquatic plants would be too large and thus a waste of bodily infrastructure. The researcher plotted a type of phase diagram for the moose diet with intake of aquatic versus intake of terrestrial plants in gram. The food composition must be above the minimal energy level and above the minimal sodium level needed by the animal, and, at the same time, it must lie below the rumen capacity. The three lines intersect and form a triangle. All values on the surface area of the triangle fulfill all constraints and are thus possible solutions. When G. E. Belovsky looked what the moose actually took, he realized that they pushed for the maximal terrestrial plant intake that still satisfied the sodium needs. In other words, moose selected their diet to maximize the energy intake within the limits of the given rumen capacity.

Extension of the Issue

What are you doing if you are a mountain goat? Its plant diet is also deficient in sodium, but since goats frequently live in quite dry environments, aquatic plants are no realistic solution. Goats discovered that licking certain stones can help them to satisfy their sodium needs. Not only goats lick stones to meet their mineral requirements, children do it, too. The following story is a famous case in pediatrics. In the nineteenth century, poor British children did not receive enough milk to meet their calcium demands for bone growth. Since the mineral part of bones is calcium apatite, quite substantial amounts of dietary calcium are needed during the growth phase. In rural Britain, the classical wall painting of farm houses was made with chalk—children, without following any chemistry course, knew about that link and met their calcium needs by licking the walls. When the early wall paints were introduced which contained lead, severe intoxications came to the attention of a physician who linked it to the licking behavior. It is quite fascinating that the body can express its needs and direct its action in form of a complex behavior to satisfy its nutritional needs. This self-control does not work in all cases: I remember a medical case record from Zurich, in which a homeless person was hospitalized with strange symptoms until the

physicians recognized their first case of scurvy that they had seen in their life. The patient lived exclusively from two food items, canned beans and biscuits, neither contained vitamin C. Apparently, he did not develop a craving for fresh food.

Nutrient-Specific Foraging

Animals frequently know their food needs very well. Nutrient-specific foraging was even reported in invertebrate predators (Mayntz et al. 2005). This observation is somewhat surprising since it was believed that the body composition of prey animals is nutritionally balanced for carnivores. These biologists used three polyphagous animals for their investigations. The first was a *Carabidae*, a highly mobile beetle (Figure 6.2). To test whether this ground rover actively selects prey according to nutrient content, they tested the food intake on locust powder mixed with either lipid or protein. They observed that the beetles preferred lipid locust powder when they were pretreated on a protein diet and a protein locust powder when pretreated on a lipid diet. In addition, when coming from a protein-rich diet, they consumed more food than when coming from a lipid pretreatment. Then the zoologist reared *Drosophila* flies on different diets, and they were surprised that they could vary the protein-to-lipid ratio in the animals over a relatively wide range, simply by offering a distinct diet. Researchers had anticipated that the body composition of the prey is relatively independent from diet. The next test animal was a wolf spider (Figure 6.3), a classical sit-and-wait predator. Again the predator tried to balance its food intake. When they came

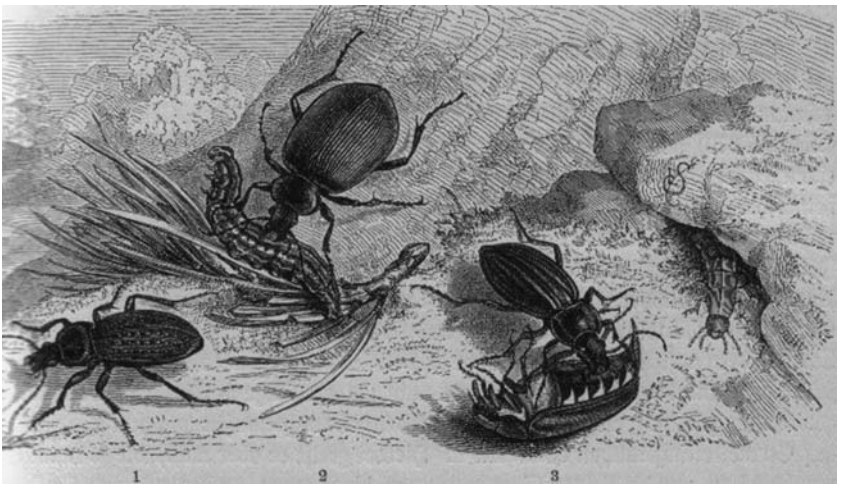


FIGURE 6.2. Carabidae or ground beetles are one of the largest families in the insect order Coleoptera. They are fierce predators that inactivate their animal prey by biting them with their strong mouth parts, then they spit a digestive juice on the prey, which rapidly liquefies the prey. The beetles then take up the predigested juice from the prey. The figure shows from *left to right Carabus hortensis*, *Calomosa sycophanta*, and *Carabus auratus* with its larva under the stone.

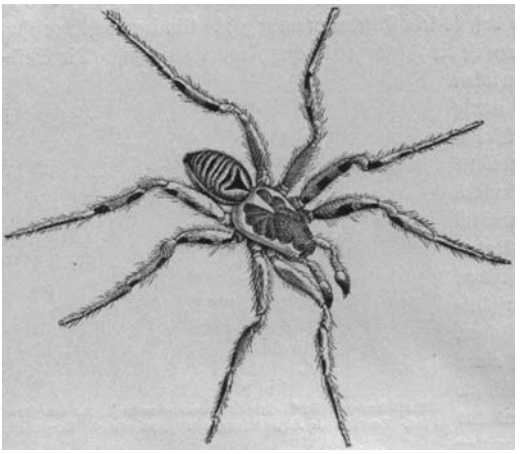


FIGURE 6.3. Wolf spider, here the tarantula of southern Europe (*Lycosa tarentula*), family Lycosidae, order Araneida. In the fourteenth century, the bite of the tarantula was linked to a dancing mania (Chorea saltatoria), which was a mere fright reaction from humans decimated by the Great Pestilence that swept across Europe in 1348 and not the effect from the poison of this spider.

from a diet on lipid-rich flies, they preferred protein-rich flies and vice versa. The next taster was a desert spider that builds durable webs. Prey items arrive spontaneously, and the spider cannot control the nutritional composition of the prey. However even these spiders control their diet composition by differential extraction of their prey. If the spiders came from a protein-poor diet, they left less nitrogen in the fly remnants after feeding than after coming from a protein-rich diet. These results now force theoretical ecologist to go back to model building and to incorporate the new observations into optimal foraging models that account not only for prey quantity but also for prey composition.

Leaves Chosen by Your Mother

In some animals, food selection is already made by the mother. Take the moth *Manduca sexta*. It lays its eggs mostly on solanaceous plants (potato, tomato). This is not an absolute rule; occasionally it lays eggs also on nonsolanaceous plants. The preference for the former plant as food source is clear: Larvae (also called tobacco hornworm) reared on solanaceous plants grow and develop much quicker on them than on alternative food sources. The larval stage is a critical step where the moth is exposed to more predators, pathogens, and parasitoids than the adult stage. So you best pass quickly through these stages. How does nature achieve fidelity of the larvae to the better food without compromising the capacity to exploit alternative food sources, if necessary? The larvae molt through different instar stages, and the researchers took fourth instar larvae reared on solanaceous foliage and put them on a solanaceous or a nonsolanaceous (cowpea) diet (del Campo et al. 2001). In the first case, all

larvae started feeding on their known food, while only 22% of the solanaceous-reared larvae started feeding on the unusual food. In fact, 35% of the larvae on the new food source preferred to starve to death, which is a remarkable observation since the hornworm can complete their development on many nonhost plants. In contrast, hornworms reared on nonsolanaceous foliage did not care whether feeding continued on this food source or changed to a solanaceous food.

The Material Basis of the Decision

A small trick led to the identification of the mechanisms underlying this food choice process. The researchers soaked cowpea leave discs with an extract of potato leaves, and solanaceous-reared larvae preferred the treated leaves over the control leaves by an overwhelming vote of 96 to 4%. This biological test guided them through the purification procedures. The feeding stimulant was indioside D—a steroid substituted with a few sugar moieties. After the chemical analysis, they did the next step and explored the neurophysiological basis of the food recognition. The mouthpart of the larvae consists of a maxillary palp and a mandibule as mechanical feeding instruments. They are surrounded on the top by antennae and at the bottom by a structure, which looks like a tiny electrical plug, the sensilla styloconica. *There is no need to be afraid of these names: zoologists have to invent a word to name the observed structures for which no words exist in our everyday language. Scientific committees encourage Greco-Latin artificial words, which sound terribly scientific while in fact you could have also called it the "sensitive electric plug."* When the scientists made electrical recordings from these plugs/styloconia, the lateral sticks of this structure responded specifically to the application of the chemical cue indioside D (*here you have the same naming problem for something which has no name in our languages*), but only in the solanaceous-reared animals. Microsurgery closed the chain of arguments: When the sensilla sticks were cut on both sides of the mouth, the solanaceous-reared animals lost their preference and started readily on the cowpea diet. In this way, Nature accomplishes that the specialist herbivore keeps to its host plant. Nature must follow a different strategy when dealing with a generalist herbivore like the locust. Its taste receptors responses to amino acids, salts, and sugars which are found in many plants and not to a specific compound found only in a single plant family.

Koala Versus *Eucalyptus*: Choices for the Food Specialist

Even food specialists show preferences and clear-cut food choices. Take the case of the koala (*Phascolarctos cinereus*; Figure 6.4), which feeds exclusively on *Eucalyptus* (Figure 6.5) trees belonging to three species (Moore and Foley 2005). *Eucalyptus* trees differ in a number of characteristics. These trees vary in size—koalas prefer larger trees simply because they represent larger food patches. However, this comes at a price. Plants elaborate secondary metabolites to deter specifically herbivores. *Eucalyptus* trees do that via the synthesis of

FIGURE 6.4. The koala (*Phascolarctos cinereus*), the arboreal teddy bear of Australia, was attributed to the family Phalangeridae from the order Marsupialia.

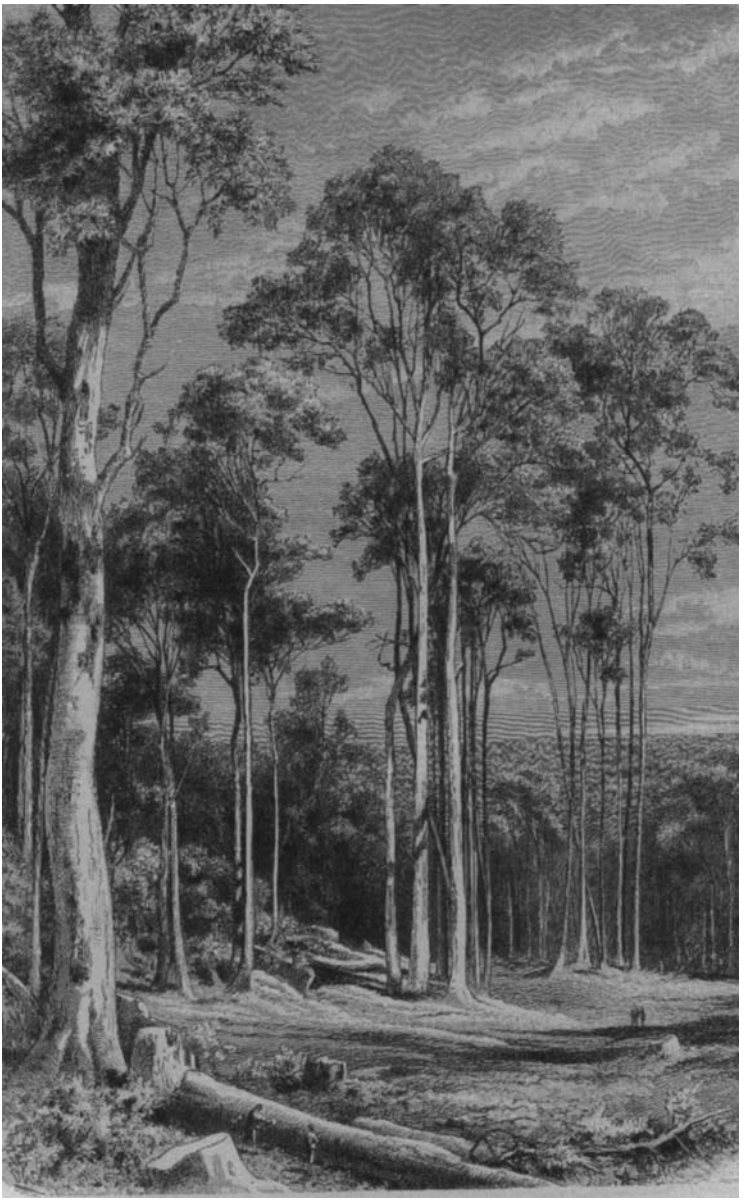


FIGURE 6.5. The eucalyptus tree, which belongs to the order Myrtales (which includes the most important genera of tropical mangrove), family Myrtaceae, is here represented by its largest member *Eucalyptus regnans*. This tree is native to Australia and reaches more than 100 m of height and is thus the largest tree of the world. It reaches a height set by the physical limit of water transport in trees (Koch et al. 2004).

formylated phloroglucinol. Koalas, as specialized *Eucalyptus* "folio-vores," are adapted to these compounds and are tolerant to it as no other animal. And this is necessary because the larger trees are also producing higher concentration of this compound. However, the detoxification of these compounds also costs energy to the koala. It is thus only consequent that within a given size class, koalas visit trees with lower toxin concentrations. Avoiding intoxication is only one side, assuring a balanced nutritious diet is another side of their food choices, which the koalas have to take into consideration. *Eucalyptus* is extremely low in nitrogen content, but when the researchers conducted extensive leave chemistry, differences in nitrogen concentrations emerged. The strategy of the koalas is clear: Trees with high toxin concentrations are avoided, trees with medium toxin concentration were overvisited because they offered satisfying nitrogen sources, while trees producing low toxin and also low nitrogen concentrations were again avoided. Thus even in an extreme food specialist, food habitat differentiation occurs and sets in motion an arms race between defense reactions of the trees (by overexploitation koalas can cause *Eucalyptus* tree mortality) and counterdefenses by the specialist herbivore.

Food Choices at the Ecosystem Level

Choosing food is not only important for the nutritional decisions of individuals or a species, it also affects the structure of the entire ecosystems. If large numbers of species share the same ecological niche, it is commonly assumed that the coexistence of so many species is the consequence of finely divided food resources. This reasoning was applied to very different ecological niches ranging from coexisting insectivorous bats, herbivorous insects, and bacterial commensals in the human gut. Yet, biologists arrived to different conclusions when looking to herbivorous insects, coexisting in a tropical forest of New Guinea (Novotny et al. 2002). When they analyzed the data for 900 herbivorous insects on 50 plant species, they found that most insect species feed on several closely related plant species. They investigated two plant genera in detail: *Ficus* and *Psychotria*. Any two species in these genera shared 50% of their herbivorous species. This overlap in herbivore community decreased gradually with increasing phylogenetic distance between the plant hosts. Large and species-rich plant genera hosted more distinct leaf-chewing communities than small genera. This reflects simply the preference of the herbivores for a larger food resource basis. Monophagous insects, i.e., animals feeding on a single plant species, were rare in the tropical forest. On the average, a single host plant species was the food resource for 30 species of Coleoptera (beetles), 26 species of Lepidoptera (butterflies, moths), and 20 species of Orthoptera (locusts, crickets, grasshoppers). These observations are at variance with the notion that extremely specialized food interactions between herbivores and plants finely divide the plant food resource and permit the coexistence of numerous herbivorous species. Actually these ecological considerations had also an impact on other branches of zoology: It also decreased the estimate of arthropod diversity from 30 million to "only" five million species.

The Star-Nosed Mole has Studied the Optimal Foraging Theory

In the 1970s, a lot of ecological thinking dealt with the concepts as to how a predator makes its food choices. It was anticipated that such an important part of the life history of animals would be under natural selection and the animal's foraging activity should therefore maximize the rate of energy intake. Some of the work sounds rather theoretical, and there are many mathematical treatments of the problems. Yet, for the animal, optimal foraging is a crucial question of survival. If the animal spends too much time with prey of too low nutritious value, it will have a suboptimal food intake. You might say that it will have to spend more time on foraging to satisfy its caloric needs. However, many animals spend essentially the whole day with foraging—prolonging the search is not an option, they will starve. Even for an animal that is not searching food the whole day, the consequence of suboptimal foraging is hard; it will simply have less time for finding a mate, caring for its young, or defending its territory.

In Charnov's classical model, the rate of energy intake R can be described by a simple equation: $R = E/(T_s + T_h)$. In this equation, E stands for the energy content of a prey item, T_s is the time spent for searching the prey item, and T_h is the time needed to handle the food item. Well, if the mole *Condylura cristata* has understood the equation, it has several options. Simple arithmetic tells it that R is high if E is high. So, its first instinct will tell it to go for an earthworm instead of a cricket, not to speak of a small invertebrate—these yield 1100, 840, or only 10 kJ, respectively, as caloric value. However the mole has done its arithmetic course in the severe school of natural selection (Catania and Remple 2005). It learned there not to neglect the denominator. Keeping T_s or T_h or better both low will also boost R. T_s is influenced by choosing the right habitat—the right one is the richest with respect to the prey. As animals can move around, they have some freedom of choice. Very interesting observations were made with birds as to how they decide when the current feeding plot is still profitable and when they have to leave the plot. This is not a major problem for the mole: Its wetland habitat contains high densities of invertebrate prey. T_s can thus be kept low. Now, it must look for keeping T_h low. Going straight for the nutritious earthworm might not be the best choice if this prey necessitates a relatively long handling time. Less nutritious prey can be more profitable because it is the ratio E/T_h that matters. In addition, is the large prey sufficiently abundant to keep T_s low? Does the mole meet every 10 s an earthworm? You might argue that the mole takes what it gets: the earthworm and the small invertebrate. However, keeping T_s and T_h low means that you need a specialized sensorium and dentition to detect and eat the prey efficiently. Thus you have to make your choices. Selection worked on star-nosed mole (Figure 6.6) and made its choice: It goes for small prey. Its dentition is tweezers-like, which are optimized for precisely grasping small preys. They are greatly reduced when compared to the dentition in the eastern mole (*Scalopus aquaticus*). As its name indicates, the star-nosed mole has a bizarre nose—many times greater than the nose of the other moles and consequently more densely populated with sensory cells. The nose is specialized into a low-resolution periphery and a high-resolution

FIGURE 6.6. With the star-nosed mole (*Condylura cristata*), family Talpidae, order Insectivora, we explore the predictions of the optimal foraging theory. This North American mole frequently leaves its burrow and even swims.

central region. The optimization of the search and eating program is such that the zoologists needed a high-speed video system to film the foraging of this mole. The sequences are really quick: a 50 ms move forward followed by a 25 ms touch time. If no prey was detected, the next cycle of move and touch follows and so on. If a prey is detected, a decision must be made: to eat or not to eat. If the mole decides "no," it continues with the move–touch cycles; if it decided "yes," it will handle the food. For this handling, the mole takes mere 230 ms to achieve the capture and eating task. These extremely fast T times allow, under experimental conditions, the processing of 10 small food items in about 3 s. The energy intake or profitability reaches 40 kJ/s and is thus at the theoretical limit of the process. The system works really at the borderline of physiological capacities: Mammals need 12 ms to process tactile information in the somatosensory cortex and 5 ms for activating the appropriate muscle cells with a motor command. The 25 ms touch time does not leave much room for central processing and reflection on a decision. One could also formulate that the mole is "blind" because it could not be such an efficient forager with distance detection (sight, sound, or smell). A positive feedback from a tactile detection system means that the mole can directly open its mouth to catch the prey. Visual information processing is slow in comparison—human eye movement takes 200 ms and then you still have to reach the perceived prey.

To Lure with Food

If animals are under the dictate of optimal foraging, other organisms can exploit these constraints for their own purpose. I will illustrate this with an example from central Europe. When walking along riverbanks one can see there a nice, colorful plant that was not there twenty years ago. As one could suspect, it is one of the many examples of successful species invasion. The plant in question is *Impatiens glandulifera*. It is native to the Himalayas; it was introduced in Europe hundred years ago and started to spread from Czechoslovakia and has now reached the

riverbanks of Austria and Germany. The native plants—like *Stachys*, *Lytrium*, and *Epilobium*, all nice and sizable flowers—are getting under pressure from this aggressive invader. Normally, invaders compete for food, water, light, and space. The Asian beauty has chosen a more insidious, but efficient strategy: It lures pollinators with food. In fact, the nectar sugar concentration of about 50% is quite normal when compared to the nectar from plants visited by bumblebees. The trick is, it produces more nectar (Chittka and Schurkens 2001). As science is about figures, the numbers are revealing: *I. glandulifera* secretes 0.5 mg nectar per flower and hour, while the other riverbank beauties achieve only 0.01–0.04 mg. Bumblebees had also "learned" their Charnov equation and realized that by visiting the Asian invader, they can reduce T_s—they get the same amount of nectar with fewer visits. Less time is spent in flying from one flower to the next, and since insect flight is a costly business, these economies count. The invader also invested strongly in advertisement using different senses. For the eyes, the flowers are big and intensively colored; for the nose, the Indian flower is strongly scented. The honey trap is prepared for the pollinator. The result was foreseeable: *I. glandulifera* experiences 2.5 visits per flower per 10-min observation period, which is four times higher than visits on *Stachys*—the highest nectar producer from the native flora. This is the investment part for the invader: To get into the new floral market, it paid a higher price. However, the reward was directly proportional to the investment. In mixed plots with *Impatiens*, the number of visits to the *Stachys* competitor was reduced by 50% and their seed set was reduced by 25%. Small wonder that the percentage of *I. glandulifera* along the riverbanks had increased over the last years. We should not blame this flower for exploiting Charnov's equation: Luring with food is a common strategy in animals. Male birds frequently present an attractive food item (or material for nest building) to the female partner in courtship. Have you ever thought about the evolutionary sense of your action when offering a flower bouquet to a lady?

Food Avoidance

There is some food that you better avoid to eat because it can make you sick. Some people experienced that food-associated illness left a lifelong aversion toward food items that were consumed just before the onset of the sickness. This phenomenon was now investigated in detail in a much simpler system—the nematode *Caenorhabditis elegans*. What to eat and what not is an important decision for *C. elegans*: In its natural habitat—the soil—this worm lives on bacteria. The soil is a complex microbial environment; the nematode will meet there more or less nutritious bacteria and also pathogenic bacteria. The pathogenic soil bacteria *Pseudomonas aeruginosa* and *Serratia marcescens* can multiply in the intestine of the nematode, and this can lead to the death of the animal after a few days. *C. elegans* protects itself from this danger by two strategies: innate immunity and food avoidance by aversive olfactory learning. Thereby they learn to associate a particular smell of the pathogenic bacterium with the visceral malaise and to avoid a second exposure. Since this nematode has a simple nervous system consisting of just 302 neurons, the identification of

molecules, cells, and neuronal circuits associated with this behavior is greatly facilitated. As a first step, the researchers developed a behavioral test (Zhang et al. 2005). When they offered a choice of two bacteria, a nutritious *E. coli* and a pathogenic bacterium, to nematodes grown up on *E. coli*, the animals showed no particular avoidance to the pathogen; they were naïve. However, when they were already trained on plates containing a food and a pathogenic bacterium, the animals avoided the pathogen on the test plate. This observation speaks for associative learning, but it does not tell you whether they develop a positive association with the harmless or a negative association with the pathogenic bacterium. An olfactory maze assay, offering a more extended bacterial food choice, demonstrated both attractive and aversive components in the learning. They could dissociate both components, since a short time exposure of 4 h to the pathogen was sufficient to induce the aversive behavior, while this short experience could not induce attractive associations. Yet, the behavioral test does not lead to the molecular basis of this learning process. The researchers looked therefore into the literature and tentatively targeted serotonin as candidate signal molecule. Why serotonin? Neuroscientists knew that mood, food, and serotonin are connected. Food, especially carbohydrates like chocolates, was known to lift the mood in periods of stress—for example, in students preparing for examinations. Measurement of serotonin in the hypothalamus showed that serotonin levels rise in the anticipation of food and spike during a meal. Drugs that elevate serotonin levels in the brain are powerful appetite suppressants and were used to treat human obesity. Therefore, it was logical to look also into serotonin as a first guess for associative learning of food avoidance with *C. elegans*. Serotonin is synthesized in the body from the amino acid tryptophan via a sequential hydroxylation and decarboxylation reaction. The *C. elegans* genome contains a single tryptophan hydroxylase homologue, and a knockout mutant was very instructive (Sze et al. 2000). The mutant animals showed no serotonin accumulation but were viable. When presented with food, the wild type but not the mutant increased the pharyngeal pumping activity. The serotonin mutant had also effects on the metabolism-regulating neurosecretory axis. The mutant accumulated more fat and 15% of the mutants entered a nonfeeding, nonreproducing "dauer" (German for "enduring") state. Like cookies in children, the bacterial food upregulates the production, release, and response to serotonin in *C. elegans*. Serotonin signaling has been implicated in the control of mammalian feeding, metabolism, and body temperature regulation by the hypothalamus. The unifying feature of many of the serotonin responses in *C. elegans* is the coupling of food sensation to various motor and endocrine reactions. Food is a major reward in animal life, and we should thus not be surprised to see serotonin also linked to associative learning in lowly invertebrates.

The tryptophan hydroxylase mutant tph-1 in *C. elegans* was not impaired in general olfactory ability or the recognition of bacteria, but it was selectively unable to associate the physiological response to pathogenic bacteria ingestion with olfactory cues (Zhang et al. 2005). As so much is known about this simple invertebrate, the researchers could implicate a simple neuronal circuit with the

associative learning. In response to bacterial infection, serotonin is produced in one specific neuron called ADF. Another neuron receives information about bacterial food from a sensory neuron and integrates at the same time the serotonin signal from ADF via a serotonin-gated ion channel leading to aversive learning. As no serotonin is emitted by the ADF neuron in the mutant animal, it has lost its capacity to avoid poisonous food.

Food Separating Species

Speciation Concepts

The rapidity of an event in biology is not an argument against gradual evolution in the context of the evolution theory. Evolutionary biologists count with the possibility of speciation occurring under our eyes at least when applying time spans used in human history. This "creation" of species under our eyes could be food for thought for creationists. Biologists have explanations for these events. It would be interesting to hear about alternative explanations from a creationist framework of thought. In science, the value of a hypothesis is commonly judged from the predictions you can make about the natural phenomenon under investigation that can be tested by observation or experimentation. As this book is about food and eating, I will illustrate the problem of speciation from the perspective of food choices by animals.

The crucial event for the origin of a new species is reproductive isolation. Reproductive isolation can be of two types. Two species are called prezygotic when they differ by courtship or mate choice or different breeding seasons. The species are called postzygotic when they interbreed but yield offspring of low viability or fertility. A commonly hypothesized situation for speciation is a new species evolving from its ancestor in geographical isolation. This process is called allopatric speciation, and the cause for isolation can be manifold (mountain range, river, disease outbreak, migration that separates an initially contiguous species). Almost all biologists accept that allopatric speciation occurs. However, the discussion between biologists starts when it concerns sympatric speciation, meaning when a new species evolves within the geographical range of its ancestor. Ernst Mayr, the great twentieth-century evolutionary biologist, who searched an extension of Charles Darwin's ideas into the biological discoveries of the twentieth century, contested in his 1942 classic *Systematics and the Origin of Species* (1999 reprint by Harvard University Press) that sympatric speciation can occur. By casting doubts, he did something very valuable in science: He stimulated others to look for evidence.

The Food Choice Shift from *Rhagoletis pomonella*

The 2004 edition of a brilliant textbook (Mark Ridley, *Evolution*, Blackwell 2004) quotes an example that comes close to sympatric speciation without fulfilling all tenets. The actor of this drama is *Rhagoletis pomonella*, a tephritid fly and pest of apples (Figure 6.7). The insect lays its eggs into apples, the maggot grows in the apple causing economical damage. As apples are under close

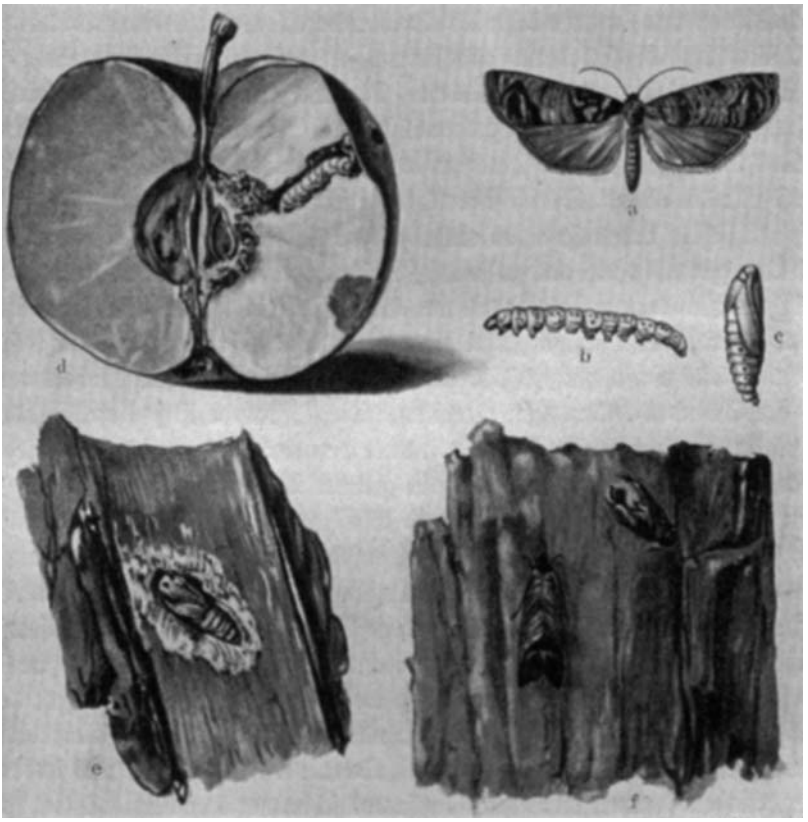


FIGURE 6.7. The codling moth belongs to the family Tortricidae, order Lepidoptera and is a major fruit pest in North America. The figure shows (a, f) the adult moth, (b) the caterpillar, (c) the pupa, (d) shows a caterpillar burrowing into the apple and (e) shows the caterpillar, after devouring the apple, emerging from the apple and pupating under a bark.

scrutiny in orchards, one can trace the first report on apple infestation with this fly to 1864 in North America. Before that date, the preferred host for oviposition was the hawthorn. In the meanwhile, this fly has included still further fruit plants (cherry, pears) as targets and did what biologists call a host shift. Females prefer to lay eggs into the fruits they grew up, and males tend to wait for mating on the fruit they grew up—the consequence is what biologists call assortative mating. *R. pomonella* from apple and hawthorn have, after about 140 generations, developed into two races that differ, for example, in their development time. Maggots in apple develop in 40 days, those in hawthorn in 60 days, and this in turn leads to a reproductive isolation because the adults are then sexually not active at the same time. However, when you put the two races together in the lab, they mate together indiscriminately, and they yield fertile offspring. In the biological species definition, no speciation has yet occurred. However, M. Ridley quoted convincing circumstantial evidence for sympatric speciation in phytophageous insects. There

are about 750 fig wasp species, and each breeds on its own fig species. A similar case could be made with leaf miners—a parasitic gall wasp, whose larvae feed on plant tissue, lead to exotic transformation of plants (Figure 6.8).

The European Corn Borer

Ostrinia nubilalis feeds on about 200 weeds. When maize was introduced into Europe about 500 years ago, the insect included maize into its food plants. In France, two races of corn borers can be distinguished that differ in food plant utilization. The first is the "hop-mugwort E race" and the second is the "maize Z race." The races display host plant fidelity for oviposition, but mating does not occur primarily on the host plant. How do they distinguish each other? There are apparently E race- and Z race-specific sex pheromone blends that could lead to assortative mating. The researchers used a nice trick to explore the genetic differentiation of the two races. As mugwort (*Artemisia vulgaris*) is a C3 plant and maize a C4 plant, the two plants handle CO_2 differently and can thus be distinguished by stable ^{13}C carbon isotope analysis (Malausa et al. 2005). The animal tissue closely mirrors the isotope distribution of its food plant. The researchers caught 400 moths from 5 sites within 4-km distance and found, both with respect to wing and spermatophor analysis, a bimodal carbon isotope distribution without overlap. All but one E race females had mated with E males, and all but one Z race females had mated with Z males. Genetic analysis differentiated Z and E animals into two clearly distinct groups. Gene flow between these two races was thus reduced to $<1\%$ in the absence of spatial and temporal isolation (the flight periods overlap). Food choice preferences might be a major force here for the genesis of races, which get close to a sympatric speciation event.

Cichlid Fish in a Crater Lake

The case for sympatric speciation is coming close to proof with a recent work analyzing cichlid fish (Figure 6.9) in a small (<5 km), but deep (200 m) Crater Lake from Nicaragua (Barluenga et al. 2006). It is a homogeneous place containing an impoverished fauna due to its geographical isolation and recent origin ($<23{,}000$ years). Allopatric speciation is thus very unlikely. Yet, the lake contains two closely related cichlids, *Amphilophus citrinellus* and *A. zaliosus*. With respect to mitochondrial DNA sequences, they differ clearly from cichlids of the next lakes. The molecular data suggest that *A. zaliosus* has evolved from *A. citrinellus*. Despite that close similarity, the two species differ visibly even for nonzoologists. The two species mate assortatively. Stable heterospecific pairs can still form, but they do not lead to successful matings. This observation suggests prezygotic isolation by differences in courtship behavior. One might stop here and suspect sympatric speciation through sexual selection. This has actually been proposed to explain the outstanding species richness of cichlids in the East African Great Lakes, which contain more than 1,500 endemic species. In fact, the strong differences in body coloration could independently suggest sexual preferences as the underlying mechanism. However, the zoologists

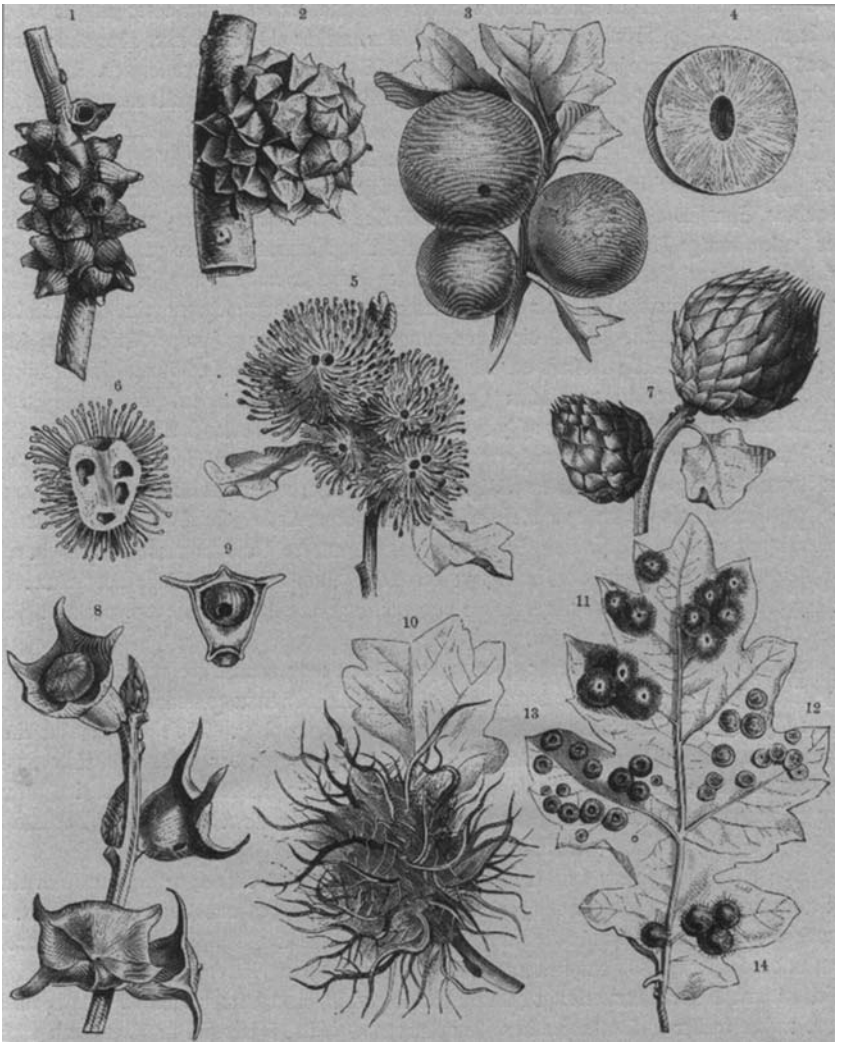


FIGURE 6.8. Gall wasps are insects from the family Cypnidae, order Hymenoptera. The female lays an egg through the long ovipositor into plant tissue, where a substance from the insect causes an abnormal outgrowth of the plant. The gall grows with the larva, which feeds on the plant tissue. The larva pupates within the gall. Oak is the host for many different gall wasp species giving rise to many diverse forms of galls as depicted in this figure. Interesting life stories can be told about some galls, e.g., the gall from *Amphilothrix sieboldi* (*top left*) produces a sweet secretion, which attracts ants that defend the gall against predators.

from a lacustrine University in Germany dived deeper into the Crater Lake and looked whether disruptive natural selection could explain the evolution of alternative habitat preferences in the cichlids of this small lake. They found that *A. citrinellus*, the form with a greater body height and the broader pharyngeal

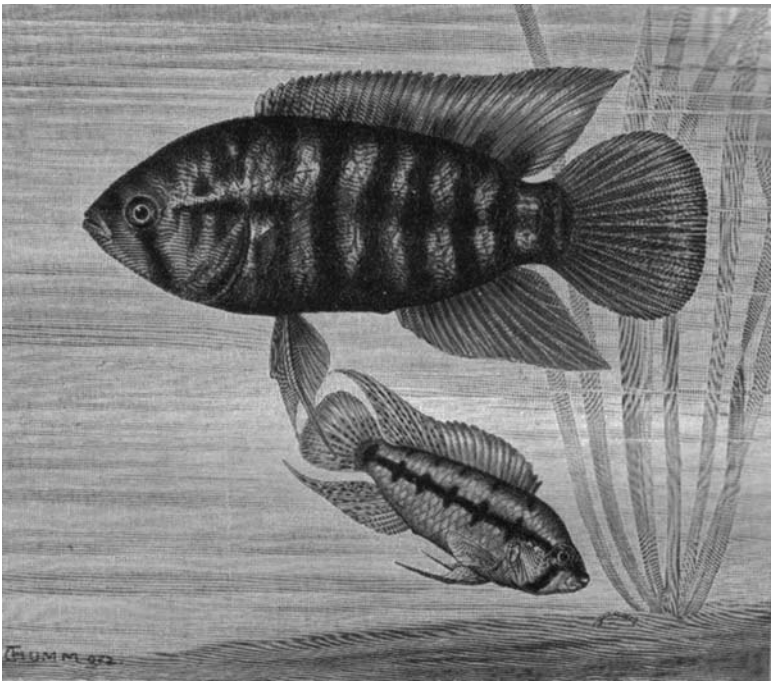


FIGURE 6.9. Cichlids are a species-rich fish family from the order Perciformes (here represented by the American *Cichlasoma facetum* at the *top* and *Heterogramma pleurotaenia* at the *bottom*). They are discussed as an example where food choice differences led to speciation.

jaw differed in habitat preference from the more slender *A. zaliosus*. The former is a benthic (bottom) forager, while the latter is living in the open water column (limnetic). Stomach content analysis indicated significant dietary differences. *A. citrinellus* feeds in decreasing order on the alga *Chara*, biofilm, insects, and other fish. *A. zaliosus* has a more restricted diet and biofilm dominated in its stomach content. These researchers suggested that sexual selection alone is unlikely to explain the speciation in cichlids from the African lakes if unaided by differentiation of the food space.

