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# DIPLOMARBEIT

Titel der Diplomarbeit

„Euglossini (Hymenoptera, Apidae):
Fluid feeding mechanisms and functional morphology of the proboscis“

verfasst von

Maria Helene Gruber

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# Contents

# 1 Introduction

## 1.1 Long-tongued insects and the evolution of suction feeding

Feeding on nectar requires specialized mouthparts that allow for the ingestion of fluids. Insects that primarily feed on nectar occur mostly in the Hymenoptera and Lepidoptera, but also a good number are representatives of Diptera and a few are Coleoptera (Proctor et al. 1996, Krenn et al. 2005).

From an evolutionary viewpoint nectaring proboscides of Hymenoptera are derived from the short and functionally united maxillae and labium, termed the labiomaxillary complex, which is characteristic in all groups of this order. Specializations first led to short proboscides for nectar-feeding, then to structures longer than the head and subsequently to extremely long formations which may exceed the body length in some taxa. It was assumed that long proboscides have evolved about 25 times convergently in Hymenoptera. Therefore many different mechanisms for nectar feeding can be found in the various taxa. Nectar uptake and ingestion can be accomplished by adhesion, capillarity, lapping, sponging, suction feeding, as well as the application of saliva and subsequent uptake. In Hymenoptera, the basic feeding mode of the labiomaxillary complex is a combination of lapping and sucking (Krenn et al. 2005).

In some of the long proboscis nectar-feeding insects, e.g. butterflies and moths, a predominately sucking mode of fluid feeding is present. The necessary pressure gradient for nectar uptake is primarily produced by cephalic muscular pumps. In this case capillarity and adhesion are of minor functional importance. Nectar-feeding insects with very long proboscides should be therefore more profitable using low viscous nectar (Kingsolver & Daniel 1995).

A closed food tube is essential for nectar intake along a pressure gradient. The food tube varies in form and function in Lepidoptera, Diptera and Hymenoptera. In Diptera and Lepidoptera the mouthparts form a food tube which is permanently sealed (Krenn et al. 2005). However, this is not the case in bees.

## 1.2 The feeding mechanism of bees and the functional regions of the proboscis

As in all insects, the mouthparts of bees consist of 4 modified extremities, namely (1) the unpaired labrum, (2) the paired mandibles, (3) the paired maxilla, and (4) the unpaired labium (Zander 1946).

Nectaring mouthparts have been studied extensively in honey bees and can be used as a model for Apidae, i.e., Apini, Bombini, Meliponini and Euglossini. According to the detailed morphological description of honey bees by Snodgrass (1956, 1993), the mandibles lose the typical biting form and have acquired a more or less flattened or spoon shape. The proboscis (Fig. 1, **A**) is composed of the parts of the maxillae and the labium coming together to form the labiomaxillary complex, which is lengthened in *Apis mellifera.* The galeae (Ga) are large flat blades and much longer than the basal part of the maxillae, the stipites. The laciniae are reduced or absent. The maxillary palps (MxPlp) vary in length in various bee genera and are reduced in *Apis*. The glossa (Gl) of the labium is greatly lengthened and capable of an active movement of pro- and retraction. The relatively small paraglossae embrace the glossa on its base. The labial palps (LbPlp), parts of the distal labium, are long and four-segmented, the two basal segments are elongated, and the two distal segments are very small. The basal part of the labium is composed of the prementum (Prmt) and the mentum (Mt), while the lorum (Lr) articulates with the maxillary cardines. The base of the ligula (glossa + paraglossae) and the membranous palpigers are partly retractile into the prementum. The glossa is long and hairy except at its base and terminates in the flabellum (Fbl) (Snodgrass 1993).

To feed, honey bee workers unfold the protracted proboscis and assemble the parts of maxillae and labium into a temporary food tube (Fig. 1, **B**). During feeding the maxillae remain relatively motionless, whereas the protracted glossa of the labium (Fig. 1, **C**) performs licking movements (Snodgrass 1956). Further, the proboscis extension depends on the activity of muscles associated with the mouthparts. During extension of the glossa, nectar moves onto it by capillarity. The fluid on the surface of the glossa causes the hairs of the glossa into an erected position so that the volume of fluid that is held between hairs is increased (Chapman 2013).

Presumably, the hair erecting is caused not only by contact with the liquid. Simpson & Riedel (1964) assume a relation between protraction and retraction of the glossa. When

the glossa is fully protracted, the membrane between each row is stretched and the bristles spread out. When the glossa is retracted, the tension of the glossal surface is relaxed and the bristles flatten (Fig. 1, **D**).

When the glossa is retracted into the food tube formed by the galeae and labial palps, the fluid is drawn into the cibarium by pumping action. In Hymenoptera the cibarial pump is functionally combined with a pharyngeal pump which has dilator muscles arising from the frons (Chapman 2013). Cephalic fluid pumps are present in all fluid-feeding insects, and are not restricted to obligatory nectar-feeders (Borrell & Krenn 2006).

Kingsolver & Daniel (1995) described the glossal movements as a three-phased licking cycle: (1) glossal extension, during which nectar is loaded onto the surface of the hairy glossa, (2) glossal retraction, during which the loaded nectar is drawn into the food tube and (3) the unloading phase, during the nectar is removed from the glossa and transported into the mouth.

When the proboscis of euglossines is not in use, the base of the glossa is retracted, and together with the labial palps and the galeae, it folds backward under the head and body (Krenn et al. 2005). Retraction of the glossa is caused by partially coiling at the base of the glossal rod into the apical region of the prementum (Snodgrass 1956, Simpson & Riedel 1964).

Fluid-feeding insects usually have chemoreceptors on the tip of the labium, on the palps, and in the walls of the cibarium (Chapman 2013). Galić (1971) examined the sensillae on the glossa, epipharynx, and hypopharynx of workers of the honey bee (*Apis mellifera*). The sensillae on the glossa are categorized as sensillum chaeticum. They probably have a chemo-mechanoreceptive function. On the epipharynx there are two sensory fields, the tips of the sensory organs are directed against the food stream. They are probably of the type sensillum trichodeum and function as contact-chemoreceptors. The hypopharynx possesses paired sensory fields near the hypopharyngeal glands. Orientation and arrangement of the sensilla are very uneven and belong to the morphological category of sensillum basiconicum, which probably function as chemosensillae.

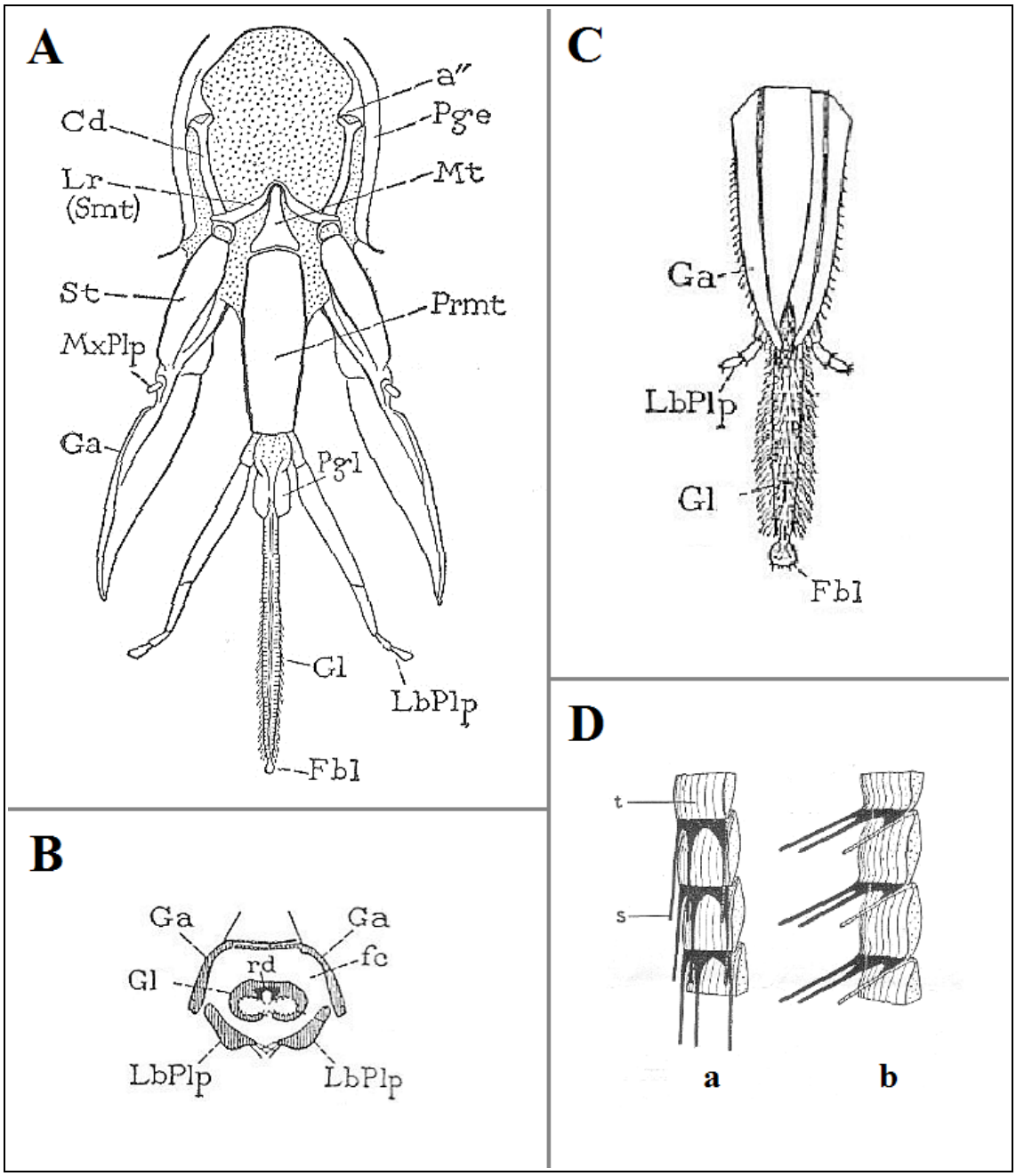


Fig. 1: **A** Schematic representation of the labiomaxillary complex of *Apis mellifera*, worker. **B** Cross section through distal part of proboscis. **C** Distal parts of proboscis in functional position, glossa protracted, anterior. **D** Portions of glossa wall showing bristles flat (**a**) and erect (**b**). The bristles are shown shorter than they are. Figure A is refered to Snodgrass (1993), figures B and C are modified after Snodgrass (1956), and figure D is refered to Simpson & Riedel (1964).

## 1.3 Form and function in short- and long-tongued bees

Since Kirby (1802) (cited in Engel 2001), bees have been segregated into major groups, the short- and long-tongued bees. Long-tongued families (Megachilidae and Apidae) have the first and second segments of the labial palps sheath-like (i.e., elongate and flattened), while short-tongued families (Colletidae, Halictidae, Andrenidae, Paleomelittidae, and Melittidae) typically have these same segments cylindrical and more or less similar to the following segments (Engel 2001).

The main function of the proboscis of bees is for the uptake of nectar. There are few comparative studies on the differences in the movements of the proboscis during the nectar intake and ingestion rates between short- and long-tongued bees. According to Harder (1982) and Snodgrass (1956), a long-tongued bee (*Bombus pensylvanicus* and *Apis mellifera*) holds its maxillae and prementum relatively stationary. In the tube formed by the galeae and labial palps, the glossa reciprocates. Observations on a feeding short-tongued bee (*Andrena carlini*) show that the prementum moves with the lapping movements of the glossa, stretching and retracting with each lapping cycle (Harder 1983b). On the basis of the observed different movements, Harder (1982, 1983b) assumes that the functional unit of the proboscis of the short-tongued bees is the labium, while in long-tongued bees the glossa is the main part. He also pointed to the lengthened and flattened labial palps, which have evolved in long-tongued bees. These changes in shape could be a result of the impossibility of full retraction of long glossae (Harder 1983b).

