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DIPLOMARBEIT

Titel der Diplomarbeit

„Comparative morphology of the mouthparts of South African Monkey Beetles (Scarabaeidae: Hopliini)“

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1. Introduction

The majority of flower visiting insects belongs to the following four orders: Hymenoptera (47%), Diptera (26%), Coleoptera (15%) and Lepidoptera (10%). The remaining 2% consist of further insects (Knuth, 1898, cited in Barth, 1991). Beetles represent a phylogenetically old group of insects with biting chewing mouthparts (Barth, 1991). They usually possess prognathous, unspecialized mouthparts (Kevan & Baker, 1983; Krenn et al., 2005) and feed on nectar, pollen and petals.

1.1. Food sources of flower visiting insects

Pollen serves as a highly nutritious food source and contains proteins, minerals, lipids, carbohydrates and fibre (Johnson & Nicolson, 2001). The protein concentration shows a great variation among different plant species, it can range from 2.5-61% (Roulston & Cane, 2000). Pollen grains possess a hard and highly resistant outer wall, the exine which must be overcome to benefit from the nutrients (Johnson & Nicolson, 2001). Therefore, insect mouthparts are highly integrated structural units, interfacing with their food source (Betz et al., 2003). To crack the pollen wall mechanically, diverse mouthpart adaptations are known. Beetles feeding on pollen show a broad mola on their mandible with various rows of teeth to squash the pollen grains (Roulston & Cane, 2000). Different mandibular adaptations to use pollen as food source are two thin and smooth lobes, lacinia mobilis and postmola, to knead the pollen grains (Fuchs, 1974). The mouthparts of pollen- and nectar feeders are densely covered with setae to mop up pollen and nectar (Johnson & Nicolson, 2001). Especially the maxillae are equipped with dense pads and tufts of specially shaped bristles (e.g. broadened, curled, crooked) and that are moistened with saliva to improve the pollen grain adhension (Fuchs, 1974; Karolyi et al., 2008). Those are used as pollen brooms or to feed on nectar from exposed surfaces. Beetles feeding on floral tissue are often destructive to the plants and do not serve as pollinators (Krenn et al., 2005). The majority of flower visiting beetles probably damage the flowers more than they are beneficial for them. Often they eat the petals and destroy their host plants (Barth, 1991).

Nectar is basically a sugar-water mixture with a total sugar content of about 40%. This amount can range from 8-76% depending on the plant species. Nectar contains in smaller amounts amino acids, proteins, organic acids, phosphates, vitamins and

enzymes as well (Barth, 1991). For nectar uptake two mechanisms are common: adhesion and suction. Specialized mouthparts for nectar uptake have an elongated tubular food canal to suck nectar along a pressure gradient. Such elongated proboscides evolved independently in Coleoptera, Hymenoptera, Diptera and Lepidoptera (Krenn et al., 2005). Species of the genera *Leptopalpus* and *Nemognatha* possess a suction tube formed by maxillae that is used for nectar uptake like a proboscis (Matthes, 1991; Wilhelmi & Krenn, 2012). In few beetles the galea is modified to wipe up nectar, wherefore the setae, located on the galea, are numerous, long and curly (Fuchs, 1974; Johnson & Nicolson, 2001).

1.2. Monkey Beetles (Scarabaeidae: Hopliini)

Monkey beetles appear to be one of the most important pollinating insects in the Western and Northern Cape Province of South Africa. This region contains the majority of the world´s monkey beetle species with more than 2/3 of the worldwide monkey beetle fauna and many of these species are endemic to southern Africa (Colville et al. 2002; Goldblatt et al., 1998; Mayer et al., 2006). They can carry high pollen loads and play a vital role in the pollination of Asteraceae and Aizoaceae (Mayer et al., 2006). Monkey beetles may feed on pollen, nectar and petals of the flowers and use the flowers as mating sites in addition (Steiner, 1998).

1.3. Pollination guilds (by Picker & Midgley, 1996)

Three pollination guilds in monkey beetles were defined by Picker & Midgley (1996) based on colour preference and feeding behaviour. The first pollination guild includes species of *Anisonyx* and *Peritrichia*. These beetles are described by the authors as densely hirsute, darkly coloured and show no marked sexual dimorphism. Their mouthparts are elongated and used to feed on pollen and possibly on nectar. They were neither observed to burrow themselves in flowers nor to damage them. Beetles of the second pollinator guild, the “embedding guild”, are rather hairless and sexually dimorphic. They dig into their host flowers and leave them damaged. This pollination guild includes beetles of the genera *Scelophysa*, *Heterochelus*, *Gymnoloma* and *Pachycnema*. A third pollination guild contains species of *Lepithrix*. These beetles are described as an intermediate guild between the two other guilds. Even though

beetles of the third guild do not feed on nectar, their feeding mechanisms are similar to those of the embedding guild (Picker & Midgley, 1996).

The purpose of the present study is to describe and examine the mouthpart morphology of these beetles and to analyse their gut content to estimate the feeding preferences of selected South African monkey beetles.
The hypothesis is that the various South African Hopliini exhibit different mouthpart morphology that is related to their feeding preferences and can be regarded as adaption to the respective flower visiting behaviour.

2. Materials and Methods

The beetles were collected during spring in August 2010 and September 2011 in the northern and western Cape of South Africa when they are common. They were identified by J. Colville (University of Cape Town, South Africa) and preserved in 70% ethanol. The studied species (Tab. 1) were grouped into feeding groups according to their mouthpart morphology.

2.1. Light microscope

For the examination using a light microscope, the heads were removed from the body and imbedded in a melted wax-rosin mixture with a soldering iron and insect pins. Dissected mouthparts were prepared using a stereo microscope and embedded in Polyvinyllactophenol on a microscopic slide. After 48 hours of drying the preparations were sealed with nail polish to prevent them from draining and from the infiltration of air-bubbles. Photos of different focal planes were taken with a light microscope (Olympus CX41) equipped with a digital reflex camera (Olympus E330). The micrographs were stitched using Helicon Focus (Version 3.10), line drawings and contrast graduations were edited with Adobe Photoshop CS5 (Version 12.0). For each of the 17 investigated species at least 3 to 11 specimen were examined and compared.
The contents of the anterior gut were extracted using a stereo microscope and microscopic slides were prepared in Polyvinyllactophenol. After air drying, the preparations were examined and the gut contents identified.

Photos of the bodies were made with an Olympus SZX2-ZB10 equipped with a CAM-UC30 Camera.

2.2. Scanning electron microscope (SEM)

The heads or mouthparts of some species were studied using a SEM (Philips XL 20, Philips XL 30 ESEM) at the Core Facility - Institution of Cell Imaging and Ultrastructure Research (University of Vienna, Austria). SEM photos were taken from 1 to 3 specimens of selected representatives of the various feeding groups. The dissected mouthparts or heads were dehydrated in a series of alcohol (70%, 80%, 90%, 100% ethanol) and Hexamethyldisilazan (HMDS). The specimens were air-dried and attached on an aluminium stub by adhesive tabs and sputtercoated with gold (Agar sputtercoater B3740 for 240 seconds).

3. Results

The studied species were classified into different feeding groups based on similarity in mouthpart morphology. In the following each feeding group is described and pictures of one species are used as example for each group. The examined structures are labrum, mandible, maxilla and labium. For each species male and female individuals were examined, differences could be found only in the size of the mouthparts. No morphological differences could be found that would allow to conclude a functional difference or different feeding preferences. Since this difference between sexes only appeared in a minor dimension they had not been further evaluated. In this research the terms setae and bristle are used synonymously, describing a hair-like structure.

Tab. 1 Studied species, sampling sites, pollination guild based on colour preference and feeding behaviour according to Picker & Midgley (1996) and feeding group based on mouthpart morphology and gut content.

