Feeding Mechanisms of Adult Lepidoptera: Structure, Function, and Evolution of the Mouthparts

Harald W. Krenn
Department of Evolutionary Biology, University of Vienna, A 1090 Vienna, Austria;
harald.krenn@univie.ac.at

Abstract

The form and function of the mouthparts in adult Lepidoptera and their feeding behavior are reviewed from evolutionary and ecological points of view. The formation of the suctorial proboscis encompasses a fluid-tight food tube, special linking structures, modified sensory equipment, and novel intrinsic musculature. The evolution of these functionally important traits can be reconstructed within the Lepidoptera. The proboscis movements are explained by a hydraulic mechanism for uncoiling, whereas recoiling is governed by the intrinsic proboscis musculature and the cuticular elasticity. Fluid uptake is accomplished by the action of the cranial sucking pump, which enables uptake of a wide range of fluid quantities from different food sources. Nectar-feeding species exhibit stereotypical proboscis movements during flower handling. Behavioral modifications and derived proboscis morphology are often associated with specialized feeding preferences or an obligatory switch to alternative food sources.

Keywords

proboscis; fluid uptake; flower visiting; feeding behavior; insects

INTRODUCTION

The Lepidoptera (butterflies and moths) are one of the most diverse taxa of animals containing about 160,000 described species in 47 superfamilies (103). Both the larval and the adult stages of nearly all species are associated with vascular plants. Most larvae feed on plant material using biting-chewing mouthparts. The majority of adults are anthophilous; they possess a proboscis that is used to imbibe floral nectar and other liquid substances. The role of Lepidoptera as pollinators has been demonstrated in many cases of mutualistic relationships with flowers and floral specialization (59, 79, 113, 125, 128). Their adaptation to flower morphology provided classical examples of reciprocal adaptations in insect-flower interactions (36). After Charles Darwin examined the flower of a star orchid possessing an approximately 300-mm-long nectar spur, he predicted the existence of a hawk moth with a proboscis of matching length (36) that was actually discovered 40 years later (114). The

fossil record of Lepidoptera dates back to the Jurassic period, yet the evolution of present-day species-rich lineages are probably related to the radiation of angiosperms during the Cretaceous within a relatively short time frame (145). The shift of larval feeding to angiosperm foliage could have been crucially linked with the evolution of adult nectar feeding and the adaptive radiation of glossatan Lepidoptera (136).

The mouthparts of Lepidoptera belong to one of the best-studied feeding organs of flower-visiting insects, in terms of anatomy, functional morphology, and evolutionary biology (91). Several benchmark morphological studies, dating from the latter half of the twentieth century, led to the establishment of a phylogenetic classification of the major lineages of Lepidoptera that was strongly supported by arguments regarding mouthpart structures (38, 95, 101, 112). This high-level classification, based on morphology, has remained robust in light of present-day molecular-based phylogenies (62, 146). The anatomy of the lepidopteran mouthparts has been reviewed comprehensively in a phylogenetic context (96, 98, 103). Here, I focus on the evolution of functionally important traits of the proboscis, the mechanisms of proboscis movements and fluid uptake, as well as feeding behavior on flowers and adaptations to other food sources.

COMPOSITION AND EVOLUTION OF LEPIDOPTERAN MOUTHPARTS

Biting-Chewing Mouthparts in Adult Lepidoptera

The origin of the lepidopteran proboscis can be traced back to the pair of small galeae of uncertain function in the plesiomorphic biting-chewing mouthparts retained in nonglossatan moths of the families Micropterigidae (Figure 1), Agathiphagidae, and Heterobathmiidae (54, 72, 87, 95, 98, 140).

The Micropterigidae possess a complete set of mouthpart structures that are well adapted for collecting and grinding angiosperm pollen or fern spores (33, 72, 97, 140). Covered by the labrum, the asymmetrical mandibles act like a mortar and pestle to crush pollen grains. The maxilla consisting of cardo and stipes gives rise to the small lacinia on the median side, as well as the short galea and the large, five-segmented maxillary palp (Figure 1 *a*). The galea is equipped with microtrichia, a row of lamellate setae, few uniporous sensilla, and bristle-shaped sensilla, as well as one small muscle attached to the stipes (33, 53, 72, 88). The maxillary palp scrapes pollen out of anthers (72). Pollen grains adhere to the paddle- and mushroom-shaped bristles of the apical segment (Figure 1*b*), which transport the pollen to the mandibles (33, 53). The labium bears a pair of short two-segmented labial palps, which bear apical sensory pit organs (33). Species of *Micropterix* feed on a variety of flowers (97), whereas those of *Sabatinca* usually feed on pollen of *Zygogynum* (Winteraceae) flowers, which are pollinated during the search for pollen (138). These moths use paddle- and spatula-shaped sensilla for pollen collecting (55). Whether adults of the Agathiphagidae feed at all is uncertain; nonetheless, their mandibles are used to open the pupal casing for emergence (97). Adult Heterobathmiidae frequent flowers of *Nothofagus* (Nothofagaceae) to feed on pollen; in addition, they have been observed to drink water (102). Their mouthparts are similar to those of the Micropterigidae (99) and are well adapted to collect and grind pollen, but only one type of so-called prehensile sensilla occurs on the maxillary palp, where pollen and fern spores are frequently found (54).

Mouthparts of Glossata and Evolution of the Proboscis

The great majority of adult Glossata possess a coilable proboscis (Figure 2), which evolved only once, thus representing an autapomorphy of this clade. Adult Glossata take up only liquid food and achieve this exclusively by way of the food tube of the proboscis, which is composed of the medially concave and interlocked galeae. The origin of the proboscis and the transition to feeding on liquids resulted in the reinforcement of the sucking pump in the head and a reduction of all major constituents of the mouthparts, except the galeae and the labial palps (136). The other components of the mouthparts play no role in food uptake but may have sensory function during foraging.

In species with a functional proboscis, the labrum forms a small plate over the basal proboscis joint, where bristles of the pilifers contact the basal galeal joint; these sensory bristles probably detect proboscis movements (53, 84, 87). The mandibles are reduced and nonfunctional. The basal maxillary sclerites—the stipes and the cardo—form a tubular component from which the coilable galea and the maxillary palp emerge (Figure 2*b*); a lacinia is absent (98).

The maxillary palps are composed of five segments in the plesiomorphic condition, but are short and reduced in the number of segments in most species of Ditrysia (98). The biological role of the maxillary palps remains unclear despite the presence of sensilla in various lineages (52, 53, 57). In the females of the yucca moth, *Tegeticula* and *Parategeticula* (Prodoxidae), the second segment of the maxillary palpus is extended into a long coilable tentacle that is used to collect pollen and to actively pollinate *Yucca* flowers (37, 119). The tentacles are as long as the proboscis and are similarly equipped with muscles and sensilla. This extraordinary and novel organ probably evolved as an adaptation to the mutualistic pollination behavior of female yucca moths (120).

The labial palps are composed of two to three segments (98). They extend from the prementum sclerite and may form prominent structures in front of the head (Figure 2*a*). They are equipped with scales, bristles, and various sensilla partly arranged in an apical pit organ (52, 53, 57, 98). The sensilla of the pit organ are sensitive to carbon dioxide (25, 68, 78, 106). They play an important role in the nectarforaging behavior of sphingid moths (139). In *Manduca sexta* (Sphingidae) the labial pit organ detects minute changes in concentration of carbon dioxide, which serves as a distant olfactory attractant to freshly blossomed flowers (65) and as a predictor of nectar volumes before actual flower probing (67).

The plesiomorphic condition of the proboscis occurs in the representatives of the family Eriocraniidae, which use their short and simply composed proboscises to drink from water droplets and sap seeping from injured leaves (93, 95). Originating from the tubular stipes, the coilable galeae are linked to each other by pointed cuticular structures on the dorsal and ventral sides of the median food canal. The outer surface of each galea bears microtrichia, few uniporous sensilla basiconica, and bristleshaped aporous sensilla trichodea. The galeal lumen contains a nerve, a trachea, and an extrinsic muscle that originates on the stipes; however, no intrinsic galeal musculature extends to the tip (87, 88, 93).

Derived from the plesiomorphic condition, the proboscis of Myoglossata is characterized by functionally specialized dorsal and ventral linking structures, three morphological types of sensilla, and additional intrinsic galeal muscles (87, 88, 101). The principal composition is similar in Myoglossata, except for the species-poor family Neopseustidae, in which each galea forms a functionally closed food tube. The short double-tube proboscis is held together by special scales that extend from the ventral side of each galea. The galeal lumen contains a slender intrinsic galeal muscle in addition to the basal extrinsic muscle (88, 100). Three types of proboscis sensilla are present, including sensilla styloconica (56, 57), which was previously regarded to be restricted to the nectar-feeding taxa (87). The food source of the neopseustid moths is still unknown.

The proboscis of the Eulepidoptera exhibits features that probably evolved in context with flower visiting: considerable length, complexly composed galeal walls, a fluid-tight food tube with a special tip region, and numerous intrinsic galeal muscles (Figures 2, 3) (87, 88). The proboscises of nectar-feeding species display amazing lengths, which range between 3.5 and 49.9 mm in butterflies (104) and between 2.5 and 280 mm in sphingid moths (4, 109). In butterflies the length normally corresponds to about 43–93% of the body length (34, 104, 118). In the family Sphingidae the body mass is positively correlated with proboscis length (2). Disproportionately long proboscises exceeding the body length occur in some species of the Hesperiidae, Riodinidae, and Sphingidae families. The current record holder among true butterflies is *Eurybia lycisca* (Riodinidae), with a 49.9-mm-long proboscis, about twice as long as its body (104). The longest proboscis yet encountered in any flower-visiting animal belongs to the Neotropical hawk moth, *Amphimoea walkeri*, and measures 280 mm (4).

The proboscises of nonfeeding adult Lepidoptera are generally more or less reduced in length and structural complexity (130), but detailed studies are lacking. Reduced proboscises are characteristic of the representatives of the superfamilies Hepialoidea, Tineoidea, Cossoidea, and Lasiocampoidea. Furthermore, rudimentary proboscises are occasionally encountered in species of other taxa, such as the Sesioidea, Pyraloidea, Bombycoidea, Noctuoidea, and Geometrioidea (98, 130). All true butterflies, the Papilionoidea, possess a fully functional suctorial proboscis.

