

Review

Mouthparts of flower-visiting insects

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Received 12 July 2004; accepted 20 October 2004

Abstract

This review deals with the morphology and function of adult insect mouthparts modified to feed on nectar, pollen or petals. Specialization to nectar-feeding is evident in formation of proboscides of various lengths and designs. Proboscides of many Hymenoptera and Diptera function according to adhesion mechanisms that load nectar onto extensible apical mouthpart regions before fluid is conveyed along the food canal to the mouth by capillarity and suction. Predominantly suctorial proboscides evolved once in Lepidoptera, probably twice in Coleoptera, variously in some Hymenoptera and several times with similar design in Diptera. Many of them are particularly long and have sealed food tubes, specialized apical regions, new proboscis resting positions and modified feeding movements. Mouthparts of obligate pollen-feeding insects can be characterized by modified mandibles, specialized bristles for pollen manipulation and elaborate feeding movements. Often saliva is crucial for pollen retention and ingestion. In Coleoptera, intact pollen is gathered by sweeping movements of mouthparts; in Diptera, it is suspended in saliva prior to suction. Pollen is crushed by asymmetrical mandibles in aglossatan Lepidoptera and one group of basal Hymenoptera. Pollen-piercing mouthparts occur in Thysanoptera and one group of Diptera. Some butterflies and few Diptera extract nutrients from pollen by mixing it externally with saliva on their mouthparts. No mouthpart specializations to petal-feeding are reported in flower-visiting insects.

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Keywords: Mouthparts; Proboscis; Anthophilous insects; Nectar; Pollen; Feeding; Morphology; Evolution

1. Introduction

The majority of flower-visiting adult insects belongs to the bees, wasps, flies, butterflies, moths and certain beetles. They obtain nutrition from floral nectar and pollen and a few from petal tissue. Occasionally, adults from other orders (Table 1) also feed on floral food. In many instances they ensure the pollination of the plants they visit. In addition to food, flowers are frequented to collect fragrances, to seek shelter, prey, larval hosts and mates.

Insect–flower associations are multifaceted and can be examined from botanical, entomological, ecological or evolutionary viewpoints which are often summarized under the heading of pollination biology (e.g. Kevan and Baker, 1983; Paulus, 1988; Thompson, 1989; Heß, 1990; Proctor et al., 1996; Pellmyr, 2002; Lunau, 2004). Paleontological evidence indicates that the co-radiation of

major groups of specialized flower-visiting insects and angiosperms took place in the Cretaceous period (Grimaldi, 1999). This was preceded by evolution in the late Jurassic and early Cretaceous of angiosperm pollinating insects with generalized mouthparts (Labandeira, 1997, 2002). Adaptation to flower-visitation has led to behavioral and learning developments, elaborate sensory apparatuses (Barth, 1991; Lunau, 1996), increased flight abilities (Dudley, 2000) and morphological specialization of mouthparts. Comparative descriptions of various insect mouthparts are given in benchmark treatises of Weber (1933), Snodgrass (1935) and Matsuda (1965). Functional aspects of adult and larval mouthpart feeding are reviewed by Smith (1985) and Chaudonneret (1990). These works, however, do not focus on flower-visiting insects.

We review and attempt to synthesize current understanding of the form and functional mode of adult mouthparts in flower-visiting insects and to discuss aspects of convergent evolution to different floral foods regardless whether the insects achieve pollination or not.

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Table 1
Insect orders which contain representatives that feed on flowers

Insect orders	Food sources and feeding behavior	References
Collembola	Facultative nectar and pollen-feeding	Porsch, 1957; Kevan and Baker, 1983
Plecoptera	Nectar-feeding rarely observed	Porsch, 1957
Dermaptera	Various floral tissues	Porsch, 1957
Blattodea	Flower visiting rarely observed	Porsch, 1957
Orthoptera	Anthers and petal-feeding	Porsch, 1957; Schuster, 1974
Mantodea	Supplementary pollen-feeding of nymphs in <i>Tenodera</i>	Beckman and Hurd, 2003
Hemiptera	Nectar-feeding in few Lygaeidae	Rammer, 1942; Porsch, 1957
Thysanoptera	Piercing sucking of pollen and floral tissue	Hagerup, 1950; Hagerup and Hagerup, 1953; Kirk, 1984; Williams et al., 2001
Coleoptera	Pollen, nectar and tissue-feeding	Fuchs, 1974; Kevan and Baker, 1983; Proctor et al., 1996
Neuroptera	Obligate pollen-feeding in <i>Nemoptera</i>	Porsch, 1957; Popov, 2002
Hymenoptera	Nectar and pollen-feeding widespread, some collect pollen as larval food. Occasional petal-feeding	Kevan and Baker, 1983; Hanson and Gauld, 1995; Proctor et al., 1996; Jervis, 1998; Jervis and Vilhelmsen, 2000
Trichoptera	Nectar-feeding uncertain	Ulmer, 1905
Lepidoptera	Mostly only nectar-feeding; pollen-feeding is plesiomorphic; derived in Heliconiini	Norris, 1936; Gilbert, 1972; Scoble, 1992; Kristensen, 2003
Mecoptera	Nectar-feeding rarely observed	Porsch, 1957
Diptera	Nectar and pollen-feeding in many taxa	Downes, 1958; Kevan and Baker, 1983; Gilbert and Jervis, 1998; Larson et al., 2001

Bold letters indicate those taxa which contain obligatory flower-visiting species. Most cited references give overviews for the respective taxa.

2. Nectar-feeding

Two principal mechanisms are deemed responsible for the uptake of surface liquids or nectar from flowers (Kingsolver and Daniel, 1995) which are not mutually exclusive: adhesion and suction. Mouthparts, which function in accordance with the properties of adhesion and capillarity possess a wettable apical surface and perform licking, lapping, dapping or sponging movements to draw fluids into the mouthparts. Mouthparts which function according to a purely suctorial mode often have greatly elongated and tubular food canals to take nectar from flowers with long and/or narrow corolla tubes. These mouthparts generally remain motionless during feeding and suck nectar along a pressure gradient according to the principle of a soda straw.

The most common resource utilized by flower-visiting insects is nectar secreted from floral glands. Nectar varies in sugar concentration from 5 to 75% and contains glucose, fructose and sucrose, as well as various amounts of amino acids and other substances (Baker and Baker, 1983; Kevan and Baker, 1983; Dafni, 1992; Proctor et al., 1996). Flowers can be broadly grouped according to floral architecture and degree of nectar accessibility into those offering only pollen, those with exposed nectaries, partially hidden nectaries (bowl-shaped flowers or under a flap of petal tissue) and nectaries concealed at the base of long, narrow, tubular corollas (e.g. Heß, 1990; Patt et al., 1997; Jervis and Vilhelmsen, 2000). Some of the most spectacular nectar-feeding mouthparts are those associated with deep flower-tubes (e.g. Nilsson, 1988; Johnson and Steiner, 1997). Various elongate suctorial proboscides have independently evolved in species of Coleoptera, in many lineages of Hymenoptera and Diptera and within the glossatan Lepidoptera. These mouthparts are

appropriately labeled ‘concealed nectar extracting apparatuses’ (Jervis, 1998; Gilbert and Jervis, 1998). In addition to these highly specialized obligatory nectar-feeding insects many others are known to feed occasionally on floral nectar with unspecialized orthopteroid or with piercing/sucking mouthparts (Table 1).

2.1. Coleoptera

Anthophilous beetles from various families consume nectar, many in addition to pollen, from open flowers (Proctor et al., 1996). Their unspecialized mouthparts normally are prognathous (Kevan and Baker, 1983) and only slightly modified from the orthopteroid composition having bristles on the mandibles and setose maxillary and labial structures. Scarabaeid beetles load nectar using sweeping movements of setose maxillary structures in a manner resembling pollen collection (Johnson and Nicolson, 2001).

Meloidae from several taxa possess elongated mouthparts that are adapted for feeding from flowers with concealed and partially concealed nectaries (Handschin, 1929; Schremmer, 1961; Kaszab, 1962; Chaudonneret, 1990). In *Lepipalpus* a proboscis is composed of the greatly elongated 4-segmented maxillary palps (Handschin, 1929). The distal segments are densely covered with short setae on their median sides. During feeding they are brought together to form a median food canal, which extends further than the head. Proximally, setae from labrum, galea, lacinia and labium join together on the posterior side to form a continuation of the food tube leading to the mouth. The tip of the proboscis bears an apical sensory pad and a subapical organ with bottle-shaped sensilla. In the resting position the proboscis is flexed at the base of the first

maxillary palpal segment and lies under the body between the coxae reaching the abdomen (Handschin, 1929). The extreme development of the maxillary palps is extraordinary since in the related genera of Nemognathinae the galeae are modified into fringed structures. In the genera *Nemognatha*, *Gnathium* and *Zonitis* the galeae are filiform coming together in form of a sucking tube (Bologna and Pinto, 2001). The galeae are loosely connected to each other along their concave inner margins which are densely covered with bristles forming a pointed brush-like structure (Schremmer, 1961). In nectar-feeding Nemognathinae the galea measures 1.5–10 mm in length, in some the proboscis is longer than the body (Lovell, 1915; Kaszab, 1962). The short galeae are equipped with relatively long bristles while the long galeae which form a true food canal have short bristles (Kaszab, 1962). Detailed studies of proboscis morphology and function, as well as, flower handling in nectar-feeding Meloidae are lacking.

2.2. Hymenoptera

Most adult Hymenoptera obtain nourishment in liquid form as floral nectar (sometimes mixed with pollen), honeydew or host fluids, although the specific feeding habits of many remain undocumented. Flower-visiting behavior is found throughout the order in various taxa of sawflies (Megalodontesioidea, Tenthredinoidea and Cephoidea); Parasitica (Ichneumonoidea, Evanioidea, Chalcidoidea and Cynipoidea); Chrysidioidea and Aculeata (Tiphidae, Sapygidae, Mutillidae, Pompilidae, Formicidae, Scolidae, Vespidae, sphecid wasps and bees) (Kevan and Baker, 1983; Gauld and Bolton, 1988; Hanson and Gauld, 1995; Proctor et al., 1996; Quicke, 1997; O'Neill, 2001).

2.2.1. Composition of adult mouthparts

The mouthparts of Hymenoptera are insufficiently typified as biting/chewing. Although the mandibles retain this function, liquids are taken up with the slightly extensible, pre-oral organ known as the labiomaxillary complex. This feeding organ is probably a derived feature common to all Hymenoptera (Königsmann, 1976; Vilhelmsen, 1997) and occurs when the labium is united to the base of the maxillae rather than to the head capsule. The role of the orthognathous mandibles during feeding is generally secondary to that of the labiomaxillary complex (Schremmer, 1961; Spradbery, 1973; Quicke, 1997). In the first instance the mandibles ensure the emergence of the adult from the cocoon, brood cell or other site of pupation. They also serve manifold industrial functions—biting, tearing, shredding, chewing, grasping and manipulation of objects.

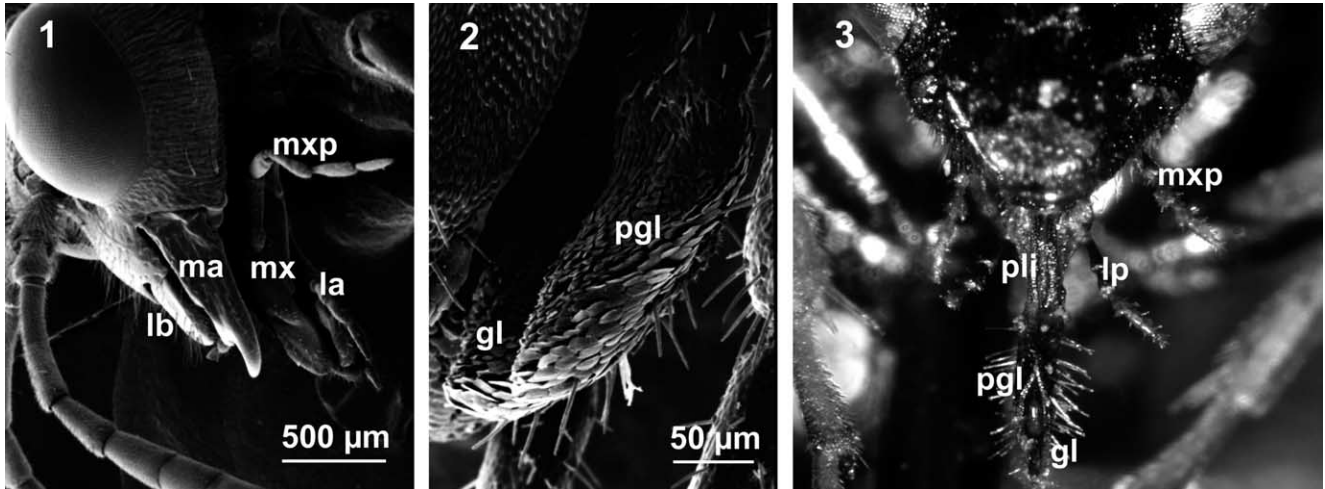
The actual feeding organ—the labiomaxillary complex is short and unspecialized in most Hymenoptera. It permits consumption of liquid food from more than one type of source such as host fluid, honeydew and/or nectar from flowers with open nectaries, e.g. umbels of Apiaceae (Jervis and Vilhelmsen, 2000). By far the most common

evolutionary adaptations of the labiomaxillary complex in Hymenoptera are those related to nectar-feeding. In some the feeding organ is drastically reduced, such as in the Siricidae, which reportedly do not feed as adults. Descriptive accounts of morphology and illustrations of the short and generalized labiomaxillary complex have been published for various 'Symphyta' (Demoll, 1909; Taylor, 1931; Arora, 1956; Matsuda, 1957; Schedl, 1991; Vilhelmsen, 1996; Jervis and Vilhelmsen, 2000), Parasitica (Hanna, 1935; Zaka-ur-Rab, 1978; Jervis, 1998) and Aculeata (Duncan, 1939; Richards, 1962; Gotwald, 1969; Bohart and Menke, 1976; Osten, 1982, 1988, 1991).

The basic feeding mode of the labiomaxillary complex in most Hymenoptera can be characterized as a combination of licking and sucking. Major steps in the feeding process are indicated in the following. The main body of the labiomaxillary complex protracts out of its resting place in the head cavity by turning of the cardines, which articulate with the head. Once protracted, the labium is suspended between the maxillae, which remain extended and more or less stationary. The ligula (glossa and paraglossae) produces a licking motion by repeated extension and retraction. An independent forward and backward motion of the entire labium probably coincides with and augments the motion of the ligula. When the labium is fully protracted, the ligula extends beyond the apical ends of the galeae. Its exposed and hairy surface initially contacts the food material (nectar loading). Retraction of the ligula brings the liquid adhering to it into the food conduction area or food canal where it is unloaded and conveyed further by capillarity, labial movements and suction force from the muscular cibarial or pharyngeal pumps.

The composition of the food canal, which leads to the actual mouth, changes along its course. Apically the floor of the canal is formed by the anterior hairy surface of the ligula and basally by the hypopharynx, which in Hymenoptera is secondarily connected with the prementum and extends from the mouth to the base of the glossa. The roof of the food canal is formed apically by blade-shaped galeae (and sometimes also laciniae) and basally it is closed by the epipharynx, a soft lobe on the under surface of the labrum. An infrabuccal pouch is formed in many Hymenoptera by an invagination of the hypopharynx in the basal region. It varies in size and significance and generally serves as a detritus and food compressor (Snodgrass, 1956; Vilhelmsen, 1996).

An outstanding feature of short and unspecialized mouthparts is the relative lengthiness of the maxillary palps. They consist maximally of six segments, are longer than the stipes and extend beyond the galea and glossa. In many taxa the palps dangle freely and are capable of movement even when the main body of the labiomaxillary complex is retracted into the fossa on the underside of the head. The palps are important as tactile and sensory outposts. They are well provided with muscles. Each of the first three segments of the maxillary palp contains at



Figs. 1–3. Examples of mouthpart variation in sawflies (scanning electron micrographs and light microscopy). Fig. 1. *Tenthredo* sp. (Tenthredinidae) head with partially exposed mouthparts, maxillary palp (mxp); labium (lb); maxilla (mx); mandible (ma); labrum (la). Fig. 2. *Tenthredo* sp. (Tenthredinidae) posterior and anterior surfaces of glossa (gl) and paraglossae (pgl) covered with scales. Fig. 3. *Euryus nitidus* (Pergidae) extended proboscis showing glossa (gl) and hairy paraglossae (pgl); grooved pre-ligular section (pli); maxillary palp (mxp); labial palp (lp).

least one pair of intrinsic muscles, e.g. in Tenthredinidae and Braconidae (Taylor, 1931; Matsuda, 1957; Zaka-ur-Rab, 1978). In Symphyta the paraglossae and glossa, which is usually larger, are often bulbous and lie together forming a single broad wettable surface (Figs. 1 and 2). In Parasitica and Aculeata the glossa alone may be broad or pointed and the paraglossae are often reduced in size or vestigial. The anterior surface of the glossa and paraglossae are covered with numerous transverse rows of hairs or sometimes scales which have hydrophilic properties (Vilhelmsen, 1996; Jervis and Vilhelmsen, 2000). Peg-like sensilla are commonly found on the ligula, inner galea, epipharynx, palps and other structures (Galic, 1971; Whitehead and Larsen, 1976; Michener and Brooks, 1984). Gustatory (pit) sensilla occur at the base of the glossa, at least in bees. The main organs of smell and taste in honeybees, however, are located on the forelegs and antennae (Whitehead and Larsen, 1976). In both sexes of several sawflies and woodwasps is a cluster of rod-like sensilla of unknown function near the tip of the labial palps, sometimes occurring in a shallow depression or cavity (Schedl, 1991; Vilhelmsen, 1996).

2.2.2. Formation of nectaring proboscides

The most frequent modification of the labiomaxillary complex is the formation of a proboscis for drinking nectar.

This is usually achieved by elongation of the main axis of the labiomaxillary complex. Occasionally, also the labrum (Fig. 27) or head capsule contribute dramatically to the elongation. The evolution of a proboscis serving predominantly for nectar intake has occurred more often than conventionally assumed in the Hymenoptera, as disclosed in the surveys by Jervis (1998) on the Parasitica and Jervis and Vilhelmsen (2000) on symphytan lineages. Examples among the Aculeata will prove to be no less abundant.

The labiomaxillary complex operates as a functional unit and its elongation generally encompasses multiple elements. Glossal elongation, for example, often occurs simultaneously with enlargement of the prementum, which contains the increased musculature needed to produce the licking movements of the glossa. Lengthening of the food canal may necessitate a conforming elongation of opposing structures. Often the middle and proximal sections of the proboscis (prementum, stipes, cardo, hypopharynx) are elongated and thus serve to increase the functional length of the proboscis, even if they do not always participate directly in the composition of the food canal. It may be noteworthy to mention that proboscis formation usually occurs at the expense of the maxillary palps which characteristically diminish in importance, size and proportion relative to the stipes and galea. Furthermore, they lose much of their

Figs. 4–17. Aspects of proboscis formation in bees (light microscopy, scanning electron micrographs and semithin sections; section method described in Pernstich et al., 2003). Fig. 4. *Agapostemon virescens* (Halictidae) proboscis with proximal section (prx) made up of cardines and hypopharynx, and middle section (med) composed of prementum and stipites; glossa (gl). Fig. 5. *Lasioglossum malachurum* (Halictidae) proboscis partly retracted; glossa (gl); prementum (pm); mandible (ma). Fig. 6. *Lasioglossum malachurum* (Halictidae) detail of partially retracted proboscis; glossa (gl); paraglossa (pgl). Fig. 7. *Lasioglossum malachurum* (Halictidae) apical region of glossa (gl) with bifid hairs. Fig. 8. *Melipona anthidioides* (Apidae) head with extended proboscis; closed mandibles (ma); overlapping galeae (ga); protruding glossa (gl). Fig. 9. *Melipona anthidioides* (Apidae) apical section of extended glossa (gl) with erected bristles; terminal segments of labial palps (lp) diverge at right angles from the glossa; galea (ga). Fig. 10. *Melipona anthidioides* (Apidae) glossal apex with hairy anterior surface of flabellum (fl); seta (s). Fig. 11. *Osmia cornuta* (Megachilidae) glossal apex with flabellum (fl) and seta (s), glossal hairs lie flat.

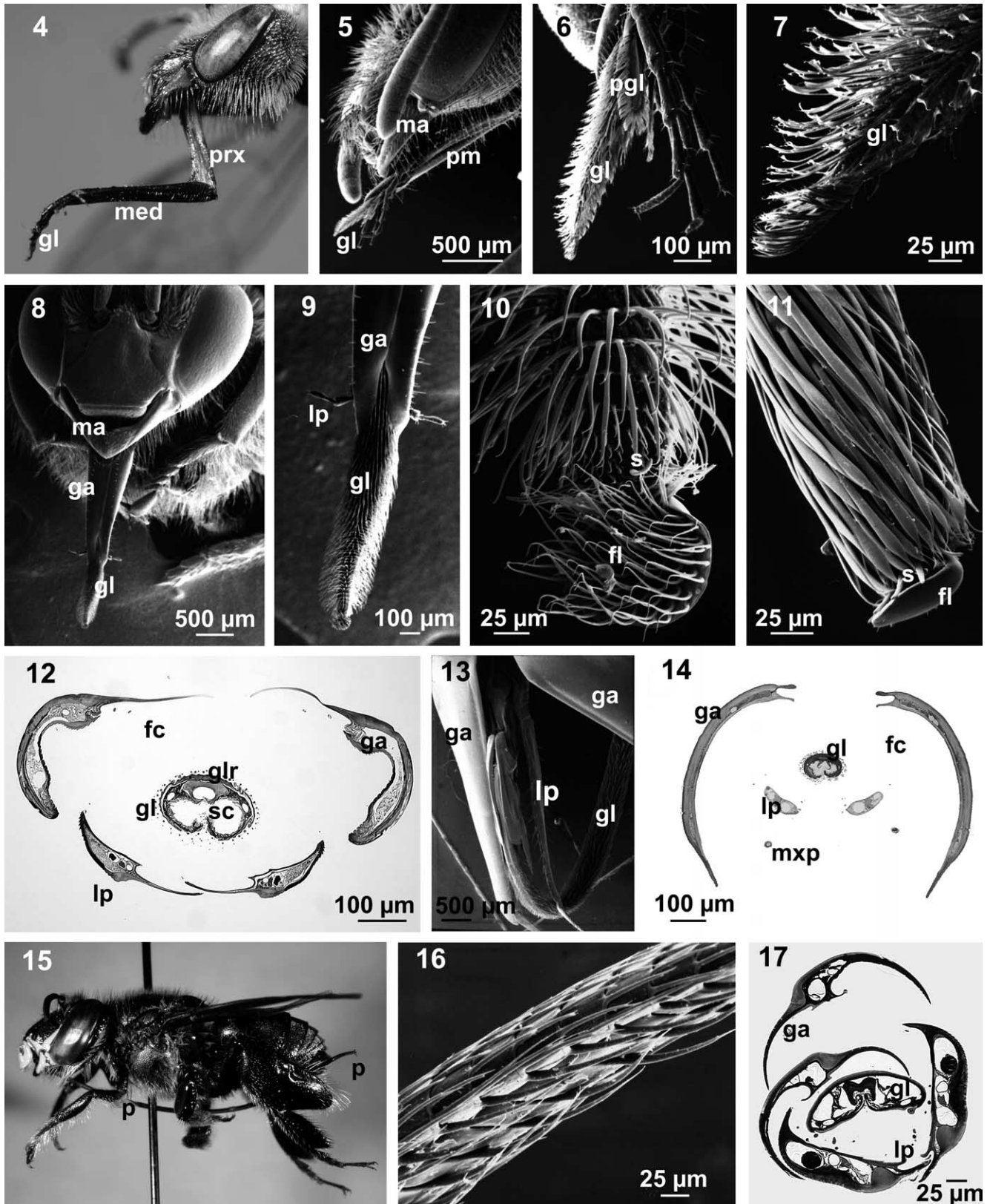


Fig. 12. *Bombus pratorum* (Apidae) cross-section of extended tongue; galea (ga); glossa (gl); glossal rod (glr); labial palp (lp); food canal (fc); 'salivary canal' (sc). Fig. 13. *Xylocopa* sp. (Apidae) proboscis with non-overlapping galeae (ga), right galea bent away to show base of glossa (gl) and labial palp (lp). Fig. 14. *Xylocopa* sp. (Apidae) cross-section of extended tongue; galea (ga); glossa (gl); maxillary palp (mxp); food canal (fc); labial palp (lp). Fig. 15. *Euglossa chalybeata* (Apidae) proboscis (p) retracted under body. Fig. 16. *Euglossa tridentata* (Apidae) non-bushy section of glossa. Fig. 17. *Euglossa tridentata* (Apidae) cross-section of tongue; galea (ga); glossa (gl); labial palp (lp); arrangement of parts does not represent a natural position.

musculature. Similarly, the labial palps become slender and small in relation to the glossa and undergo loss of muscles (Snodgrass, 1925; Matsuda, 1957; Zaka-ur-Rab, 1978).