Behavior

Sharing Food and Other Goods: On Cheating and Altruism

Great Expectations with Capuchins

Biologists like to play with animals. Sometimes they find even an employer that pays them to play with animals and occasionally this playing provides deep

insights into the human nature. Take the following scene where food choice becomes context dependent in a way that tells us that the "sense of fairness" is not an exclusively human trait. The plot is the following: The biologist gives capuchin monkeys (*Cebus apella*; Figure 6.10) token, which they exchange against food (in this example, a cucumber; Brosnan and de Waal 2003). They play the game. Then they introduced a second monkey, which also gets a cucumber against a token. No problem, both monkeys play the game. Then the second monkey gets for its token a grape, a higher appreciated food, or even worse they receive a grape without being obliged to return a token. The reaction of the first monkey can be violent: It might not only refuse to play the game, but it will throw the token or the cucumber out of the test chamber. Apparently, food takes another role—social context, fairness, and pride are now at stake. The animal refuses a food item, it would always have accepted when trading alone. However, now the human player has violated the fair trade social contract. Nonhumane primates apparently have a precise idea how food resources should

FIGURE 6.10. Capuchin monkeys, family Cebidae, are an example for the sense of justice in food sharing and for tooth wear of fruit-eating monkeys.

be divided in a social context. Interestingly, there was a strong gender difference: While female monkeys showed the described behavior, male capuchins were indifferent toward the interventions of the biologist, possibly suggesting an effect of hormones on the perception of social fairness.

To test the sense of fairness in capuchins, scientists constructed a special table, where food items could only be reached when both monkeys cooperated—they did this in 89% of the cases (de Waal and Berger 2000). In the next series of experiments, the effort of both animals was needed but only one animal was rewarded by food. The cooperation rate fell—as one could expect—to 39%. However, capuchins shared food spontaneously by dropping crumbs while the cooperating partner reached for the food. Significantly more pieces of food were shared after successful cooperation trials and helper capuchines pulled two to three times more often in cooperation trials if the preceding trial had been successful.

Deception with Chimps

In the view of biologists, humans are an unusually prosocial species—humans accept costs when helping congeners in one-way situations without expecting a direct reward. One might therefore expect a gradual increase in cooperative behavior and the concern for the welfare of others when moving from *C. apella* to higher nonhuman primates. For example, chimpanzees show cooperative hunting, food sharing, and coalitionary aggression (Figure 6.11). What about their sense of fairness when sharing food? To test that trait, anthropologists set out a simple but revealing test system (Silk et al. 2005). Chimps were trained to handle an apparatus to get a desired food item, and they were rarely making mistakes. When their own food was on stake, they chose the correct handle in 92% of the trials. To make the device instructive for the researcher, the apparatus had two options. The chimp could get the food only for itself or it could manipulate the system such that an unrelated, but long year cage mate would also get food. Importantly, the food came to the observing chimp without incurring an extra cost to the manipulating animal. The response was clear: In about half of the cases, the acting chimpanzee chose the food-sharing option, and the figure was exactly the same whether a second animal was present or not. To be sure, the outcome could have been worse. The acting chimpanzee could have followed an antisocial preference by avoiding food sharing in the presence of a second chimp. This was not the case. However, the chimpanzees were clearly indifferent to the welfare of the unrelated group member. The scientists assured that the first animal could see and hear the second, and the second understood the consequence of the action from the first animal as it displayed begging gestures. The sense of fairness has thus not evolved gradually in primates but is a derived property of the human species and might be linked to cultural learning and the evolution of moral thinking and the feeling of justice.

How strong this latter feeling is in humans was shown by Swiss researchers interested in the motivation of humans in economical interactions.

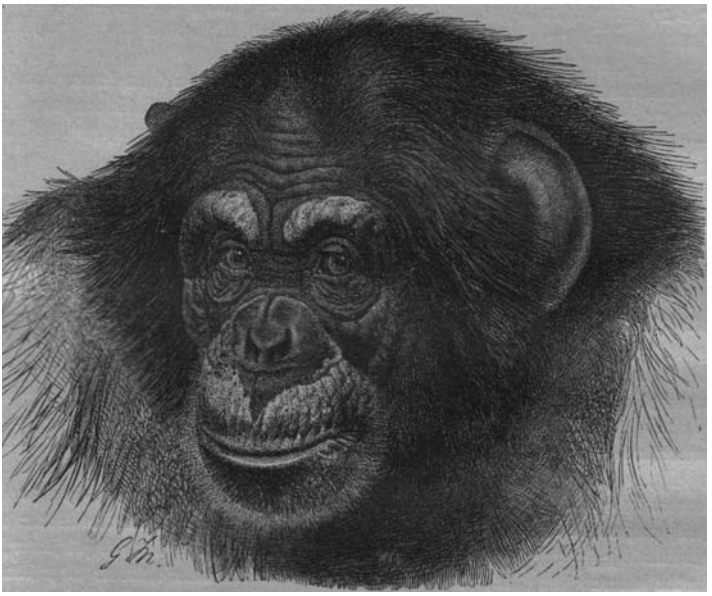


FIGURE 6.11. A juvenile chimpanzee (*Pan troglodytes*), man's closest relative, is explored for its tool use and culture development. The evolution of social behavior and food sharing is discussed with experiments conducted with chimpanzees.

Before switching to this interesting, although for biologists somewhat unconventional, reasoning, I should mention that German anthropologists detected a spontaneous inclination for altruistic helping in as young as 18-month-old children (Warneken and Tomasello 2006). The children helped adults unable to conduct a given action (e.g., open a door of a cabinet when the adult's hand were full). Notably, the children did help without hesitation—they reacted with an average latency of 5 s, needed no verbal request for help, eye contact, reward, or praise. These researchers from Leipzig were not convinced that altruism is a new evolutionary invention in humans. They argued that selfish reactions were provoked in the above-mentioned animal experiments because they involved food. Under natural conditions, chimpanzees have to compete over food, and the drive to acquire food for themselves might preclude their capacity to act on behalf of others. Therefore, they studied the reactions of young chimps in the same tasks as the infants. Notably, all chimps helped reliably in the tasks involving reaching. The animals needed a verbal encouragement to help and kept the object longer than infants before handing it over. In other tests, the chimps did not help, but the researchers noted that these were more demanding tasks. They concluded that children and chimpanzees are both willing to help but differ in their ability to interpret the other's need for help. The same group of Max Planck researchers conducted another revealing experiment with chimpanzees allowing insights into the evolution of cooperative behavior (Melis et al. 2006). In fact, according to their tests, their capacity for cooperation evolved already in the ancestor of

chimpanzees and humans. I will skip the technically amusing details of this test. Briefly, a chimpanzee can try to solve a food-rewarded task either alone or in collaboration. Not surprisingly, they invited a collaborator significantly more often when they realized that the food-reaching task needed two actors compared to a situation where they could get the food in solo action. The fascinating story unfolds with the choice of the collaborator. When confronted with two potential collaborators for a task necessitating cooperation, the test animal chose a partner apparently on a random basis. However, chimpanzees differ in dexterity and insight into a given situation. There are good and poor collaborators. In cooperation with a poor collaborator, no food could be gained. The animals recalled this difference very well. In a repeat session, they regularly recruited the better collaborator. As this means better nutrition for both, the researchers argued for a strong selective pressure for good collaboration in animals that address food-seeking problems in teams. Actually, the strong human trend for collaboration between nonkin individuals might find here an evolutionary explanation.

Homo reciprocans

Sharing food became an issue for us because humans evolved in social groups. When man was hunting big game in the ice ages, the evolution of human cooperation was accelerated. Hunting animals as large as mammoth was a daring exercise and could only be achieved as teamwork. When the hunt was successful, a lot of meat was there to share. *Historians, biologists, social scientists, and economists have their own approaches how this sharing was settled. As a biologist, I reviewed mostly biological research literature, which treat humans somewhat as a naked ape, a usual professional deformation of biologists. Worse, I transferred conclusions from the biological context into the human society. To reverse this trend, I will now deliberately report on approaches from Swiss economists that have a bearing on the biological and philosophical "know yourself."* Their reasoning starts with the big game argument. Every member of the group benefits from the hunted meat and should participate at the hunt. Well, not all were physically fit to do so, restricting the hunting group to strong adult males. However, some were perhaps not inclined to do so. Hunting is dangerous, so isn't it more practical to keep a rear position during the hunt and fight for a front position during the sharing ceremony? What led people to participate in dangerous exercises? Biologists proposed the kin selection hypothesis where cooperation is the result of interactions between closely related individuals—the arguments of the selfish gene weighs less under this condition. Others pointed to reciprocity, a long-term tit-for-tat as the basis for this cooperation. Humans are like many animals very interested in a social position; part of the costly cooperation might derive from a social interest in reputation. You might also argue that unwritten laws developed quite early that punished free riders in such hunting operations. However, if you stay in a biological framework, punishment is costly for the punisher, an individual must identify the free rider and punish him running a personal risk in this conflict. The punishment hypothesis will only work when there are enough humans that are willing to do this as an altruistic punishment.

E. Fehr from an economy research group in Zurich and colleagues set out to look whether this behavior exists in human populations (Fehr and Gachter 2002). By lack of mammoths, he sent his Swiss students out to hunt for mammon. The details of their thoughtful money game do not interest here. In short, the students could invest in this game for the public good or cheat and reap a selfish benefit. Without punishment, it happened what happens everywhere. The students started with an average level of cooperation, and this level decreased sharply. Even smart students from Zurich are still the selfish naked apes. Then the game was repeated with punishment for the free rider. Yet, the punishment was costly to the person who did the punishment. The rules of the game were so that the student could not expect to meet the same players again, he could not count on reaping a future profit by educating his coplayer. As predicted by the authors, the level of cooperation increased to top levels. What are the mechanisms for this costly altruistic punishment? We are getting back to the capuchin monkeys—it is negative emotions, anger. The anger grew proportionally greater, the larger was the difference in the noninvestment of the cheater from the group norm. Remarkably, the cheater knew about these negative emotions and when asked about it, he anticipated even stronger averse reaction than actually occurred.

In fact, when biologists anticipate that the selfish gene theory comes from their field, they should read David Hume, who wrote in the eighteenth century: "every man ought to be supposed to be a knave and to have no other end, in all his actions, than his private interest." E. Fehr tells us that humans have a strong tendency for altruism if only in social punishment. This observation might explain some trends in human societies that are not easily understood from the selfish gene theory. It highlights why humans are so willing to punish those who violate social norms (Bowles and Gintis 2002).

On Human Altruism and Sanctions

As if he was feeling that his concept of the altruistic punishment as the fabric of human society will not flatter our self-perception, E. Fehr designed another economical game (Fehr and Rockenbach 2003). As food is not very motivating in an affluent society, real money was at stake, a quite obvious choice for an economist. In a clever game design, they played now investor and trustee. The investor had to trust the other person, but the trusted person was free to cheat. To be somewhat protected, the investor could impose in some games a fine for cheating trustees, but the investor could also voluntarily renounce on this punishment. They measured the back transfer of the trustee to the investor. Three major observations came out: (1) Overall, the money returned by the trustee was proportional to the money invested. (2) When a fine was imposed, less money was returned by the trustee than when no fine could be imposed. (3) When the investor renounced voluntarily on the fine, the highest amount of money was returned by the trustee. Apparently the trustee acknowledges being trusted. If it comes to the famous sticks and carrots, the carrots might be the better argument in human societies. Remarkably, the investor—once informed about the better feedback of the trusted trustee—did not change his behavior: The same

percentage preferred to impose a fine for cheaters even when knowing that this reduces his return. Apparently, we are not simple automates that calculate the optimal result for our selfish interest—we have strong opinions on the moral legitimacy of sanctions even when they are against our selfish interest. Irrational human behavior that is against survival instinct like revenge or suicide bombing might have a root in this apparently deeply human feeling.

Empathy

Neurobiologist went to the neural basis of altruistic punishment (de Quervain et al. 2004) and empathy—the sharing of emotions, pain, and sensations with others (Singer et al. 2006). These neural responses were modulated by the perceived fairness of the other partner. In the experiments, the study subjects started a money game, where they could behave as fair or unfair players. In the next level, the subjects observed the fair or unfair players experiencing a painful punishment inflicted by the experimental system. The neuroscientist looked for the empathy reaction in the insular and cingulate cortex by neuroimaging methods. Less empathic activity was elicited in the brain of the observer when an unfair player was in pain. Then the neuroscientists looked into the reward center, the nucleus accumbens. People shared empathy with fair players but also liked the punishment of unfair players. Interestingly, men showed a stronger desire for revenge than women. There is thus a neural foundation for theories of social preferences and a predominant role for males in the maintenance of justice.

Kin-Altruism and "Food" Sharing

Of course, the field of food sharing has not been entirely left to economists and neurobiologists. The genetic basis for the evolution of social behavior has been studied by W. Hamilton in the 1960s, and now, also economists ask genetic questions ("how hungry is the selfish gene?"). The inclusive fitness model predicts that people favor those to whom they are most closely related. In humans, the model has explicit predictions for commonly observed behaviors like within-household violence, allocation of food, or childcare. Anthropologists have investigated food sharing in tribesmen from South America, and the effects of kin-altruism appeared to be modest. References for the above statements can be found in Bowles and Posel (2005). These authors had the idea to submit the predictions of the inclusive fitness model to a rigorous statistical test. They collected data on the remittances sent by South African migrant workers to their rural households of origin. They collected many further data that allowed an evaluation of the rural households with respect to the composition of the household and degree of relatedness with the sender of the remittance. Since the predictions of the model do not depend only on the degree of relatedness but on the age, sex, and health and other characteristics relevant to the so-called reproductive value of the beneficiary, they also collected these data. The model is rather complex: The sender should give more to his adolescent children instead of his infants (high infant mortality will

prevent many from reaching reproductive age) or his parents (they have no reproductive activity). He should give more when at the end than at the beginning of his reproductive years. The authors accounted also for the foundation of secondary households at the place of migrant work. Overall, the effect of kinship was modest. Less than a third of the variation in the remittances could be explained by the applied kin-altruism model. The only observation sticking out was the wife's presence in the household, which resulted in 45% increase over the mean remittance. As the wife is genetically not related to the worker, the interpretation is ambiguous. There might be selfish-gene reasons (care of the migrant's children, expected future reproductive success with his wife) or altruistic motives toward nonkin, documented in behavioral experiments (Fehr and Fischbacher 2003).

Food Help and Social Queues

Kin selection for explaining eusocial animal behavior came also under criticism from zoologists working with Stenogastrinae hover wasps. These hymenopteran insects live in groups of up to 10 females. A single rank 1 female lays nearly all the eggs but rarely leaves the nest. Helper females collect food to feed the larvae of the dominant female. The problem is twofold: There is substantial variation in the help provided by the assisting females, and only 10% is explained by variation in relatedness. Kin selection is here apparently not the key to the understanding of help. The system is accessible to a quantitative analysis because there is a strict age ranking in the females with promotion of the next oldest female in the queue when the top female has died (Field et al. 2006). The help could be easily measured as the time spent outside of the nest. Notably, the researchers observed that the helpers worked harder when they were of lower rank. The helping effort dropped dramatically when a female was lifted from rank 3 to rank 2. They suggested an interesting explanation. Helpers will gain indirect fitness benefits through aiding natal nest-mates. If you are low on the social ladder, helping is your best option. However, the situation is different for a rank 2 female. She can hope for laying eggs herself and reaping the full genetic benefit. Yet, she must survive to achieve this position. Foraging is dangerous, you might meet predators and pathogens and that will negatively affect your survival probability. Staying home is then the safer bet. Furthermore, helpers should work less hard when the group of helpers increases because this is like rising in the rank—a large work force promises a larger survival of larvae should the individual become the first ranking female. The behavior of animals in experimentally manipulated groups where ranks were shifted and where the workforce was increased, concurred with the predictions of their model.

On Trust, the Amygdala and Oxytocin

Trust in other people has a clear physiological basis. Patients with bilateral damage to the amygdala showed marked effects. They rated people as trustworthy from their facial expressions, who were rated as untrustworthy by a control population. This defect was restricted to the visual interpretation of

facial expressions and did not extend to verbal evaluation of people when short biographies of different characters were presented to them (Adolphs et al. 1998). E. Fehr added a new facet to his research when teaming up with clinical psychologists. They repeated the investor–trustee game, but half of the subjects were now treated with a nasal sniff of the peptide hormone oxytocin, best known for its physiological action in milk letdown and labor. This treatment significantly increased the investments of the donor when he was aware that he played with humans, but not when playing with a computer program (Kosfeld et al. 2005). Apparently, oxytocin rendered subjects more optimistic about the likelihood of a good outcome in social interactions by inhibiting the defense behaviors.

Evolution of Eating Strategies from First Principles

This chapter has made a wide swing around the quest for food topic, using approaches coming from different nonbiological disciplines. I would like to still add a pure mathematic analysis (Burtsev and Turchin 2006), which transgresses the constraints of game theory. The latter is characterized by a simple structure of the payoffs and only a small number of possible strategies. The model divides the world into patches that contain food resources or are empty. The eating agents can rest, eat the resource (but can store only a fixed maximal amount of energy), divide, move to the next patch (when the resource in the initial one is empty or consumed), or attack other agents in a neighboring patch. An agent that has exhausted its reserves dies. The number of possible behavioral strategies is extremely large, but in a simple run of the model only those emerged that were already determined by J. Maynard Smith using the theory of games in the 1970s. These were doves that never attack and flee when attacked; the hawks attacked other agents, and finally the bourgeois, which stays in the patch, attacks invaders, and does not care about neighbors. If the carrying capacity is large, the bourgeois strategy dominates. However, below a threshold, only doves and hawks compete. If the agents are now allowed to evolve cooperative strategies, new populations emerged: cooperative doves, ravens (predators recognize and do not attack in-group members), and starlings (which mob large intruding invaders). The researchers claim that their computer simulations have implications for the evolution of territoriality in animals (and private property in humans) but also admit limitations on their model. One strategy, well known in zoology, namely the cooperative attack (wolf strategy), did not evolve in their simulation. In a future extended model, they want to allow for horizontal ("cultural") and not only vertical ("genetic") transmission of traits to check whether this allows the evolution of human ultrasociality, i.e., cooperation between genetically unrelated individuals, so characteristic for humans in the animal kingdom.

Altruism or Personalized Nutrition in a Social Mammal

I will end the chapter with a peculiar eating culture in a eusocial animal. In eusocial organisms, there is division of labor between morphologically distinct

castes. These species show communal breeding where "queens" are responsible for producing all the offspring, while workers forego reproduction and assist others to reproduce. Eusociality has interested biologists because it represents an extreme form of altruism in biology; it is best known from insects. In mammals only two strange species of African mole rats show this social structure (Figure 6.12). These are nearly hairless and sightless subterranean animals that disperse by extending their burrow system. In *Cryptomys* three types of animals were observed: the queen and the frequent workers, which perform more than 95% of the daily work performed by the colony, and finally there are the "lazy" types, which the zoologists called respectfully the "infrequent" worker (Scantlebury et al. 2006). In fact, the infrequent workers contribute between 25 and 40% of the individuals of the colony but perform less than 5% of the total work. The infrequent workers were heavier than the frequent workers and showed both higher amounts of fat and muscle mass. The likely reason for these two nutritional classes of workers became clear after heavy rainfall. Rainwater softened the soil and now allowed prospective forays by the infrequent workers. They now invest their fat reserves to tunnel through the earth in search for other colonies of mole rats. The heavier and lazier individuals are thus the reproductive form of the animals in the colony, and they need their fat stores to meet the high energy demands to find a partner without getting above ground where they would be helpless against predators.

Communicating on Food

Honeybee's Waggle Dance

One of the most complex systems in animal communication is honeybee's waggle dance. The dance resembles a miniaturized reenactment of the flight to the food source. The direction and distance to the food source are encoded by the elements of the dance. Karl von Frisch made his first observations on the

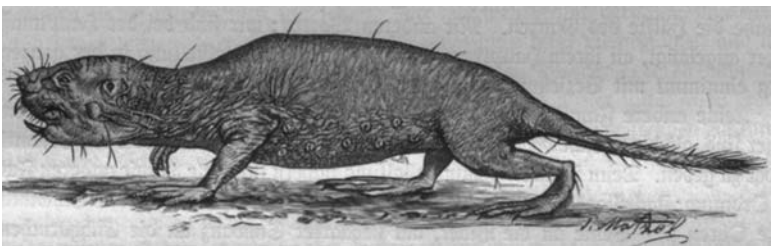


FIGURE 6.12. Mammals are defined by the possession of hairs, but the naked mole rat, a burrowing mammal from the plains and deserts of Africa, mostly lacks hairs. The figure shows a species from Somalia, *Fornarina phillipsi*, a close relative of the better known *Heterocephalus*. These animals nearly lack eyes and ears and dig tunnels by their front claws and incisors. They feed mainly on roots and bulbs of plants. This animal is also a eusocial mammal that has evolved nutritional castes.

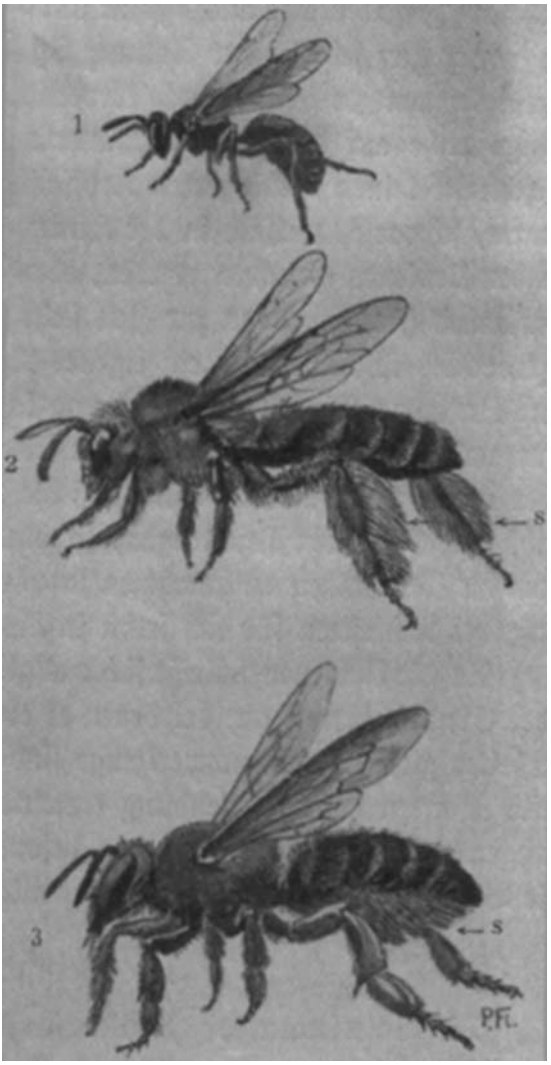


FIGURE 6.13. Bees (Apidae) come in different forms. The most primitive are the Proapina (*1*) here represented by *Prosopis*, they forage only on flowers with easily accessible nectar. The next group is Prodilegina with collecting hairs (S) on the hindlegs, here represented by *Dasypoda* (*2*) and then Gastrilegina with a collecting brush under the belly, here depicted with *Megachile* (*3*). These are all solitary bees.

bee (Figures 6.13 and 6.14) language in 1921, but it took him decades before he could decode the information for a human observer. For example, the direction of the waggle run corresponds to the angle of heading to the food source relative to the current sun azimuth and is performed relative to a sensory reference. Sounds complicated? I can reassure you, not only for you: Even for the bees,

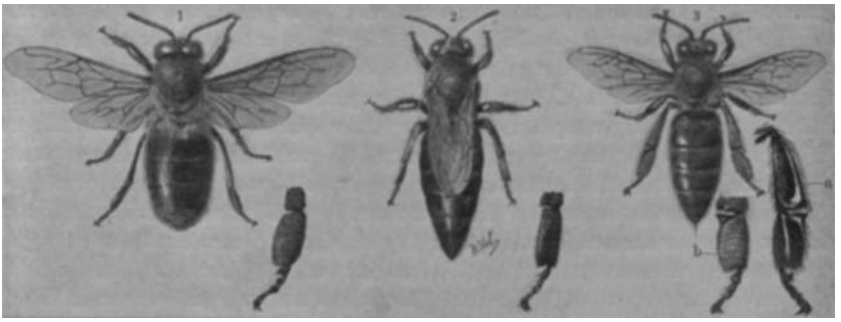


FIGURE 6.14. Social bees are bumblebees (*Bombinae*) and of course the honeybee, *Apis mellifica*, here represented by a male (*1*), a queen (*2*), and a worker (*3*). Their legs are magnified.

this behavior is rather difficult to learn, and the bee recruits might need more than an hour to decide what direction to take. The bees have to follow the successful forager-dancer to learn this information. They thereby also learn the odor of the food.

Bumblebees

Bumblebees have a simpler information system in place that is also fairly efficient. The forager returns to the nest and makes minutes-long excited runs across the nest, frequently bumping into other bumblebees, and it distributes the odor by buzzing the wings. The nest mates get aroused by this action and leave the hive in large numbers. In field experiments, they seek the odor of those flowers brought into the nest by the forager. Biologists believe that this is the evolutionary origin of the complex behavior in honeybees (Dornhaus and Chittka 1999). The rougher bumblebees are in many other aspects a useful reference for the more sophisticated behavior of the honeybee. In color-discriminating task (only one artificial flower offered sucrose, the others nothing), bumblebees showed a continuum of behavior. Some were making careful and correct decisions for the right rewarding color, but this took time. Other bumblebees opted for a quick and dirty strategy and visited any flower since the time to check a wrong source was anyway short. However, they could do better. When the landing on the wrong artificial flower was linked to a punishment (they were penalized with bitter quinine), also these looser bumblebees showed an increased discrimination capacity but at the expense of longer response times (Chittka et al. 2003).

Fitness Through Dancing?

Bees are more sophisticated in their food search behavior and must have an impressive cognitive capacity to work through all the information necessary for successful foraging. However, recently many biologists were rather critical about

the basic tenets of the discoveries of K.v. Frisch. In one recent report, they asked whether honeybee colonies really achieve a higher ecological fitness through dancing. To test for that correlation, they disturbed the bees by alternatively offering diffuse light and orienting light. In one case, the dances were disoriented, and the bees could not transmit precise information on food location to the recruited bees. As an outcome parameter, they measured the mass of the hive serving as an indicator of foraging success. During the periods with oriented dancing, the colonies showed an overall greater amount of collected food, but this difference did not manifest in all seasons. In the autumn, no difference was associated with oriented dancing (both colony types lost weight); in the summer, both gained weight, but the oriented dancers gained somewhat more. Only in the winter (the study site was California), a marked effect was found, the colonies with the disoriented dancers lost weight, while the oriented dancers gained weight. Apparently, the waggle dance is ecologically important only when the food sources are hard to find or variable in richness (Sherman and Visscher 2002).

Precision of Communication

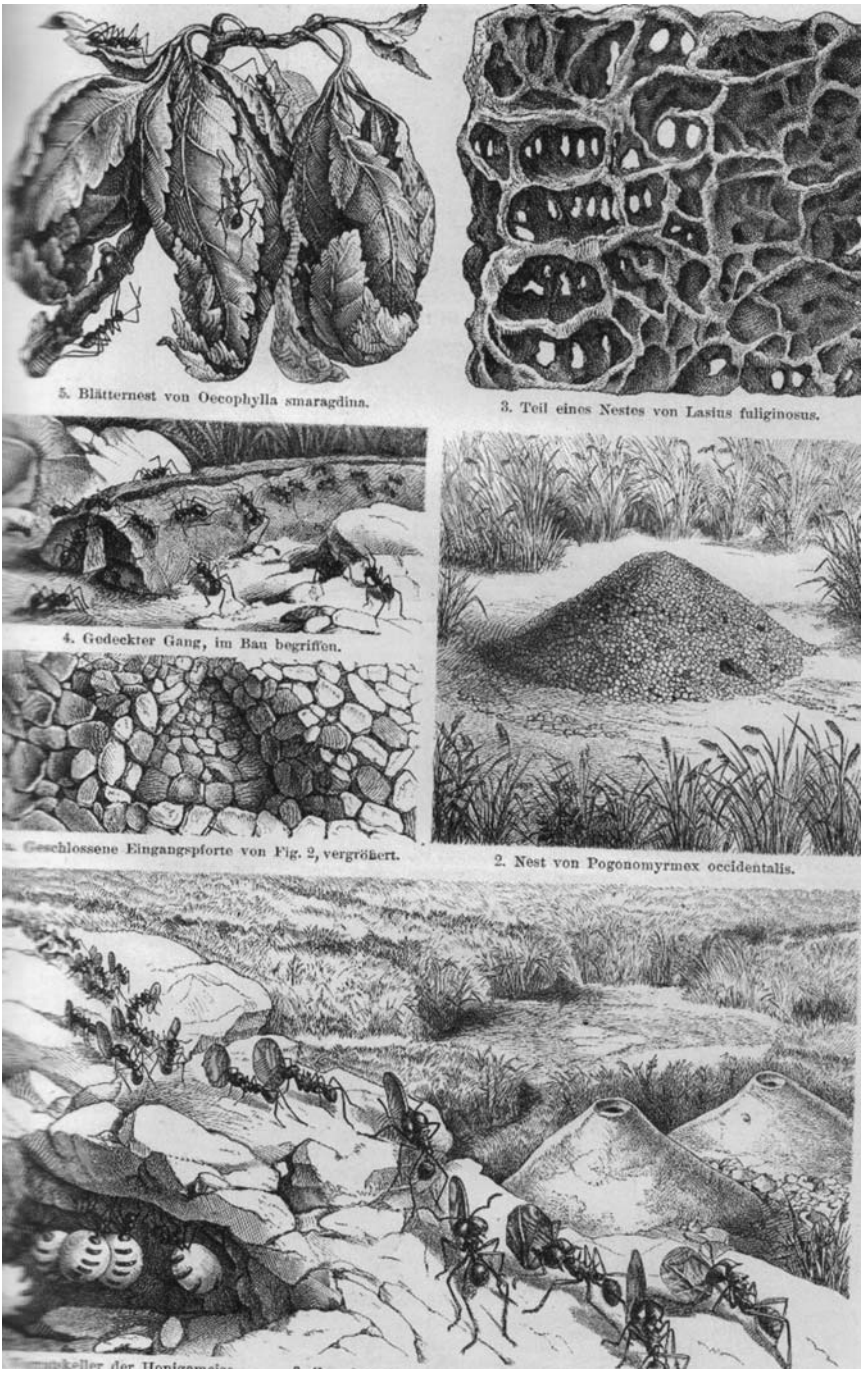
When these critical questions were asked, other followed. What is actually the precision of the conveyed information? If the coding of honeybees were really as precise as described by K.v. Frisch, it would be the most sophisticated nonprimate communication system in the animal kingdom. Doubts came up because recruits had to go through different dance sessions to get the message, some hesitated, still others did not find the food source at all. In a recent report, the biologists captured the recruited bees as they left the hive and attached them a harmonic transponder such that the researchers could track their paths. The scout bees had to convey the information that the artificial feeder was at right angle to the coordinates defined by the Sun and at 200-m distance. Overall, the recruited foragers performed very well. All but three of the electronically marked 19 bees arrived at the feeder, although some arrived just a few meters aside without finding the feeder and then returned without food to the hive. Despite some side wind, the bees kept very precisely the indicated angle and deviated only when trespassing the set 200-m mark. In these experiments, one could still argue that the bees used additional cues like the odor marks of the dancers for orientation. To exclude that possibility, the researchers displaced the hive and observed that the recruited bees followed as precisely the transmitted path information from the new release point as from the original start point (Riley et al. 2005). However, other researcher could trick out honeybees by sending them into a narrow tunnel for foraging. The scouts transmitted then a too long distance for food location to the recruited bees. Apparently, the bees calculate distance according to retinal image flow that they experience during the search. Their brain misreads the distance because the close tunnel walls increase the perceived optic flow (Esch et al. 2001). These experiments do not refute the precision navigation system of bees but reveal the physical parameters that the bees use for their distance counting.

Teaching

The ant *Temnothorax* has developed a way to teach its nest mates the way to a food source by a process called tandem running (Franks and Richardson 2006). The teaching leader ant goes ahead followed by the naïve learning ant. The teacher continues to run only when touched on its legs and abdomen by the antennae of the learning ant. The run is frequently interrupted by stops where the learner ant walks around probably memorizing landmarks—the teacher waits patiently. During the tandem run, both ants coordinate their speed: If the gap between the ants gets larger such that the physical contact is interrupted, the teacher slows down and the learner speeds up to remain in contact. Tandem running has no advantage for the teacher—actually it is fourfold slowed down in its foraging trip—but the learner reaches food in a significantly shorter time period. The gain is 30% acceleration in time. The exercise becomes cost-efficient for the nest because the behavior is "contagious." The former pupil, once it had detected the food source, runs back to the nest and becomes a teacher in turn. In this way, these ants propagate time-saving knowledge among foragers. Tandem running is thus superior to the strategy where workers from the same ant species carry nest mates to the food source. The carried ant does not become a teacher probably because it was transported with the head pointing rearward, and it was thus prevented from memorizing landmarks. Other ant species carry their nest mates with the head looking forward, and these carried ants become then carriers for the next run. Apparently, a big brain is not a requisite for teaching to occur in animals.

Decision Processes

Orientation by waggle dance plays a role in still another situation of the life history of the beehive—when the swarm leaves the old hive and searches for a new site. The swarm then sends the scouts out, which explore the environment searching a good site for a new hive in a promising food surrounding. The scouts dance again a waggle dance, but it follows different rules. The question is no longer to convey precise information on a food source, now competing places are proposed by different scouts. In house hunting, the number of waggle runs, which is initially proportional to the perceived quality of the site, declines with each successive dance. Other bees follow the dance of the scouts, some check it physically, and then the popularity of the different proposals is assessed by attrition. The dance with the most persistent scouts wins, and this is usually the highest quality site (Visscher 2003). This subject touches an interesting current research area about decision-making in animal groups on the move. This can be migrating grazing mammals in search of the most promising grassland, schools of fish, large groups of insects or birds. The group has now a difficult point to settle: How do uninformed individuals recognize those that are informed, and how do groups come to a collective decision (Couzin et al. 2005)? It is also a question of leadership since mathematical models showed that only a very small proportion of informed individuals are required to achieve great accuracy in the prediction as observed in the migrating beehive example. The mathematical model showed


5. Blätternest von Oecophylla smaragdina.
3. Teil eines Nestes von Lasius fuliginosus.
4. Gedeckter Gang, im Bau begriffen.
Geschlossene Eingangspforte von Fig. 2, vergrößert.
2. Nest von Pogonomyrmex occidentalis.

that successful group foraging needs only limited cognitive ability. Biologists differentiate two basic decision modes: One is the despotic mode, where the decision is made by the most experienced group member. Again, mathematical treatment of the process tells us that this process only pays when the group size is small and the difference in information is large. In all other cases, they tell us that the second mode, the democratic mode, is more beneficial. The benefit derives from the property of the system to avoid extreme decisions, "democracy" in animals is a type of insurance system. It is not likely that each individual has the possibility to influence the decision process by a personal voting (Conradt and Roper 2003). The stage is mathematically prepared, and the ground is now free for the experimentalists to test the predictions.

Animal Technology

The Invention of Agriculture: Fungal Gardens of Ants

A Riddle

If you hear agriculture, your first idea might be the neolithical revolution by Homo sapiens about 10,000 years ago, but this figure is not tenable any longer—a better guess is 50,000,000 years ago. If you count, slightly astonished, the digits of this number, you will realize that this figure reaches back into the time just after the demise of the dinosaurs. Who has taken the step from hunting to targeted food production that merits the name of agriculture? If I wanted to push you on a wrong track, I would say the animals have the size of a cow and also consume daily an amount of leaves that the cow is getting as feed. If you try now to check vertebrates for this capacity, then you are definitively on a wrong track. Of course, I voluntarily misguided you: When I said the weight of a cow, I referred to the biomass of a single colony of leaf-cutter ants from the American tropics, which counts several millions of animals.