Most of the work is based upon research of *Apis* and *Bombus*, both representatives of the so-called long-tongued bees. Within this group are representatives that extend the proboscis far beyond that in *Apis* or *Bombus*.

The proboscis in representatives of the orchid bees (Euglossini) can reach lengths of twice the body length (Roubik & Hanson 2004) and even longer (Parra-H. 2006). The functional morphology and the foraging behavior of Euglossini have been studied by Borrell (2003ab, 2005, 2006, 2007). He concluded that orchid bees have shifted from the lapping-sucking mode of feeding to a purely suctorial mode (2003b). He observed 30 species of the four main genera (*Eufriesea, Euglossa, Eulaema and Exaerete*) and exemplified his feeding observations in *Euglossa imperialis*.

When feeding on sucrose solution, offered in micropipettes, “the glossa was always fully extended and stationary, reaching ca. 6 mm beyond the apical end of the feeding tube formed by the galeae and the labial palps” and he thus assumes that the glossa is not an essential component for nectar transport (Borrell 2003b).

Kingsolver & Daniel (1995) predicted a greater dependence on fluid viscosity in suction feeders than in lappers.

It was demonstrated that sucrose solutions below 35–40% are not sufficiently viscous to affect the ingestion rates of bumblebees (Harder 1986) and stingless bees (Roubik & Buchmann 1984). However, higher concentrations, rapidly increase the viscosity and decrease ingestion rates. Sucrose solutions of 50–65% were ingested much slower in bumblebees (Harder 1986).

Ingestion rates in bumblebees can also decline with increasing flower depth (Harder 1983b, 1986) since morphologically dissimilar bees drink at different rates because glossa length affects lapping rate and volume ingested per lap, and body mass affects lapping rate.

Data from 33 species of euglossine bees suggest that nectar intake rates decline with proboscis length, when the effects of body size were statistically removed (Borrell 2003a).

Euglossini feed on flowers with 30–45% sugar content and prefer an average sugar content of 38%, but the concentration of the nectar is always lower than 60% (Roubik et al. 1995). Borrell (2003b) presents similar results that indicate optimal nectar concentration of 30-40% sucrose.

## 1.4 Euglossine bees

Euglossini belongs to the subfamily Apinae within the family Apidae. Apinae are segregated into three major lineages, the Eucerine-line, Anthophorine-line and Apine-line. The Apine-line contains several non-corbiculate and corbiculate tribes to the latter belong Euglossini, Bombini, Apini and Meliponini (Plant & Paulus 2013).

Orchid bees or euglossine bees are an interesting group of strictly Neotropical long-tongued bees which constitute a relatively well studied group of tropical insects. The common name of these bees refers to their special relationship to orchids. Male Euglossini are the exclusive pollinators of nearly 700 orchid species (Dressler 1982, Roubik & Hanson 2004). They are most diverse in wet forests, but a few species range into savannas and gallery forests (Dressler 1982).

As mentioned above, euglossine bees have relatively long proboscides, especially bees of the genus *Euglossa* achieve remarkable proboscis lengths (Dressler 1982, Michener 2007). The folded proboscis of *Euglossa rugilabris* measures about 28 mm and is more than twice as long as the body (Dressler 1982). *Euglossa natesi* represents the bee with the longest proboscis relative to body length. The proboscis in repose reaches 28.35 mm, which is equivalent to about twice the body length (Parra-H. et al. 2006).

Using their long proboscides these bees are able to exploit a wide array of deep tubular flowers that are inaccessible to other bees, except by robbing (Dressler 1982). They tend to follow foraging traplines, which are often visited day by day (Janzen 1971, Ackerman et al. 1982).

To ingest nectar, Euglossini visit flowers belonging to different plant families, e.g., Apocynaceae, Gesneriaceae, Rubiaceae and Marantaceae (Dressler 1982). They are the major group of pollinators for the New World Marantaceae. The flowers of Marantaceae have a "trigger" mechanism that deposits the pollen in the proboscidial fossa. The genus *Calathea* is pollinated mainly by species of the genera *Eulaema* and *Euglossa*. Some *Calathea* has become specialized for pollination by large Euglossini, since their flowers must be forcible opened by the bee. Smaller bees and other flower-visiting insects use them as a source of nectar, but without achieving pollination (Kennedy 1978, Bauder et al. 2011).

General morphology of euglossine proboscides and other representatives of long-tongued bees have been studied (Winston 1979). However, greater morphological detail is needed to better understand nectar feeding in these bees.

## 1.5 Aims and objectives of the present study

The aim of the present study is the comparison of mouthparts and feeding capacity in 2 *Euglossa* species. At first sight, the two orchid bees have similar body sizes; however, their proboscides distinctly vary in length. The following questions are examined:

(1) Are there differences in the composition of the proboscis between these two representatives of the genus *Euglossa*?

(2) Are there differences in handling times on flowers or on nectar intake volume in feeding trials?

It is hypothesised that extremely elongated proboscides show non-allometric biometry in those components that form the food tube and elongations which are associated with costs on flower handling times. According to Kunte (2007), longer proboscides cause longer handling times in Neotropical butterflies.

# 2 Methods

## 2.1 Study site and studied species

The study was conducted in February 2010 in the Tropical research station La Gamba (N 8°42"61', W 83°12'97"), adjacent to the Piedras Blancas National Park in the southwestern part of Costa Rica. With an altitude of about 70 m, it is characterized by tropical lowland rainforest. The Golfo Dulce region (Puntarenas province), where the study area is situated, is one of the most humid areas in Costa Rica. The average number of rainy days is 286.5 per year and the average annual rainfall is about 6000 mm. December to March are the driest months with an average rainfall of about 300 mm. During the months with the highest precipitation (August-November) it rains nearly every day. The relative humidity is constantly high, averaging 88.3% at the station and 97.7% inside the forest. The mean monthly temperature averages 27.3°C in February (Weissenhofer & Huber 2001).

The Piedras Blancas National Park shows high euglossine species diversity, and more than a third of the species known from Costa Rica occur in the park (Gruber et al. 2008). The fragrance-dependence of the male bees makes it possible to attract them for studies (Williams & Dodson 1971, Dressler 1982, Janzen et al. 1982), and many of these perfume components are well known (Roubik & Hanson 2004).

For my study, I selected males of two species (*Euglossa imperialis* and *Euglossa championi*), that are relatively similar in body size, but show marked differences in proboscis length. Other reasons for selecting these species were that they are relatively easy to determine in the field compared to other species, and *Euglossa imperialis* was a common object of study in the observations of Borrell (2003-2007).

Orchid bee males were attracted by fragrance baits of three different aromas which are known to be present in orchid flower fragrances (Williams & Dodson 1971). Cineol, eugenol and methyl salicylate where chosen, since they are known to be attractive to *E. imperialis* and *E. championi* (Tab. 1) (Roubik & Hanson 2004). The bees were allured and captured in the adjacent Piedras Blancas National Park.

Tab. 1: Bees allured and collected for feeding observations and biometric analyses

| **Attracted species** | **N males** | **Fragrances** |
|---|---|---|
| *Euglossa imperialis* COCKERELL, 1922 | 29 | cineol, eugenol, methyl salicylate |
| *Euglossa championi* CHEESMAN, 1929 | 31 | cineol, methyl salicylate |

## 2.2 Morphometry of the bees' body and proboscis

After collection, the bees were immobilized in the refrigerator for about half an hour to better enable taking the measurements (Tab.2).

Fresh weight determination was taken with a digital pocket carat balance (Kern CM 50-C2N), body length, head and thorax width, and the proboscis in folded resting position were measured using an electronic digital caliper.

Species determination was done using Roubik & Hanson (2004) and a stereomicroscope in the laboratory.

Tab. 2: Morphometric data studied on the bees' body in cold-immobilized state

| | | |
|---|---|---|
| 1 | Fresh weight [g] | before the feeding trials |
| 2 | Body length [mm] | from the anterior of the head to the posterior tip of the metasoma |
| 3 | Head width [mm] | at the widest point, from eye to eye |
| 4 | Thorax width [mm] | from outer edge to outer edge of tegulae |
| 5 | Proboscis length [mm] | in folded position; from the mandibles to the tip of the proboscis |

After the body measurements were taken, the feeding experiments were conducted (chapter 2.3).

After all tests were carried out, the animals were preserved in 70% ethanol, some were previously killed with ethyl acetate ($C_4H_8O_2$) and then stored in 70% ethanol. Treatment with ethyl acetate causes protraction of the glossa (Harder 1983b). Every bee was stored separately and labeled individually, starting with the collection of morphometric data, followed by the feeding trials, and further studies on the proboscides at the University of Vienna.

For measurements on the different parts of the proboscis, it was necessary to sever the mouthparts from the head capsule. For this purpose, the bee was fixed with pins, the mandibles, which embrace the proboscis on its base, were opened with a preparation needle and the proboscis was lifted out of the head capsule. Muscles were cut with a scalpel, and by grasping the cardines with tweezers the proboscis could be completely taken out of the capsule.

They were placed on laminated graph paper for photography with a Nikon D70 camera with a Nikkor 55 mm micro lens. To prevent dehydration and to provide a better grip on the surface, the proboscis was coated with a liquid-film of ethanol. Using the photos, the mouthparts were measured with the measuring tools of the program ImageJ on a personal computer.

The mouthparts were mounted on microscopic slides in glycerin for examining the morphology of the proboscis with a Nikon Eclipse 800 microscope equipped with a Nikon DS-Fi2 camera.

### 2.3 Feeding observations of orchid bees

The feeding experiments were carried out with natural and artificial nectar sources in a mosquito tent in the garden of the tropical research station. To ensure that the bees were ready for experiments after cooling for biometrical studies, they were acclimatized for at least half an hour and flight ability of the individuals was awaited.

Various flowers were freshly cut from the garden as natural nectar sources for each test run and the bees presented as a bouquet. The flowers of *Calathea lutea* have been found to be very attractive. The flowers of *Lantana* sp. and *Stachytarpheta frantzii* were hardly visited. Consequently *Calathea* was mainly used for the experiments. In order to test artificial nectar (30% sucrose solution) artificial flowers were built and tested for their attractiveness to bees in color and form. The main focus was placed on ensuring that the feeding tube was transparent in order to be able to observe the proboscis movements well during feeding. Large amounts of sugar solution were offered using 200 µl micropipettes whereas small drops offered in feeding trials had a volume of 10 µl in comparison.

For the experiment to determine the ingestion rate (ingested amount of sugar solution in µl/s) drops per 10 µl were applied on natural rubber plates. Natural rubber has proven to be very practical in these experiments, as the bees found enough grip and small drops formed on the surface. So the loss of fluid during the intake by the bees could be observed well.

Various feeding observations were made in 11 individuals of *E. imperialis* and 7 of *E. championi.* A Sony V50 digital camera was used for video recording.

Nectar concentrations of natural and artificial sources were determined with a Zeiss refractometer (maximal sugar concentration 85%). Nectar volume was measured in flowers with micro capillary tubes. Corolla tube length was measured with an electronic digital caliper.

### 2.4 Statistics

Statistical analyses where performed with IBM SPSS Statistics 20. To compare the morphometric data of the two species, the nonparametric Mann-Whitney-U-Test was performed. The significant level was set at $p < 0,05$.

# 3 Results

## 3.1 The proboscis of *Euglossa championi* and *Euglossa imperialis*

Fig. 2 and 3 show the prepared proboscis of the two species in lateral view. The components of the proboscis are artificially disassembled by preparation.