Species	Sampling sites	Collection date	Pollination guild	Feeding group
Anisochelus inornatus (BURMEISTER 1844)	Grasbergroad, Hantam Botanical Garden	26.08.2010 27.08.2010		2
Anisonyx ursus (FABRICIUS 1775)	Darling	09.2011	1	1
Chasme decora (WIEDEMANN 1823)	Malmesbury	09.2011		4
Chasme jucunda (PÉRINGUEY 1902)	Kamieskroon	09.2011		2
Clania glenlyonensis (DOMBROW 1997)	Nieuwoudtville; Grasbergroad; Hantam Botanical Garden	26.08.2010		2
Clania macgregori (DOMBROW 1997)	Grasbergroad	27.08.2010		2
Congella sp. (PÉRINGUEY 1902)		03.2012		3
Dolichiomicroscelis gracilis (PÉRINGUEY 1902)	Darling	09.2011		2
Heterochelus pickeri (DOMBROW 1997)	Hantam Botanical Garden	26.08.2010	2	5
Kubousa gentilis (PÉRINGUEY 1902)	Malmesbury	09.2011		3
Lepisia ornatissima (BURMEISTER 1844)	Kamieskroon	09.2011		3
Lepisia rupicola (FABRICIUS 1775)	Darling	09.2011		2
Lepithrix sp. (NIETNER 1857)	Kamieskroon	09.2011	3	4
Monochelus nieuwoudtvillensis (DOMBROW 1997)	Butterkloof-Pass	29.08.2010		3
Pachycnema calcarata (BURMEISTER 1844)	Kamieskroon	09.2011	2	1
Pachycnema flavolineata (BURMEISTER 1844)	Kamieskroon	09.2011	2	6
Pachycnema crassipes (FABRICIUS 1775)	Surroundings of Nieuwoudtville; Grasbergroad	27.08.2010	2	1
Scelophysa scheffoldi (DOMBROW 1999)	Kamieskroon	09.2011	2	2

3.1. Feeding group 1

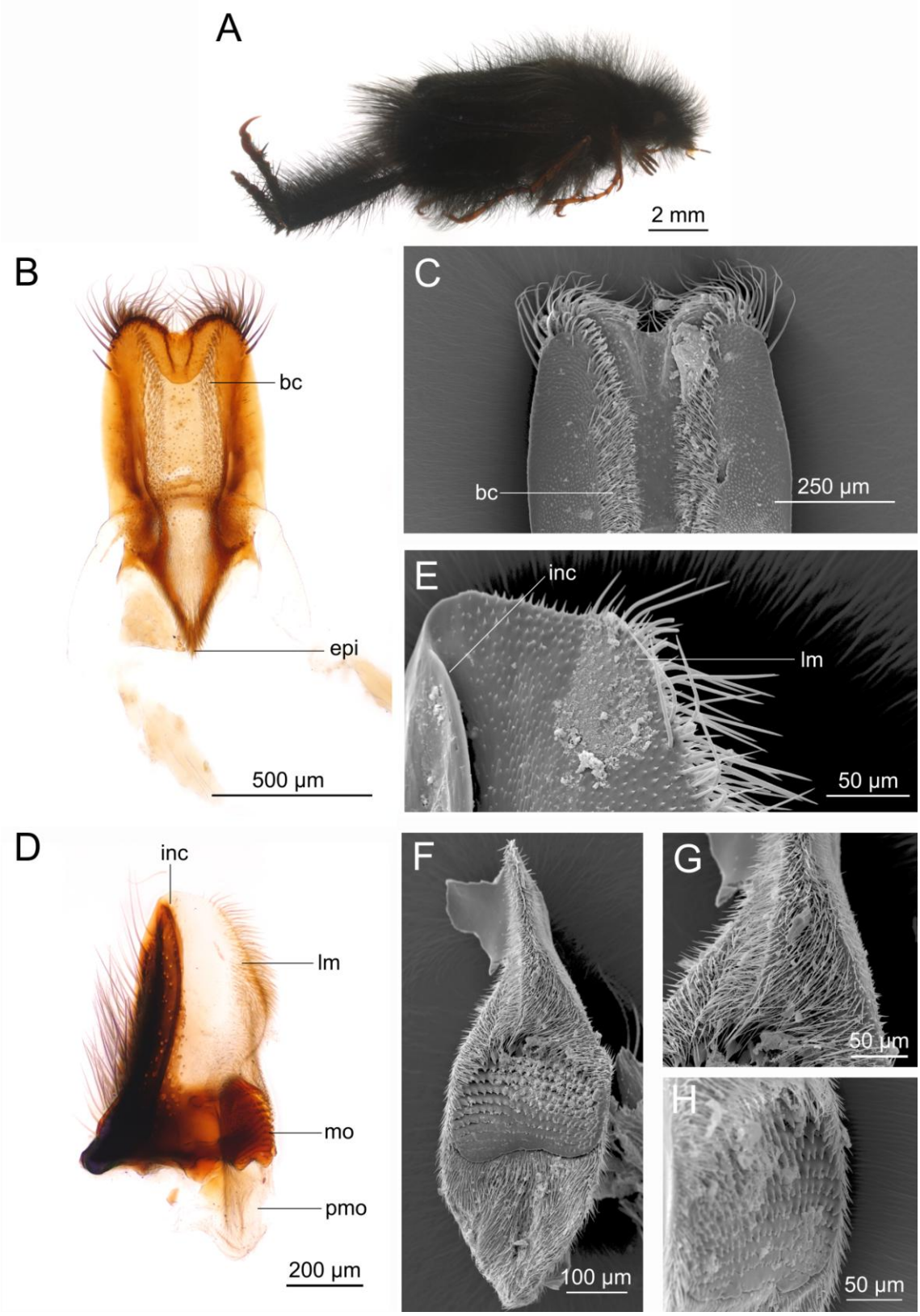

Fig. 1: Body and morphology of labrum and mandible of *A. ursus* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Male of *A. ursus* (LM). **B** Ventral view of the labrum (LM). **C** Inner surface of the labrum (SEM). **D** Left mandible, ventral view (LM). **E** Left mandible, detail of the incisor part and the lacinia mobilis, ventral view (SEM). **F** Medial side of the mandible (SEM). **G** Lacinia mobilis, medial view (SEM). **H** Mola, ventral view (SEM). *bc* bristle crest, *epi* epipharynx, *inc* incisor, *lm* lacinia mobilis, *mo* mola, *pm* postmola

Three of the investigated species were categorized as members of the first group. These species are *A. ursus*, *P. calcarata* and *P. crassipes* (Tab. 1). The first group is described by the example of *A. ursus* (Figs.1, 2). The mouthpart morphology of this feeding group is summarized in table 2.

The body of *A. ursus* is densely hirsute (Fig. 1A) and possesses elongated mouthparts, especially the maxillary palps and the galea bristles. However the other two species, *P. calcarata* and *P. crassipes*, are not as pilose as *A. ursus*. These species even show a greater sexual dimorphism than *A. ursus* whose females are nearly as pilose as the males and the hind legs do not differ in size and shape between sexes.

Tab. 2: Characteristics of the mouthpart morphology of feeding group 1.

Labrum	distal margin curved inwardly, numerous and long setae
Mandible	large postmola, incisor part smooth, without cutting edges
Maxilla	galea covered with numerous and curled bristles, lacinia possesses bristles, cutting edges or tooth are lacking
Labium	ligula elongated

Labrum (Figs. 1B, C)

On the distal edge the labrum is curved inwardly and equipped with numerous and long bristles. The labrum is elongated, slender and deeply curved on the distal edge extending into a u-shaped indentation (Fig. 1C). This prominent indentation could only be found in *A. ursus*. The labrum possesses a v-shaped bristle crest that ends in the epipharynx (Fig. 1B). The bristle crest is composed by a number of bristle rows. The lateral bristle row points anterior while the inner row of bristles points median to the middle of the labrum, where several pores are located. The proximal part of the inner rows is pointing toward the epipharynx and differs from the other setae through their shape and number. Whereas the distal setae are longer and thicker, the proximal ones are shorter and thinner and the median part is equipped with denser placed setae. In comparison to the other pollination groups the labrum of these three species is not as much sclerotized.

Mandible (Figs. 1D-H)

The mandible of *A. ursus* is elongated and located on the proximal part of the labrum at the end of the bristle crest. Due to this position, labrum and maxilla are not separated by the mandible and lay against each other. The left and right mandibles of these species are symmetric, composed of an incisor part on the distal edge, a lacinia mobilis, a mola and a postmola in the proximal part (Fig. 1D). The incisor is smooth without cutting edges (Fig. 1E). It is not distinctly delineated from the lacinia mobilis, which terminates the incisor part. The distal apex of the mandible is not formed by the incisor but the lacinia mobilis. The lacinia mobilis or prostheca is a smooth, thin and not sclerotized lobe, reaching from the incisor part till the mola (Figs. 1D, F). The median margin of the lacinia mobilis possesses bristles in a large number (Fig. 1G). Above the mola the lacinia mobilis is curved and covered with setae pointing downwards toward the mola. The mola (Figs. 1F, H) is a plate-like strongly sclerotized structure and its grinding area bears several rows of small peaked teeth. This ridged structure is equipped with longer teeth in the distal region while the teeth in the proximal region are smaller and flattened, lacking in the proximal apex. Although the mola surface is not large it is covered with numerous teeth. The postmola is a setose lobe like the lacinia mobilis, beginning in the proximal termination of the mola (Fig. 1F). The large surface of the postmola possesses plenty of bristles similar in shape and number to those of the lacinia mobilis.