History of Leaf-Cutting Ants

The fungal gardens of these Central and South American ants became a showcase for an evolution-oriented ecological research that created new paradigms for the theory of symbiotic interactions (Figures 6.15 and 6.16). The

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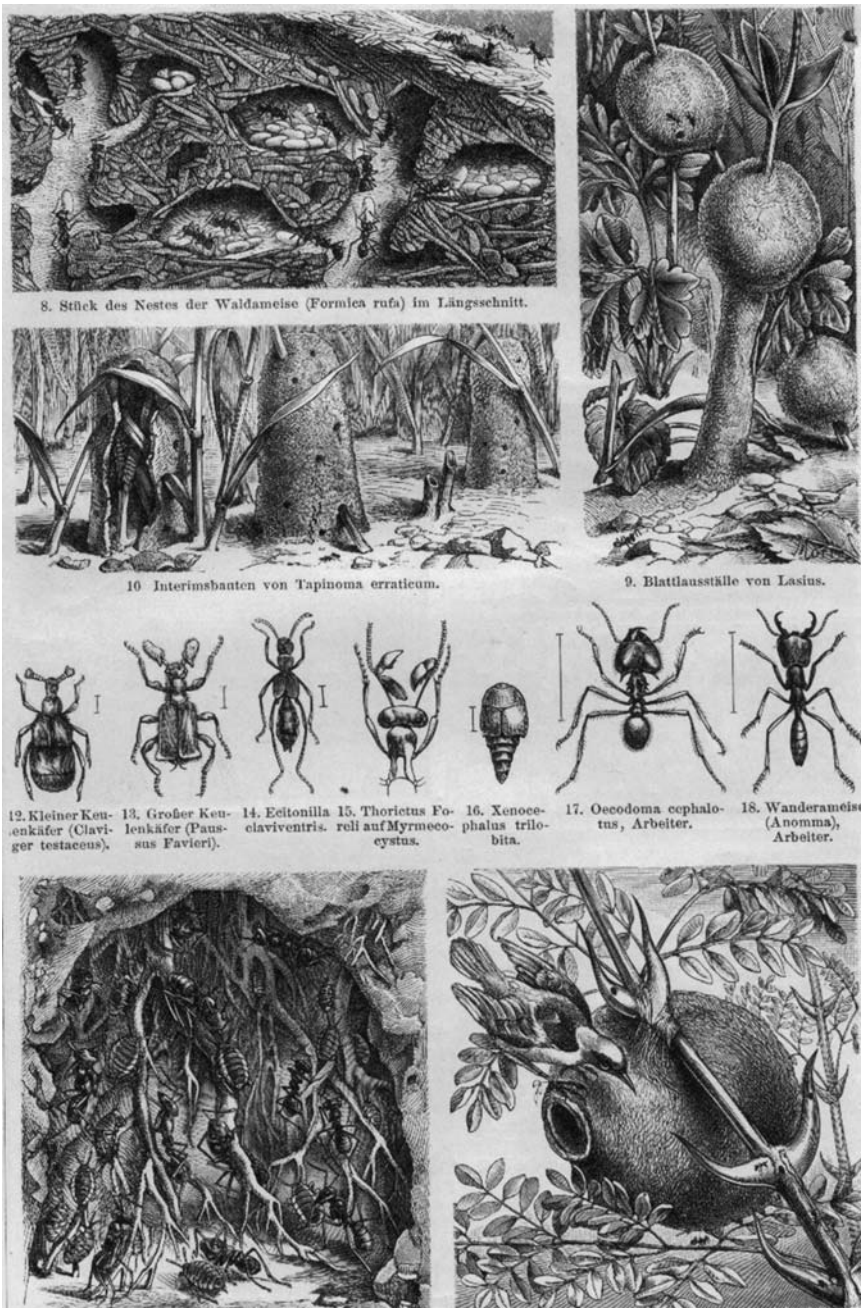
FIGURE 6.15. As social insects, ants build a variety of nests. In forests the common European ant *Formica rufra* constructs characteristic ant-heaps with many entrances (Figure 6.16, *8* shows a cut through the colony with brood chambers), while the agricultural Texan ant *Pogonomyrmex barbatus* builds a hillock with a central opening at the top (bottom, right), *P. occidentalis* covers the hillock with small stones and even closes the entrance (center, right). The nest of *Lasius fulginosius* is built from chewed wood (top, right), those of *Oecophylla smaragdina* are sewn from leaves (*top left*) using their silk-excreting larvae as sewing needles. Along their foraging ways, leaf cutter ants keep lanes free of grass (bottom, center), some of these lanes can even be covered (center, top left).


8. Stück des Nestes der Waldameise (Formica rufa) im Längsschnitt.
10 Interimsbauten von Tapinoma erraticum.
9. Blattlausställe von Lasius.
12. Kleiner Keulenkäfer (Claviger testaceus).
13. Großer Keulenkäfer (Paussus Favieri).
14. Ecitonilla claviventris.
15. Thorictus Foreli auf Myrmecocystus.
16. Xenocephalus trilobita.
17. Oecodoma cephalotus, Arbeiter.
18. Wanderameise (Anomma), Arbeiter.

inquiry into this fascinating system is also a good illustration as to how science is stepwise unfolding the secrets of nature. The leaf-cutters (Figure 6.17) are so characteristic when they come back from their foraging to the colony, each charged with a leaf and one after the other, that they attracted quite early the attention of human observers. Their earliest mentioning is in the Popul Vuh of the Mayan civilization in the nonscientific language of a creation myth. The first but wrong scientific conjecture was made by the British naturalist Bates. He proposed in 1863 that the leaves were used to protect the broods in the nest against the tropical rain. Ten years later, the engineer Thomas Belt got it right when he stated that the leaf-cutter ants use "leaves on which they grow a minute species of fungus, on which they feed. The ants are mushroom growers and eaters" (quoted from Schultz 1999). As frequently in science, the breakthrough discovery was done twice in the same year. The other person was a professional biologist, Fritz Müller, who described his discovery in a very early issue of the science journal *Nature*. After them several generations of zoologists have worked on ants, and entire books have been dedicated to ants, social insects, and gardening ants. Research on ants led also to the conception of an entire new branch in biology: sociobiology. I will not retrace this history, interesting as it is, but try to convince you that what these ants are doing is really an agricultural activity. After that outline, I will illustrate current research around this fascinating symbiosis system that got more and more trophic levels over the years.

Gardening Activity

First to the natural history of leaf-cutting ants (Currie 2001): When a foundress queen leaves the old nest, she takes care to carry a small clump of the fungus stored in a type of a mouth pocket on her nuptial flight. Once inseminated, the queen digs a small chamber, spits out the fungus and starts tending for it. She either uses her fecal fluids as manure or forages for substrate. Then she rears the first generation of workers, which then take over the task of tending the garden and foraging for the garden substrate. When they come back to the colony with a leaf, the ants lick the leaves to remove the wax layer that the plant has evolved to protect its leaves from fungal attack. Then follows a mastication, which cuts leaves to 2-mm pieces. This is supposed to remove the leaf-specific microbiota.

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FIGURE 6.16. Various ants produce special breeding devices, e.g., *Tapinoma erraticum* build elongated structures along grasses and use them as brood chambers for their eggs (center, left). Still other ants like *Lasius flavius* construct shelters for their milking cows, the aphids (top, right; bottom, left). Ant-heaps are visited by beetles, some are tended by ants (center, left two animals), others are living on ants (center, fourth from left), still others display ant forms to mix into the colony (center, third from left). Some ants associate with plants, which they protect against leaf-cutter ants or herbivorous animals. On these "ant plants" the ants form air-borne nests. Some birds prefer ant plants also for their own nest-building activity, they probably profit from the protection conferred by the ants defending their trees (bottom, right).

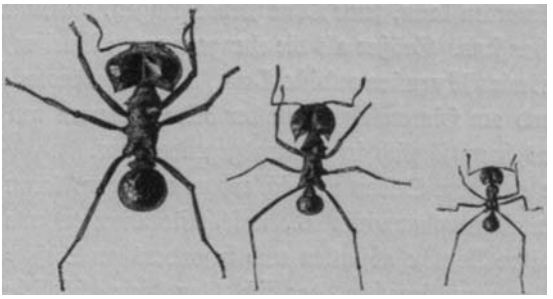


FIGURE 6.17. Leaf-cutting ants—here three differently sized workers from *Atta cephalotes*, family Formicidae, order Hymenoptera—do not eat leaves, but feed at home fungi with the plant material. They became thus inventors of gardening activities and had to solve many problems associated with biological food processing.

The resulting pulp is then enriched with a fecal droplet to provide some enzymes. The pulp is then posed on the top of the fungal garden, and it takes 6 weeks for the complete decomposition process. During that time, fresh material is continuously added on the top and the spent material is regularly removed from the bottom of the fungal garden. The workers take great care with the spent material, which is deposited in real refuse heaps at some distance from the colony. The ants have some gardening activity; they move around, eat parts of the fungus, and distribute the fungal enzymes with their fecal pellets over the culture. The ants prune the fungus, they open and close tunnels to the surface to achieve optimal humidity and temperature for the decomposition. The ants neither eat the leaves nor the fungus, but the gongylidia—special nutrient-rich hyphal tips that sprout out of the fungal biomass. Like a riddle in a fairy tail, the ants are thus the dominant herbivore of the Neotropics without eating a single leaf. The entomologist Wilson marveled that leaf-cutting ants have such "an efficient utilization of almost all forms of fresh vegetation that their invention can be properly called as one of the major breakthroughs in animal evolution." Individual colonies survive for 10 years. I think we can agree that this is true agriculture.

Diversity in Ants and the Associated Fungi

However, not all what glitters is gold—this description of early agriculture is overoptimistic. Recent research has revealed that life for leaf-cutter ants is not that easy. I will try to retrace the major steps of research in gardening ants over the last 10 years. Major efforts were invested in the molecular phylogeny of the fungus-growing ants. The *Attini* tribe is thought to have originated 50 million years ago, and the separation between the *Cyphomyrex* genus, which uses insect feces and corpses as gardening substrate, and *Trachymyrex* genus, which uses dead vegetative matter as food substrate, is older than 25 million years and backed by molecular data and animals included in amber (Hinkle et al. 1994). Only the higher attines (*Acromyrmex* and *Atta*) use fresh leaves and flowers of many plants as nutritional support for their gardens. The congruent evolutionary relationships of the higher ants and their fungal symbionts initially suggested

cospeciation and asexual clonal propagation of the fungi for millions of years. This simple picture got cracks when a larger set of ants and their associated fungal gardens were investigated. The fungi are not of a monophyletic origin but came in three groups. Two belong to *Lepiotaceae*. Relatives of this group of mushrooms are also appreciated by human gourmets—a cousin is *Agaricus campestris* (the "champignon de Paris" of the French restaurants) and greater brother is *Macrolepiota procera*, a fine mushroom with a nut flavor. A third group of fungi from ant garden belongs to the *Apterostigma* group, which are distant relatives of the *Tricholoma* mushrooms (containing some comestible, but also some poisonous mushrooms). Particularly between the primitive ants and their fungi, numerous topological incongruency was detected on the respective phylogenetic trees suggesting horizontal transfer of fungi across the ant species and the secondary acquisition of fungi from a pool of free-living fungi (Chapela et al. 1994). Subsequent work showed that any single attine ant nest contains only a single fungal cultivar, whereas nests of the same ant species may contain distantly related cultivars even if they were only separated by a few centimeters. The same fungi might also be cultivated by distantly related ants (Mueller et al. 1998). These data refuted the long-standing model of fungal clonality spanning million of years, and this model was already questioned on theoretical grounds because asexuality should pose problems with the accumulation of deleterious mutations (Muller's ratchet argument). In fact, after accidental loss of the cultivar, ants are apparently forced to search replacements from neighboring colonies. Even if this "borrowed" fungus does not match their original clone, incompatibility is quickly overcome.

From Two to Three Players: *Escovopsis*

But what are these accidents that lead to the collapse of the fungal gardens? Fungus-growing ants maintain axenic (single species) "monocultures" of fungi, despite the continuous exposure of the substrate to microbes adapted to the plant material, which are passively carried with the leaves into the nest. Apparently, ants arrive to weed out their gardens from alien microbes. Humans have great difficulty to maintain monocultures of genetically homogeneous crops—parasites have frequently a devastating effect on these crops. How do ants succeed to keep their gardens pathogen-free? The answer is simple: They don't. When Cameron Currie and colleagues sampled thousands of fungal gardens from Panama, about 40% of the gardens yielded nonmutualistic fungi. Notably, the nonmutualists were dominated by a single fungus, *Escovopsis*. Nonmutualist is actually a euphemism, *Escovopsis* is a highly virulent pathogen of the fungal garden. After intentional infection, the fungal garden collapses within days. They are so radical that they leave no apparent microscopic evidence of the mutualistic fungi. *Escovopsis* is highly specialized to fungal garden and cannot be isolated from the environment. It is apparently horizontally transmitted from colony to colony, although it is not imported by the founding queen (Currie, Mueller et al. 1999). Phylogenetic studies demonstrated that *Escovopsis* is monophyletic and comes from a dubious parent company, which includes parasites of commercially cultivated mushrooms and the famous cereal

fungal parasite *Claviceps purpurea*. At ancient levels, the phylogenies of the three organisms ant/mutualistic fungus/parasitic fungus are perfectly congruent, suggesting that what was initially described as an ant–fungus symbiosis is actually a tripartite coevolution. At recent evolution levels, frequent host switches were observed demonstrating traits of a fierce arms race (Currie et al. 2003).

A Fourth Player: *Streptomyces*

There is a German word saying the deeper you get into a forest, the more trees you are seeing. This sounds pretty trivial, but this means that you need to concentrate if you want to find your way out of this forest. This applies not only to forests of the brothers Grimm but even to the much smaller fungal garden. The Smithonian outpost at Panama added a new player to the garden party. To keep the symmetry, the turn is now at the helper side. Behind the curtain are *Streptomyces* bacteria. Actually, they do not stay behind the scene, they are found in a long-overlooked powdery whitish crust under the thorax of ants, in other ants they are found under the forelegs. While the place of association was variable, they were regularly associated with all groups of attine ants underlining their ecological importance. *Streptomyces* is actually a good choice for the ants, because it is the most notorious of all bacteria with respect to antibiotic production. In fact, most antibiotics developed for human pharmaceutical use are actinomycete (to which *Streptomyces* belongs) metabolites. *You see the humiliation of human pride after Copernicus is a never-ending story. First, I had to tell you that agriculture was not a human invention, and, now, leaf-cutter ants are also the inventors of a grass roots pharmaceutical industry*.

Streptomyces associated with attine ants are doing what they are expected to do. They do not produce antibiotics against saprophytic or entomopathogenic or other common fungi but show exclusive inhibitory activity against *Escovopis*. At the same time, it produces growth-promoting compounds for the mutualistic fungi (Currie, Scott et al. 1999). We have here the fourth partner in this ant symbiosis, which makes this system one of the most complex symbiotic associations discovered in nature.

If you have such a valuable antibiotic producer, ants have all interest to treat them carefully. This is indeed the case. The bacteria, which belong to a single genus, *Pseudonocardia*, are associated with all attine ant species examined and occur on each species in a given location on the cuticule. Females carry them away during their mating flights to transmit them to the offspring colonies. The location of the bacteria differs between ants: The paleo-attines, as the name indicates the oldest phylogenetic group of these gardening ants, have them under the forelegs. The "higher" attines have them under the propleural plates on the trunk. Cameron Currie and colleagues recently took a closer look on these propleura and carefully removed these filamentous bacteria. Below this filth, they detected crescent-shaped cavities. The ants have developed homes for their mutualistic bacteria to house them. Not enough with that, the cavities are underlain with an exocrine gland, and it seems that the ant feeds the bacteria by its glandular secretions. Actually, some worker ants have cavity openings essentially over the entire cuticle. A phylogenetic analysis demonstrated that the mutualistic association is of an early evolutionary origin.

As we live currently an antibiotic resistance crisis in medicine, this observation raises also the intriguing question as to why the parasitic fungus has over these long evolutionary periods not evolved a resistance against the antibiotic produced by the filamentous bacterium (Currie et al. 2006).

Why a Fungal Monoculture?

Recent research has added still further layers of complexity to the system. When ants weed their garden, they apparently do not remove only the parasitic fungi but also the mutualistic fungi that happen to contaminate their garden. Why do they do that? Wouldn't it be in the interest of the ants to abandon the monoculture to be more stable in case of parasite attack like humans are doing (Zhu et al. 2000)? *A possible answer to this paradox is that ant's weeding is actually an extended phenotype à la Dawkins of the symbiont, which does not like the idea to share the food resources with a competitor. This is a sound selfish instinct, which governs all of biology*. If garden fungi are brought together, they show incompatibility reactions, which are proportional to their genetic distance. All fungus-growing ants manure newly grown mycelia with their own feces. As the ants feed on the resident fungus, the latter can use the ants for spreading incompatibility factors via its digestion. In fact, these factors survive the gastric passage, and ants are now used as a mobile spraying unit for incompatibility factors whose molecular nature was not yet defined (Poulsen and Boomsma 2005).

On Inventions

Ants are clever animals, but a good idea in biology runs the risk to be copied. We should therefore not be surprised to hear about fungus-growing termites. This insect-fungus symbiosis has a single African origin. In contrast to the ant system, in termites no secondary domestication of other fungi than those belonging to the *Termitomyces* group has occurred, which do not exist any longer as free-living species (Aanen et al. 2002).

Some biologists think that ants are especially inventive animals and recent research showed that you can also quote them as the inventors of group hunting, which developed traps. This strategy is seen in Amazonian arboreal ant *Allomerus*. They live in leaf pouches of the ant-plant Hirtella. They cut hairs from the stem of the host plant and stitch them together by the mycelium of a purpose-grown fungus building a type of gallery with numerous holes. Workers hide within the gallery and wait for a large prey landing on the gallery in ambush position with their mandibles wide open. If a locust has landed, the first wave of ant aggressors grasps legs, wings, and antenna of the prey through these holes. They then stretch the prey on the gallery such that the next waves of ants can sting it to death (Dejean et al. 2005).

Ant Plants

I will finish our excursion into the fascinating world of ants with plants that use ants for their purpose (Figure 6.18). If you want to use somebody in biology,

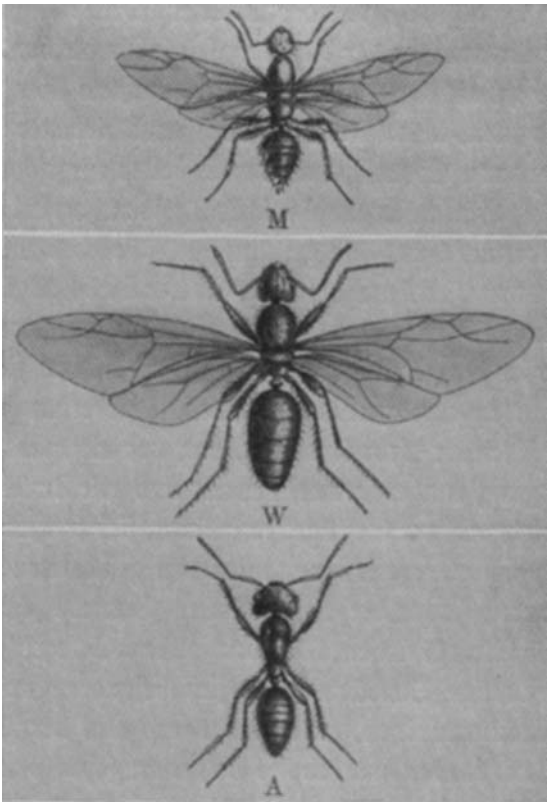


FIGURE 6.18. Class society in ants: male (M), female (W), and sexually not active worker (A) from the European ant *Camponotus ligniperda*. Its American cousin *C. femoratus* is known for the construction of ant gardens.

you need a shrewd strategy of exploitation or you must offer something for the service provided by a partner. Plants have learned to use insects and their offer is nectar produced in their flowers. With that free meal trick, they attract insect or bird pollinators that take over an important function in the propagation strategy of plants. Some plants also produce extrafloral nectar on vegetative parts, and myrmecophytes (in plain English "ant-plants") house and nourish specialized ant colonies on their leaves. In turn ants defend then their hosts against herbivores. The deal in this mutualistic relationship is fair and clear: food for defense. But there is a problem: What about cheater ants that take the nectar but do not show any inclination to defend the plant? In fact, there are enough nonsymbiotic ants foraging in the vegetation to spoil the tit-for-tat game. Researchers from the Max Planck Institute of Chemical Ecology in Jena found an interesting cue. Mutualistic ants preferred the nectar from "their" *Acacia* plants, while nonsymbiotic ants preferred the nectar of other plants. How was that achieved? Ant plants produce the disaccharide sucrose into the nectar as normal plants do, but they

produce into the secretion also the enzyme invertase (also known as sucrase) that hydrolyses sucrose into glucose and fructose. Nonsymbiotic ants prefer sucrose over monosaccharides, and the converse is true for the symbiotic ants. This preference pattern forms an efficient filter against exploitation by cheater ants. However, why should the symbiotic ants prefer the monosaccharides? The reason became quickly clear: The symbionts, in contrast to the nonsymbionts, lack a sucrase activity in their intestines. As disaccharides cannot be absorbed by the intestinal epithelia, the symbiotic ants become tied to "their" host. This nutritional trick stabilizes the mutualistic relationship, and we have here a fascinating case of specific coevolution (Heil et al. 2005).

Tool Use and Caches in Crows

From New Caledonia to Old England: Corvus Betty

Traditionally, the manufacture and use of tools were seen as a specific attribute of humanity. Ethologists told us that we have to share this property with apes. Since apes are our cousins, we were not too much upset that our uniqueness was violated. However, then came bird watchers with surprising observation that question some of our prejudices on tool use, culture, and animal intelligence. The story started with G. Hunt, an eyewitness of tool use in the New Caledonian crow *Corvus moneduloides*. When this resourceful bird searches for prey in the holes of dead wood, it uses twigs with a hook. The tools were made on purpose and carefully carried during foraging. They placed the tool under their feet when on a perch and in the bill when flying. These tools are used many times, and they are made with a shrewd technique. The birds removed secondary twigs along the primary twig, which then becomes the hook. They spend several minutes to remove the leaves and the bark to get a neat hooked stick. These crows used another tool made from the tough leaves of the plant *Pandanus* forming a stepped-cut tool. This pointed, but sturdy leaf with rigid barbs along the uncut end was held longways in the bill when foraging for spiders, millipedes, and alike under detritus (Hunt 1996). The researcher returned to Grand Terre, the only island where wild crows were observed to manufacture tools of this great complexity. He observed a population-wide handedness (or should one better say footedness in birds) in toolmaking. This laterality in tool manufacture, which was independent of ecological factors, speaks in favor of the involvement of a neural program in this process. It was compared to the right-handedness in humans that may be a consequence of the evolution of language, which favors the left hemisphere (Hunt et al. 2001). Later observations confirmed that tool use was not a cultural trait linked to this island like in some monkeys. In the latter, the classical case is that of macaques from a tiny Japanese island, where one juvenile female invented 50 years ago the washing of sweet potatoes in the river to remove the dirt. Since then the potato washing has spread through the population and passed as a tradition to the next generations (de Waal 1999). That this process of toolmaking can be spontaneously learned was shown with a clever Caledonian crow called Betty. In her Oxford captivity, she learned to

bend wires to retrieve food that she could not reach otherwise. Betty did the toolmaking in a minute and got the food within 2 min (Weir et al. 2002). The Oxford zoologists wanted then to settle whether toolmaking is a hard wired property of the bird's brain or whether it had to be learned from adult birds. For this purpose, they raised birds from the egg, half of them got teaching lessons in toolmaking from the zoologist, which they attended with apparent interest. The other half got no training. Food retrieval with hooked twigs was observed in both groups of animals at about 70 days of age. From Kew Botanical Garden, the researchers got also *Pandanus* leaves, which they used also as tools, although none fashioned the tools as their relatives from Grande Terre. While tool use is thus genetically acquired, the special tool form might still be influenced by social factors (Kenward et al. 2005).

Avian Tricks

Corvids are probably the most intelligent birds and are only rivaled by parrots and within mammals by monkeys and apes. In many respects, one can distinguish them as rule learners from rote learners like pigeons. They solve many tasks easily. One such task is the pulling of a piece of meat attached to a string and hanging from a perch. The raven has to pull the string with the beak, fix it in the new position with the feet, and pull again until it can reach the prey. It does not get mixed up when alternatives are offered like additional strings or stones fixed to the string or a piece of meat so heavy that he judges it useless to try it are offered (quoted from Emery and Clayton 2004).

Corvids are exceptional but not the only case of tool use in birds. Herons float feathers as tools to attract fish, woodpeckers use small sticks, and the burrowing owl *Athene* waits silently next to its nest when it has placed mammalian dung around its burrow to entice its prey. Indeed, the dung beetle *Phanaeus* attracted by this bait makes a sizable part of its diet (Levey et al. 2004).

The Complicated World of Food Hoarding

Some corvids (jays (Figure 6.19), nutcrackers, and magpies) like squirrels hoard food in times of plenty, and they return to these caches in time of need, which can be after hours, days, or in the next winter. The scrub jay does it also in the laboratory, which allowed zoologists to explore its food retrieval strategies. Corvids managed the classical three memory Ws: *What* happened, *where*, and *when*? The tasks they solved required phenomenal memory capacities since they remembered the whereabouts of more than a thousand caches. Their home computer showed remarkable processing qualities. Captive jays were given wax moth larvae, their favorite but perishable food item or peanuts, a stable but less likened food. They hoarded this food but were allowed to retrieve it only after either a short- or long-waiting period. First they go for their favorite food, but they quickly learned that after several days of waiting the larvae became degraded and unpalatable. This experience made, they do not even try to search

FIGURE 6.19. The Eurasian jay (*Garrulus glandarius*), family Corvidae, order Passeriformes.

the larvae, and the next time, they go directly to the otherwise less-favored peanut. If the researchers replaced the larvae with a fresh one and they did not make the degradation experience, the jays continued to go for the worms because they did not make this negative experience. These experiments were the first

conclusive behavioral evidence of episodic-like memory in animals (Clayton and Dickinson 1998). In the wild, the construction of caches is complicated by the social context. If jays are observed when hoarding food, they quickly come back and recache the food item. However, they do that only when they had previously made the experience of pilfering, either themselves as a pilferer or as a victim of food stealing. No such strategy was chosen when the jay could cache the food in private, i.e., unobserved (Emery and Clayton 2001). These experiments were the first demonstration that animals can remember the social context of past events and can adjust their present behavior to avoid potential detrimental consequences in the future. Different corvids differed in their memory capacities, e.g., jays remembered the caches of other birds for 2 days, while nutcrackers remembered only their own caches after this time period. We have here again an arms race between storers and pilferers, which leads to remarkable behavioral strategies, like waiting until a potential pilferer is distracted or lead the competitor arbitrarily away or even making false caches containing inedible food like a stone or nothing at all (quoted from Emery and Clayton 2004). A recent report added a further layer of complexity when Cambridge scientists discovered that food-caching scrub jays kept track of who was watching when (Dally et al. 2006). The scientists arranged for a situation where the storers cached in the presence of a dominant or a subordinate bird, or their partner or in private. Item recaching was greatest in the dominant condition, while partners were not perceived as a risk to cache safety.

Corvids gain increasingly a living within urban settlements, and sometimes use human civilization for food acquisition in astonishing ways. Corvids were previously observed to let nuts fall on rocks to get them opened. In a recent TV news item, I saw crows to drop nuts on streets in a Japanese city. They waited so that cars would crack the nut to recover the edible part. The news item showed that crows also used pedestrian crossing for this exercise to recover the nuts during the pedestrian's green period thereby avoiding getting accidentally under the cars.

On Stone Tools and Culture in Apes

What is Culture?

We associate our existence with culture, although when speaking of earlier hominids (species more closely related to humans than to chimpanzees) their tools are frequently referred to as industries to avoid the pretentious word of culture. This shy to use the term culture for animal behavior is probably again rooted in our anxiety to draw a firm line between us and the animals; such that we can maintain our Biblical God-like existence against the Darwinian Ape-like roots (Figure 6.20). One researcher brought this dilemma to the point when stating: The question of whether animals have culture is a bit like asking whether chicken can fly. There are certainly differences in the flying capacity of chicken and the albatros, but both can fly (de Waal 1999).

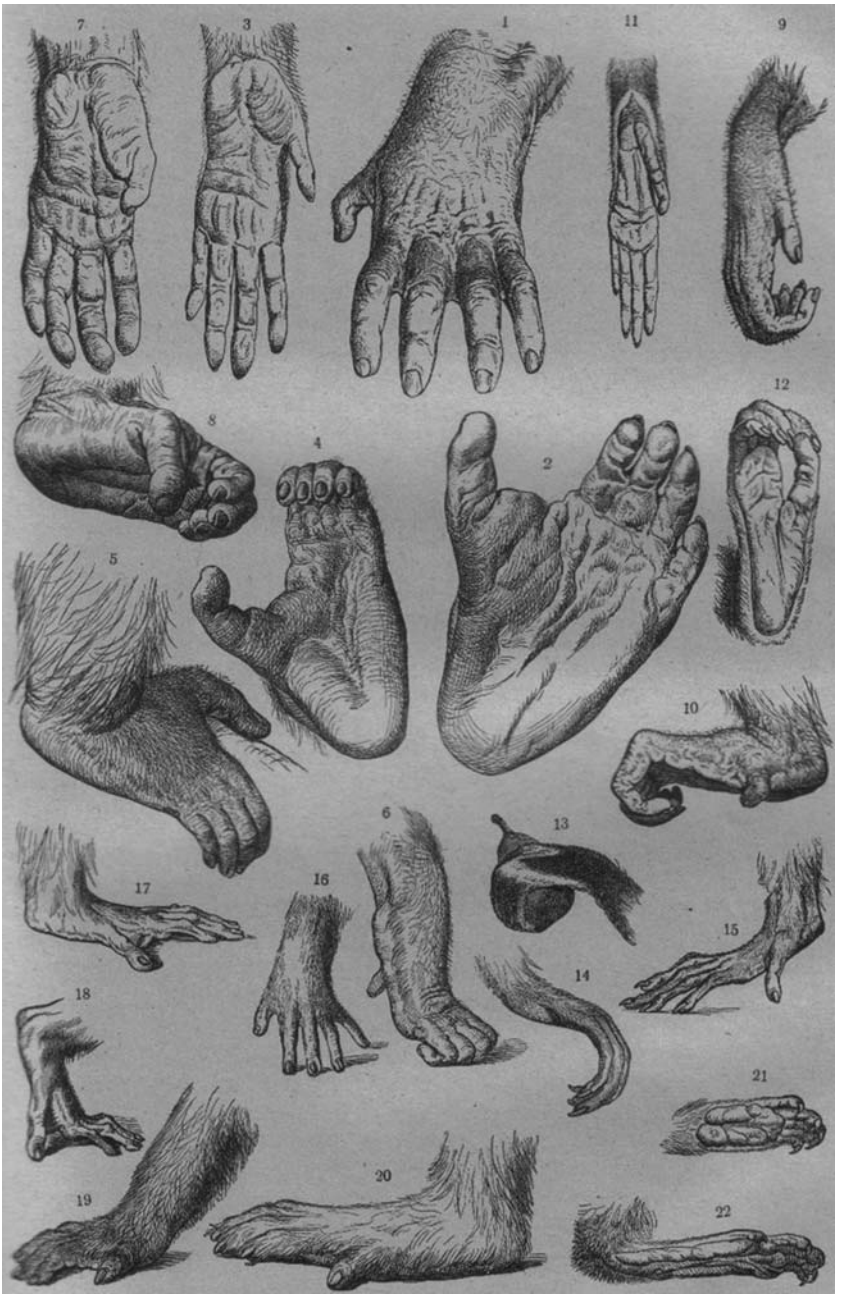


FIGURE 6.20. On the way to the handy man or the evolution of dexterity: Hands from the gorilla (*1, 2*), chimpanzee (*3–8*), orangoutang (*9, 10*), gibbon (*11–13*), the baboon (*19–20*) and the marmoset *Callithrix (21–22)*.

Nutcracking Culture

One of the best-studied cultural practices of chimpanzees is nutcracking. Mothers share the nuts that they have just cracked with their youngsters, which thus immediately get the first lessons in nutcracking by onlooking. Nongenetic, demonstrated, and learned transmission of techniques is one of the definitions of culture. Observers estimated that it takes up to 5 years for a chimpanzee to learn an efficient way of cracking hard nuts like the *Panda* nut from West African rainforests. The reward is high: If the animal masters the technique, it can obtain more than 3,000 kcal of food per day. However, to get to the *Panda* seed, which sits in one of the hardest kernels, is not an easy task. The compression force to crack it open can only be achieved by using stone tools. The trick is to crack the kernel without smashing the seed. Management of this trick is essential if you want to consume a lot of nuts without loosing time to pick nut fragments from kernel remnants. Chimpanzees from a remote area in the Tai National Park in Cote d'Ivoire were observed to use stone hammers of igneous rocks weighing between 3 and 15 kg for this task (Mercader et al. 2002). They carry these stones for 100 m to 2 km from the source rock bed to the nutcracking place. Once at the place, they curate the hammers intensively and transport them from site to site. Notably, the scientists who explored this site were not zoologists or ethologists but anthropologists, and they took an unusual but interesting approach. They knew from their zoologist colleagues that the site was used between 1975 and 1996 (when the *Panda* tree died). Nevertheless, they applied formal archaeological techniques as if this was a human excavation site. They carefully documented 40 kg nutshells and 4 kg of broken stone. They concluded that the stones and the nutshells were associated by a behavior, that anvils were used and that the stones are limited to a zone around the anvils. In a conventional archeological site, the stones would be classified as hammer edges, flakes, and shatters. These stone tools were produced unintentionally by the chimpanzees but resembled the objects found in the Olduwan industry of the earliest hominin technologies. Stone tool use is not limited to chimpanzees. Also capuchin monkeys from dry forests in Brazil use stones to dig out tubers, roots, or insects; to crack seeds or to get to the inner pitch of thorny fruits. The researchers concluded that tool use became essential during the dry season with low food abundance; in their view, the nutritional need led to the invention (Moura and Lee 2004).

Chimp Cultures

But is stone use already a culture? Cultural anthropologists insist on the use of language for the definition of culture and make it thus an exclusive human trait. Biologists have more inclusive criteria and define culture as intergeneration transmission of behavior through social or observational learning. This definition covers what one could also call "traditions" like dialects in songbirds or potato washing in macaques. Actually, when chimpanzees from two western and four eastern African sites were compared based on accumulated 150 years

of chimpanzee observation by field biologists, they listed their behavior into that shared by all, ecologically explained behavior and cultural variants (Whiten et al. 1999). To the cultural category belonged the nutcracking in western chimpanzees or, for example, distinct ant-eating habits. One ant-dip technique is done with a long wand in one hand stirring an ant nest, and the other hand is used to wipe off the ball of ants clawed into the wand and to lead it to the mouth. The other ant-dip "culture" is characterized by the use of a small stick, which collects a smaller number of ants and is directly transferred into the mouth. Chimpanzees are thus not so different from humans, in which differences between cultures are constituted by a multitude of variations in technology, social customs, and eating habits.

Cultural Conformism in Tool Use

The similarity in human and chimp culture goes even further. We tend to associate culture with creativity and novelty. One should not overlook that conformity to cultural norms is also an important ingredient of human and chimp culture. Conformity in tool use was demonstrated by psychologists working with captive chimps. Scientists have criticized that critical elements of chimpanzee behavior cannot be studied in captivity but only at the population level with wild animals. However, this limits the scientist to observational studies. To bridge the gap between the two types of research, scientists studied social learning where an animal teaches another animal a naturalistic foraging task. The psychologists educated a high-ranking female chimpanzee in the handling of an instrument that provided a desired food item, when correctly manipulated (Whiten et al. 2005). In fact, the food could be obtained in two alternative ways, either by lifting a level with a stick or by poking with a stick into an opening. The psychologists showed only one technique to the animal. When the instrument was introduced to naïve control animals, they manipulated it, but no animal succeeded to get the food item out. Then the researchers introduced the trained expert. The members of his group showed great interest in the food searching activity of the expert and most animals quickly learned the task—how to get the food. All animals practiced the mode that was taught to the expert. Then a follower individual discovered the second mode and practiced both techniques, some animals became then proficient in both techniques. Then the apparatus was removed. When reintroduced two months later, the chimps initially introduced into the poke or the lift technique, nearly exclusively practiced the first introduced technique despite the knowledge about the alternative technique. Despite the capacity to acquire particular local variants of a technique, most animals showed powerful conformist tendency to copy others. They discounted personal experience in favor of adopting perceived community norms. Apparently, the animals valued social bonds very high. Social norms contribute to the integration of groups. In macaques these norms are enforced by policing function of a small subset of respected individuals, which do conflict management. Removal of these individuals from the group destabilized the social niche and the group members disintegrated into smaller, less divers, less interacting subgroups when

measured with respect to grooming, play, and contact-sitting. Policing thus not only controls conflict but also plays a critical role in social learning and cultural traditions (Flack et al. 2006).

Sex Differences

I want to mention another similarity between the chimp and human cultures, which concerns sex differences in learning. Scientists observed chimpanzee mothers in Tanzania teaching their offspring the local technique of fishing termites with a stick (Lonsdorf et al. 2004). The striking observation was that the daughters learned the termite fishing technique from their mothers nearly 2 years earlier than sons. Daughters were also more proficient as measured by the number of termites gathered per dip. The reason became also clear: Daughters observed the mothers more carefully than the sons—which spent more time on playing—and imitated carefully the stick technique, while the sons were relatively careless in that respect. The biologists were quite impressed by this difference since similar sex differences in social learning were found in human children.

Orangoutang Cultures and We

The classical question is again whether chimpanzees are special or whether their case can be generalized. A subsequent study documented similar geographical variation in orangoutang (Figure 6.21) behavior from Sumatra and Borneo (van Schaik et al. 2003). The list of cultural variants in behavior again included eating habits like using leaf gloves to handle spiny fruits, tool use to poke holes into the nests of social insects, and breaking hollow twigs to suck ants out of their nests. These two studies push back the origin of manual skills and material culture to about 14 million years ago when the ancestor of orangoutangs, chimpanzees, and humans lived. Human culture differs clearly in having symbolic elements, stressing the cognitive elements. This study addressed another question, which can perhaps in the human context not be addressed due to the complexity and the contentiousness of the issue. The researchers asked what factors correlated positively with the inventiveness of orangoutangs. *Many languages keep proverbs that address this question. In German one word is "need is the best inventor" or stated negatively "a full stomach does not like studies." Is there a basis to this statement? The researchers formulated the question more scientifically and asked whether higher rates of innovation are linked to marginal ecological conditions ("necessity"). When they used percent feeding time of orangoutangs on tree cambium as an index of food scarcity, they obtained no support for the necessity hypothesis. Other words link creativity with playful exploration (free time; the poet F. Schiller stated "humans are only then really humans when they play"). The idea of our purpose-free fundamental research culture is partially based on this idea. The inventiveness was significantly linked with playtime, but the two factors were correlated negatively. Interestingly, the*

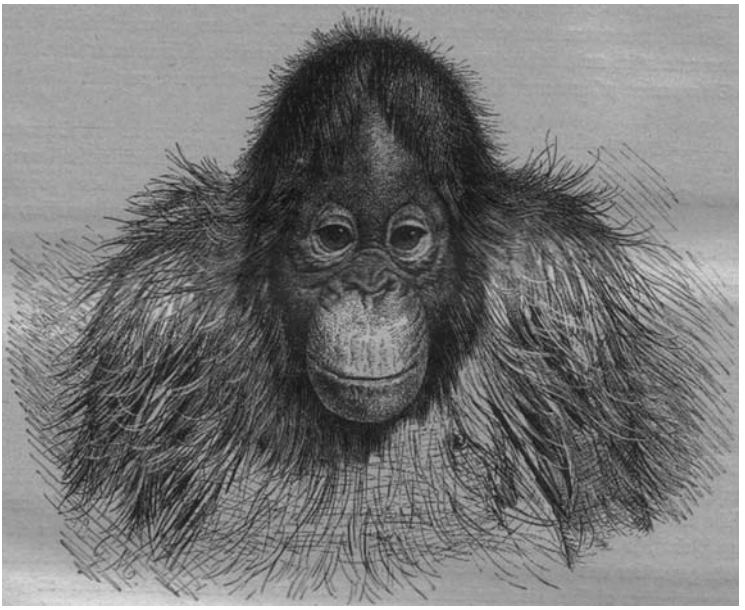


FIGURE 6.21. Juvenile orangoutang (Malay: man of the wood; Latin: *Pongo pygmaeus*), large man-like ape from Borneo and Sumatra, family Pongidae.

relationship between the time spent in association and inventiveness were significantly correlated but only for nondependant animals. This is actually an index to opportunities for social learning.