From a morphological and functional point of view three categories of nectaring proboscides can be distinguished with reference to Hymenoptera, i.e. *short*, *long* and *extremely long*. In short proboscides a slight to moderate length is achieved (Figs. 25 and 26), the mode of feeding and general morphology deviate only little from unspecialized mouthparts. Proboscides which are long (Figs. 8, 27–29) to extremely long (Figs. 15 and 19) differ notably from unspecialized mouthparts with respect to composition of the elongation, design of the food tube, method of extension and retraction, feeding movements and mode of operation. Jervis (1998) and Jervis and Vilhelmsen (2000) distinguished eight types of mouthpart elongations in Hymenoptera based on the composition of the food canal. All elongated mouthparts were referred to as concealed nectar extraction apparatuses, although they are not always associated with or restricted to flowers with completely hidden nectaries. Here, nectaring proboscides in Hymenoptera are referred to as short, long or extremely long and then according to their composition.

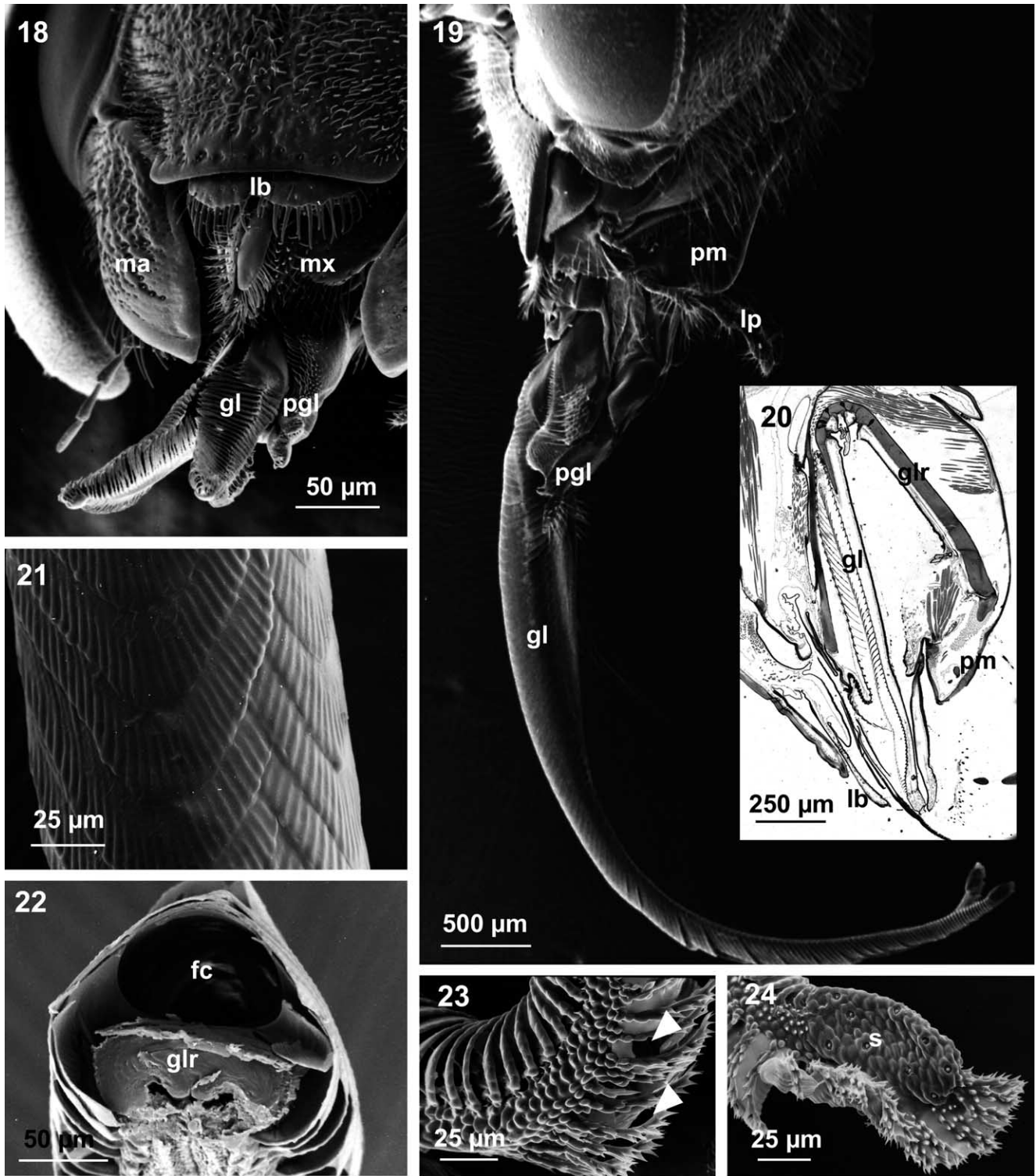
2.2.3. Short proboscides

A short proboscis is defined as slightly to moderately elongated, whereby the glossa is generally shorter than the prementum or about as long. The licking/sucking mode of feeding predominates. Nectar is loaded onto the exposed section of the glossa and passes along the food canal as in unspecialized mouthparts. The apex of the glossa is often narrow and pointed, however exceptions are known in which both the glossa and paraglossae present a broad wettable surface. Although detailed morphological and functional studies are generally lacking a short proboscis is evident in at least some members of about 35 genera of sawflies (Schedl, 1991; Jervis, 1998), e.g. *Megalodontes* (Megalodontesoidea), *Cephus* (Cephoidea) (Vilhelmsen, 1996), *Tenthredo* and relatives such as *Allantus*, *Cuneala*, *Elimora* and *Elimopsis* (Tenthredinoidea) (Plant, unpubl.). In the Parasitica at least 50 such genera can be enumerated (Jervis and Vilhelmsen, 2000) including *Gasteruption* (Evanoidea), *Polistomorpha* and *Leucospis* (Chalcidoidea) (Plant, unpubl.). The mouthparts within several genera of Braconidae (Ichneumonoidea) range from unspecialized to moderately elongated in either apical (glossa, paraglossae, galea) and/or basal regions (stipes, prementum, cardo) including intermediate forms (e.g. *Cardiochiles*, *Vipio*, *Bracon*, *Chelonus*, *Agathis*, *Agathirsia*) (Jervis, 1998). A preliminary survey of the Aculeata indicates that a short proboscis is found in at least some representatives of the following genera: Chrysididae: *Stilbum*, *Spinolia*, *Pseudochrysis*, *Euchrocos*, *Parnopes*, *Hedychridium*, *Omalus*, *Allocoelia*, *Pseudohexachrysis* (Plant, unpubl.); Tiphidae: *Meria*, *Hemithynnus*, *Myzinum* (Osten, 1982), *Elis* (Osten, 1988), *Epomidiopteron* (Osten, 1991), *Plesia*; Sapygidae:

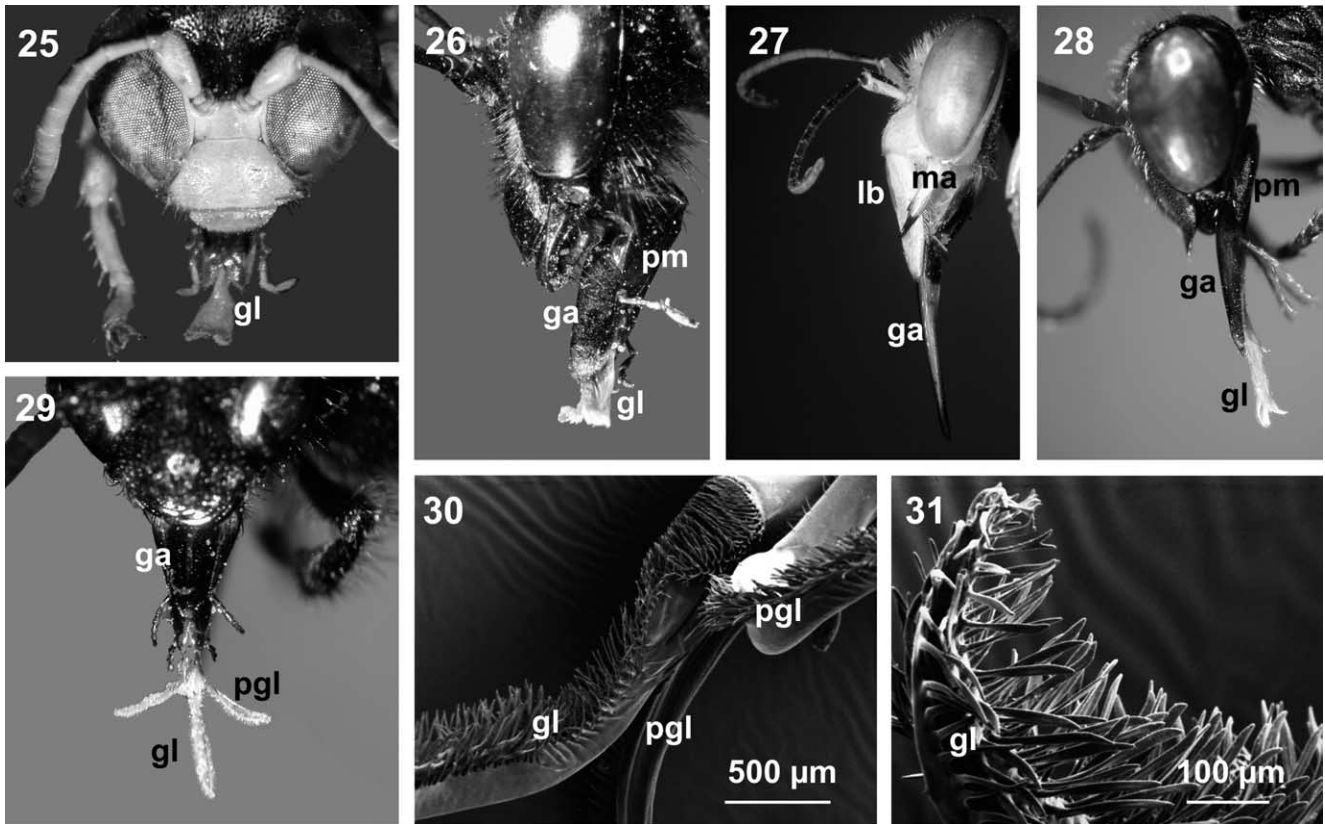
Sapyga (Osten, 1982), *Huarpa* (Hanson and Gauld, 1995), Pompilidae: *Anoplius*, *Episyron*, *Pepsis*, *Notocyphus* (Plant, unpubl.); Scoliididae: *Dasyscolia*, *Scolia* (Fig. 30), *Campsoscolia* (Osten, 1982); Vespidae: *Euparagia*, *Gayella*, *Paramasaris*, *Paragia* (Fig. 18) (Richards, 1962), *Priscomasaris* (Gess, 1998), *Vespula* (Duncan, 1939), *Vespa* (Demoll, 1909), *Eumenes* (Osten, 1982), *Ancistrocerus* (Richards, 1962), *Eustenogaster*, *Pterocheilus* and other eumenids (Plant, unpubl.); Sphecidae (Figs. 25–28): *Scepliphron*, *Dynatus*, *Sphex*, *Isodontia*, *Entomosericus* (Bohart and Menke, 1976), *Palmodes*, *Prinoyx*, *Stangeella* (Fig. 26), *Tachysphex*, *Oxybelus*, *Sphecius*, *Stizus*, *Bembecinus* (Fig. 25), *Bicyrtes*, *Philanthus*, *Tachytes* (Plant, unpubl.). Additionally all members of ‘short-tongued’ bees (Andrenidae, Colletidae, Melittidae and Halictidae) (Figs. 4–6) have, at least, a moderately developed nectaring proboscis. Although the glossa is typically short in these bees, the middle section of the proboscis, e.g. prementum, is elongated (Fig. 4).

The movements of the proboscis of the short-tongued bee *Andrena carlini* were filmed and described by Harder (1983). To feed, the bee unfolds the fully contracted proboscis to a functional feeding position by swinging it out of its resting space in the proboscidial cavity on the underside of the head. This is achieved by rotation of the cardines, which connect with the head capsule. The base of the proboscis is otherwise attached to the head by flexible membranes which become fully stretched. The galea, glossa and other parts must unfold from their rest position and straighten out before the proboscis can be deployed. A temporarily closed food canal is formed from the mouth to the tips of the galeae. Two licking movements of the labium are primarily responsible for liquid intake. The entire labium rapidly slides to and fro between the stationary maxillae, assisted by the rocking motion of the postmentum. Simultaneously, the glossa augments the lapping action of the labium by its own extension and retraction. The short and pointed glossa repeatedly plunges into the nectar, which adheres to its hairy anterior surface and passes into the food conduction area covered by the overlapping galeae. Nectar ascends the food canal to the mouth presumably by application of suction from the pharyngeal pump. The structure of the postmentum is critical for the motion of the labium (Plant and Paulus, 1987). In Halictinae and some Hylaeinae a simplified postmentum denies an independent licking movement to the labium as a whole. Instead the postmentum serves as an elbow joint flexing the particularly elongated proximal and middle sections of the proboscis. The proboscis in these bees is functionally elongated yet the galea and glossa typically remain short (Figs. 4–7).

The proboscis in social Vespidae such as *Polistes*, *Vespa* and *Vespula*, is not specialized for nectar-feeding but functions as a large licking apparatus to ingest fluids from masticated prey and a variety of other sources including floral nectar. The short and weakly bilobed glossa presents a



Figs. 18–24. Proboscis in pollen-wasps (Vespidae) (scanning electron micrographs and semithin sections; section method described in [Pernstich et al., 2003](#)). Fig. 18. *Paragia decipiens* head with extended proboscis; labrum (lb); mandible (ma); maxilla (mx); bifurcate glossa (gl) with bands of lamellae; paraglossa (pgl). Fig. 19. *Ceramius hispanicus* head and extended glossa (gl); prementum (pm); labial palp (lp); paraglossa (pgl). Fig. 20. *Ceramius hispanicus* sagittal section of retracted proboscis showing course of sclerotized glossal rod (glr); bunched up mantle of glossa (gl); prementum (pm); labrum (lb). Fig. 21. *Ceramius hispanicus* region of glossa showing system of overlapping lamellae. Fig. 22. *Ceramius hispanicus* section of broken off glossa revealing highly elastic glossal rod (glr) and food canal (fc) closed by overlapping lamellae. Fig. 23. *Ceramius hispanicus* section of bifurcated glossal arm for uptake of liquids (arrowheads). Fig. 24. *Ceramius hispanicus* sclerotized acroglossal button at tip of bifurcation; sensilla (s).



Figs. 25–31. Nectaring proboscides in sphecids and *Scolia* (light microscopy and scanning electron micrographs). Fig. 25. *Bembecinus pulchellus* (Sphecidae) head with extended proboscis; glossa (gl). Fig. 26. *Stangeella cyaniventris* (Sphecidae) head with extended proboscis; glossa (gl); galea (ga); prementum (pm). Fig. 27. *Bembix flavescens* (Sphecidae) head with elongated labrum (lb) and extended proboscis; galea (ga); mandible (ma). Fig. 28. *Ammophila* sp. (Sphecidae) head with extended proboscis; glossa (gl); galea (ga); prementum (pm). Fig. 29. *Scolia sexmaculata* (Scoliidae) head with extended proboscis; galea (ga); paraglossae (pgl) diverge at right angles to glossa (gl). Fig. 30. *Scolia* sp. (Scoliidae) only hairs at base of glossa (gl) are arranged in transverse rows; paraglossa (pgl). Fig. 31. *Scolia* sp. (Scoliidae) tip of glossa (gl) with cuticular hair-like projections.

broad wettable surface and executes scooping movements (Spradbery, 1973).

2.2.4. Long and extremely long proboscides

The formation of long to extremely long proboscides (Table 2) is characterized by innovation and variation in design of the food tube, in methods of extension and retraction, in storage positions and feeding movements. The principal mode of nectar intake, namely lapping/sucking, may increasingly give way to a purely suctorial feeding mode (e.g. long tongued pollen wasps, *Euglossa*) or to one characterized by broad sweeping movements (e.g. *Scolia*). We generally regard a hymenopteran proboscis as long when the length of the glossa is greater than the prementum and as extremely long when the extended proboscis is longer than the head. The definition depends on relative lengths, not absolute measurements. In some cases the glossa is not the predominately elongated structure. For example, in *Nipponorhynchus* the enormously long and rigid proboscis is mostly formed by the prementum, stipites and possibly laciniae (Jervis and Vilhelmsen, 2000). The opposing surfaces of the stipites and prementum are concave

and align together so that they form a closed food tube on each side of the prementum. The remaining parts—glossa, paraglossae, galeae, palps—are not particularly modified, except the hypopharynx which extends over the glossa and may therefore be involved in nectar loading. Mechanisms for retraction and storage of proboscis are uncertain. The uniquely constructed nectaring proboscis in some species of the sawfly *Eurys* is also difficult to classify. In *Eurys laetus*, *E. rutilans* (Jervis and Vilhelmsen, 2000; Schedl, 1991) and, to a lesser extent, *E. nitidus* (Fig. 3) (Plant, unpubl.) the glossa, paraglossae and other parts (galeae, stipites, prementum, ligula and pre-ligula area) are only moderately elongated. Together, however, they permit considerable extension of the labium. The feeding mechanisms are not fully understood. Possibly the maxillae remain tucked in near the head during feeding and nectar adhering to the outstretched ligula is unloaded between the galeae in a scooping motion when the labium retracts.

In Aculeata an extremely long proboscis is found for example in *Raphiglossa*, *Psiloglossa* (Vespidae) (Plant, unpubl.) and several species of *Parnopes* (Chrysididae) (Bohart and Kimsey, 1982; Plant, unpubl.). The long and

slender food tube is formed by the galeae, which encase the linear glossa. During rest the proboscis cannot be retracted fully under the head and lies for the most part under the thorax sometimes extending to the hind coxae or further.

In ‘long-tongued’ bees, Megachilidae and Apidae (classification after Michener, 2000), the food tube consists of elongated galeae and labial palps which align together to form a temporary canal completely ensheathing the linear and hairy glossa (Fig. 12). This condition is also found in some ‘short-tongued’ bees, such as the Panurginae and Rophitinae, except that the first two segments of the labial palp are usually not flattened or trough-like as in most ‘long-tongued’ bees. The galeae overlap each other along their posterior margins. This mechanism enables the food canal to easily vary in width. In carpenter bees, *Xylocopa*, however, the posterior galeal margins fit into each other tongue-and-groove style. The bee uses its robust galeae as a wedge to force entry into flowers and to perforate flowers for nectar-robbing (Schremmer, 1972). The galeae amply enclose and protect the labial palps and glossa (Figs. 13 and 14).

The honeybee, *Apis mellifera*, is the first insect whose mouthparts were illustrated and described with aid of a compound microscope, published documents date back to the year 1625 (Freedberg, 2002). Morphology and function have been extensively investigated, in particular by Snodgrass (1956). As in other long-tongued bees nectar is ingested by a licking/sucking mode. Prior to actual feeding, the honeybee unfolds the completely contracted proboscis to the initial functional feeding position. The galeae, labial palps and glossa assemble themselves into a temporarily formed food tube. During feeding the maxillae remain relatively motionless while the labium rapidly and repeatedly performs two licking movements. Much as in *Andrena*—the entire labium slides back and forth by rotation of the postmentum; simultaneously the glossa protracts and retracts by muscles attached to the base of the glossa. The movements of the glossa are divided into a three-phased licking cycle by Kingsolver and Daniel (1995): (1) glossal extension, during which nectar is loaded onto the wettable exposed surface of the glossa, (2) glossal retraction, during which nectar is drawn into the food tube and (3) unloading of nectar in the tube to be sucked into the mouth by action of the pharyngeal pump. The principal organ of fluid loading is thus the long and flexible glossa. Its surface is covered by transverse rings each bearing long stiff hairs; the rings or annuli are separated by intervals of looser membrane. Variation in shape and density of the glossal hairs are evident in long-tongued bees (Michener and Brooks, 1984). For example, in *Anthophora* and *Eucera* the glossal hairs at least in the latter half of the glossa are oar-shaped and flat, thus increasing the wettable surface area (Proctor et al., 1996). The glossa is internally reinforced along its entire length by the conspicuous and elastic glossal rod (Fig. 12); the hair-fringed groove of the glossal rod and the internal glossa canal were designated the salivary

channel of the tongue by Snodgrass (1956). However, in a rarely cited paper Simpson and Riedel (1964) showed that by placing a color stain over the salivary orifice of a honeybee, copious amounts of saliva flow down the outside of the glossa. When the galeae and labial palps were experimentally held back, saliva would accumulate over the edges of the paraglossae; however, it would not travel down the glossa. It is thus not necessary to postulate the existence of an extra channel for saliva descent inside the glossa. The authors further showed that bees alternate between periods of wetting the food with saliva and sucking.