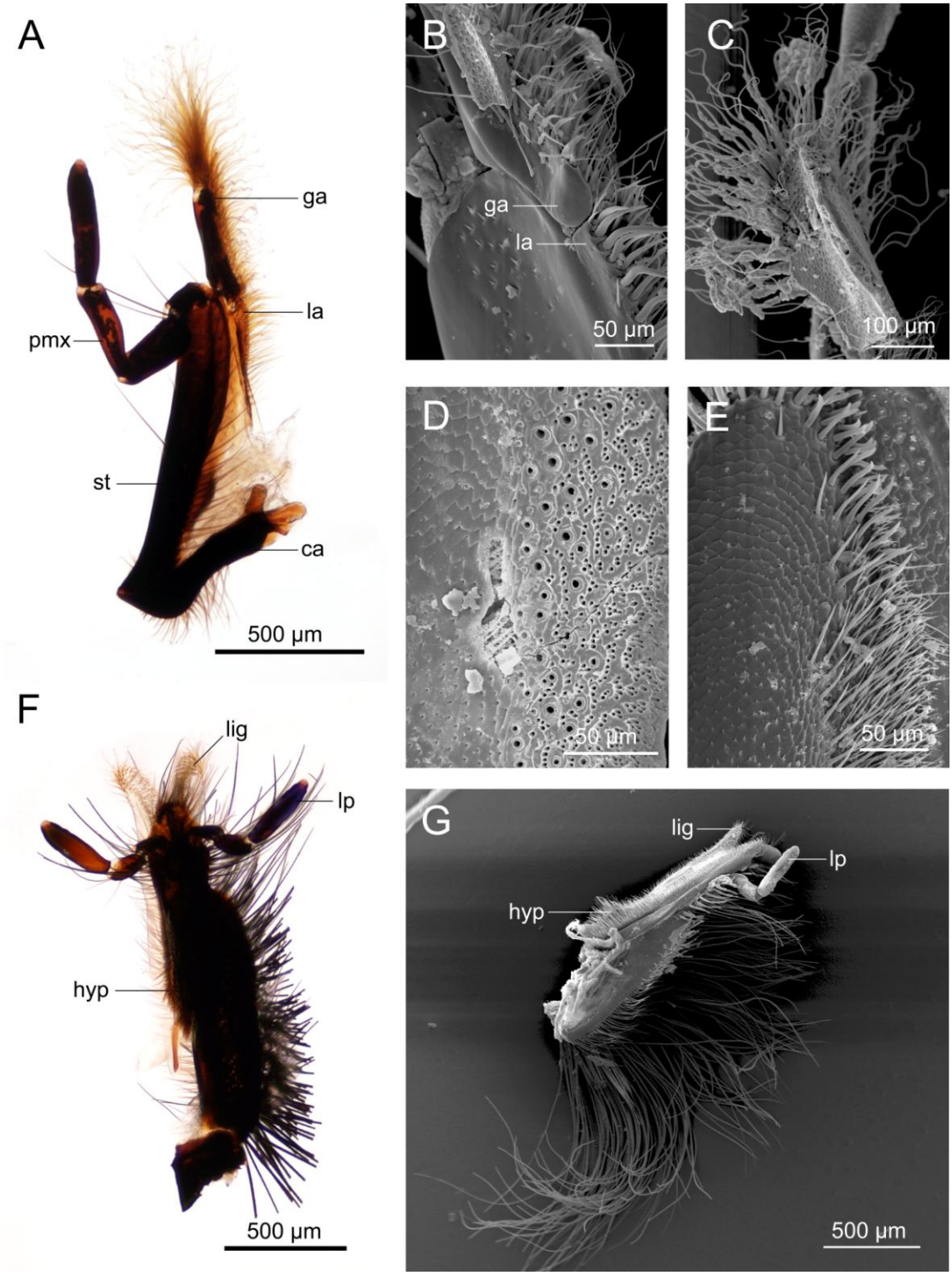

Fig. 2 Morphology of maxilla and labium of *A. ursus* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Right maxilla ventral view (LM). **B** Detail lacinia and galea (SEM). **C** Galea covered with liquid (SEM). **D** Detail fluid (SEM). **E** Detail labrum surface, ventral view (SEM). **F** Labium dorsal view, ventral bristles cut off (LM). **G** Labium (SEM).
ca cardo, *ga* galea, *hyp* hypopharynx, *la* lacinia, *lig* ligula, *lp* palpus labialis, *pmx* palpus maxillaris, *st* stipes

Maxilla (Figs. 2A-D)

The left and right maxillae are symmetric in size and shape and consist of cardo, stipes, lacinia, galea and the maxillary palp. In all studied species belonging to feeding group 1 the cardo is elongated and slender. The proximal apex bears forked apodem and presumably allows a higher movability of the maxilla (Fig. 2A). The lacinia bears numerous bristles that differ from those of the galea in size and shape. Whereas those of the lacinia are shorter and thicker, those of the galea were thinner and curled (Figs. 2A, B). The three representatives of this group show identical maxillae. None of them revealed tooth-like structures or cutting edges, the surface of the galea is covered with numerous and thin bristles covered with some fluid matter (2C). This substance adhered on the mouthparts during the preparation for the SEM. Measurements revealed that its imprints (Fig. 2D) are equal in size and shape to the surface of the labrum (Fig. 2E). The smaller holes seem to be from the inner row of setae on the labrum, while the bigger holes are from the lateral bristle rows and even the lateral pattern of the labrum surface is visible.

Labium (Figs. 2F, G)

The labium of *A. ursus* is elongated and covered with numerous long bristles on the ventral side (Fig. 2G). The ligula, a membranous lobe formed by glossa and paraglossa, reaches forward between the labial palps (Fig. 2F).

Gut content and pollen grains and fluid on mouthparts

In *A. ursus* and *P. calcarata* no pollen grains were found in the dissected guts. A colourless or orange substance was found in the foregut. The galea of all three species was covered with some substance that could be seen in the SEM pictures. *P. crassipes* showed Asteracea pollen grains in the for-, mid- and hindgut, as well as intact pollen grains on the mola.