The composition of the galeal wall ensures the elasticity for coiling and uncoiling without deformation of the food tube. The outer galeal wall is composed of darkened cuticle rings that lie embedded in the lighter-hued cuticle, giving the proboscis an annulated appearance (73, 82, 118). The dark cuticle is probably hard exocuticle, whereas the light cuticle is interpreted to consist of flexible mesocuticle and endocuticle. Resilin is found in particular areas of the proboscis wall (73). In many species, distinct ribs, visible on the convex outer surface, may have cuticular spines, hair-like cuticular processes, or scales (82, 87, 118, 134). The concave median surface that forms the food tube is composed of smooth plates that may be vertically fluted (73, 87, 118).

The galeae are held together by rows of interlocking cuticular processes, termed legulae, that exhibit different shapes on the dorsal and ventral sides of the food canal (Figure 3*b*) (44, 73, 87). The dorsal linkage consists of flat horizontally extending lancet-shaped plates. They overlap those of the opposite galea to form the roof of the food tube. Their principal

variation in Glossata concerns the number of rows (87). Single-celled glands are situated in the galeal epidermis and empty toward the dorsal legulae; their secretion serves to lubricate and seal the dorsal linkage in butterflies (44). Two rows of ventral legulae are plesiomorphic in Eulepidoptera; in certain lineages of Ditrysia the lower legulae are modified into hooks that interlock with their counterparts, like a zipper (Figure 3b), providing firmness to the proboscis linkage (87).

Dorsal and ventral linking structures seal and firmly link the food tube; they are regarded as a functional precondition for a suctorial proboscis that takes up fluid along a pressure gradient (28). The fluid-tight food tube necessitates a specialized region for fluid intake. Near the tip, the dorsal legulae are particularly elongate and between them are drinking slits, which permit the uptake of fluids (Figure 2b,c). This region comprises 5–20% of the proboscis length in butterflies (92, 118, 123). Nymphalid butterflies and probably all other Macrolepidoptera assemble their proboscises after emerging from the pupal stage, because the galeae develop separately from each other. This behavioral process renders the proboscis functional and has to occur immediately after eclosion (83).

The sensory equipment of the proboscis was comprehensively reviewed by Faucheux (53). The sensilla trichodea or sensilla chaetica have an aporous sensory bristle that extends from a collared socket. They occur only on the external surface of the proboscis and become shorter and more scattered toward the tip; in most butterflies they are longer on the ventral side of the proboscis than on the dorsal side (84, 118). On the basis of ultrastructural studies, these sensilla are regarded as mechanosensitive (5, 84). They might provide information on the width and depth of tubular flowers during probing (84). Flower-handling efficiency relies heavily on mechanosensory input, as shown for species of sphingid moths (66). Bristle-shaped sensilla probably also provide tactile information concerning the correct resting position of the proboscis, as scanning electron micrographs confirm that they contact the surface of the adjacent coil (82).

The sensilla basiconica of the external proboscis surface are arranged in irregular rows, whereas in the food canal they form a single row (52, 75, 84, 87). They consist of a short dome-shaped socket and sensory cone that may be elongate or short, blunt or sharply tipped; sometimes it barely extends beyond the surface sculpture of the galeal wall (3, 5, 52, 53, 84, 118, 123, 131, 141). A terminal pore may be present or absent; in exceptional cases the cone is multiporous (53). Deduced from their ultrastructure, these sensilla are regarded as chemo- and/or mechanoreceptive (84, 135, 141). In electrophysiological tests, the sensilla of the food canal respond to sucrose solutions (75) and may provide information on flow rates by means of gustatory cues received from the imbibed fluid (84). In addition, sensilla ampullacea occur near the proboscis tip in the Sphingidae (53).

The sensilla styloconica are composed of a variously shaped stylus and a shorter terminal sensory cone (Figure 2c). Sensilla styloconica are regarded to be derived from sensilla basiconica (3, 53, 131) and do not occur in nonglossatan Lepidoptera (87). They are arranged in one to three regular rows in the distal half of the proboscis and are restricted to the tip region, where the drinking slits occur in butterflies (84, 87, 118, 123, 131) and in the noctuid moth *Heliothis virescens* (105). Their number may range from 7 to 144 per galea

and their length from 10 to 237 μm in butterflies (53, 118, 123). An astounding diversity of sensilla styloconica lengths and shapes are found in taxa of the true butterflies (the Papilionoidea) and the families Noctuidae, Geometridae, and Pyralidae. Cross-sections reveal the stylus to be either smooth and ellipsoid or longitudinally ribbed and star-shaped; some species exhibit terminal spines around the sensory cone, whereas in others the ribs are serrate or very short and practically absent (52, 53, 84, 87, 92, 105, 118, 123, 131, 141). In species of the Sphingidae the short sensilla styloconica are located in pits and never extend beyond the surface of the proboscis (53). Comparative morphological studies suggest that a stylus with cuticular ridges is the plesiomorphic condition in Glossata (57, 87). Derived sensilla shapes evolved in adaptive context with derived feeding habits (32, 92, 110). The internal ultrastructural composition is similar in all examined taxa despite the variety of external shapes. The sensory cone is uniporous; in some species wall pores were also detected. Each sensillum contains three to four receptor cells with dendrites extending to the terminal pore. One dendrite ends with a tubular body at the base of the cone, indicating that the sensillum serves as a combined chemo- and mechanosensory organ (3, 84, 105, 111, 141). Sensilla styloconica are sensitive to certain mono- and oligosaccharides and a variety of other substances (22, 127). For example, in butterflies that feed on fermenting fruits, the sensilla also respond to ethanol (117). The central projection pattern of the sensory neurons can be divided into two categories, which presumably reflect the functions of these sensilla (105). The axons of the receptor neurons enter the tritocerebrum and terminate near the antennal gustatory neurons. Stimulation of sensilla styloconica with sucrose increases proboscis movements and food ingestion (76).

In species of Myoglossata, the galeal musculature consists of extrinsic and intrinsic galeal muscles (88, 101). The extrinsic galeal musculature, i.e., the basal galeal muscle, originates near the stipital-galeal junction and extends into the basal galea (Figure 3*a*). The intrinsic galea musculature extends in the galeal lumen distal from the base (Figure 3*b*) and is regarded as a functional adaptation that enables the lengthy proboscis to perform its characteristic flower-probing movements. A hypothetical pathway proposes four key events for the evolution of novel proboscis musculature: (*a*) the recruitment of muscles from the basal galeal muscles by shifting the attachment site beyond the basal joint, (*b*) the shift of the muscle origin site into the galea resulted in the intrinsic galeal muscles in species of Eulepidoptera; followed by (*c*) the multiplication of the musculature in context with proboscis elongation in the lineage of Ditrysia. (*d*) The split into two series of overlapping muscles resulted in a more dense arrangement of intrinsic musculature as found in most members of Apoditrysia as well as all Macrolepidoptera, including butterflies (Figure 3*b*) (88, 89).

FUNCTIONAL MECHANISMS OF PROBOSCIS AND FLUID UPTAKE

Movements of the Proboscis

Compared with the proboscis of other nectarfeeding insects, the proboscis of Lepidoptera has several unique features. It forms a flat, vertical spiral when at rest (Figure 2*a*), it consists of merely two components, and it functions primarily by means of a hydraulic mechanism (82). How the proboscis works has long been a source of controversy (7, 44, 94, 129).

Comparative and experimental studies (7, 82, 85, 142) provide strong evidence that the same mechanisms of movements operate in all species regardless of proboscis length or the various arrangements of galeal muscles or behavioral adaptations to particular food sources.

In the resting position the proboscis is coiled into a spiral of 2.5 to 7 turns (82, 94). The proboscis is tightly wound onto itself so that there is no space between the coils. It lies against the labium (Figure 2*a*) between the labial palps (82).

The uncoiling process relies on a hydraulic mechanism (7, 82, 129, 142). The proboscis is first unlocked from its resting position—it is elevated by the basal galeal muscle. Owing to its elasticity, the coil of the proboscis loosens somewhat. Further uncoiling is enabled by contraction of stipes muscles, whereby movements of the sclerotized part of the stipes compress the stipital tube (Figure 4*a*). The repeated compressions of the stipes force hemolymph into the attached galea. Because the structures of the stipes form a valve, the proboscis is stepwise uncoiled when the hemolymph pressure inside the galeae increases. The increased internal pressure results in an outwardly arched dorsal wall in the uncoiled proboscis (85). The uncoiled proboscis normally assumes a bent position with a more or less distinct flexion, termed the bend region or knee-bend (Figure 5*a*) (7). The bend region is probably caused by the elasticity of the proboscis (82, 85). Increased hemolymph pressure can lead to a nearly straight position of the proboscis; in some cases, the distal proboscis bends slightly upward (7, 143). During flower handling, the proboscis is elevated by contraction of the basal joint muscles, while forward or backward movements of the region distal to the bend region (Figure 5*a*) are caused either by an increase in pressure due to stipital pumping or by action of the intrinsic galeal musculature of the proboscis, respectively (82).

After the stipes valve opens, proboscis coiling is achieved by the elasticity of the cuticle, which loosely recoils the spiral into 1.5 to 2.5 turns. The contractions of the intrinsic galeal muscles (Figure 4*b*) are responsible for tightening the coil as indicated by experiments and electromyogram recordings (85, 142). The final resting position is achieved after the coiled proboscis has been flexed under the head by contraction of a single stipital muscle (Figure 4*b*). Presumably, after relaxation of the intrinsic galeal muscles, the proboscis unwinds slightly until it contacts the labium (82). The sculpture and cuticle processes of the proboscis wall provide the grip needed to hold the coiled proboscis under the head without further muscular contraction, and microtrichia on the median sides of the labial palps are hypothesized to assist in fixing the final position (82, 91).

Capacity of Fluid Uptake

Glossatan Lepidoptera take up fluid along a pressure gradient in the food tube of the proboscis that is created by a sucking pump in the head. A biophysical model based on the Hagen-Poiseuille equation shows that the flow rate is proportional to the pressure drop produced by the sucking pump and the diameter of the food tube, but it is inversely proportional to proboscis length and viscosity of the fluid, which depends on the sugar content (80). This model predicts an optimal nectar concentration of 30–40% sucrose to maximize energy intake in butterflies and hawk moths (35, 77, 107). In natural habitats, however, flower choice depends on additional parameters such as available nectar

concentration and volume, flower morphology, availability and density of flowers, as well as handling and transit time between flowers (23, 28).