Erection of glossal hairs in long-tongued bees, such as *Apis*, *Bombus* and *Anthophora*, is postulated to contribute to nectar loading (Snodgrass, 1956; Simpson and Riedel, 1964). When the glossa is fully extended the membrane between each row is stretched and the bristles in the apical half of the glossa spread out (Figs. 8–10). They flatten when tension is relaxed and the glossa is retracted (Fig. 11). The glossa thus expands when immersed into liquid and when retracted food is squeezed off of it (nectar unloading) by the pressure of surrounding walls of the food canal. Two separate retractor muscles effect hair erection and flattening.

The glossa retracts by a partial coiling at the base of the glossal rod into the apical region of the prementum (Snodgrass, 1956; Simpson and Riedel, 1964). In *Anthophora* the coiling of the glossal rod is particularly strong, while in other long-tongued bees, such as *Osmia*, it is less obvious (Plant, unpubl.). When stored and not in use, only the base of the glossa is retracted, the rest bends under the outside of the prementum so that the glossa together with the labial palps are pointing backward and covered by the folded-back galeae (Figs. 15 and 17).

Bumblebee feeding has been examined by high-speed film for *Bombus pennsylvanicus* workers (Harder, 1982). The licking movements are refined, in contrast to *Andrena* and *Apis*; the entire labium no longer contributes to the licking motion, but remains stationary. The glossa alone is repeatedly projected into the liquid food and retracted into the food tube. If nectar is just beyond the reach of the extended glossa, the bumblebee however can protract its prementum lending a greater reach to the entire labium. The shape of the postmentum augments this protraction (Plant and Paulus, 1987).

Orchid bees (Euglossini) have switched to a suction mode of feeding (Borrell, 2003). Their mouthparts are extremely long compared to body size. They range from 5 to 30 mm long and are thus among the longest in bees (Kimsey, 1982; Roubik, 2004). The proboscis cannot be fully retracted under the head; it lies between the coxae on the ventral side of the thorax and in *Euglossa* sometimes extends beyond the tip of the abdomen (Fig. 15). Unlike other long-tongued bees, the glossa is considerably less hairy (Fig. 16) (Michener and Brooks, 1984). The components of the food canal appear to mechanically interlock (Fig. 17). When taking up liquids, the proboscis and glossa are fully extended and remain stationary, as

Table 2
Occurrence of long to very long proboscides and their compositions in Hymenoptera

Taxa	Elongated parts								References
	Glossa	Paraglossa	Galea	Labial palp	Max. palp	Lacinia	Stipes	Prementum	
Tenthredinoidea									
Tenthredinidae, Selandriinae	<i>Nipponorhynchus</i>					+	+	+	Schedl, 1991; Jervis and Vilhelmsen, 2000
Pergidae, Euryinae	<i>Eurys laetus, rutilans</i>	+	+	+			+	+	Schedl, 1991; Jervis and Vilhelmsen, 2000
Pergidae, Euryinae	undetermined species				++				Houston, 1983
Ichneumonoidea									
Braconidae, Braconinae	<i>Bracon</i> sp.				++				Jervis, 1998
Braconidae, Cheloninae	<i>Chelonus longipalpis</i>				++				Jervis, 1998, also <i>C.hungaricus, palpator</i>
Braconidae, Cardiochilinae	<i>Cardiochiles minutus</i>	++							Jervis, 1998
Ichneumonidae, Banchinae	<i>Agathilla bradleyi</i>	++							Jervis, 1998
Ichneumonidae, Labeninae	<i>Cerionotus monticola</i>	++							Jervis, 1998
Ichneumonidae, Ophioninae	<i>Agathophiona fulvicornis</i>	++							Jervis, 1998
Braconidae, Agathidinae	<i>Agathis nixonii</i>	++		++	++				Jervis, 1998, also <i>Agathirsia</i> sp.
Braconidae, Cheloninae	<i>Chelonus rostratus</i>	+			+				Jervis, 1998
Braconidae, Agathidinae	<i>Agathis longipalpus</i>				++				Jervis, 1998
Aculeata									
Sphecidae, Ammophilinae									
	<i>Ammophila</i>	+		+					Ulrich, 1924; Osten, 1982
	<i>Podalonia, Eremnophila</i>	+		+					Plant, unpubl.; (most species)
Vespidae, Eumeninae	<i>Zetha</i>	+	+	+					Plant, unpubl.
Sphecidae, Sphecinae	<i>Prinox</i>	+	+	+					Plant, unpubl.
Sphecidae, Bembicinae	<i>Bembix, Bicyrtes</i>	+	+	+					Plant, unpubl.
Sphecidae, Bembicinae	<i>Stizus lineata</i>	+	+	+					Plant, unpubl.
Chrysididae	<i>Parnopes grandior, fischer</i>	++		++					Plant, unpubl.
Vespidae, Eumeninae	<i>Rhagiglossa, Psiloglossa</i>	++		++					Plant, unpubl., Mediterranean species
Sphecidae, Bembicinae	<i>Steniolia, Zyzzyx chilensis</i>	++		++					Plant, unpubl., e.g. <i>S.longirostris, obliqua</i>
Vespidae, Masarinae	Masarina	++							Krenn et al., 2002
	<i>Metaparagia</i> (Paragiina)	++							Carpenter, 1996
Scoliidae	Scoliinae, Campsomerinae	+	+			+	+	+	Osten, 1982; Plant, unpubl.
Bees									
Colletidae, Xeromelissinae	<i>Chilimelissa, Xeromelissa</i>				+		+	+	Plant, unpubl.
Andrenidae, Andreninae	<i>Andrena violae</i>	+							LaBerge, 1986
Melittidae	<i>Pseudophilanthus</i>	+							Michener, 1981; e.g. <i>P. tsavoensis</i>
Colletidae, Hylaeinae	<i>Palaeorhiza papuana</i>	+							Michener, 1965 (males only)
Halictidae, Rophitinae	<i>Dufourea longiglossa</i>	+							Ebmer, 1993
Halictidae, Nomiinae	<i>Lipotriches testacea</i>	+							Pauly, 1984
Halictidae, Halictinae	<i>Ariphanarthra palpalis</i>							+	Eickwort, 1969
Colletidae, Euryglossinae	<i>Euthesma tubulifera</i>							++	Houston, 1983
Colletidae, Hylaeinae	<i>Hylaeus (Pseudhylaeus)</i>							++	Michener, 1965; Houston, 1983
Colletidae, Colletinae	<i>Niltonia virgilia</i>				++				Laroca et al., 1989
Colletidae, Colletinae	<i>Leioproctus filamentosus</i>			++ ^a	++				Laroca et al., 1989
Apidae, Megachilidae	most species	+		+	+				Michener, 1944; Winston, 1979
Halictidae, Rophitinae	many species	+		+	+				Michener, 1965
Andrenidae, Panurginae	species of several tribes	+		+	+				Michener and Brooks, 1984
Andrenidae, Andreninae	<i>Andrena micheneriana</i>	+		+	+				LaBerge, 1978
Andrenidae, sePanurginae	<i>Perdita hurdi</i>	++		+			+	+	Hurd and Linsley, 1963
Andrenidae, Panurginae	<i>Neffapis, Nolanomelissa</i>	++			++				Rozen and Ruz, 1995; Rozen, 2003
Megachilidae	Lithurgini	++		++	++				Plant, unpubl.
Apidae	Euglossini, Anthophorini	++		++	++				Also, <i>Melitoma</i> (Emphorini)

Proboscis components particularly elongated (+), greatly elongated (++). Not included are cardo, subgalea, labrum and head which in some cases are elongated. Taxa listed may contain exceptions or may not include all examples.

^a Filaments of galea.

shown by a video film study of *Euglossa imperialis* (Borrell, 2003). Nectar is capable of ascending the enormously long food tube by capillarity and suction force. Whether other bees (e.g. *Lithurgus*, *Melitoma* or the Anthophorini) with extremely long mouthparts, which are also held against the ventral thorax when not in use, feed primarily by suction, is not known.

A proboscis can be characterized by elongation of a single structure rather than a combination of multiple components as is common in Hymenoptera. For example, the glossa alone may be enormously long relative to the prementum and galea (which themselves may be slightly enlarged). In several Ichneumonoidea (Jervis, 1998) the glossa is exposed for much of its length and modified to serve as its own food canal, in that the deeply bifid lobes align together to form a temporary food tube. A predominantly glossal proboscis is also found in many pollen-wasps (Masarinae, Vespidae) (Fig. 19) (Richards, 1962; Carpenter, 1996). This unique proboscis has been studied from functional-anatomical and evolutionary points of view (Schremmer, 1961; Osten, 1982; Krenn et al., 2002). In the apical bifid section of the glossa, each glossal lobe contains its own food tube, which is an arch-way formed by hair-like cuticular structures of the posterior glossa. In the non-bifid section of the glossa, the food canal is formed by overlapping arched lamellae of the anterior surface (Figs. 21 and 22). The lamellae are arranged in transverse rows and are present even in ancestral taxa of Masarinae with a short glossa (e.g. *Priscomasaris*, Gess, 1998) and are most likely homologous with glossal hairs. Nectar drawn into the food canals of the glossal lobes merges into the central food canal of the non-bifid glossa (Figs. 22–24). Further ingestion occurs by suction, licking movements are not apparent. Particularly modified is the region between the glossa and prementum containing several large lingular sclerites (Richards, 1962). They are responsible for the initial protraction of the glossa and subsequent retraction. The problem of storing the enormous glossa is solved by forcing the glossal rod to the back of the prementum, while much of the mantle covering of the glossa formed by the rows of lamellae bunches together and does not retreat as deeply as the glossal rod (Fig. 20) (Krenn et al., 2002). This design appears to limit glossal length to about twice that of the prementum. Greater glossal lengths are achieved in the subtribe Masarina, e.g. *Celonites* and others, by storing the glossal rod in a special sac which protrudes out the back end of the proboscis over the prosternum (Schremmer, 1961). Interesting is the convergent development of a glossal proboscis within a second clade of pollen-wasps, *Metaparagia* (Carpenter, 1996). It is similarly retracted deep into the prementum and the lingular sclerites are well-developed as in *Paragia* but the composition and functioning of the food canal is not known.

In only a few species of bees is the glossa extremely long and exposed for much of its length while the remaining parts of the proboscis remain unmodified from their respective

genera, i.e. *Perdita hurdi*, *Andrena violae*, *Pseudophilanthus tsavoensis* and males of *Palaeorhiza papuana* (Hurd and Linsley, 1963; Michener, 1965, 1981; LaBerge, 1986). In females of the latter the glossa is unmodified, short and truncate. How the extremely long glossa serves to load and conduct nectar, and the position it assumes when retracted, are not known.

In some Hymenoptera only the maxillary palps are greatly elongated for nectar-feeding (Jervis, 1998). They form a drinking tube by closely aligning their flattened or concave inner margins. Nectar may be drawn up the entire length of the palps by capillary force and conveyed further by lapping motions of the glossa and by suction force (Jervis and Vilhelmsen, 2000). Although some Symphyta and Parasitica feed on nectar with enormously long maxillary palps, most examples occur in colletid bees. In *Chilimelissa* and *Xeromelissa* the maxillary palps possibly align during feeding. In particular, segments two and three are laterally flattened and hairy (Plant, unpubl.). They could form a functional extension to the glossa, which is short and apically truncate. In *Euhesma tubulifera* the very long maxillary palps are channeled on their inner surfaces and cohere to form a tube to extract nectar (Houston, 1983; Jervis, 1998). An extremely long proboscis that is formed mostly by the labial palps is found in a small number of Hymenoptera. Most examples stem from colletid bees. The inner surfaces of certain segments may be deeply concave or compressed. When brought together they form a functional feeding-tube. Whether nectar is taken by suction or capillarity force is not known.

An entirely unique structure for nectar intake is found in the colletid *Leioproctus filamentosus* (Michener, 2000). The proboscis itself resembles that of other *Leioproctus* except that the labial palps are modified to long, slender filament-like strands and combine with several strands of enormous, filament-like setae arising from the galea to form a pencil of filaments. Possibly, nectar would be drawn by capillary action along the filaments until it reaches the glossa. It has been suggested that the particular morphology of the colletid glossa is associated with its functioning as a brush to apply a secretion to the wall of the brood chamber (McGinley, 1980; Michener, 1992). If true, the importance of nest construction as a secondary function may act as an evolutionary constraint keeping the glossa short and broad in female Colletidae. There are no records of elongated glossae among colletid females. It should be noted, however, that in some colletids (Diphaglossinae, *Colletes nasutus*) the bifid arms of the glossa are long and brushy, yet the short basal region of the glossa retains the special appearance typical for colletid females (Plant, unpubl.).

Feeding and mouthpart function has been described for various Scoliididae, in particular *Megascolia maculata* and compared to other Aculeata by Osten (1982, 1988, 1991). Although the proboscis is relatively long (Fig.

29), it can be used on flowers with open and unconcealed nectaries such as umbels of Apiaceae. When feeding the glossa and paraglossae rapidly protract and retract. At full extension, they are entirely exposed and the paraglossae diverge off laterally. The anterior surfaces of both structures are densely covered with peg-like cuticular projections (Figs. 30 and 31). On retraction the paraglossae converge, sweeping nectar and pollen toward the glossa. Food is caught between glossa and paraglossae and adheres to their special hairs. The glossa and paraglossae are about as long as the prementum and during retraction they are pulled straight back into a deep pocket within the prementum. The galeae are remarkably short. During feeding the maxillary and labial palps are in constant motion.

2.3. *Trichoptera*

The mouthparts of adult Trichoptera are normally weakly developed but in some species of Plectrotarsidae, Kokiriidae and Stenopsychidae they are adapted for ingestion of liquid food by formation of an elongated proboscis (Ulmer, 1905; Chaudonneret, 1990; Neboiss, 1991). In some genera, which probably exhibit flower-visiting behavior, the proboscis is considerably longer than the head. In *Plectrotarsus* the head forms a rostrum and both the labrum and labium are greatly elongated (Ulmer, 1905). In the South African *Dipseudopsis* (Dipseudopsidae) the proboscis seems to be formed by distal parts of the maxillae which enclose a median food groove and which are annulate on the external side (Ulmer, 1905). The morphology of these mouthparts has been investigated only in dried museum specimens and the manner in which they are used to extract nectar is poorly understood.

2.4. *Lepidoptera*

2.4.1. *Mouthpart morphology*

All adult Lepidoptera except those of the three most basal taxa possess a coilable proboscis which is predominantly composed of the elongated galeae (Fig. 32). It is the feeding organ used for sucking up fluids and is regarded as synapomorphic for the Glossata (Kristensen, 1984, 1998). The remaining mouthparts play a less direct role in feeding. The labrum is represented only by a short plate which covers the dorsal base of the proboscis (Fig. 33). The mandibles and laciniae are vestigial or absent. The basal elements of the maxilla (stipes and cardo) are fused together; their inner cavities and attached muscles form a hemolymph pump (Fig. 43). The stipes bear the maximally 5-segmented maxillary palp and articulate with the galeae on the frontal side to form the basal joint of the proboscis (Fig. 33). The two galeae interlock dorsally and ventrally to enclose the food canal (Figs. 35 and 44). The concave inner surface of each galea forms one half of the food canal allowing fluid uptake along a pressure gradient (Kingsolver and Daniel,

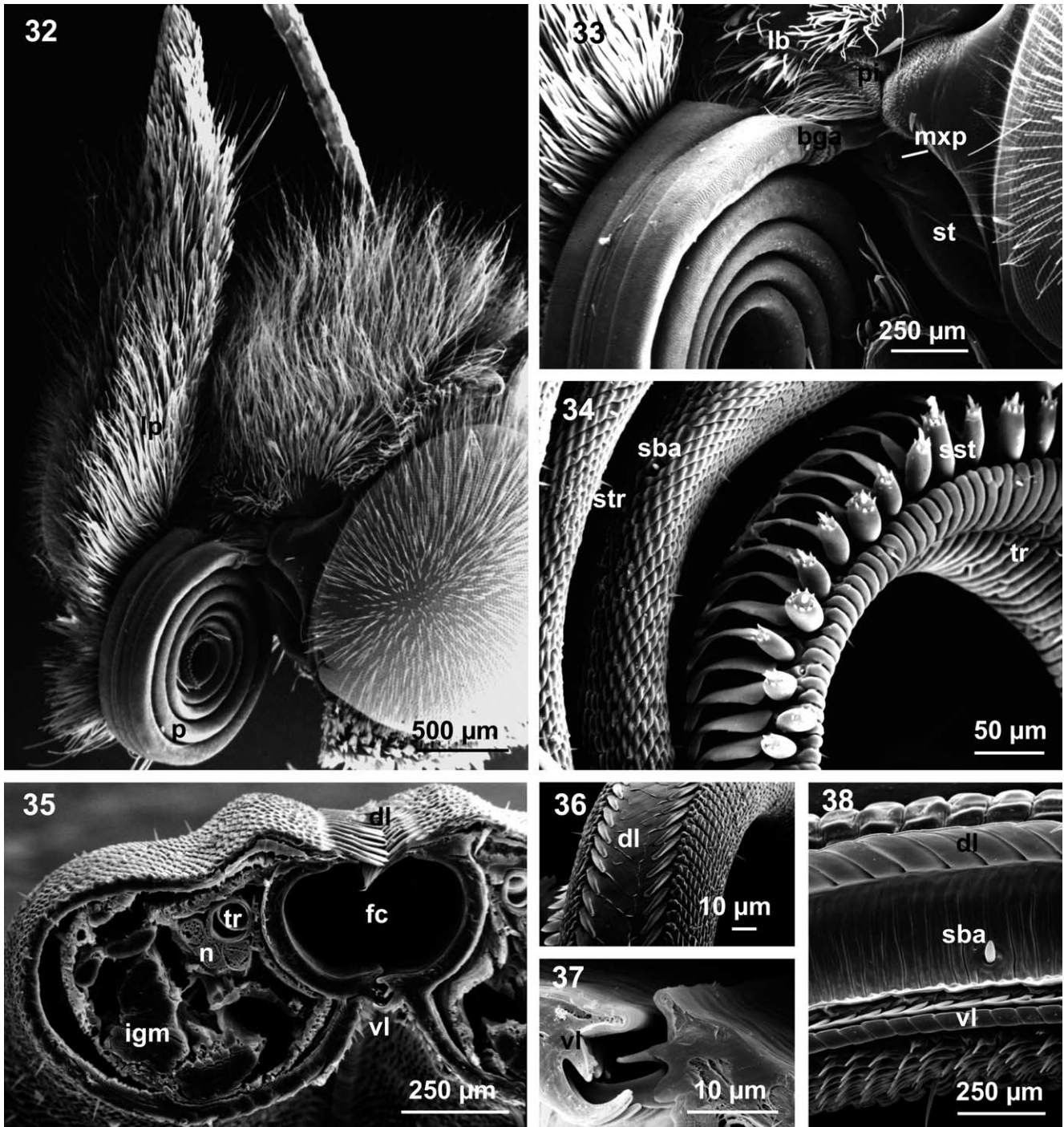
1995) created by the cibarial sucking pump (Eastham and Eassa, 1955; Kristensen, 1968a; Eberhard and Krenn, in press). The labium is flat and bears the 3-segmented labial palps which are densely covered with bristles and sensory setae (Fig. 32) (Faucheux and Chauvin, 1980a; Zwick, 2001). A basal area of microtrichia, the basalfleck (Reuter, 1888) presumably keeps the coiled proboscis in its resting position (Fig. 44). At the tip of each labial palp is an assemblage of sensilla in a cavity (Faucheux and Chauvin, 1980a; Lee et al., 1985; Bogner et al., 1986; Faucheux, 1991a, 1999). General proboscis morphology has been studied under various aspects in monotrysian Glossata (e.g. Tillyard, 1923; Philpott, 1927; Kristensen, 1968a,b; Kristensen and Nielsen, 1981a; Davis, 1986; Nielsen and Kristensen, 1996; Krenn and Kristensen, 2000, 2004), in Ditrysia (e.g. Schmitt, 1938; Pradhan and Aren, 1941; Rammert, 1993; Krenn and Kristensen, 2000, 2004) and, in particular, in many Rhopalocera (true butterflies) (e.g. Breitenbach, 1882; Eastham and Eassa, 1955; Vasudeva, 1956; Chaudonneret, 1990; Krenn, 1990, 1998, 2000; Paulus and Krenn, 1996; Krenn and Mühlberger, 2002). A recent review of the lepidopteran mouthpart anatomy in phylogenetic context is given by Kristensen (2003).

The only exception to the typical formation of a single food canal in fluid-feeding Lepidoptera, is the double-tubed proboscis of Neopseustidae, monotrysian moths whose feeding habits are not known. In this group each galea forms a separate food canal resulting in two independent sucking tubes which are interlocked by rows of conspicuous cuticle processes (Kristensen and Nielsen, 1981b).

2.4.2. *Nectaring proboscis*

The mouthparts of the basal groups of Glossata are used for intake of water and non-floral plant fluids which is regarded as the ancestral diet of Glossata (Downes, 1968; Kristensen, 1968a, 1984). Plesiomorphic characters of the galea of Glossata include a microtrichiated external galeal wall and the spinose galeal linking structures on the dorsal and ventral margins of the smooth plates of the food groove. Sensory equipment comprises a few sensilla trichodea on the external galea and uniporous sensilla basiconica on both the external galea and the median food groove (Krenn and Kristensen, 2000). Extrinsic muscles extend between the stipes and the basal galeal joint and are present in all Glossata while the intrinsic galeal musculature characterizing the Myoglossata evolved in context with elongation of the galeae prior to nectar-feeding behavior (Kristensen and Nielsen, 1981a; Krenn and Kristensen, 2004).