3.2. Feeding group 2

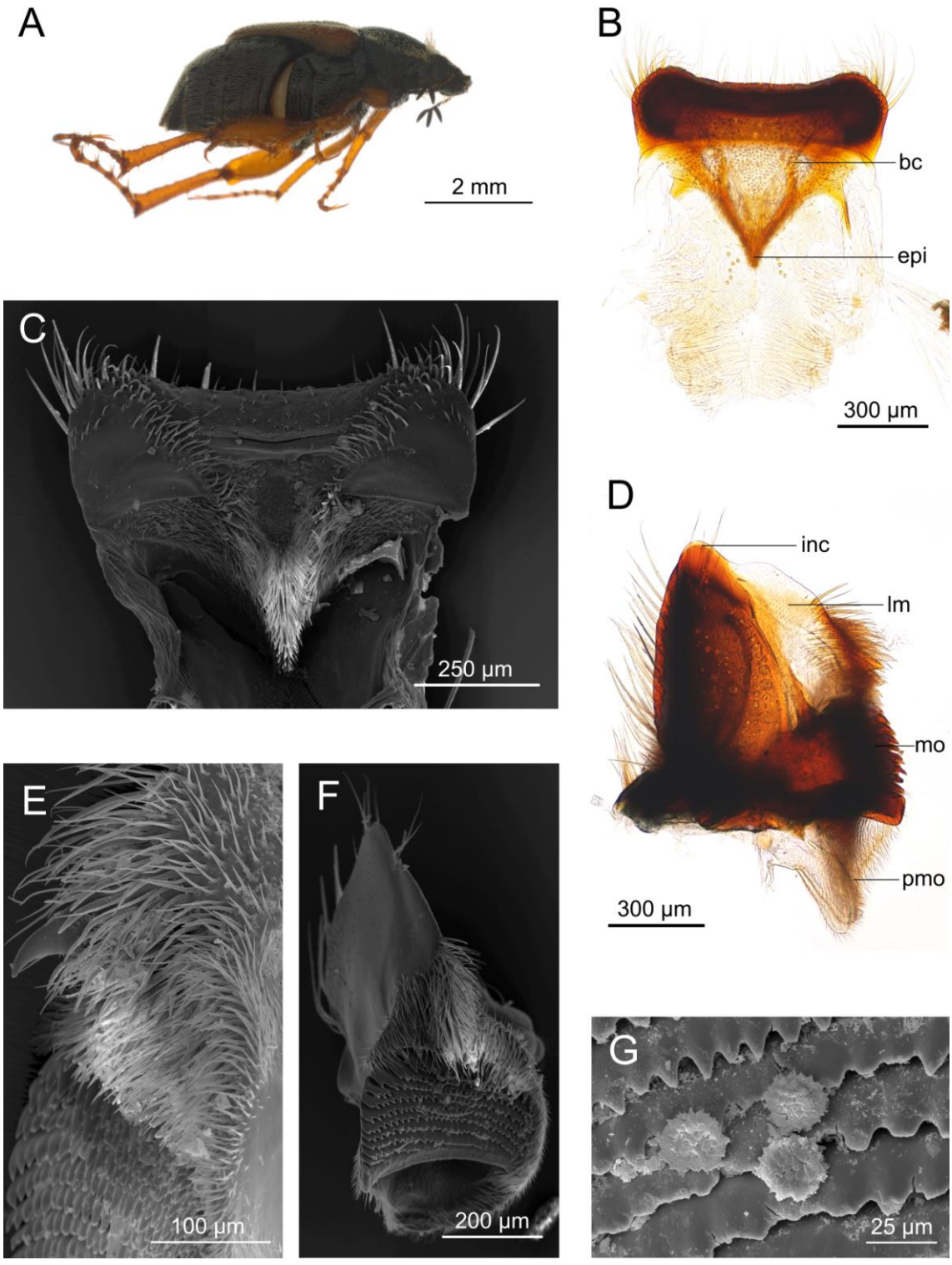

Fig. 3: Body of *D. gracilis*, labrum and mandible of *C. glenlyonensis* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Female of *D. gracilis* (LM). **B** Labrum ventral view (LM). **C** Labrum ventral view (SEM). **D** Right mandible ventral view (LM). **E** Detail lacinia mobilis (SEM). **F** Medial side of the left mandible, mola, postmola and lacinia mobilis (SEM). **G** Detail mola with pollen grains (SEM).
bc bristle crest, *epi* epipharynx, *inc* incisor, *lm* lacinia mobilis, *mo* mola, *pm* postmola

Seven out of eighteen studied species were characterized as representatives of the second feeding group. The characteristic mouthpart morphology of this group is summarized in table 3. Following species belong to this feeding group : *A. inornatus*, *C. jucunda*, *C. glenlyonensis*, *C. macgregori*, *D. gracilis*, *L. rupicola* and *S. scheffoldi*. (Tab. 1). In the following this group is illustrated by the example of *D. gracilis* and *C. glenlyonensis* (Fig. 3, 4).

The body of representatives of this feeding group is relatively hairless and most of these seven species showed no marked sexual dimorphism. With few exceptions the body of the feeding group 2 is small with long and thin hind legs (Fig. 3A).

Tab. 3: Characteristics of the mouthpart morphology of feeding group 2.

Labrum	distal margin curved inwardly only a little bit or straight and covered with few, short bristles
Mandible	incisor part smooth, lacinia mobilis bears a sclerotized tooth
Maxilla	galea toothed and covered with long bristles, lacinia possesses sclerotized bristles
Labium	ligula not elongated

Labrum (Figs. 3B, C)

The distal edge of the labrum is strongly sclerotized and straight or curved inwardly only a little bit (Fig. 3B). It bears a few short bristles on the distal margin (Fig. 3B) and a v-shaped bristle crest that ends in the epipharynx. The proximal part of the bristle crest is composed of numerous dense bristles (Fig. 3C).

Mandible (Figs. 3D-G)

The mandible of *C. glenlyonensis* is about as high as broad and located proximal the bristle crest of the labrum. Left and right mandibles are symmetric, consisting of an incisor part, a lacinia mobilis, a mola and a postmola (Fig. 3D). The apex of the incisor is rounded without cutting edges. The lacinia mobilis ends proximal of the incisor and can clearly be distinguished (Fig. 3D). The median margin of the lacinia mobilis possesses numerous setae and a sclerotized tooth in the proximal area while the rest is free from bristles (Fig. 3E). The mola is broad with several rows of teeth as chewing surface (Fig. 3F). Intact Asteracea pollen grains could be found on the mola (Fig. 3G). The postmola is small, covered with various and small setae (Fig. 3D).

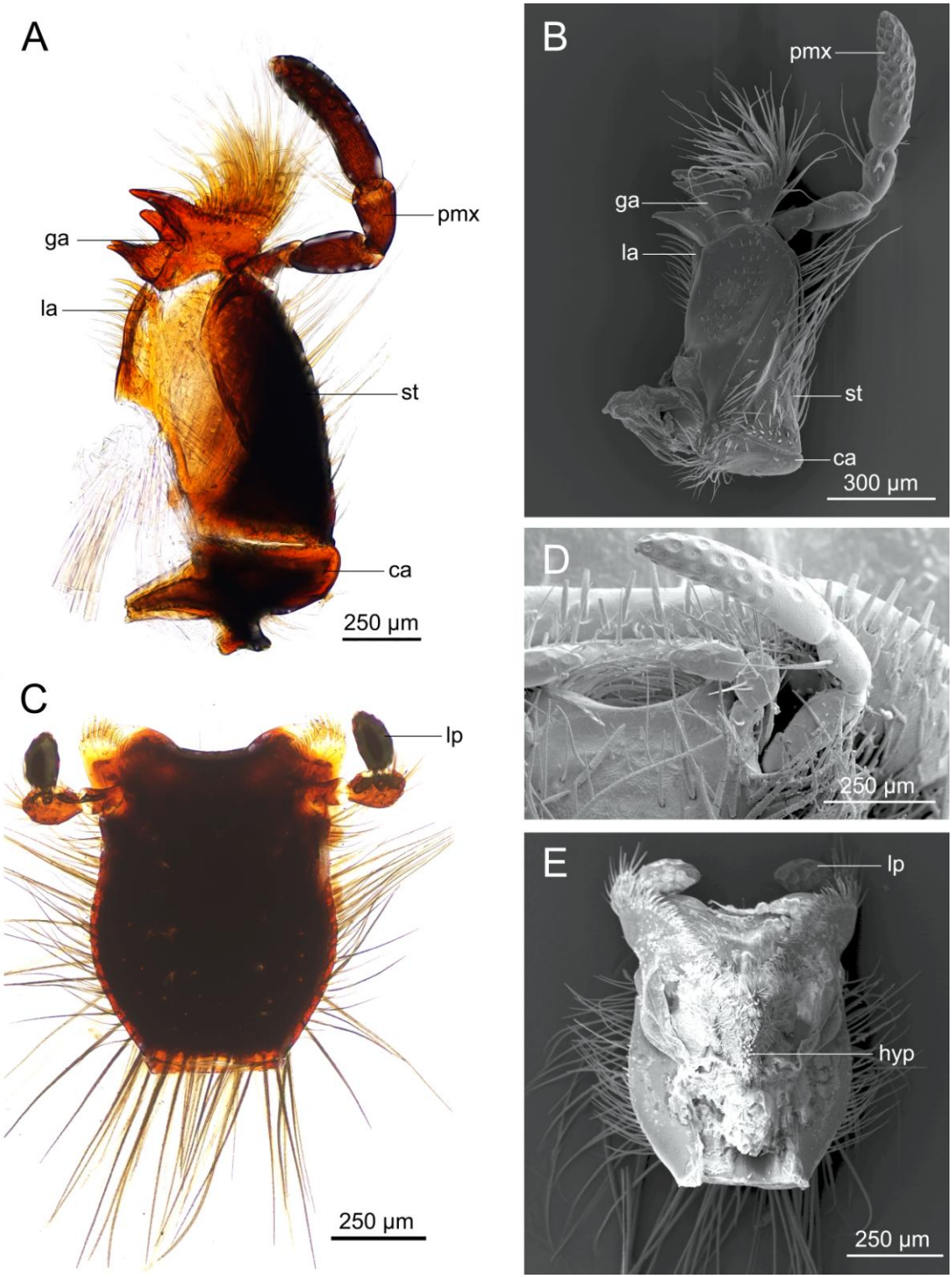

Fig. 4: Morphology of maxilla and labium of *C. glenlyonensis* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Left maxilla ventral view (LM). **B** Right maxilla dorsal view (SEM). **C** Labium ventral view (LM). **D** Head capsule ventral view (SEM). **E** Labium ventral view (SEM).
ca cardo, *ga* galea, *hyp* hypopharynx, *la* lacinia, *lp* palpus labialis, *pmx* palpus maxillaris, *st* stipes

Maxilla (Figs. 4A, B, D)

The left and right maxillae are symmetric in size and shape and consist of cardo, stipes, lacinia, galea and the maxillary palp. The maxilla has a short and thickened cardo (4A, B). The stipes is broadened and bears thickened muscles. The galea forms several strong and sclerotized teeth on the median part while the proximal margins bears numerous bristles. These bristles are long and straight without hooks or curls. In the resting positions the setae are pointing inwardly like the teeth (4D). The lacinia is a rudimentary lobe located on the distal margin of the galea on the median side of the stipes. It bears various bristles that differ from those of the galea in size and shape. The setae on the galea are fewer and shorter but stronger sclerotized than those of the galea (4A).