Human's Progress?

The Diet of Australopithecus

Hominid Successions

The term hominid refers to the human clade subsequent to the divergence from our common ancestor with chimpanzees. Until quite recently, a hominid specimen attributed to the genus *Ardipithecus* from the 5.8 My old Middle Awash formation in Ethiopia fitted best with the suggested divergence of the human/chimpanzees lineages dated to 6.5 My by molecular methods (Haile-Selassi 2001). Spectacular fossil finds have now pushed back this time horizon. The current hominid family tree starts with *Sahelanthropus tchadensis* at about 7 My ago (Brunet et al. 2002). This specimen is currently the closest position in the hominid clade to the last common ancestor of chimpanzees and humans. Actually, the similarity with apes were so marked that some researchers proposed the genus name *Sahelpithecus* instead of *Sahelanthropus* (Wolpoff et al. 2002). The original authors insisted on the belonging to the hominid lineage with a virtual

reconstruction of the deformed cranium of the specimen by computer tomography, which even suggested bipedalism in this earliest hominid (Zollikofer et al. 2005). The hominid tree continues with *Ardipithecus ramidus*, which bridges the time period from 5.8 to 4.2 My. At 4 My, the first *Australopithecus* is distinguished with *A. anamensis*, then comes the famous "Lucy", the 1-m high *A. afarensis* women. This branch ends perhaps with *A. africanus* (the "Taung child") at the 2.5 My time point. If one accepts this chronology and taxonomy, one could argue that until that evolution stage, no stone industry had developed in these early hominids since the oldest findings of the Olduvai stone culture goes only back to 2.5 My ago.

The "Gracile" *Australopithecus*

The aforementioned australopithecines are summarized as "gracile" (lightly built) types, characterized by a size of up to 1–1.5 m and a weight between 25 and 50 kg (there was a considerable dimorphism between the sexes; a rule of thumb in primates tells that intellectual progress was linked to the disappearance of this sex difference). Brain size was 400–500 cc, which is comparable to that of chimpanzees when corrected for body mass. Possibly, its intellectual capacity did not surpass that of extant chimps, which could explain why these hominids never learned to manufacture tools. However, australopithecines were bipedal as demonstrated by the famous footprints of Laetoli (Day and Wickens 1980). Their habitat was relatively open consisting of grassland intermingled with trees.

From the critical time period around 4 My ago where we place the origin of *Australopithecus*, we possess now fossils from a woodland context in Ethiopia as judged from the associated vertebrate assemblage (White et al. 2006). This contrasts with the aquatic, grassland, and bush land with gallery forest context described australopithecines found 1,000 km to the south in Kenya (Leakey et al. 1995). In comparison with *Ardipithecus*, the oldest australopithecines had crossed the threshold of megadontia (big teeth). The craniodental features of the fossils display hypertrophy, evolved under the selection for intensified mastication of the food. This trend keeps on over the next two million years and is only violated by the genus *Homo*, but only subsequent to the appearance of stone tools, which apparently relieved the pressure on teeth during eating.

Diet Deduced from Tooth Size and Shape

Intensive efforts were made to deduce the food eaten by australopithecines from the fossil remains (Teaford and Ungar 2000). Information was garnered from tooth size, tooth shape, enamel structure, dental microwear, and jaw biomechanics displayed by the fossils. Australopithecines showed small incisors, but large flat molars and the postcanine teeth became larger and larger. Tooth size analysis suggests seed, leaf, and berry eating. The tooth shape analysis can provide further hints. Comparative analysis in primates demonstrated that tough, difficult to fracture food is sheared between the edges of sharp crests. In contrast, hard, brittle food, which is difficult to penetrate, is crushed between planar

surfaces. Insect exoskeletons and leaves are best manipulated by concave crested teeth. Fruit eaters use flatter cusped teeth. According to the tooth shape analysis, australopithecines were capable of processing buds, flowers, shoots, nuts, and soft fruit, but not coated seeds or leaves. Notably, they were dentally not prepared to eat meat. However, after some decomposition meat becomes less tough. Via a scavenger lifestyle, some meat might thus have found entrance into the diet of australopithecines as indirectly suggested by isotope evidence (Sponheimer and Lee-thorp 1999). *Australopithecus* was probably a scavenger and ate what remained from the prey made by larger animal predators. This interpretation was deduced from dental scratches on the bones of the prey first by the animal predator and only later by *Australopithecus*.

Tooth Wear

The thick enamel of australopithecines suggests abrasive food in the diet. The scanning microscope can reveal tiny pits and scratches on the tooth enamel ("microwear patterns"), diagnostic of the diet. Grass feeding leads to linear scratches on teeth; leaves in contrast polish the teeth; bone eating results in tiny pits in the enamel. Unfortunately, the established methods of studying microwear are error-prone and therefore anthropologists looked for more reliable methods combining scanning confocal microscopy with fractal analysis (Scott et al. 2005). They first calibrated their method with the monkeys *C. apella*, which eats fruit flesh and hard, brittle seeds, and *Alouatta palliata*, which consumes leaves and other tough food. With these data they analyzed the microwears on teeth of *Australopithecus africanus* and *Paranthropus robustus*. They deduced tough food for the former and a diet composed of more hard and brittle food for the latter. However, they warned to oversimplify this pattern into a dichotomous food preference because it may only reflect fall-back food choices consumed during some critical periods of seasonal food shortage.

In other studies, australopithecine teeth showed evidence for a fruit-containing diet like in chimpanzees and not for the tough plant material ingested by orangoutangs. *Homo erectus*, in contrast, showed teeth with signs of heavy wear and tear with pits, striation, and polish suggesting a nonspecialized omnivore. Dental microwear showed at the same time gorilla-like fine wear striae and baboon-like pits indicating a wide range of diets.

Trends for Dental Robustness

The australopithecines finally showed thick mandibular bones capable of developing a substantial torsion and bite force with a high occlusal load. These hominids had the mastication properties to eat fibrous, coarse food. When looking for time trends, *A. anamensis* adapted to hard abrasive food, *A. afarensis* developed the increased mandibular robustness, and *A. africanus* the increase in postcanine tooth size. Overall the comparison of *Australopithecus* with *Ardipithecus* suggested a dietary shift in face of climatic variability. Hard abrasive food became apparently increasingly important in the Pliocene. For

the paleontologists, this change signals an ecological breakthrough involving a niche and food expansion with an intensified exploitation of more open African Pliocene habitats.

From Hominid Stone Tools to the Control of Fire

The Oldest Industrial Complex: Olduvai

The Olduwan stone-tool industry was named after the 1.8-My-old stone artifacts after the Olduvai Gorge in Tanzania, but these are not the oldest pieces of this form. This culture can be traced back to 2.5 My ago from Gona in Ethiopia (Semaw et al. 1997) or to 2.3 My in Turkana, Kenya (Roche et al. 1999). Human technology had a humble beginning here: It only needed to select a suitable pebble from a streambed, to strike it with another stone to produce sharp-edged flakes or crude choppers. The stone cores show evidence of pitting and bruising. The working edges are very sharp. Late Pliocene hominids had already mastered the basics of stone-tool manufacture, although only multipurpose tools like hammerstones suitable for pounding activities were made. Knapping stones, understanding of the fracture mechanics was already well understood. Refits of flakes to the original stone showed how they decided to strike the original pebble.

The tools cannot be dated directly, their age must be inferred from the archaeological stratum that contained the artifacts. The faunal remains include many mammals and within them mainly grazing species like bovids, suids, equids ("cows," "swines," "horses"), fish, reptiles (shell fragments of large tortoise) and ostrich-egg fragments. While this demonstrates perhaps some hominid collection strategy, no evidence of man-made action was found on the animal remains. The most striking aspect of this stone industry is that it did not change over a long time period, spanning 2.5—1.5 My ago; in the literature, this is called the technological stasis of the Oldowan industrial complex. It is tempting to link this era to the life span of a specific hominid lineage. Hominids living before 2.5 My were unable to this technological "achievements," while new populations emerging at 1.5 My ago climbed to new heights of stone technology due to higher brain capacities and thus technical intelligence.

The Maker of the Olduvai Tools

But what face do we fix to the Oldowan industry? Here, one must probably directly confess our current ignorance. Human remains regularly make headlines in newspapers and fill also the columns of research journals like *Nature* and *Science*. However, basically the populations of early hominids were small, the likelihood of fossilization was low, therefore the fossil record is still very fragmentary. Actually, the number of skeletal remains is not so bad, but we frequently do not know whether this lineage died out or led to modern humans. The case is vividly demonstrated with the maker of the Olduwan industry. The maker was variably referred to as *Homo rudolfensis* (a name now mostly rejected

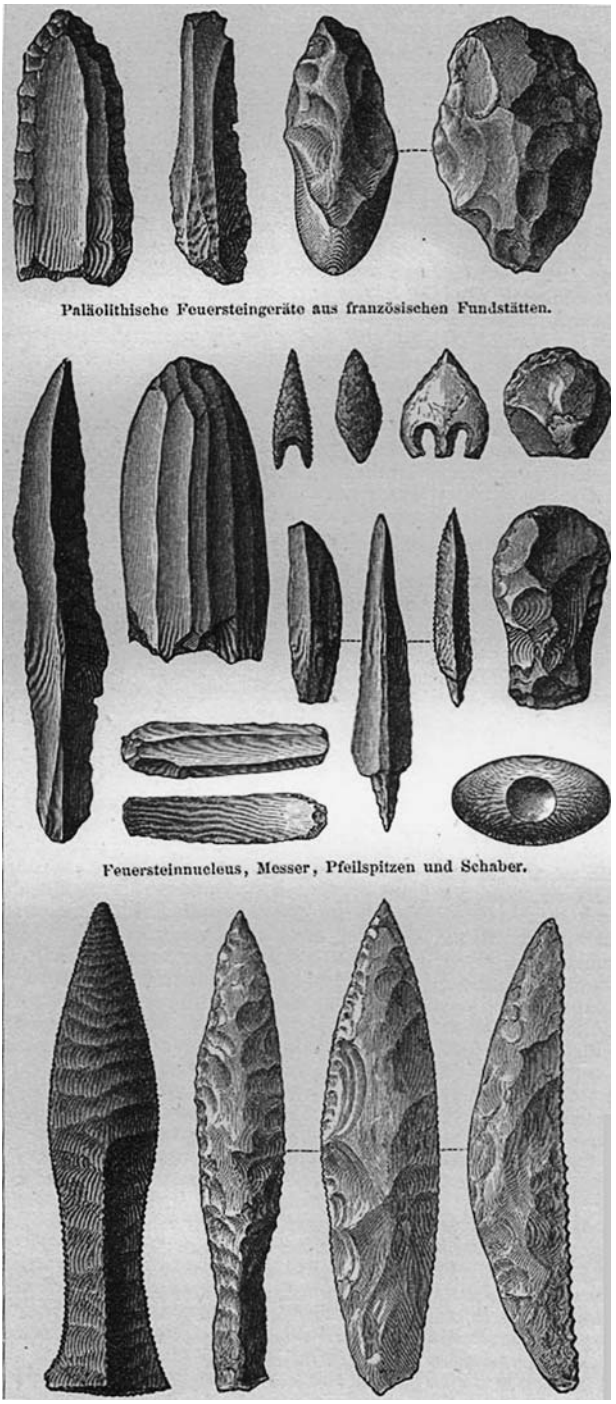
by anthropologists) or *Australopithecus rudolfensis*, while most researchers prefer a new genus name with *Kenyanthropus rudolfensis*.

From the "gracile" australopithecines, the actors of the previous section, the makers of the Olduvai tools were differentiated by paleontologists as "robust" australopithecines. These were heavily built hominids with small brains and large jaws and big chewing teeth. These hominids are currently placed in at least two different genera *Australopithecus* (controversially also called *Homo* or to avoid conflict *Kenyanthropus*) *rudolfensis* and *Paranthropus* with two lines *P. robustus* and *P. bosei*. From these hominids, we possess as oldest remains the fairly complete skull from Lake Turkana dated at 2.5 My ago. These robust hominid types are found in eastern Africa between 2.3 and 1.3 My ago. The robust stature is commonly attributed to their diet that required heavy chewing and possibly consisted of low quality vegetable food, such as roots and nuts. Morphologically, *Paranthropus* showed initially a rapid dental evolution, which was then followed by a long stasis. The apparent conformity between a consistent dietary adaptation, dental, and technological stasis makes a powerful circumstantial case for linking *Paranthropus* with the Olduvai industry (Wood 1997).

The genus *Homo* is currently thought to start with *Homo erectus/ergaster* and not with *Homo habilis*, which is currently delegated to the *Australopithecus* lineage. However, from its brain size (500–650 cc) and its extension in time, which fits at least part of the Olduwan industry period, *Homo* (alias *Australopithecus*) *habilis* could also still fit the ticket. This would justify the older name of this hominid as the "handy man." As in many cases of hominid evolution, we must conclude that the jury is still out and we do not yet know in what hands to lay the Olduvai stones.

The Face Behind the Acheulean Technology

As abrupt as the Olduvai technology made its appearance, so suddenly was the striking change to the Acheulean stone technology at about 1.6 My (Figures 6.22 and 6.23). This industry impressed as bifaces, teardrop-shaped hand axes that were worked around all of the margins. They persisted until about 150 Ky ago and became the most popular "Swiss Army knife" of the Paleolithic. The earliest finds are from Konso in Ethiopia where roughly made biface hand axes and picks of up to 27-cm length were manufactured (Asfaw et al. 1992). The flakes are untrimmed. In contrast to the Olduvai stone tools, the Acheulean tools are not only closely associated to large mammal bones but the bones showed hominid-induced modifications like percussion pits, flake scars, and cut marks. Butchery is their apparent task, while the food use of the Olduvai stone tools is less clear, but might be linked to resistant plant material. Again in contrast to the previous period, the Acheulean culture provided already in the Konso sediment a hominid mandible that allowed the identification of the carrier of this culture. It is *H. erectus*. African specimens are sometimes called *H. ergaster*, and *H. erectus* is reserved to fossils found outside of Africa. To circumvent this ambiguity some anthropologists use the clumsy name *H. erectus/ergaster*. The Nariokotome boy described by Walker and Leakey is the most complete early hominid ever found.



Paläolithische Feuersteingeräte aus französischen Fundstätten.

Feuersteinnucleus, Messer, Pfeilspitzen und Schaber.

It dates from 1.6 My ago and comes from Lake Turkana in Kenya. It is a male, young adolescent 1.5-m tall, which would have reached modern proportions as an adult (1.8 m and 68 kg), but showed a significantly smaller brain size (900 cc vs. 1,500 cc for modern humans). Its large body size would have provided heat and dehydration tolerance; together with its advanced tool kit it would have contributed to the success of this early species of our genus *Homo*. It lived in many ecological settings and saw a wide geographical distribution: *H. erectus* was found in Indonesia and China more than hundred years ago and became famous as Java Man and Peking Man, respectively. *H. erectus* was also found with a mandible in Dmanisi, Georgia, dated to 1.6 and 1.8 My ago (Gabunia and Vekua 1995). It shared a number of similarities with both African and Chinese representatives. A clear-cut specimen of *H. erectus* dated to 1 My ago was also found in Awash, Ethiopia making the distinction of an African *H. ergaster* from an Eurasian *H. erectus* doubtful (Asfaw et al. 2002).

Butchery

In Ethiopia *H. erectus* lived in an open grassland habitat with water margins as demonstrated by equid, bovine, and also hippo fossils. Butchery of these large mammals is evident. The different African and Eurasian specimens represent probably demes, i.e., communities below the species level. Many aspects of *H. erectus* remain still elusive: Its origin is undefined and the direction of its dispersal is not clear. Did he emigrate from Africa to Eurasia, stood in the Caucasus at the gates of Europe without intruding this continent (was the climate too cold or the carnivores too big?) and taking route to Asia? Or was he an immigrant from Asia into Africa? The stone tools are traditionally differentiated into a western and eastern Acheulean separated by the Movius Line extending from the Caucasus to the Bay of Bengal. However, at 800 Ky ago, the eastern and western industries were not so different to justify speaking of different cultures associated with different species (Yamei et al. 2000; Goren-Inbar et al. 2000). The lithic findings both at Gesher Benot in Israel and in Bose, China, reflect adroit technical skills and in-depth planning abilities suggesting complex hominid behavior at the beginning of human globalization.

Old Age Food Care

A beautifully preserved nearly complete skull from the same layer in Dmanisi yielding the *H. erectus* mandible demonstrated an astonishing insight into the complexity of our genus 1.7 My ago. It shows an edentate (toothless) skull, all the

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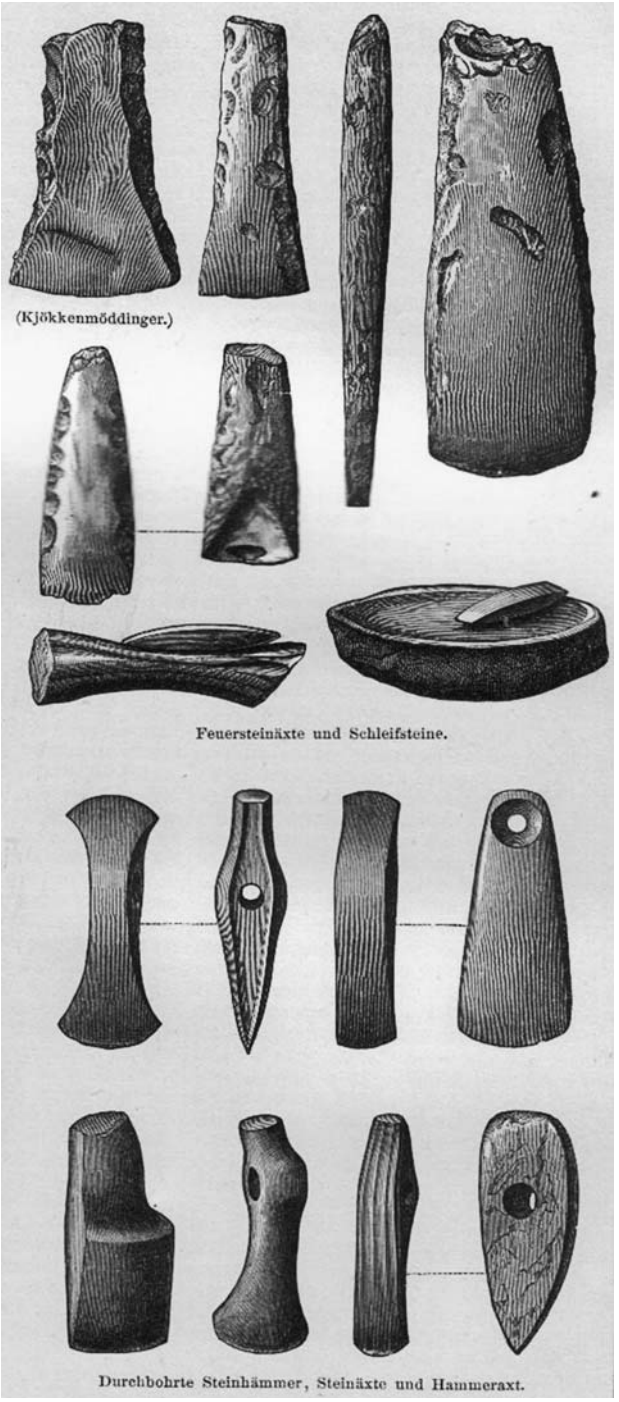
FIGURE 6.22. The figures illustrate the evolution of the stone tools used by humans through the different periods of the Stone Age. The Stone Age is commonly divided into a Paleolithic period, where further subperiods can be distinguished according to the stone technology. The periods are named according to French archeological sites as Acheuléen, Moustérien, and Magdalénien in this temporal order.


(Kjökkenmöddinger.)
Feuersteinäxte und Schleifsteine.
Durchbohrte Steinhämmer, Steinäxte und Hammeraxt.

maxillary and most of mandibular teeth were lost due to aging or a pathological process (Lordkipanidze et al. 2005). The remarkable observation is that this occurred well before death as the mandibular bone showed substantial resorption. The skull was associated with stone artifacts and animal bones showing cut and percussion marks. Meat consumption was probably the nutritional basis for this population living at this high latitude. The survival of a toothless individual suggests that it fed on soft tissue like bone marrow, brain tissue, and soft plants or depended for the mastication on the help of other individuals from his clan.

Fire Use

Mythology and fairy tales do not place the events in a historical time frame. Hänsel and Gretel from the Grimm brother would probably loose a lot of their attraction to a broader audience, when a cultural anthropologist would place the event to a famine that occurred 1625 in Marburg, Germany (this is purely fictive). However, scientists are a curious blend of people and cannot resist to search for indications of a place and a time even when reading fairy tales. To them it might come as a satisfaction that a famous act of the Greek mythology can now be located and dated. Prometheus feels pity with the earthlings that live under miserable conditions, and he steals the fire from the jealous Greek gods who do not want to share it with humans. There is definitively something special with the Holy Land: Israeli archaeologists found the earliest evidence of hominid control of fire. The place is again the above-mentioned Gesher Benot at the Dead Sea associated with the Acheulean stone industry, and the time is about 800,000 years ago. The site shows evidence for localized burned flint and wood (wild olive), heated to 500 °C, which they interpret as hearths. Alternative explanations were discarded: peat fire by lack of substrate, wildfire following lightning by the localized nature of the heating and the sparing of adjacent wood, and finally underground fire as burning roots because it would not have developed the 500 °C heat observed in the purported hearths (Goren-Inbar et al. 2004). If confirmed such an early use of fire would have led relatively early to dramatic changes in hominid behavior with respect to food preparation, defense against wild animals, and social interaction (light and heat in the night). Other archaeologists found indirect evidence for the controlled use of fire at the much younger Peking Man site dated to 500,000 years ago but noted the absence of ash residues and hearth features (Weiner et al. 1998).

FIGURE 6.23. The stone artefacts at the top are from a Danish culture known as the *Kjökkenmöddinger*. These people lived through the period described as Mesolithic. This was a difficult period when compared to the period of the great hunters. From their diet they left mainly heaps of oyster and clamshells, but few big games. At the lower part of the figure are stone tools from the Neolithic.

On Cooking and a Varied Diet

Homo erectus is also the inventor of cooking. This habit did not only contribute substantially to food safety but it also reduced the advantage of big teeth. Cooked food requires much less cutting, tearing, and grinding than raw food. One of the distinguishing features of *H. sapiens* from *H. erectus* is the further diminution in the size of the teeth. Extant hunters like Kalahari Bushmen or Australian Aborigines do not live from the meat of big game alone. Snakes, birds and their eggs, locusts, scorpions, centipedes, tortoise, mice, hedgehogs, fish, crustaceans, and gastropods figure on their menu plan. These animal morsels were complemented by plant delicacies. The latter included fleshy leaves, fruits, nuts, roots, and seeds like hackberry. *This type of variable diet was probably not far from that of early hunters. When considering the effect of diet on human health, one should keep in mind that we were selected by evolution for this type of food. Members of early and poor agricultural societies have a monotonous diet in comparison, and our food has diverged substantially from that of our ancestors.*

Palaeofaeces

For example, paleofecal deposits from a place in Texas that showed archaeological evidence for 10,000 years of intermittent occupation by prehistoric hunter-gatherers were recently investigated by DNA technology (Poinar et al. 2001). These 2000-year-old samples identified—in the plant diet—agave, yucca, sunflower, hackberry, acorn, edible nightshades, legumes were detected by amplification of a chloroplast gene, and cactus was identified microscopically. The animal diet consisted, according to DNA analysis, of sheep, goat, pronghorn antelope, and cottontail rabbit. Microscopy identified small mammals (packrat, squirrel) and fish as part of the diet. The authors pointed to two important implications of the data. One is more technical: Archaeologists emphasize the role of small mammals in hunter-gatherer diets. The sampling methods underestimate systematically the contribution of large animals. They were butchered at the kill site and only the pure meat was carried back to the occupation site, leaving thus only few large animal remains. The other is nutritional: An individual stool sample contained food derived from four animal and four plant sources. These humans were clearly omnivores. In addition, this is a remarkably rich diet. Cave hunter-gatherers had a more varied and nutritionally sound diet than humans dependent on early agriculture.

Hunters and Gatherers: The Origin of Grandmother's Recipe

The Reinsdorf Spear

Archaeology is literally finding the needle in the haystack, but this improbability of findings does not discourage the followers of this science. Apparently, it

spurns only the age-old instinct of the hunter and gatherer in us. And then there are always these stories of the absolute lucky characters that struck gold. Here, I am not alluding to Heinrich Schliemann who decorated his wife with the gold treasure of Priamos at Troy. I think here of H. Thieme, a curator in Germany, who fights an impossible battle against a 50-m-high shovel-excavator that digs through a brown coal mine. His task is to stop the engine should it unearth an interesting archeological find, in its tons per minute progress. What he found made his fellow archaeologists speechless (Dennell 1997). In the Reinsdorf Interglacial dated to 400,000 years ago, he found notched pieces of wood for holding stone tools and 1-m-long sticks for stunning small prey or a stabbing spear for killing an already wounded or corned animal at short distance. But the best is still to come: He found three complete wooden spears, 2-m long, made out of very hard wood, carefully manufactured from a 30-year-old spruce tree. The spear has the aerodynamic form of a modern javelin and is certainly destined for big game hunting (Thieme 1997). Associated with these finds were a thousand of large mammalian bones, some of them with cut marks from butchery. The bones included those of straight-tusked elephants, rhinoceros, red deer, bears, and horses. The site also yielded a hearth. According to this site meat from hunting may have provided a great share to the diet of the hunters. Although this picture fits well to that widely distributed in laymen, professional archaeologists were wary with the issue of big game hunting in the Lower and even the Middle Paleolithic. They saw hominids more as scavengers competing with hyenas for animal prey, killed by big carnivores. The evidence were tooth marks from hominids on animal bones overlaying and not underlaying those of bigger carnivores, which according to this evidence killed the prey and only the leftover was the meager meal of hominids. Evidence for purposeful hunting was too fragmented to convince archaeologists and big game hunting was delayed until the arrival of fully modern humans at about 40,000 years ago. The spears from Schöningen changed this judgment: They had the same proportions, with the center of gravity a third of the way from the sharp end, and the tip of the spear came from the base of the tree trunk where the wood is the hardest. The spears are not the work of a 15 min culture; substantial planning activity was necessary to achieve these hunting weapons. The finds added to other evidence.

Homo heidelbergensis as Hunter

Although with an age of 120,000 years much younger, another spear from Lehringen in Germany was found where you would expect it: between the ribs of a straight-tusked elephant. A tip of a likely spear was found in Clacton, England, from a comparable period as that of Schöningen and a 500,000-year-old scapula from a rhinoceros unearthed in Boxgrove, England, showed a circular hole pointing to wounding with a spear. Boxgrove delivered also the hunter; to be precise, it was the tibia from the earliest Englishman. The size and robustness of the leg bone left no doubt about the male sex, the hunter's weight was calculated to 80 kg. He had the strength to throw the Schöningen spear. The stratum

containing the tibia was associated with typical flint bifaces of the Acheulean industry, but the tibia was attributed to another species of the genus *Homo: H. heidelbergensis* (Roberts et al. 1994). This species has a larger brain than *H. erectus* (1,200 cc vs. 900 cc) and has a wide distribution over Europe. The type species is the famous mandible from Mauer 1 near Heidelberg, Germany. Other finds are from Greece (Petralona cranium), Ethiopia (Bodo cranium), and even footprints from volcanic ash in Italy (Mietto et al. 2003). Most anthropologists think that *H. heidelbergensis* originated from *H. erectus* in Africa at about 1 My ago and gave rise to more recent *Homo* species, including *H. sapiens*. Taken together the data mean that Europe was well colonized with *H. heidelbergensis* at 500,000 years ago, while evidence for an earlier human occupation of Europe by for example *H. erectus* is lacking (Gamble 1994).

The Gatherer

The traditional view sees the tribes with adult males as specialized hunters and women as gatherers. Although direct evidence for this scenario is lacking, it would fit classical prejudices and probably natural inclinations. Extant male humans have a greater aggressiveness and a better 3-D orientation in the environment predisposing them for hunting. On the other side, one sees women caring for children, gathering fruits, mushrooms, tubers, roots, grains, and small animal prey. Probably, cooking also became part of their task in that time period. We still see this heritage in psychological tests of modern women who easily outcompete their male counterparts if the parallel execution of multiple tasks is requested. Food preparation and not only food foraging became part of the everyday activity. We see this trend when we look to a hominid tree that depicts the hominid fossils on 2-D graph with an age and postcanine teeth size as axes. It has a definitive Y-shape. At the stem is the hypothetical chimp-like, forest-dweller, arboreal and fruit-eating ancestor of the hominid tree. The australopithecine trunk is then bifurcating into the *Paranthropus* branch with big teeth and the *Homo* branch with small teeth. The small teeth of the *Homo* branch does not necessarily indicate meat eating, but vegetable material was perhaps prepared to make it more palatable to smaller teeth.

Anthropologists on Grandmothers

In a *Nature* editorial titled "We Are What We Ate" anthropologists discussed the value of observations in a hunter and gatherer population in Tanzania (Wood and Brooks 1999). What struck the anthropologists was the role of the postmenopausal grandmothers. They cared for themselves, and their grandchildren by using foraged tubers. Thus their daughters are released to gather food and to become pregnant again. *Hunter-gatherer societies must follow the animals imposing a substantial mobility on the clan. The spacing of birth is therefore anticipated to be 4 years that a mother has only to carry a single child during their migration. Infanticide was supposed to be frequent as excessive child caring could overstretch young women. Here physically fit grandmother*

could play an important, and some would say decisive, role in the development of modern humans. Via selection, this cooperation of grandmothers could lead to important changes ranging from longer lifespan, an extended growth phase with delayed maturity giving more time to social learning, and also an increased adult body mass. The fertility of the clan would profit from the cooperation of the grandmothers (the "grandmother hypothesis"). But what is the evidence for this hypothesis?

Life Histories in Mammals

First, some facts: Human children, unlike other primates including chimpanzees, are unable to feed themselves when they reach the weaning age. The food we eat is too difficult that a young child could handle it. Assistance in food provisioning, food preparation, and even feeding will be important. If you see assistance in animals you see more frequently premenopausal individuals, which help their parents to breed.

Mammals fall along a continuum of life histories. At one end are species were maturation is quick, fertility is high, and adults die young (e.g., mice). At the other end, maturity is delayed, reproduction is slow, and adults usually live long enough to grow old (e.g., elephants). Interestingly, chimpanzees and woman have comparable life histories; both show female fertility peaks before 30 years of age and virtually none after 45 years. However, then the curves dissociate: chimpanzee survival rates fall along with fertility; in the wild less than 3% of the adults are older than 45. In contrast, even in the hunter-gatherer population a third of the women are over 45 years (Hawkes 2004). *Grandmothers could be useful and the toothless Georgian* H. erectus *individual demonstrates that its clan shared this belief. Formulating a hypothesis and proving evidence for it are, however, two different things.*

Epidemiologists on Vital Statistics

Recently, a cooperation between biologists and epidemiologists set out to test the hypothesis with demographic data from a multigenerational individual database, involving 3,000 women from traditional farming societies in Finland and Canada in the preindustrial age. Indeed, the evaluation showed that after extensive control for confounding factors, women gained two extra grandchildren for every decade they lived after age of 50 years. Both sons and daughters experienced this granny effect; they show greater fecundity and raise more children to adulthood and start reproducing at a younger age. This grandmother effect disappeared when the grandmother lived more than 20 km away (Lahdenperä et al. 2004). These data have enormous implications for current life history discussions. It shows not only that grandmothers contribute to the survival of the tribe by increasing the fertility of their children and by decreasing childhood mortality; the implications go farther: Senescence and lifespan can now be interpreted as a selected evolutionary trait. Notably, the study showed that the hazard of death in the grandmother increased sharply when their daughters passed through menopause. Now they

can slip into the role of the grandmother and the grand-grandmother becomes dispensable. Notably, the data showed that the grandmother effect showed some attrition when their age increased beyond 60 years, which is intuitively plausible since their physical fitness will decrease. *There is some food for thought in these data. One might postulate that the current trend of delaying childbearing in European societies could lead to a further increase in lifespan. Then for the male readership, they could ponder the question why females outlive male in most industrial societies. Is the stronger sex selected for physical robustness during active hunting adulthood, but since we do not contribute so much to childcare, men are from an evolutionary viewpoint dispensable at an earlier age? A complicating factor is certainly that male fertility declines with age, but does not know an andropause. How does the preference of many women for older man and men for younger women influence evolutionary life histories?*

Grandmother's Recipe: Another Hypothesis

There is another hunter-gatherer effect that might still exist in our subconsciousness and that influences our food preferences. In the food industry, marketing groups have two contradictory strategies to sell their products. One is the label "New," which is perceived as an attractive argument to buy a better food; the other, although less frequently used, is "Grandmother's recipe." I think we have here a basic dilemma of human nutrition, which is explained by the grandmother hypothesis in the gatherer societies. Let's do the theoretical experiment to hunt with early humans. We have seen that mammals were the favorite game—the only question was to find them and to kill them. We heard of toxic animals that discourage the appetite of their predators with poisons. I am not aware that mammals use this strategy: they run, they fight, they hide, perhaps they stink, but once culled there is practically no risk associated with the consumption of the meat (parasites and infectious agents put aside). Hunters did not need much toxicology knowledge in their business. The situation is very different for the gathering women. Plants use the chemical club extensively in their fight against herbivores. This might be just antinutrients or bitter compounds to dampen the appetite, but many vegetables do not shy away from frankly killing the predator with potent toxins. Making a distinction and knowing plants, their nutritional and pharmacological properties, became essential for the survival of the clan. And here we are back with the contradictory marketing strategy of the food industry. If you are too conservative in your food selection (a German proverb says "The farmer eats only what he knows"), you avoid intoxication, but in a clan, which lives below its nutritional needs, survival depends also on the finding of new, better, and more nutritious food items. The farmer has no problem, he has sown what he is eating and he weeds out of his field what does not belong there. The situation was different for the women gatherer. She had to choose what Mother Nature was offering her. Worse, since hunting dictates the migration behind the game, they get in constantly changing places. Geographical landmarks became useless for remembering nutritious plant material; they had to memorize the plant. While only a handful of games existed, the plants get into

the thousands. Small errors like confusion of A. campestris, *the champignon of Paris, with a poisonous* Amanita *mushroom could literally wipe out the family. Women had therefore to learn to distinguish and the best teacher would be her own mother, who has one generation more experience. However, to what extent can you trust the judgment of your mother? Here, humans apparently chose a simple, but efficient criterion: Ask the oldest women of the clan. She has the largest botanical knowledge and she has never made a fatal error, otherwise she would simply not have reached old age.*

Extensions

All traditional societies follow this scheme (old men have aspirated to this position perhaps with the transition from matrimonial to patrimonial family structures, but this characteristically did not extend to eating and cooking, except for the chefs in Western restaurants). Before the industrialization of food production, any food item was a potential risk and substantial knowledge was necessary to prepare a healthy meal. It is to these basic instincts of survival that the advertisement "Grandmother's recipe" alludes. Men distrusted women throughout history for poisoning them, and they knew that women did know a lot about plants and their secret powers (not only toxins, but also hallucinogens and even medicinal properties). The borderline between an old women knowing herbs and their healing power to witches that could in their imagination wipe out entire clans and societies was small and delicate. I suspect also that the resistance of substantial parts of the European population against the perceived and, frequently, rather theoretical risks of genetically modified food strikes an ancient emotional string of the gatherer societies. You had to eat, but you were never really sure whether you would see the next morning when using a new food item in your diet. All scientific arguments of a young male scientist in a white lab coat will not placate the deeply emotional concerns of the consumers (which include many individuals who studied science), they probably need a grandmother addressing their concerns after a lifetime consumption of GMO (genetically modified organism) food.

On Neanderthals and Cannibalism

His Place on the Tree

In the previous section, I took the liberty to anticipate relatively humane thinking, but we lack clear evidence whether we can do that. With respect to our evolutionary ancestry, most anthropologists see us as the follower of H. heidelbergensis. *Thus genes from the Schöningen hunter should be in us. However, we are not the only offspring of this tree: Long before* H. sapiens *walked on earth another* Homo *species deviated from the* H. heidelbergensis *branch, namely* H. neanderthalensis. *This is actually the first early human where the art of ancient DNA analysis could complement the fossil finds. The museum guarding the historical remains of the first Neanderthal find offered a bone piece on the*

altar of molecular biology, and they were rewarded. The scientists succeeded to amplify some mitochondrial DNA out of it (Krings et al. 1997). More recently mitochondrial DNA of even better quality was recovered from a Neanderthal child in the Caucasus who was dated to 29,000 years BP. Now even a Neanderthal genome sequencing project is on its way (Green et al. 2006). The extinction of the Neanderthal line is currently fixed at 28,000 years BP; the child is thus one of the last survivors of this lineage. The German and the Caucasian Neanderthal subjects were separated not only by 2,500 km geographical distance but also by about 200,000 years from their common ancestor. The last common ancestor of *H. sapiens* and *H. neanderthalensis* lived according to the mitochondrial DNA argument perhaps 700,000 years ago (Ovchinnikov et al. 2000). The split of *H. sapiens* from the ancestor branch (being it *H. heidelbergensis* or other offshoots of *H. ergaster* like *H. rhodensis* is controversial, see Stringer 2003) is also well documented now. The Herto find in Ethiopia gives a minimum fossil age to our ancestors of 160,000 years (White et al. 2003), while the Kibish find, also from Ethiopia, would push the earliest well-dated anatomically modern humans to nearly 200,000 years BP (McDougall et al. 2005). In contrast, the expansion of our species did not occur before 60,000 years ago. There is thus clear fossil and archaeological evidence that *H. sapiens* and *H. neanderthalensis* are contemporary. How much contact they had is not clear.