Nectar-feeding behavior is reported for the Incurvarioidea and Ditrysia which comprise about 98% of lepidopteran species (Pellmyr, 1992; Kristensen, 2003). The long proboscis of nectarivorous Lepidoptera has a number of features, which evolved in context with nectar intake and flower handling. These include a tightly sealed food canal, a specialized tip region, novel sensory equipment, complexly textured galeal wall and modified intrinsic galeal



Figs. 32–38. Suctorial mouthparts of butterflies (scanning electron micrographs). Fig. 32. Head of *Vanessa cardui* (Nymphalidae) with proboscis (p) in spirally coiled resting position, labial palp (lp) has been removed on left side. Fig. 33. Labrum and basal parts of maxilla of *Vanessa cardui* (Nymphalidae); triangular labrum (lb) covers entrance into sucking pump; its lateral lobe, pilifer (pi), bears long bristles which touch the proboscis base. Stipes (st) bears the one-segmented maxillary palp (mxp) and is adjoined to the basal galeal region (bga). Fig. 34. Lateral view of coiled proboscis of *Vanessa cardui* (Nymphalidae); tip region (tr) is characterized by slits leading into food canal and by rows of sensilla styloconica (sst). Ripped lateral galeal wall bears bristle shaped sensilla trichodea (str) and short blunt-tipped sensilla basiconica (sba). Fig. 35. Cross section of the proboscis of *Vanessa cardui* (Nymphalidae); galeae are interlocked dorsally (dl) and ventrally (vl) enclosing the central food canal (fc). Lumen of each galea contains two series of intrinsic galeal muscles (igm), nerves (n) and tracheae (tr). Fig. 36. Dorsal linking structures, dorsal legulae (dl) of *Polyommatus icarus* (Lycaenidae); rows of cuticular platelets alternating overlap and form fluid tight linkage of the galeae. Fig. 37. Ventral legulae (vl) of *Vanessa cardui* (Nymphalidae) extend from ventral galea wall; hook shaped cuticular structures firmly interlock with those of the opposite galea. Fig. 38. Median side of the galea of *Melitaea cinxia* (Nymphalidae); food canal (fc) composed of vertically arranged smooth plates bearing sensilla basiconica (sba) which project into food canal; dorsal margin shows one row of dorsal legulae (dl), ventral side shows double row of ventral legulae (vl); ventral galeal wall has microtrichia.

musculature (Krenn and Kristensen, 2000, 2004). These indispensable features of nectar-feeding Glossata have been mainly studied in Macrolepidoptera, in particular in the Rhopalocera (Figs. 32–38).

2.4.2.1. Length of proboscis. The proboscis varies considerably in length, the longest is found in the sphingid moth, *Amphimoea walkeri* (Amsel, 1938). With a length of 280 mm it represents the longest known sucking device in insects. In European butterflies proboscis lengths range between 4.9 and 17 mm (Paulus and Krenn, 1996). In true butterflies the longest is reported in *Eurybia* (Riodininae) (De Vries, 1997) measuring up to 45 mm (Krenn, unpubl.). The proboscis tapers progressively to the tip, while the diameter of the food canal remains nearly unchanged (Krenn, 2000; Krenn and Mühlberger, 2002).

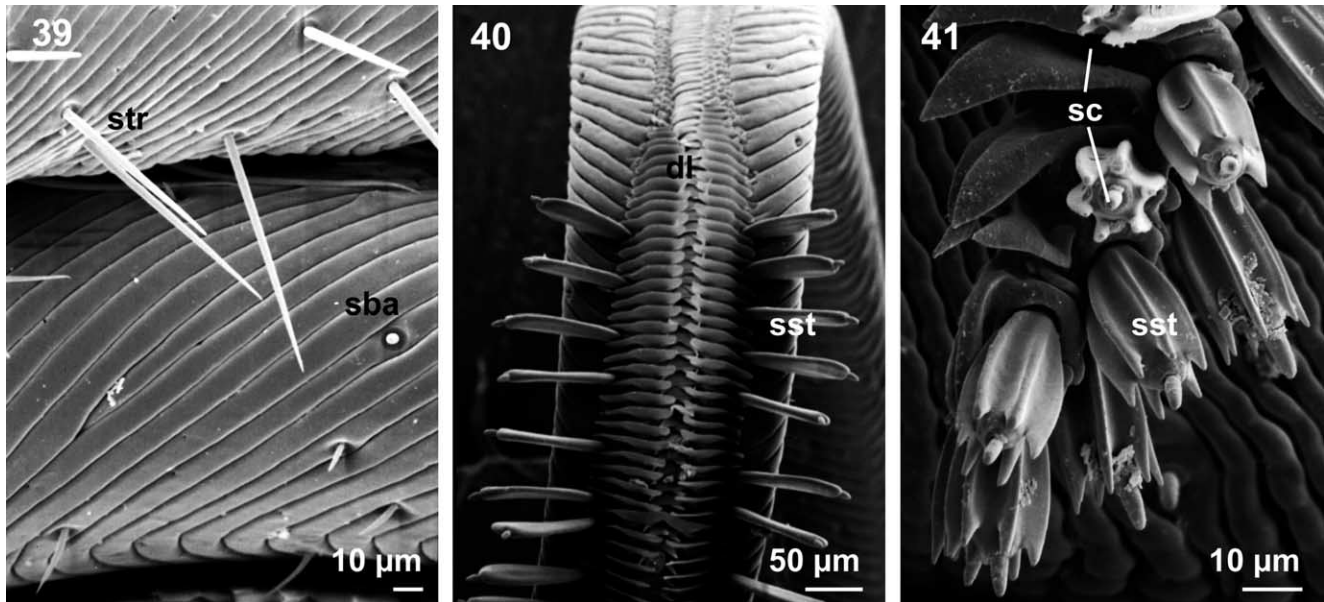
2.4.2.2. Composition of food canal. The intake of nectar with an enormously long proboscis requires a completely sealed food canal (Fig. 35). The galeae are permanently linked by interlocking rows of cuticular structures, called legulae (Davis, 1986) on the dorsal/anterior (Fig. 36) and ventral/posterior sides (Fig. 37) (Eastham and Eassa, 1955; Hepburn, 1971; Krenn and Kristensen, 2000). The dorsal legulae are flat, lancet-shaped, extend horizontally from the dorso-median galeal wall and closely overlap with those of the opposite galea (Fig. 36) (Eastham and Eassa, 1955; Hepburn, 1971; Krenn and Kristensen, 2000). Glandular cells described in *Pieris brassicae* were interpreted to produce a secretion that may serve to ensure the tight sealing of the galeae (Eastham and Eassa, 1955). The slender ventral legulae extend in two rows below the food groove and interlock with their counterparts on the opposite galea (Figs. 37 and 38). In most Ditrysia the processes of the lower row are modified into blunt hook-shaped structures which engage with similar hooks on the opposite side (Fig. 37) (Hepburn, 1971; Krenn and Kristensen, 2000).

The galeae develop separately from each other in the pupae. In nymphalid butterflies the food tube is assembled by a distinct sequence of galeal movements that can only occur within a short period after emergence from the pupae. This procedure is irreversible and the galeal interlocking is finalized by hardening of the cuticle (Krenn, 1997).

2.4.2.3. Tip region. A distinct apical region is recognizable in all Glossata by the modified dorsal legulae (Paulus and Krenn, 1996; Krenn and Kristensen, 2000). The single dorsal legulae are remarkably curved and interlock at their tips with those of the opposite galea. Due to their curvature and extension they form slits between them, which allows fluid intake into the otherwise tightly sealed food canal (Figs. 34 and 40). One row of these slits is found on the dorsal side of each galea in the tip region which makes up 5–20% of total proboscis length in Rhopalocera (Paulus and Krenn, 1996; Krenn and Penz, 1998; Krenn et al., 2001). Thus there is no apical opening of the food canal, the intake-

slits of the tip-region must be immersed in fluid prior to sucking.

2.4.2.4. Sensory equipment. The morphology of sensilla on the proboscis has been studied in various nectar-feeding Lepidoptera (e.g. Goldware and Barnes, 1973; Städler et al., 1974; Sellier, 1975; Faucheux and Chauvin, 1980b; Altner and Altner, 1986; Baker and Chan, 1987; Faucheux, 1978, 1991a,b, 1995, 1999; Paulus and Krenn, 1996; Walters et al., 1998; Krenn, 1998; Krenn and Kristensen, 2000). In context with nectar-feeding, novel sensory equipment evolved which includes three kinds of sensilla and the pilifers near the proboscis base (Krenn and Kristensen, 2000). (1) Bristle-shaped sensilla trichodea (sensilla chaetica of Faucheux, 1999) are scattered over the external galeae usually becoming shorter toward the tip of the galea. Presumably they function as mechanoreceptors (Fig. 39) (e.g. Städler et al., 1974; Faucheux, 1991b; 1999; Krenn, 1998). (2) The rather short sensilla basiconica are arranged in longitudinal rows on the external sides and in the food canal (Figs. 34, 38 and 39). They are composed of a short socket and a dome or peg-shaped sensory cone of various lengths (Faucheux and Chauvin, 1980b; Altner and Altner, 1986; Krenn, 1998; Walters et al., 1998; Faucheux, 1991b, 1999). The sensilla possess two to four sensory cells whose dendrites extend into the cone to a single terminal pore (Krenn, 1998; Walters et al., 1998; Faucheux, 1999). Multiporous sensory cones are found in Adelidae and Pyralidae (Faucheux, 1995; 1999). To judge by their ultrastructural features, they probably have a contact-chemoreceptive function (Städler et al., 1974; Krenn, 1998; Faucheux, 1999). Walters et al. (1998) propose a bimodal chemo-mechanical function. (3) Sensilla styloconica are restricted to the external galeae of Incurvarioidea, Palaephatoidea and Ditrysia and probably evolved in context of nectar-feeding (Krenn and Kristensen, 2000). They are composed of a long, variously sculptured shaft (or stylus) and a shorter terminal sensory cone (Figs. 34, 40 and 41) (e.g. Städler et al., 1974; Sellier, 1975; Altner and Altner, 1986; Paulus and Krenn, 1996; Walters et al., 1998; Krenn, 1998; Faucheux, 1999). They are arranged in rows in the distal half of the proboscis (Fig. 40) where they may extend beyond the terminal end of the galea (Fig. 41). In the Rhopalocera these sensilla are restricted to the tip region (Paulus and Krenn, 1996). The plesiomorphic shape of the stylus is characterized by several longitudinal ribs which form apical spines around the terminal uniporous sensory cone (Fig. 41) (Krenn and Kristensen, 2000). Numerous apomorphic sensilla shapes have been described in Rhopalocera (Figs. 34 and 40) (Sellier, 1975; Paulus and Krenn, 1996; Krenn et al., 2001), in Geometridae and Noctuidae (Möller, 1986; Büttiker et al., 1996). In Sphingidae the smooth and short sensilla styloconica are located in pits (Faucheux, 1999). They are sensitive to various mono- and oligosaccharids and a variety of other substances (Salama et al., 1984; Blaney and Simmonds,



Figs. 39–41. Proboscis sensilla of butterflies (scanning electron micrographs). Fig. 39. Bristle shaped sensilla trichodea (str) of various lengths on lateral side of the proboscis of *Dryas julia* (Nymphalidae) function as mechanosensilla, sensilla basiconica (sba) as contact chemosensilla. Fig. 40. *Dryas julia* (Nymphalidae), rows of flat sensilla styloconica (sst) in tip region; sensilla styloconica are combined contact chemo–mechanosensilla; extended dorsal legulae (dl) form slits in the food canal. Fig. 41. Terminal end of a galea of *Brintesia circe* (Nymphalidae); plesiomorphic shape of sensilla styloconica (sst) features longitudinal ribs and spines around the uniporous sensory cone (sc).

1988). In contrast to the diversity of external morphology, the sensilla in all examined species contain three to four sensory cells whose dendrites mostly extend to a terminal pore of the sensory cone, yet one leads to a tubular body at the base of the cone (Altner and Altner, 1986; Walters et al., 1998; Krenn, 1998; Fauchaux, 1999). Presumably sensilla styloconica are bimodal chemo–mechanosensilla (Altner and Altner, 1986; Krenn, 1998; Walters et al., 1998; Fauchaux, 1999). In an arctiid moth, Altner and Altner (1986) found a second subtype with additional wall pores on the sensory cone. These multiporous sensilla styloconica are assumed to be involved in the specialized feeding behavior of this moth.

The distribution pattern of proboscis sensilla can be interpreted in connection with food localization and flower-probing. Bristle shaped sensilla trichodea may serve to monitor the diameter of the corolla and the depth of proboscis insertion. Chemosensitive sensilla provide information on the presence of nectar inside the food tube as well as externally. The combined mechano–chemosensitive sensilla styloconica in the tip region are crucial for detecting the opening of the corolla tube. Once the proboscis is inserted into the corolla, they may serve to localize the nectar source using chemical and mechanical cues (Krenn, 1998).

In nectar-feeding Lepidoptera bristles arising from the lateral lobes of the labrum, the pilifers, make contact with the proboscis near the basal joint (Fig. 33) (Davis, 1986; Fauchaux, 1991a; Krenn, 1998; Krenn and Kristensen, 2000). Since the bristles are innervated, they probably serve

as mechanoreceptors involved in perception of proboscis movements relative to the head (Fauchaux, 1991b; Krenn, 1998). Their function is indicated by the fact that tineid moths and monotrysian moths with a well-developed proboscis, generally possess normal pilifer setae, while reduction of the proboscis is accompanied by various stages of pilifer reduction (Davis, 1986; Robinson and Nielsen, 1993). The proprioceptive function of the sensilla might be an adaptation to flower-handling (Krenn and Kristensen, 2000), an alternative functional hypothesis, however, suggests that the bristles maintain the two halves of the galeae together (Chaudonneret, 1990). The auditory role of the pilifers in Sphingidae (Roeder, 1972; Göpfert and Wasserthal, 1999) is regarded to be derived.

2.4.3. Proboscis functioning

The functioning of the proboscis can be explained by the action of various maxillary muscles and the elastic properties of the cuticle (Schmitt, 1938; Eastham and Eassa, 1955; Bänziger, 1971; Krenn, 1990, 2000; Wannemacher and Wasserthal, 2003).

2.4.3.1. Resting position and galeal wall composition. In the resting position the proboscis is coiled between 3.5 and 7 times depending on its total length (Fig. 32) (Krenn, 1990). The coils are tightly packed and touch each other for the entire length. The coiled proboscis is held between the setose labial palps and contacts the labium on the ventral side of the head (Fig. 44) (Krenn, 1990). The complexly textured wall confers to the proboscis the elastic properties

necessary to loosely coil it about 1.5–3.5 times (Bänziger, 1971; Krenn, 1990). The convex dorsal, lateral and ventral sides of the galea are composed of alternating dark and light cuticle which gives it an annulated appearance in many Macrolepidoptera (Fig. 45). The lightly colored cuticle was interpreted as flexible endo- and mesocuticle within which the darkly colored and hard exocuticular ribs are embedded (Hepburn, 1971). The shape and arrangement of the sorts of cuticle vary from continuous longitudinal bands—mainly on the dorsal side with transverse rings of dark cuticle running from the lateral to the ventral side—to single dark patches of various shapes (Fig. 45) (Paulus and Krenn, 1996). The external surface shows distinct ribs (Figs. 34 and 39) which may bear hairs or spine-like cuticular processes (Fig. 38) (Krenn, 1990; Speidel et al., 1995/96; Paulus and Krenn, 1996). The concave food canal wall is composed of smooth semicircular cuticular plates which are vertically fluted in many species (Fig. 38) (Paulus and Krenn, 1996; Krenn and Kristensen, 2000).

2.4.3.2. Proboscis uncoiling and stipes pump. Prior to feeding, the proboscis uncoils primarily due to a hydraulic mechanism (Schmitt, 1938; Bänziger, 1971). To a minor degree the elastic properties of the proboscis help to unwind the coiled proboscis (Krenn, 1990). During the uncoiling process the proboscis is elevated at the basal joint while it uncoils in several stepwise movements (Fig. 42A) (Krenn, 1989, 1990). Extension of the basal joint lifts the proboscis due to the extrinsic galeal muscles which extend between the stipes sclerite and the dorsal/anterior wall of the joint region (Eastham and Eassa, 1955; Bänziger, 1971; Krenn, 1990; Krenn and Mühlberger, 2002; Wannemacher and Wasserthal, 2003). The stepwise uncoiling is caused by stepwise increase of internal hemolymph pressure. Contractions of stipital muscles cause several simultaneous compressions of both stipital tubes (Fig. 43) which propel hemolymph into the attached galeal lumen (Schmitt, 1938; Bänziger, 1971; Krenn, 1990; Wannemacher and Wasserthal, 2003). Relaxation of the stipital muscles is followed by an expansion of the stipital tubes that allows hemolymph to enter from the head capsule through a slit-like opening. The hemolymph pressure inside the galea is upheld by the valve-like composition of the stipital tubes (Fig. 43) (Eastham and Eassa, 1955; Bänziger, 1971; Krenn, 1990). A comparative investigation of the head anatomy showed that the stipital musculature may vary, but in species with a functionally intact proboscis at least two stipital muscles are present (Schmitt, 1938).

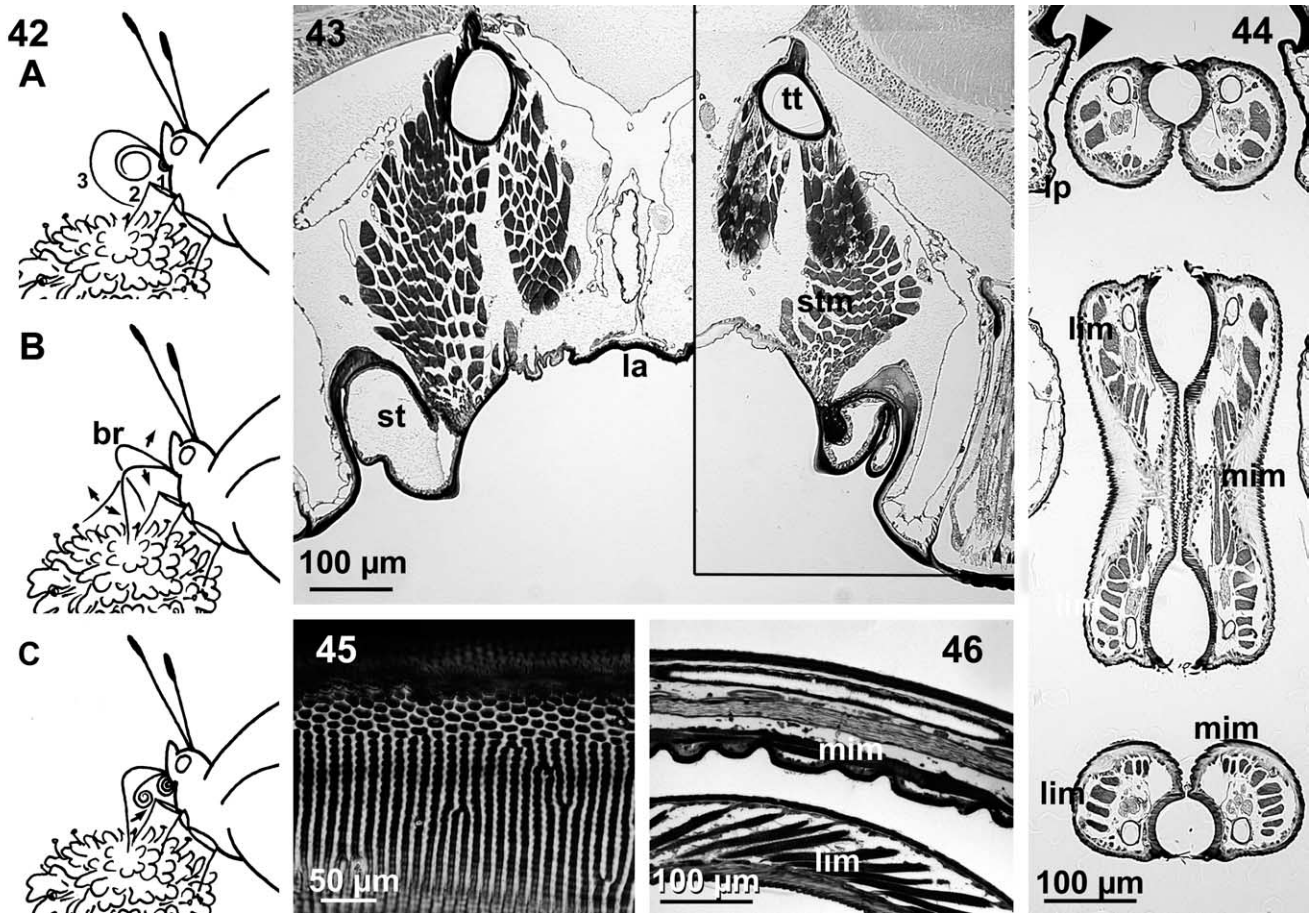
2.4.3.3. Feeding position and flower-handling behavior. In most Macrolepidoptera the proboscis assumes during feeding a flexed position which is characterized by a bend region (sometimes referred to as the knee bend) at about one third of its length (Fig. 42B) (Eastham and Eassa, 1955; Bänziger, 1971; Krenn, 1990, 1998; Paulus and Krenn, 1996; Krenn and Penz, 1998; Knopp and Krenn, 2003). The

formation of the bend region is probably due to changing elasticity distal from the bend (Krenn and Mühlberger, 2002). The flexed feeding position and the characteristic pattern of movements are associated with the ability to handle variously shaped flowers without moving the whole body. During probing behavior the entire proboscis moves up-and-down combined with forward and backward motions of the distal proboscis (Fig. 42B). Extension of the basal galeal joint lifts the proboscis while flexion of the joint pushes the proboscis deeper into a corolla tube (Krenn, 1989, 1990; Penz and Krenn, 2000). The up-and-down movements are probably due to the extrinsic galeal muscles and an antagonistic stipital muscle (Eastham and Eassa, 1955; Krenn, 1990). The to-and-fro-movements of the distal region serve to detect the corolla tube entrance and are caused by greater and lesser flexion of the bend region (Krenn, 1989, 1990, 1998). The extension is due to further increase of hemolymph pressure in the proboscis recognizable by simultaneous stipital compressions while greater flexion is caused by elasticity and intrinsic galeal muscles (Krenn, 1990). At times, the proboscis can be fully extended for its entire length and may even slightly bend upward in a movement described as hyperuncoiling (Bänziger, 1971) which was illustrated in Sphingidae (Wasserthal, 1997). Furthermore, the tip region can be bent to the sides or can be flexed in a way that the dorsal side lies upside down. The position of the inflow slits on the dorsal side of the galeae is the reason for this double-bent posture of the proboscis which can be primarily observed during fluid intake from even surfaces (Krenn, 1990; Knopp and Krenn, 2003).

2.4.3.4. Proboscis coiling and galeal musculature. The coiling process starts at the tip and proceeds toward the basis of the proboscis (Fig. 42C) (Krenn, 1990). The coiled proboscis is brought to its ultimate resting position under the head by alternating stipital movements (Krenn, 1990; Wannemacher and Wasserthal, 2003). If the coiling process is interrupted, the proboscis unwinds due to its elasticity until the outermost coil touches the ventral side of the head. In this way the tightly coiled proboscis maintains its position without muscular activity (Krenn, 1990).