The capacity of the feeding apparatus is best measured by uptake volume during feeding experiments. The volume of fluid ingested by nymphalid butterflies varies from 36–133 μl of artificial nectar depending on body size (70, 81, 110). Under near-natural conditions the meal size of *Vanessa cardui* was 28 ± 9.3 μl (S.D.), in which an average of 145 ± 56 flowers were probed in 48 ± 24 min, with an average volume rate of 19.3 ± 10.4 nl per second (70). Stimulated *V. cardui* butterflies consumed artificial nectar (30% sucrose) from artificial flowers, which is equivalent to an average of 15.23% of its body weight within 2 min, or it consumed mean nectar amounts, which are equivalent to 41.6% of its body weight when feeding until satiation (81). The larger sized *Morpho peleides* consumed nectar equivalent to an average of 23.6% of its body weight within 2 min and equivalent to 43.7% of its body weight in approximately 10 min. The uptake of highly viscous sugary fluids from rotting fruits probably involves a dilution of the sugar with salivary fluid (81). An oral valve permits an alternating flow of saliva and nutritive fluid through the food tube (46).

Tropical hawk moths consume between 0.4 and 1 g of nectar per night (143). Their average meal size decreased linearly with increased sugar concentration, from 0.35 g at 10% to 0.11 g at 50% (137). The intake rate of hawk moths was analyzed as a function of sucrose viscosity (by adding tylose as an inert polysaccharide) in a 30% sucrose solution. Because the intake rates decreased with increasing viscosity, it was concluded that the gustatory input effects fluid ingestion independent of viscosity (77).

Males of a notodontid moth *Gluphisia septentrionis* take up large amounts of water, although their proboscis is rudimentary and they do not feed on sugary fluids. The moth can pump an equivalent of 12% of its body mass per minute through the digestive tract, which amounts to more than 600 times its body mass in 3.4 h of fluid uptake (132).

Mechanism of the Sucking Pump

The functional anatomy of the sucking pump has been studied mainly in butterflies (44, 47, 50) and the hawk moth *Manduca sexta* (39, 108). The majority of head muscles are associated with the sucking pump (136), which is an expandable cavity located between the proboscis and esophagus and is outfitted with valve structures. Discontinuous fluid transport is achieved by coordinated and rhythmic contracting of dilator, compressor, and sphincter muscles. As demonstrated in real time, X-ray imaging of feeding butterflies shows that fluid is drawn into the pump by dorsal expansion of the chamber. Contraction of circular compressor muscles transports discrete boluses of fluid into the esophagus (133). A neuroanatomical study of the sucking pump in *M. sexta* indicates that the frontal cibarial valve and one pair of the dilator muscles must have originated from the cibarium, whereas the remaining dilator muscles, the compressor musculature, and the sphincter muscle to the esophagus belong to the stomodeum. This led to the new hypothesis that the sucking pump developed from the anterior stomodeum rather than the cibarium (39). The sucking pump muscles are innervated by the frontal ganglion and can be triggered into action by application of a sucrose solution to the proboscis. As indicated by electrophysiological studies, the dilation phase begins with contraction of the esophageal sphincter and is

followed by contraction of the cibarial opener muscle (39, 108). The principal composition of the sucking pump and its mechanism appears identical in glossatan Lepidoptera. In nymphalid butterflies, cibarial components form a valve that controls the outflow of saliva into the food canal of the proboscis during the compression phase of the sucking pump (47).

ADAPTATIONS TO VARIOUS FOOD SOURCES

Nectar-Feeding and Flower-Handling Behavior

Most nectar-feeding Lepidoptera are opportunistic flower visitors (64) and probe flowers of various sizes with open or concealed nectaries. Most descriptions of flower-handling behavior concern butterflies and hawk moths (44, 82, 86, 125). Butterflies approach flowers with a loosely coiled proboscis and uncoil it after landing. In the feeding position, the proboscis shows a distinct bend after approximately one third of its length (Figure 5*a*), enabling the proboscis to adjust to various flower depths (7, 44, 82). A typical sequence of probing movements consists of an elevation of the proboscis at the basal joint until the tip loses contact with the surface, followed by extension or flexion of the bend region to move the tip of the proboscis forward or backward, and lowering of the proboscis until its tip again contacts the flower at another location (Figure 5*a*). Butterflies often produce several short series of such probing movements lasting between 0.2 and 0.5 s and consisting of two to five cycles (82, 86). Once a butterfly has located the entrance to a flower, it lowers its proboscis at the base, enabling the tip to project into the flower. Depending on the length of the proboscis and the depth of the flower, the proboscis is inserted up to the bend region or even further; sometimes this is accompanied by flexion of the legs and bowing of the head. Brief poking movements often follow in which the proboscis is partially lifted and immediately inserted again. During flower probing, the sensilla styloconica presumably provide information on both nectar and the position of the tip inside a flower (84). The proboscis may remain motionless for a moment when nectar is ingested. When the flower is depleted, the proboscis is pulled out. If the butterfly is visiting an inflorescence, it rapidly turns to the next flower and repeats the flower-probing sequence. In this manner a butterfly can swiftly probe one flower after another by simply rotating its body (86). A study of handling times in butterflies indicates that species with a disproportionately long proboscis may require significantly greater length times compared to species with an average sized proboscis, thus amounting to reduced foraging efficiency (104).

Hawk moths often exploit flowers while hovering in front of or over them; at times, the flower is grasped with the legs (125). The Sphingidae are particularly capable of extracting nectar from long-spurred flowers; nonetheless, they can skillfully handle shallow flowers (2, 69, 109, 144). Stereotypical swing-hovering flight behavior was observed in some hawk moths (144). The tip of the proboscis is introduced into the corolla as far as possible whereby the distal proboscis is often bent upward (7). Mechanosensory input is crucial for proboscis insertion since three-dimensional features of the flower, such as grooves, significantly enhance foraging performance by decreasing the time it takes for the hawk moth to discover the nectar (66).

There is convincing evidence that the evolution of extremely long proboscises is associated with adaptations to long-spurred flowers, in particular orchids (36, 114, 115, 128). However,

an alternative hypothesis argues that the evolution of the extremely long proboscis of the hawk moth *Xanthopan morgani* from Madagascar could have resulted from selective pressure to escape predators, such as spiders, that lurk on flowers. Long-spurred orchids are adapted to hawk moths, exploiting them as particularly valuable pollinating vectors (143, 144).

Pollen Feeding and Additional Sources of Food

The Neotropical butterflies of the closely related genera *Heliconius* and *Laparus* (Nymphalidae) rely on pollen, in addition to floral nectar, as a food source (24, 51, 63). The pollen grains are actively collected on the outside of the proboscis during flower probing. After a lump of pollen has been collected, it is agitated in a fluid for hours by coiling and uncoiling movements of the proboscis (Figure 5*b*). The resulting liquid is ingested, but the pollen grains remain outside the body (63). During this process essential amino acids are extracted from the pollen grains (116). Nitrogen obtained from amino acids benefits the production of eggs, nuptial gifts, and antipredatory substances, and it greatly extends life span (24, 43, 63, 116). A morphologically based phylogeny suggests that pollen feeding is convergent in *Heliconius* and *Laparus* (121). However, recent molecular-based phylogenies indicate a single origin for pollen feeding with a loss in one lineage (21). The proboscises of *Heliconius* butterflies are longer than those of related nonpollen-feeding nymphalids, and they bear a greater number of long sensory bristles in the proximal half where the pollen is accumulated (90). Flower-probing movements last significantly longer on flowers when pollen is collected (86). Fluid exuded from the tip helps pollen stick to the proboscis and is used for pollen processing (122). The fluid, likely saliva, contains proteases that probably extract the amino acids (45). A comparative study of the salivary glands revealed no histological differences between pollen-feeding and nonpollen-feeding Heliconiinae (46). However, both the length and the volume of salivary glands were greater in pollen-feeding species (48).

Some species of Ithomiinae are specialized to supplement their nutrition with nitrogen from bird droppings. Females ingest liquid from fresh excrement of antbirds, which hunt insects flushed out by predatory marches of *Eciton* army ants (126).

In addition to floral nectar, many Lepidoptera obtain sugar from other sources such as extrafloral nectaries, squashed fruit, and honeydew, as well as mineral substances from perspiration on human skin and from moist soil. The latter phenomenon is common to males of many taxa and sometimes involve large aggregations of different species on sodden earth, dung, mammalian urine, mud puddles (1, 20, 42) and, according to a single report, on marine algae mats (124). Butterflies perform dabbing movements with the tip of the proboscis when consuming fluid from moist surfaces. Compared to flower probing, the uncoiled proboscis shows a less conspicuous bend region and either the tip region is directed toward the body (Figure 5*c*) or the proboscis is held in a nearly straight position with the tip region flexed upside down so that the drinking slits contact the moist surface (86).

Many adult members of the moth family Arctiidae and male Danainae and Ithomiinae butterflies are attracted to plants that contain pyrrolizidine alkaloids. They take up and incorporate the poisonous plant substances, using them as a defense against predators and, in

modified form, during courtship behavior. The pharmacophagous butterflies discharge a fluid from the proboscis tip that dissolves alkaloids from wilted leaves and dried parts of certain Boraginaceae and Asteraceae (26, 27).

Sweeping Technique of Feeding from Surfaces

A considerable number of species of the family Nymphalidae, and certain butterflies of the Riodinidae, Lycaenidae, and some moths of the Noctuidae, have never been observed to visit flowers (40, 41, 49, 71). Instead of nectar feeding, they feed on fruit, honeydew or decaying substances. The nonflower-visiting butterflies of the Nymphalidae have a shorter proboscis than their nectar-feeding relatives. The tip region is equipped with long, numerous, and densely ordered sensilla styloconica, which form a flat brush (Figure 5*c*) that functions as a structure for accumulation of fluid (81, 92, 110). The brush-shaped tip region is interpreted to be an adaptation to feeding on wet surfaces and presumably evolved independently in various phylogenetic lineages (92). Most nonflower-visiting butterflies perform a sweeping technique along with dabbing movements to ingest fluid from wet surfaces of various kinds. Butterflies of Nymphalinae and Satyrinae apply the dorsal side of the tip region to the feeding surface and either raise the tip and place it elsewhere or sweep it over the surface. Proboscis movements differ greatly in frequency across substrates, probably depending on the texture and fluidity of the fruit (110). The butterfly *Morpho peleides* scans a wide area without having to move about by simply rising and lowering the uncoiled proboscis and by sideward bending of the particularly flexible tip region. Further, it liquefies dried fruit juice and dilutes thick juices for ingestion by discharging saliva (81).