Cold and Food Adaptations

In Spain, the late Neanderthal and *H. sapiens* occupied different territories separated by the Ebro River. Archaeologists did not find evidence that behavioral and technological transfer occurred between both populations (Mellars 1998). The relatively short, stocky bodies of the Neanderthals were interpreted as a cold adaptation to the periglacial north of Europe. Yet, most of the Neanderthals lived in the temperate areas of southern Eurasia. Their large noses and faces were probably due to the pressures of heavy chewing of their diet and the use of jaws as tools and not for the warming of cold air streams in nasal passage as was also proposed. In France, both populations occurred side by side: Neanderthals are associated with the "Mousterian" stone culture, which is developed from the Levallois technique. These tools were shaped by removing flakes from a core, followed by removal of one final flake, which formed the tool itself. Fireplaces are regularly found, and hunting remained the basis foraging activity. The relatively cold climate restricted fruits probably to a few berries. Parallel you find the "Aurignacian" tools associated with *H. sapiens*. In addition to stone tools, you find numerous bone tools, many are pointed and might have served as spear tips.

Emancipation

The French "Châtelperronian" culture led to an archaeological emancipation of the Neanderthals (Bahn 1998). Bone tools were found and a wealth of ornaments were found. Animal teeth, ivory beads, and bones with perforations suggested necklaces. These Neanderthals had objects created for visual

display on the body, we have to anticipate that these ornaments communicated some meaning; Neanderthals thus elaborated and transmitted autonomous codes. Anatomical investigations showed that the hand of the Neanderthals was capable of substantial dexterity (Niewoehner et al. 2003), other investigation of the larynx suggested the use of speech. Suddenly, the shaggy, subhuman brutes transformed into cultured human beings. Tool use became more sophisticated. Levallois flakes of the Mousterian level dated to 40,000 years age showed a black substance on their surface. Chemical analysis identified it as remnants of a hafting material used by Middle Paleolithic people to glue handles on their tools. The raw bitumen glue was heated to extreme temperature before application (Boëda et al. 1996). We do not know with certainty whether we can attribute these complex multicomponent tools to the Neanderthals. However, the initial simple idea of archaic hominids making simple tools that were replaced by anatomically modern hominids that made complex tools cannot any longer be maintained.

Dark Sides: Cannibalism?

The appreciation of the Neanderthals has lived cycles of extremes. If you enter the archaeological museum in Neanderthal near Düsseldorf, Germany, you see a pretty Neanderthal woman receiving you in the entrance hall. She looks as if she would have appreciated the Arcy necklace. But beware: Despite all speculation on sexual attraction between human species in science fiction movies, anatomical hybrids between both human forms have not yet been clearly identified. Some anthropologists speak of the Neanderthals as a subspecies of H. sapiens. *However, the postulated morphological continuity between both forms could not be demonstrated, even the late Neanderthals showed very distinct anatomical features, which suggest a reproductive barrier between both populations (Hublin et al. 1996).*

The dark side of the Neanderthal man was a subhumane brute with a club in his fist as he was represented near the old museum in Düsseldorf. Archaeology has experienced rather dramatic swings in the assessment of the Neanderthal culture. The dark side started with archaeological findings in the 1930s that were interpreted as cannibalism in Neanderthals. The early cannibalism signs on the Monte Circeo skull turned out to be a misinterpretation; they were caused by gnawing hyena. Somewhat better is the evidence from a finding in Valence, France, where Neanderthal bones showed cut marks from a flint tool and fresh bone breakage (Defleur et al. 1993). This looks like quite good evidence, but we should not precipitate a conclusion; ethnographic studies showed mortuary practices involving bone defleshing and secondary burial of bones, but we are not aware of sophisticated burial rites in Neanderthals.

American Cannibalism

Cannibalism in humans is a very contentious subject that touches psychological barriers (Diamond 2000). We should not blame the Neanderthals; cannibalism was widespread in modern humans, too, and this as recent as in the aftermath

of the Russian Revolution. There it was a widespread phenomenon that was not only explained by starvation as documented in an excellent historical account (O. Figes *A People's Tragedy*). Many opponents have refused to accept the evidence for cannibalism, but archaeologists have gone very far to prove the case (Marlar et al. 2000). Excavation at a prehistoric Puebloan site in Colorado that was precipitously abandoned for unknown reason showed the bodies of people of both sexes, disarticulated, defleshed, and apparently cooked. The cutting stone tools showed molecular evidence for blood and the cooking pots demonstrated traces of myoglobin of human origin. A coprolite (ancient fecal deposit) of human origin was found near one hearth. It contained no starch granules from a vegetarian diet but again showed human myoglobin. This observation does not show how common cannibalism was on the territory of the USA.

Modern Cannibalism: From Mourning Rites to Kuru

Cannibalism in contrast never became a widespread eating habit, and there might be good reasons for it, which have nothing to do with religious or ethical feelings. The case is best illustrated by a ritual cannibalism practiced by modern humans in the Fore region of Papua New Guinea. Endocannibalism is, in that region, a rite of mourning and respect for the dead kinsmen. The exploration of this rite was actually not done by ethnologists but by neurologists of the National Institutes of Health in Bethesda, especially D.C. Gajdusek, who lived himself through glory and misery like few of his fellow scientists. In his report, women opened the dead with their bare hands when they prepared the tissue for consumption. Horrible as it sounds, they scooped the liquefied brain by hand in bamboo cylinders. What followed brought the tribes to the brink of extinction and changed the male/female ratio in the Fore region to 3:1. The reason became tragically clear a few years after the start of epidemiological investigations. Children of both sexes crowded around the women during these rites, while men stood apart. Women and children apparently got infected by a mysterious agent that defied for a long time a molecular definition. Yet, epidemiological observations gave no indication for its contagion. No disease was ever seen in foreigners living in this area, while many children from the Fore tribes developed, sometimes after decades, the illness when living for years abroad. More than 2,500 cases were reported since the medical investigations started in the late 1950s. Kuru, as the disease was called, has been disappearing gradually during the last 40 years since the rites were suspended. The remaining cases showed a conspicuous rise in age of onset that pointed to an exposure at these cannibalistic rites.

The Symptoms

Even if the incubation period could be very long (which earned the illness the qualifier a "slow virus disease" in its early days), when the symptoms of Kuru set in, death within a year or so was the inevitable outcome. The subjects had self-diagnosed unsteadiness of stance and gait, they searched support of a stick for

walking, tremor and ataxia set in and the patients needed the help of tribesmen to walk. Kuru means shivering, which is a cardinal symptom, in this period. Then follows a sedentary phase characterized by emotional instability with outburst of pathological laughter and gradual loss of speech, while dementia was not observed. In the third stage, sitting becomes impossible; the patients become incontinent, dysphagia leads to starvation and then to death within 9 months. The pathology is restricted to the brain, showing a spongiform encephalopathy and amyloid-containing plaques. The laboratory findings are unlike to any other infectious disease, no immune or inflammatory response is induced, but the brain material of the victim contains high titers of infectious material that could after much testing be transmitted to laboratory animals. The mysterious agent belongs to an entirely new class of infectious proteins (prions, more on it later in the BSE section). At the moment it is sufficient to conclude that cannibalism is evolutionary a dangerous strategy since it involves dietary exposure to congeners – thus no species barrier provides protection against disease transmission.

The Hobbit: Wanderer Between the Worlds

Are we Orphans?

Humans are fascinated by the idea to establish a contact with other intelligences on a different planet. Martians visited at least in science fiction films our home planet. The hope for life on Mars or on the Jupiter satellite Europe has not yet faded, but even the most optimistic biologists do not expect more than microbial life forms at these places. Astrophysicists are used to look for planets in other solar systems and designed the SETI program emitted into the cosmos. Until now we have not received an answer to our messages. Perhaps the probability of extraterrestrial life has increased after the observation of planets circling around other suns. After the demise of the Neanderthals, H. sapiens *saw itself as a cosmic orphan. Then a team composed of Australian and Indonesian archaeologists took the scientific and the lay world by surprise: They found another member of* Homo *family whose demise was dated as recent as 18,000 years ago. We were not alone, the Cro Magnon modern man, the painter of the caves of Lascaux and Altamira, who is so close to our feelings when we look to his artistic remains, could entertain a conservation with two other species of humans if he had some sense of tourism and cross-species language capacities, if the third contemporary of H. sapiens was capable of speech.*

Homo florensis

It needed traveling to the Indonesian island of Flores, but this should not have presented a major problem; 40,000 years ago, a spectacular expansion of the modern humans started which led over the next few ten thousands of years to a colonization of the entire globe. This was not a that remarkable feat—*H. erectus*, the likely ancestor, was already a daring explorer and did not shy away to cross the street of Sunda as a seafarer as demonstrated by stone tools dated to 900,000

years ago. The lack of a land bridge was also suggested by an impoverished fauna that consisted of giant reptiles (the Komodo dragon), giant rats, tortoise, and a pygmy elephant (*Stegodon*; Morwood et al. 1998). This wide radiation of early humans calls for a reappraisal of the intellectual capacity of *H. erectus*. However, no skeleton remains accompany the stone tools. This is the more unfortunate because the descendant of this early invasion is a particularly strange member of the human branch. The archaeologists called it *Homo florensis*, but it was quickly dubbed the Hobbit even in scientific journals. The cranium and skeleton from a likely female individual suggests a human being of a mere 1-m size and less than 28-kg weight and a spectacular low brain volume of 380 cc (Brown et al. 2004). All figures are lower than the estimates for australopithecines, which existed several millions of years earlier. Anthropologists made a virtual endocast of the skull. The investigation of the original is delicate: The skull was not fossilized and had the consistency of wet papier mâché. It was slightly damaged during the excavation and redamaged by an Indonesian scientist that could not believe the finding (*a worthy story of Pride and Prejudice on its own*). This study excluded a microencephalic individual, and the statistical analysis of the brain form, using principle component analysis, puts it closest to *H. erectus*, the likely first colonizer of Flores (Falk et al. 2005).

Size Reduction and Diet

A human pygmy was also excluded: African pygmies are taller than 1.4 m and have brain volumes well above 1,000 cc. Explanations of the small body size of African pygmies are based on thermoregulatory advantages of small size for life in hot and humid forests either as enhanced evaporative cooling or reduced internal heat production. The reduction in size is achieved by reduced production of the insulin-like growth factor in puberty when brains are already fully outgrown. The most likely explanation for small size of *H. florensis* is insular dwarfism. The Hobbit is most likely the product of a long period of evolution from probably normal-sized *H. erectus*, who arrived on this island 900,000 years ago. On this relatively small island, small body size was adaptive. In the absence of agriculture, tropical rainforests offer a very limited supply of calories for hominids. The scientists argued that selection should favor smaller individuals with reduced energy requirements. The impoverished fauna means also lack of predators, the Komodo dragon being the sole danger. Like in domesticated animals that loose the predator pressure, the sensory system is reduced, which might result in the observed dramatic reduction in brain size. The bones found in the cave point to fish, snakes, frogs, tortoise, birds, and rodents as food sources (Morwood et al. 2004). The only big game of this human species was neonates from the pygmy elephant *Stegodon*, which disappeared from this island 12,000 years ago. We know that *H. sapiens* arrived in this region by island hopping, some 55,000–35,000 years BP. Apparently, both human species coexisted thousands of years. We ignore whether there were contacts between both species and whether *H. sapiens* could communicate with a hominid of such small brain size. The small brain size also raises an important question with

respect to the stone tools that accompanied the *H. florensis* skeletons. The stone tools associated with the cave are simple, but they show clear signs of designed elaboration. Some anthropologists doubted that a small-bodied hominin with a brain size of about 400 ccm and thus comparable to that of an *Australopithecus* could have mastered stone tool use. The question was now settled positively by the description of stone tools from a much older cave in Flores dated to 800,000 years BP (Brumm et al. 2006). The tools from both caves are in the same technological tradition suggesting *H. florensis* as a stone-tool maker, which apparently challenges our preconceptions on the necessary brain size for such technological activities.

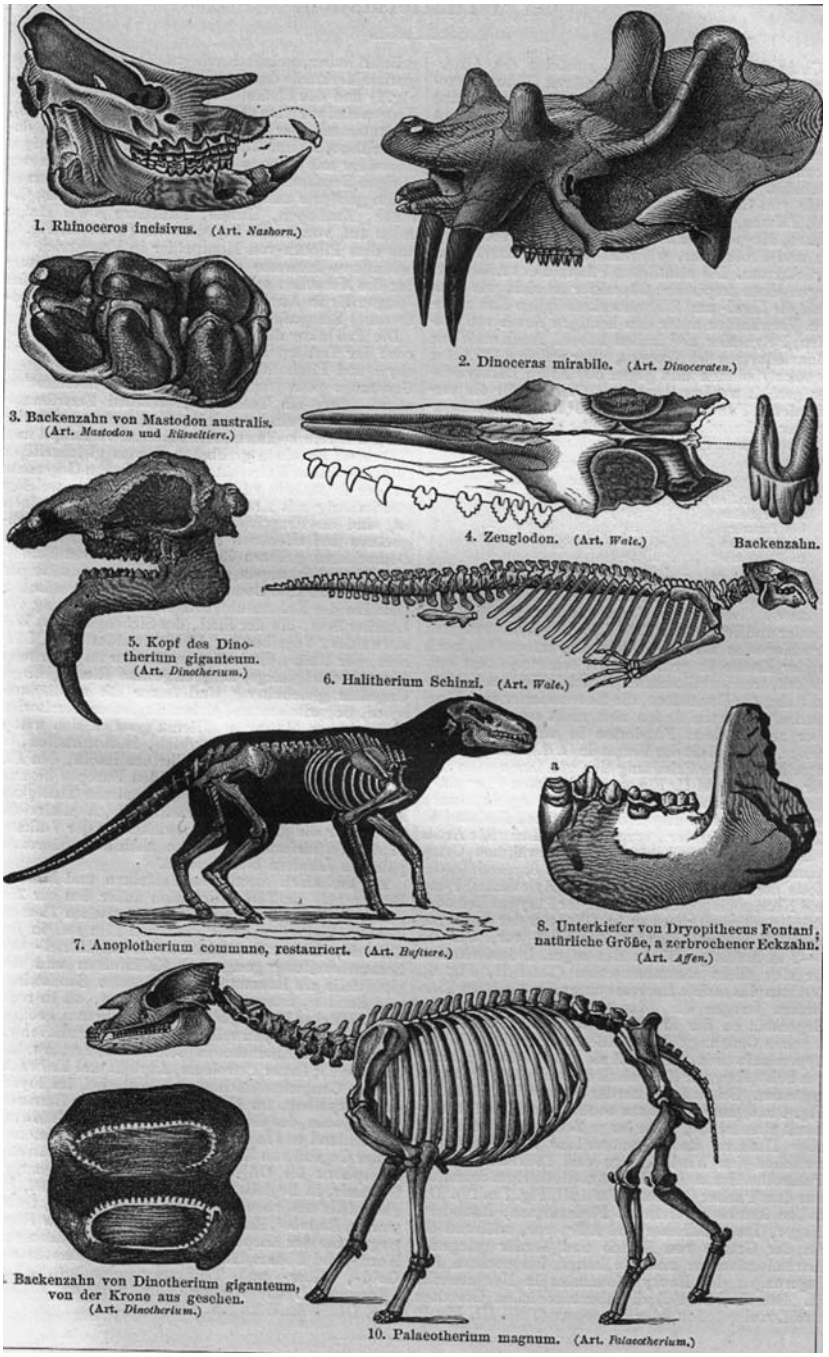
Late Pleistocene Megafauna Extinction: An Early Blitzkrieg?

An Australian "Blitzkrieg"?

Was H. sapiens *responsible for the disappearance of* H. florensis? H. sapiens *has a bad reputation on the fifth continent*. The Cenozoic is commonly divided into the Tertiary (Figures 6.24 and 6.25) and the Quaternary Period. The latter is divided into the Pleistocene and the Holocene. In the Pleistocene (Figure 6.26), Australia sported 24 genera of megafauna: giant marsupials like the 3-m high, short-faced kangaroo *Procoptodon*, marsupial equivalents of rhinoceros and leopards, 1-ton carnivorous lizards like a too-big Komodo dragon, giant crocodiles, the giant bird *Genyornis*. In the Late Pleistocene, 23 of the 24 genera of megafauna disappeared leaving behind only the *Macropus* kangaroos (Diamond 2001; Figure 6.27). Two theories were proposed to explain this collapse of the megafauna. One is the overkill theory, where human hunters drove the megafauna to extinction. There is even a "blitzkrieg" version of this scenario, where the newly arriving humans quickly culled the large herbivores out of existence and thereby killed indirectly also the large carnivores that lost their food source. Despite all courage attributed to the early humans, it is judged unlikely that humans attacked the 1-ton lizards looking like a blown-up version of the extant Komodo dragon. The alternative hypothesis is extinction due to climate and vegetation change. The dilemma can only be solved by precise data of human arrival and the kinetics of megafauna disappearance.

Timing

The arrival of humans in Australia can relatively precisely be dated to 56 ± 4 thousand years ago. All Australian land mammals, reptiles, and birds weighing more than 100 kg experienced a continent-wide extinction at 46 ± 2 thousand years ago with remarkable synchrony in eastern and western Australia. It occurred at least 20,000 years before the Last Glacial Maximum and also before the aridity increased dramatically in Australia. The data are consistent with a human role in extinction, but the blitzkrieg version can be discarded since it took 10,000 years after human arrival to take effect (Roberts Flannery et al. 2001).


1. Rhinoceros incisivus. (Art. Nashorn.)
2. Dinoceras mirabile. (Art. Dinoceraten.)
3. Backenzahn von Mastodon australis. (Art. Mastodon und Rüsseltiere.)
4. Zeuglodon. (Art. Wale.)
Backenzahn.
5. Kopf des Dinotherium giganteum. (Art. Dinotherium.)
6. Halitherium Schinzi. (Art. Wale.)
7. Anoplotherium commune, restauriert. (Art. Huftiere.)
a
8. Unterkiefer von Dryopithecus Fontani, natürliche Größe, a zerbrochener Eckzahn. (Art. Affen.)
Backenzahn von Dinotherium giganteum, von der Krone aus gesehen. (Art. Dinotherium.)
10. Palaeotherium magnum. (Art. Palaeotherium.)

Humans therefore first triggered ecosystem disruption, as a result of which the megafauna became extinct. Other biologists observed an interesting trend: The likelihood of extinction was actually not correlated with the body size but with slow reproduction rate. In their words, it was an extinction of the "bradyfauna" ("*brady*," Greek for "slow") and not of the megafauna ("*mega*," Greek for "great"). Exceptions to this rule were arboreal and nocturnal animals, inhabitants of dense forests and animals living in high altitudes and high latitudes. These are all regions where humans had less access and where the predation pressure was consequently lower (Cardillo and Lister 2002).

Recent statistical analysis showed that threatened and nonthreatened terrestrial mammals differed in mean body weight (1.4 vs. 0.14 kg; Cardillo et al. 2005). When taking 3 kg as a cutoff, regression models showed no intrinsic biological traits that correlated with extinction risk in smaller animals, while such traits were found in larger animals (population density, neonatal weight, and litters per year). Larger animals are more affected by forest fragmentation and predation pressure. For example, in neotropical forests, subsistence hunters' prey preference increases abruptly for mammals above 6.5 kg.

Smoking Gun in Australia

Researchers tried to decipher the events around the ecosystem collapse that occurred with human arrival in Australia by analyzing eggshells and teeth from herbivorous animals (Miller et al. 2005). Plants that use the C3 or C4 pathway of carbon fixation leave a distinct isotopic composition, which can still be detected in the minerals of the fossils. They thus reconstructed the diet of the extant emu (*Dromaius novaehollandiae*) and the extinct giant flightless bird *Genyornis newtoni* over the critical time period. Before human arrival, the emu ate a wide range of food sources and utilized abundant nutritious grasslands constituted by C4 plants in wet years and relied more on shrubs and trees, i.e., C3 plants, in drier years. After the arrival of humans, emus shifted to C3 dietary sources. *Genyornis* consumed a more restricted diet and relied heavily on C4 plants. The emu can in contrast tolerate a pure C3 plant diet. Also teeth of the herbivorous marsupial wombat told the same story. The same emu eggshell observation was made in three places characterized by three different climates,

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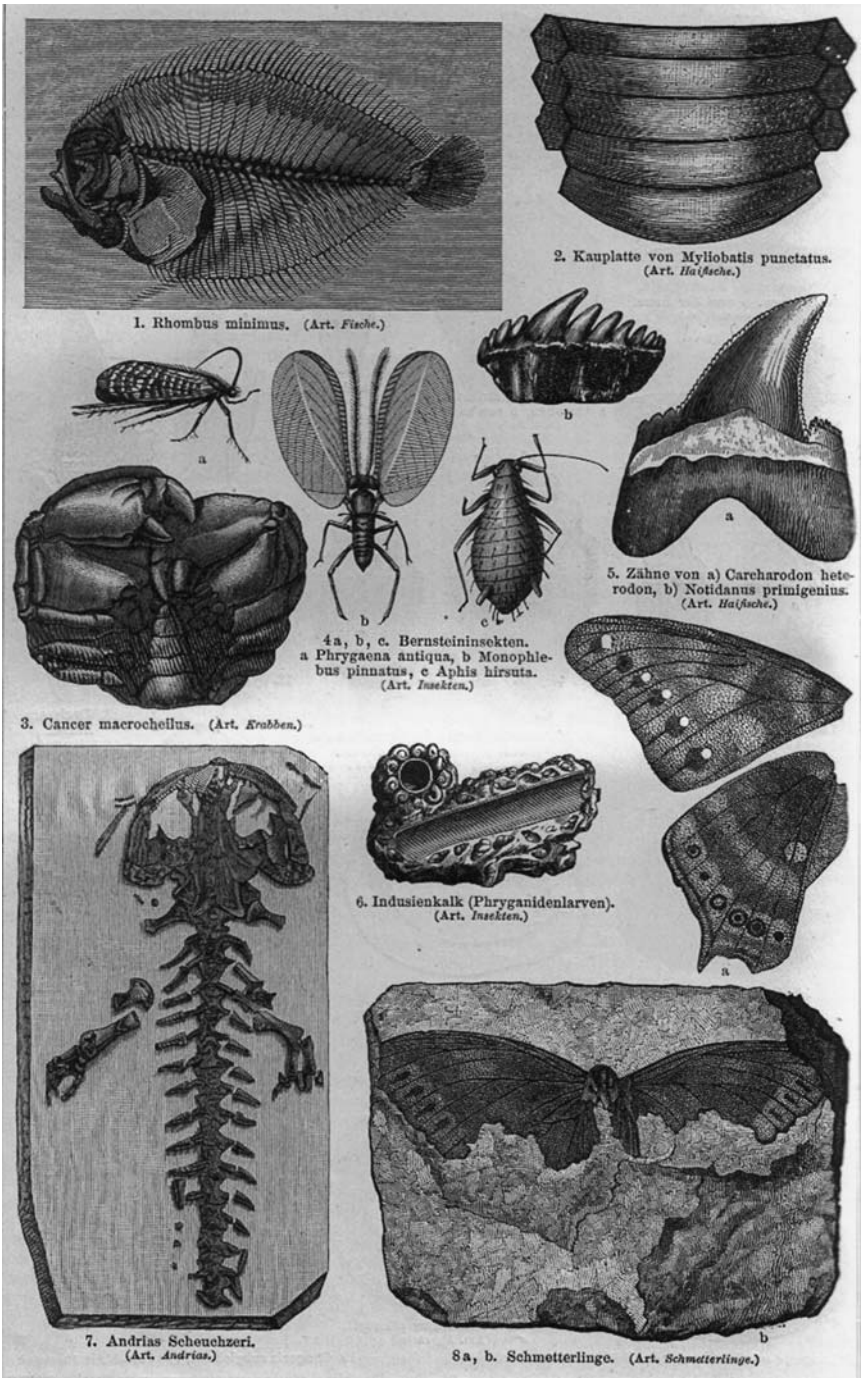
FIGURE 6.24. Tertiary 1. The Tertiary Period opens the Cenozoic era; it began 65 million years ago. Tertiary life forms are distinctly modern. The most remarkable development was the diversification of mammals. Exaggerated skull forms like in *Dinotherium* (*5*, *9*) and *Dinoceras* (*2*) strike the eyes. Molars from elephant-like Mastodons (*3*) were found and early rhinoceros fossils (*1*) were described. Cuvier made his famous investigations describing an early hoofed animal, *Anoplotherium* (*7*), and *Paleotherium* (*10*). Monkeys are represented with the famous jaw of the ape *Dryopithecus* (*8*), a tree-dwelling fruit eater with some relationship to the ancestry of humans. Other mammals returned from the land back into the water as documented by *Zeuglodon* (*4*), an ancestor of whales and *Halitherium* (*6*).


1. Rhombus minimus. (Art. Fische.)
2. Kauplatte von Myliobatis punctatus. (Art. Haifische.)
a
b
c
4a, b, c. Bernsteininsekten. a Phrygaena antiqua, b Monophlebus pinnatus, c Aphis hirsuta. (Art. Insekten.)
5. Zähne von a) Carcharodon heterodon, b) Notidanus primigenius. (Art. Haifische.)
3. Cancer macrocheilus. (Art. Krabben.)
6. Indusienkalk (Phryganidenlarven). (Art. Insekten.)
7. Andrias Scheuchzeri. (Art. Andrias.)
8a, b. Schmetterlinge. (Art. Schmetterlinge.)

making climate factors an unlikely explanation. The authors favored fire use by humans as a cause. They speculated that humans might have hunted along the fire front, cleared passageways, or promoted the growth of preferred fire-resistant plants. Thus a drought-adapted tree/shrub/grassland mosaic was transformed into modern chenopod/desert scrub. According to this interpretation, dietary specialization and not feeding strategy (browsing vs. grazing) was the predictor of extinction.

Alaska Paints a Different Picture

A US arctic biologist used the excellent preservation state of large mammalian species in the permafrost from Alaska to explore the critical time period around the human arrival to explore the effect of humans on the megafauna with radiocarbon dating of the animal remains (Guthrie 2006). Humans became visible to archaeologists at about 12,000 BP. This time period coincides precisely with the demise of the horse *Equus ferus*. However, the researcher does not believe that humans were the cause for the extinction of the horse. He proposes several arguments against this interpretation. The horse shrank in size before extinction pointing to a causal nutritional factor for its disappearance. The mammoth coexisted with humans for about one millennium, before it got extinct. Furthermore, the bison, sparse before the arrival of humans, expands around the time of the human arrival and remains in place despite being traditional a favorite human hunting target. The wapiti (*Cervus canadensis*) and the moose arrive with humans and stay there. This is apparently not the Australian blitzkrieg scenario. Looking for alternative ecological explanations, the biologist investigated the pollen record and deduced for the time period, before human arrival, a very cold dry mammoth steppe with xerophyllic grasses, sedges, and sages. This period is followed by a warmer and wetter transition period—the grasses explode and edible woody plants like *Salix* become abundant. This climate and vegetation change attracts humans and wapiti from northern Eurasia. Shortly after the climate changes to taiga and tundra vegetation, the dwarf birch (*Betula*), highly defended against herbivory by its toxin content, becomes the dominant plant in the pollen record. Three thousand years later the willow (*Populus*) follows, whose leaves have the highest nutrient content of northern plants. Wapitis and bisons

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FIGURE 6.25. Tertiary 2. Other vertebrates are also documented in the fossil record, like modern-looking bony fishes (*Rhombus, 1*), sharks are represented with many teeth (*5*) and rays with dental plates (*2*). A historically particularly interesting fossil is that of a giant salamander (*7*). Scheuchzer described this fossil in 1732 as "Homo diluvi testis"—as a fossil evidence for humans that drowned during the deluge described in the Biblical record. Invertebrates like fragile butterflies are also documented in the Tertiary (*8*). Of outstanding beauty are many insects trapped in amber. They are frequently preserved in great detail (*4*). Insert 3 shows a crab fossil and insert 6 shows a characteristic chalk from the Tertiary formed by the larvae of caddisflies (Phryganeidae).

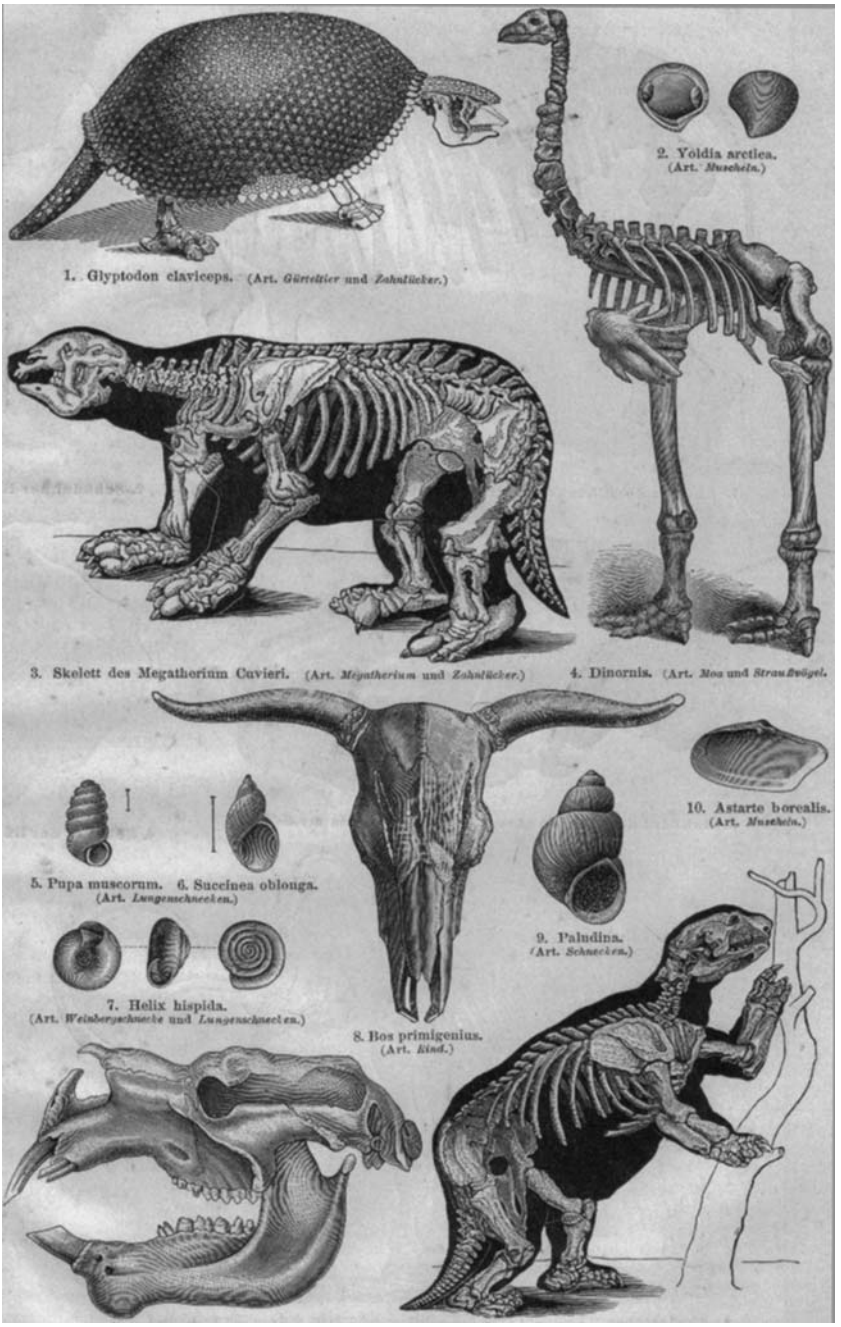
1. Glyptodon claviceps. (Art. Gürteltier und Zahnlücker.)
2. Yoldia arctica. (Art. Muscheln.)
3. Skelett des Megatherium Cuvieri. (Art. Megatherium und Zahnlücker.)
4. Dinornis. (Art. Moa und Straußvögel.
5. Pupa muscorum. 6. Succinea oblonga. (Art. Lungenschnecken.)
7. Helix hispida. (Art. Weinbergschnecke und Lungenschnecken.)
8. Bos primigenius. (Art. Rind.)
9. Paludina. (Art. Schnecken.)
10. Astarte borealis. (Art. Muscheln.)

FIGURE 6.26 I.

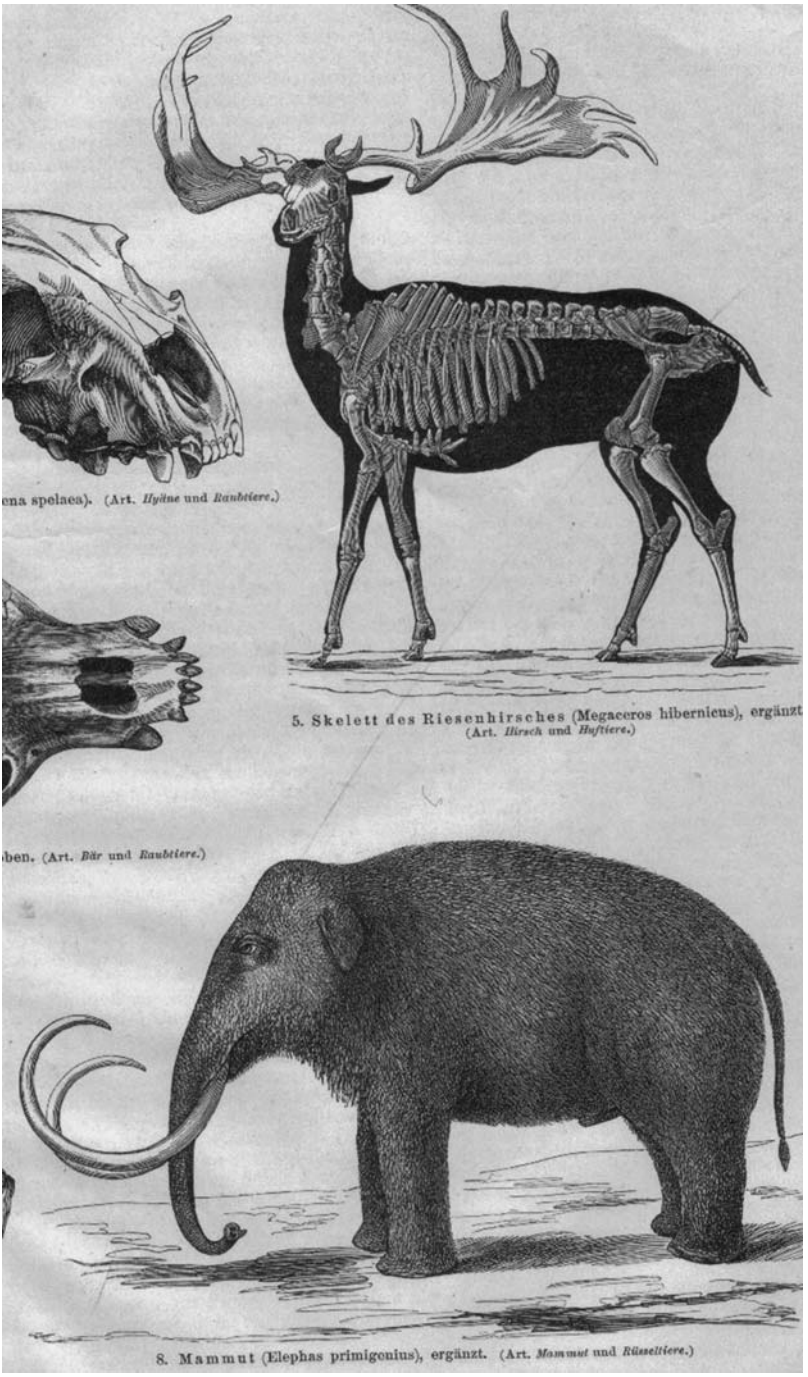

FIGURE 6.26 II.

can make heavy use of this new food. Caecalids, animals like the horse, elephant, and rhinos—characterized by a large hindgut diverticulum (cecum)—loose their competitive advantage. Under poor vegetation conditions, they can tolerate high volumes of poor quality forage due to the higher food throughput through their gut. Climate change, not human hunters, are behind the fauna changes in Alaska.

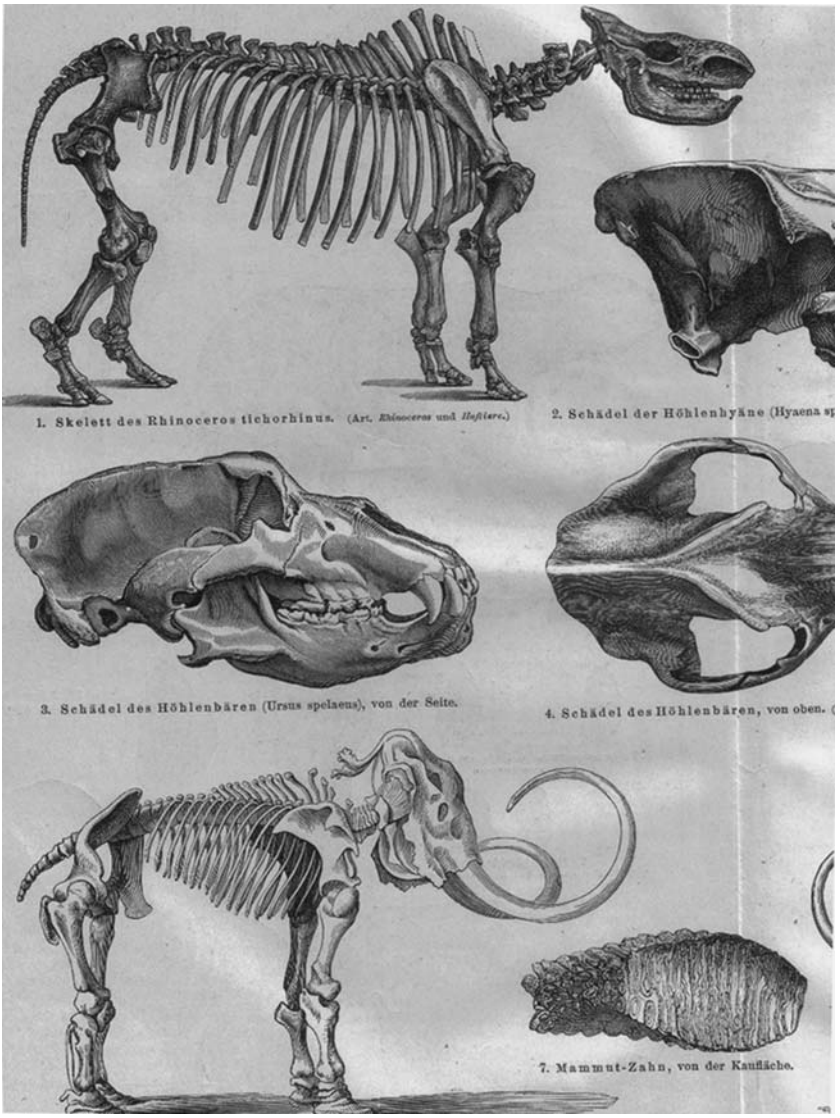

FIGURE 6.26 III.