The elasticity of the proboscis is only sufficient to recoil it into a loosely coiled position (Bänziger, 1971; Krenn, 1990; 2000). The role of the intrinsic galeal muscles for complete coiling was long suspected (Réaumur, 1734; Schmitt, 1938; Bänziger, 1971; Krenn, 1990) and recently demonstrated (Krenn, 2000; Wannemacher and Wasserthal, 2003). Since the most basal taxa of Glossata do not possess intrinsic galeal muscles, it must be assumed that their tiny proboscis is coiled by the elasticity of the cuticle alone (Kristensen, 1968c; Nielsen and Kristensen, 1996).

In the proboscis of the Myoglossata (Kristensen and Nielsen, 1981b), intrinsic muscles occur beyond the basal galeal joint (Krenn and Kristensen, 2004). Monotrysian Heteroneura are characterized by one or few longitudinal intrinsic muscles extending along the ventral galeal wall and



Figs. 42–46. Anatomy and movements of the proboscis of butterflies (scanning electron micrographs, light microscopy, and semithin sections; section method described in Pernstich et al., 2003). Fig. 42. Movements of the proboscis in a butterfly; schematic drawings from 16 mm film footage (Krenn, 1989). A. Uncoiling movements; stepwise extension illustrated in three consecutive positions of the proboscis (1, 2, 3). B. Flower-probing combines up-and-down movements of whole proboscis at the basal joint (vertical arrows) with to-and-fro movements of the distal proboscis at the bend region (br) (horizontal arrow); three positions are shown. C. Proboscis coiling starts at the tip and proceeds to the proximal region which is coiled, at last, under the head; arrow indicates direction of movement, three positions are shown. Fig. 43. Head and basal parts of maxillae in cross section of *Zerynthia polyxena* (Papilionidae); combined from two micrographs. Stipes (st) forms a tubular connection between the cervical lumen to the galeae. Inset photo shows stipital tube in compressed position during proboscis uncoiling. Contraction of stipital musculature (stm) extends to tentorium (tt) folds stipital tube and pumps hemolymph into galea. Fig. 44. Proboscis of *Zerynthia polyxena* (Papilionidae) in cross section; coiled proboscis (pr) lies between labial palps (lp); microtrichia of the lateral galeal wall engage with such cuticle structures of labial palps (arrow head). Musculature of galea composed of lateral intrinsic muscles (lim) and median intrinsic muscles (mim) is responsible for coiling the proboscis. Fig. 45. Composition of the lateral galeal wall (light microscopy) of *Papilio machaon* (Papilionidae); complex pattern of light and dark cuticle ensures elastic properties of the proboscis. Fig. 46. Longitudinal section through coiled galea of *Zerynthia polyxena* (Papilionidae). Series of lateral intrinsic galeal muscles (lim) extend obliquely from the dorso-lateral wall to the ventral galeal wall; the series of median intrinsic galeal muscles (mim) extend along the ventral wall.

most Ditrysia by, at least, one series of obliquely running muscles (Kristensen and Nielsen, 1981a; Krenn and Kristensen, 2004). In most Macrolepidoptera the intrinsic galeal musculature can be classified into two series according to both its position and course (Fig. 44). The lateral intrinsic muscles overlap each other and extend from the lateral to the ventral wall where they attach on tendons to the exocuticular ribs of the wall (Fig. 46). The second series, the median intrinsic galeal muscles, runs a more longitudinal course along the ventral wall or extends slightly obliquely from the medioventral wall to the middle of the ventral wall (Fig. 46) (Eastham and Eassa, 1955; Krenn, 1990, 1998; Krenn and Mühlberger, 2002). The presence of

two series of intrinsic muscles is ancestral in butterflies as well as in Macrolepidoptera (Krenn and Mühlberger, 2002; Krenn and Kristensen, 2004). This complex pattern of galeal muscles probably evolved in context with the functional demands of the extremely long proboscides in Ditrysia (Krenn and Kristensen, 2004). Derived patterns of muscle arrangements mainly concern partial reduction of the median intrinsic galeal muscles that was found in some Rhopalocera (Krenn and Mühlberger, 2002).

2.5. Diptera

Adult Diptera feed from a wide variety of liquid or

semi-liquid foods. The mouthparts of all species regardless of the food source are functionally linked to form a proboscis which in its plesiomorphic design is composed of multiple elements: paired mandibles and maxillae and the unpaired labrum, hypopharynx and labium (Fig. 47). The mandibles are absent in most flower-visiting Diptera, although they are functional mostly in females of some blood-feeding taxa. The basal sclerites of the maxillae (cardo and stipes) bear the slender laciniae and maxillary palps. The labrum is usually deeply grooved and combines with the epipharynx to form the food canal. The canal is ventrally closed by the hypopharynx which is traversed by the salivary duct (Fig. 52). The prominent labium consists of the labial stalk, bearing at its distal end the paired labella. In many Diptera the labella are traversed by a system of small channels, the pseudotracheae (Fig. 51). The labium usually takes the form of a gutter in which the other mouthparts lie.

In many Brachycera structures of the head capsule contribute to the formation of the proboscis. Such a proboscis is distinguished lengthwise by three sections from basal to apical, i.e. rostrum, haustellum and labella (Figs. 47 and 49). The rostrum, which is composed of the clypeus and cibarium, forms a novel moving unit (Gouin, 1950b; Szucsich and Krenn, 2000). It increases both the maximal operational length and maneuverability of the proboscis. The haustellum is a complex of functionally interconnected mouthparts (Fig. 51). It supports the labella which constitute the primary organs for fluid uptake (Figs. 47, 49 and 51).

The diversity of mouthpart modifications in Diptera is treated in numerous comparative studies (Dimmock, 1881; Hansen, 1884; Peterson, 1916; Gouin, 1949; Hoyt, 1952; Denis and Bitsch, 1973; Nagatomi and Soroida, 1985; Elzinga and Broce, 1986; Chaudonneret, 1990). Mouthparts of blood-feeding and predatory Diptera have been dealt with in detail for the Culicidae (Schiemenz, 1957; Snodgrass, 1959), Tabanidae (Bonhag, 1951), Empididae (Bletchly, 1954; Krystoph, 1961), Rhagionidae (Bletchly, 1955) and Asilidae (Whitfield, 1925). The morphology of nectar-feeding proboscides in Diptera has been examined in detail only in Bombyliidae (Szucsich and Krenn, 2000, 2002) and Syrphidae (Schiemenz, 1957; Gilbert, 1981; Schuhmacher and Hoffmann, 1982).

2.5.1. Nectar-feeding Diptera

Although the feeding habits of many Diptera are inadequately known, many adult flies feed on floral nectar, to a lesser extent on pollen and some are specialized pollinators of particular plants (Proctor et al., 1996; Zizka, 1999). Diptera from about 52 families are mentioned to contain representatives known to feed on nectar, members of 14 families are obligate nectar-feeders (reviewed in Kevan and Baker, 1983; Proctor et al., 1996; Gilbert and Jervis, 1998; Larson et al., 2001). However, the mouthparts of few taxa have been studied with regard to nectar-feeding.

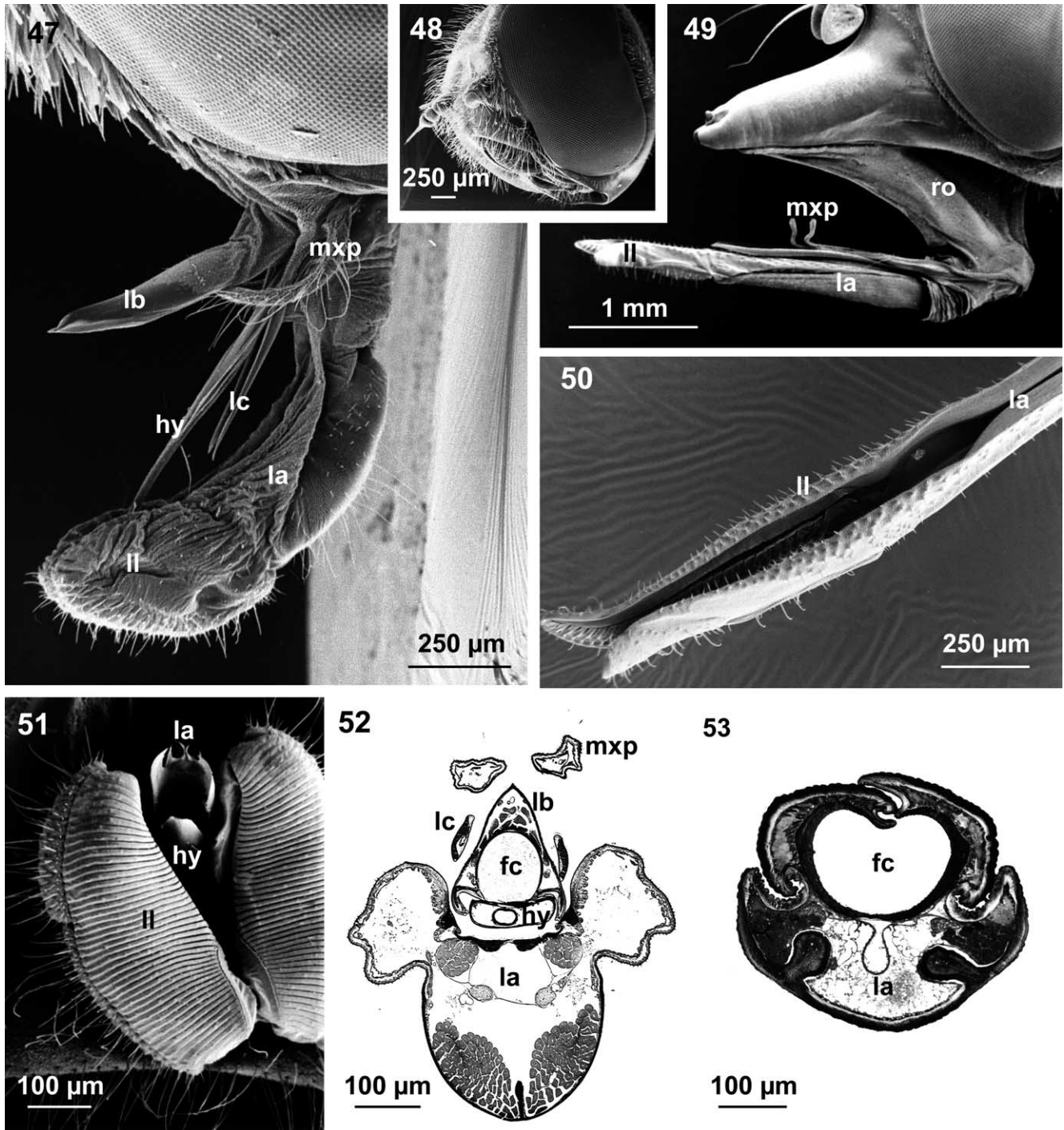
2.5.1.1. *Nematocera*. About one third of Nematoceran families obtain food from flowers, as well as other sources (Gilbert and Jervis, 1998; Larson et al., 2001). Obligate nectar-feeders occur apparently only in tropical Culicidae (Snodgrass, 1959; Schremmer, 1961) and Simuliidae (Gilbert and Jervis, 1998). So far, no particular mouthpart adaptations to nectar-feeding have been reported except the loss or a reduction of piercing stylets in males of blood sucking Culicidae (e.g. Hoyt, 1952) and Ceratopogonidae (Downes, 1958) and in both sexes of obligatory nectar-feeding Culicidae (Snodgrass, 1959).

2.5.1.2. *Brachycera*. Of all Diptera, nectar-feeding is the most widespread in Lower Brachycera. Obligate nectarivorous flies are recorded in the Vermilionidae, Nemestrinidae, Acroceridae, Bombyliidae and Mydidae (Gilbert and Jervis, 1998). In many of these groups elongated proboscides are interpreted as adaptations to deep corolla tubes. Detailed studies on the morphological adaptations of feeding from flowers exist only for Bombyliidae (Szucsich and Krenn, 2000; 2002). Representatives from about one quarter of all cyclorrhaphan families are reported to feed on nectar. Obligate nectar-feeders occur in the Syrphidae, the only well-studied group in context with feeding (Gilbert, 1981, 1985), as well as in Conopidae, Chryomiidae, Drosophilidae, Muscidae, Anthomyiidae and Tachinidae (Gilbert and Jervis, 1998).

2.5.2. Proboscis formation

Most flower-visiting Diptera with a short proboscis take nectar from flowers with open and easily accessible nectaries (e.g. Gilbert, 1981, 1985). The proboscis operates according to a sponging/sucking mode of feeding. While in predatory and blood-sucking Diptera, the primary organ for food-uptake may be the labrum, the hypopharynx or the labella, in nectarivorous flies it is always the labella. Nectar loading is facilitated by capillarity and adhesion forces and fluid is sucked into the food canal which is formed by the interconnecting parts of the haustellum. The haustellum in nectar-feeding flies, as opposed to predatory and blood-feeding flies, is associated with a high degree of maneuverability. An even greater amount of proboscis maneuverability is achieved in many Brachycera with the incorporation of the rostrum. This basal most part of the proboscis enables flower-probing movements and retracts the proboscis into its resting position in the oral cavity (Fig. 48). The sponging/sucking mode of feeding as performed by a short proboscis represents the ancestral method of fluid uptake in Diptera. Specialized modes of feeding, such as purely suctorial, are in many cases associated with the formation of a greatly elongated proboscis as well as significant modifications of the labella, the food canal composition and proboscis movements (Figs. 49, 50 and 53).

2.5.2.1. *Labella—organ of fluid uptake*. In the sponging/



Figs. 47–53. Proboscis of Diptera (scanning electron micrographs and semithin sections; section method described in Pernstich et al., 2003). Fig. 47. Head of *Hemipenthes morio* (Bombyliidae) with extended proboscis. Decoupling of mouthparts is due to the drying process during preparation; hypopharynx (hy); labium (la); labrum/epipharynx (lb); lacinia (lc); labellum (ll); maxillary palp (mxp). Fig. 48. Head of *Hemipenthes morio* (Bombyliidae) with proboscis in resting position. Proboscis is totally withdrawn into oral cavity. Fig. 49. Head of *Rhingia campestris* (Syrphidae) with partially extended, elongated proboscis. Snoutlike protrusion of head capsule enables a resting position similar in species with short proboscides; labium (la); labellum (ll); maxillary palp (mxp); rostrum (ro). Fig. 50. Elongated labella of *Rhingia campestris* (Syrphidae). The labella (ll) constitute a prolongation of the main axis of the proboscis; labial stalk (la). Fig. 51. Labella of *Dasyrphus albostratus* (Syrphidae) in the sponging feeding position. Inner surfaces of labella, equipped with the pseudotracheae, form the so-called oral disc; labium (la); labellum (ll); hypopharynx (hy). Fig. 52. Haustellum of *Eristalis tenax* (Syrphidae) in cross section. The single components are functionally coupled, with labrum/epipharynx (lb) and hypopharynx (hy) forming the food-canal (fc) and lying in labial gutter (la). Hypopharynx is interlocked with labrum/epipharynx in a tongue-and-groove-like fashion. labium (la); lacinia (lc); maxillary palp (mxp). Fig. 53. Distal labium of *Prosoeca ganglbauri* (Nemestrinidae) in cross section. In the distal part of the elongated proboscis the food canal (fc) is built up by the labium (la) alone.

sucking proboscis of the greater part of flower-feeding Diptera nectar is taken up by the broad and fleshy labella, which are spread onto the surface during feeding. The resulting oral disc constitutes the organ of primary fluid-uptake (Gilbert, 1981; Szucsich and Krenn, 2000) (Fig. 51).

The surface of the labella is traversed by a series of channels (pseudotracheae) which are strengthened by opened chitinous rings and form a system of slits. Individual pseudotracheae merge into collecting channels which empty into the distal end of the food canal (Figs. 50 and 51). In some taxa prestomal teeth are present at the base of the labella, which generally serve as cutting and scraping organs (Graham-Smith, 1930; Elzinga and Broce, 1986). Based on the structural differences between the chitinous rings, Zaitzev (1983) distinguished two categories: (1) dentate pseudotrachea which open zipper-like and presumably close by an increase in hemolymph pressure and (2) spinose pseudotrachea which cannot be closed. This distinction however is based solely on examination of the family Bombyliidae. Intermediate stages are found in Muscomorpha (Elzinga and Broce, 1986). Spinose pseudotracheae are the most common except in Syrphidae. In a study of 181 species in 34 families of Muscomorpha, Elzinga and Broce (1986) found pseudotracheal diameters of 3–8 μm to be predominant in nectar-feeding species. However, much larger diameters are found in nectarivorous Bombyliidae (Szucsich, unpubl.).

Most authorities (Peterson, 1916; Elzinga and Broce, 1986) suggest that the pseudotracheal system serves for the distribution of saliva onto the labellar surface when feeding on solidified nectar and for the transport of food in the opposite direction. However, with respect to the Syrphidae, Schuhmacher and Hoffmann (1982) maintain that only saliva is transported by the pseudotracheae and that food is conducted along furrows which overlie the canals and which are formed by interpseudotracheal folds (Fig. 69). This separation of passageways for food and saliva does not apply to all nectar-feeding Diptera, since some species lack interpseudotracheal folds, e.g. *Bombylius major* (Szucsich and Krenn, 2000). The development of pseudotracheae has been treated as an autapomorphy of the Brachycera (Nagatomi and Soroida, 1985). Since, they also occur in the Tipulidae, Mycetophilidae and Ptychopteridae (Peterson, 1916) they may be a synapomorphy of the entire order (Hennig, 1981) or a major part of Diptera (Peterson, 1916).

2.5.2.2. Labella movements. Morphologists mostly describe feeding positions in which both proboscis and labella take stationary postures (Graham-Smith, 1930; Szucsich and Krenn, 2000, 2002). It is true that movements of the labella and proboscis serve to attain the respective feeding position, however, they are also directly involved in food uptake.

Graham-Smith (1930) delineated six positions or stages attainable by the proboscis in *Calliphora erythrocephala*, which likewise occur in other Brachycera. In addition to the resting position, only two of these feeding positions pertain

to nectar-feeding Diptera (Elzinga and Broce, 1986). The resting position in most nectarivorous Diptera is characterized by juxtaposition of the labella so that their matching pseudotracheal surfaces oppose each other (stage I, Graham-Smith, 1930) (Fig. 55A). To attain the functional feeding position the labella are flexed against the labial stalk by contraction of intrinsic muscles in the labial stalk (Fig. 55B). A subsequent retraction of the furca, a basal sclerite of the labella, opens up the labella, thus forming a flat oral disc (stage II or filtering position, Graham-Smith, 1930) with exposed pseudotracheae (Fig. 55C). Further extension of the labellar margins produces a cup-like shape to the oral disc (stage III or cupping position, Graham-Smith, 1930).

Gilbert (1981) described how nectar is taken up by Syrphidae. The proboscis is extended until the tips of labella reach the nectar. The labella separate so that they come to lie flat on the surface of the fluid (Fig. 56A). Nectar is ingested by the force of consecutive sucking pumps. As the level of fluid lowers, the proboscis is not projected further, rather the labella are gradually closed (Fig. 56B). When fluid level is 1–2 mm below the tip, the proboscis is further extended and the process repeated. This implies that nectar can travel along the labella without being contained within the labral sucking tube. The inner surface of the labella is obviously hydrophilic. Solidified nectar and honeydew are dissolved with saliva prior to sucking.

2.5.2.3. Composition of food canal. In most Diptera the food canal is composed of the labrum-epipharynx which forms a large half-pipe structure closed by the hypopharynx (Fig. 52). In some taxa—e.g. Tipulidae (Gouin, 1949) and Tephritidae (Vijaysegaran et al., 1997), the hypopharynx is very short or reduced. Ventrally the food canal is sealed by the floor of the labial gutter. In most obligate nectar-feeding Diptera the general composition of the food canal is retained, however in some species additional elements ensure closure of the food canal, such as the laciniae in Bombyliidae which support the non-sclerotized folds of the hypopharynx (Szucsich and Krenn, 2002).

2.5.2.4. Food conduction. The passage of food through the mouthparts in Diptera involves the interplay of successive suction pumps (Bonhag, 1951; Schiemenz, 1957; Schuhmacher and Hoffmann, 1982). As yet, six different pumps are known. (1) The prelabral pump in Syrphidae draws liquids from the margins of the labella to the center. It generates a rhythmic pulse (5–10 cycles/s), which can be observed in feeding flies, by contraction of the epifurcal muscle (Schuhmacher and Hoffmann, 1982). Although the pump is described only in Syrphidae, it probably occurs in many taxa, which rely on a sponging/sucking mode of feeding. (2) A labial pump is present in species in which the labial stalk forms a great proportion of the food canal. The diameter of this labial part of the food canal can be increased by abduction of the paraphyses (Szucsich, unpubl.). (3) The labro-epipharyngeal pump draws fluids

toward the cibarium by contraction of intrinsic labral muscles which widens the diameter of the epipharyngeal food canal (Szucsich and Krenn, 2000). (4) The cibarial pump expands the lumen of the cibarium by action of clypeo-cibarial musculature. It is the strongest pump in most Brachycera. Its efficiency is increased by the fusion of the clypeus and the cibarium (Gouin, 1950b; Szucsich and Krenn, 2000). (5) The precerebral pharyngeal pump is diminished in taxa in which the cibarial pump is strengthened. (6) The postcerebral pharyngeal pump is present in Nematocera (Schiemenz, 1957) and some basal Brachycera (Bonhag, 1951).

2.5.2.5. Proboscis movements. When feeding, the entire proboscis is barely moved in many Nematocera and some lower Brachycera. The resting and feeding positions are reportedly not differentiated from each other. The individual parts of the proboscis move more or less independently. To feed, many Brachycera however can alter the orientation of the whole proboscis. At least in lower Brachycera ('Orthorrhapha') an increased maneuverability of the proboscis appears to occur in taxa that feed on flowers.

In most Tabanidae the proboscis is inclined downward when feeding or at rest. However, in *Corizoneura longirostris* (Tabanidae) the extremely elongated proboscis is held straight out in front of the head in the rest position. To feed, the proboscis is held perpendicular to the long axis of the body (Mitter, 1918; Dierl, 1968). At rest the proboscis is entirely retracted into the oral cavity in Stratiomyidae (Gouin, 1950a), Bombyliidae with short proboscides (Dimmock, 1881; Szucsich and Krenn, 2000), Therevidae (Irwin and Lyneborg, 1981), Scenopinidae (Kelsey, 1981), some Empididae (Krystoph, 1961) and most Cyclorrhapha (e.g. Graham-Smith, 1930; Schiemenz, 1957). When not feeding, Acroceridae (Schlinger, 1981) and Nemestrinidae (Taskes, 1981) hold the proboscis backward against the underside of the body. Bombyliidae with long proboscides (Szucsich and Krenn, 2002) and Apioceridae (Peterson, 1981) project it forward. Most groups, however, feed in an orthognathous position.