Some Asian species of the family Lycaenidae feed on honeydew produced by aphids, coccids, and membranicids. They also consume extrafloral nectar, but they never visit flowers. To entice these sap-feeding insects to release droplets of honeydew, the butterfly taps them with its proboscis, presumably mimicking antennal stimulation performed by guarding ants (60, 61).

Techniques of Fruit and Skin Piercing

Apart from surface feeding, some Lepidoptera pierce their food sources to obtain the fluid inside. Nymphalid butterflies of the subfamily Charaxinae plunge the proboscis into soft fruit, dung, or carrion (110). The butterflies search for injuries on the fruit through which they thrust their proboscises, employing movements of the whole body. Unlike the sweeping technique of fruit feeding, the proboscis is held straight, without bending (Figure 5*d*). After the fruit is penetrated, the entire proboscis moves forward and backward without being withdrawn. Fruit-piercing butterflies have higher intake rates from soft fruit compared with other fruit-feeding Nymphalidae when standardized for body size (110). The proboscis is rather short, thick, and robust; the tip is pointed and outfitted with short sensilla styloconica (Figure 5*d*) (92, 110).

A number of noctuid moths employ a different mechanism to pierce fruit (12, 13, 18) that may inflict damage to citrus crops (58). These moths possess a sharp-tipped proboscis that bears an armature of acute erectile structures, hooks, and spines (6). The erectile structures are composed of a socket and an acute shaft corresponding to the composition of sensilla

styloconica, the hooks are probably homologues of sensilla basiconica, and the spines correspond to dorsal legulae of the galeal linkage (32). Bänziger (6) described the elaborate technique, whereby even thick-walled fruit can be pierced. It begins with a rapid vibration by which a small hole is drilled, and the hooks anchor the proboscis. Penetration is accomplished by antiparallel movements of the galeae (Figure 5*e*), in which one and then the other galea is pushed further into the fruit. Tilting movements of the head compensate for sideward bending of the proboscis when one galea is pushed forward. The erectile structures are extended by a bulging of the cuticle due to increased hemolymph pressure inside the galea resulting from stipital pumping similar to the uncoiling process. The erected structures of one galea provide resistance so that the other galea can be pushed further into the tissue. After feeding, hemolymph pressure is decreased inside the galeae by opening the stipes valve. The flexion of the erectile structures reverses and antiparallel movements of the galeae withdraw the proboscis.

Males of seven Asian species of *Calyptra* facultatively pierce skin and suck blood from large mammals, including humans (6, 9, 10, 11, 15, 18, 147). The proboscis armature is similar to that in fruit-piercing moths (Figure 5*e*). The proboscis tip drills a hole into the skin by torsion, and penetration results from antiparallel movements of the galeae (Figure 5*e*). Erectile structures provide the resistance needed to advance the proboscis into the skin (10, 11). There is no doubt that hemophagy is derived from fruit-piercing behavior (18).

Eye Frequenting and Tear Feeding

A considerable number of nocturnal species of the Pyralidae, Noctuidae, and Geometridae, and few species of the Thyatiridae, Notodontidae, and Sphingidae, in tropical regions of the world regularly feed on wounds and lachrymal fluid from the eyes of large mammals, including humans (8, 14, 16, 17, 29, 30). These zoophilous moths are mainly males. They approach their hosts at night and settle near the eye to imbibe lachrymal fluid (Figure 5*f*).

All obligatory lachryphagous moths possess a soft proboscis tip, which is characterized by projecting sensilla and long dentate dorsal legulae, giving the tip region a serrate appearance (Figure 5*f*) (29, 32). The shape of the proboscis and its jerky probing movements irritate the eye (humans experience pain) and cause an increase in lachrymal secretion (16, 17, 19). Because the particular tip morphology is similar to that in unrelated tear-feeding taxa, it is regarded as an adaptation that evolved convergently in eye-frequenting species (32). An examination of the midgut of these moths demonstrated the presence of leukocytes and epithelial cells (31). Proteases present in the gut of many but not all lachryphagous moths would allow for digestion of protein contents of tears (8, 18).

In contrast, the tear-feeding noctuid moth *Hemiceratoides hieroglyphica* from Madagascar possesses a sharp-tipped proboscis, although it feeds from the eyes of sleeping birds. The tip is characterized by hooks and spines, similar to that in species of fruit-piercing Noctuidae (74). Details of the armature indicate a different evolutionary line than other tear-feeding Lepidoptera (18).

Acknowledgments

Glossary

Plesiomorphic	character of ancestral condition, present before the last common ancestor of the taxon
Autapomorphy	derived character, unique to a taxon
Glossata	taxon of Lepidoptera comprising more than 99% of species; characterized by the coilable proboscis, among other traits
Ditrysia	taxon of Lepidoptera characterized by specialized female genital apparatus
Myoglossata	taxon of Glossata characterized by intrinsic proboscis musculature
Eulepidoptera	primary nectar-feeding Lepidoptera
Macrolepidoptera	medium to large, broad-winged Lepidoptera with exophagous larvae

LITERATURE CITED

1. Adler PH. Soil- and puddle-visiting habits of moths. J. Lepid. Soc. 1982; 36(3):161–73.

2. Agosta SJ, Janzen DH. Body size distributions of large Costa Rican dry forest moths and the underlying relationship between plant and pollinator morphology. Oikos. 2005; 108:183–93.

3. Altner H, Altner I. Sensilla with both terminal pore and wall pores on the proboscis of the moth, *Rhodogastria bubo* Walker (Lepidoptera: Arctiidae). Zool. Anz. 1986; 216:129–50.

4. Amsel HG. *Amphimoea walkeri* Bsd., der Schwärmer mit dem längsten Rsssel. Entomol. Rundsch. 1938; 55:165–67.

5. Baker GT, Chan WP. Sensilla on the antennae and mouthparts of the larval and adult stages of *Oleuthreutes cespitata* (Lepidoptera: Tortricidae). Ann. Soc. Entomol. France. 1987; 23:387–97.

6. Bänziger H. The piercing mechanism of the fruit-piercing moth *Calpe* [*Calyptra*] *thalictri* Bkh. (Noctuidae) with reference to the skin-piercing blood-sucking moth *C. eustrigata* Hmps. Acta Trop. 1970; 27:53–88.

7. Bänziger H. Extension and coiling of the lepidopterous proboscis: a new interpretation of the blood-pressure theory. Mitt. Schweiz. Entomol. Ges. 1971; 43:225–39.

8. Bänziger H. Biologie der lacriphagen Lepidopteren in Thailand und Malaya. Rev. Suisse Zool. 1972/1973; 79:1381–469. [PubMed: 4671232]

9. Bänziger H. Skin-piercing bloodsucking moths I: ecological and ethological studies on *Calpe eustrigata* (Lepid., Noctuidae). Acta Trop. 1975; 32(2):125–44. [PubMed: 240258]

10. Bänziger H. Skin-piercing bloodsucking moths II: studies on a further three adult *Calyptra* [*Calpe*] sp. (Lepid., Noctuidae). Acta Trop. 1980; 36:23–37. [PubMed: 35931]

11. Bänziger H. Skin-piercing bloodsucking moths III: feeding act and piercing mechanism of *Calyptra eustringata* (Hmps.) (Lep., Noctuidae). Mitt. Schweiz. Entomol. Ges. 1980; 53:127–42.

12. Bänziger H. Fruit-piercing moths (Lep., Noctuidae) in Thailand: a general survey and some new perspectives. Mitt. Schweiz. Entomol. Ges. 1982; 55:213–40.

13. Bänziger H. Biological and taxonomical studies on immature and adult fruit-piercing moths in Nepal, with reference to Thailand. Nat. Hist. Bull. Siam Soc. 1987; 35:1–17.

14. Bänziger H. The heaviest tear drinkers: ecology and systematics of new and unusual notodontid moths. Nat. Hist. Bull. Siam Soc. 1988; 36:17–53.

15. Bänziger H. Skin-piercing blood-sucking moths V: attacks on man by five *Calyptra* spp. (Lepidoptera, Noctuidae) in S and SE Asia. Mitt. Schweiz. Entomol. Ges. 1989; 62:215–33.

16. Bänziger H. Remarkable new cases of moths drinking human tears in Thailand (Lepidoptera: Thyatiridae, Sphingidae, Notodontidae). Nat. Hist. Bull. Siam Soc. 1992; 40:91–102.

17. Bänziger H. Microstega homoculorum sp. n.: the most frequently observed lachryphagous moth of man (Lepidoptera, Pyralidae: Pyraustinae). Rev. Suisse Zool. 1995; 102(2):265–76.

18. Bänziger H. Skin-piercing blood-sucking moths VI: fruit-piercing habits in *Calyptra* (Noctuidae) and notes on the feeding strategies of zoophilous and frugivorous adult Lepidoptera. Mitt. Schweiz. Entomol. Ges. 2007; 80:271–88.

19. Bänziger H, Büttiker W. Records of eye-frequenting Lepidoptera from man. J. Med. Entomol. 1969; 6(1):53–58. [PubMed: 5813263]

20. Beck J, Mühlenberger E, Fiedler K. Mud-puddling behavior in tropical butterflies: in search of proteins or minerals. Oecologia. 1999; 119:140–48.

21. Beltrán M, Jiggins CD, Brower AVZ, Bermingham E, Mallet J. Do pollen feeding, pupal-mating and larval gregariousness have a single origin in Heliconius butterflies? Inferences from multilocus DNA sequence data. Biol. J. Linn. Soc. 2007; 92:221–39.

22. Blaney WM, Simmonds SJ. Food selection in adults and larvae of three species of Lepidoptera: a behavioural and electrophysiological study. Entomol. Exp. Appl. 1988; 49:111–21.

23. Boggs, CL. Ecology of nectar and pollen feeding in Lepidoptera. In: Slansky, F.; Rodriguez, JG., editors. Nutritional Ecology of Insects, Mites, and Spiders. Wiley; New York: 1987. p. 369-91.

24. Boggs CL, Smiley JT, Gilbert LE. Patterns of pollen exploitation by *Heliconius* butterflies. Oecologia. 1981; 48:284–89.

25. Bogner F, Boppré M, Ernst K-D, Boeckh J. CO_2 sensitive receptors on labial palps of Rhodogastria moths (Lepidoptera: Arctiidae): physiology, fine structure and central projection. J. Comp. Physiol. A. 1986; 158:741–49. [PubMed: 3090241]

26. Boppré M. Leaf-scratching: a specialized behavior of danaid butterflies (Lepidoptera) for gathering secondary plant substances. Oecologia. 1983; 59:414–16.