The Irish Elk

Also in other regions, megafauna extinction was observed, but it showed distinct kinetics and causes: Sabre-toothed tigers, mastodons, woolly mammoths, and the Irish elk survived until the end of the Pleistocene epoch, while the mammoths roamed their last exiles still at the time of the Egyptian pharaohs. With respect to the causes, let's take the example of the Irish elk (*Megaloceros giganteus*; Figure 6.26; Pastor and Moen 2004; Stuart et al. 2004). Female elks are probably to be blamed for the demise of the species. They selected males with large antlers, their instinct has told them that this is a sign of fitness for males if they find sufficient food to build and shed these antlers each year. This task should not be underestimated from the nutritional side. The animal's huge antlers weighed 40 kg and spanned 3.5 m. It was calculated that the antlers contained 8 kg calcium and 4 kg phosphate, which is a tremendous burden of mineral intake for the bulls. Furthermore, the extreme antlers prevented them the access into dense forests. All went well as long as the Irish elk could forage in its native willow and birch shrub habitat, existing 20,000 years ago in central and Western Europe. Then the climate cooled in the Last Glacial Maximum around 20–12,000 years ago. The vegetation in Europe changed to short-stature and unproductive tundra. Open grass-shrub plant communities persisted only near the Urals, the exile of the elks. After the great cold, the Irish elk came back to the British islands and Denmark, during the Late Glacial Interstadial. The rapid warming resulted in a productive

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FIGURE 6.26. Cenozoic era, Quaternary Period. The Pleistocene (Diluvium) started one million years ago and preceded the most recent geological period, the Holocene. The figures document some giant animal forms: within birds the emu-like *Dinornis* (I, *4*) from New Zealand dwarfed its nineteenth-century describer Owen; within marsupials the Australian *Diprotodon* reached the size of a rhinoceros (I, bottom left); *Megatherium* (I, *3*) the largest ground sloth, an edentate mammal, reached the size of an elephant. As suggested by the reconstruction of *Mylodon* (I, bottom right), another ground sloth, this giant fed on leaves from trees and bushes. Also from South America comes *Glyptodon* (I, *1*), a giant armadillo-like mammal. Its heavy armour suggests harsh predation pressure. It probably fed on plants, carrion, and insects. Leading fossils of the Northern German Diluvian loess are the snails Pupa, Uccinea, Helix and Paludina (1, 5, 6, 7, 9). Giant forms were also described for the Pleistocene rhinoceros (III, *1*), the giant Irish elk *Megaceros* (II, *5*), and the mammoth (III, bottom left). The specimens of the mammoth preserved in the permafrost soil showed a heavy fur as an adaptation to global cooling during the Ice Ages (II, 8). Caves yielded a rich fauna like the cave bear *Ursus speleus* (III, *3*). Also the precursor of the domesticated cattle *Bos primigenius* is documented on this figure (I, *8*). The Irish elk (*Megalocerus giganteus,* II, *5*) shows increased growth of the antlers induced by sexual selection. The female's sexual preferences drove this species into extinction when the food basis of the animal changed with the changing climate. The mammoth (*Mammuthus primigenius*) is an extinct genus of elephants, which was still depicted in the cave paintings of the hunter–gatherers from early Europe.

FIGURE 6.27. Red kangaroo (*Macropus rufus*), one of the few large marsupials surviving the arrival of humans in Australia.

grass and sedge vegetation. At about 10,000 years, the temperatures dropped again, the open steppe-tundra returned, and the animals were again forced out of Europe back to the Urals, where their fate became sealed at 7,000 years ago. Western populations tried to survive by trading reduced sexual display organs against nutritional relieve (Gonzalez et al. 2000). The final blow was probably given by the Mesolithic hunters.

The Woolly Mammoth

A different extinction history was reconstructed for the woolly mammoth *Mammuthus primigenius* (Figure 6.26) (Lister 1993; Stuart et al. 2004; Guthrie 2004). The mammoth is special for extinct animals. You can admire nice specimen displaying trunk and fur in Russian museums because they were exquisitely preserved in the permafrost soil of Northern Siberia. The mammoth is, with the cave bear, a prominent example for paleogenomics. Its genome is about to be reconstructed from frozen samples. Actually, it is a metagenome project since only half of the DNA (but this is a remarkably high amount for ancient DNA samples) is elephant DNA (Poinar et al. 2006). The analysis of the mitochondrial DNA allowed placing the mammoth closer to the Asian than to the African elephant, which separated 6 Ma ago. The mammoth split from the Asian line 0.5 Ma later (Krause et al. 2006). The nonelephant half of the "mammoth" DNA is also interesting for this book since it allows a glimpse into the ancient gut microbiota and the decomposers of the mammoth carcass. Numerically, bacteria

dominated the non-mammoth DNA with proteobacteria, firmicutes, actinobacteria, bacteroidetes, and chlorobi bacteria, in this decreasing order. Archaea were found with lesser frequency as were fungal taxa like *Ashyba*, *Aspergillus*, *Neurospora* and *Magnaporthe*. The last rank was filled with soil-inhabiting eukaryotes like *Dictyosteliida* and *Entamoeba*. Although the researchers clearly targeted the ancient mammoth DNA, the associated microbial DNA might be a bonus for researchers interested in the organisms following sequentially in the mineralization of dead mammalian bodies. After this short excursion into paleogenomics, back to the extinction history of the woolly mammoth, which differs from that of the Irish elk. The mammoth's presence in Europe does not show the large gaps as the giant elk; its natural habitat apparently persisted through this time, and it was well adapted to the cold. Warming of the climate replaced the previous rich, mosaic vegetation of herbs and grasses (the steppe-tundra) by a less diverse and less productive boggy tundra, mixed with coniferous forests. The mammoths left Europe to seek refuges in Northern Siberia and on islands in the Arctic Sea. On the Wrangel island, they persisted until 3,500 years ago. Paleo-Eskimos arrived only 3,000 years ago and are thus not a likely cause of their extinction. Food limitations and lack of predation caused the development of dwarf mammoths. Island dwarfism is a common phenomenon and produced 1-m small elephants (*Elephas falconeri*) on Malta. The extinction of mammoths on small islands in the Bering Street was linked to habitat destruction by sea level rises and inbreeding depression by too small populations. Hunting was probably not involved.

Mesolithic Marasm

Large mammals were well adapted to the arid and windy conditions with a treeless, short grass–sedge–sage sward. Mammoth, bison, and reindeer found their different optimal diets and habitats. In North America the transition to the Holocene brought dramatic changes. Landscape changes included the creation of lakes, bogs, shrub tundra, forests, soil paludification, low-nutrient soils, and plants highly defended against herbivory. Horses experienced a rapid body size decline before they went extinct (Guthrie 2003). The decline reflected on one side a restricted access to optimal food sources, but on the other side also increasing competition with other herbivores. Zoologists observed a general replacement of caecalid species that use a large cecum gut-diverticulum in food processing (woolly mammoth, woolly rhino, and horses) by ruminants (bison, moose, and reindeer).

Reindeers, the favorite game animal of the European paleolithic hunters, followed the retreating glaciers to maintain their preferred habitat. With the evasion of their preferred meat source, the hunter-gatherers entered a severe crisis, which is by some historians called the "Mesolithic marasm." The open landscape ideal for hunting disappeared; the retreating glaciers left many lakes and bogs; forests reclaimed large areas. People were plagued by myriads of mosquitoes, and we have in addition ample evidence for strife between the tribes. In Denmark the former hunters lived mainly of mussels, and the diet was sometimes so small that you also find the bones of the earliest domesticated dogs

on the refuse heaps. *The cultural heights of the hunters who created 15,000 years ago the wonderful paintings in the caves of Altamira in Spain and Lascaux in France were forgotten. The Mesolithic art is primitive in comparison, the tribes were poor, fighting for their nutritional survival and weakened by frequent feuds with neighboring groups. The time was ripe for a next major invention in the quest for food, which changed not only the foraging strategy of humans but also the face of the planet. Over the last thousand years, humans became the world's greatest evolutionary force linked to mass extinction and habitat destruction that was before only seen with climate changes.*

The Spread of Early Agriculture

A Transition Period

In the words of a prominent scientist, plant and animal domestication is the most important development in the past 13,000 years of human history (Diamond 2002). A surprising observation is that the step from a hunter-gatherer to a farmer society was done at about the same time (i.e., 9,000–4,000 years ago) in several regions of the world: The Near East and China in Asia; the Sahel, West Africa and Ethiopia in Africa; the Andes, Amazonian, Mesoamerica, and the Eastern US in America; New Guinea in Oceania. There is a clear east–west alignment in the Old World imposed by the ease of spread between comparable climate zones along similar latitudes. Only in the New World do we see a north–south gradient dictated by the form of the continent. Europeans tend to look to the Fertile Crescent in the Near East as the cradle of agriculture because here their crops and animals were first domesticated and because this region soon also became the birthplace of their civilization. *Some historians see these links between agriculture and culture as a necessity. However, neither the farmers from New Guinea nor those from the Eastern USA developed a higher civilization.*

Agriculture relieved humans from the obligation to follow the hunted game animals on their migratory paths. They could settle down, found villages, and develop new tools like pottery that was too fragile or forges that were too heavy that hunters could carry them on their migrations. Hunter societies could only grow slowly because over-hunting of their game would destroy their food basis. In contrast, farmers could produce a surplus of food: They could nourish more mouths, and their wives could raise more infants due to the sedentary life style. The storable food sources freed some people from food production, and they became craftsmen, inventors, soldiers, bureaucrats, and nobles. The moving tribe that had to split when it became too big contrasted with the village that could grow, and fuse with other villages to become the many "kingdoms" mentioned in the Bible.

Hardship

One should refrain to paint a too rosy picture of this transition time. Actually, many memories of this historical process were kept in the Biblical report. With

a little fantasy, you still recognize the good old time of the heydays from the "Altamira" hunter society in the Paradise. Humans were expelled from this hunter Paradise, where everything was for free; you just had to stretch out your hand. You might want to interpret the archangel who guarded the entry to the paradise as the climate change that occurred after the last glaciation. Adam is condemned to agricultural activity, and he perceives this as a punishment. Early farming was probably a lot of hardship. Indeed, the fieldwork is expressively cursed in the Old Testament. Surely, the regular work on the field was much less fun than following the old human instinct of hunting and gathering, which is still so strong in modern man as everybody can tell from self-observation. Deadly conflicts as reported between the first sons of man ("Adam"), suggesting splits between those that tamed animals and became pastoralists (Abel) and those domesticating the plants and working on the fields (Cain). The former still kept more traditions of the hunter society, but Abel was slain by Cain, disproving from the beginning the concept of the peaceful vegetarian that conquered the world by the superiority of his inventions. The transition to agriculture was really a dangerous, if not murderous period. Medical epidemiologists tell us that many infectious diseases were not efficiently transmitted in the sparsely populated hunter societies. The crowding of humans in villages and their close living with their domesticated animals created new possibilities for the transmission of infectious diseases. It is probably no chance observation that humans share more serologically related microbes with cattle than with lemurs. We should also not keep a too idealistic idea about food abundance in the early farming society. The efficiency of the early crops was still low, the basic inventions in animal husbandry had still to be made. The diet was surely less varied than in the hunter-gatherer society. In short, the transition was characterized by more work, worse nutritional condition as demonstrated by lower adult stature and heavier disease burden.

Anthropologists noted poor dental health, but amazingly also an early neolithic tradition of dentistry in farmers from Pakistan (Coppa et al. 2006). Holes were apparently quite skillfully drilled into the enamel on occlusal surfaces of teeth, and the patients continued to chew on these tooth surfaces. The protodentists probably used a bow-drill tipped with a flint head. This technique was practiced for 1,500 years but abandoned at 6,500 BP. The reason why it was given up is not clear since the population continued to suffer from poor tooth health.

A Point of No Return?

Why should this step be done? There are several answers. First, the early farmers could not foresee the consequence of their action. Another problem was that there was no way back into the hunter society. The big herds had disappeared from Europe, and the growing population needed more and more food, which could anyway not be provided by hunting. After the first growth, there was no way back except in the form of a collapse of the civilization. In the Classic Maya period at about 750 AD, the Yucatan lowlands counted perhaps up to 10 million inhabitants. The Maya experienced after the Terminal Classic period a

demographic disaster as profound as few in human history. Multiyear droughts ruined the food basis of this society, and the densely populated urban centers were abandoned permanently (Haug et al. 2003). How vulnerable even modern societies are with respect to their agricultural basis is illustrated by the Dust Bowl event in the USA.

The Expansion

However, once established, the farmer society developed a dynamic that pushed aside all hunter-gatherer societies. For example, European agriculture originated in the Near East about 9,000 years ago. The Neolithic revolution reached in Europe almost all areas suitable for agriculture, and the precise contour waves of its progress can be projected on the European map in 500 years intervals starting from east to west Anatolia, reaching the Aegean basin from where three different trajectories can be deciphered. A southern route goes westward over Italy, Southern France to the Iberian Peninsula. The propagation was quick with a spread of 10 km per year suggesting a maritime transport. The neolithic populations can easily be identified by their fully terrestrial diet, while the Mesolithic populations showed a 50% marine component in their diet. In Portugal, a stepwise replacement of late Mesolithic by early neolithic settlements occurred between 6,000 and 5,000 years ago (Zilhao 2001). A second wave goes from the Aegean world into what is today Romania where it split into a western wave progressing via Germany to Ireland and another wave via Ukraina, Russia, and Scandinavia (Sokal et al. 1991). However, it was not only the new agricultural technique that spread, but at the same time the Indo-European language family replaced all other dialects in Europe (and as the name suggests also to the east as far into Asia as India), with the remarkable exception of the Basque language.

The Ukranian Horse Versus the Anatolian Cattle

As we will see below, the domestication of the major European crops originated in a small region of eastern Anatolia. Anatolia is also the home of one, if not the oldest Indo-European language, the Hittite. Was the Proto-Indoeuropean language given as part of the cultural package that included agricultural techniques as well as domesticated crops and animals (Diamond and Bellwood 2003)? Linguists have tried to deduce the home of the Proto-Indoeuropean by searching their shared words. The most widely shared vocabulary concerns the horse associated with transport (wheel, chariot) and riding, then comes cattle herding and milking, followed by words describing many other domesticated animals (pig, sheep and wool, goat, dog, goose, duck, bee). Interestingly, plant crops and trees do not belong to this linguistic package. This is the dictionary of a pastoral society, not that of a sedentary, agrarian crop-oriented population. Was horse the motor of this dispersal of the early agricultural life style? The horse had multiple functions: They were eaten by the hunters, used for working on the field and also for riding. Riding became, however, only possible with the invention of the bit. Archaeologists argued that the use of the bit should leave a

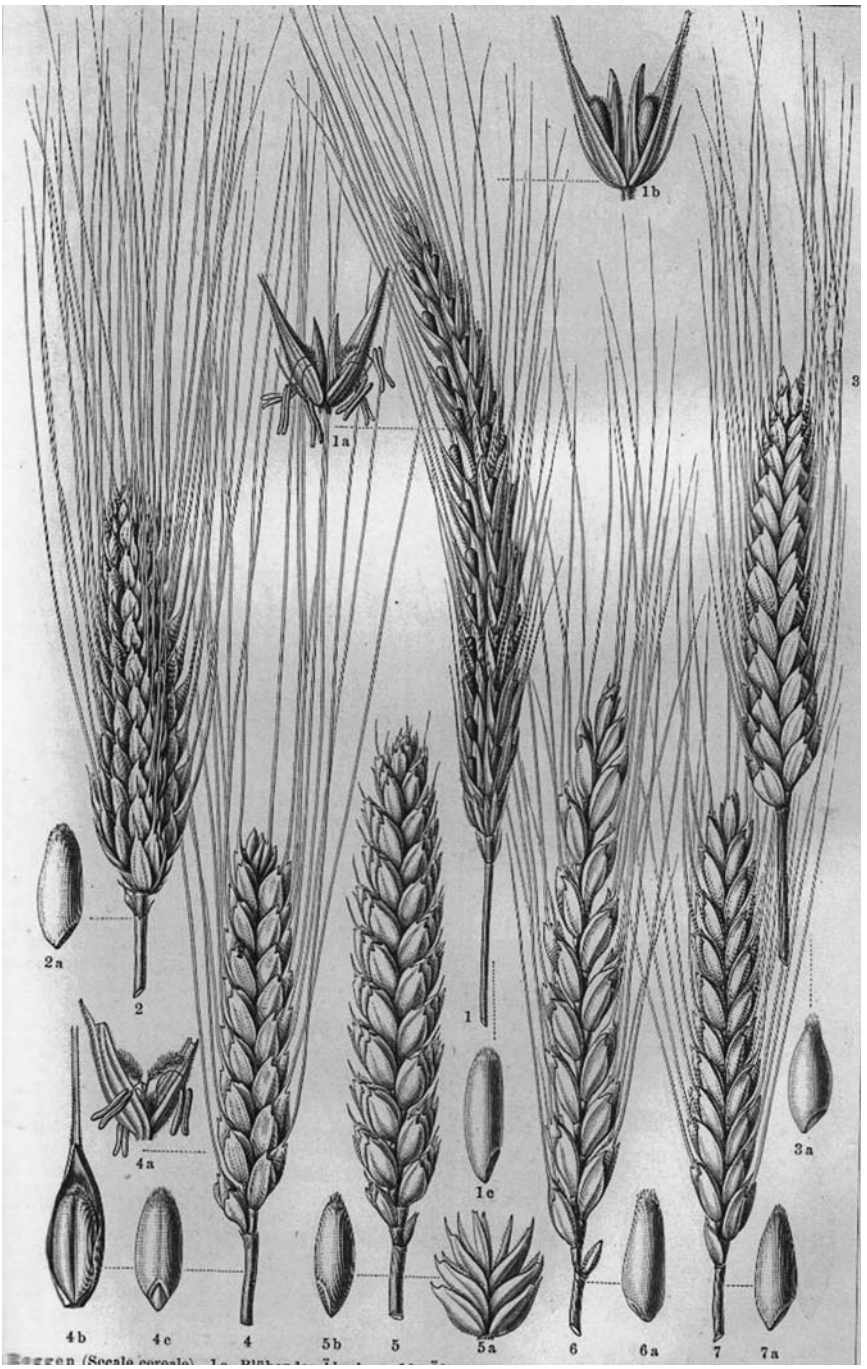
trace on the teeth of the horses, and they searched for the earliest signs of horse teeth with signs of wear. This observation should lead them to the propagator of the Proto-Indoeuropean language. The oldest finds of horses with used teeth were preserved by the Ukrainian Sredny Stog culture dated to 4000 BC (Diamond 1991). This archaeological evidence fits remarkably well with the linguistic analysis of N.S. Trubetzkoy, who placed the home of this language family to the north of the Black Sea. It fits also with the superior role that the horseman played in military-driven colonization throughout history as still demonstrated much later by the conquest of Latin America through the Spaniards. Does such a warrior model speak in favor of a stronger demic diffusion than in the case of the spread of Anatolian cattle culture? Human geneticists are undecided, they speak currently of a 22% Neolithic versus a 30% Paleolithic contribution to the current European gene pool, and they distinguish with classical markers a southeast to northwest gradient. Y chromosome and mitochondrial DNA data also show gradients, but they are difficult to compose in a single picture. *As in the analysis of the central metabolism, one can borrow here the term "palimpsest" from archaeologists, a document that was overwritten in later time but which still allows to read partly the original text. Too many later genetic intrusions have occurred in the long history of Europe to expect a clear message*. The situation is clearer in other regions of the world. Genetic evidence for the demic diffusion model of agriculture could be provided for India (Cordaux et al. 2004). Demic diffusion of the Han languages in China could also be demonstrated.

Domestication

The Garden of Eden: Domestication of Crops

The Garden of Eden at Karacadag?

Let's now review the paleobotanical evidence, which allows to localize the Garden of Eden or at least the East of Eden. This claim sounds astonishing, but the evidence is quite convincing. Near East neolithic agriculture was based on three cereals (einkorn wheat, emmer wheat, and barley (Figures 6.28 and 6.29)), four pulses (lentil, pea, chickpea, and bitter vetch), and a fiber crop (flax). If you map the native distribution area of these plants, you define a core area between the upper Tigris and Euphrates rivers as the center for the innovation. Apparently, the cool, dry climate of the Younger Dryas (about 9000–8000 BC named after the Alpine plant *Dryas octopetala*) triggered the end of the nomadic life style and the beginning of farming. A number of archaeological data support this conclusion: Excavations indicate a wealthy society with plenty of food that used stone sickles and "stepped" stone quern for grinding cereal crops. Glossed flint sickle blades from the Jordan valley suggested that wild emmer wheat was harvested as early as 7800 BC (Lev-Yadun et al. 2000). Wheat became the major cereal in Europe and countries colonized by Europe. The wild einkorn wheat *Triticum monococcum* subspecies *boeticum* is the wild relative of


1b
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the domesticated einkorn wheat *T. monococcum* subspecies *monococcum*. Plant geneticists characterized 1,300 lines of einkorn, which were localized to 5 km with respect to their origin, for agronomical and taxonomical traits (Salamini et al. 2002). The genetic distance within this group was evaluated using multiple DNA markers. Phylogenetic tree analysis showed that one group originating from the volcanic Karacadag mountain in southeast Turkey is distinctly separated from the remaining groups, while all cultivated "einkorns" are closely related among themselves. This observation raises the possibility that the Karacadag lines are the closest relatives of the wild progenitor that gave rise to cultivated einkorn about 10,000 years ago.

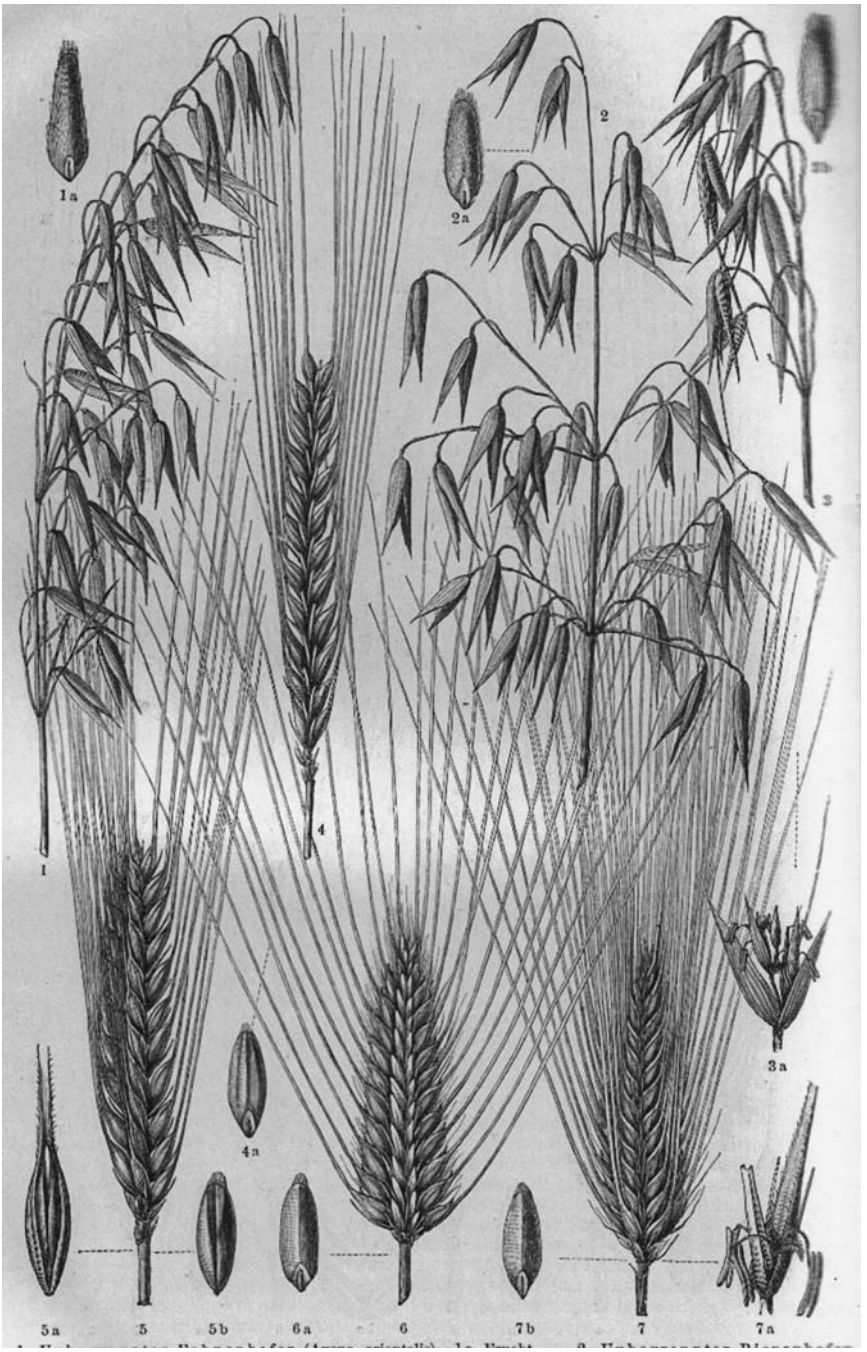
The Selection Process

The morphological traits of the Karacadag lines show, however, a wild cereal with low seed weight and a very brittle rachis. The early farmers selected for three basic characters when dealing with wheat. For an optimal nutritional value, they selected first for larger seeds. But this was not enough; in the wild forms, the spikelets of the ear fall apart at ripening through fragmentation of the rachis ("shattering"). The early farmers therefore selected for plants with a tough rachis. This is lethal for a wild form since it would effectively prevent dispersal of the seeds but an essential property for harvesting.

As shattering is such a visible marker of domestication, agricultural archaeologists working in the Near East could date the domestication process (Tanno and Willcox 2006). They investigated many charred wheat spikelets and dated the sites. Wild cereals with dehiscent ears shatter at maturity into spikelets identified by smooth scars. Domesticated cereals do not shatter, but separate when threshed producing jagged scars. A site dated to 10,000 years BP yielded no indication for domesticated wheat. This mutant form represented 30% of the spikelets between 9,300 and 8,500 and rose to 60% by 7,500 years BP. The mutant took thus more than a millennium to become established. The archaeologists suspected that the early farmers probably harvested before the spikelets fell to avoid loss of grains—the work of selection was thus slowed down. Also selection for larger grain size was slow, the size was maintained between 9,500 and 6,500 years BP.

The selection for reduced shattering was also crucial for rice domestication. Plant geneticists working with the domesticated rice *Oryza sativa* and *O. nivara*, a closely related wild relative, identified a genetic locus where one allele made that

FIGURE 6.28. Wheat and rye. 1-Rye (*Secale cereale*) with the flower (*1a*) and grain (*1c*). The other depicted plants are various varieties of wheat: *Triticum turgidum* (*2*) was cultivated in England, the diploid *T. monococcum* (*3*) and the tetraploid *T. dicoccum* (*7*) was popular in Germany, but have largely disappeared from the fields; the tetraploid *T. durum* (*4*) is used to make pasta. The most important variety is the hexaploid *T. aestivum* = *T. vulgare* (*5*), which is used to make bread. *T. spelta* (*6*) is still relatively popular in southern Germany.


1a
2
2a
2b
3
1
4
3a
4a
5a
5
5b
6a
6
7b
7
7a

the plant shed all mature grains when hand-tapped, while another allele allowed only partial shedding under vigorous hand shaking. Many of the agronomically important characteristics of domesticated plants are determined by quantitative trait loci (QTL). These traits are typically affected by more than one gene, as well as by the environment. There can also be interactions between QTLs ("epistasis"), which further complicates analysis. The rice geneticists were lucky: They could link the reduced shattering to a single gene expressed in the pedicel junction, where mature grains separate from the mother plant (Li et al. 2006). This is a logical finding. The falling of old leaves and of ripe fruits is crucial for proper plant function and regulated in an abscission zone. In *O. nivara* a nicely marked abscission zone consisting of a one-cell layer is histologically clearly visible, while in *O. oryzae* this layer is discontinuous and even lacking near vascular bundles. Domestication of cereals was a delicate balance. The abscission zone should be sufficiently stabilized to prevent spontaneous shattering after grain maturation. However, the abscission zone should not be too much suppressed to avoid problems with threshing. Yet, there are still other problems with domestication that had to be solved.

In the wild form the leaf-like structures that protect the seed ("glumes") are attached tightly to the seed ("hulled" genotype). The farmers selected forms that released the seed during threshing ("free-threshing" genotype). The first domesticated einkorn was a diploid species. This form was abandoned in the Bronze Age and replaced by a tetraploid form. This form was accidentally crossed with the wild cereal *Aegilops tauschii*, yielding a hexaploid hybrid, which was most suitable for baking and became thus the world's leading crop. This hexaploid bread wheat (*Triticum vulgare*) and the tetraploid hard wheat (*T. durum*) represent the final steps of *Triticum* domestication. The genetic analysis of the mutant genes in wheat is complicated by the high degree of ploidy and the large genome of this crop (Salamini et al. 2002).

Still Earlier Steps in the Jordan Valley

Some plants left their imprints in the Bible: in the Old Testament the primogenitur of a hunter (Esau) is sold against a lentil meal from a farmer/pastoralist (Jacob). The choice of the lentil as the plant with the closest amino acid profile to animal

FIGURE 6.29. Barley and oats. At the *top*, you see three varieties of oats: *Avena orientalis* (*1, 3*) and *A. sativa* (*2*), only the latter is economically important. Oats are mainly used a livestock feed, but they have also a place in breakfast cereals and cookies. At the *bottom*, different varieties of barley are depicted: *Hordeum distichum* (*4*), *H. vulgare* (*5*), *H. zeocriton* (*6*), and *H. hexastichum* (*7*). Half of the barley is used as livestock feed, the rest goes in human consumption; 10% is used in beer production. The history of wheat (*T. dicoccum*) and barley cultivation reaches back to the neolithical revolution. Barley was the main bread cereal of the land of the Bible, Greece, and Rome and remained in Europe the prominent bread cereal until the sixteenth century. Rye and oats were introduced only in the Bronze and Iron Age.

proteins is probably an intended allusion. In the New Testament the fig tree (*Ficus carica*) plays a prominent role in parables. We should thus not be surprised when Israeli agro-archaeologists recently came up with good evidence for the domestication of figs in a pre-pottery Neolithic village near Gilgal in the Jordan valley (Kislev et al. 2006). The finds consisted of carbonized figs and drupelets that were stored in a site dated to 11,400 years ago and thus fully a thousand years before previous early estimates for the Neolithic Revolution. A major player in this plot is the parasitoid fig wasp *Blastophaga* that inserts her ovipositor into the style of the female flower. This infestation prevents the dropping of the fruit and allows maturation of the fruit. Actually, villagers picked up a mutant that evolved parthenocarpy—the development of a fruit without pollination and fertilization. The fruit became soft, sweet and edible, while the wildtype was nonpalatable. Without human intervention, the mutant would have been lost due to its sterility—embryoless fruits do not produce new trees. However, figs were an easy early domestication because cuttings of the sterile fig developed roots more easily than any other fruit tree and could thus be propagated vegetatively. This easy growing of fig roots should not surprise since the *Ficus* genus is known for its abundant growing of air roots (Figure 6.30). The genus comprises a number of species (e.g., *F. benjaminica*) that literally strangulate trees on which they grow by descending a large mass of air roots. In Gilgal the figs were stored

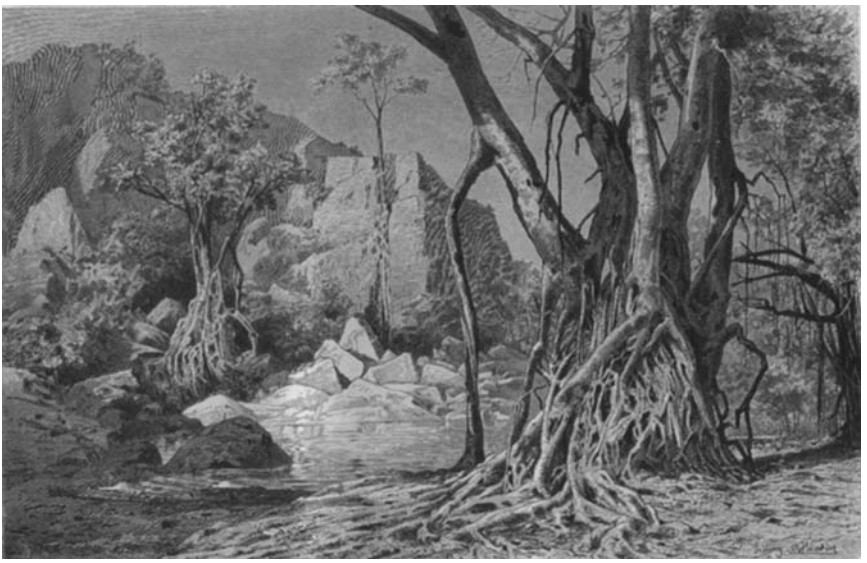


FIGURE 6.30. Ficus trees with characteristic oversized roots. The strong development of roots allows parasitic ways of life to several members of the *Ficus* genus. However, the ease of growing roots from a cut branch of *Ficus* is also at the basis of the vegetative propagation of *Ficus carica* which was the key to the early domestication of the fig in the Jordan valley.

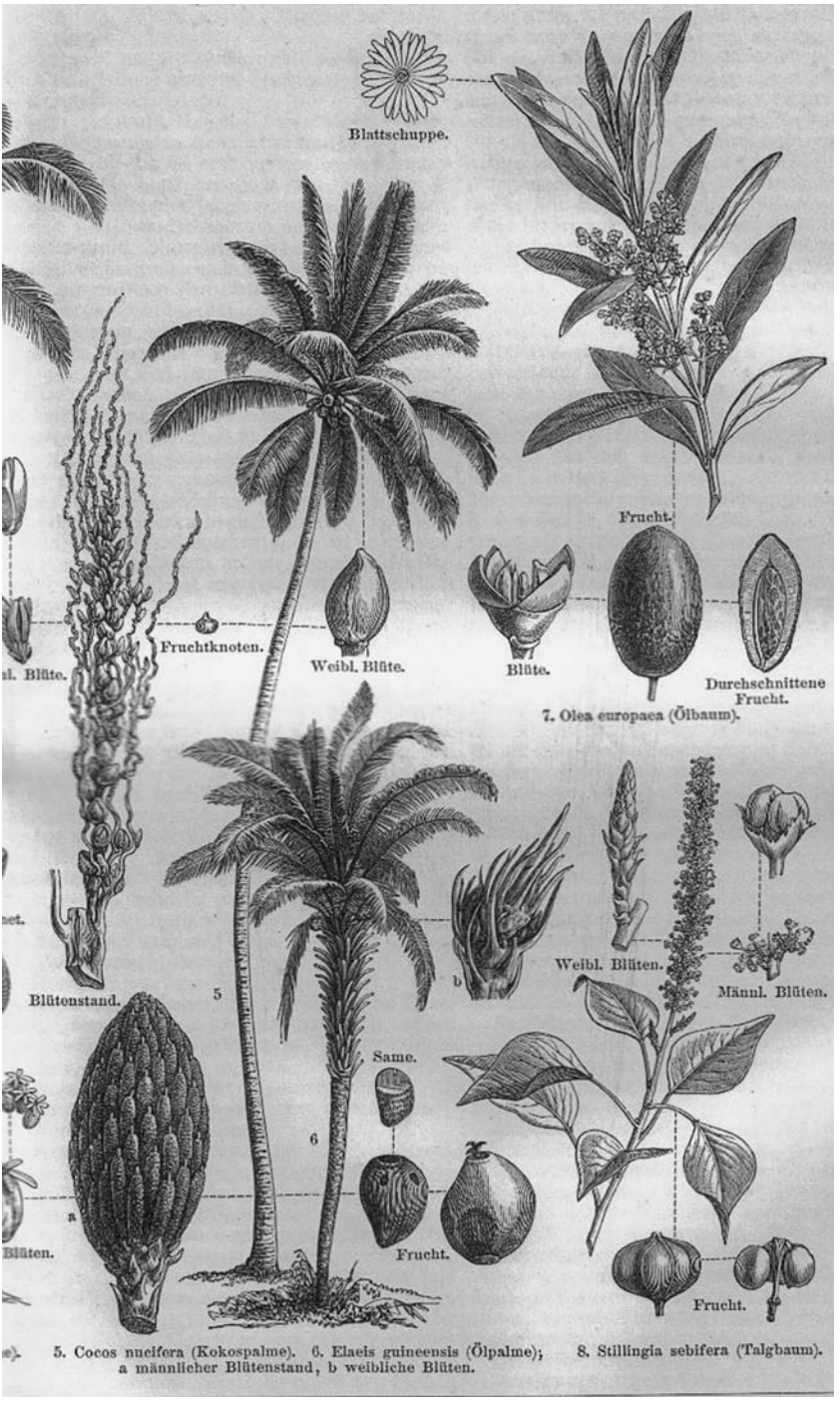
with wild barley and wild oat suggesting a subsistence strategy consisting of a gathering of annual plants from wild stands together with early domestication.

The ancient world revered the fig and its tree, it was associated with the cult of Bacchus; figs became the food at the public table of the Spartans; figs were the major source of the food for the slaves from antiquity. In public display the fig tree gave shadow to the founder twins of Rome in front of their wolf cage and the tree became a symbol of prosperity.

Surviving stores of lentils from the same period showed that wild lentils (*Lens orientalis*), the progenitor of *L. culinaris*, were gathered in Syria. Its domestication was initially impossible due to a 90% seed dormancy. Since wild lentils yield only 10 seeds per plant, its cultivation was impossible. Israeli archaeologists dated a hoard of a million lentils found in the Biblical city of Nazareth at 8,800 years ago. As this store of lentils was contaminated with seeds from a weed of present-day lentil fields, namely *Galium tricornutum*, the lentil dormancy mutant was found and the lentil was cultivated by this time. A large granary with wild barley (*Hordeum spontaneum*), the progenitor of *H. vulgare* contaminated with wild oat (*Avena sterilis*) was also found in Gilgal, the site of the fig findings. Clearly, the inhabitants of this village sowed a number of wild crops and were engaged in predomistication cultivation at this early time (Weiss et al. 2006).

Tomato Fruit Size

In contrast to the slow increase in wheat grain size, rapid evolution of fruit size has accompanied the domestication of most fruit-bearing crop. The precursor of the domesticated tomato (*Lycopersicon esculentum*) probably weighted only a few grams. Fruits are seed dispersal organs of plants, they must thus be sufficiently large to house enough seeds, but small enough to be commensurate with the size of the animals, which disperse the seeds. On most continents these are small rodents and birds setting a clear upper limit for the fruit size. A notable exception is New Zealand, whose isolated geographical island position prevented the colonization with small mammals. Here giant, 7-cm-long, flightless grasshoppers (*Deinacrida rugosa*) take at least for some plants the role of small rodents as seed disperser. Their seeds pass the intestinal tract of the insects intact and show even a higher germination rate than undigested control seed (Duthie et al. 2006). A tomato fruit larger than a 1 cm would be unsuitable for seed dispersal. However, tomatoes have a substantial unused genetic capacity: Modern tomatoes can weigh as much a 1 kg. US plant geneticists identified a QLT, which contributed about 30% of the fruit size (Frary et al. 2000). They narrowed their analysis down to a single gene whose highest expression level was in carpels, the structure which ultimately develops into fruit. Carpels of large-fruited tomatoes were already heavier at flowering. The gene controlled the number of carpel cells. The mutation was located in the upstream promoter region of the gene and the geneticists suspected a negative regulator of cell division as the gene function, which concurs with similarities to the *ras* oncogen.