The functional mechanisms of the movements have only been described in detail in Cyclorrhapha (e.g. Graham-Smith, 1930; Schiemenz, 1957) and Bombyliidae (Szucsich and Krenn, 2000; 2002). In these groups, the increased flexibility of the proboscis is attained by a new moving unit, the rostrum. Szucsich and Krenn (2000) differentiated two submovements, a folding of the haustellum against the rostrum and a rotation of the rostrum out of the head capsule (Fig. 54). In addition to the labella, movements of the proboscis are also often involved in the process of feeding. During feeding many flies can be observed performing tapping movements with their proboscis (Fig. 54E,F).

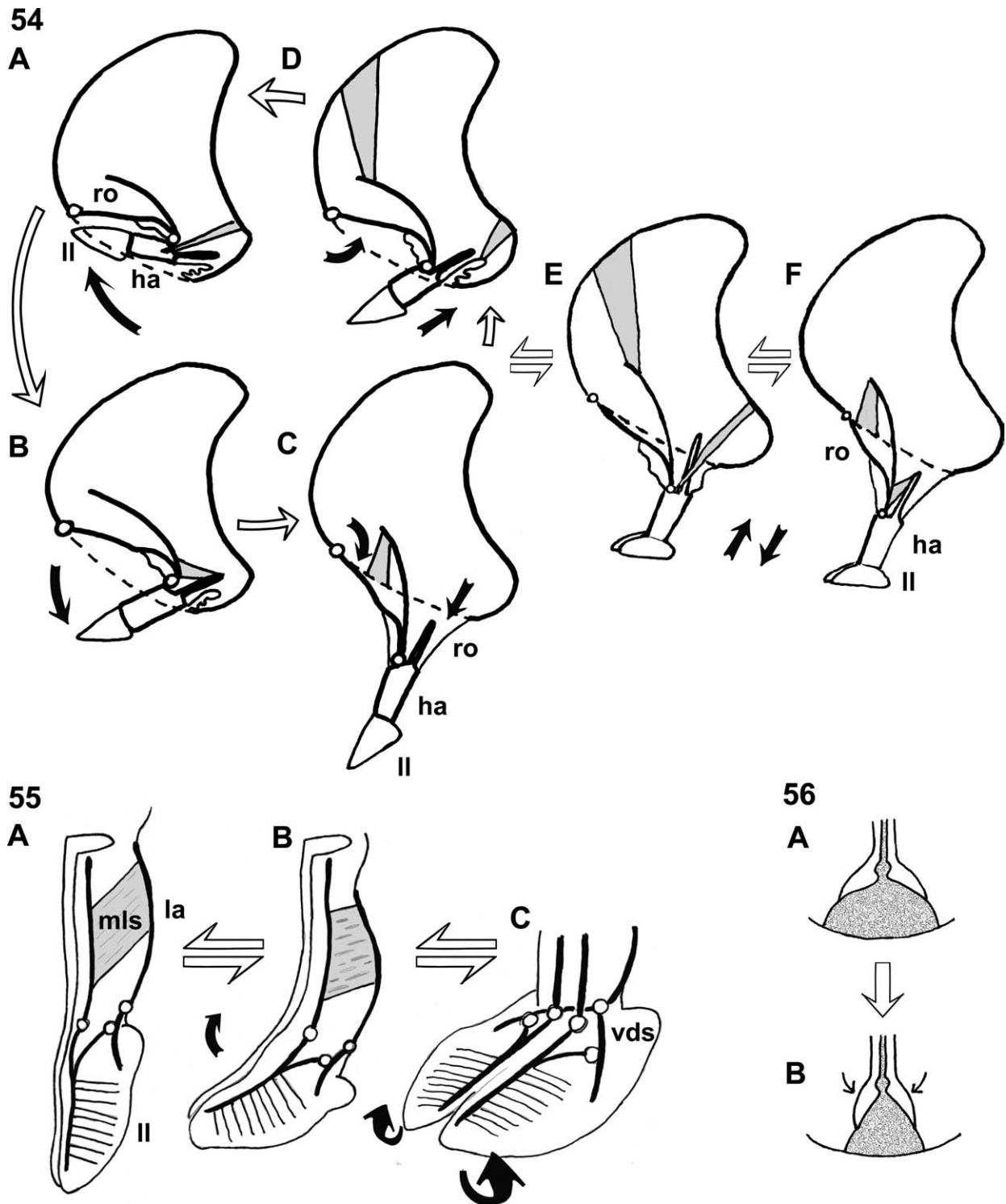
2.5.3. Suctorial proboscides

The mouthparts of Diptera with generalized feeding

habits hardly show adaptations to nectar-feeding which can be distinguished from those which feed on other food sources such as honeydew and rotting materials. Morphological specializations are more obvious and diverse in elongated proboscides, which take nectar from flowers with deep corolla tubes or concealed nectaries. Long to extremely long proboscis formations have been noted in several Diptera (Mitter, 1918; Schremmer, 1961; Dierl, 1968; Nagatomi and Soroida, 1985), however the morphological details and functional mechanisms are seldom studied. The evolutionary interplay between elongated proboscides and the depth of corolla tubes in the visited flowers is frequently commented on with respect to the Diptera (Johnson and Steiner, 1995, 1997; Manning and Goldblatt, 1996; Szucsich and Krenn, 2002) (Table 3). Adaptations to other floral traits, such as the narrowness of corolla tubes and to flowers that open to the side have been examined in the Bombyliidae (Szucsich and Krenn, 2002) and to a lesser extent the Syrphidae (Gilbert, 1981).

Bombylius major, a fly with a maximal functional proboscis length of 10.5–12.5 mm, shows several unique morphological features such as interlocking bristles which close the ventral sides of the labella (Szucsich and Krenn, 2002). Further, the pseudotracheal system is reduced to three channels, which extend in the longitudinal axis of the proboscis and open at the tips of the labella. A unique feeding position with the proboscis in a horizontal posture is attained by the lengthened ventral part of the rostrum (Szucsich and Krenn, 2002) (Table 3).

Various elements partake in the elongation of a suctorial proboscis (Table 3). Usually, it is the haustellum as a whole, which undergoes a major increase in length. However, when the length of the labium exceeds that of other mouthparts or when the labium is the sole elongated mouthpart structure then the distal part of the food canal is formed by the labium alone (Szucsich, unpubl.). The sidewalls of the labial stalk join together at the top to form a closed food tube (Fig. 53). The lengthening of the labium can be due to elongation of the labial stalk as in *Prosoeca ganglbauri* (Nemestrinidae) and *Conops flavipes* (Conopidae) or to the weakly sclerotized labial base as in *Eulonchus halli* (Acroceridae). Some nectar-feeding representatives of *Corizoneura* (Tabanidae) have an extremely elongated labium (about 30 mm long) yet they retain the short piercing/sucking mouthparts (about 8 mm long) typical of many tabanids (Mitter, 1918; Dierl, 1968). Little is known about the functional morphology of the highly elongated proboscides in Acroceridae and Nemestrinidae which reach lengths of about 80 mm (Johnson and Steiner, 1995). In numerous Diptera the labella are elongated in addition to the labial stalk (Fig. 50). However, in many Conopidae and others with long proboscides the length of the labellar lobes is reduced (Elzinga and Broce, 1986). When the rostrum is elongated, it is usually accompanied by a beak-like protrusion of the head-capsule, which protects the elongated proboscis during rest (e.g. *Rhingia campestris*, Syrphidae) (Fig. 49).



Figs. 54–56. Proboscis movements in Diptera. Fig. 54. Proboscis movements of *Hemipenthes morio* (Bombyliidae) (simplified from Szucsich and Krenn, 2000), circles indicate positions of joints, contraction of muscles, shaded in gray are necessary to attain the given postures. A. resting position, where proboscis is totally withdrawn into the oral cavity (see Fig. 48) attained from position (D) by flexion of haustellum (ha) against rostrum (ro). B. Haustellum is folded out of the oral cavity. C. Rostrum is rotated out of oral cavity, proboscis attains its maximal operational length. D. Rostrum is rotated into oral cavity and ventral rostral membrane retracted into head capsule. E. and F. Feeding in a sponging/sucking mode often encompasses tapping movements of proboscis. After spreading open the labella (II) in position (C), the rostrum is slightly rotated in and out of the oral cavity, accompanied by slight movements of haustellum against rostrum to keep the oral disc in a fixed plane labrum/epipharynx (la); labellum (II); hypopharynx (hy). Fig. 55. Labellar movements of *H. morio* (Bombyliidae) (modified from Szucsich and Krenn, 2000), circles indicate positions of joints, intrinsic muscle of the labial stalk (mls) shaded in gray. A. Labium (la) in resting position—the labella (II) are held in the longitudinal axis of the labial stalk, the intrinsic muscle of the labial stalk is relaxed. B. Labella are flexed toward the labial stalk by contraction of intrinsic muscle of labial stalk. C. Adjacent labella open on their ventral sides by spreading of ventral

Adaptations to narrow corolla tubes are mainly diagnosed in Bombyliidae (Szucsich and Krenn, 2002) and to a smaller degree in Syrphidae (Gilbert, 1981). Feeding from such narrow flower tubes physically prevents opening of the labella. Adaptive pressure to obtain nectar from deep corollas can be seen in the shape of the labellum in *Rhingia* which is narrow and pointed, apparently functioning as an extension to the proboscis (Gilbert, 1981) (Fig. 49). A main characteristic of Bombyliidae that extract nectar from flowers with narrow corolla tubes is the narrow labella with few pseudotracheae which open into the labellar margin (Szucsich and Krenn, 2002). In Conopidae, the number of pseudotracheae ranges between 2 and 7 and the collecting canal is absent (Elzinga and Broce, 1986). The pseudotracheal rings are free at the tip and attenuated into numerous hair-like filaments at the margin of the labella. Prestomal teeth, gustatory setae and nodules are absent. The labella form a single preoral tube for ingesting nectar (Elzinga and Broce, 1986). Since, the labella cannot be opened once inside a narrow corolla tube, a reduction of labellar movements was expected to be found. This, however, was not confirmed in *Bombylius major* since this species also feed on pollen (Szucsich and Krenn, 2002).

Adaptations to other floral traits have passed largely unnoticed. Yeates (1994) suggested that elongated mouthparts in Bombyliidae are an adaptation to feeding while hovering. Szucsich and Krenn (2002) proposed that at least in Bombyliidae greatly elongate mouthparts with increased maneuverability and hovering capacity could be essential for feeding from zygomorphic flowers.

A long nectaring proboscis has arisen independently on numerous occasions in the majority of families of flower-visiting Diptera, which supports the idea that behavior promotes evolution of a concealed nectar extracting apparatus (Gilbert and Jervis, 1998). Characteristic for long proboscides of nectar-feeding Diptera are long and slender labella, a reduced number of pseudotracheae and modification of pseudotracheae into nectar-conducting channels which sometimes open into the labellar margin.

3. Pollen-feeding

Pollen serves as a valuable food source for numerous flower-visitors. It is rich in nutrients and contains proteins, free amino-acids, lipids and occasionally starch (Kevan and Baker, 1983; Roulston and Cane, 2000). Given the appropriateness of pollen as a potential and readily available source of protein/nitrogen, it is surprising that only few adult insects feed exclusively on it. Representatives from many orders of insects are reported to feed, at least, occasionally on pollen, including uncustomary examples in

Collembola (Kevan and Baker, 1983) and Mantodea (Beckman and Hurd, 2003) (Table 1). Obligate pollen-feeding insects are evident in several taxa of Coleoptera, Hymenoptera, Diptera and Lepidoptera. Some representatives of these orders have evolved a variety of specialized mouthpart structures and feeding techniques which comply with their diet.

3.1. Thysanoptera

Some Thysanoptera are the only known non-holometabolous insects known to feed extensively on pollen. Several thrips serve as specialized pollinators (e.g. Hagerup, 1950; Hagerup and Hagerup, 1953; Thien, 1980; Kirk, 1984; Williams et al., 2001). Pollen-feeding behavior is documented for adults of eight species from different families (Kirk, 1984). The piercing/sucking mouthparts of thrips, which enables them to feed on plant tissue, are unmodified in pollen-feeding species. The mouthparts form an asymmetrical mouthcone which is ventrally directed and composed of the labrum, a single mandible, the paired mandibular stylets, labial and maxillary palps (Moritz, 1982). It is placed over a pollen grain, the mandibular stylet punches a hole through one of the pores and the nutrient-rich content is sucked out. The maxillary stylets interlock in a tongue-and-groove fashion to form a feeding tube that is extended through the opening. During suction the pollen grain is held unsupported by forelegs or palps on the end of the mouthcone (Kirk, 1984).

3.2. Neuroptera

Adults of several species of Nemopteridae feed on pollen, as confirmed by gut content and excrement analysis (Monserrat, 1985; Picker, 1987). *Nemoptera sinuata*, for example, feeds exclusively on pollen as shown by field observations (Popov, 2002). To feed it inserts the rostrum into the flower to pry it open. The galeae and labial palps, together with the strongly elongated labium, remove pollen grains from the anthers and transfer them to the mouth with simultaneous and rapid up-and-down movements. The mandibles and labrum are more or less stationary during feeding. The insect also harvests pollen by grooming the tarsi of the forelegs with the mouthparts and swallowing the accumulated pollen (Popov, 2002). The pollen harvesting structures of the galea and labial palps are not investigated in detail.

3.3. Coleoptera

Pollen-feeding beetles are recorded from representatives in a number of families (Table 4). In many of these, the

divergent sclerites (vds) of the labellar base. Thus they form an oral disc where fluid is taken up by adhesive forces. Fig. 56. Labellar feeding movements on fluid droplets: during feeding the labella gradually close as the meniscus of the fluid descends (A–B) (adopted from Vijayasegaran et al., 1997 according to the description of Gilbert, 1981).

Table 3
Examples and composition of suctorial proboscides in selected species of Diptera

Family	Species	Elongated parts							Number of pseudotracheae	References	
		Rostrum	Haustellum					Labella			
			Labrum	Hypopharynx	Maxillae	Mandibles	Labial base				Labial stalk
Tabanidae	<i>Pangonius funebris</i>		+	+	+	+		+	?	?	Nagatomi and Soroida, 1985
Tabanidae	<i>Corizoneura longirostris</i>		+	+	+	+		++	?	7	Mitter, 1918
Vermileonidae	<i>Lampromyia intermedia</i>		++	++	++	--		++	?	?	Nagatomi and Soroida, 1985
Nemestrinidae	<i>Prosoeca ganglbauri</i>		+	+	+	--		++	+	26	Szucsich, unpubl.
Acroceridae	<i>Eulonchus halli</i>		+	+	+	--		++	+	?	Schlinger, 1981
Bombyliidae	<i>Bombylius major</i>	+v	++	++	++	--		++	++	3	Szucsich and Krenn, 2000, 2002
Syrphidae	<i>Rhingia campestris</i>	+	++	++	++	--		++	++	25	Gilbert, 1981
Conopidae	<i>Conops flavipes</i>					--		++	-	?	Peterson, 1916
Conopidae	<i>Stylogaster biannulata</i>					--		++	++	1	Elzinga and Broce, 1986
Chloropidae	<i>Olcella cinerea</i>		?	?	?	--		++	++	-	Elzinga and Broce, 1986
Tachinidae	<i>Siphona illinoensis</i>					--		++	++	3	Elzinga and Broce, 1986
Tachinidae	<i>Siphoteskia occidentalis</i>	+				--		++		7	Elzinga and Broce, 1986

Extent of elongation and reduction in the single components of the proboscis are noted: (--) totally reduced, (-) reduction in length, (+) elongation and (++) greater elongation. (+v) in *Bombylius* indicates that only the ventral part of the rostrum is lengthened, enabling an enhanced maneuverability of the proboscis. (?) indicates that data are not available from the cited source.

Table 4

Coleopteran families mentioned to include pollen-feeding representatives; bold letters indicate occurrence of mouthpart adaptations to pollen-feeding at least in some species of the taxon

Taxa	References	Remarks
Staphylinidae, Omaliinae	Klausnitzer, 2003	
Scarabaeidae: Cetoniini, <i>Cetonia</i> , <i>Trichius</i> , <i>Trichostetha</i> , Hopliini	Schremmer, 1961; Fuchs, 1974; Kevan and Baker, 1983; Johnson and Nicolson, 2001	Sweeping brushing mode of pollen-feeding, mostly in addition with nectar, some feed also on petals
Buprestidae	Fuchs, 1974; Kevan and Baker, 1983	
Elateridae	Fuchs, 1974	
Lycidae	Klausnitzer, 2003	
Cantharidae	Fuchs, 1974; Kevan and Baker, 1983	
Dermestidae	Fuchs, 1974; Kevan and Baker, 1983	
Cleridae	Fuchs, 1974; Kevan and Baker, 1983	
Malachiidae: <i>Malachius</i>	Schicha, 1967	Pollen-sweeping mouthparts
Nitidulidae	Fuchs, 1974; Kevan and Baker, 1983	
Boganiidae	Klausnitzer, 2003	
Mordellidae	Fuchs, 1974; Kevan and Baker, 1983	
Largiidae	Fuchs, 1974	
Alleculidae	Fuchs, 1974; Kevan and Baker, 1983	
Cephaloidae	Kevan and Baker, 1983	
Oedemeridae	Fuchs, 1974; Kevan and Baker, 1983	
Meloidae	Kevan and Baker, 1983	Adaptations to nectar-feeding in various genera
Cerambycidae: Lamiinae , Cerambycinae	Goldman, 1933; Fuchs, 1974; Kevan and Baker, 1983	
Pyrochroidae	Fuchs, 1974	
Chrysomelidae	Fuchs, 1974; Kevan and Baker, 1983	
Nemonychidae	Klausnitzer, 2003	
Oxycorynidae: Allocoryninae	Klausnitzer, 2003	
Curculionidae	Kevan and Baker, 1983	

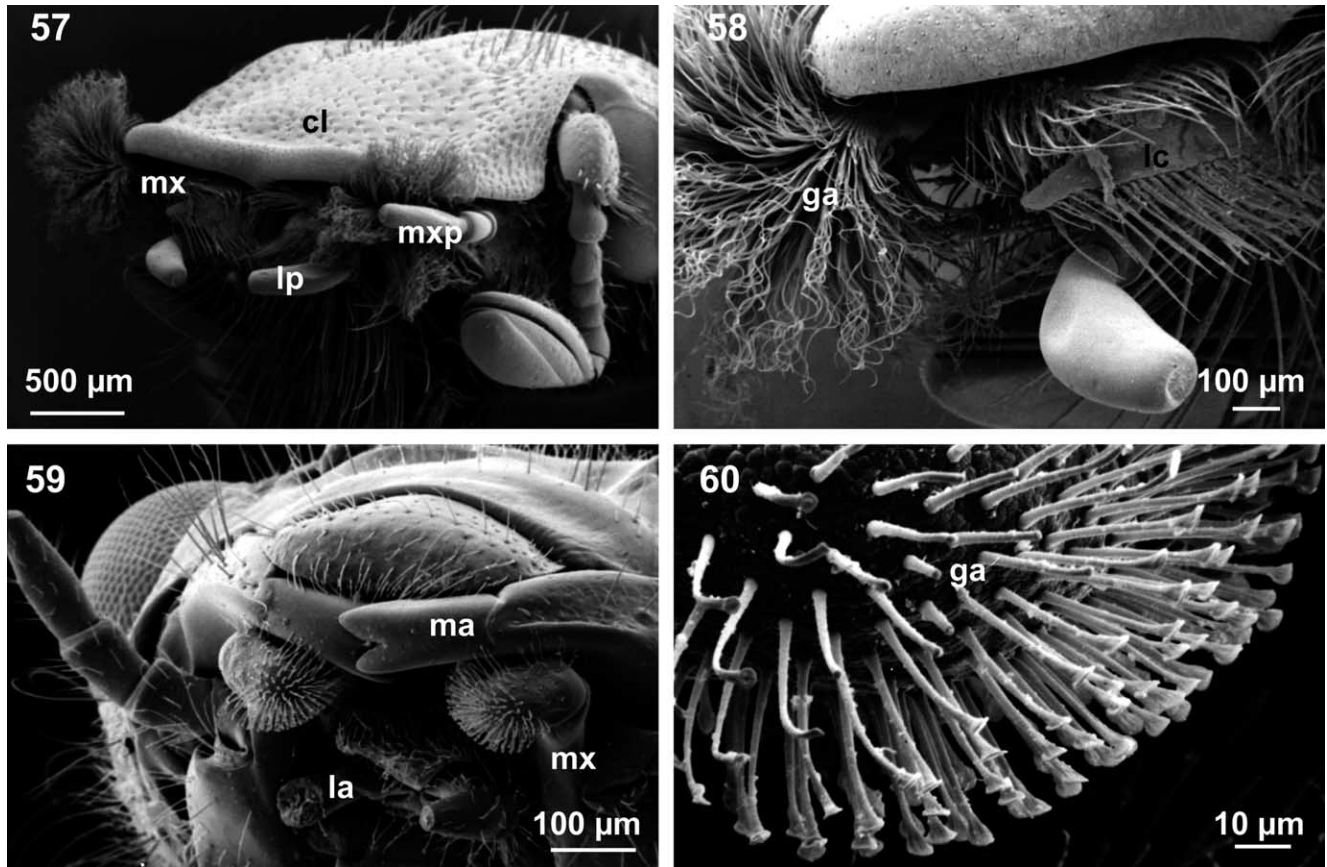
mouthparts are prognathous and may serve equally for pollen and nectar uptake. Since the mouthparts are short, beetles are usually found on flowers with exposed pollen. However, small and slender beetles can exploit flowers with concealed food sources by crawling or pushing their way into the flower (Barth, 1991).

Characteristic for many pollen-feeding Coleoptera are several modifications of the mandibles such as hairiness, a soft lacinia mobilis and a postmola which kneads and conveys pollen (Schremmer, 1961; Fuchs, 1974; Nel and Scholtz, 1990). The mandibles may have reduced biting capacity and serve for pollen manipulation. The apical parts of the maxillae bear pads and tufts of bristles, which help take up pollen and transport it to the mouth in conjunction with movements of the labrum/epipharynx unit, labium and hypopharynx. Pollen-harvesting structures such as comb-like bristles and/or specially shaped bristles to which pollen grains adhere were described in Scarabaeidae, Oedemeridae, Cerambycidae, Cantharidae, Bruchidae, Meloidae and Mordellidae. The bristles may be spatulate, spoon-shaped or with various other apical widenings (Fuchs, 1974).