The galeae of the maxilla and the labial palps and glossa of the labium are extremely elongated and flattened. They are much longer as the basal parts of the maxilla, the stipites and maxillary palps, and much longer as the basal parts of the labium, post- and prementum (Fig. 2, 3 **A**). The maxillary palps (**B**) are relatively short. The labial palps are four-segmented. The two basal segments are elongated and sheath-like, and the two distal segments (**C**) are very small and cylindrical in shape. The basal part of the labium is composed of the prementum and the postmentum, they articulate with the cardines of the maxilla. The postmentum is a V-shaped unit that closes and opens. The proximal components are responsible for unfolding of the proboscis as well as for pro- and retraction. The base of the glossa and paraglossae are partly contracted into the prementum in retracted position of the glossa. The greatly elongated galeae and labial palps form the food tube which encloses the glossa. The greatly elongated glossa is very hairy with broadly lanceolate hairs on its distal end, which is the part of the glossa that reaches out beyond the food tube in protracted position of the glossa. The glossa terminates in the flat and lanceolate flabellum (**D**), covered with short hairs on its anterior surface. The glossa constitutes the main organ of nectar uptake by adhesion.

*E. championi* and *E. imperialis* are similar in basic structure of the proboscis with the same components; the striking difference is the much longer distal parts of the galeae, labial palps and glossa in *E. imperialis*.

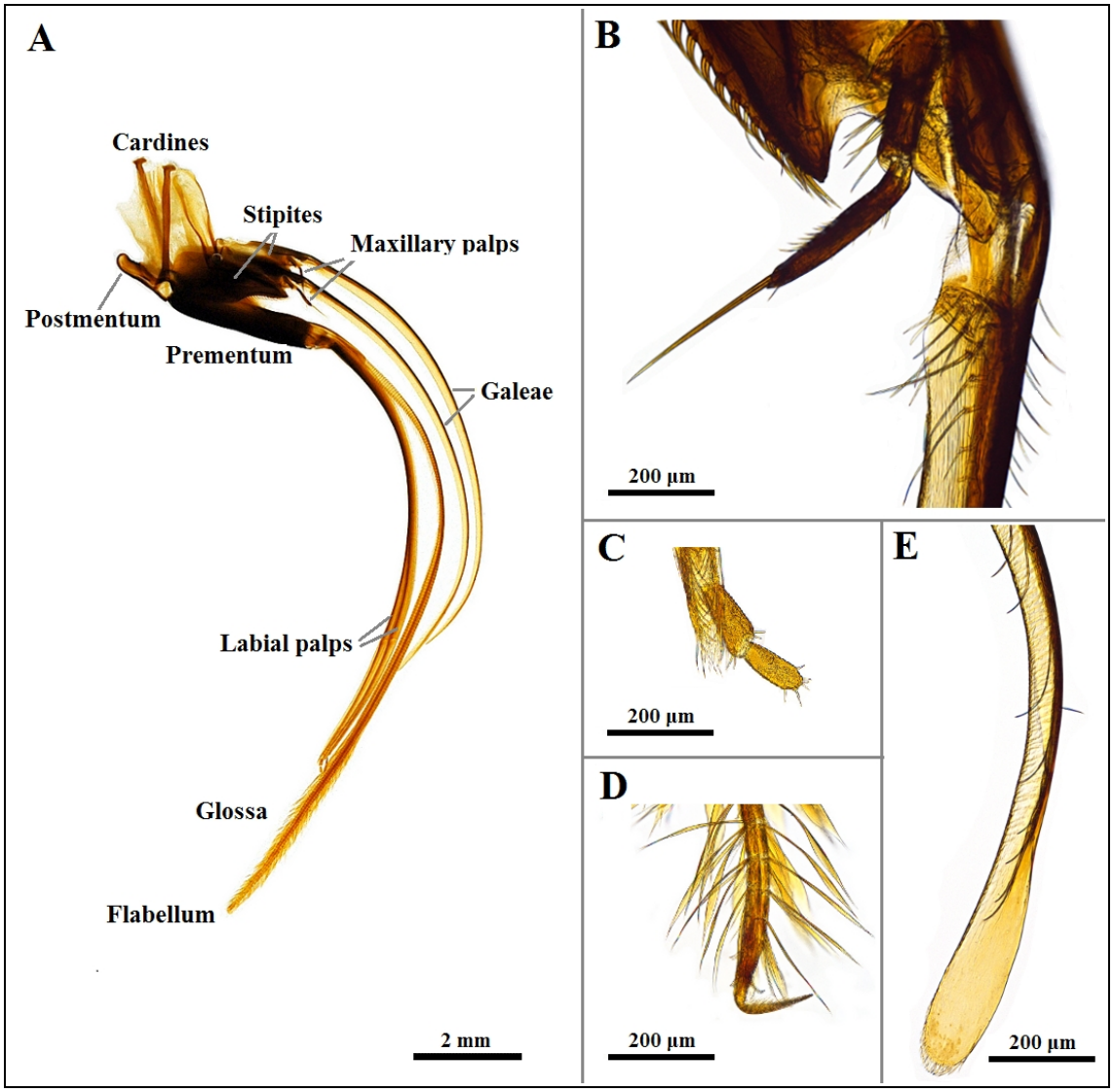


Fig. 2: **A** Proboscis of *E. championi* with its basal parts (cardines, stipites, postmentum, prementum) and distal parts (galeae, labial palps, glossa); lateral view; artificially disassembled **B** Maxillary palp in detail. **C** Tip of labial palp with the two small distal segments which show sensilla on the distal end of each segment. **D** The tip of the glossa show the broadly lanceolate and long hairs and a hairless region until it termintes in the flabellum. The hairless distal reagion of the glossal tip is equipped with sensillae. **E** Tip of galea with setae on the anterior margin is covered with a row of small hairs on the distal margin.

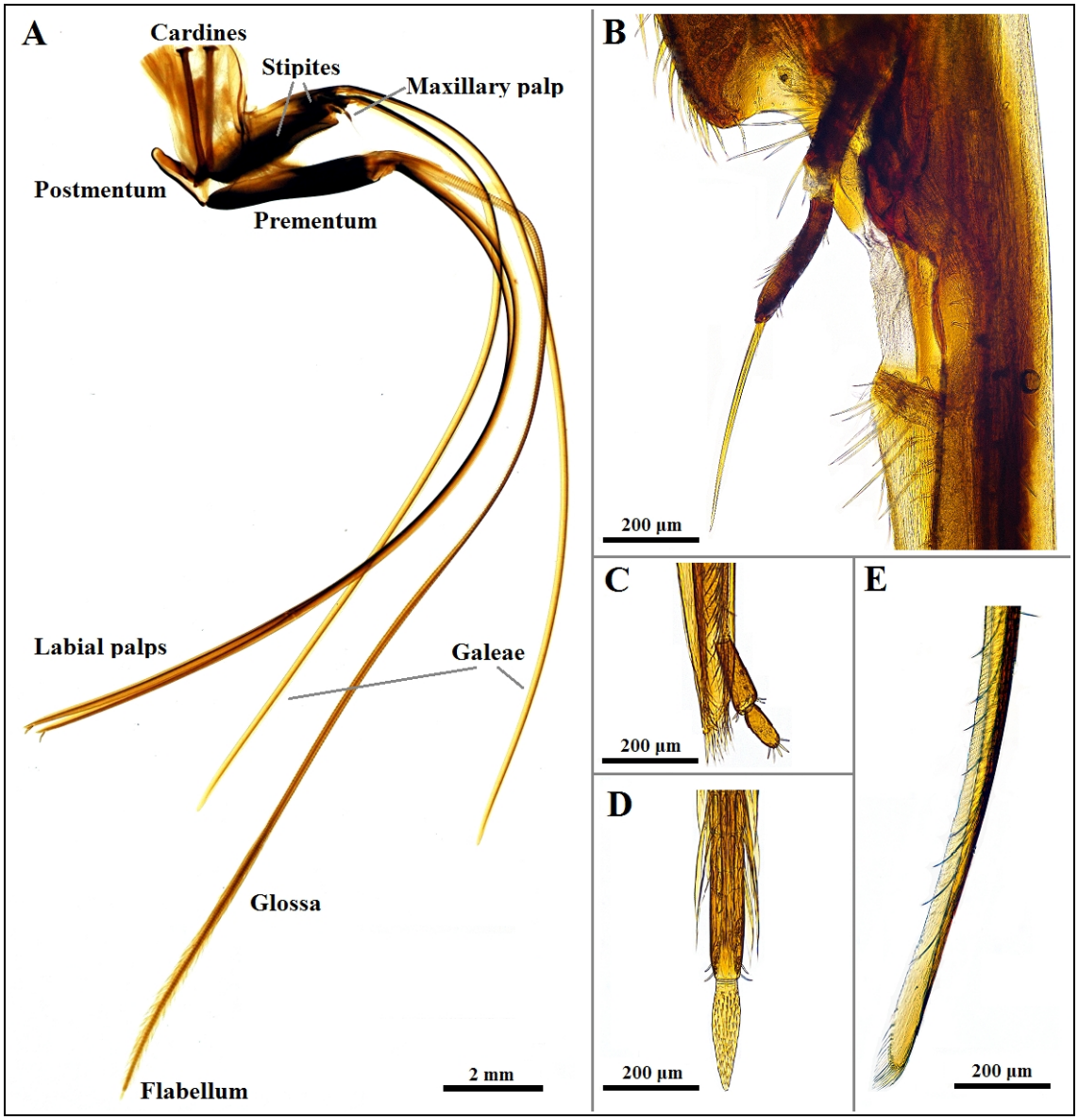


Fig. 3: **A** Proboscis of *E. imperialis* with its basal parts (cardines, stipites, postmentum, prementum) and disproportionately elongated distal parts (galeae, labial palps, glossa); lateral view; artificially disassembled. **B** Maxillary palp in detail. **C** Tip of labial palp with the two small distal segments which show sensillae on the distal end of each segment. **D** Tip of the glossa with the flabellum. The hairless distal reagion of the glossal tip is equipped with sensilla. **E** Tip of galea with setae on the anterior margin is covered with a row of hairs on the distal margin.

### 3.2 Measurements on body and proboscis

Data of measurements on body and proboscis are listed in Tab. 3 and 4.

*Euglossa championi* and *E. imperialis* differ significantly in absolute body mass (n = 63, Z = - 4.604, p < 0.001) and absolute body length (n = 65, Z = - 6.679, p < 0.001). However, body length relative to body mass (body length/body mass) shows no significant differences (n = 63, Z = - 1.131, p = 0.258). The proportions of head and thorax are on first sight nearly the same, but the results differ significantly in head width (n = 65, Z = - 4.061, p = < 0.001) and thorax width (n = 65, Z = - 2.555, p = 0.011).

All absolute measurements on the components of the proboscis result in highly significant differences between the two species (p < 0.001), whereas relative lengths (length/body length) divided by body mass, the cardo shows slightly significant differences (n = 48, Z = - 2.048, p = 0.041), while the stipes (n = 48, Z = - 1.305, p = 0.192), and prementum (n = 48, Z = - 0.968, p = 0.333) have no significant differences. In both absolute and relative data, all distal components of the proboscis (galea, labial palp, glossa), as well as the folded proboscis in rest position, differ highly significantly (p < 0.001). In *E. championi* the folded proboscis is shorter than body, extending to sternum 2, in *E. imperialis* it is longer than the body. Fig. 4 illustrates the disproportionally longer distal parts in comparison to the proximal components of the proboscis.