5. Cocos nucifera (Kokospalme). 6. Elaeis guineensis (Ölpalme); a männlicher Blütenstand, b weibliche Blüten. 8. Stillingia sebifera (Talgbaum).

Ethiopia

Not everything was invented in the Fertile Crescent (Figure 6.31). Important mutants were selected in other cradles of agriculture like Ethiopia. Resistance to fungal pathogens is an important trait for a cereal to become an important crop. Barley (*Hordeum vulgare*) has played an important role in Old World agriculture. The majority of the cultivated elite varieties of barley are resistant to the widespread powdery mildew fungus. Plant geneticists could now show that the resistance is the consequence of a loss of gene function. The seven-membrane Mlo protein is not any longer expressed because a complex tandem repeat array in the 5' regulatory sequence leads to an aberrant transcript. Since this gene product is essential for the infection process, the mutant shows a strong resistance phenotype. In line with this hypothesis, excision of the repeat induced in the laboratory led to the restoration of the Mlo function and restored also the sensitivity to the fungus (Piffanelli et al. 2004). Interestingly, this mutation was detected in landraces from traditional farmers in Ethiopia during the 1930s and might reflect the breeding efforts of their ancestors to achieve pathogen-resisting barley.

Maize in Mesoamerica

We get a genetically even clearer picture when changing to maize (Figure 6.32), a crop that was domesticated in Mesoamerica. Archaeological research in the humid lowlands at the Gulf Coast of Mexico provided the earliest record of maize cultivation. Large pollen typical of domesticated maize (*Zea mays*) appeared about 5000 BC. A single manihot pollen characteristic for domesticated manioc was sighted at 4600 BC, while sunflower seeds and cotton were only spotted 2500 BC when farming had already expanded (Pope et al. 2001).

Already in 1939 the prominent geneticist George Beadle argued that maize could have been selected as a new variant of teosinte. He speculated that maize was only separated by five major mutations from the wild plant

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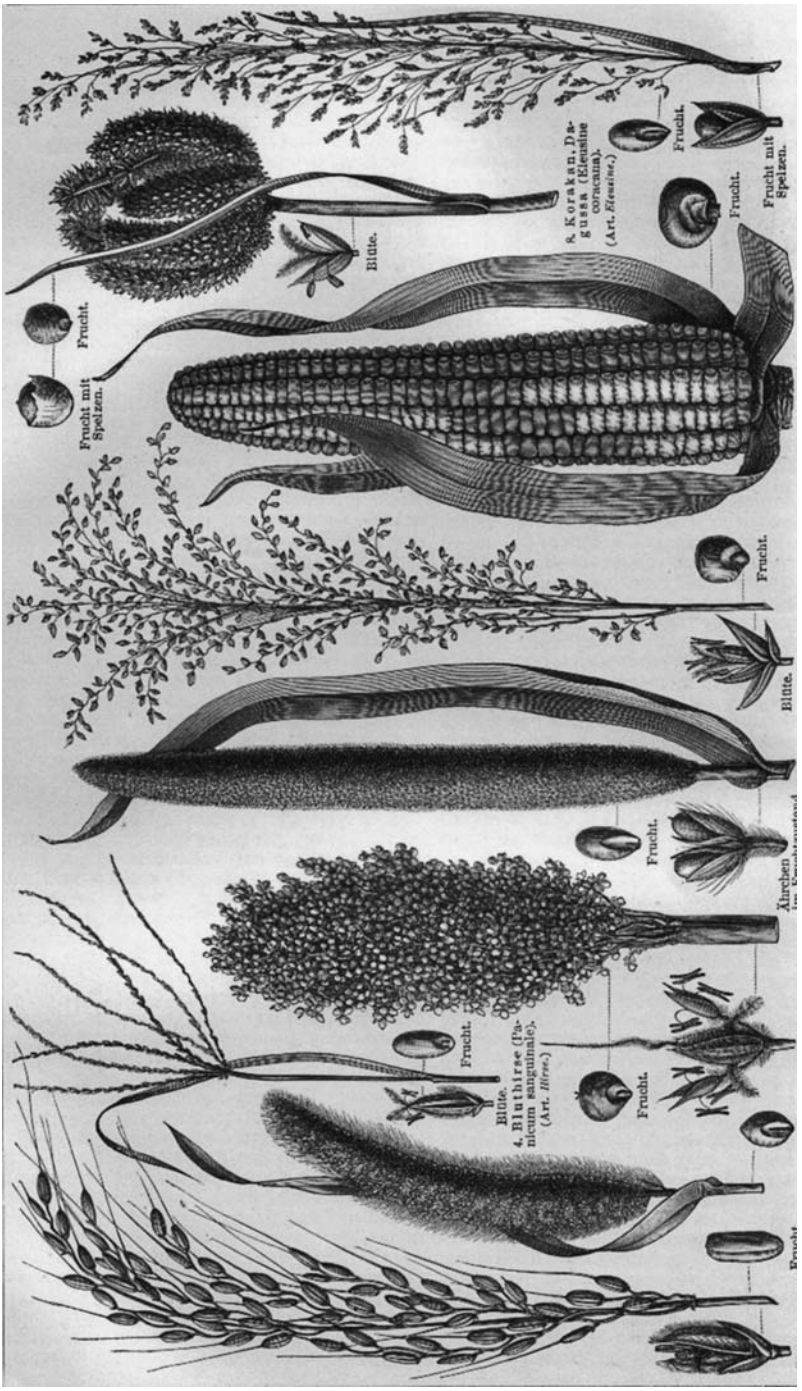
FIGURE 6.31. Fat- and oil-providing plants. At the *left* you see the coconut (*Cocos nucifera*, 5), which yields cocobutter, which is rich in saturated fatty acids and free of cholesterol. It is used for margarine, ice cream, and chocolate. This palm tree (up to 30 m tall) was domesticated 3,000 years ago in Malaysia and was exported from there over the entire Pacific and Indian Ocean. Next to it is the oil palm (*Elaeis guineensis*, *6*) from West Africa. With a harvest of 6 tons palm oil per hectare of cultivated land, it provides the highest yield for any oil-producing plant and is after soybean the second important source of vegetable oil. The two palms are shown with their male (**a**) and female (**c**) flowers. The fruit of the olive (*Olea europea*, *7*) contains 40% oil and has thus the highest caloric content of all known fruits (200 kcal/100 g). It was cultivated in the Near East and became a characteristic tree for the Mediterranean basin from antiquity to now. From Biblical times onwards it was associated with many values, the olive twig became a symbol of conciliation and peace. *Stillingia sebifera* (*8*) is a Euphorbiaceae from China, its seeds are surrounded by a fat layer.


Frucht mit Spelzen.
Frucht.
Blüte.
8. Koraka n. Dagusa. (Eleusine coracana). (Art. Eleusine.)
Frucht.
Frucht.
Frucht mit Spelzen.
Frucht.
Blüte.
Frucht.
Ährchen
Frucht.
Blüte.
4. Blutbirse (Panicum sanguinale). (Art. Hirse.)
Frucht.
Frucht.

(Martienssen 1997). One of these major mutations was indeed identified in 1997 and called *teosinte branched 1*, (in short *tb1*; Doebley et al. 1997). It affects the apical dominance of the plant. Whereas teosinte plants bear many long axillar branches that are tipped by male inflorescences (tassels), maize plants are upright and not branched and show only few, short axillar branches tipped by female ears. The growth of the ears is controlled by *tb1* and the *terminal ear 1* genes. The *tb1* gene was cloned and offered a surprise: it did not differ from the gene sequence of teosinte. The protein showed similarity to the *cycloidea* gene product from snapdragon, which decides whether a radially or a bilaterally symmetrical flower is built. However, the maize *tb1* gene is expressed at twice the mRNA level of the teosinte allele. This observation suggests that gene regulation changes underlie the transition from teosinte to maize. This was proven subsequently.

The plant breeder selects seeds from the preferred form and culls out the undesired forms during a series of crossing experiments. The trait of interest increases in frequency and becomes thus finally fixed. One should thus expect that the genetic diversity is drastically decreased in the crop when compared to the wild type. This was, however, not the case for the protein-coding part of the *tb1* gene. This explains why maize is still today such a variable crop. However, the regulatory 5′ noncoding part of the *tb1* gene showed evidence for a strong selection (Wang et al. 1999). The geneticists deduced that it took only a few hundred years to fix the *tb1* mutation and that Balsas teosinte from the southwestern Mexico was the ancestor of maize.

Plant geneticists suspect, however, that maize domestication was a complex process that acted on a large number of traits and genes. Important morphological differences between teosinte and maize are currently attributed to genetic changes in five chromosomal regions. Recently, US scientists added another gene to this list (Vollbrecht et al. 2005). It is called *ramosa1* and it is a transcription factor, which controls inflorescence architecture by imposing a short branch identity. The mutant was detected a century ago on the field of a farmer. The plant showed branched tassels and ears and looked so different that it was initially described as a new species, *Zea ramosa*.

The Southward Spread of Maize

The rise of historical states in ancient South America like that of the Wari or Inca was maize-dependent. However, the arrival of maize from Mesoamerica

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FIGURE 6.32. The figure shows extra-European cereals, from *left to right*: rice (*Oryza sativa* with flower and grain, *1*) and various forms of millet—the foxtail millet *Setaria italica* (*2*), Durra *Sorghum* (*5*), pearl millet *Pennisetum* (*6*) and the broomcorn millet *Panicum miliaceum* (*3*), *Panicum sanguinale* (*4*). At the *right* side you see the finger millet *Eleusine coracana* (*8*) and the teff *Eragrostis abyssinica* (*9*). Millets are important staple food in Asia and western Africa. During the Middle Ages millet provided major grains in Europe. America's contribution to the cereals is maize or simply corn (*Zea mays, 7*).

into the Andes was poorly documented. Recent archaeological evidence pushed the beginning of Andean maize cultivation back to 4000 BP and that at an impressive altitude of 3,600 m above sea level in Peru (Perry et al. 2006). At this level two agricultural zones meet: In the temperate *qheshwa* zona between 2,300 and 3,600 m, maize is produced under intensive irrigation, while in the cool *echadero* zone from 3,600 to 4,000 m, tuber cultivation is practiced. The investigation of starch granules and phytoliths identified mainly maize, half of them with evidence of onsite processing into flour by grinding. Interestingly, the agricultural archaeologists found also remains of arrowroot (*Maranta*), which is a typical plant of the lowland tropical zone that cannot be grown above 1,000-m altitude. The scientists interpret this as evidence for the deliberate transport of plant foods and thus human traffic between the tropical forest and the highland.

Agricultural Archeology

An outpost of the Smithsonian Institute in Panama showed that simple microscopic methods could contribute to the elucidation of the history of early plant domestication in humid tropical areas that are hostile to the preservation of organic remains. In one study, they used phytoliths, microscopic siliceous remains of plants. In a prehistoric site from coastal Ecuador, they found phytoliths with forms and sizes characteristic for domesticated *Cucurbita* (squash and gourd), which produced oil- and protein-rich seeds appreciated by the latest foragers and earliest farmers in America (Piperno and Stothert 2003). The remains were dated to 9,000 years ago. Since stone tools occasionally contained still identified remains from blood, the researchers argued that milling stones might preserve in crevices starch grains that can be identified and dated and thus allow to retrace part of the domestication history of roots and tubers that are otherwise only poorly documented in the archaeological record. In fact, on milling stones from a shelter in Panama dated between 7,000 and 5,000 years ago, they found starch grains (Figure 6.33) identifiable as manioc (*Manihot esculaenta*), yams (*Dioscorea*) and arrowroot (*Maranta*) mixed with maize starch (Piperno et al. 2000).

A Filled Cooking Pot

In fortunate situations we can have a direct look into the food bowl and are not obliged to rely on microscopic analysis of the food item. A nice archeological paper (Lu et al. 2005) describes a Late Neolithic dish, which might also provide a strong argument on the question who invented noodles. Spontaneously, you might associate Italians with this popular staple food, but also Arabs and Chinese claimed to have invented them first. Some data point to pasta that was already prepared by the Romans, giving noodles the respectable age of 2,000 years. The abovementioned bowl was filled with what looks like noodles. It was found in a 4,000-year-old Neolithic settlement near the Yellow River in China. To make the Chinese claim to the invention of noodles clear, the Chinese authors noted a resemblance between these 0.3-cm thin, 50-cm long yellow noodles

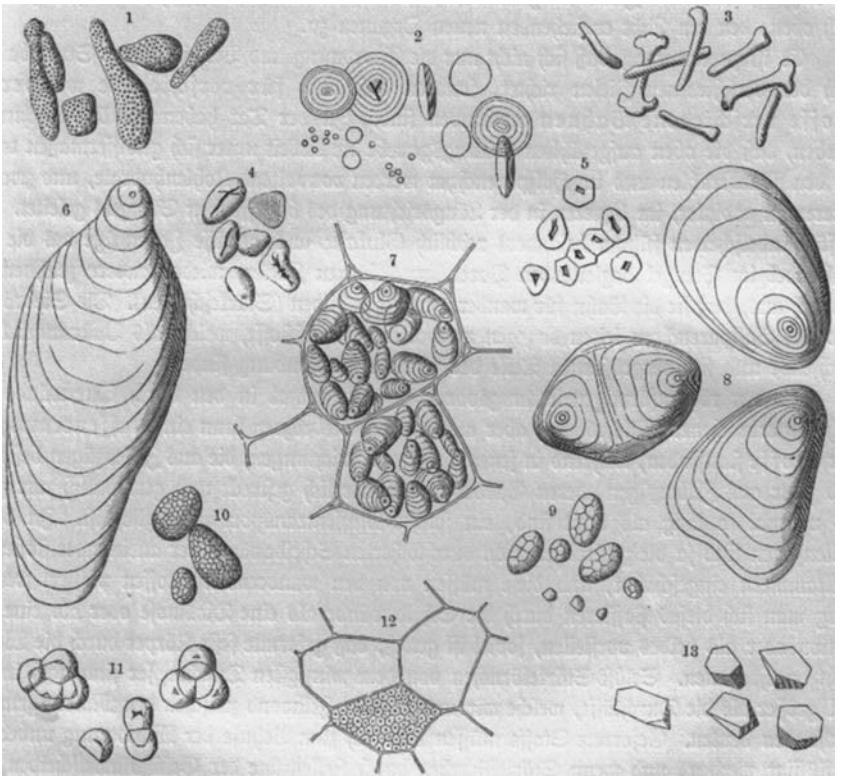

FIGURE 6.33. Agricultural archaeologists deduce the nature of domesticated plants from starch remains associated with stone tools on. This is possible since different plants show distinct forms of starch grains as demonstrated here with some examples (*1* Agrostemma; *2* wheat; *3* Euphorbia; *4* beans; *5* maize; *7, 8* potato; *9* oat; *12* rice; *13* millet).

with modern La-Mian noodles from China. Bad luck for the Roman noodle's claim to fame and antiquity. The authors provide us some further details on these proto-noodles. Modern pasta and noodles are made from durum and bread wheat. Phytolith and starch grain analysis, however, identified modern millet as the basis of this early food item, which would also explain the very delicate character of these noodles.

New Guinea

Also the remote New Guinea belongs to the cradles of agriculture. As the early farmers collected plants from their environment, each center has its own local character. In excavations of the Kuk Swamp, archaeologists found stone tools dated to 7,000 BP. They contained raphids (calcium oxalate crystals) and phytoliths of two starch-containing plants. They were identified as remains from taro (*Colocasia esculenta*) and banana (*Musa*, for other tropical fruits

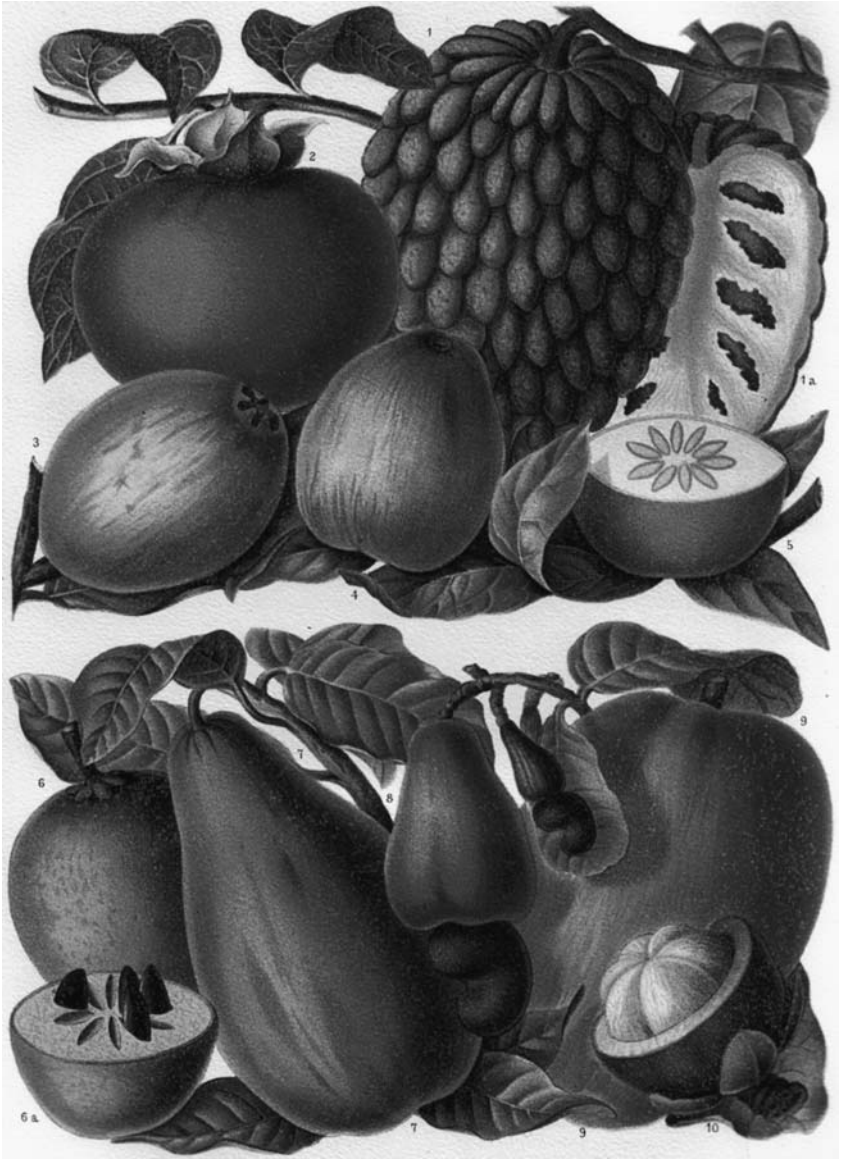

FIGURE 6.34. Tropical fruits. From *left to right*, *top*: guava (*Psidium guajava*, *3*) from Central America, one of the richest sources of vitamin C; persimmon (*Diospyros kaki*, *2*) from China and Japan is rich in vitamin A; an "apple" from Malaysia (jambu, *4*); the custard apple (*Annona*, 1). *Bottom*: sapodilla (*Achras zapota*, *6*) from Central America—a traditional food plant of the Mayas and Aztecs, initially a basis for the chewing gum; the avocado (*Persea americana*, *7*) is an unusual fruit since it was appreciated by the Aztecs more for its lipid content (linoleic acid) than its sweetness; cashew nut (*Anacardium occidentale*, *8*) from Brazil; mango (*Mangifera indica*, *9*) was cultivated 4,000 years ago in Indomalaysia; mangosteen (*Garcinia mangostana*, *10*) from Malaysia is rated as one of the most delicious tropical fruits.

see Figure 6.34), the most important food staples in New Guinea before the European introduction of sweet potato. At the same time mountain rainforests were cleared by fire to grassland. Soon followed wetland agriculture with mounding (phase 2) and ditched cultivation (phase 3; 4,000 years ago; Denham et al. 2003). However, in other respects New Guinea did not follow the familiar aspects of agricultural societies in other world regions. New Guinea represents one of the most colored patchwork of languages, no demic diffusion was observed and no social stratification and civilization developed in New Guinea. The invention of agriculture is thus not a one-way into a technical culture.

Taming the Beast

Conditions for Breeding

Despite substantial variability in plant and animal species that were domesticated in the different world regions, it remains striking that a relatively small set of species got a place in agriculture. Humans have tried in vain to domesticate many animals, a number of examples are documented in the written documents of ancient Egypt that will amuse a modern farmer. A more recent famous fiasco is the unsuccessful taming of the zebra by European settlers in South Africa. The zebra turned out to be incurable vicious and endowed with a much better peripheral vision than horses. They escape the lasso even of experienced rodeo cowboys. There is thus a minimal list of requirements the animal breeder expects to be fulfilled (Diamond 2002): The diet should be easily provided, the growth rate should be quick, no long birth spacing, no nasty disposition (aggression toward the breeder), possibility to breed in captivity, and no panic in enclosures, and the animal should follow the leader dominance of the breeder.

Goat

Notably, we have to return to the Fertile Crescent when we want to retrace the early history of animal domestication. The initial domestication of goats (*Capra hircus*) could be traced to 10,000 years ago in the Zagros mountain of western Iran. The researchers deduced their claim from studying the distribution of animal bones associated with human activities. First they established a bimodal distribution curve between the sexes and then searched for the selective culling of young males and delayed slaughter of females as indication of herding. In hunted populations, adult males were well represented, then the first shift was seen when herding started first within the geographical distribution range of goats in the mountain, followed by dispersal of goat herding into the lowlands (Zeder and Hesse 2000).

Cattle

The limited geographic ranges of the wild progenitors of many of the primary European domesticated species excluded a central European origin for them and

pointed again to eastern Anatolia or the Near East as their homeland. This is not the case for the cattle, humans' favorite beast of burden. Central Europe knows the wild ox (*Bos primigenius*) or aurochs, which became extinct in the seventeenth century when the last animal was killed in Poland. Scientists collected 400 samples from Europe (including four extinct British wild oxen from museums), Africa, and the Near East, and determined mitochondrial DNA sequences. They argued that genetic loci from a center of origin are expected to retain more ancestral variation, while lineage pruning through successive colonization should lead to a reduction of genetic variability in derived populations. Phylogenetic tree building set first as expected the zebu (*Bos indicus*) apart from the European ox (*Bos taurus*); they are separated by about 100,000 years. It should be noted that the distinction of both oxen as different species is not justified from the biological species definition. Both taxa are completely interfertile. The aurochs from the museum clusters near the *B. taurus* branch. The African cattle diversity is clustered around a haplotype that is absent from the European samples and occurs only with low frequency in the Near East. The haplotype analysis traced the origin of the European cattle to east Anatolia and the Near East (Troy et al. 2001). What about the situation of cattle domestication in Africa? Livestock research institutes located in Africa set out to sample cattle from 50 populations of 23 African countries and investigated them for 15 microsatellite markers (Hanotte et al. 2002). *They got some advance help from painters. Rock artists showed that the earliest African cattle was the humpless* B. taurus*, the humped cattle was first depicted in Egyptian tomb paintings of the XII dynasty. As suggested by the painters, the geneticists got a mixed message. The zebu influence was the highest at the horn of Africa and suggested import of the zebu by Arabian contact. The zebu was actually domesticated in the Indus valley 6,000 years ago. Arabs brought the zebu together with the domesticated chicken and the camel. These contacts were no one way paths since India received cereals domesticated in Africa like sorghum and the finger millet. However, the initial expansion was by* B. taurus *most likely derived from a single region of origin and it reached the southern part by traveling an eastern route. The genetic structure of the African cattle population was markedly influenced by the rinderpest epidemics in the late nineteenth century and by the fact that it experienced population bottlenecks due to attrition from tropical livestock diseases*. The statistical analysis of the genetic data pointed to at least three centers of domestication contributing to the current genetic make-up of cattle in Africa.

Horse

An even more complicated genetic structure was revealed when about 200 domesticated horses were investigated for mitochondrial DNA sequences. In the analysis the modern horse lineages coalesce only 300,000 years BP, much too early when compared to the domestication of horses, which took place according to archaeological evidence 6,000 years ago. Numerous matrilines (mitochondria are only inherited from the mother) must have been incorporated into the gene pool of the domestic horse. The genetic data suggest that horses were initially

captured over a wide geographical area and used for nutrition and transport. When the supply of wild horses dwindled because of overexploitation or environmental changes, captive breeding started in many different regions. In the history of horse use, the technique of capturing, taming, and rearing of wild animals was transferred between the populations and not the domesticated breeds (Vila et al. 2001).

Pig

Archaeological record of pig bones suggested that pigs were first domesticated 9,000 years ago in the Near East. We have here a case as in cattle where central Europe has an own wild boar population. Did the domesticated pig come in an early agricultural import package with the cattle and sheep from the Near East? Mitochondrial sequences from 700 wild and domesticated pigs revealed that the European wild boar is the principal source of modern European domesticated pigs. The sequence data placed the origin of the wild boar in Southeast Asia from where they dispersed across Eurasia. There were also multiple centers of pig domestication across Eurasia (Larson et al. 2005).

Domestication of Moulds: Aspergillus

Microorganisms are frequently overlooked when recalling the history of domestication despite the fact that they played important roles for food and feed production. We mentioned already the important cultural role of lactic acid bacteria in milk fermentation, practiced in dairy countries. A similar cultural role was played by *Aspergillus* moulds for the fermentation of soy sauce, miso, and sake in Asia and especially in Japan. *Aspergilllus* (Figures 6.35 and 6.36) belongs to the Deuteromycetes (Fungi imperfecti) and produces sexual ascospores or asexual conidiospores on a highly characteristic structure called an aspergillum. Its recruitment into food production also involved substantial taming. In the *Aspergillus* genus you find one of the most useful food fermenting microorganism, *Aspergillus oryzae*, which is the source of industrial enzymes and organic acids, but also *A. flavus*, a saprophyte growing on crops like corn, peanuts, cottonseed, and tree nuts. However, it is not just a food spoilage organism: *A. flavus* produces aflatoxin B1, which is one of the most potent liver toxins. In fact, a strong epidemiological link between dietary exposure to aflatoxin and hepatocellular carcinoma was demonstrated in populations from China and sub-Saharan Africa. Scientists showed that this was not a trivial domestication process. *A. oryzae* was used for thousands of years in oriental food manufacturing and carries its scientific name from its common association with rice plants. In old Japanese reports, the seed culture was derived from rice smut, where *A. oryzae* is found in association with a fungal plant pathogen. Also the analysis of the genome sequences from *A. oryzae* demonstrated that it was itself once a toxic mould. It contains all the 25 genes that *A. flavus* needs for the biosynthesis of aflatoxin (Machida et al. 2005). However, in *A. oryzae* these genes are not expressed, possibly due to a regulatory mutation. *A. oryzae* shows a 37-Mb genome encoding 12,000 genes and is thus 8 Mb larger

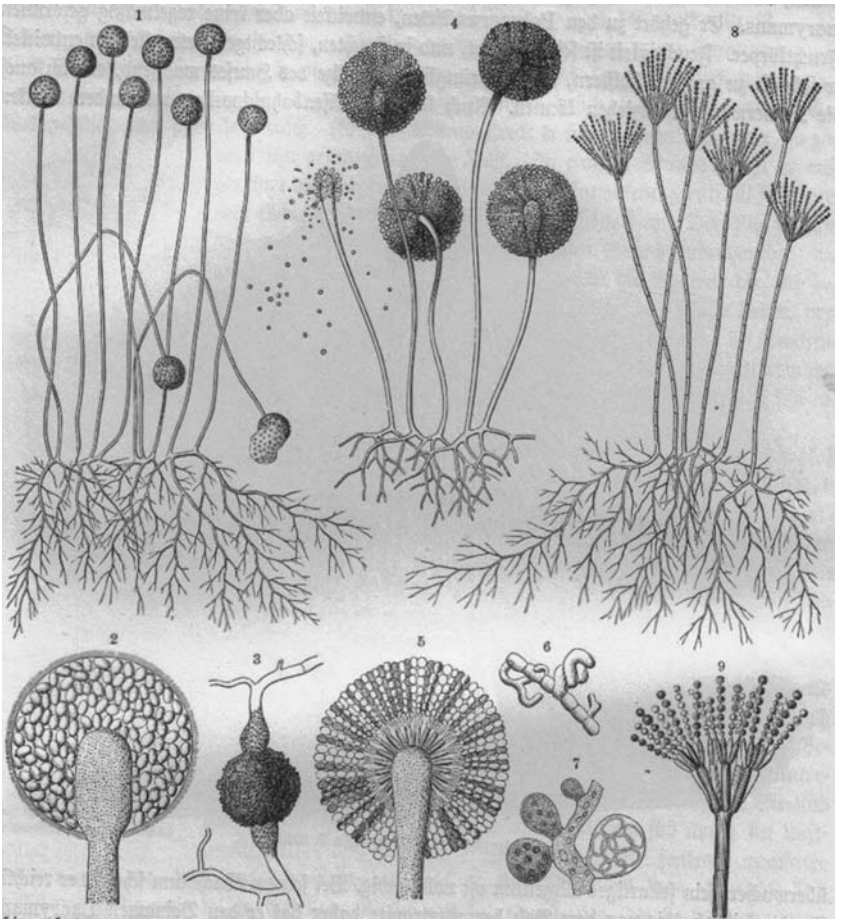

FIGURE 6.35. Different fungi. *1–3 Mucor mucedo* (order Zygomycetales, class Phycomycetes, *2* sporangium), *4, 5, 7 Aspergillus niger* and *6, 8, 9 Penicillium crustaceum* (order Plectascales, class Ascomycetes). *2, 5, 9* sporangia with conidia. These organisms are commonly called moulds. Mould is not a systematic name, only the indication for superficially growing fungal hyphae. Moulds play an important role in food processing, both in the positive and in the negative sense.

than the genome of the pathogenic and allergenic fungus *Aspergillus fumigatus*. The latter mould is a prolific conidia producer, which might explain its allergic properties. However, none of the nine major allergens is a spore surface protein. *A. fumigatus* is an opportunistic pathogen in immunocompromised patients, but the genome sequence showed few cues to the underlying pathogenic mechanisms. The authors observed many genes that are upregulated at temperatures higher than in the environment (Nierman et al. 2005). However, this does not reflect an adaptation to the warm-blooded host. *A. fumigatus* is quite thermotolerant (up to 70° C) because it is frequently isolated from compost. Its primary niche is rotting vegetable.

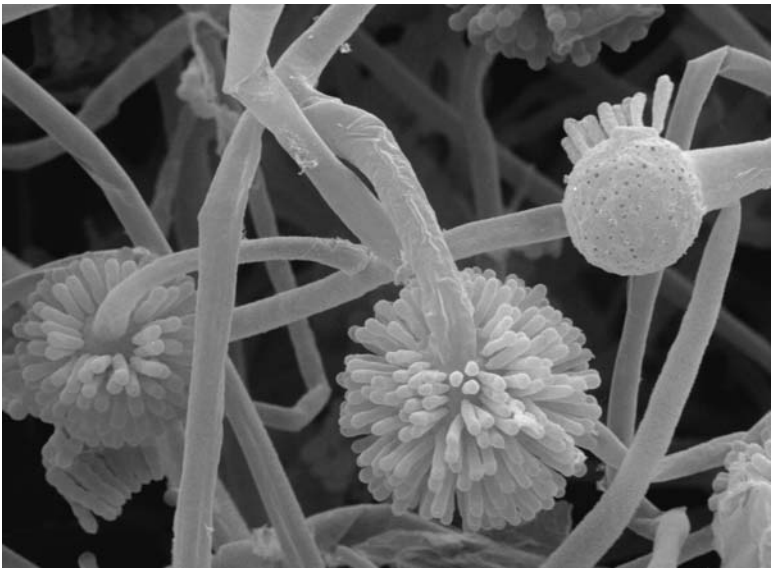

FIGURE 6.36. Hundred years later: molds seen with the scanning electron microscope. Sporangia with conidia from the molds *Aspergillus restrictus* (*top*) and *Syncephalastrum racemosum*.

Alignment of these two and a third *Aspergillus* genome revealed the presence of similarly organized genome segments (syntenic regions) and *A. oryzae*-specific genome segments in a mosaic pattern. The latter gene segments are enriched for genes involved in metabolism. *A. oryzae* produces copious amounts of industrially useful enzymes like amylases and proteinases. The reason is clear: Within the koji culture, *A. oryzae* grows on the surface of steamed rice or ground soybean, where it has to digest starch and proteins to get the sugars and amino acids it needs. In fact, *A. oryzae* encodes 135 secreted proteinase genes, more than 1% of the total genome is dedicated to this single task. Even more impressive is the expansion of genes involved in secondary metabolism. However, in contrast to yeast, no duplication of the *A. oryzae* was diagnosed; the *A. oryzae*-specific DNA segments are most likely the result of horizontal gene transfer.

Fishery

Contemporary Fishery Problems

Sustainable Fishery?

The introduction of a new top predator, humans, into the food chain raised a number of problems. I will illustrate the problem with some figures taken from a report that questioned whether the current rate of global fishery is sustainable

(Pauly and Christensen 1995). If you subdivide the global primary productivity in dry weight of annually created biomass, about 60% is produced by terrestrial ecosystems. Humans take a disproportional part of this primary productivity: estimates are between 35 and 40%, which is used directly (food, fiber) or indirectly (animal feed) or foregone (urban sprawl). The authors calculated that 8% of the world's aquatic primary productivity is required to sustain the current rate of fishery. This figure was based on the world fishery statistics from 1988 to 1991 (annually 95 million tons of fish), augmented by the discard of bycatch (27 million tons), and a recalculated average rate of energy transfer of 10% from one trophic level to the other. The latter figure indicates that 1 kg biomass of prey at trophic level x creates 100 g biomass in its direct predator at trophic level $x+1$. The food chain is efficient and short in the ocean: for example in the open ocean, the catch (major species are tunas, bonitos) is on average at trophic level 4, in upwelling systems (major species: anchovy, sardine) it is lower (2.8), and intermediate at nontropical shelves (major species: cods, hakes, and haddocks; trophic level: 3.5). Upwelling and shelves provide the major catches, and in these ecosystems, about 30% of the primary productivity is needed to sustain the current rate of fishery. The authors concluded that the prospect of increasing these catches is dim. They contradicted also earlier conclusions that "human influence on the lowest trophic levels in the ocean outside of severely polluted areas is minimal and human exploitation of marine resources therefore seems insufficient." The discussion over the last 10 years since this report appeared has amply verified the bleak prospect for some areas of fishery. What are possible consequences? Do we have to catch the prey of tuna (mainly small pelagic fish), i.e., do we have to go down the trophic level with our fishery? Or do we need better management of the available stocks? Or do we even need a complement of agriculture for the oceans?

In Cod We Trust

The Collapse Which Could be Forseen

Fishing is the catching of aquatic wildlife and was likened to the hunting of bison (Pauly et al. 2002). The comparison was taken by the authors on purpose to point to two facts: Modern men returned to the food supply practices of the gone hunter-and-gatherer society and when used to feed a large population and when using modern technology, the prey population as big as it might appear will finally collapse. The bisons of the Great Plains were hunted down with the help of the gun, and high-tech fleets netted the cod out of the ocean. *I like reading old biology books, one has the illusion to be a bit cleverer than our ancestors and one can ask whether the bright minds of their time could foresee future events. One of my favorite books is the late-nineteenth-century zoology book series known in Germany as the "Brehm" from which already Darwin quoted extensively in his book The Descent of Man. The author of the article on the North Atlantic cod reported with much surprise on the unbelievable abundance of cod off Norway, which nourished an entire industry in Northern Europe.*

With the same awe, eighteenth-century zoologists would have reported on the bison herds. Both populations have collapsed. However, the author of the Brehm was already asking himself whether this exploitation rate of the cod would be sustainable without knowing what late-twentieth-century hunting technology we would lash on the cod. The problematic strategy of the "harvesting without sowing" was already apparent to biologists around 1900.

History of Fishing

Fishing is associated with *H. sapiens* nearly from its biological beginnings. A finely worked bone tool industry containing barbed bone points was found at an archaeological site in Zaire, which was dated to 90,000 years BP (Yellen et al. 1995). The site was characterized by abundant catfish remains. Fish exceeding 2 m in length was apparently harpooned in shallow water during spawning and thus provided a major meat input for the hunters. Very similar tools were found in this region about 50,000 years later pointing to a remarkable conservation of a fishing culture. The long-term exploitation of this meat source was possible since the population apparently consisted only of nuclear family units. Fishery researchers distinguish three periods of human impact on marine ecosystems. The aboriginal use refers to subsistence exploitation of near shore ecosystems by human cultures using simple watercraft and fish extraction technology. Colonial use comprised a systematic exploitation of shelf seas by foreign mercantile powers (Jackson et al. 2001). The last period was called the global pattern of maritime resource consumption and is characterized by a rapid worldwide depletion of predatory fish communities, both in the open ocean and the continental shelves (Myers and Worm 2003).

Signs of Depletion

The first step to an analysis providing a scientific basis for future restoration efforts is an exact quantification of the extent of fish depletion. Data were therefore compiled from standardized research trawl surveys over the last 40 years. The large demersal (bottom-dwelling) fish such as cod, flatfishes, skates, and rays all showed a sharp decline in different geographical areas. Data for the open ocean were obtained from the Japanese fishing fleet that uses pelagic longlines as the most widespread fishing gear. Longlines contain many hooks in a single line and thus represent a long baited transect through the water. Most world regions still yielded between 8 and 10 catches per 100 hooks in the 1960s, but these values dropped to 2 in the 1980s with decreasing trend. Formerly productive areas had to be abandoned and higher catches were only found at the periphery of exploited areas. Calculations showed an initial decline of 16% per year and the global ocean has lost more than 90% of the large predator fish species. The researchers suspected that most fish managers might not be aware of the true magnitude of the fish decline since the majority of the decline occurred in the first years of exploitation. For example, during the first 5 years of

industrialized trawl fishing, the Golf of Thailand lost 60% of the large demersal fish. The researchers warned furthermore that reliance on recent data might be misleading since the data provide only minimum estimates for the unexploited communities, and referred to this as the "missing baseline" problem.

