Chapter 1
Introduction: Ecological Importance of Insect Feeding

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Abstract Insects are extremely diverse arthropods with highly diverse lifestyles. All kinds of organic material may be used by insects as food. Their feeding activities have an enormous ecological impact on all terrestrial and freshwater ecosystems. Insect feeding contributes to pollination, nutrient recycling, pest control and water purification, whereas it can be destructive to wild and cultivated plants and stored products and may transmit pathogens to plants and animals including humans. In this context, form and function of mouthparts are crucial to understand the feeding behaviour as well as the ecological and economic importance of insects.

1.1 Insect Feeding

Insects are the most diverse and abundant group of arthropods. They are the dominant group of invertebrates in most terrestrial and freshwater habitats of the world; and their activity, for instance, feeding, provides many important ecosystem functions. Insects have evolved diverse lifestyles comprising a great number of feeding preferences, feeding modes and specialized adaptations to various food sources. The nutrition of different groups ranges from phytophagy (i.e. feeding on various plant tissues; plant sap, nectar and pollen; and seeds, as well as aquatic grazing and consumption of tissue from induced plant galls), carnivory (i.e. feeding on, within or off other animals), fungivory (i.e. feeding on spores, hyphae and fungal bodies) and detritivory (i.e. feeding on decaying organic matter including saprophagy, coprophagy and xylophagy) to filter-feeding on suspended particles. Phytophagous insects make up to 25% of all living species of animals and have an enormous impact on plants and terrestrial food webs (Bernays 2009). At least a quarter of all insects are estimated to be parasites, parasitoids or predators of other arthropod species (Chapman et al. 2016). Detritivorous insects comprise a significant component of soil arthropods and are an integral part of subterranean food webs (Bagyaraj et al. 2016). Many insect species are highly specialized on particular food sources, while others are generalized and omnivorous showing various combinations of the major feeding types.

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H. W. Krenn (ed.), *Insect Mouthparts*, Zoological Monographs 5,
https://doi.org/10.1007/978-3-030-29654-4_1

During their life cycle, many insects switch their feeding style, which is often combined with a change in habitat, for example, a shift from aquatic immatures to terrestrial imagines or from soil-dwelling larvae to epigaeic or phytophilous adults.

1.2 Importance of Insect Feeding

Through their feeding activity, insects perform essential ecological roles in terrestrial and freshwater ecosystems. The estimated number of 5.5 million species (Stork 2018), each with innumerable individuals, makes it impossible to gain a realistic view of how much food insects consume in their habitats per year. However, the enormous impact of insect feeding on natural habitats and human-dominated environments including indoor habitats has been demonstrated (e.g. Scudder 2009; Chakravarthy and Sridhara 2016; Leong et al. 2017). This includes mutualistic interactions like pollination, the dispersal of seeds and decomposition but also antagonistic interactions, such as phytophagy, predation and parasitism. In this way, insects significantly contribute to vital ecosystem functions that are directly or indirectly associated with their feeding activities and the performance of their mouthparts (Fig. 1.1). The ecosystem services provided by insects may be beneficial to humans with a high economic value (Losey and Vaughan 2006; Chakravarthy and Sridhara 2016). However, insect feeding activities can also have a significant adverse impact on human beings, agricultural crops and livestock.

1.2.1 Pollination

The most important beneficial activity that is directly related with insect feeding is the pollination of angiosperms. When insects search for floral food resources, i.e. mainly pollen and/or nectar, they transfer pollen onto the stigma of conspecific flowers. Through this activity, insects pollinate about 90% of the flowering plants on Earth (Ollerton et al. 2011). This mutualistic interaction between plants and insects was the starting point in the evolution of flowering plants in the Cretaceous (Grimaldi and Engel 2005; Hu et al. 2007). Still in the present, insect pollinators play a significant role in diversification and evolution of angiosperms (Van der Niet and Johnson 2012; Gervasi and Schiestl 2017).

Insects provide pollination services for a range of crop plants in agricultural landscapes. For the 100 most economically important crops used for human food, the economic value of insect pollination was estimated at 153 billion euros per year (Potts et al. 2010). Considering that only a small fraction of plants are used by humans, the feeding activities of flower-visiting insects are invaluable in the reproduction of many angiosperm plants.