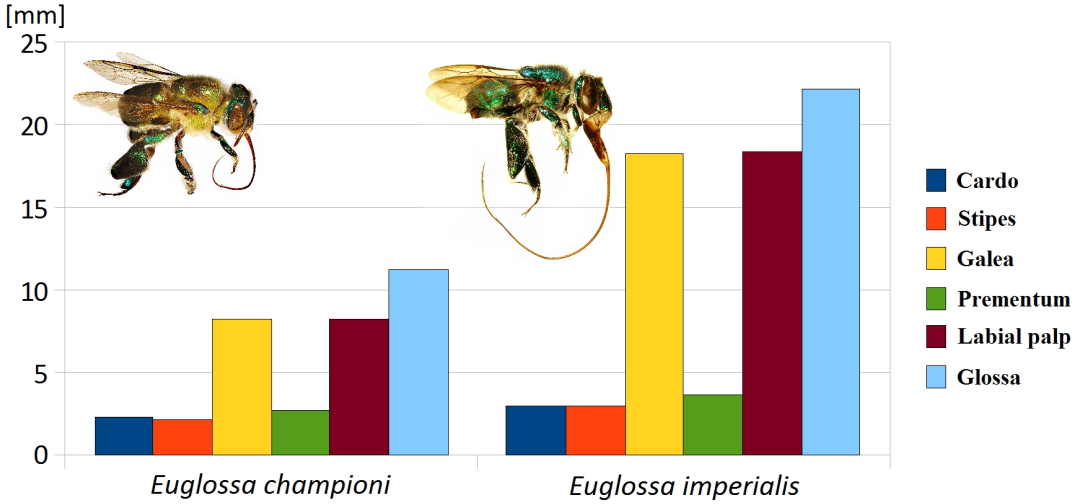


Fig. 4: The basal maxillary cardo and stipes, and the basal labial prementum show slight differences in proportions, whereas the maxillary galea, labial palp and glossa are disproportional elongated in *E. imperialis*.

Tab. 3: Body measurements on the cold-immobilized bees: Fresh body mass, body length, head width, thorax width and length of proboscis in folded rest position.

| | Species | N | Mean | SD |
|---|---|---|---|---|
| **Body mass** [g] | *E. championi* | 34 | 0.12 | 0.02 |
| | *E. imperialis* | 29 | 0.14 | 0.02 |
| **Body length** [mm] | *E. championi* | 36 | 12.70 | 0.68 |
| | *E. imperialis* | 29 | 14.82 | 0.62 |
| **Head width** [mm] | *E. championi* | 36 | 5.06 | 0.14 |
| | *E. imperialis* | 29 | 5.21 | 0.12 |
| **Thorax width** [mm] | *E. championi* | 36 | 5.06 | 0.18 |
| | *E. imperialis* | 29 | 5.20 | 0.23 |
| **Proboscis length** (folded) [mm] | *E. championi* | 25 | 7.58 | 0.64 |
| | *E. imperialis* | 25 | 16.66 | 0.46 |

Tab. 4: Measurement of the components of proboscis in 70% Ethanol.

| | Species | N | Mean [mm] | SD |
|---|---|---|---|---|
| **Cardo** | *E. championi* | 30 | 2.28 | 0.06 |
| | *E. imperialis* | 18 | 2.98 | 0.08 |
| **Stipes** | *E. championi* | 30 | 2.15 | 0.08 |
| | *E. imperialis* | 18 | 2.90 | 0.08 |
| **Galea** | *E. championi* | 30 | 8.30 | 0.27 |
| | *E. imperialis* | 18 | 18.26 | 0.70 |
| **Prementum** | *E. championi* | 30 | 2.67 | 0.06 |
| | *E. imperialis* | 18 | 3.65 | 0.11 |
| **Labial palp** segment 1+2 | *E. championi* | 30 | 8.26 | 0.24 |
| | *E. imperialis* | 18 | 18.39 | 0.65 |
| **Glossa** | *E. championi* | 30 | 11.25 | 1.01 |
| | *E. imperialis* | 18 | 22.22 | 1.45 |
| **Labium with glossa protracted** | *E. championi* | 16 | 15.07 | 0.35 |
| | *E. imperialis* | 5 | 28.11 | 0.66 |
| **Labium with glossa retracted** | *E. championi* | 14 | 11.91 | 0.73 |
| | *E. imperialis* | 11 | 23.54 | 0.75 |

Comparison of the protracted and retracted glossae (Fig. 5) shows a mean difference of 3.16 mm (N = 30) in *E. championi* and 4.57 mm in *E. imperialis* (N = 16). These lengths correspond to the lengths of the glossae, reaching out of the food tube after protraction. In *E. championi* the relative protraction to total glossa length is greater than in *E. imperialis*. Functional length of the proboscis can be increased by protraction of the glossa by 17% in *E. imperialis* and by 21% in *E. championi*.

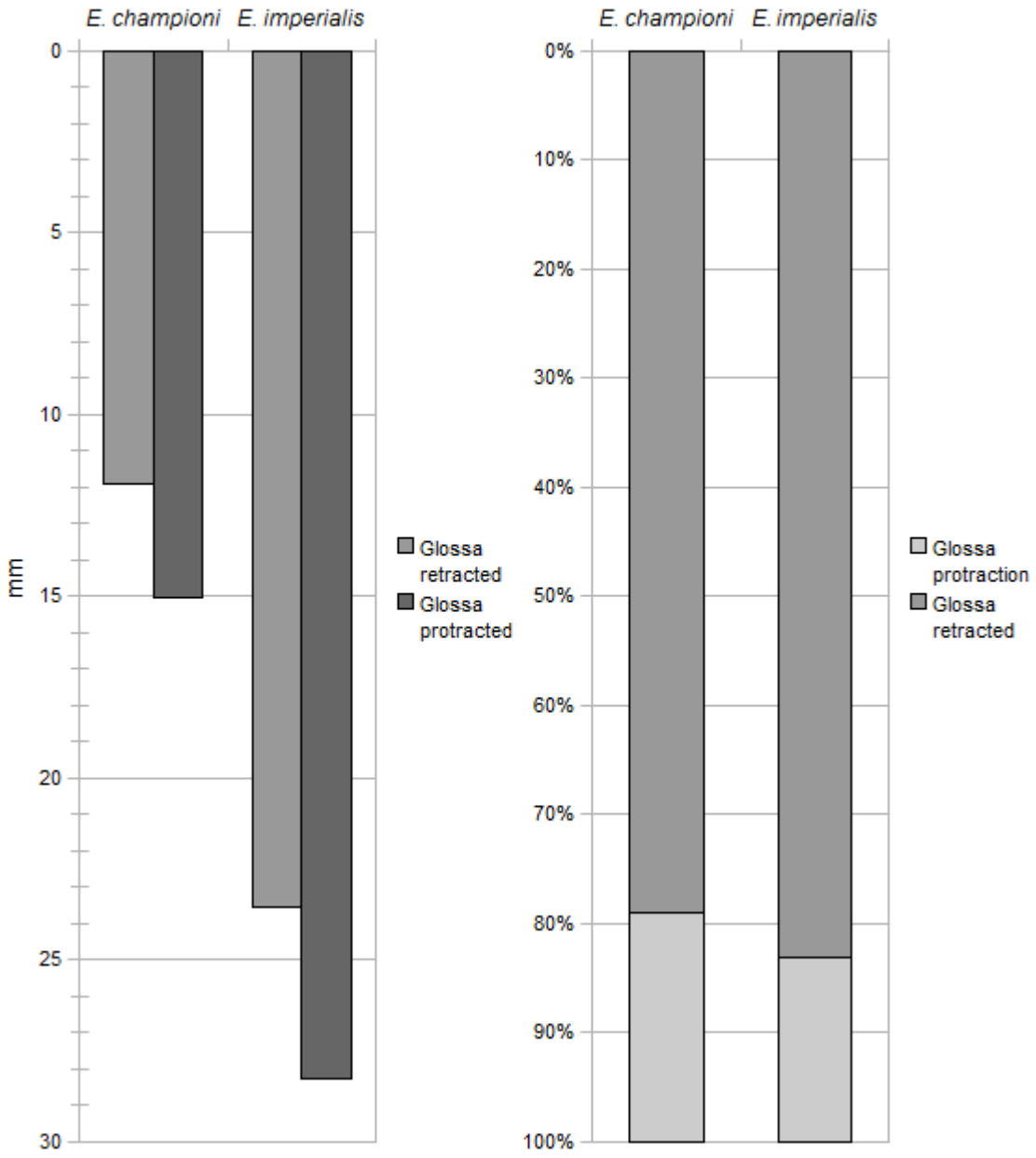


Fig. 5: Comparison of protracted and retracted glossal lengths in *E. championi* and *E. imperialis*. Left: absolute lengths, right: relative lengths.

## 3.3 Feeding observations of orchid bees

### 3.3.1 Feeding on natural nectar sources

Feeding behavior of *E. imperialis* was studied in an observation tent using flowers of *Calathea lutea*. After a bee was set free in the observation tent, it took only several seconds until it approached the presented bouquet of flowers. The bee usually unfolded its proboscis before landing after it had chosen a flower. After landing, the entrance of the flower tube was probed with the tip of the long proboscis. This seems to be no easy task, sometimes requiring body acrobatics, sometimes the bee hung on the flower clinging with the midlegs or standing vertically on the corolla in order to be in a position to enable insertion of the the extremely long proboscis into the flower tube. When the proboscis was inserted into the opening of the flower, it protracts and deeply immerses itself into the long flower tube of *Calathea*. The deep penetration into the flower can trigger the pollen transfer mechanism in *Calathea lutea* (Fig. 6). After feeding the proboscis is removed from the corolla by dragging it out when the bee leaves the flower by crawling or flying away. Of the flowers visited by *E. imperialis*, one third (N = 6) were triggered by the visitation, 7 flowers were probed without triggering and 5 flower visits occurred on already triggered flowers. The bees probed the flowers between 1 to 5 times. The number of flowers probed by the individual bees, and the condition of the flowers (triggered, not triggered and already triggered) are shown in Tab. 5. The bees switched from one flower to the next by flying or crawling.

Additional photographs of several flower visits are presented in the Appendix.

The mean probing time of *E. imperialis* (N = 8) on *Calathea lutea* flowers (N = 18) was 55.6 seconds ± 40.1 S.D. (Tab. 6). The mean sugar content of *C. lutea* (N = 12) was 39.4%, and the mean nectar volume was 12.13 µl ± 5.7 S.D. The mean corolla tube length of flowers of *C. lutea* measured 29.68 mm ± 1.75 S.D. The flower-handling times (total time the bee spent on the flower with proboscis unfolded) differed considerably and reached in some cases to double the time of probing (time from when the proboscis was inserted into the corolla tube until it was pulled out) due to the mentioned difficulties bees can have due to the long proboscis.