27. Boppré M. Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaliods). Naturwissenschaften. 1986; 73:17–26.

28. Borrell, BJ.; Krenn, HW. Nectar feeding in long-proboscis insects. In: Herrel, A.; Speck, T.; Rowe, NP., editors. Ecology and Biomechanics: A Mechanical Approach to the Ecology of Animals and Plants. Taylor & Francis/CRC Press; Boca Raton, FL/London/New York: 2006. p. 185-212.

29. Büttiker, W. Biological and morphological notes on the fruit-piercing and eye-frequenting moths; XI Int. Kongr. Entomol. Wien; 1960; Vienna. 1962. p. 10-12.

30. Büttiker W. Biological notes on eye-frequenting moths from N. Thailand. Mitt. Schweiz. Entomol. Ges. 1967; 39:151–79.

31. Büttiker W. Midgut structure and contents in some higher moths, especially in eye-frequenting taxa. Entomol. Basiliensia. 1997; 20:57–80.

32. Büttiker W, Krenn HW, Putterill J. The proboscis of eye-frequenting and piercing Lepidoptera. Zoomorphology. 1996; 116:77–83.

33. Chauvin G, Faucheux M. Les pièces buccales et leurs recepteurs sensoriels chez l'imago de *Micropterix calthella* L. (Lepidoptera: Micropterigidae). Int. J. Insect Morphol. Embryol. 1981; 10:425–39.

34. Corbet SA. Butterfly nectaring flowers: butterfly morphology and flower form. Entomol. Exp. Appl. 2000; 96:289–98.

35. Daniel TL, Kingsolver JG, Meyhofer E. Mechanical determinants of nectar-feeding energetics in butterflies: muscle mechanics, feeding geometry, and functional equivalence. Oecologia. 1989; 79:66–75.

36. Darwin, C. On the various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and the Good Effects of Intercrossing. Murray; London: 1862.

37. Davis D. A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae). Bull. U.S. Natl. Mus. 1967; 255:1–170.

38. Davis D. A new family of monotrysian moths from austral South America (Lepidoptera: Palaephatidae), with a phylogenetic review on the Monotrysia. Smithson. Contrib. Zool. 1986; 434:1–202.

39. Davis NT, Hildebrand JG. Neuroanatomy of the sucking pump of the moth, Manduca sexta (Sphingidae, Lepidoptera). Arthropod Struct. Dev. 2006; 35:15–33. [PubMed: 18089055]

40. DeVries, PJ. The Butterflies of Costa Rica and Their Natural History. Princeton Univ. Press.; Chichester, UK: 1987. p. 327

41. DeVries, PJ. The Butterflies of Costa Rica and Their Natural History. Princeton Univ. Press.; Chichester, UK: 1997. p. 288 Volume II: Riodinidae

42. Downes JA. Lepidoptera feeding at puddle-margins, dung, and carrion. J. Lepidop. Soc. 1973; 27(2):89–99.

43. Dunlap-Pianka H, Boggs CL, Gilbert LE. Ovarian dynamics in Heliconiine butterflies: programmed senescence versus eternal youth. Science. 1997; 197:487–90. [PubMed: 17783249]

44. Eastham LES, Eassa YEE. The feeding mechanism of the butterfly *Pieris brassicae* L. Philos. Trans. R. Soc. London Ser. B. 1955; 239:1–43.

45. Eberhard SH, Hrassnigg N, Crailsheim K, Krenn HW. Evidence of protease in the saliva of the butterfly *Heliconius melpomene* (L.) (Nymphalidae, Lepidoptera). J. Insect Physiol. 2007; 53:126–31. [PubMed: 17210163]

46. Eberhard SH, Krenn HW. Salivary glands and salivary pumps in adult Nymphalidae (Lepidoptera). Zoomorphology. 2003; 122:161–67.

47. Eberhard SH, Krenn HW. Anatomy of the oral valve in nymphalid butterflies and a functional model for fluid uptake in Lepidoptera. Zool. Anz. 2005; 243:305–12.

48. Eberhard SH, Nemeschkal HL, Krenn HW. Biometrical comparison of the salivary glands between pollen-feeding and nonpollen-feeding nymphalid butterflies (Lepidoptera). Biol. J. Linn. Soc. 2009; 97:604–12.

49. Ebert, G.; Rennwald, E. Die Schmetterlinge Baden-Württembergs. Band 5 Noctuidae. Stuttgart; Ulmer: 1991.

50. Ehrlich PR, Ehrlich AH. The head musculature of butterflies (Lepidoptera: Papilionoidea). Microentomology. 1962; 24:85–133.

51. Estrada C, Jiggins CD. Patterns of pollen feeding and habitat preference among *Heliconius* species. Ecol. Entomol. 2002; 27:448–56.

52. Faucheux MJ. Morphology and distribution of sensilla on the cephalic appendages, tarsi and ovipositor of the European sunflower moth, *Homoeosoma nebulella* Den. & Schiff. (Lepidoptera: Pyralidae). Int. J. Insect Morphol. Embryol. 1991; 20:291–307.

53. Faucheux MJ. Biodiversité et unité des organes sensoriels des Insectes Lépidoptères. Bull. Soc. Sci. Nat. Ouest Fr. Suppl. Sér. 1999:1–296.

54. Faucheux MJ. *Heterobathmia pseuderiocrania* (Heterobathmiina): mouthparts, mouthpart sensilla, and comparison with other nonglossatan suborders (Insecta, Lepidoptera). Rev. Mus. Argent. Cienc. Nat. 2005; 7(1):57–65.

55. Faucheux MJ. Les sensilles des pièces buccales du papillon australien broyeur de pollen *Sabatinca sterpos* Turner (Lepidoptera: Zeugloptera: Micropterigidae). Comparaison avec *Micropterix calthella* Linné. Bull. Soc. Sc. Nat. Ouest Fr. 2005; 27:169–82.

56. Faucheux MJ. L'apparition des sensilles styloconiques sur la trompe au cours de l'evolution des Lépidoptères: les pièces buccales d'*Apoplania valdiviana* Davis&Nielson 1984 (Glossata: Neopseustoidea: Neopseustidae). Bull. Soc. Sc. Nat. Ouest Fr. 2007; 29:178–89.

57. Faucheux MJ. Mouthparts and associated sensilla of a South American moth, *Synempora andesae* (Lepidoptera: Neopseustidae). Rev. Soc. Entomol. Argent. 2008; 67(1-2):21–33.

58. Fay HAC, Halfpapp KH. Fruit maturity and soundness relevant to feeding choice by fruit-piercing moths (Lepidoptera: Noctuidae) in citrus crops in northeast Australia. Int. J. Pest Manag. 2006; 52(4):317–24.

59. Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD. Pollination syndromes and floral specialization. Annu. Rev. Ecol. Syst. 2004; 35:375–403.

60. Fiedler K. The remarkable life history of two Malaysian lycaenid butterflies. Nat. Malays. 1993; 18(2):35–43.

61. Fiedler K, Maschwitz U. Adult myrmecophily in butterflies: the role of the ant *Anoplopis longipes* in the feeding and oviposition behavior of Allotinus unicolor. Tyô to Ga. 1989; 40(4):241–51.

62. Friedlander TP, Regier JC, Mitter C, Wagner DL, Fang QQ. Evolution of heteroneuran Lepidoptera (Insects) and the utility of dop decarboxylase for Cretaceous phylogenics. Zool. J. Linn. Soc. 2000; 130:213–34.

63. Gilbert LE. Pollen feeding and reproductive biology of *Heliconius* butterflies. Proc. Natl. Acad. Sci. USA. 1972; 69:1403–7. [PubMed: 16591992]

64. Gilbert LE, Singer MC. Butterfly ecology. Annu. Rev. Ecol. Syst. 1975; 6:365–97.

65. Goyret J, Markwell PM, Raguso RA. Context- and scale-dependent effects of floral CO_2 on nectar foraging by *Manduca sexta*. Proc. Natl. Acad. Sci. USA. 2008; 105(2):4565–70. [PubMed: 18212123]

66. Goyret J, Raguso RA. The role of mechanosensory input in flower handling efficiency and learning by *Manduca sexta*. J. Exp. Biol. 2006; 209:1585–93. [PubMed: 16621939]

67. Guerenstein PG, Hildebrand JG. Roles and effects of environmental carbon dioxide in insect life. Annu. Rev. Entomol. 2008; 53:161–78. [PubMed: 17803457]

68. Guerenstein PG, Yepez EA, van Haren J, Williams DG, Hildebrand JG. Floral CO_2 emission may indicate food abundance to nectar-feeding moths. Naturwissenschaften. 2004; 91:329–33. [PubMed: 15257387]

69. Haber WA, Frankie GW. A tropical hawkmoth community: Costa Rican dry forest Sphingidae. Biotropica. 1989; 21(2):155–72.

70. Hainsworth FR, Precup E, Hamill T. Feeding, energy processing rates and egg production in painted lady butterflies. J. Exp. Biol. 1991; 156:249–65.

71. Hall JPW, Willmot KR. Patterns of feeding behavior in adult male riodinid butterflies and their relationship to morphology and ecology. Biol. J. Linn. Soc. 2000; 69:1–23.

72. Hannemann HJ. Die Kopfmuskulatur von *Micropteryx calthella* (L.) (Lep.). Morphologie und Funktion. Zool. Jb. Anat. 1956; 75:177–206.

73. Hepburn HR. Proboscis extension and recoil in Lepidoptera. J. Insect Physiol. 1971; 17:637–56.

74. Hilgartner R, Raoilison M, Büttiker W, Lees DC, Krenn HW. Malagasy birds as hosts for eyefrequenting moths. Biol. Lett. 2007; 3(2):117–20. [PubMed: 17251126]

75. Inoue TA, Asaoka K, Seta K, Imaeda D, Ozaki M. Sugar receptor response of the food-canal taste sensilla in a nectar-feeding swallowtail butterfly, *Papilio xuthus*. Naturwissenschaften. 2009; 96:355–63. [PubMed: 19083195]

76. Jørgensen K, Kvello PJ, Almaas TJ, Mustaparta H. Two closely located areas in the suboesophageal ganglion and the tritocerebrum receive projections of gustatory receptor neurons located on the antennae and the proboscis in the moth *Heliothis virescens*. J. Comp. Neurol. 2006; 496:121–34. [PubMed: 16528726]

77. Josens RB, Farina WM. Nectar feeding by the hovering hawk moth *Macroglossum stellatarum*: intake rate as a function of viscosity and concentration of sucrose solutions. J. Comp. Physiol. A. 2001; 187:661–65. [PubMed: 11763964]

78. Kent KS, Harrow ID, Quartararo P, Hildebrand JG. An accessory olfactory pathway in Lepidoptera: the labial pit organ and its central projections in *Manduca sexta* and certain other sphinx moths and silk moths. Cell Tiss. Res. 1986; 245:237–45.