Honey bees (*Apis mellifera*) may provide an estimate of the number of flowers visited by a pollinating insect and the mouthpart performance during food gathering. Mouthparts can be seen as minute tools for collecting of even very small amounts of nectar from

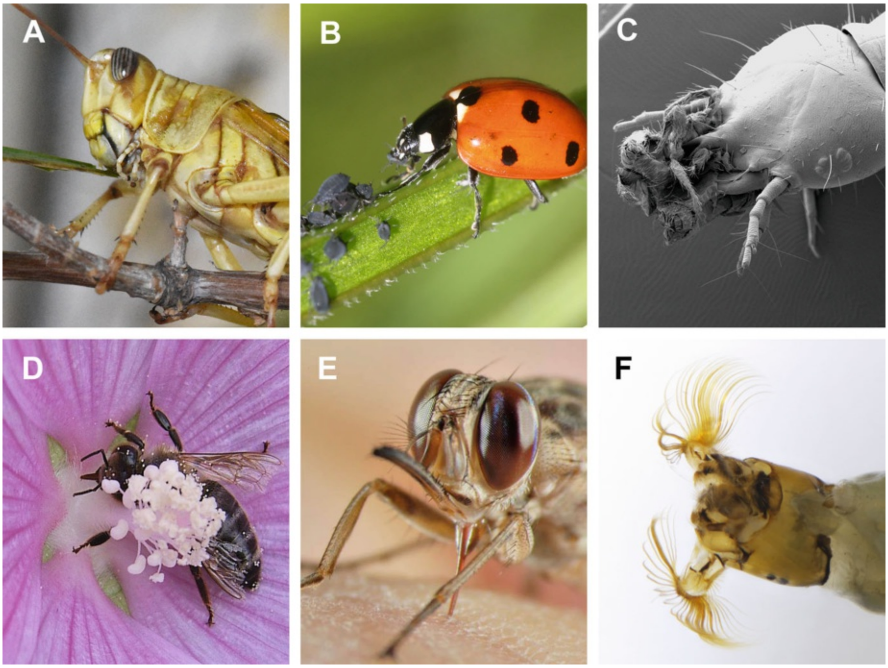

Fig. 1.1 Insects feeding activities; (**a**) herbivorous locust (*Schistocerca gregaria*) takes up grass; (**b**) carnivorous lady beetle (*Harmonia axyridis*) feeds on plant sap-sucking aphids (photo by courtesy of H. May); (**c**) carnivorous ground beetle larva (*Nebria* sp.) eats a soil-living springtail; (**d**) nectar-feeding honey bee (*Apis mellifera*) with pollen grains on the body; (**e**) blood-feeding tsetse fly (*Glossina morsitans*) may transmit trypanosomes, the pathogen of sleeping sickness (photo by courtesy of R. Pospischil); (**f**) aquatic larva of *Simulium* sp. (Simuliidae) feeds on suspended particles in freshwater

flowers. Depending on the available nectar in flowers, approximately 1 million apple blossoms, about 3.3 million rapeseed flowers, or more than 10 million red clover flowers need to be visited by workers of the western honey bees (*Apis mellifera*) to produce 1 kg of honey (Farkas and Zajacz 2007; Morawetz pers. comm.). When considering these numbers in the context of global honey production, estimated to be 1,003,627 tons (FAO 2018), an inordinately large number of flower visits would be required.

In addition to honey bees and other Apidae, the significant role of non-bee pollinators in the global agricultural production is well supported (Rader et al. 2016; Ssymank et al. 2017). The activity of all flower-visiting insects would significantly add more flower visits by countless numbers of species in the global annual pollination service, without which there would be only inconspicuous flowers and less fruits or vegetables available on Earth. Considering that only a small fraction of plants are used by humans, the feeding activities of all flower-visiting insects are invaluable in the reproduction of angiosperm plants. In this way, pollination by insects crucially supports the primary production of biomass and plant biodiversity in terrestrial ecosystems by their feeding activities linked to the action of their mouthparts.

1.2.2 Nutrient Recycling

Many insects and other arthropods are responsible for litter breakdown, dung burial, turnover of soil through burrowing activities and accelerating the return of nutrients to the soil through their feeding behaviour and defecation. Detritus-feeding activities of myriads of soil-dwelling insects and non-insect hexapods achieve decomposition and nutrient recycling in terrestrial ecosystems that represent an enormous economic value (Scudder 2009). For example, the leaf-cutter ants are indirectly responsible for improving soil fecundity in Neotropical forests. Billions of worker ants cut off leaves by using their mouthparts; they carry the plant material into their underground nests and feed it to a symbiotic fungus which serves as food for these ants (Hölldobler and Wilson 1990). The waste generated by the ant colony and the metabolic products of the fungi are essential for soil fertility. In the same sense, termites are regarded as eco-engineers that are perhaps the most impressive decomposers of dead wood and plant material in the subtropical and tropical regions of the world (Scudder 2009; Bagyaraj et al. 2016). Furthermore, in freshwater habitats, many insects perform an essential ecosystem function by filter-feeding suspended organic microparticles. Vast numbers of insects help maintain clear water bodies through their feeding activities and provide purification of freshwater systems (Gullan and Cranston 2014). In this way, aquatic immatures and larvae are important contributors to link food webs through the uptake of nutrients in water and returning them to terrestrial ecosystems by the winged adult insects via their dispersal flights.