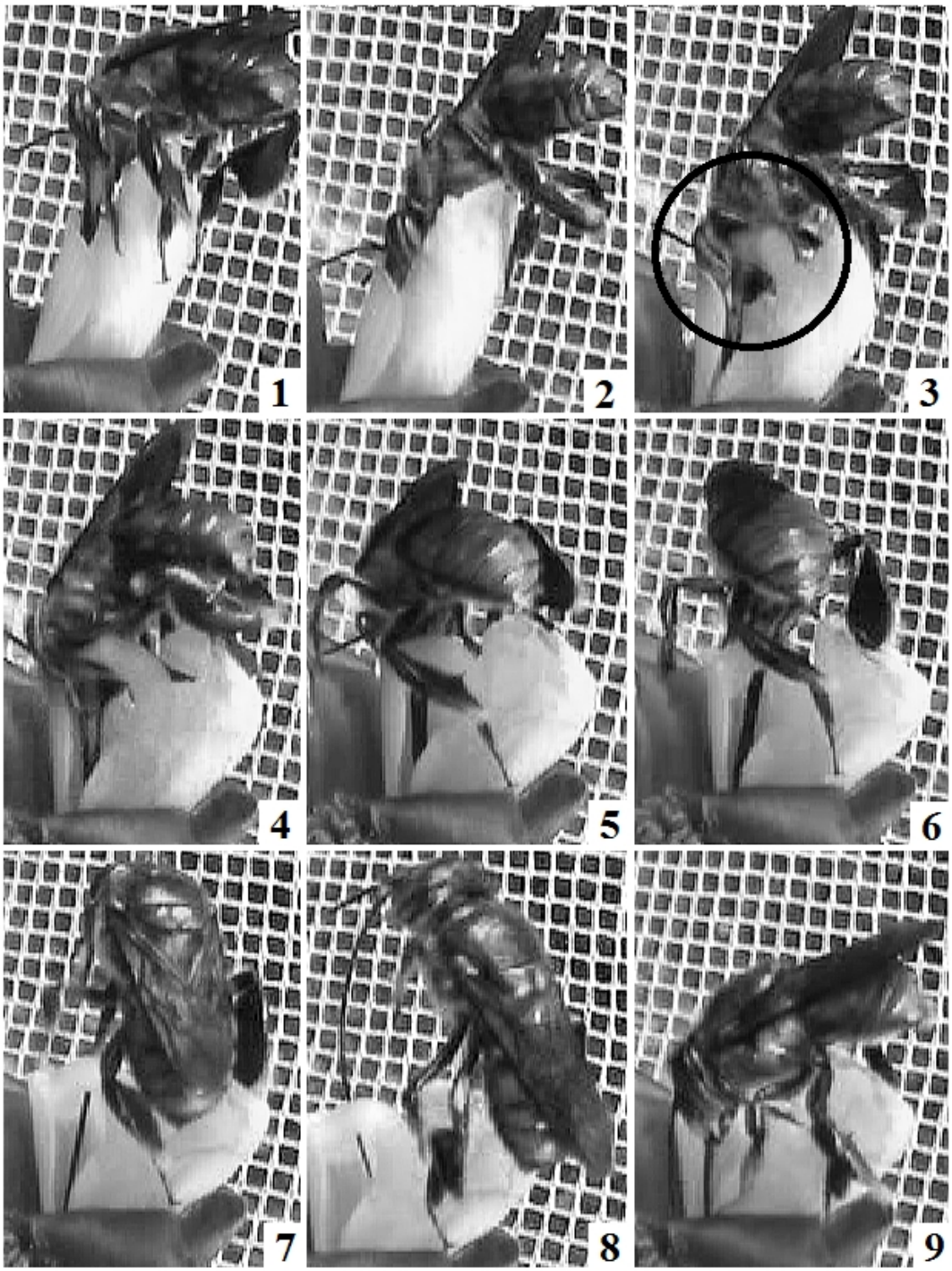


Fig. 6: *E. imperialis* handling a flower of *Calathea lutea*. The deep immersion of the proboscis (**1**) and the force caused by head (**2**) trigger the release of the style (**3**) and pollen is placed in the proboscidial fossa of the bee (**4**). Trapped head and proboscis are freed by a lateral movement of the body (**5**, **6**). The proboscis is withdrawn from the flower by straightening the body (**7**, **8**), and again inserted into the flower tube (**9**). The positional change enables deeper insertion of the proboscis. The time from first insertion to insertion after style release (1-9) is 8.2 s. The spring forward movement of the triggered style takes approx. 0.16 s. (Single frames of video footage)

Tab. 5: Number of probed *Calathea lutea* flowers and their condition when visited by *Euglossa imperialis*.

| Individuals | N probed flowers | N flowers probed and triggered | N flowers without triggering | N already triggered flowers |
|---|---|---|---|---|
| *E. imperialis* 02 | **2** | 1 | - | 1 |
| *E. imperialis* 05 | **4** | 2 | 1 | 1 |
| *E. imperialis* 12 | **1** | - | 1 | - |
| *E. imperialis* 13 | **5** | - | 4 | 1 |
| *E. imperialis* 14 | **3** | 2 | - | 1 |
| *E. imperialis* 15 | **1** | - | - | 1 |
| *E. imperialis* 16 | **1** | 1 | - | - |
| *E. imperialis* 26 | **1** | - | 1 | - |
| Total probed flowers | **18** | **6** | **7** | **5** |

Tab. 6: Probing times of *E. imperialis* on *Calathea lutea* flowers.

| Individuals | N probed flowers | Min – max [s] | Mean probing time [s] | S.D. |
|---|---|---|---|---|
| *E. imperialis* 02 | ***2*** | 46 - 82 | 64 | 25.5 |
| *E. imperialis* 05 | ***4*** | 14 - 54 | 31.8 | 18.3 |
| *E. imperialis* 12 | ***1*** | | 173 | |
| *E. imperialis* 13 | ***5*** | 13 - 61 | 39.2 | 19.6 |
| *E. imperialis* 14 | **3** | 4 - 57 | 35.7 | 28 |
| *E. imperialis* 15 | **1** | | 104 | |
| *E. imperialis* 16 | **1** | | 84 | |
| *E. imperialis* 26 | **1** | | 82 | |

*Euglossa championi* was seldom observed on natural flowers, since this species was very sensitive, or simply too demanding in terms of flower selection. *Calathea lutea* was probed only on a single occasion, when an individual of *E. championi* was placed on a flower directly. The probing in this individual took 142 seconds.

However, 4 individuals of *E. championi* could be observed during visits on *Stachytarpheta frantzii*. Mean probing times ranged from 11.6 to 39 seconds ± 39 S.D. (Tab. 7). The mean sugar content of *S. frantzii* (N = 10) was 24%, and mean nectar volume was 1.7 µl ± 1.0 S.D. The mean corolla tube length of flowers of *S. frantzii* measured 11.45 mm ± 0.46 S.D.

Tab. 7: Mean probing times of *E. championi* on *Stachytarpheta frantzii.*

| Individuals | N probed flowers | Min – max [s] | Mean probing time [s] | S.D. |
|---|---|---|---|---|
| *E. championi* x | **8** | 1 - 38 | 11.6 | 12.1 |
| *E. championi* 24 | **13** | 3 - 145 | 39 | 52.6 |
| *E. championi* 26 | **1** | | 32 | |
| *E. championi* 28 | **5** | 4 - 26 | 12.8 | 10.4 |

### 3.3.2 Feeding on artificial nectar sources

In *Euglossa championi,* the uptake of one drop (10 µl volume) on a surface was fastest when the entire free part of the glossa has contacted the liquid, slower when only half of the glossal tip was in the drop and slowest when mainly the tips of the galeae and labial palps were in contact with the fluid. In contrast, nectar uptake in *Euglossa imperialis* lasted longer when only the glossal tip came into contact with the sugar solution. It was the fastest when mainly the tips of the galeae and labial palps were in contact with the fluid. *Euglossa championi* is thus slightly faster in the intake of fluids (Tab. 8). After feeding on a drop of artificial sugar solution the bees searched for more food by busily "scanning" the surface with the tip of the proboscis. Due to the long mouthparts they had to straighten their bodies to a nearly vertical position to reach the ground with the tip of the proboscis (Fig. 7).

Tab 8: Artificial sucrose solution (30%) offered as 10 µl drops on natural rubber plates.

| Individuals | N ingested drops | Ingesting rate [µl/s] | Min | Max | Total ingested nectar [µl] |
|---|---|---|---|---|---|
| *E. imperialis* 17 | 7 | 0.62 | 0.33 | 0.77 | 70 |
| *E. championi* 15 | 3 | 0.66 | 0.56 | 0.83 | 30 |
| *E. championi* 12 | 5 | 0.68 | 0.50 | 0.77 | 50 |

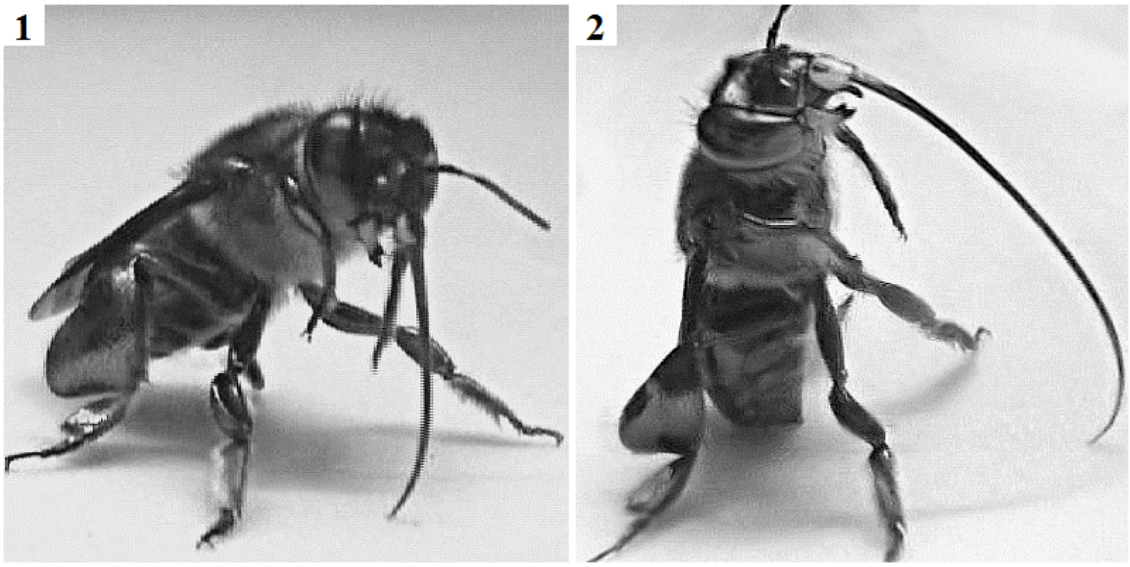


Fig. 7: *E. championi* (**1**) and *E. imperialis* (**2**) searching for more food after feeding of droplets of sugar solution (30%). The forelegs are not involved and bent, the midlegs are stretched in both species. The hindlegs of *E. championi* are bent, so the bee's body is at an angle of approx. 45 degrees to the ground. The hindlegs and the body of *E. imperialis* are vertically straight.

### 3.3.3 Proboscis movements during fluid-feeding

The intake of artificial nectar occurred in several modes and with varying use of the proboscis. The individuals of *E. imperialis* observed to feed on small and large amounts of nectar (N = 5) and *E. championi* (N = 4) showed 3 different ways in which the glossa is used during nectar uptake (Tab. 9):

1) Glossa remained motionless
2) Glossa was mainly motionless, but sometimes with lapping movements
3) Glossa with typical lapping-sucking motions, rhythmically repetitive (licking cycles)

In all observations the glossa was protracted. In one and the same individuals different glossal movements were possible. For example, in an individual of *E. championi*, which ingested a drop of sugar solution with glossa fully motionless, displayed licking cycles when feeding from an artificial flower.

Small amounts of artificial nectar were offered in drops of approximately 10 µl. In the 3 observed individuals of *E. championi* and *E. imperialis* (Tab. 8), nectar ingestion occurred with the glossa motionless (Fig. 9) as long as enough contact with the fluid was possible; the remains of the sugar solution were licked up by the glossa.

Large amounts of artificial nectar were offered in 200 µl micropipettes. In most cases the extended glossa remained motionless, sometimes with sporadic lapping movements. In 2 individuals of *E. imperialis* and 1 of *E. championi* typically lapping-sucking motions of the proboscides occurred (Fig. 10).

There are also differences in the motion of the basal proboscis parts. There is no observed protraction of stipites and prementum during feeding on drops that are presented on a flat surface.

Feeding from 200 µl micropipettes led to more or less partially or to fully protracted basal parts. Lapping motions of the glossa involved simultaneous motions of the basal parts not necessarily but in some cases.