In the European rose chafer (*Cetonia aurata*, Scarabaeidae) the mouthparts are short and covered by the broad, heavily sclerotized and protruding clypeus (Fig. 57). Pollen is acquired by outward sweeping movements of the galeae which bear dense hair brushes (Fig. 58). The pollen is then conveyed over the lacinial combs (Fig. 58) to the region between the mandibles, which are extraordinarily modified.

They lack cutting edges, dentition and cannot be used for biting (Schremmer, 1961). The outer surface is developed into a rounded and paper-thin plate of unknown significance. Attached to the inner base of the mandible is a flexible palp-like structure (lacinia mobilis) which is densely covered with short hairs and works in conjunction with back-and-forth movements of the epipharynx and hypopharynx to transport pollen to the mouth (Schremmer, 1961). Similar mouthpart modifications and a sweeping/brushing mode of feeding on intact pollen grains are found in various scarabaeid beetles, for example monkey beetles (Hopliini) (Johnson and Nicolson, 2001). Likewise, remarkably hairy mouthparts have been described in the pollen-feeding longhorn beetles in the subfamilies Cerambycinae and Lamiinae (Goldman, 1933).

The mouthparts of *Malachius bipustulatus* (Malachiidae) are specialized for pollen-feeding (Schicha, 1967). This beetle feeds on non-sticky grass pollen by stretching out the galeae to dab anthers. Pollen grains adhere to the concave tips of trumpet-shaped bristles on the galeae (Fig. 60) and are transferred to spoon-shaped bristles of the labium when the galeae retract. Bristles of the lacinia pass the food onto the mandibles which are symmetrically dentate with sclerotized cutting edges and mola (Fig. 59). The lacinia mobilis and postmola are soft and the latter is covered with bristles. The mandibles knead the pollen and together with simultaneous movements of the labrum-epipharynx and labium-hypopharynx convey it to the mouth.



Figs. 57–60. Mouthparts of pollen-feeding Coleoptera (scanning electron micrographs). Fig. 57. Sweeping/brushing mouthparts of the pollen-feeding beetle *Cetonia aurata* (Scarabaeidae). Special shaped bristles of the maxilla (mx) take up and transport pollen to the mandibles which are hidden under the labrum and clypeus (cl); short maxillary palp (mxp) and labial palp (lp). Fig. 58. Maxillary bristles of *Cetonia aurata* (Scarabaeidae); undulated hairy bristles on the galea (ga) collect pollen and a comb-like arrangement of bristle on the lacinia (lc) transport them to the mandibles. Fig. 59. Head and mouthparts of *Malachius bipustulatus* (Malachiidae); slightly modified mandibles (ma); maxillae (mx) and labium (la) equipped with specialized bristles for pollen-feeding. Fig. 60. In *Malachius bipustulatus* (Malachiidae) trumpet-shaped bristles of the galea (ga) help to attach pollen grains to the mouthparts.

3.4. Hymenoptera

Pollen-feeding is reported to occur in many adult Hymenoptera (Kevan and Baker, 1983; Gauld and Bolton, 1988; Hunt et al., 1991; Schedl, 1991; Vilhelmsen, 1996; Jervis, 1998; Jervis and Vilhelmsen, 2000). The amount ingested is generally relatively small. Bees, pollen-wasps (Masarinae) and a Sri Lankan sphecid wasp, however, collect enormous amounts of pollen and carry it back to their nests to provision the larvae (Mauss, 1995; Gess, 1996; Krombein and Norden, 1997; Mauss and Müller, 2000). Secondly they may consume pollen for their own nutritional purposes (Michener, 2000). Pollen is either transported internally in the crop and regurgitated in the nest (Hylaeinae, Euryglossinae and pollen-wasps) or it is loaded into external, pollen-carrying structures (scopa and corbícula) as in most bees (Thorp, 1979, 2000; Wcislo and Cane, 1996).

Flower-visiting Hymenoptera may inadvertently consume pollen while feeding on nectar accidentally mixed with pollen grains. A common method of acquiring pollen is

to groom it with the forelegs from the surface of the head where it has accumulated during flower visitation. The forelegs transfer the pollen to the mouthparts. All Hymenoptera groom the tibia and tarsi of the foreleg by scraping them through the mouthparts (Farish, 1972). The inner surfaces of the labiomaxillary complex may be outfitted with combs, pectens and brushes to serve to handle pollen. In short-tongued bees the forelegs are drawn between the labium and the maxillae passing over the well-developed inner galeal comb. In long-tongued bees a functionally analogous comb is situated on the outer stipes (Schremmer, 1972; Jander, 1976). The pollen wasps and ‘crop-collecting’ bees, such as *Hylaeus*, lacking scopal brushes for pollen transport groom pollen from the head or forelegs into the proboscis, but pollen on the thorax and abdomen cannot be conveyed forward to the mouthparts and is discarded by normal grooming movements (Michener et al., 1978; Michener, 2000). This restriction presumably applies to other pollen-feeding Hymenoptera too.

In addition to inadvertent pollen-feeding and ‘pollen grooming’ after visitation, pollen can be harvested directly

from flowers by actions of unspecialized mandibles and forelegs (Patt et al., 1997). Robust pollen-removing hairs (straight or curved, but usually hooked) are sometimes found on the exposed surfaces of the proboscis in short-tongued bees (species of *Leioproctus*, *Colletes*, *Andrena*, *Calliopsis*) and in long-tongued bees (*Proteriades* group of *Hoplitis*, *Cubitalia* and species of *Osmia* and *Melissodes*) (Thorp, 1979, 2000; Michener, 2000). They are associated with pollen removal from tubular flowers with hidden anthers. In several species of *Ancylloscelis* (Alves-dos-Santos and Wittmann, 1999), for example, the females use their proboscis to obtain nectar at the bottom of the flower, simultaneously the brushes of hooked hairs on the prementum and stipes remove pollen. The sockets of many hairs are expanded to permit a passive switching in the direction of the hairs. After several visits the foraging bee combs the pollen from the retracted proboscis with its forelegs and transfers the pollen to the hind leg scopa. Some pollen-feeding Mutillidae and Scoliidae are reported to scoop up pollen with elongated maxillary and labial palps which bear a dense covering of curved hairs (Jervis, 1998).

Many Xyelidae feed exclusively or predominantly on gymnospermous and angiospermous pollen. Others such as *Macroxyela ferruginea* eat leaves, parts of flower buds as well as pollen, yet none are recorded to feed on nectar (Vilhelmsen, 1996; Jervis and Vilhelmsen, 2000). Several features of the mouthparts in both sexes likely pertain to pollen-feeding. (1) The mandibles are highly asymmetrical (Fig. 62), the inner base of one is concave and that of the other is bulbous, together they apparently crush pollen like a mortar and pestle (Jervis and Vilhelmsen, 2000). (2) Maxillary palpal segments III and IV are greatly elongated. In *Xyela* and related genera they are bizarrely expanded near the apex (Figs. 61 and 62) (Arora, 1956; Snodgrass, 1960; Jervis and Vilhelmsen, 2000). The significance of this structure for feeding is not known. (3) Hypopharynx forms a very large cavity (infrabuccal pouch) lined with rows of teeth which serves to further process pollen (Vilhelmsen, 1996). (4) Glossa and paraglossae are reduced and lack the

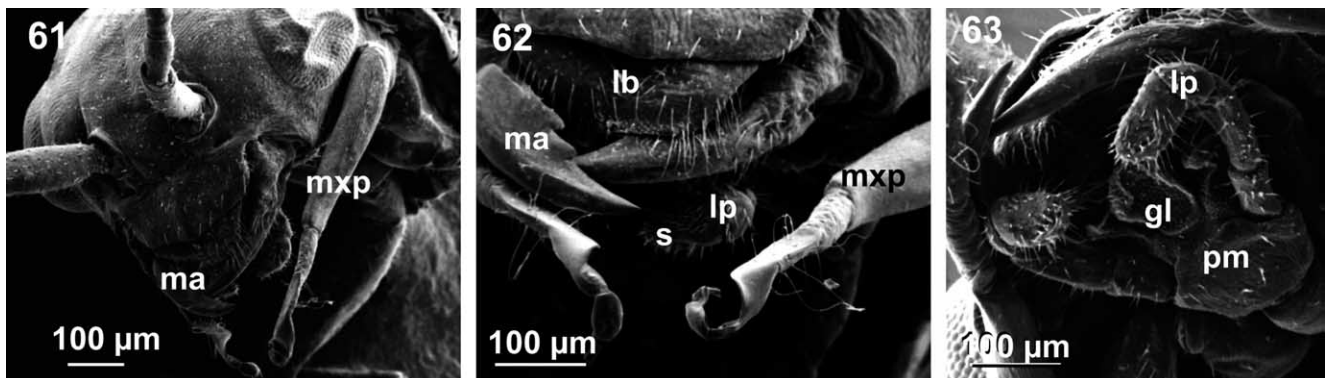
transverse rows of flattened hairs or scales found in most Hymenoptera. Both the anterior and posterior surfaces of the glossa in *Xyela* are beset with numerous small peg-like projections (Fig. 63), only at the apex is there a fringe of short cuticular hair-like structures which however do not extend beyond the glossal apex. In Macroxyelinae the glossa is reported to be absent (Vilhelmsen, 1996). These mouthpart features do not comply with the conventional ground plan for the Hymenopteran labiomaxillary complex. Although Xyelidae represent the most basal taxa of Hymenoptera according to fossil record and phylogenetic studies (Ronquist, 1999; Nieves-Aldrey and Fontal-Cazalla, 1999; Schulmeister, 2003), the adult mouthparts possibly reflect a secondary specialization to pollen-feeding.

3.5. Lepidoptera

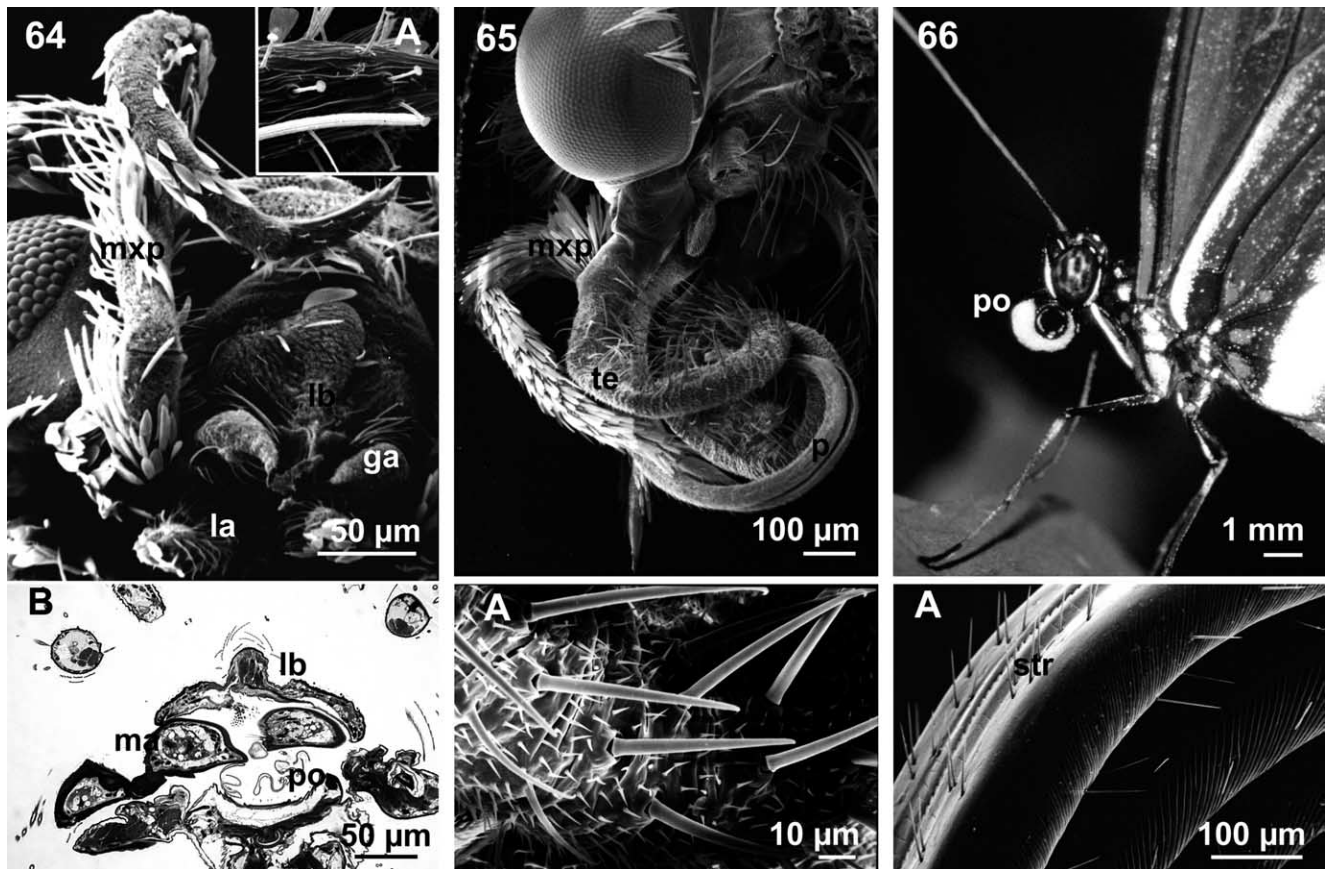
3.5.1. Pollen grinding moths

Aglossatan Lepidoptera of the families Micropterigidae and Heterobathmiidae subsist predominantly on a pollen-diet. *Micropteryx* visits a great variety of angiosperm flowers while *Sabatinca* moths feed on fern spores and pollen from grasses and *Zygogynum* trees (Winteraceae) (Thien et al., 1985; Kristensen, 1998). Heterobathmiidae moths are found on the flowers of beech trees (*Nothofagus*) and are considered to be pollen-feeders (Kristensen, 1998).

The mouthparts of the various groups of basal Lepidoptera show striking resemblances to each other as seen in *Micropteryx* (Fig. 64) (Hannemann, 1956; Chauvin and Faucheux, 1981), *Sabatinca* (Tillyard, 1923) and *Heterobathmia* (Kristensen and Nielsen, 1979). They retain the complete set of orthopteroid structures and show adaptations to pollen-feeding. Pollen is harvested directly from the anthers by a scraping motion of the long maxillary palps. Pollen adheres to the terminal palpal segments which bear blade-like structures and mushroom-shaped setae (Fig. 64A) (Chauvin and Faucheux, 1981). The pollen is transferred to the galeae and laciniae which convey it to a preoral cavity (infrabuccal pouch) (Hannemann, 1956), which is found in



Figs. 61–63. Mouthparts of pollen-feeding Xyelidae (scanning electron micrographs). Fig. 61. *Xyela alpigene* head with mouthparts, large maxillary palp (mxp); mandible (ma). Fig. 62. *Xyela alpigene* hook-shaped terminal section of maxillary palp (mxp); labial palp (lp) with sensilla cluster (s); labrum (lb); mandible (ma). Fig. 63. *Xyela alpigene* view of labium with labial palps (lp) and glossa (gl) flanked by smaller paraglossae; prementum (pm).



Figs. 64–66. Mouthparts of pollen-feeding Lepidoptera (scanning electron micrographs). Fig. 64. Grinding mouthparts of *Micropterix aruncella* (Micropterigidae); tip of maxillary palp (mxp) takes up pollen which possibly adhere to the mushroom shaped bristles of the terminal palp segment (inserted photo A); pollen (po) is ground between the mandibles (ma) which is shown in a head semithin section, photo (B); galea (ga), labium (la); labrum (lb). Fig. 65. Head of female *Tegeticula yuccasella* (Prodoxidae); first segment of the maxillary palp (mxp) extends into a tentacle (te). This novel mouthpart structure is coiled lateral to the proboscis (p) and is used for pollen collection and pollination of yucca flowers. Photo (A) shows details of the annulated tentacle wall which is equipped with hooked bristles and microtrichia. Fig. 66. Pollen extracting proboscis of *Heliconius hecale* (Nymphalidae); pollen (po) is attached outside on the proboscis by salivary fluid and is agitated by uncoiling and coiling of the proboscis; in this way the salivary fluid extracts amino acids from the pollen grains. Proximal region of the proboscis is equipped with numerous long sensilla trichodea (str) in the region where the pollen load is formed (photo A).

Micropterigidae, Aglossata and Heterobathmiidae (but not Glossata) (Kristensen, 1984). The mandibles receive the pollen and grind it like a mortar and pestle with their asymmetrically modified bases (Fig. 64B). The right base is depressed to receive the projecting molar of the left mandible. The ground pollen is eventually directed to the mouth by asynchronous movements of the mandibles over the epipharynx, which is asymmetrically sclerotized and covered with setae (Hannemann, 1956).

3.5.2. Pollen-collecting yucca moths

The specialized pollination relationship between yucca plants (Agavaceae) and yucca moths, *Tegeticula* and *Parategeticula* (Prodoxidae) is an excellent example of one-to-one coevolution (reviewed by Powell, 1992; Pellmyr, 2003). Adult female moths harvest pollen and pollinate yucca flowers with the help of long tentacular appendages on the mouthparts. In pollinating species of *Tegeticula* a setose tentacle arises from the distal portion of the first

segment of the maxillary palp and is about as long as the proboscis (Fig. 65) (Pellmyr, 1999). Its surface is annulated, covered with dense microtrichia and bears a large number of hook-tipped trichoid sensilla giving this organ a setose appearance (Fig. 65A) (Pellmyr and Krenn, 2002). The tentacles rake pollen from the anthers and together with the forelegs compress it for storage under the head. Female moths do not feed on the collected pollen, instead they lay eggs into the floral ovary on a suitable flower of the host plant and subsequently they remove a small portion from the pollen batch with the tentacles to pollinate this flower (reviewed and illustrated by Pellmyr, 2003). The larvae feed on the developing seeds. The tentacle is capable of coiling and contains a prominent longitudinal musculature consisting of numerous small muscles, which are distributed mostly along the ventrolateral walls. These muscles permit recoiling and are distinctly separate from muscles attached to the base of the second segment of the maxillary palp which serve as flexors and extensors (Pellmyr and Krenn,

2002). The complexly shaped tentacle is unique and not homologous to any structure found in related prodoxide moths. Since, it shares similarities with the galea, the tentacle may have evolved by ontogenetic duplication of the galea at an apical growth bud on the first segment of the maxillary palp (Pellmyr and Krenn, 2002).

3.5.3. Pollen-nutrient extracting nymphalidae

Although butterflies regularly come into contact with pollen, only representatives of *Heliconius* and *Laparus* (Nymphalidae) feed on pollen of particular plants using their proboscis (Fig. 66) (Gilbert, 1972; Boggs et al., 1981; Estrada and Jiggins, 2002). The long nectaring proboscis is morphologically similar to that in related non-pollen-feeding nymphalids, except for the greater number and length of sensory bristles in the proximal region of the galeae (Fig. 66A) (Krenn and Penz, 1998). Flower-probing movements occur conspicuously longer on individual flowers when collecting pollen so that eventually pollen adheres and accumulate on the proboscis (Penz and Krenn, 2000). The grains are suspended, presumably, in saliva on the outside of the proboscis and are agitated for hours by coiling and uncoiling movements of the proboscis. During this process amino acids are extracted from the pollen grains. The resulting liquid is ingested and subsequently the pollen grains are discarded. Consumption of pollen benefits the development of eggs in females, the production of nuptial gifts and heightens longevity in these butterflies (Gilbert, 1972; Dunlap-Pianka et al., 1977; Boggs et al., 1981).

3.6. Diptera

Pollen-feeding represents derived behavior for Diptera

and must have evolved several times independently in the major groups of flower-visiting flies. Detailed accounts of pollen-feeding exist for the Syrphidae (Holloway, 1976; Gilbert, 1981; Schuhmacher and Hoffmann, 1982), Drosophilidae (Nicolson, 1994), Ceratopogonidae (Downes, 1955) and, to some extent, Bombyliidae (Szucsich and Krenn, 2000). Diptera from numerous other families are reported to feed on pollen, i.e. Bibionidae, Mycetophilidae, Simuliidae, Scatopsidae, Empididae, Calliphoridae, Scatophagidae, Anthomyiidae, Muscidae and Tachinidae (Table 5). Pollen-feeding flies generally also consume nectar; only a few syrphid flies feed nearly entirely on pollen (Gilbert, 1981).

3.6.1. Pollen-feeding mechanisms and behavior

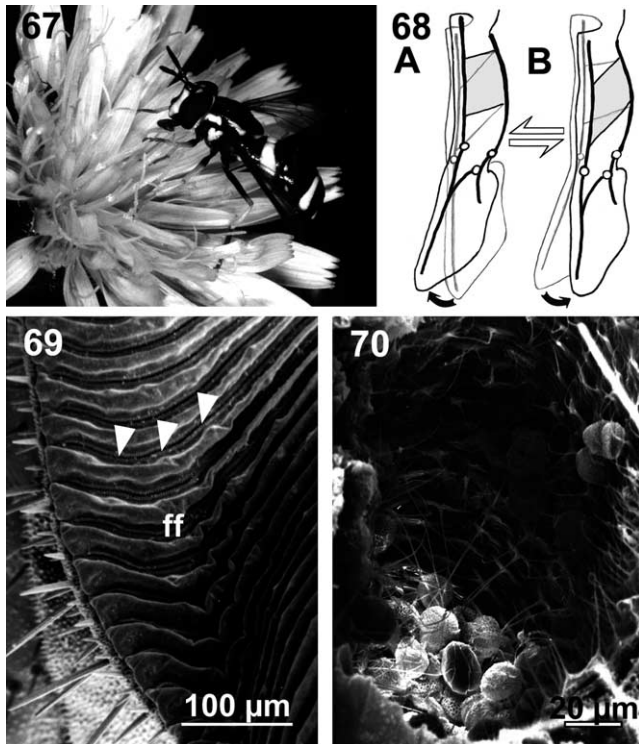
In most Syrphidae the labella are vital both for gathering pollen from the anthers and for conveying it to the labral food canal. Pollen is harvested in some Syrphidae by a repeated tapping movement of the opened oral disc of the labella directly on the anthers; pollen adhering to it is ingested (Fig. 67) (Szucsich, pers. obs.). In other Syrphidae and Bombyliidae the labella surround the anthers and perform rubbing and twisting movements to scrape off pollen (Fig. 68) (Dimmock, 1881; Gilbert, 1981; Szucsich and Krenn, 2002). The labella are released from the anthers and fold together capturing pollen between them. Finally, pollen is also conveyed to the mouth by movements of the forelegs either by self-grooming as described for *Eristalis* (Syrphidae) (Holloway, 1976) or directly from anthers as in various Bombyliidae (Deyrup, 1988; Neff et al., 2003).