Detailed investigation off Newfoundland where Canada introduced severe restrictions on cod fishing painted a bleak picture for some large, once widely distributed demersal fishes. Skates (*Raja*) occurred in the St Pierre Bank with 0.6 million individuals in the 1950s, this dropped to 0.2 millions in the 1960s to a mere 500 individuals in the 1970s, and in the last 20 years none has been caught (Casey and Myers 1998; Figure 6.37). This 1-m-large elasmobranch (cartilageous-fish-like sharks) has few natural enemies but gets accidentally into the nets of fishers. Consequently, it once sported a leisurely life history. It grows slowly, mature at about 11 years, and lays only about 50 eggs per year.

The Overlooked Biology

Bony fishes like the cod invest heavily in many eggs and could thus have a fabulous fecundity and appear therefore better equipped to cope with the problem of overfishing. However, fishing is a very selective process going for the larger animals and this dramatically compromises the egg production. A ripe female red snapper (*Lutjanus campechanus*) measures 61 cm, weighs 12.5 kg, and produces 9,300,000 eggs. You need 212 younger females of 42-cm length and 1.1-kg weight to produce the same amount of eggs (Pauly et al. 2002). Going for the larger animals as is done with the current extraction technologies means that you

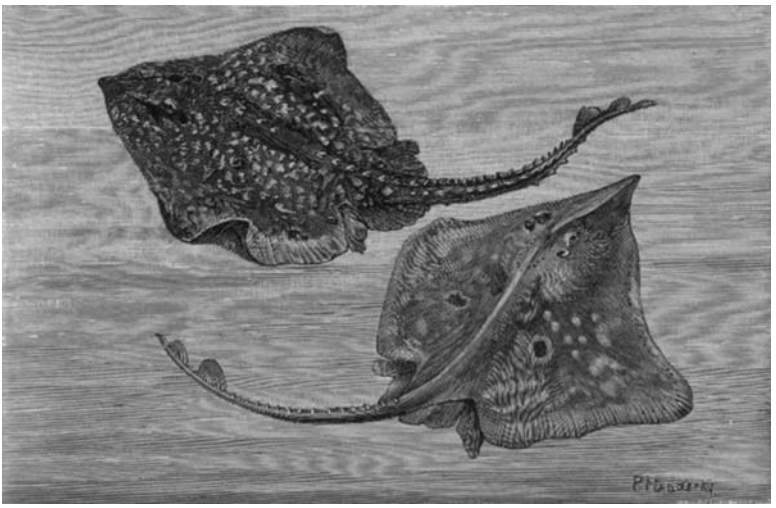

FIGURE 6.37. Skates (*left*: *Raja clavata*; *right*: *R. batis*), skates feed on mollusks, crustaceans, and fishes, dropping down on the prey from above. We speak about skate depletion as a sign of over-fishing the oceans.

target the Achilles' heel even of prodigiously fertile bony fish. Cod can live for many years and only reaches sexual maturity by the age of 4 years. However, cod is fully exploited by the year of two. Substantial mortality sets in before many fish had a chance to reproduce. Currently, only about 4% of 1-year-old cod survive to maturity. The result is clear, even when formulated in fishery jargon: low survival of recruits into the spawning stock. Or more bluntly as stated in the title of the report: *Potential Collapse of the North Sea Cod Stock*" (Cook et al. 1997) and this came just on the heels of the Canadian cod demise.

A Bit of Politics

The Canadian government reacted and ordered in 2003 an end to all cod fishery off Newfoundland and Labrador, while the EU only tighten the cod quota. The reason for the distinct reaction is differences in the extent of cod decline in both regions (99% off Canada and "only" 90% in the North Sea) and a stronger fishery lobby in Europe (Schiermeier 2003). At the moment there is a discussion between scientists and fishery managers about the burden of proof for the effect of fishery on the marine ecosystem (Dayton 1998). Scientists argue that traditional fishery management aims to optimize the catch of commercially important species, but eventually cause the collapse of the targeted species itself. They complain that those profiting from the public resources are not required to prove that their actions cause no damage. Much higher margins of safety are requested from industries running nuclear power plants or selling drugs for human use. They argue that thousands of square kilometers of benthic (sea bottom) habitat and invertebrate communities have been obliterated by trawling. Other scientists argue that the sea bottom is literally ploughed by trawling. Still others found this analogy inappropriate and likened trawling to clear cutting forests in the course of hunting deer (Pauly et al. 2002). Some fishery scientists would put a rather long list of well-known fishes on the extinction threat list, while fishery managers claim that the declines are still statistically blurred by natural variability in abundance.

Recovery?

To shed more light on these statistics, more data evaluation is needed. When 90 marine fish stocks that experienced a 15-year decline were followed 40% continued with the decline, 50% showed some recovery, and only 7% had fully recovered. The latter belonged all to clupeids (herring and relatives). The recovery of clupeids was attributed to their younger maturation age and the high selectivity of the clupeid catch technology (mid-water trawls on schools identified acoustically). Gadeid (cod and relatives) did not recover (Hutchings 2000). The latter observation disappointed and surprised fishery researchers. The Canadian government had already closed the directed fishing for the northern cod in 1992, but even after a decade-long moratorium, its population size remained at a historical low. What went wrong? Or are our models inadequate? Scientists draw attention to the fact that the life history of cod changed even before

overt evidence for population decline became evident (Olsen et al. 2004). They had observed that cod continually shifted toward maturation at earlier ages and smaller sizes. Actually this is exactly what life-history theory predicts: Increased mortality at a given age and size of maturity selects for an earlier age of maturity. In parallel with the drop in annual survival that cod experienced over the last 20 years, age at 50% maturity decreased from 6 to 5 years. Ecologists have here a theoretical explanation: With reduced biomass, the remaining fish experience greater resource availability and could thus grow quicker. However, the cod collapse period was characterized by poor conditions for growth and the early maturing females were also smaller.

Darwinian Selection

The analysis actually supported another hypothesis, namely that fishery pressure selected for an early-maturing genotype. The concern is now great that current fishery practices have induced a strong evolution in cods, perhaps also by immigration of genotypes that fixed the population at lower stock levels. *This would not be the first case that human intervention has selected for an unwanted phenotype; think on the use of antibiotics to fight bacterial infections, which resulted perversely, but logically in a growing population of antibiotic-resistant germs*. In fact, there are experimental data with fish that we should not ignore, namely the Darwinian consequences of selective harvest by fishery (Conover and Munch 2002). Fishing mortality is highly selective, regulatory measures impose minimal sizes for the catches. Exploited stocks therefore typically show truncated size and decreased age distribution. This pressure could easily favor genotypes with slower growth and earlier age at maturity. US scientists sampled silversides (*Menidia menidia*) from a large gene pool of fish. They took 1,100 juveniles and imposed 10% mortality by harvesting the largest, in another experiment the smallest, and in a third experiment random 10% of the individuals over multiple generations. Interestingly, the small-harvested line showed much higher total harvest and mean weight of the individuals than the large-harvested line. The random-line took an intermediate position. Clearly, the selection on adult size caused the evolution of a range of traits (e.g., egg size, larval growth rate). The genetic changes might be irreversible, challenging the hopes for the recovery of severely battered fish stocks. These researchers called for a rethinking of our current regulation (all fish below a given size range are protected) and suggested a contrary protection policy, namely that all fish above a given size are protected. With respect to current fish extraction technology, this might not be an easy task. The definition of marine reserves could there be a more practicable solution. Fish would be under no size selection pressure and could diversify outside of artificial fishery constraints. Such reserves were propagated both as conservation as well as fishery management tools. Available data indicate that reserves lead to rapid increase in biomass, abundance, average size of organisms, and increased species diversity. In the Caribbean, the combined biomass in the reserve tripled

in 3 years. Notably the biomass doubled also in adjacent fishing areas. Apparently, increased egg-output supplied juveniles and large-sized adults into the neighboring fishing grounds (Roberts, Bohnsack et al. 2001).

Trophic Interactions

We now get to trophic cascades, which we encountered in the previous chapter with the introduction of a top predator, the fox. Here we see cascading effects by the fishery-induced removal of a top predator, the cod. Parallel to the cod decline, the Canadian shelf saw an increase in pelagic (water column) fish and shrimps and crabs, which were the preferred prey of cod (Frank et al. 2005). Their commercial landing now increased substantially reflecting a population relieved from predation. Interestingly, seal biomass also increased in this area. Seals got now unlimited access to the pelagic fish prey. However, the disappearance of cod had also effects at lower levels of the food chain. Zooplankton larger than 2 mm diminished in numbers. They are the food basis for pelagic fish and shrimps and crabs. In contrast, smaller zooplankton and phytoplankton increased numerically. The takeout of the cod restructured the entire food web and the data should remind you the story of the otter and the kelp, which I told you before. We have here a general ecological principle emerging from different food web conditions. It is not clear whether this new equilibrium can get fixed or whether cod can again gain ground. As a recovery of the Canadian cod was not yet observed, one might suspect that the reestablishment of the old equilibrium will take much longer than suspected, if it occurs at all.

Fishing Down the Food Web

Interestingly, the combined shrimp and crab landings from the aforementioned study area now far exceed that of the groundfish fishery it replaced. This illustrates a phenomenon, which became known in the scientific fishery literature as "Fishing down the marine food web" (Pauly et al. 1998). Landings from global fisheries have shifted in the last half-century from large piscivorous fishes toward smaller invertebrates and planktivorous fishes. When the catches for this time period are plotted as a function of their trophic level, the scientists observed a decrease from 3.3 to 3.1 in marine areas and from 3.0 to 2.8 for freshwater areas. This trend was seen over many regions of the world, but a number of exceptions were observed. Part of the variation was due to the high temporal variation in anchovy landings in the South Pacific or the sharp decline in Antarctic catches, which are now dominated by krill. Ecological food web theory wants that catches of organisms from lower trophic level should exceed those of organisms at higher trophic level as observed in the previous study. However, when applied to larger geographical areas, the highest landings are not associated with the lowest trophic levels. Curious backward-bending features were observed when both parameters were plotted against each other. This discrepancy with theory probably indicates that we have a very incomplete

picture of the complexity of marine food webs. Anyway, fishing down the food web is not a good alternative: As the authors stated, zooplankton is not going to reach our dinner plates in the foreseeable future. Actually, there are also theoretical limits to this practice.

Effect of Overfishing

Overfishing in a lower trophical level will only decrease the predation pressure in the next lower trophical level. These populations will increase in size and become so dense that they are much more susceptible to infectious diseases (Jackson et al. 2001). Indeed, there are some indications for emerging marine diseases as a consequence of both climatic changes and anthropogenic factors (Harvell et al. 1999). The final specter is a "microbialization" of the global coastal ocean. Overfishing was linked to population explosions of microbes and areas like the Chesapeake Bay and the Baltic Sea are now bacterially dominated ecosystems with a trophical structure totally different from what they showed only a century ago (Jackson et al. 2001). *Microbiologists are anyway convinced that microbes are the silent rulers of the world. We should think twice whether we should act in a way that we see us confronted more or less alone against the microbes without any intermediate fauna. This is likely a battle, which we cannot win. Are "no take zones" the only remedy against the decline of fishery or should we conduct fishery not with a hunter-gatherer, but a farmer mentality? In other words is aquaculture a sustainable alternative?*

Aquaculture

Farmed Fish

Is aquaculture the transition from the hunting to the farming type of fish production? This question cannot be answered in a single sentence and as usual in science a differentiated picture must be painted (reviewed in Naylor et al. 2000). First a few numbers as orientation: Over the last decade, the weight and value of farmed fish and shellfish has doubled. Currently about a quarter of all fish consumed by humans is farmed fish. Asia accounts for 90% of the global aquaculture production: China takes here with two-thirds, the lion's share. With respect to the trophic level, very different types of species are farmed: At one end are giant clams, which obtain most of their energy from symbiotic algae; followed by filter feeders like mussels; then come herbivorous fish like the carp; at the other end are carnivorous fish like salmon. Carp is mainly produced in China for low-income households and its production does not need extra feed input (Figure 6.38). The situation is different for salmon (Figure 6.39) farmed in Norway and catfish farmed in the USA. Both need compound feed in the form of fish biomass. Salmon farming can thus not relieve the fish extraction stress from the oceans since the fishmeal and fish oil are derived from ocean catches of small pelagic fish. There are other ecological problems associated, for example, with salmon farming: The intensive fish farming leads to wastewater

FIGURE 6.38. The carp (*Cyprinus carpio*) illustrates why it makes a difference to use herbivorous instead of piscivorous fish in aquaculture.

laden with uneaten feed and fish feces. The high fish concentration favors the transmission of infectious diseases. The latter problem is also relevant for the ocean population since escape of farmed salmon is a common problem. In the Northern Atlantic, as much as 40% of the salmon caught on sea are escapees from fish farms. This contribution now sensitively alters the genetic makeup of the wild population.

Shifting the Problem

It is not easy to replace fishmeal and fish oil by plant-derived material. Fish convert carbohydrates to energy inefficiently, and plant material is deficient in two essential amino acids (lysine and methionine) and some fatty acids. In contrast, farmed carp is mostly reared without the use of compound feed and is grown in inland ponds. Carp production is thus independent from the marine ecosystem. However, other aquaculture systems depend on wild seeds to stock the aquaculture ponds instead of relying on hatchery-reared finfish or shellfish larvae. Other aquaculture systems like shrimp (Figure 6.40) ponds have transformed large areas of mangroves (Figure 6.41) and coastal wetlands. Earlier, they provided food and shelter to many juvenile fish that was caught in the past as adults in offshore fishery. It was calculated that about 400 g of fish is lost by habitat conversion for every kilogram of shrimp produced in Thailand. To return to our initial question, it was concluded that if the growing aquaculture is to contribute fish in a sustainable way, it must reduce wild fish inputs in feed and adopt ecologically sound management practices. Otherwise it will only cause a shift of the problem of sustainability of fishery from one to the next ecological system.

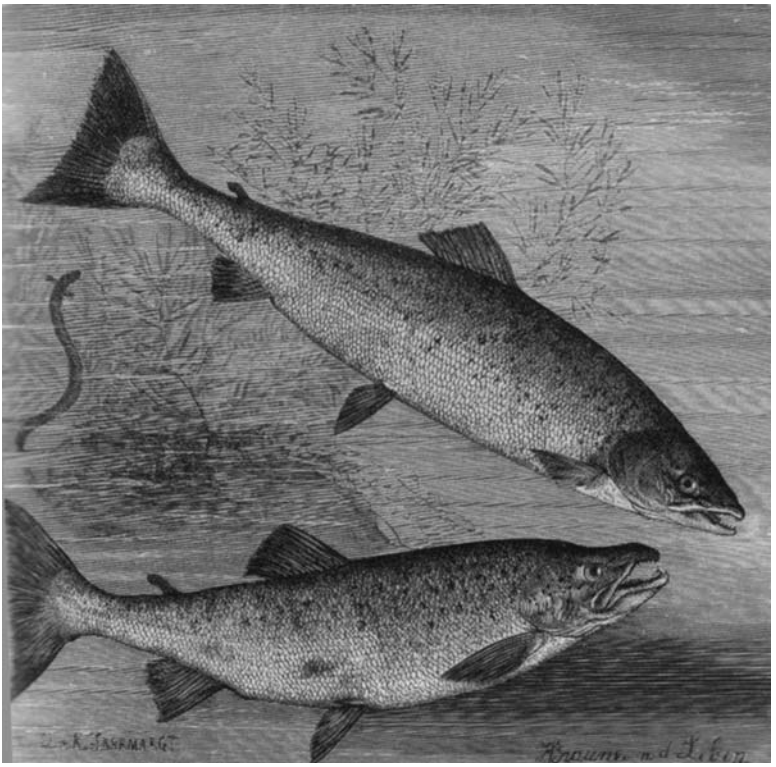

FIGURE 6.39. Salmon (*Salmo salar*) and salmon trout (*S. trutta*), typical piscivorous fishes are shown here.

The Lesson of the Lake Victoria

History of a Lake

The region around Lake Victoria became a disaster zone because of the compound impact of tribal feud, genocide and wars, and the AIDS epidemic. This was not always so: It was once a fertile contact zone between diverse African agricultural traditions (Phillipson 1986). Cereals like millet and sorghum came from the north and met bananas, yams, and sweet potatoes. Bananas came to Africa via the Indian subcontinent. Harpoon-fishing settlements were dated as early as 11,000 years ago in this region. Like in Europe the change from a hunter-gatherers to a food-producing economy was accompanied by the spread of a language, here that of the Bantu languages into southern Africa. Lake Victoria has nearly twice the area of Switzerland and is the home of a rich and diverse fish population. The lake harbors an estimated 500 endemic species of cichlid fishes, which are herbivores and detritus feeders. Mitochondrial DNA sequences

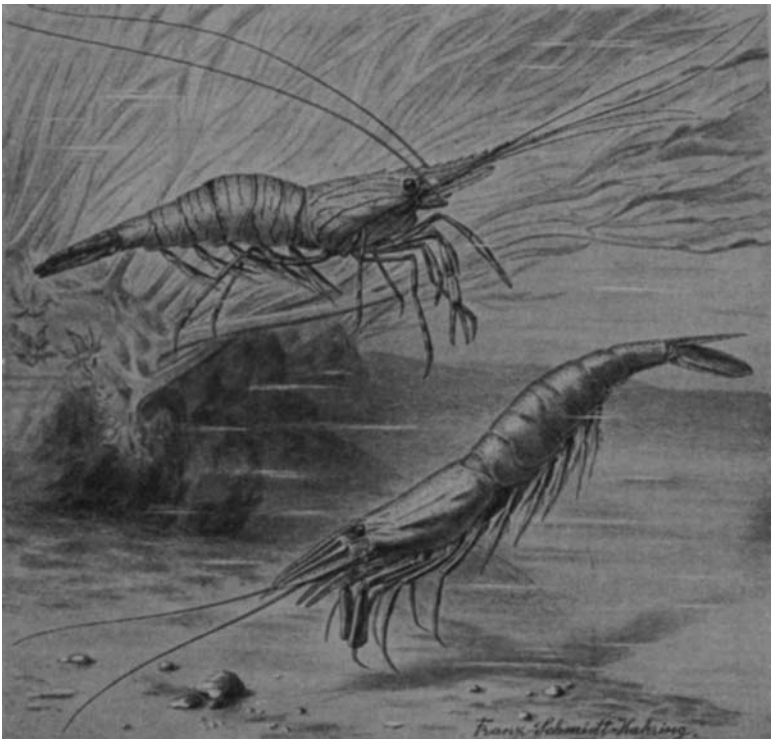

FIGURE 6.40. Shrimps are together with crabs and lobsters members of the order Decapoda, subphylum Crustacea, here represented with *Palaemon serratus* (*top*) and *Crangon vulgaris* (*bottom*). They are important in trophic interactions in the sea.

identified them as members of a genetically closely related superflock (Meyer et al. 1990). The degree of sequence variation was lower than in the human species and pointed to a recent origin of this superflock. Teleosts (bony fishes) represent with about 25,000 species half of all living vertebrate species, but such a diversification into 500 species within a single lake is astonishing. Initially it was suspected that the diversification occurred within the lake, but more recent sequencing work revealed that the Lake Victoria flock was several times seeded from cichlids living in the lake Kivu (Verheyen et al. 2003). This lake harbors much less fish species (26, of which 15 are cichlids), but the lake is much deeper (it belongs to the East African rift system) and is thus geologically much more stable. Lake Victoria is relatively shallow and experienced a nearly total dryness as recently as 15,000 years ago. This dramatic event has not sterilized the lake. However, another event in the recent historical past has upset the biological equilibrium of the lake. Fishery biologists fear that this manmade event will not only endanger the biological diversity in the lake but also lead to the destruction of the economical basis for the population living around the lake, as vividly depicted in a prize-winning documentary film ("Darwin's Nightmare"). There

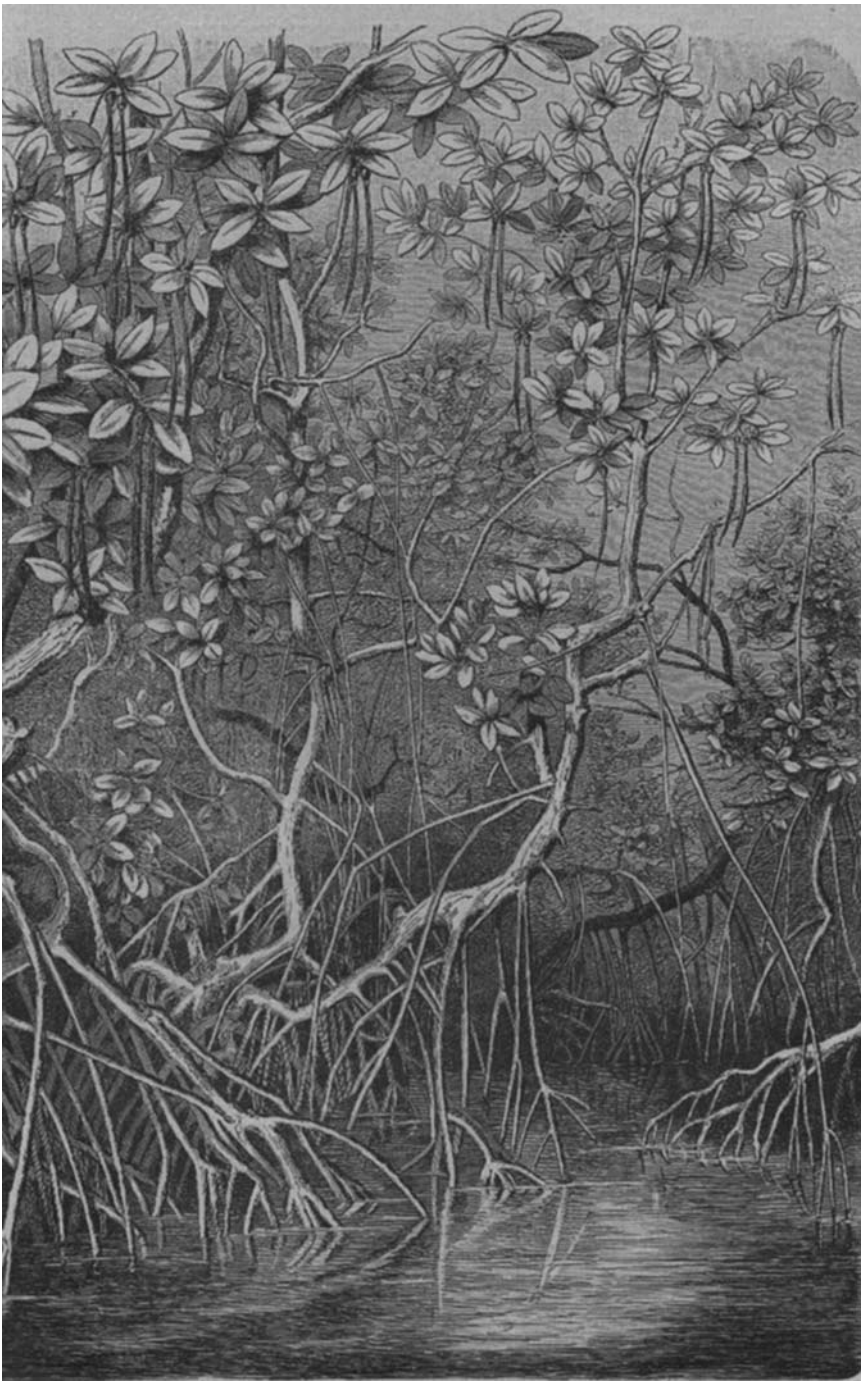

FIGURE 6.41. *Rhizophora conjugata* forms mangrove, i.e., dense thickets of shrubs and trees along tidal estuaries characterized by exposed, supporting roots. Respiratory roots are common to many species through which air enters into the plant aquaculture.

are fundamentally different methods between journalists and scientists when they report on events. Scientists essentially make experiments in the laboratory or observe events in the field and report their data in peer-reviewed scientific journals. In addition, they meet at conferences where they discuss data and exchange interpretations of the observations. However, they generally do not travel to the spot. So I cannot comment on the political and economical implications of the events documented in the film. I will limit the story to data, which were published in scientific journals and they are dramatic enough.

Species Introduction

In the public discussion, there is a misconception such that natural and artificial introduction of new life forms are distinguished. The natural introductions are considered as safe, while genetically modified organisms containing a few well-characterized alien genes capture media attention. Biologists would argue that the true dangers lurk in the incautious introduction of natural species into new environments. Virologists also distrust certain agricultural practices like the proximity of pig and poultry rearing in Asia, which favors the mixing of avian and mammalian influenza genes, raising the specter of an imminent human influenza pandemic. We should not forget that Nature is not only our loving mother, but also the greatest bioterrorist.

The Nile Perch

In the 1950s, the proposal to introduce the Nile perch, *Lates nilotus*, into Lake Victoria was made. Ecologists warned against this introduction because it is a large piscivorous fish that grows to a size larger than humans. This introduction was against ecological commonsense since short food chains are ecologically the most efficient and the yields of the predator can never be as great as that of its prey (Barel et al. 1985). In 1960 the Nile perch was introduced and the drama took its way. The local fishery was based on the catch of cichlids. Trawl fishery had already some effect on this fish stock, which represented the food basis for the local fishery. Now cichlids experienced another stress, the heavy predation by the much larger perch. The explosion of the perch—it already represented, in several lake areas, 80% of the biomass—is clearly not sustainable and will be followed by the decline of the predator when the prey population comes down. *The local population did not like the oily flesh of the perch. It cannot be sun-dried as the cichlids and must be smoked, which led to deforestation around the lake. Important sociological consequences were observed. The small fishers lost their cichlid catches, but they could not switch to perch catching since it needed stronger nets and better boats. The processing of the fish filets is now done in modern fish factories in Mwanza associated with airstrips, where the fish is directly imported to Europe. Wealth was created only for a small part of the population, and the rest fell in even deeper poverty and now live from the discards of the Nile perch processing in the factories. Ecologists complain that the introduction of the Nile perch is irreversible and that the biomass- and species-rich fish population of the Lake Victoria is perhaps gone forever.*

Risk Perception

This tragic introduction of an alien fish reminds us that fishery technology is sometimes more advanced than the ecological knowledge about the consequences of such actions. We should thus think twice before we change the environment by deliberate introduction of new species. This practice caused a lot of human tragedy, but the human mind has apparently an inclination to deal more with perceived theoretical risks (I would argue that GMO belong to them) than with real dangers.

On Fishery, Bushmeat, and SARS

Fishing off Ghana: Economics and Ecosystem Resources

Science journals report relatively rarely on economical research questions. Yet, we live only in one reality, and it is only the human mind that divides the exploration of our interior and our environment into different branches of knowledge. Especially macroecological research questions cannot be separated from economical decisions of the human society. The modern democratically governed societies are pluralistic and they follow sometimes contradictory strategies reflecting distinct interests of different pressure groups. To illustrate this point in our quest for food survey, I have chosen a recent research article in Science (Brashares et al. 2004). One camp is represented by a new branch in biology called Conservation Biology, which deals with the dramatically accelerated decline of species loss due to human transformation of the planet. Many biologists argue that mankind and its economical activity has become a major evolutionary force on a multitude of organisms (the "terminator," in the movie language). The species richness and at the same time the ecological vulnerability of the tropical rainforest made this zone a focus of conservation efforts. "Green" groups encourage us to buy or adopt parcels of the tropical rain forest to decrease the decline of biological diversity. At the other side, the European Union follows a subsidizing policy that goes sometimes straight against this goal. For example, industrialized countries possess—at least in the view of many ecological scientists—a too large and too industrialized fishing fleet. This industry is increasingly subsidized, EU financial support increased from $6 mio in 1981 to $350 mio in 2001. Owing to the decrease of catches in northern seas, we now see increasingly foreign fishing fleets off West Africa, the lion's share coming from the EU. What were the consequences? At a simple level, the fish stocks declined and may face imminent collapse. Furthermore, the technically superior European fleets outcompeted the local fishery with the consequence that the fish supply to the local markets declined and prices increased. In Ghana the supply of fish varied between 230,000 and 480,000 tons a year and showed up to 24% changes between consecutive years. As fish is the primary source of animal protein in the diet from West Africans, there are only two consequences: Either the population goes into temporary protein malnutrition or it seeks alternative animal protein sources.

The Shift to Bushmeat

The latter link was investigated in the *Science* report by the conservation biologists. They observed that monthly bushmeat sales in local markets and the estimated hunting intensity in wildlife reserves were negatively correlated with regional fish supply. Bushmeat selling and the counts of hunters reported by wildlife rangers were furthermore closely related to annual rates of wildlife decline. Over the last 30 years, the biomass of 41 mammals in the reserves declined by 76% and a number of species became locally extinct. The researchers tested this association of observations. The correlation decreased with increasing distance of the reserve from the coast, speaking for a causal connection between the observations. Apparently, we see here a transfer of harvest pressure from aquatic to terrestrial resources. *Thus by subsidizing fish industry, the EU endangers the wildlife survival in West Africa. One might argue—as in the case of the Lake Victoria—that some ecological consequences of economical decisions could not be foreseen and they became only evident after substantial research efforts. A posteriori, one gets the impression that some of the consequences could have been anticipated by pure logical reasoning. As a biologist, I wonder whether governments should have more professional ecologists on decision boards to explore the potential ecological consequences of political decisions. Leaving this job to emotionally and politically motivated environmentalists led, to my opinion, to a concentration on minor issues that deal more with sentimental concerns of citizens of wealthy societies than with ecological disasters of the developing world.*

Food Safety

Food industry spends a lot of energy and money on food quality and safety. Due to these efforts, cases of food poisoning that can be tracked to industrial food sources came substantially down over the last century. However, fresh food that is consumed raw represents still an important concern. Oysters are an illustration, and the Centers of Disease Control in Atlanta traced, as another example, large numbers of gastroenteritis in the USA to the import of raspberries from Central America. Irrigation of the plants from the bottom with contaminated water was not a problem for the fruits. In this specific case, contaminated water was used to dilute pesticides that were sprayed from the top with airplanes and could thus contaminate the fruits. *Bushmeat belongs to a different category for food microbiologists. Virologist will remember the discussions in the early phase of the AIDS epidemic, where exposure of humans to apes and monkeys was discussed for the origin of the new human virus. Nowhere is the contact between wildlife and humans so close as in the bushmeat handling, which is a multibillion-dollar trade in the tropics. During handling and butchery of the wild animal, exposure to the blood of the animal is inevitable and creates an opportunity for viral transmission. We have somewhat forgotten that the quest for food is a dangerous business not the least because our animal prey can infect us.*

SARS

This risk was recently demonstrated again by the SARS epidemic. Severe acute respiratory syndrome, as it reads in full, emerged as a new human disease associated with pneumonia in November 2002 in the Guangdong Province of China. The early phase remained largely unrecognized or underreported. The disease attracted attention when a major outbreak occurred in a hospital of Guangzhou and a hotel in the nearby Hong Kong in February 2003. Epidemiologists call this a superspreader event where single patients infected as many as 300 other individuals (Dye and Gay 2003). Outside of these events, which mark the middle phase of the epidemic (Chinese Consortium 2004), the transmission dynamics was, with 2.7 secondary infections per case, less dramatic such that public health interventions could finally cope with the epidemic (Riley et al. 2003), leading to the decline of the case numbers in the third, late phase. However, at that time the disease had already spread to 25 countries around the world with epicenters as far away as Canada. The epidemic ended in July 2003, the nightmare of a pandemic did not become a reality. Despite all public disarray, the international and the Chinese research community, assisted by the WHO as a fireworker, organized a relatively structured approach to the disease. A contributing factor was certainly the early warning by avian influenza infections in Hong Kong, which led to fatalities in humans and heightened the alert of virologist for the possible emergence of a devastating influenza epidemic from China.

Coronaviruses

You might now ask what SARS has to do with food production: a lot in fact. The connection became clear when laboratories in the USA, Canada, Germany, and Hong Kong isolated and then sequenced a coronavirus as the causative agent of this epidemic (e.g., Rota et al. 2003, Marra et al. 2003). These isolations followed directly on the heel of the epidemic and the various reports were published in the first half of 2003. The agent turned out to be a known virus. It belonged to the coronavirus group, which are large, enveloped, positive-strand RNA viruses—in virological parlance, this means that the viral genome encodes the information for the viral proteins. Coronaviruses cause respiratory and enteric diseases in humans and animals. Human coronaviruses were up to that epidemic only, associated with mild upper respiratory tract infections, but some animal coronavirus like TGE cause deadly enteric infections in swine. Coronaviruses contain the largest genomes of any RNA viruses, and the SARS isolates showed genome lengths that clustered around 29,750 nucleotides. The genome organization resembled closely that of the known coronaviruses, but its sequence forms a distinct group that is not closely related to any of the previously characterized coronaviruses.

The Epidemiologists

Under such conditions, the task is commonly passed to the epidemiologist to provide hints to the potential source of a new virus. A review of the early patient

data by a WHO fact-finding mission in April 2003 revealed to an epidemiologist that 9 of the 23 early patients worked in the food industry. Also people working in the vicinity of food markets and workers in specialty food restaurants were overrepresented (Normile and Enserink 2003). These data were later substantiated by serological surveys: 13% of 508 animal traders whose blood was sampled during the outbreak in May 2003 tested positive for IgG antibodies in the quickly developed SARS virus immunoassay. Control groups showed only 1–3% prevalence rates. Notably, traders that handled the masked palm civet, a distant relative of the house cat, were the most likely to show SARS-specific antibodies (Enserink and Normile 2003). This is not an unlikely finding: Civets are regularly eaten in China. In fact, they are preferred for their tasty meat and are handled as a delicacy by a growing sector of wealthy consumers. In China, a lot of folklore surrounds food items, civets are for example fabled to strengthen the body against winter chills. The demand for wildlife cuisine in China is thus high, and illegal poaching and husbandry of wildlife is widespread. Many families in the rural area make a living by providing this wildlife to cities (Liu 2003).

The Virus Hunters

Now the race was open for the virus hunters. This is unfortunately a respectable business for professional virologists. One needs in addition to technical skills a detective nose for this business. Guided by the epidemiological data, Yi Guan et al. (2003) went into live animal markets where they borrowed animals from vendors. None of them was found to be ill, but PCR diagnosis tools showed that from the many sampled species four of the six palm civets scored positive, the two negative animals yielded a live virus isolation from nasal secretions. They were sequenced, and it was 99.8% identical to the human isolates and differed mainly by a 29-nt insertion, upstream of the structural N gene. Interestingly, the earliest human SARS virus isolates still contained this 29-nt segment but later isolates lost this segment possibly as an adaptation to human-to-human virus transmission. The researchers cautioned that their isolation of the SARS virus from civets might not have identified the true animal reservoir of the virus. Civets might have got infected in the markets and much larger investigations in feral animals are needed to settle the question. In fact, also a raccoon dog from the investigated market yielded a closely related virus.

Indeed, experimental infection of civets with human SARS virus resulted in overt clinical disease, which is not expected for a viral reservoir where asymptomatic infection should dominate. Chinese virus hunters then went after bats. Bats are a good bet since flying mammals can be dynamic transmitters of disease. Bats are known to do that with rabies and more recently with Hendra and Nipah viruses, two other emerging zoonotic viruses. Furthermore, with 4,800 described species, bats represent 20% of all mammalian species. *Finally, the Chinese virologists knew that bat meat is considered a delicacy by Chinese gourmets and another strong link is the use of bat feces in traditional Chinese medicine*. Equipped with that knowledge, they screened nasopharyngeal and anal swabs of bats, rodents, and monkeys in the Hong Kong area. They detected a coronavirus

sequence related to the SARS virus in 40% of the anal swabs from the insectivorous Chinese horseshoe bats (*Rhinolophus sinicus*) by using PCR technology (Lau et al. 2005). None of the positive bats showed clinical symptoms, but many showed an antibody response and, interestingly, high serum titers correlated with low anal virus excretion. A parallel study from mainland China confirmed the findings (Li et al. 2005). Both studies showed closely related sequences for this coronavirus, much closer related to SARS than to another recently isolated bat coronavirus. *Rhinolophus* roosts in caves and feeds on moths and beetles. However, the cave-dwelling fruit bat *Rousettus leschenaulti* also showed serological evidence for coronavirus infection. These fruit bats (Figure 6.42) were found by the virus detectives in the markets of southern China. The current hypothesis imagines that they were the asymptomatic source for virus spillover to susceptible animals exposed in the markets like the civet. The spread of the virus to susceptible animals might have provided the necessary amplification to achieve intrusion into the human population. Notably, the greatest genetic variation existed between the bat and human coronavirus in the S1 domain of the S protein, which is involved in receptor binding of the virus. Coronaviruses

FIGURE 6.42. The dog-faced bat (*Rousettus*), a member of the Megachiroptera; flying foxes forage mostly on fruits and flowers.

apparently have the genetic diversity and flexibility to create variant S proteins that might enable them to cross the species barrier.

Transmission Dynamics

The SARS epidemic did not spread worldwide not because of our superior scientific knowledge, but because we were lucky that its transmission dynamics could be countered by age-old containment measures, which might not be the case for other respiratory infections. However, the havoc that this limited epidemic, involving about 7,000 cases and 700 deaths, spelled on the world economy can give us a foretaste on a new influenza pandemic that might lurk somewhere in China. Also in this case, agricultural practices might be at the basis of the problem. In the case of influenza, it is the proximity of poultry, pigs, and the human producer/consumer that provide an appropriate combination of viral incubation vessels to initiate a new influenza pandemic. The prospects and stakes are clearly formulated in scientific journals (see the series of reports on the threat of an avian flu epidemic in the May 26, 2005 issue of *Nature*; Aldhous and Tomlin 2005). *International air traffic will assure the quick transport of human patients in the incubation period and have already realized the One-World concept for infectious diseases. The bottom line of these reports was that we are not necessarily much better prepared to such an event as in the case of the 1918 Spanish flu, and the WHO estimates that such an avian influenza pandemic could again claim millions of human lives worldwide.*

Again a Bit of Politics

Governments and the public are relatively complacent about these prospects and deal with—in the view of many biologists—minor issues of food safety like the GMOs in the food chain at a time when another – and this time a real-biological bomb is ticking. Political economy is the art of shifting limited resources to the most urgent public needs. This means that research money spent on the health impact of electric powerlines (apparently a non-issue according to leading medical journals) and the safety of GMOs in food (probably of greater psychological than technical concern), cannot be spent on virological food safety and agricultural food production issues. The SARS crisis showed that the WHO was already overstretched with its resources when confronting a numerically still limited epidemic. Money problems at the WHO are perennial, and the WHO is definitively understaffed to face a major influenza epidemic, for example. The discussion in this chapter centered on SARS not because it is the only case. Viruses coming from traditional Asian animal husbandry condition are manifold, and similar warnings could be drawn from other emerging viral infections like Nipah virus that affected the Thai pig farmers. We should thus not see us as the ultimate predator on earth, where only food limitation puts a break on our population growth. We should realize that we are also the food for many organisms, or in more benign cases, the involuntary feeders of many organisms. This subject will be the content of the next chapter in our quest for food survey.