Labium (Figs. 4C, E)

The labium of *C. glenlyonensis* is about as broad as high and covered with numerous bristles on the ventral side. The ligula, a membranous lobe formed by glossa and paraglossa, is only a short lobe on the proximal margin (Fig. 4C). The hypopharynx is a v-shaped bristle crest of numerous and dense setae (4E).

Gut content and pollen grains and fluid on mouthparts

Numerous intact Asteracea pollen grains were found on the mouthparts and in the guts of the dissected species. Some of them showed a not clearly identifiable orange structure. Almost all dissected individuals of this feeding group had parts of foliage in their gut.

3.3. Feeding group 3

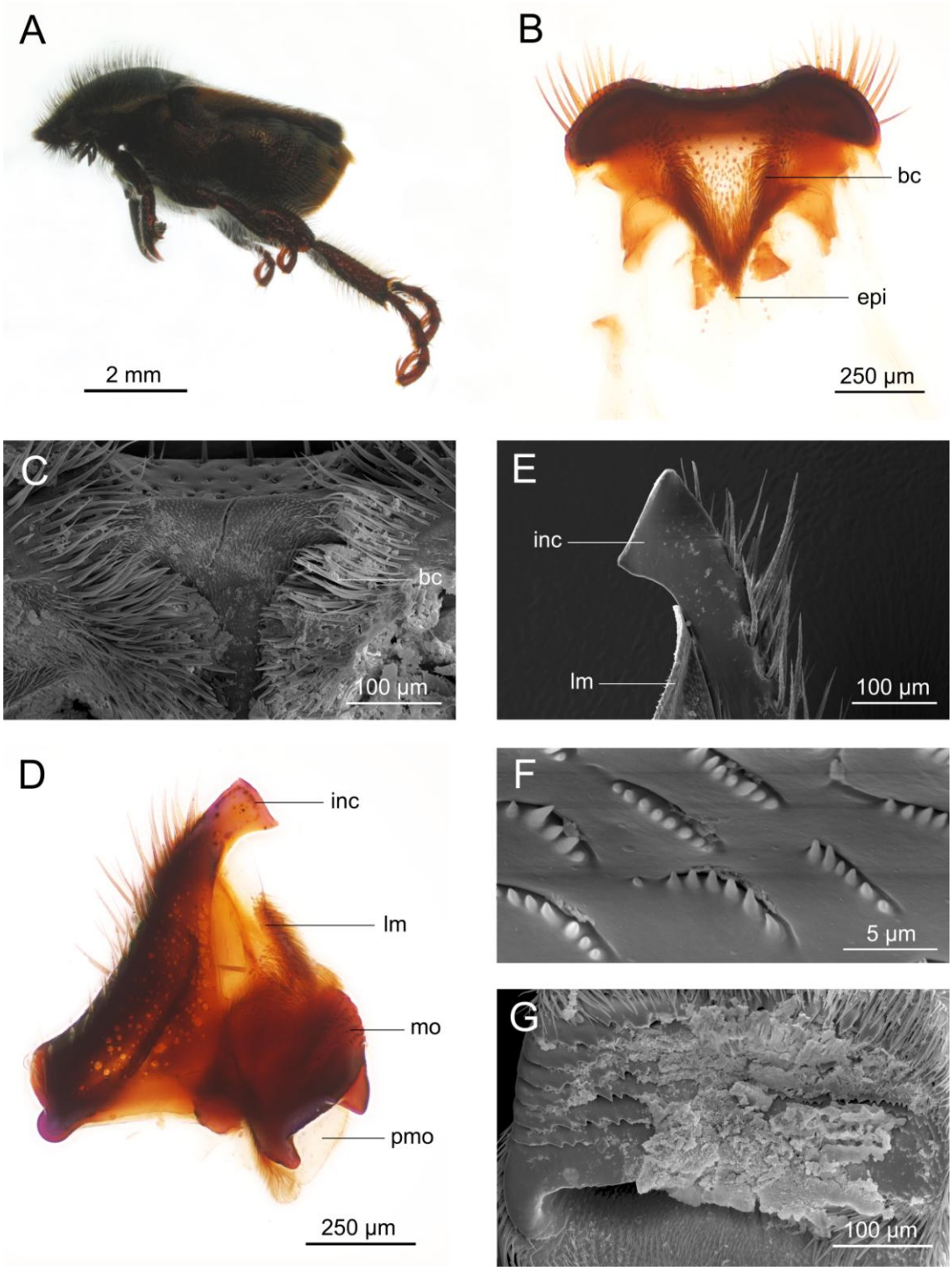

Fig. 5: Body of *K. gentilis*, morphology of labrum and mandible of *M. nieuwoudtvillensis* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Male of *K. gentilis* (LM). **B** Labrum ventral view (LM). **C** Detail bristle crest, ventral view (SEM). **D** Right mandible ventral view (LM). **E** Detail incisor (SEM). **F** Detail surface of lacinia mobilis (SEM). **G** Detail mola, medial view (SEM).
bc bristle crest, *epi* epipharynx, *inc* incisor, *lm* lacinia mobilis, *mo* mola, *pm* postmola

The feeding group 3 contains species which differ only in the morphology of their mandible, especially in the shape of the incisor, from the second feeding group (Tab. 4). Members i.e., *Congella* sp., *K. gentilis*, *L. ornatissima* and *M. nieuwoudtvillensis* of this feeding group 3 are small and covered with short hair (Fig. 5A). They showed no marked sexual dimorphism except for *M. nieuwoudtvillensis*. This group is described by the example of *K. gentilis* and *M. nieuwoudtvillensis* (Figs.5, 6).

Tab. 4: Characteristics of the mouthpart morphology of feeding group 3.

Labrum	distal margin curved inwardly only a little bit or straight and covered with few, short bristles
Mandible	small postmola, incisor part with cutting edges
Maxilla	galea bears big sclerotized teeth and is covered with few bristles, lacinia possesses sclerotized bristles
Labium	ligula not elongated

Labrum (Figs. 5B, C)

The labrum is similar to those of the feeding group 2 in size and shape. On the distal edge the labrum is strongly sclerotized and straight (Fig. 5B). The distal margin bears a few short bristles (Fig. 5B) and a v-shaped bristle crest that ends in the epipharynx. The bristle crest is composed of numerous dense bristles covered with some fluid matter (Fig. 5C).

Mandible (Figs. 5D-G, 6H)

The mandible of *M. nieuwoudtvillensis* is about as high as broad and located proximal the bristle crest of the labrum. The mandibles consist of an incisor part, a lacinia mobilis, a mola and a postmola (Fig. 5D). In *M. nieuwoudtvillensis* the lacinia mobilis ends proximal of the incisor and those two structures can be distinguished clearly (Fig. 5E). The apex of the incisor is rectangular with cutting edges with a smooth surface (Figs. 5D & E, 6H). The median margin of the lacinia mobilis possesses numerous setae, a sclerotized tooth is absent (Fig. 5D). The distal margin of the lacinia mobilis is covered with bundles of bristle-like short structures, arranged in small rows (Fig. 5F). The mola is broad with numerous rows of teeth as chewing surface and the postmola is covered with various and small setae (Fig. 5G). The mandible is located on the distal margin of the maxilla (Fig. 6G) and terminates the tube-like mouth (Fig. 6F).