79. Kevan PG, Baker HG. Insects as flower visitors and pollinators. Annu. Rev. Entomol. 1983; 28:407–53.

80. Kingsolver, JG.; Daniel, TL. Mechanics of food handling by fluid-feeding insects. In: Chapman, RF.; De Boer, G., editors. Regulatory Mechanisms in Insect Feeding. Chapman and Hall; New York: 1995. p. 32-73.

81. Knopp MCN, Krenn HW. Efficiency of fruit juice feeding in *Morpho peleides* (Nymphalidae, Lepidoptera). J. Insect Behav. 2003; 16:67–77.

82. Krenn HW. Functional morphology and movements of the proboscis of Lepidoptera (Insecta). Zoomorphology. 1990; 110:105–14.

83. Krenn HW. Proboscis assembly in Lepidoptera: a once in a lifetime sequence of events. Eur. J. Entomol. 1997; 94:495–501.

84. Krenn HW. Proboscis sensilla in *Vanessa cardui* (Nymphalidae, Lepidoptera): functional morphology and significance in flower-probing. Zoomorphology. 1998; 118:23–30.

85. Krenn HW. Proboscis musculature in the butterfly *Vanessa cardui* (Nymphalidae, Lepidoptera): settling the proboscis recoiling controversy. Acta Zool. 2000; 81:259–66.

86. Krenn, HW. Feeding behaviours of Neotropical butterflies. In: Weissenhofer, A.; Huber, W.; Mayer, V.; Pamperl, S.; Weber, A.; Aubrecht, G., editors. Natural and Cultural History of the Golfo Dulce Region, Costa Rica. Stapfia. Vol. 88. Biol. Oberösterr. Landesmus; Linz: 2008. p. 295-304.

87. Krenn HW, Kristensen NP. Early evolution of the proboscis of Lepidoptera (Insecta): external morphology of the galea in basal glossatan moths lineages, with remarks on the origin of the pilifers. Zool. Anz. 2000; 239:179–96.

88. Krenn HW, Kristensen NP. Evolution of proboscis musculature in Lepidoptera. Eur. J. Entomol. 2004; 101:565–75.

89. Krenn HW, Mühlberger N. Groundplan anatomy of the proboscis of butterflies (Papilionoidea, Lepidoptera). Zool. Anz. 2002; 241:369–80.

90. Krenn HW, Penz CM. Mouthparts of *Heliconius* butterflies (Lepidoptera: Nymphalidae): a search for anatomical adaptations to pollen-feeding behavior. Int. J. Insect Morphol. Embryol. 1998; 27:301–9.

91. Krenn HW, Plant JD, Szucsich NU. Mouthparts of flower-visiting insects. Arthropod Struct. Dev. 2005; 34:1–40.

92. Krenn HW, Zulka KP, Gatschnegg T. Proboscis morphology and food preferences in Nymphalidae (Lepidoptera, Papilionoidea). J. Zool. London. 2001; 253:17–26.

93. Kristensen NP. The anatomy of the head and the alimentary canal of adult Eriocraniidae (Lep., Dacnonypha). Entomol. Meddr. 1968; 36:239–315.

94. Kristensen NP. The morphology and functional evolution of the mouthparts in adult Lepidoptera. Opusc. Entomol. 1968; 33:1–2.

95. Kristensen NP. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). Steenstrupia. 1984; 10:141–91.

96. Kristensen, NP., editor. Lepidoptera: moths and butterflies. Vol. 1. Walter de Gruyter; Berlin/New York: 1999. p. 491 Handbook of Zoology Vol. 1: Evolution, systematics, and biogeography

97. Kristensen, NP., editor. Lepidoptera, moths and butterflies. Walter de Gruyter; Berlin/New York: 1999. The non-Glossatan moths; p. 41-49. Handbook of Zoology Vol. 1: Evolution, systematics, and biogeography

98. Kristensen, NP., editor. Lepidoptera, moths and butterflies. Walter de Gruyter; Berlin/New York: 2003. Skeleton and muscles: adults; p. 39-131. Handbook of Zoology Vol. 2: Morphology, physiology, and development

99. Kristensen NP, Nielsen ES. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). Steenstrupia. 1979; 5:69–147.

100. Kristensen NP, Nielsen ES. Double-tube proboscis configuration in neopseustid moths (Lepidoptera: Neopseustidae). Int. J. Insect Morphol. Embryol. 1981; 10:483–86.

101. Kristensen NP, Nielsen ES. Intrinsic proboscis musculature in nonditrysian Lepidoptera-Glossata: structure and phylogenetic significance. Entomol. Scand. Suppl. 1981; 15:299–304.

102. Kristensen NP, Nielsen ES. The *Heterobathmia* life history elucidated: Immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). Z. Zool. Syst. Evol. 1983; 21:101–24.

103. Kristensen NP, Scoble MJ, Karsholt O. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa. 2007; 1668:699–747.

104. Kunte K. Allometry and functional constraints on proboscis lengths in butterflies. Funct. Ecol. 2007; 21:982–87.

105. Kvello P, Almaas TJ, Mustaparta H. A confined taste area in a lepidopteran brain. Arthropod Struct. Dev. 2006; 35:35–45. [PubMed: 18089056]

106. Lee J-K, Selzer R, Altner H. Lamellated outer dendritic segments of a chemoreceptor within wall-pore sensilla in the labial palp-pit organ of the butterfly, *Pieris rapae* L. (Insecta, Lepidoptera). Cell Tiss. Res. 1985; 240:333–42.

107. May PG. Nectar uptake rates and optimal nectar concentrations of two butterfly species. Oecologia. 1985; 66:381–86.

108. Miles CL, Brooker R. The role of the frontal ganglion in the feeding and eclosion behavior of the moth *Manduca sexta*. J. Exp. Biol. 1998; 201:1785–98. [PubMed: 9576889]

109. Miller WE. Diversity and evolution of tongue length in hawkmoths (Sphingidae). J. Lepidop. Soc. 1997; 51(1):9–31.

110. Molleman F, Krenn HW, Van Alphen ME, Brakefield PM, DeVries PJ, Zwaan BJ. Food intake of fruit-feeding butterflies: evidence for adaptive variation in proboscis morphology. Biol. J. Linn. Soc. 2005; 86:333–43.

111. Nagnan-Le Meillour P, Cain AH, Jacquin-Joly E, Francois MC, Ramachandran S, et al. Chemosensory proteins from the proboscis of *Mamesta brassicae*. Chem. Senses. 2000; 25:541–53. [PubMed: 11015326]

112. Nielsen ES, Kristensen NP. The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera-Glossata. Invertebr. Taxon. 1996; 10:1192–302.

113. Nilsson LA. The evolution of flowers with deep corolla tubes. Nature. 1988; 334:147–49.

114. Nilsson LA. Deep flowers for long tongues. TREE. 1998; 13:259–60. [PubMed: 21238293]

115. Nilsson LA, Jonsson L, Rason L, Randrianjohany E. Monophyly and pollination mechanisms in *Angraecum arachnites* Schltr. (Orchidaceae) in a guild of long-tongued hawk-moths (Sphingidae) in Madagascar. Biol. J. Linn. Soc. 1985; 26:1–19.

116. O'Brien DM, Boggs CL, Flogel ML. Pollen feeding in the butterfly *Heliconius charitonia*: isotopic evidence for essential amino acid transfer from pollen to eggs. Proc. R. Soc. London Sci. Ser. B. 2003; 270:2631–36.

117. Ômura H, Honda K, Asaoka K, Inoue TA. Tolerance to fermentation products in sugar reception: gustatory adaptation of adult butterfly proboscis for feeding on rotting foods. J. Comp. Physiol. A. 2008; 194:545–55.

118. Paulus HF, Krenn HW. Vergleichende Morphologie des Schmetterlingsrüssels und seiner Sensillen: Ein Beitrag zur phylogenetischen Systematik der Papilionoidea (Insecta, Lepidoptera). J. Zool. Syst. Evol. Res. 1996; 34:203–16.

119. Pellmyr O. Yucca, yucca moths, and coevolution: a review. Ann. Missouri Bot. Gard. 2003; 90:35–55.

120. Pellmyr O, Krenn HW. Origin of a complex key innovation in an obligate insect-plant mutualism. Proc. Natl. Acad. Sci. USA. 2002; 99:5498–502. [PubMed: 11960006]

121. Penz CM. Higher level phylogeny of the passion-vine butterflies (Nymphalidae, Heliconiinae) based on early stage and adult morphology. Zool. J. Linn. Soc. 1999; 127:277–344.

122. Penz CM, Krenn HW. Behavioral adaptations to pollen-feeding in *Heliconius* butterflies (Nymphalidae, Heliconiinae): an experiment using Lantana flowers. J. Insect Behav. 2000; 13:865–80.

123. Petr D, Stewart KW. Comparative morphology of sensilla styloconica on the proboscis of North American Nymphalidae and other selected taxa (Lepidoptera): systematic and ecological considerations. Trans. Am. Entomol. Soc. 2004; 130(4):293–409.

124. Pola M, Garcia-Paris M. Marine puddling in *Papilio polytes* (Lepidoptera: Papilionidae). Fla. Entomol. 2005; 88(2):211–13.

125. Proctor, M.; Yeo, P.; Lack, A. The Natural History of Pollination. Harper Collins; London: 1996. p. 479

126. Ray T, Andrew CC. Ant butterflies: butterflies that follow army ants to feed on antbird droppings. Science. 1980; 210:1147–48. [PubMed: 17831470]

127. Salama HS, Khalifa A, Azmy N, Sharaby A. Gustation in the lepidopterous moth *Spodoptera littoralis* (Boid.). Zool. Jb. Physiol. 1984; 88:165–78.

128. Schiestl FP, Schlüter PM. Floral isolation, specialized pollination, and pollinator behavior in orchids. Annu. Rev. Entomol. 2009; 54:425–46. [PubMed: 19067636]

129. Schmitt JB. The feeding mechanism of adult Lepidoptera. Smithson. Misc. Coll. 1938; 97:1–28.

130. Scoble, MJ. The Lepidoptera Form, Function and Diversity. Oxford Univ. Press.; Oxford/New York: 1992. p. 404 Nat. Hist. Mus. Publ.