1.2.3 Pest Control

Numerous insect predators, parasitoids and parasites are invaluable for biological control and the balance of ecosystems. The activities associated with the feeding behaviour of these insects provide natural population control of other insects, arthropods, invertebrates and even some vertebrates. There is no estimate available for the number of insects that are eaten by other insects or are parasitized by larvae. However, biological pest control by wild or native insects is valued to be approximately USD$13.6 billion per year in the USA (Losey and Vaughan 2006). This estimate does not include mass-reared insect species, like parasitoid wasps or lady beetles that are regularly used in large numbers to protect crops grown in open fields or greenhouses against pest insects, without the use of insecticides.

1.2.4 Adverse Effects of Insect Feeding

Insects can destroy crops, parasitize livestock and humans or become a nuisance and health hazard to other organisms (McGavin 2016). In terms of the significant negative impact on the human population, feeding activities of many insects can have tremendous adverse effects on agriculture and horticulture and may be harmful to domestic animals and humans by transmitting pathogens. Defoliation caused by insects can alter ecosystems, and the feeding activities of keystone species cause a strong top-down effect on habitats (Carson et al. 2004), such as the feeding of a swarm of desert locusts with devastating effects on dryland habitats (Baron 1972). It was estimated that approximately one-fifth of all crops grown worldwide and stored products are lost to herbivorous insects annually (Sallam 1999), and further damage is caused by plant diseases transmitted by feeding insects. Destructive feeding activities of insects can also cause damage to wooden structures and a wide range of natural materials and fabrics. Despite this, less than 2% of phytophagous insects are potential pests of crops and agricultural products (Scudder 2009). Yet more severe, over 15% of human beings are affected by an insect-borne illness such as sleeping sickness, river blindness, yellow fever, malaria, etc., predominantly in tropical and subtropical regions of the world. More than 500 million people are at risk of exposure, and more than 1 million die from such diseases every year (Murray et al. 2012). The transmission of pathogens to plants, animals and humans occurs during insect feeding; thus, these activities have great importance for other organisms. Therefore, the knowledge on life history and feeding ecology of insects is significant and helps to recognize dangers from insects.

1.3 Why Study Insect Mouthparts?

All feeding activities are of crucial importance in the various ecological roles of insects, and feeding performance is always associated with form and function of the mouthparts. Most entomological textbooks provide descriptions of insect mouthparts and discuss various examples of functional anatomy, feeding behaviour and techniques of food uptake. The study of insect feeding organs and their function was recognized in the classical textbook of Berlese (1909) and in the benchmarking volumes of Weber (1933) and Snodgrass (1935). They illustrated many examples in detail and discussed how homologous structures developed according to functional demands in context with feeding ecology and particular food sources. Similarly, this applies to recent textbooks such as Gullan and Cranston (2014), Beutel et al. (2014), Chapman et al. (2016) and Grimaldi and Engel (2005)—the latter focuses on fossil insects. All devote chapters to these complex organs and give much emphasis to morphology, feeding ecology, physiology and evolution or the fossil records of mouthparts. Furthermore, a number of comparative studies emphasized the eco-morphology of insect mouthparts (e.g. Smith 1985; Krenn et al. 2005; Krenn and Aspöck 2012).

Studying mouthparts provides information about the feeding ecology of a particular insect species. The morphology of mouthparts allows for inference as to what type of food is consumed, such as plants or animals, solid or liquid food or dead or living organisms, even when only dead museum specimens or fossils are available.

Mouthparts of fossil insects may give information about past feeding preferences and can shed light on the evolution of food webs and the ecological roles of extinct insects millions of years ago (Labandeira 1997; Nel et al. 2018; see also Chap. 17). Furthermore, mouthparts provide fascinating examples of organ evolution that can be easily used to argue in favour of evolutionary theory since feeding organs impressively demonstrate the power of natural selection. Recently, biophysicists discovered the amazing functional performance of insect mouthparts and have started investigating feeding organs using principles of biomechanics, material science and biomimetics (e.g. Kornev et al. 2016; Li et al. 2017; Zhang et al. 2018; see also Chaps. 8 and 9). These new perspectives likewise give explanations for feeding performance under various ecological aspects. Thus, studying mouthparts provides a variety of information that can be used to understand different aspects of insect feeding and can help to better evaluate the significance of insects in the ecosystems on Earth.

Acknowledgements I thank Annalie Melin for linguistic help and Barbara-Amina Gereben-Krenn and Florian Karolyi for comments and suggestions to improve the manuscript. I am grateful to Reiner Pospischil and Helge May for providing excellent photos of feeding insects.

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