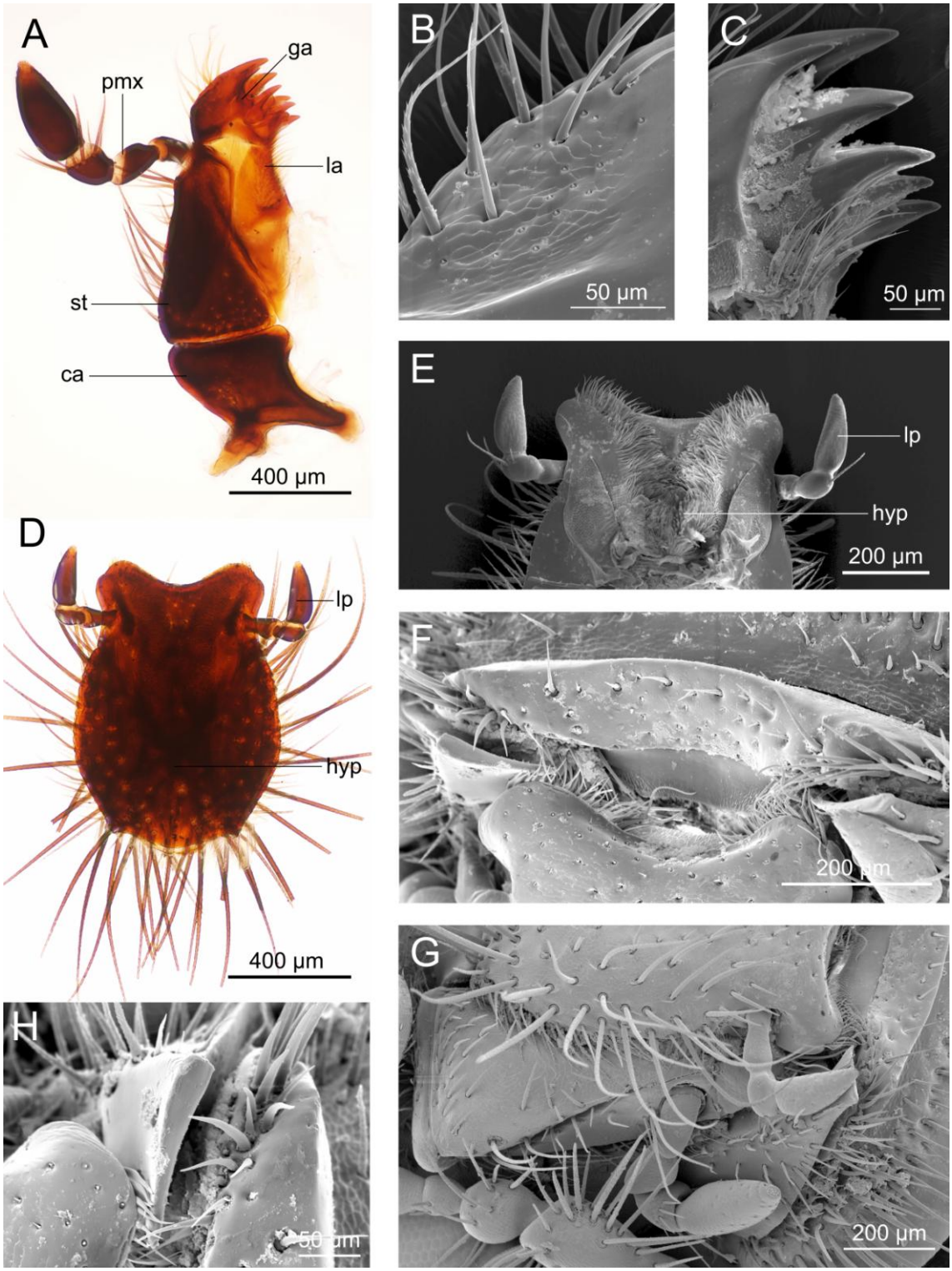

Fig. 6: Morphology of maxilla and labium of *M. nieuwoudtvillensis* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Right maxilla dorsal view (LM). **B** Detail galea dorsal view (SEM). **C** Detail galea dorsal view (SEM). **D** Labium dorsal view (LM). **E** Detail labium dorsal view (SEM). **F** Head capsule frontal view (SEM). **G** Head capsule ventral view (SEM). **H** Incisor frontal view (SEM).
ca cardo, *ga* galea, *hyp* hypopharynx, *la* lacinia, *lp* palpus labialis, *pmx* palpus maxillaris, *st* stipes

Maxilla (Figs. 6A–C)

The maxilla has a short and broad cardo (Fig. 6A) that causes a limited movability, noted during the preparation. The galea forms several strong and sclerotized teeth (Figs. 6A, C) on the median part while a few bristles are located in the lateral area (Fig. 6B). These bristles are short and neither hooked nor curled and are pointing forward. The lacinia is a reduced lobe located on the distal margin of the galea on the median side of the stipes. It bears a small number of short sclerotized bristles (Fig. 6A).

Labium (Figs. 6D–F, G)

The labium of *M. nieuwoudtvillensis* is covered with numerous bristles on the ventral side and strongly sclerotized (Fig. 6D). The hypopharynx is formed by a v-shaped bristle crest of numerous and dense setae (Fig. 6E). The surface within the bristle crest is smooth and forms a tube like structure (Fig. 6F).

Gut content and pollen grains and fluid on mouthparts

Only a small amount of pollen grains with a smooth surface were found in the guts. Those pollen grains could not be further identified. Most of the studied species had a brown-orange mixture in their gut. This material also appeared on the mouthparts, especially on the mola (e.g. Fig. 5G).

3.4. Feeding group 4

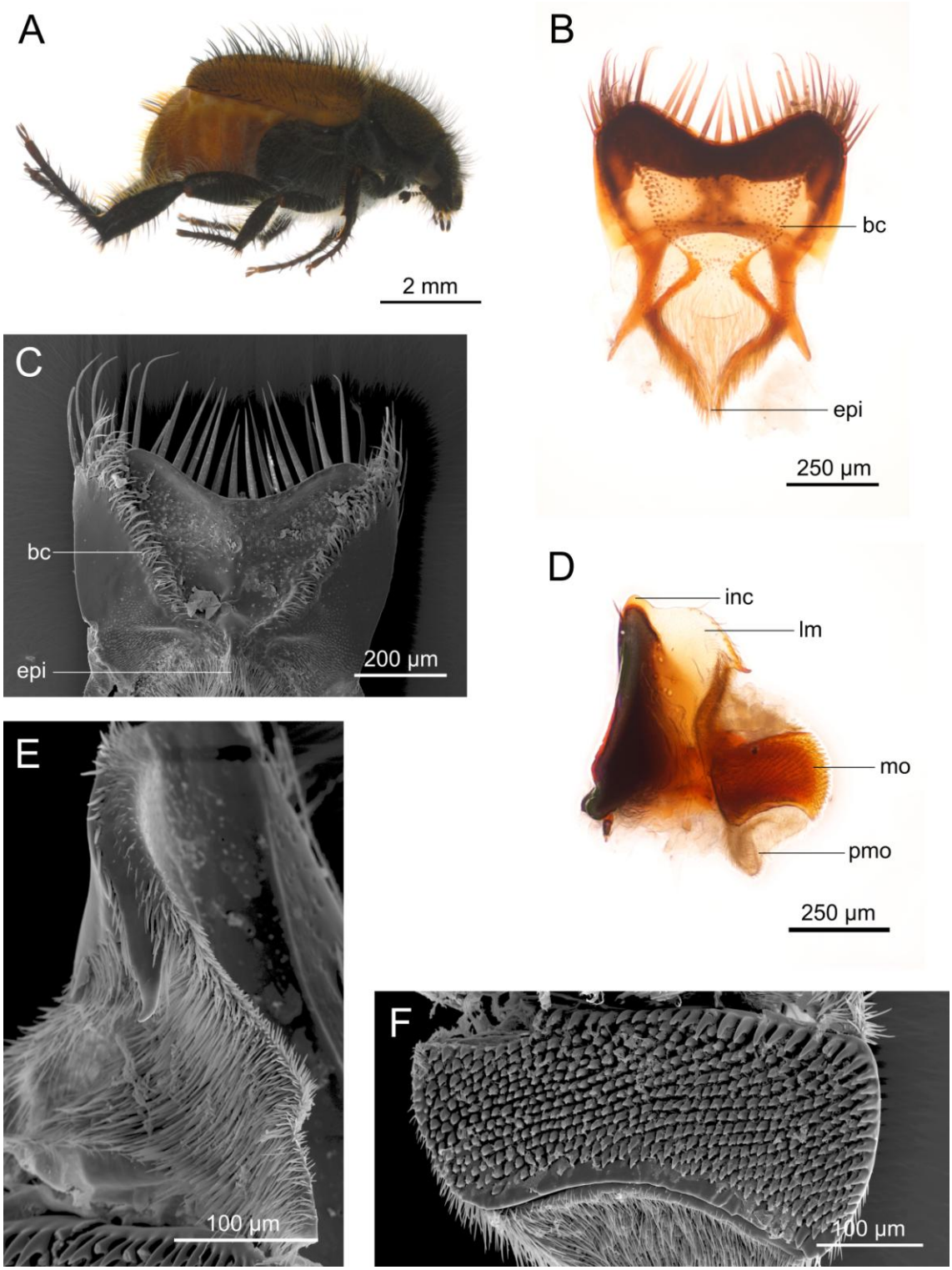

Fig. 7: Body of *C. decora* and morphology of labrum and mandible of *Lepithrix* sp. in light microscopy (LM) and scanning electron microscopy (SEM). **A** Female of *C. decora* (LM). **B** Labrum ventral view (LM). **C** Labrum ventral view (SEM). **D** Right mandible ventral view (LM). **E** Medial side of the lacinia mobilis (SEM). **F** Detail mola medial view (SEM).
bc bristle crest, *epi* epipharynx, *inc* incisor, *lm* lacinia mobilis, *mo* mola, *pm* postmola

The examined individuals of *C. decora* and the undetermined species of the genus *Lepithrix* were categorized as members of the feeding group four. Their characteristic mouthpart morphology is summarized in table 5. The body of the studied species is small and sparsely covered with short hair (Fig. 7A). The investigated species showed no marked sexual dimorphism. In the following this group is illustrated by the example of *C. decora* and *Lepithrix* sp. (Fig. 7, 8).