131. Sellier R. Étude ultrastructurale en microscopie électronique par balayage des organes sensoriels de la trompe des Lépidoptères rhopalocéres. Alexanor. 1975; 9:9–15.

132. Smedley SR, Eisner T. Sodium uptake by puddling in a moth. Science. 1995; 270:1816–17. [PubMed: 8525374]

133. Socha JJ, Westneat MW, Harrison JF, Waters JS, Lee W-K. Real-time phase-contrast x-ray imaging: a new technique for the study of animal form and function. BMC Biology. 2007; 5:6. [PubMed: 17331247]

134. Speidel W, Fänger H, Naumann CM. The surface microstructure of the noctuid proboscis (Lepidoptera: Noctuidae). Zool. Anz. 1995/1996; 234:307–15.

135. Städler E, Städler-Steinbrüchel M, Seabrock WD. Chemoreceptors on the proboscis of the female eastern spruce budworm. Mitt. Schweiz. Entomol. Ges. 1974; 47:63–68.

136. Stekolnikov AA, Korzeev AI. The ecological scenario of Lepidopteran evolution. Entomol. Rev. 2007; 87(7):830–39.

137. Stevenson RD. Feeding rates of the tobacco hawkmoths *Manduca sexta* at artificial flowers. Am. Zool. 1992; 31:57A.

138. Thien LB, Bernhardt P, Gibbs GW, Pellmyr O, Bergström G, et al. The pollination of *Zygogynum* (Winteraceae) by a moth, Sabatinca (Micropterigidae): an ancient association? Science. 1985; 227:540–42. [PubMed: 17733478]

139. Thom C, Geurenstein PG, Mechaber WL, Hildebrand JG. Floral CO_2 reveals flower profitability to moths. J. Chem. Ecol. 2004; 30(6):1285–88. [PubMed: 15303329]

140. Tillyard RJ. On the mouth-parts of the Micropterygoidea (Order Lepidoptera). Trans. Entomol. Soc. London. 1923; 1923:181–206.

141. Walters BD, Albert PJ, Zacharuk RY. Morphology and ultrastructure of sensilla on the proboscis of the adult spruce budworm, *Choristoneura fumifereana* (Clem.) (Lepidoptera: Tortricidae). Can. J. Zool. 1998; 76:466–79.

142. Wannenmacher G, Wasserthal LT. Contribution of the maxillary muscles to proboscis movement in hawkmoths (Lepidoptera: Sphingidae): an electrophysiological study. J. Insect Physiol. 2003; 49:765–76. [PubMed: 12880657]

143. Wasserthal LT. The pollinators of the Malagasy star orchids *Angraecum sesquipedale*, *A. soroium* and *A. compactum* and the evolution of extremely long spurs by pollinator shift. Bot. Acta. 1997; 110:343–59.

144. Wasserthal, LT. Verh. Westdsch. Entomol. Tag. Löbbecke-Museum; Düsseldorf: 2001. Anpassungen bei Sphingiden zur Vermeidung von Spinnen- und Fledermausattacken; p. 13-30. 2000

145. Whitfield JB, Kjer KM. Ancient rapid radiation of insects: challenges for phylogenetic analysis. Annu. Rev. Entomol. 2008; 53:449–72. [PubMed: 17877448]

146. Wiegmann BM, Regier JC, Mitter C. Combined molecular and morphological evidence on the phylogeny of the earliest lepidopteran lineages. Zool. Scr. 2002; 31:67–81.

147. Zaspel JM, Kononenko VS, Goldstein PZ. Another blood feeder? Experimental feeding of a fruitpiercing moth species on human blood in the Primorye Territory of far eastern Russia (Lepidoptera: Noctuidae: Calpinae). J. Insect Behav. 2007; 20:437–51.

SUMMARY POINTS

1. The evolution of the suctorial proboscis from biting-chewing mouthparts in adult Lepidoptera is one of the best-studied examples among flower-visiting insects.

2. The evolution of the proboscis is characterized by the formation of a food tube that is sealed by linking structures, by modifications of the sensory equipment, and by novel musculature. Each of these features can be reconstructed from the plesiomorphic condition of the tiny galeae in biting-chewing mouthparts that have been retained in some lineages.

3. In context with nectar feeding, the proboscis length may increase almost 100-fold; extremely long proboscises evolved in the families Sphingidae, Hesperiidae, and Riodinidae.

4. A primarily hydraulic mechanism uncoils the proboscis, whereas spirally recoiling is caused by the proboscis musculature in addition to cuticular elasticity.

5. A discontinuous flow of fluid is created by the cranial sucking pump, which allows uptake of quantities that approximate half the body weight in a single feeding event.

6. Repeated sequences of characteristic proboscis movements permit a butterfly to swiftly probe flowers, in particular on inflorescences.

7. Exploitation of additional or alternative food sources often is associated with modified proboscis movements and derived proboscis traits that display novel functional roles in the feeding mechanisms.
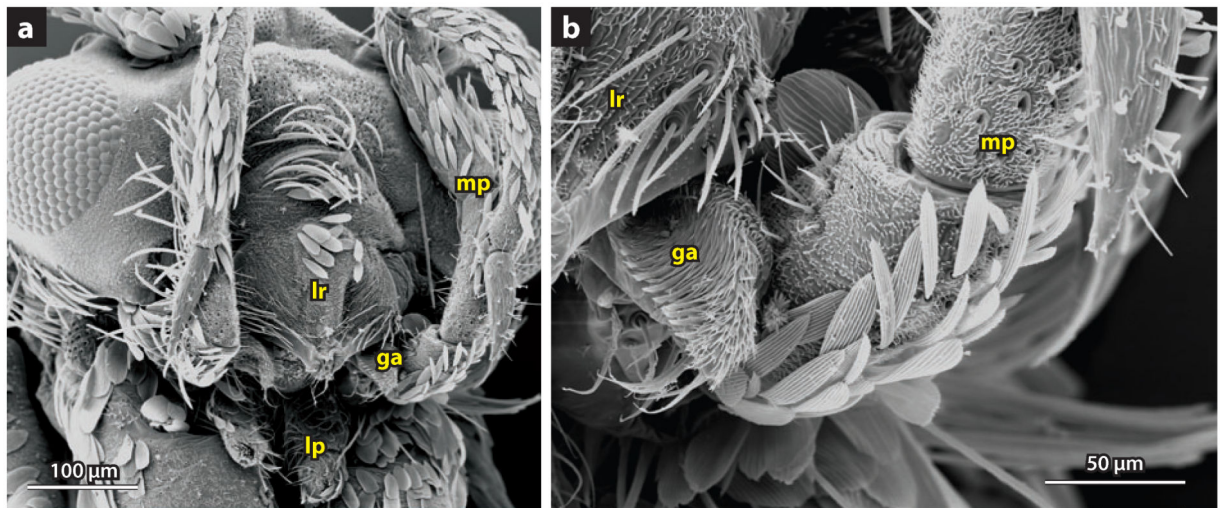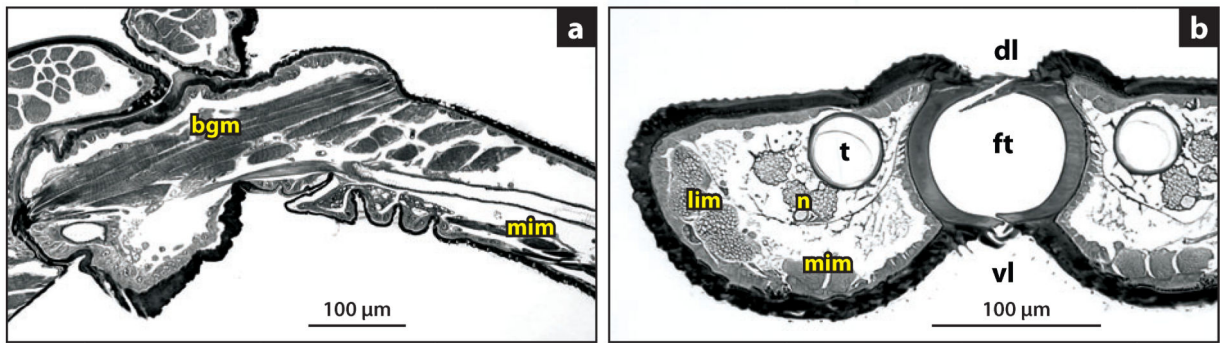
Figure 1.