Tab. 9: Observed proboscis movements of individuals of *E. championi* and *E. imperialis* during feeding on artificial nectar with 30% sugar content. Offered sources were 200 µl micropipettes and 10 µl drops.

| Individuals | Glossa motionless | Mainly motionless / occasionally lapping | Lapping / rhythmically repetitive |
|---|---|---|---|
| *E. championi* 14 | + | | + |
| *E. championi* 12 | + | + | |
| *E. championi* 13 | + | + | |
| *E. championi* 15 | + | + | |
| *E. imperialis* 01 | + | + | + |
| *E. imperialis* 03 | + | + | |
| *E. imperialis* 14 | + | + | + |
| *E. imperialis* 17 | + | | |
| *E. imperialis* 26 | + | | |

During the observations of *Euglossa imperialis* feeding on *Calathea lutea*, protraction of the proboscis occurred (Fig. 8 **B-D**). In addition to the basal movements of the proboscis when feeding on artificial flowers, an additional elongation of the proboscis could be observed. It was caused by the rotation of the cardines (**E**), which turn completely out of the head capsule, and by the fully stretched postmentum. The prementum moved in front of the stipites, and the distal entrance to the food tube is temporarily disassembled. Final fluid-handling movements are sometimes characterized by repetitive protraction (**C,D**) and retraction (**B**) of the proboscis. These observations are similar to proboscis movements in *E. championi* probing *Stachytarpheta frantzii*, but the final protraction and retraction movements occur more frequently.

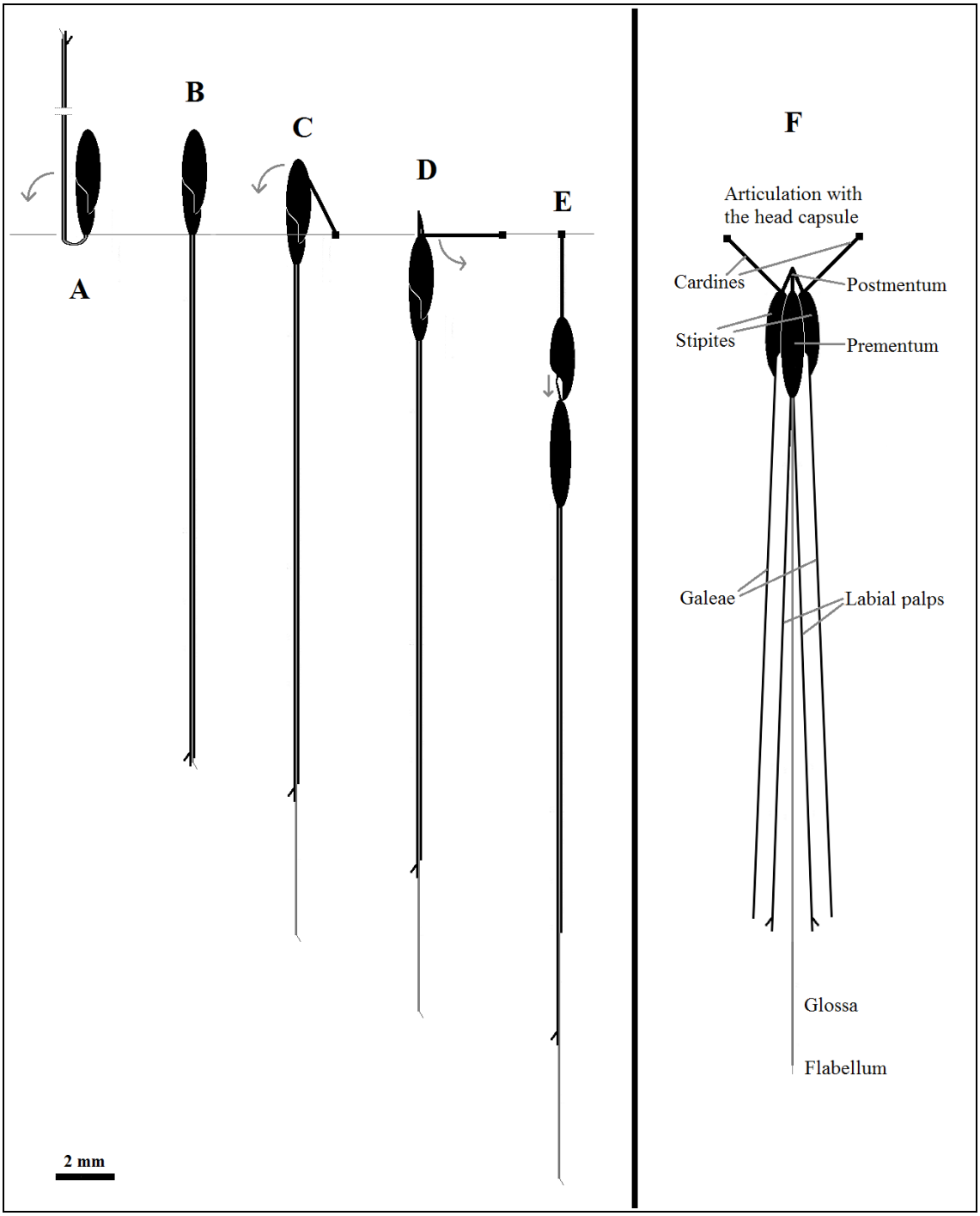


Fig. 8: Schematic illustration of the proboscis of *E. imperialis* in different positions; lateral view with paired parts shown as single for a better overview. **A** Rest position with folded distal parts of the proboscis. **B** Unfolded with distal parts protracted, glossa retracted. **C** Partially protracted basal parts and protracted glossa. **D** Protracted basal parts. **E** Additional elongation is possible by rotation of the cardines and stretching of the postmentum. **F** The paired distal parts, i.e. galeae and labial palps, are shown artificially spread for better representation and are normally merged to the food tube enclosing the glossa; anterior view.

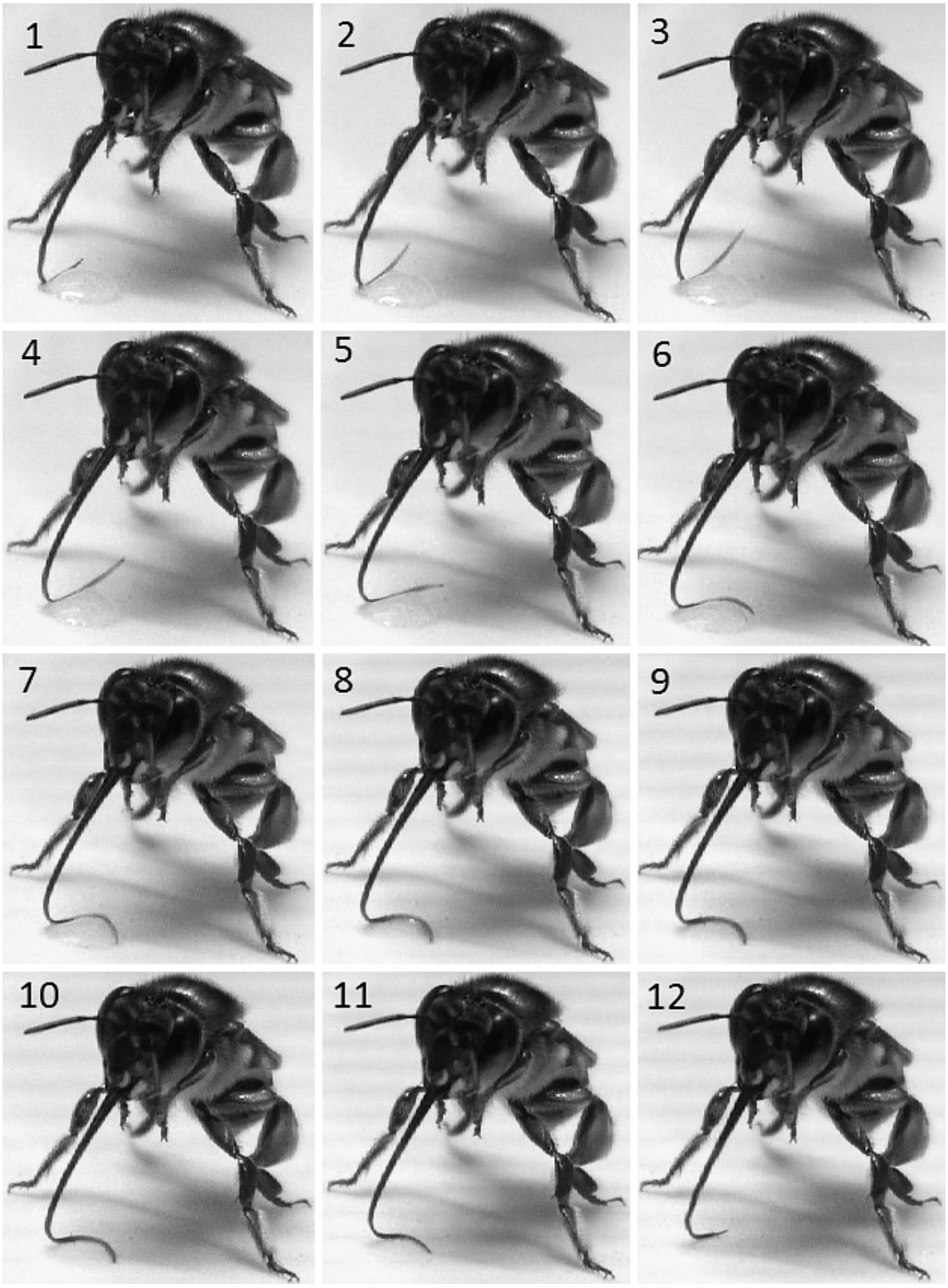

Fig. 9: *E. championi* during ingestion of a 10 µl drop of sugar solution (30%) on a natural rubber plate. The glossa is the only protracted part of the proboscis and is held motionless during fluid-uptake and ingestion. **1-3** Protraction of the glossa. **4-5** The tip of the glossa sinks into the fluid, and the shrinkage of the drop is clearly visible beginning with photo **6**. **9-12** Retraction of the glossa after fluid-uptake. (Single frames of video footage)