Tab. 5: Characteristics of the mouthpart morphology of feeding group 4.

Labrum	distal margin curved inwardly and covered with long bristles
Mandible	small postmola, large mola, incisor part without cutting edges, lacinia mobilis bears a crooked teeth
Maxilla	galea and lacinia covered with bristles
Labium	ligula elongated

Labrum (Figs. 7B, C)

The distal edge of the labrum is strongly sclerotized, curved inward and covered with numerous and long bristles (Fig. 7B) The v-shaped bristle crest is composed of a few short bristles and ends in the epipharynx (Fig. 7C).

Mandible (Figs. 7D-F)

The mandible of *Lepithrix* sp. is about as high as broad and located on the proximal edge of the bristle crest of the labrum. The mandible consists of an incisor part, a lacinia mobilis, a mola and a postmola (Fig. 7D). The median margin of the lacinia mobilis possesses numerous setae and a curved sclerotized tooth and forms a convex area (Fig. 7E). The mola is broadened with numerous rows of pointed teeth and the postmola is covered with various setae (Fig. 7F).

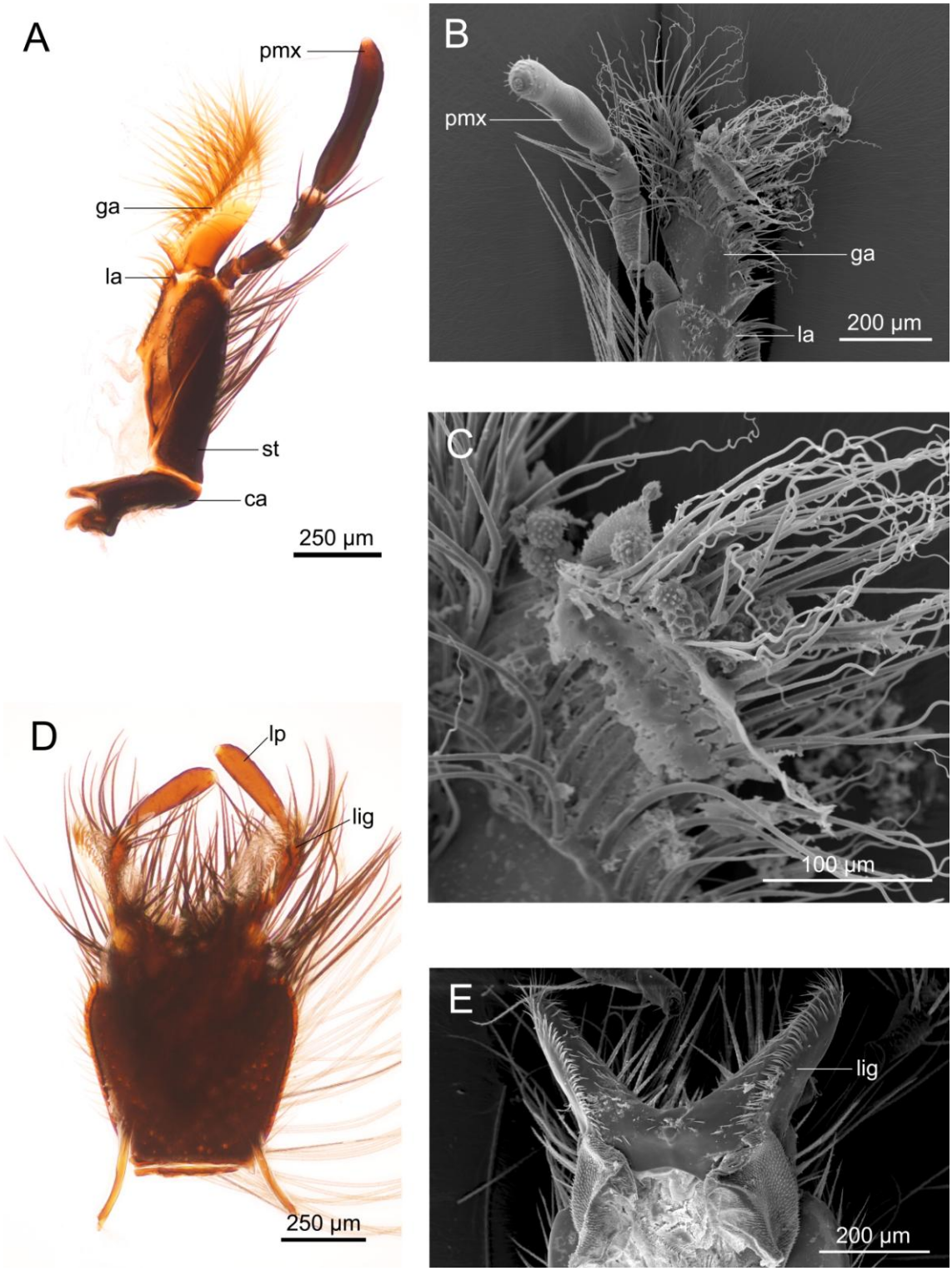

Fig. 8: Morphology of maxilla and labium of *Lepithrix* sp. in light microscopy (LM) and scanning electron microscopy (SEM). **A** Left maxilla ventral view (LM). **B** Right maxilla ventral view of galea (SEM). **C** Detail galea (SEM). **D** Labium dorsal view (LM). **E** Detail labium dorsal view (SEM).
ca cardo, *ga* galea, *la* lacinia, *lig* ligula, *lp* palpus labialis, *pmx* palpus maxillaris, *st* stipes

Maxilla (Figs. 8A–C)

The cardo is slender and allows an advanced movability which could be noted during the preparation (Fig. 8A). The galea is covered with numerous and long curled bristles (Fig. 8C). The lacinia is a reduced lobe located on the distal margin of the galea on the median side of the stipes. It bears a small number of short sclerotized bristles (Figs. 8A, B).

Labium (Figs. 8D, E)

The labium is covered with numerous and long bristles on the ventral side (Fig. 8D). The ligula, a membranous lobe formed by glossa and paraglossa, is elongated and reaches forward between the maxillary palps (Figs. 8D, E).

Gut content and pollen grains and fluid on mouthparts

The representatives of this feeding group had a huge amount of intact Asteracean and other not identified pollen grains in their guts. On the mouthparts intact Asteracean pollen grains and some dried up substance could be found (Fig. 8C).