Head of *Micropterix aruncella* (Micropterigidae) (scanning electron micrographs) illustrating the plesiomorphic biting-chewing condition of mouthparts in adult Lepidoptera. (*a*) The labrum (lr) covers the mandibles. The maxilla bears the galea (ga) and the five-segmented maxillary palp (mp). The labium bears a pair of two-segmented labial palps (lp). (*b*) Concave short galea (ga); apical segment of the maxillary palp (mp) is equipped with mushroom-shaped sensilla for the uptake of pollen grains.
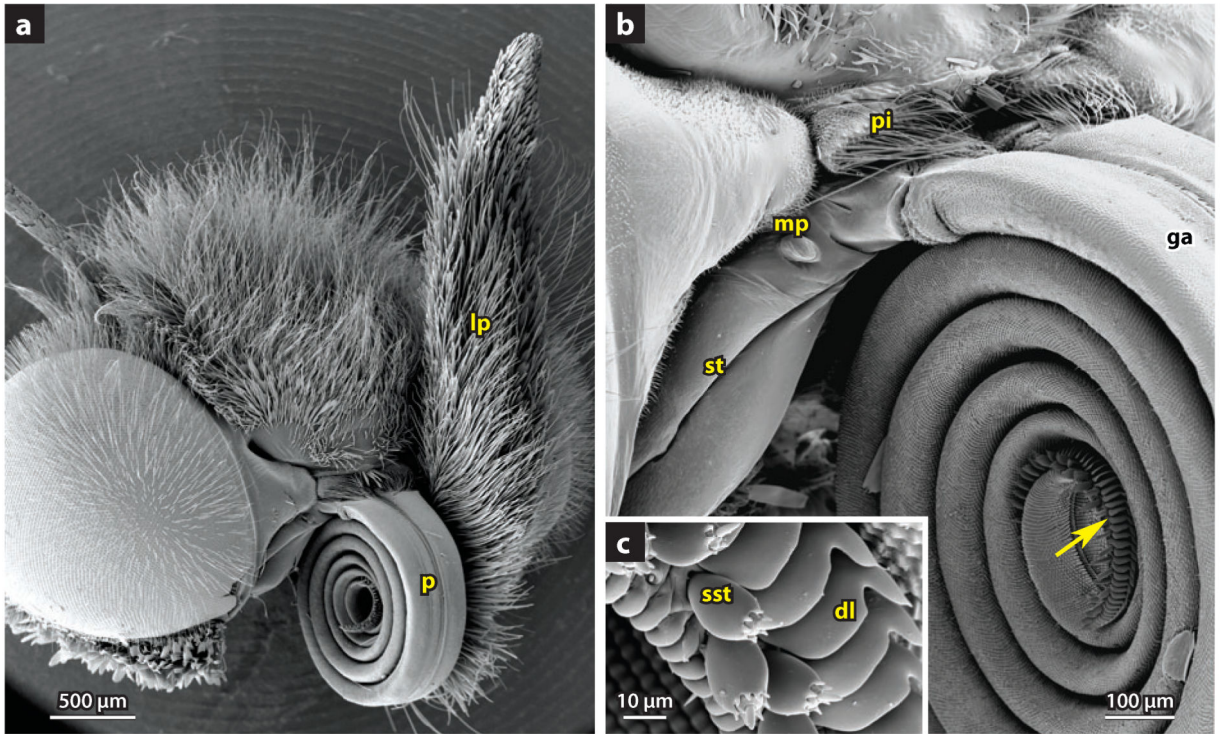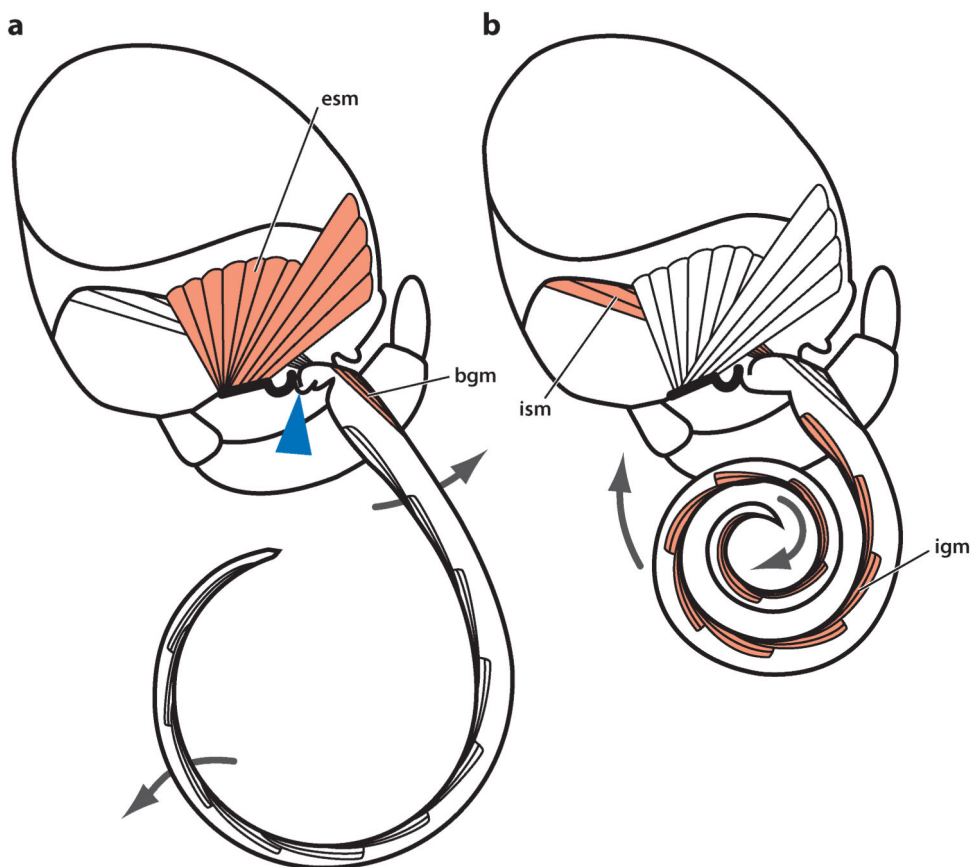
Figure 2.
Head of the butterfly *Vanessa cardui* (Nymphalidae) (scanning electron micrographs). (*a*) The proboscis (p) is coiled in the resting position; one labial palp (lp) is shown (the other one has been removed). (*b*) The pilifers (pi) contact the basal proboscis. The galea (ga) extends from the foldable stipes (st) and bears the minute maxillary palp (mp); the arrow points to tip region. (*c*) The tip region is characterized by sensilla styloconica (sst) and slits between the dorsal linking structures (dl).
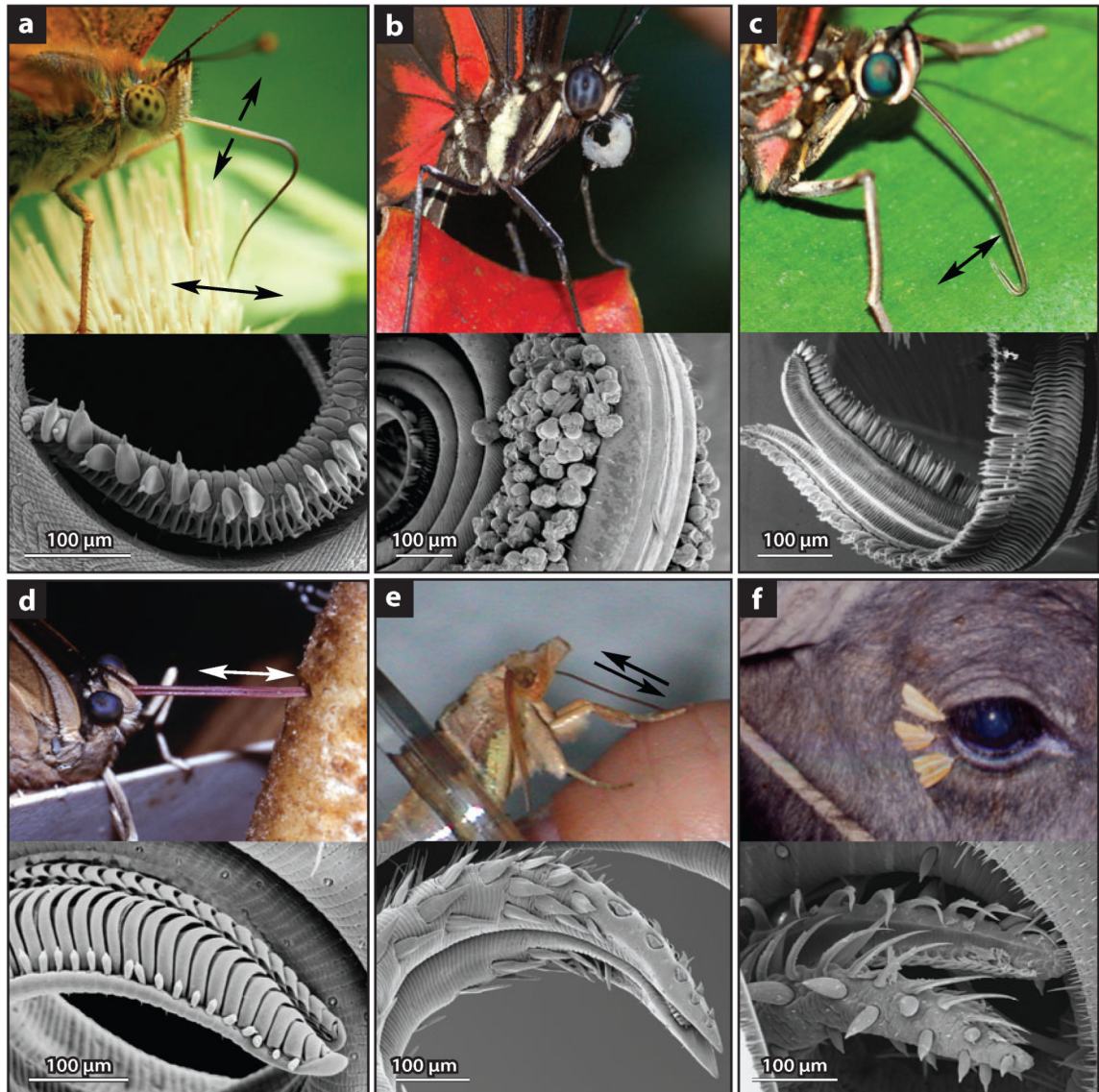
Figure 3.
Proboscis anatomy of the butterfly *Vanessa cardui* (Nymphalidae). (*a*) Longitudinal section through the basal joint region shows the basal galeal muscle (bgm) and the median intrinsic muscle (mim). (*b*) The lumen of the galea contains a trachea (t), nerves (n), and two series of muscles, the median intrinsic muscles (mim) and the lateral intrinsic muscles (lim). The food tube (ft) is closed by the overlapping dorsal linking structures (dl) and the ventral linking structures (vl), which are hooked with their counterparts.

Figure 4.
Functional mechanisms of the proboscis movements in Lepidoptera. Schematic illustration of a lateral view of an opened head. Arrows indicate direction of proboscis movement; contracted muscles are shaded red. (*a*) Hydraulic mechanism of proboscis uncoiling. External stipes musculature (esm) compresses the tubular part of the stipes (*blue arrowhead*) and pumps hemolymph into the attached galea. Basal galeal muscle (bgm) elevates the proboscis. (*b*) The coiling process involves contractions of the intrinsic galeal muscles (igm) and proboscis elasticity; contraction of internal stipes muscle (ism) flexes the proboscis into the resting position.

Figure 5.
Examples of Lepidoptera feeding on various food sources (arrows indicate proboscis movements) and corresponding characteristic proboscis morphology (scanning electron micrographs). (*a*) A nectar-feeding butterfly, *Argynnis paphia* (Nymphalidae), possesses a slender proboscis tip. (*b*) A pollen-feeding butterfly, *Heliconius pachinus* (Nymphalidae), with a load of pollen on the proboscis. (*c*) The nonflower-visiting butterfly *Morpho peleides* (Nymphalidae) uses a sweeping technique and a brush-shaped tip to feed from surfaces. (*d*) A fruit-piercing butterfly, *Archaeoprepona demophoon* (Nymphalidae), pushes its robust proboscis tip into fruit. (*e*) A piercing, occasionally blood-sucking moth, *Calyptra thalictri* (Noctuidae), employs antiparallel galeae movements (photo courtesy of J. Zaspel); the acute proboscis bears piercing armature. (*f*) The tear-feeding moth *Lobocraspis griseifusa* (Noctuidae) feeds from a buffalo's eye (photo courtesy of W. Buttiker); the proboscis tip is equipped with rasping structures.