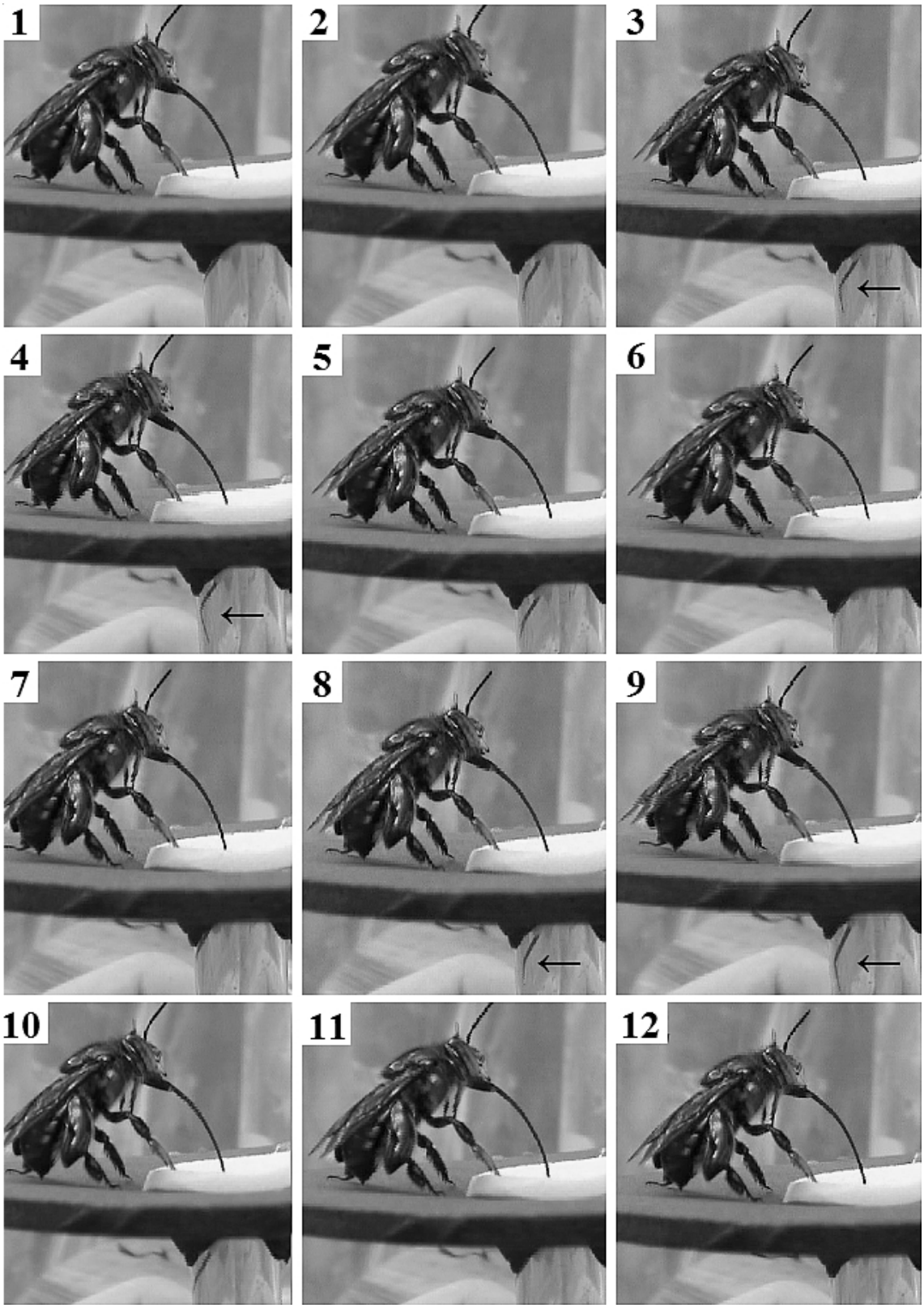


Fig. 10: Two licking cycles of an individual of *E. imperialis* feeding on an artificial flower with 200 µl sugar solution (30%). First cycle (**1-6**) lasts 0.72 s, second cycle (**7-9**) lasts 0.96 seconds. The total fluid-handling time was 35.6 s, during which 25 lapping cycles occured. The licking frequency was approximately 1 Hz when measured from the total feeding time, yet 1-2 Hz when measured from the single protraction and retraction movements. The time difference is due to short pauses between the individual licking cycles. The basal parts are not fully protracted and barely move with the glossal protraction. (Single frames of video footage; arrows point to glossa)

# 4 Discussion

The longest insect proboscides have evolved in context of nectar-feeding within the Hymenoptera, Lepidoptera and Diptera (Krenn et al. 2005). The Nemestrinidae (Diperta) represent the insects with the longest proboscis in relation to body length up to 90 mm in the genus *Maegistorhynchus* (Borrell & Krenn 2006). In Lepidoptera the genus *Eurybia* (Riodinidae) is the record holder in proboscis length and reaches an impressive 49.9 mm (Kunte 2007). In bees the Euglossini are the leaders in proboscis length (Roubik & Hanson 2004, Parra-H. 2006).

## 4.1 Comparison of the proboscis of *Euglossa championi* and *Euglossa imperialis*

*E. championi* is a species with a moderately elongated proboscis, while *E. imperialis* has a disproportionally longer proboscis. Both show similarities in the basic composition of the proboscis. The disproportionate parts are in particular the distal components of the labiomaxillary complex, the galeae, the labial palps and the glossa. The differences between the food tube forming components and the glossa are significant between the two species, whereas the basal components, which are responsible for proboscis motions, such as protraction and retraction, are almost allometric. Of the basal components only the cardines show slightly significant differences in length.

Thus the hypothesis can be considered as confirmed, that the extremely elongated distal proboscis components with its disproportionate elongation show non-allometric biometry.

## 4.2 Benefits and costs of long proboscides

Flower-handling times increase when corolla tubes are longer than the bee's glossa, and this causes a decrease in the energetic advantage (Harder 1983a). Thus, bees should feed from flowers with tube length which fits approximately the lengths of their glossa (Harder 1985). Ingestion rates in bumblebees can also decline with increasing flower depth (Harder 1983b, 1986), since morphologically dissimilar bees drink at different rates. This is due to the fact that glossal length affects lapping rate and volume ingested per lap.

Since *E. championi* was not observed to visit flowers of *Calathea lutea*, a direct

comparison of fluid-handling or probing times was not possible. *Calathea lutea* with its long corolla tubes is probably not as attractive to *E. championi*, the species with the medium sized proboscis, as to *E. imperialis*, the bee with a proboscis length that corresponds to the length of the corolla tube or presumably is a bit longer. The protracted proboscis extends with a mean length of 28.11 mm and additional elongation is possible due to extension of the postmentum at the base of the corolla tube of *C. lutea* (mean corolla tube length: 29.68 mm). Due to the 3-dimensional V-shaped postmentum, precise measurements of it were not possible, but the length of the fully out stretched postmentum approximately corresponds to the length of the stipes (mean length of stipes of *E. imperialis*: 2.90 mm). However, *E. championi* with a mean proboscis length of 15.07 mm and an additional elongation of approximately 2.15 mm (mean stipes length) results in an elongation of the functional proboscis length to about 17.22 mm.

The observations of Kunte (2007) on flower visiting Neotropical butterflies showed that the deep corolla tube of *Calathea crotalifera* restricts access. This plant species also grows in the Tropical Research Station La Gamba, where the present study occurred, but flowering time had already ended by the time the present study commenced. *Calathea crotalifera* has a relatively small spectrum of visiting butterflies, euglossine bees and hummingbirds, and pollination occurs by euglossine species which are able to trigger the flower's pollentransfer mechanism (Bauder et al. 2011). *Calathea lutea* was naturally visited by several euglossine species of all 4 genera (e.g. male *Euglossa imperialis*, male *Eulaema meriana*, male *Eulaema cingulata*, female *Exaerete smaragdina* and female *Eufriesea* sp.) occurring in the area where the present study was conducted. Euglossini tend to follow foraging traplines on a few nectar-rich resources, which are often visited daily (Janzen 1971). Since the Station's garden is directly adjacent to the rainforest, and several species also occur in the local gallery forests (Gruber et al. 2008), it is likely that the *Calathea* species in the Station's garden represent safe and profitable nectar sources on a daily basis for these bees.

Euglossini are generalists in nectar foraging, they visit various flowers from which they can physically extract nectar (Borrell 2007); however, they do not visit flowers strictly matching their proboscis length (Borrell 2005). Bees with long proboscides enjoy the advantage of having access to nectar in a greater variety of flowers and to consume nectar from more plant species than short-tongued bees do (Harder 1985).

Due to the extremely long proboscis of *E. imperialis*, the time necessary to probe a flower of *C. lutea* can be noticeable long. The bees often attempted several times to insert their proboscis into the corolla tube before they were successful. In addition, triggering the mechanism to gain access to a flower of *C. lutea* costs time and requires positional changes and repeated insertions of the proboscis. Extended flower-handling times reduce foraging efficiency (Kunte 2007) but this cost is presumably balanced by a large amount of available nectar, which is reserved for visitors with matching proboscides (Bauder et al. 2011). Handling times during foraging may decrease if there is a good match between flower and pollinator morphology (Harder 1983a).

### 4.3 Proboscis movements during fluid-feeding

According to the feeding observations of Borrell (2003b), orchid bees never lapped nectar, even when they were offered low nectar volumes. These observations do not coincide with mine. While in his study, the proboscides were always protracted and held motionless, I was able to clearly document different methods of nectar intake. Even one and the same individual imbibed nectar by differently using the glossa: (1) glossa motionless, (2) sporadic lapping movements, and with (3) cyclic licking-motions.

In sum, observations to date show that the orchid bee species are very flexible in the method of nectar consumption, ranging from lapping-sucking to – as claimed by Borrell (2003b) - pure sucking. Which method of fluid uptake is utilized by the bees is probably dependent on (1) the available nectar amount, (2) the flower morphology of nectaring plants (long corolla tube or short or dish-shaped flowers), and (3) the viscosity of the liquid (Kingsolver & Daniel 1995), as well as other possible factors.

The movements of glossa contribute remarkably to how much nectar can be drawn, especially from flowers with long corolla tubes (Harder 1995). The glossa has the longest extension of any part of the labiomaxillary complex, and its movements can be changed to ingest by capillary action to obtain residual liquids deep in the tube. The feeding experiments in which *E. championi* and *E. imperialis* were offered drops of sucrose solution on a surface, it was noticeable that *E. championi* was clearly faster in nectar uptake due to fully using the protracted glossal tip. Nectar uptake in *E. imperialis* was the fastest, when the tips of the galeae and labial palps were positioned within the drop of fluid. It is assumed that the glossa plays a greater role in nectar uptake in the

mediate sized proboscis of *E. championi*. This is supported by the greater relative protraction of the glossa in *E. championi*.

The fact that some euglossine individuals were observed to use the lapping-sucking-mode, when feeding on large fluid amounts is curious, since they are fully able to imbibe the nectar by suction alone. It would be interesting to know, if frequences of licking in euglossine bees are independent on viscosity, as in *Bombus* (Harder 1986, Chapman 2013), and if sucking necessitates more energy than lapping. Licking frequences of an observed individual of *E. imperialis* were about 1-2 Hz. Between each licking motion, the glossa remained retracted for approximately the time of a single licking motion. Probably this is the time that is required for suction nectar to ingest by musculature action of the cibarial pump. The licking frequency is very slow in contrast to *Bombus* with 4-5 Hz (Chapman 2013, Harder 1986). One reason for this may be that the much longer glossa in Euglossini must travel a greater distance before it can be retracted.

The tip region of many nectar-feeding insects are equipped with specialized sensilla (Krenn et al. 2005). According to Galić (1971), the sensilla on the tip of glossa are chemoreceptors. They presumably function for the detection of food.

### 4.4 Functional proboscis length

The observation of one individual of *Euglossa imperialis* showed that in relatively short flower tubes (*Lantana* sp.) the proboscis was not fully extended, in a way that the basal parts did not protract, however it was fully extended when inserted into the long corolla tube of *Calathea lutea.* It is assumed that the stretching of the basal part of the proboscis is only neccessary to reach nectar in deep corolla tubes. Harder assumed (1982, 1983b) on the basis of the observed different movements in short and long-tongued species that the functional unit of the proboscis length of the short-tongued bees is the labium, while in long-tongued bees it is the glossa. I disagree with his conclusion with respect to the long-tongued bee due to the important role of the food tube formed by the galeae and labial palps and the role it plays in the elongation by protracted basal parts of the proboscis which greatly affect the functional proboscis length. One should also not exclude the possibility that even within the proboscis food tube, capillarity could be an important action.

### 4.5 Probing and fluid intake

Euglossini tend to follow foraging traplines on a few nectar-rich resources, which are often visited each day (Janzen 1971). Borrell & Krenn (2006) concluded that fluid-handling times may be more of a significant problem than probing times.

Probing time is comprised of access time and ingestion time. The access time increases linearly in deeper feeding tubes, and if the flower is deeper than the glossal length, ingestion time varies due to a decline of the nectar ingestion rate (Harder 1983a).