Schuhmacher and Hoffmann (1982) assume the inter-pseudotracheal folds to be the key feature for transfer of pollen from the labella toward the epipharyngeal food canal.

Table 5
Dipteran families mentioned to include pollen-feeding representatives in literature

	Families	Proctor et al., 1996	Gilbert and Jervis, 1998	Larson et al., 2001	Additional references	
'Nematocera'	Ceratopogonidae		+	+	Downes, 1958	
	Bibionidae	+			Willis and Burkill, 1895–1908	
	Mycetophilidae	+			Willis and Burkill, 1895–1908	
	Scatopsidae	+		+	Willis and Burkill, 1895–1908	
Brachycera	Simuliidae				Wenk, pers. comm.	
	'Orthorrhapha'			??		
	Acroceridae			??		
	Bombyliidae	+	+	+	Deyrup, 1988; Neff et al., 2003; Szucsich and Krenn, 2000, 2002	
	Cyclorrhapha	Empididae		+	+	
		Syrphidae	+	+	+	Gilbert, 1981; Haslett, 1983
		Drosophilidae		+		Nicolson, 1994
		Scatophagidae			+	
		Calliphoridae	+			
		Muscidae	+		+	Kevan, 1972
Anthomyiidae	+		+	Kevan, 1972		

Paraphyletic groups in quotes.



Figs. 67–70. Pollen-feeding in Diptera. Fig. 67. *Chrysotoxum bicinctus* (Syrphidae) feeding on pollen. Fig. 68. Labellar movements while feeding on pollen. A rubbing motion is achieved by counteracting movements of the adjacent labella (compare Fig. 40a, b). Circles indicate positions of joints, intrinsic muscle of the labial stalk (mls) shaded in gray. Fig. 69. Labella of *Eristalis tenax* (scanning electron micrograph). Food furrows (ff) overlying the pseudotracheae (arrow heads), through which, according to Schuhmacher and Hoffmann (1982), pollen is transported toward the food canal. Fig. 70. Pollen in esophagus of *Bombylius major* (scanning electron micrograph) indicating that intact pollen grains are consumed.

A change in hemolymph pressure causes membranes between the pseudotracheal canals to fold outward, creating furrows overlying the pseudotracheal canals (Fig. 69). When the inner matching surfaces of the labella are juxtaposed, the furrows from each labellar half unite to form numerous tiny food-tunnels with diameters that correspond to the size of the pollen grains taken by the flies (Schuhmacher and Hoffmann, 1982). Saliva flows through the pseudotracheal canals and into the food-tunnels where it mixes with the pollen. The liquid mixture is conveyed by action of the pre-labral pump toward the epipharyngeal food canal, reversing the course taken by the saliva. The extent to which food furrows overlying the pseudotracheae represent an adaptation for pollen-feeding is questionable, since they are lacking, e.g. in *Bombylius major* a species which is known to feed on pollen (Fig. 70) (Szucsich and Krenn, 2002).

Since, intact pollen is suspended in fluid prior to uptake only few mouthpart features evolved in this context. Gilbert (1981) found a high correlation between number and density of pseudotracheae and pollen-feeding in Syrphidae. He deduced that broad and fleshy labella might be

advantageous in pollen-feeding since they reduce the time required to crop pollen from anthers and thus increase the rate of ingestion. Species with narrow labella (e.g. *Eristalis tenax* and *Rhingia campestris*) were shown to feed to a minor degree of pollen (Haslett, 1983). Both species have short labellar hairs whereas the hairs are much longer in pollen-feeding species (Gilbert, 1981). Wacht et al. (2000) studied the chemosensory control of pollen ingestion by labellar taste hairs in the hoverfly *Eristalis tenax* and found that the salt receptor cells were sensitive to proline, an amino acid commonly found in pollen. Holloway (1976) noted that *Eristalis* uses its legs to collect pollen and regarded cleaning behavior in which pollen grains adhering to the body are combed to the mouthparts as an adaptation to pollen-feeding. Legs as pollen collecting organs were likewise described in different Bombyliidae (Deyrup, 1988; Neff et al., 2003).

Gilbert and Jervis (1998) predicted a syndrome of short mouthparts with broad labella and a large number of pseudotracheal channels in all Diptera that mainly feed on pollen. However, at least in *Bombylius major*, a species with a highly elongated proboscis, pollen-feeding is clearly established (Deyrup, 1988; Grimaldi, 1988). The maneuverability of the labella suggests the same principle mechanism as described in Syrphidae (Szucsich and Krenn, 2002). Although pollen-feeding is widespread in Diptera no species have been identified which display mouthpart structures exclusively for pollen-feeding (Gilbert and Jervis, 1998). The only described adaptations to pollen-feeding are the labellar food furrows (Fig. 69) (Schuhmacher and Hoffmann, 1982) and the rubbing labella movement (Fig. 68). A clear adaptational value of either is questionable, since the food furrows are lacking in many pollen-feeders but are present in species that do not feed on pollen, while the latter can presumably be recruited from grooming movements.

Pollen-suspension is the most common feeding method by which intact pollen grains (Fig. 70) are mixed with exuded saliva and the resulting highly viscous mixture is ingested. Since Dipteran mouthparts in their ancestral condition are already adapted to fluid-feeding, there are few mouthpart specializations for pollen consumption. Pollen-nutrient extraction is another technique used, for example, in *Erioschia brassicae* (Anthomyiidae) which feeds on grass pollen (Finch, 1974). In *Drosophila flavohirta* pollen accumulates on the ventral surface of the proboscis and its nutrients are subsequently extracted by rapid vibrations of the proboscis (Nicolson, 1994). Pollen-piercing is utilized by females of *Atrichopogon pollinivorus* (Ceratopogonidae) (Downes, 1955).

4. Petal-feeding

Insects from various orders are reported to feed occasionally on floral tissues (Table 6). The majority of

Table 6
Representatives of the listed taxa at least occasionally feed on petals, all with unmodified mouthparts

Taxon	Mouthpart category	References
Orthoptera Tettigoniidae	Biting/chewing mouthparts	Porsch, 1957; Schuster, 1974; Kevan and Baker, 1983
Dermoptera Forficulidae	Biting/chewing mouthparts	Porsch, 1957; Kevan and Baker, 1983
Thysanoptera Coleoptera Scarabaeidae, Elateridae, Cleridae, Nitidulidae, Chrysomelidae, Staphylinidae, Meloidae, Cerambycidae, Mordellidae, Oedemeridae, Melyridae	Piercing/sucking mouthparts Biting/chewing mouthparts, many taxa also feed on nectar and pollen	Hagerup, 1950; Kirk, 1984 Kevan and Baker, 1983; Scholtz and Holm, 1985; Gottsberger, 1989a,b
Hymenoptera Cimbicidae, Tenthredinidae	Biting/chewing mouthparts	Kevan and Baker, 1983; Jervis and Vilhelmsen, 2000

them are destructive to the plants and do not pollinate with the exception of some beetles and thrips.

Many florivorous Thysanoptera feed on petals by piercing plant cells with their mandible and maxillary stylets and ingest fluid from the ruptured cells (Moritz, 1982; Hunter and Ullman, 1989). However, there is no evidence that species found in flowers evolved specialized mouthparts for floral tissue (Mickoleit, 1963).

Petal-feeding Coleoptera belong mainly to Nitidulidae, Curculionidae, Scarabaeidae and in particular the genus *Cylcocephala*. They are attracted by the fruity odor of flower-petals particularly of basal angiosperms such as Annonaceae. The flowers of these plants trap the beetles inside where they feed on the fleshy tissue of the petals and become covered with pollen (Gottsberger, 1989a,b, 1999). The beetles have well-sclerotized mandibles to bite off and chew small pieces of tissue, while maxilla and labium manipulate the food (Proctor et al., 1996). Similarly meloid beetles of the genus *Mylabris* are reported to predominantly feed on petals and have unmodified chewing mouthparts (Scholtz and Holm, 1985). Although it is commonly asserted that mouthparts are unmodified in petal-feeding Coleoptera, their morphology has not been adequately examined.

Floral tissue is an uncommon source of food for adult Hymenoptera, being reported in some species of *Corynis* (Cimbicidae) and *Tenthredo* (Tenthredinidae). The food sources utilized by these sawflies range from nectar, pollen, arthropod prey, floral tissue to tree sap, in particular in the specious genus *Tenthredo* (Liston, 1980; Jervis and Vilhelmsen, 2000).

5. Discussion

Insects which regularly feed on nectar or pollen stem largely from the holometabolous orders Coleoptera, Hymenoptera, Diptera and Lepidoptera. In addition, few representatives of Neuroptera and possibly some Trichoptera are specialized on floral foods. Non-holometabolous insects

except some Thysanoptera feed only occasionally on flowers (e.g. Kevan and Baker, 1983; Proctor et al., 1996). Mouthpart adaptation to nectar uptake and pollen-feeding are found only in Holometabola, probably because complete metamorphosis permits a radical differentiation of mouthparts between larva and adults. Why only few non-holometabolous insects regularly consume nectar or pollen is not entirely certain. Larvae of Holometabola normally do not feed on nectar or pollen (except when provisioned by females), possibly because single flowers offer insufficient quantities of food and due to the absence of flight and search abilities of immature insects.

5.1. Nectaring proboscides

One of the more remarkable modifications of insect mouthparts is the development of a nectaring proboscis which copes with minute amounts of nectar in various degrees of viscosity and with floral architecture that may obstruct the nectaries. Mechanisms responsible for the uptake and ingestion of nectar include adhesion, capillarity, proboscis movements such as lapping or sponging, suction pumps and the application of saliva. Nectaring proboscides have evolved once in Lepidoptera, in a few Coleoptera, many Hymenoptera and several lineages of Diptera. In flower visitors with rather short to moderately long proboscides, fluid initially adheres to a distal and expandable uptake region and is then conveyed along a food route to the mouth by capillary force, suction and sometimes proboscis movements. In Hymenoptera nectar loading usually occurs on the wettable and hairy glossa (sometimes also paraglossae) in conjunction with licking movements. In Diptera the distal parts of the labium, the broadened and spreadable labella, are equipped with a system of minute channels (pseudotracheae) for loading liquids. These methods of fluid feeding proceed by adhesion and rely on the hydrophilic properties of the cuticle particularly along the food conduction area. The possibility that a combination of hydrophilic and hydrophobic cuticle areas may

substantially direct the passage of fluids through the mouthparts is unexamined. The adhesive mode is prevalent in the mouthparts of most Hymenoptera and in short-tongued flies and probably in beetles and it is regarded to be ancestral. It forms the basis for general fluid feeding and explains why a wide array of insects without mouthpart specialization can facultatively feed on floral nectar.

In contrast to adhesion modes, a predominantly sucking mode of fluid feeding is found in some of the long proboscides of nectar-feeding insects. The flow of nectar along the food canal is primarily achieved by a pressure gradient produced by muscular pumps. Capillary forces and adhesion are of minor functional importance. Biomechanical reasoning holds that extremely long mouthparts should be restricted to low viscous nectar (Kingsolver and Daniel, 1995). However, the role of saliva as a diluting factor was not taken into account and may be important in butterflies (Eberhard and Krenn, 2003). Suctorial proboscides are characterized by a lack of direct feeding movements (such as licking, sponging, sweeping), a sealed food canal and a modified uptake region. They are especially associated with removal of nectar from long and narrow tubular flowers. These greatly elongated proboscides have evolved convergently with different components in various lineages of Hymenoptera, on multiple occasions with similar composition in Diptera and only once in the glossatan Lepidoptera. In some taxa the proboscis attains a length several times that of the body. It is presumed that the extremely long proboscis in sphingid moths is the result of co-evolution with the long-spurred orchids that these moths pollinate (Nilsson, 1988, 1998). However, it was alternatively suggested that extremely great lengths might have evolved to ensure a safe distance between the hovering moth and potential predators (e.g. spiders) lurking on the flower (Wasserthal, 1997).

Formation of a closed food canal is essential for the operation of a nectaring proboscis. The tube may be composed of multiple components (e.g. galeae and labial palps), of a single paired element (e.g. interlocking galeae) or a highly modified unpaired element (e.g. the glossa of pollen-wasps). In many Hymenoptera the food canal is assembled anew for each feeding act then disassembled when not in use. In Diptera and Lepidoptera the components of the food canal are permanently sealed together by interlocking structures. The biomechanics of temporarily closed or permanently sealed structures have received scant attention.

The existence of hydraulic mechanisms for proboscis movement has been verified in Lepidoptera (Bänziger, 1971; Krenn, 1990; Wannemacher and Wasserthal, 2003). These mechanisms have also been proposed to play a role in certain proboscis movements of Hymenoptera (Snodgrass, 1956) and Diptera (Van der Starre and Ruigrok, 1980). Hydraulic means are particularly important in long, narrow and tubular mouthparts since the muscle bulk required to create increased hemolymph pressure can be located in the

head or basal regions of the proboscis whereas large internal proboscoidal muscles would be weighty, space-consuming and would require greater proboscis diameters.

The separation between feeding and resting positions, i.e. between full extension and complete retraction, of nectaring proboscides is widespread except in some Diptera. Different resting positions evolved in various insects with greatly elongate proboscides presumably to reduce the drag in flight and in this context new mechanism of movements evolved that likewise are used for flower handling. At rest the proboscis may be folded under the body (e.g. in bees), held forward projecting in front of the body (e.g. beeflies) or coiled up under the head (in butterflies and moths).

5.2. Evolutionary pathways

The evolution of nectaring proboscides in Hymenoptera has undoubtedly proceeded from the short, unspecialized labiomaxillary complex, which still occurs widely throughout the order. It led first to the development of a short proboscis specialized for nectar-feeding, then to long and very long formations. Each mouthpart category represents a structural/functional stage that ultimately places limitations on further lengthening and which cannot be escaped without considerable morphological changes. A short nectaring proboscis has developed well over 100 times convergently in the Hymenoptera and a long proboscis perhaps about 25 times. Bumblebees have taken a step toward the development of a stationary suctorial proboscis by partial suppression of licking movements. Very long proboscides that have been shown to be largely suctorial have evolved on few occasions (Euglossini bees, pollen-wasps). Though, the mode of feeding is not known in other bees with very long proboscides (e.g. Anthophorini, *Melitoma*, Lithurginae, *Nolanomelissa*).

Multiple taxa of Diptera have convergently made the behavioral shift from a generalized liquid diet to specialization on nectar. Since the uptake of fluids is the ancestral mode of feeding in this order, it is often difficult to identify morphological adaptations specific to nectar-feeding. One of the early steps in the evolution of a relatively short nectaring proboscis was a broadening of the labella and increased participation of labellar movements during fluid uptake. The evolution of a purely suctorial mode of nectar-feeding, often accompanied by proboscis elongation, is characterized by a reversal of these trends, i.e. a narrowing of the labella and reduction of feeding movements. Extremely elongated sucking proboscides have arisen either from sponging/sucking mouthparts of short-tongued flower-visiting flies, such as some Bombyliidae and Syrphidae or from piercing/sucking mouthparts of blood-feeding and predatory groups, e.g. Culicidae, Tabanidae and Empididae.

In contrast to Hymenoptera and Diptera, the construction

of the suctorial proboscis of Lepidoptera is astoundingly uniform and probably evolved only once. It is thus regarded as a morphological key innovation of the Glossata. This means that a single evolutionary event must have occurred centering on the transition in adult food preferences from the ancestral diet of non-floral fluids to nectar (Pellmyr, 1992). The proboscis of the nectar-feeding Eulepidoptera (Kristensen, 2003), which contains more than 100,000 species, exhibits several modifications from the ancestral suctorial proboscis morphology including elaborate proboscis linkage, new sensory equipment and modified intrinsic galeal musculature (Krenn and Kristensen, 2000, 2004).

In rare cases a highly advanced nectaring proboscis has undergone further modification in accord with a change of diet. Studied mainly in Lepidoptera, representatives of several lineages have switched from nectar to alternative liquid foods, such as juice of rotting fruits, decaying organic matter, wound exudates, lachrymal fluid and blood (reviewed by Scoble, 1992). All derived feeding preferences are correlated with specialized external features of the proboscis (e.g. Bänziger, 1970; Büttiker et al., 1996; Krenn et al., 2001; Knopp and Krenn, 2003). The blood-sucking mouthparts of some muscoid flies (e.g. *Stomoxys*) are probably derived from general fluid feeding mouthparts which also serve for nectar consumption. However, many species from various taxa either no longer feed on nectar or only imbibe water with their rudimentary mouthparts. Some lepidopteran species with a secondarily shortened proboscis exhibit a behavior by which large amounts of water, and thus minerals, are ingested (Smedley and Eisner, 1995).

5.3. Mouthparts and pollen-feeding

Pollen feeders must cope with the task of gathering a more or less sticky powder of small durable particles which is available in small quantities on flowers. Many facultatively flower-visiting insects (e.g. beetles) feed on pollen from openly accessible flowers with unspecialized orthopteroid biting/chewing mouthparts, which serve equally well for the intake of nectar and for chewing petals. The same is true for flower-visiting Thysanoptera, which use their unmodified mouthparts to pierce single pollen grains and cells of floral tissue.

Most obligate pollen-feeding insects, however, have specialized mouthparts for efficient pollen harvest and ingestion. Structural adaptations of the mouthparts for pollen-feeding are less evident than those for drinking nectar. They include specialized bristles, which form combs and brushes to gather pollen in many Coleoptera. The mouthpart modifications partly resemble those of spore-feeding mycophagous beetles (Betz et al., 2003). Mandibular movements serve to convey pollen to the mouth where intact pollen is ingested. The assumption that the symmetrical mandibles are used to crush pollen grains has not been substantiated (Roulston and Cane, 2000). More likely pollen

grains are macerated and enzymatically broken down in the gut (Johnson and Nicolson, 2001). Pollen grains, however, are crushed by asymmetrical mandibles in Micropterigidae (Lepidoptera) and possibly also Xyelidae (Hymenoptera). In both groups the asymmetrical mandibles function in a mortar and pestle fashion to grind pollen prior to ingestion. The consumption of whole pollen grains is achieved in the typical dipteran proboscis by suspending pollen in salivary fluid and subsequently sucking up the mixture. In Micropterigidae special bristles help attach the pollen grains to the mouthparts. Likewise hooked setae on the mouthpart tentacle of female yucca moths are crucial in pollen loading and modified bristles play a major role in attaching pollen to the suctorial proboscis of *Heliconius* butterflies. The latter do not ingest pollen but externally extract its nutrients in salivary fluid (Boggs, pers. comm.). At least one species of *Drosophila* and possibly some Anthomyiidae extract pollen nutrients externally on the mouthparts similar to *Heliconius* butterflies. In summary, it can be concluded that mouthparts of pollen-feeding insects are characterized by specialized bristles that form devices to retain and transport pollen; furthermore, saliva is particularly important during pollen-feeding.

The extent to which mouthparts are involved in pollen acquisition, manipulation and ingestion varies in adult insects. They may play little or no role in the initial procurement of pollen or its digestion. In bees, some flies and beetles, for example, pollen adhering to hairs of the head may be collected by grooming movements of the forelegs and directed to the mouthparts. Many bees and bee flies also harvest pollen directly from anthers with unspecialized mandibles or hairbrushes and combs on the forelegs. Pollen collection and transport is also found in fig wasps; however, the pollen is not consumed and the mouthparts reportedly play no role (Cook and Rasplus, 2003).

Mouthparts that serve well for both nectar and pollen-feeding are found in Coleoptera, Hymenoptera, *Heliconius* butterflies (Nymphalidae) and some Diptera. The hairy mouthparts of Coleoptera can simultaneously take in nectar and pollen. In pollen extracting *Heliconius* butterflies and suspension feeding Diptera (e.g. some Syrphidae) the mouthparts and their movements, which are adapted to nectar drinking, are only slightly modified for pollen consumption. The various techniques for harvesting pollen and acquiring its nutrients are reflective of multiple evolutionary origins from different plesiomorphic modes of feeding within various lineages of insects. Specialized pollen feeding in adult insects has evolved from carnivory (in some beetles e.g. Malachiidae), from nectar-feeding in various Diptera (e.g. Syrphidae) and Lepidoptera (*Heliconius*), from spore-feeding in aglossatan Lepidoptera and from generalized phytophagous or petal-feeding beetles (e.g. Scarabaeidae).

The earliest fossil insects which presumably fed on pollen and/or floral tissues are Coleoptera from the

Cretaceous period (Grimaldi, 1999). These early flower-visiting beetles, together with other insects with generalized feeding habits, such as mandibulate moths, sphecid wasps and short-tongued flies, are cited by Grimaldi (1999) to mark the evolutionary onset of insect-angiosperm pollination. In particular, the variety of early Diptera is regarded as decisive for the pollination and evolution of early Cretaceous flowering plants. Fossil evidence shows that the evolution of bees, Masarinae, Ditrysia and Syrphidae occurred after radiation of the major lines of Angiosperms. The earliest record of greatly elongated mouthparts and thus presumably nectar-drinking, is attributed to the lower Brachycera, such as Nemestrinidae from the Upper Jurassic (Ren, 1998); however, Grimaldi (1999) argues that these flies may instead have fed on gymnospermous pollen.

5.4. Outlook

The best studied examples of mouthparts in flower-visiting insects are the proboscides of butterflies and bees. They have been investigated from morphological, functional, evolutionary and ecological points of view. Variation in the mouthparts of Hymenoptera and Diptera is complex and diverse and it warrants further study. The extremely long proboscis in many Diptera has only been examined superficially, in particular, the Nemestrinidae, which possibly possess the phylogenetically earliest nectaring proboscis. Mouthpart morphology and feeding ecology in minor groups of flower-visiting insects such as Coleoptera, Neuroptera, Trichoptera and others, which infrequently visit flowers are not well-known and deserve future investigation. The study of insect feeding and the corresponding mouthpart adaptations contribute to our understanding and reconstruction of the evolution of one of the most important global plant-animal interactions, namely angiosperm pollination, which has become one of the major ecological fundamentals of the present world.

Acknowledgements

The authors wish to thank S. Schödl (Nature History Museum, Vienna) for permission to examine material in the Hymenopteran collection. In addition we thank P. Huemer (Tiroler Landesmuseum, Innsbruck), S. D. Johnson (University of Natal), N. P. Kristensen (Zoologisk Museum, København), V. Mauss (Staatliches Museum für Naturkunde), E. Meyer (University of Innsbruck), H. F. Paulus (University of Vienna), O. Pellmyr (University of Idaho) and C. M. Penz (Milwaukee Public Museum) for providing material. We are indebted to G. Dutzler-Stark, U. Hannappel, S. Matus, and A. Pernstich for technical help; to the EM-laboratory of T. Klepal (Institute of Zoology, University Vienna) for use of their facilities and to G. Spitzer and D. Gruber for assistance.

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