Short-tongued bees are more rapid in nectar intake than long-tongued bees with labia of equivalent size. The observed dissimilarities in ingestion rates were attributed by Harder (1983b) to the differences in the different proboscis mechanisms (Harder 1986). Borrell (2003a) also found a negative effect of proboscis length on intake rates in euglossine bees. Although meaningful observations regarding this are lacking in the present study, there is a trend toward the suggested effect in *E. imperialis*, which is slightly less efficient when feeding of small amounts of nectar.

With respect to *Bombus*, the intake rate of sucrose solutions at concentrations up to about 40% lies around 1.75 µl/s (Chapman 2013). More viscous nectar causes lower ingestion rates, probably because the glossa can load less fluid. This effect on bumblebees is explained by the constant lapping rate regardless of viscosity (Harder 1986). The mean nectar intake of *Euglossa* ranges from 0.62 µl/s (min 0.33 – max 0.77) in *E. imperialis* to 0.68 µl/s (min 0.50 – max 0.83) in *E. championi* when feeding on 10 µl drops. The slower intake of *E. imperialis* is probably due to the small amount of artificial nectar, if my assumption is correct that the glossal use during nectar uptake is less important than in *E. championi*.

In summary it can be concluded that an orchid bee with a particularly long proboscis has to bear costs in slower nectar intake rates.

# 5 Abstract

Orchid bees (Euglossini, Apidae) possess the longest proboscides among bees. Proboscis lengths can reach approximately twice the body length, and maybe more in several species. The extremely elongated mouthparts enable the use of a very broad spectrum of plant species as a nectar source, from which short-tongued insects are excluded from feeding due to the long corolla tube.

The aim of this study was to compare the mode of nectar feeding in two species of the genus *Euglossa*. *E. championi*, an Euglossini bee with a relatively moderate length of proboscis, and *E. imperialis*, an Euglossini bee with one of the longest proboscides.

In addition to measurements and comparison of the mouthparts which are involved in fluid-feeding, feeding experiments were conducted with both natural and artificial flowers. Main attention was paid to the proboscis movements during feeding.

The two studied species are similar in general structure of the proboscis; however, in *E. imperialis* there are noticeable disproportionate extensions of the distal components of the proboscis (galeae, labial palps and glossa), which form the food tube and make it a functional unit. These components differ highly significantly between the two investigated species. In contrast, the basal parts, which are responsible for the protraction and retraction, hardly show any differences between the two species.

In conclusion, Euglossini are not presumed to be purely suction-feeders, they exhibit different proboscis movements of distal and basal proboscis parts during feeding, and lapping-sucking motions typical of other long-tongued bees actually occur. Regarding the flexible use of the proboscis, Euglossini are quite possibly at an advantage compared to other long-tongued flower-visiting insects, since they can choose the most efficient method to handle floral liquids.

# 6 Zusammenfassung

Prachtbienen (Euglossini, Apidae) sind jene Bienen mit den längsten Saugrüsseln, die eine Länge bis zu doppelter Körperlänge erreichen können. Mit diesen langen Mundwerkzeugen können sie ein sehr breites Pflanzenspektrum für die Nektaraufnahme nutzen, das für kurzrüsselige Insekten unerschlossen bleibt.

Die Arbeit umfasst vergleichende Untersuchungen an 2 Arten der Gattung *Euglossa. E. championi,* mit einer für Euglossinen relativ moderaten Rüssellänge, sowie *E. imperialis* mit, innerhalb der Gattung, einem der längsten Rüssel. Neben Messungen und dem Vergleich der einzelnen an der Nahrungsaufnahme beteiligen Rüsselteile, wurden Fütterungsversuche mit natürlichen wie auch künstlichen Blüten durchgeführt. Das Hauptaugenmerk wurde dabei auf die ausgeführten Bewegungen der Proboscis gelegt.

Die beiden untersuchten Arten gleichen sich im Aufbau der Proboscis, auffällig sind jedoch in *E. imperialis* die überproportionalen Verlängerungen der distalen Proposcisteile, die als funktionelle Einheit das Nahrungsrohr bilden (Galeae, Labialpalpen und Glossa). Sie unterscheiden sich in der Länge hoch signifikant von jenen der Art mit der relativ moderaten Rüssellänge, *E. championi*. Die basalen Teile, die für die Proboscisbewegungen verantwortlich sind, zeigen im Vergleich der beiden Arten kaum Längenunterschiede.

Nektaraufnahme erfolgt bei den Prachtbienen nicht ausschließlich saugend, wie für die Prachtbienen angenommen, sondern es konnten auch diese für langrüsselige Bienen typisch leckend-saugenden Bewegungen beobachtet werden. Mit dem flexiblen Einsatz des Rüssels sind Euglossini vermutlich anderen langrüsseligen Blütenbesuchern in gewisser Hinsicht im Vorteil, weil sie flexibler Flüssigkeiten von unterschiedlichen Blüten aufnehmen können.

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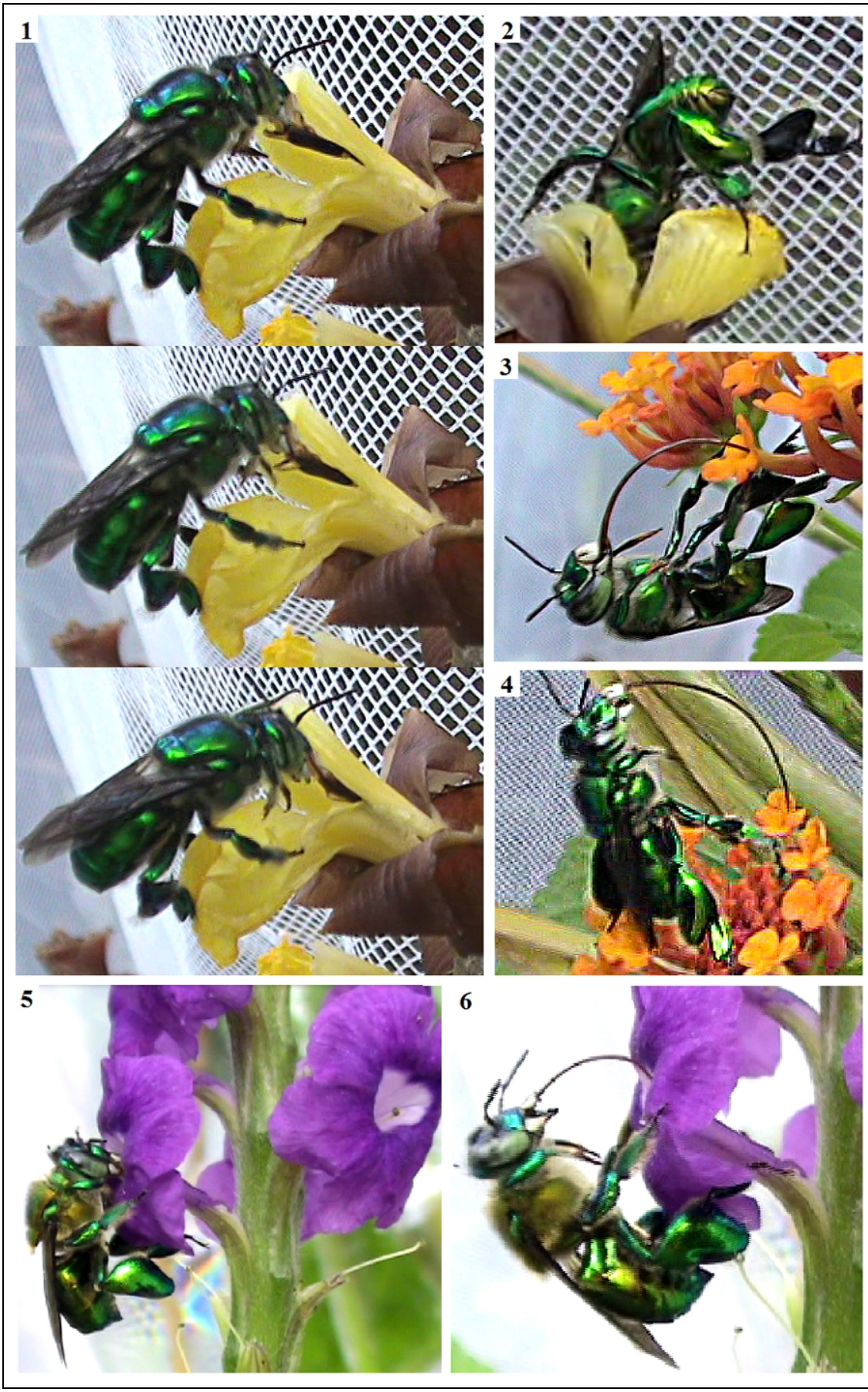
# Appendix

**1:** *Euglossa imperialis* probing a flower of *Calathea lutea*. The protracted proboscis is inserted into the corolla tube and gets additional elongation due to the stretched postmentum. Photos from top to bottom show the stretching action. **2:** For reaching the base of the corolla tube this individual of *E. imperialis* performs a headstand. This is possible if the corolla is in a vertical position. **3** and **4**: *E. imperialis* probing flowers of *Lantana* sp. requires a balance act from hanging on mid and hind legs to straigthen up the body by stretching mid and hind legs. **5** and **6**: *Euglossa championi* probing flowers of *Stachytarpheta frantzii*.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# Curriculum vitae

## Personal Details

| | |
|---|---|
| Name | Maria Helene GRUBER |
| e-mail | m.h.gruber@gmx.at |
| Citizenship | Austria |

## Education

| | |
|---|---|
| 10/2009 - 9/2013 | Diploma thesis at the Department of Evolutionary Biology: "Euglossini (Hymenoptera, Apidae): Fluid feeding mechanisms and functional morphology of the proboscis" (FWF-project P 22248 B17 "Extremely long mouthparts in flower-visiting insects: form, function and evolution") |
| 2/2013 - 5/2013 | Basic course in beekeeping at LV für Bienenzucht, Vienna |
| 3/2009 - 10/2009 | Course in environmental education at WWF Austria, Vienna |
| since 2003 | Studies in Biology / Ecology at the University of Vienna, Faculty of Life Sciences; major subject: Terrestrial Ecology |
| 2002 - 2003 | Qualification for university entrance (natural scientific studies) |
| 1998 - 2001 | College for social professions / LHB Vienna |

## Work Experience

| | |
|---|---|
| since 4/2009 | Social work at KoMiT GmbH, Vienna (educational leave 1/2012 - 12/2012) |
| 7/2005 - 12/2011 | Freelance in environmental education at WWF Austria, Vienna |
| 8/2007 - 12/2008 | Freelance on an adventure playground (environmental education and animation) at Wiener Kinderfreunde, Vienna |
| 10/1996 - 11/2001 | Social work at Institut Hartheim GmbH, Alkoven |

## Training Courses & Field studies

| | |
|---|---|
| 2013 | Field course: Habitats and vegetation of seminatural landscapes, Ötschergräben |
| 2012 | Field course: Methods in Biodiversity research, NP Donauauen<br>Course: Determination of native Apidae |
| 2010 | Ultrastructural laboratory course: Submicroscopic anatomy and preparation techniques for TEM and SEM<br>Field studies for my diploma thesis at the Tropical Research Station La Gamba, Costa Rica (3 weeks) |
| 2009 | Course and field trips: Protected area management<br>Laboratory course: Morphology and evolution of Arthropoda |
| 2008 | Course: Analog and digital photography for scientific documentation |
| 2007 | Field course: Ecology and behavior of native flower visitors<br>Field course: Biodiversity of animal communities in Costa Rica, Tropical Research Station La Gamba, CR<br>Alpine excursion and zoological field study<br>Course: Scientific film in biology |
| 2006 | Course: Reproduction ecology of tropical plants |
| 2005 | Volunteer at Naturschutzbund Oberösterreich ("Umweltbaustelle Koaserin"; 1 week) |

## Publications

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