3.5. Feeding group 5

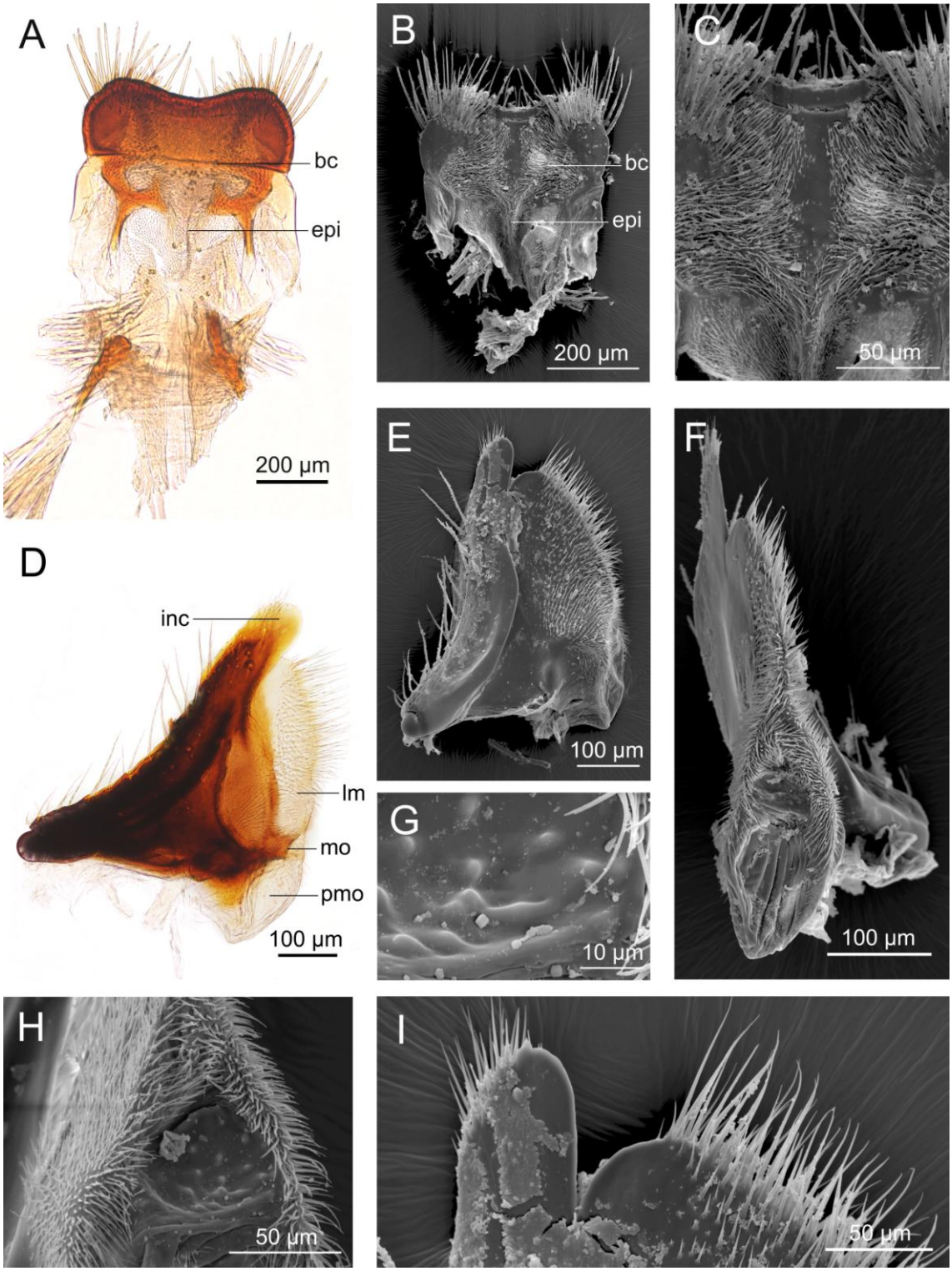

Fig. 9: Morphology of labrum and mandible of *H. pickeri* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Labrum ventral view (LM). **B** Labrum ventral view (SEM). **C** Detail of the labrum ventral view (SEM). **D** Right mandible ventral view (LM). **E** Right mandible ventral view (SEM). **F** Medial side of the left mandible (SEM). **G** Detail mola medial view (SEM). **H** Detail mola and lacinia mobilis (SEM). **I** Detail incisor (SEM).
bc bristle crest, *epi* epipharynx, *inc* incisor, *lm* lacinia mobilis, *mo* mola, *pm* postmola

The feeding group 5 contains only individuals of *H.pickeri* (Tab.1). The mouthpart morphology is summarized in Table 6.

Tab. 6: Characteristics of the mouthpart morphology of feeding group 5.

Labrum	distal margin curved inwardly only a little bit or straight and covered with few, short bristles
Mandible	very small mola without any teeth, incisor part smooth
Maxilla	galea bears one row of small teeth on the distal margin and is covered with numerous bristles, lacinia bears numerous bristles
Labium	ligula not elongated

Labrum (Figs. 9A-C)

On the distal edge the labrum is strongly sclerotized, curved inwardly a little bit (Fig. 9A). It is equipped with long and straight bristles on the proximal margin (Figs. 9A, B). It possesses a v-shaped bristle crest which is composed of a numerous bristles and ends in the epipharynx (Fig. 9C). This bristle crest differs from those of the other feeding guilds in its appearance (Fig. 9C).

Mandible (Figs. 9D-I)

The mandible of *H. pickeri* is composed of an incisor part on the distal edge, a lacinia mobilis, a mola and a postmola in the proximal region (Fig. 9D).The incisor part can clearly be distinguished from the lacinia mobilis and cutting edges are lacking (Fig. 9E). It is a smooth and rounded structure on the proximal margin (Fig. 9I). The lacinia mobilis possesses numerous setae covering most of this structure and pointing into median direction (Fig. 9E). The shape of the mandible differs from the others due to its thinness. The mola is a reduced structure that causes no broadening of the mandible (Fig. 9F). Furthermore the mola differs by its surface structure. While the mola of other feeding groups are equipped with numerous rows of teeth this is covered with a few small exaltations (Fig. 9G). *H. pickeri* has a convex mola (Fig. 9H). The postmola is a small lobe located on the proximal edge of the mola (Fig. 9D). Its small surface is covered with a few short bristles (Fig. 9F).

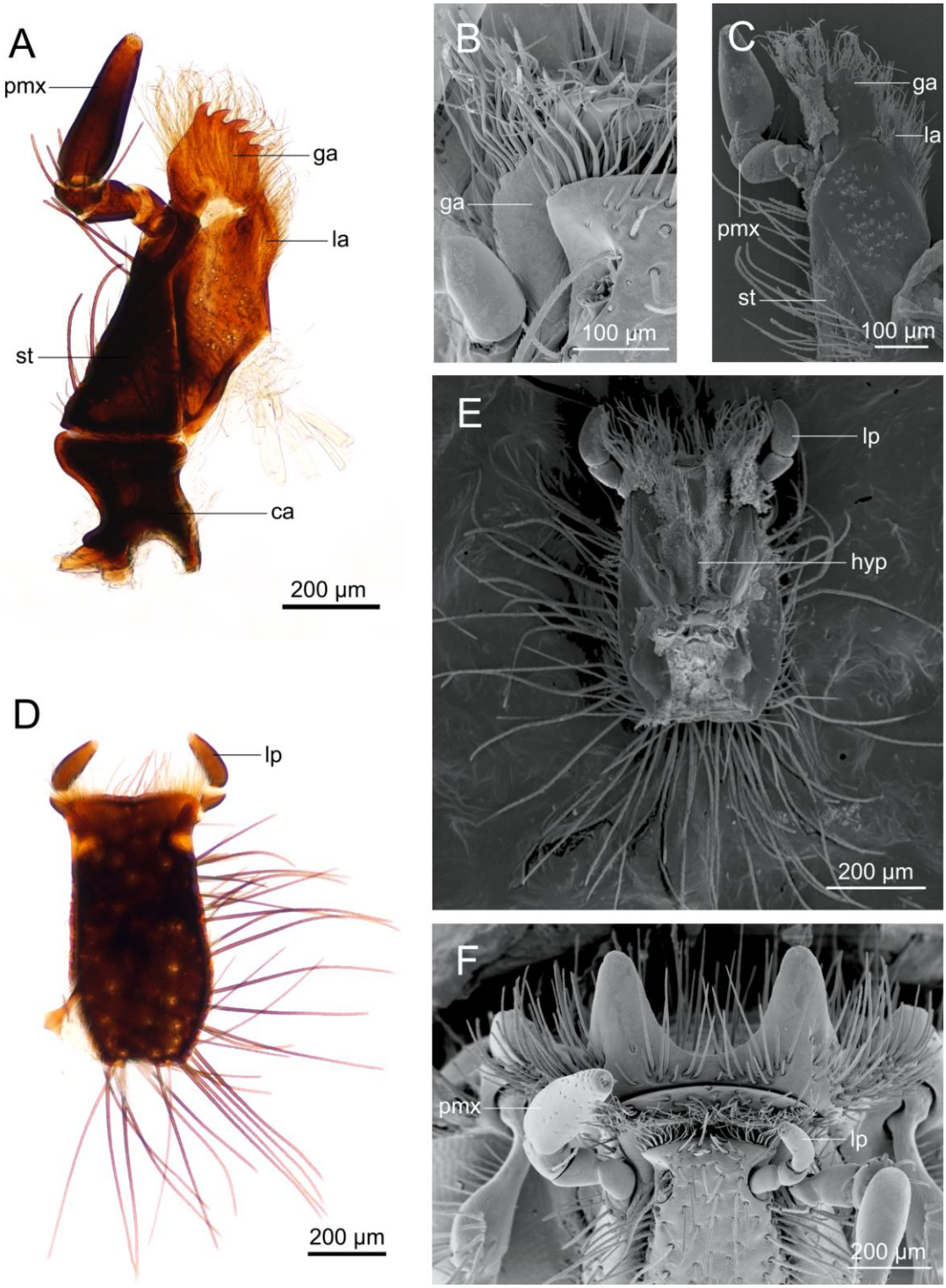

Fig. 10: Morphology of maxilla and labium of *H. pickeri* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Left maxilla dorsal view (LM). **B** Ventral view of the head capsule, palpus labialis broken off (SEM). **C** Right maxilla ventral view (SEM). **D** Labium dorsal view (LM). **E** Labium dorsal view (SEM). **F** Head capsule frontal view (SEM).
ca cardo, *ga* galea, *hyp* hypopharynx, *la* lacinia, *lp* palpus labialis, *pmx* palpus maxillaris, *st* stipes

Maxilla (Figs. 10A–C)

The maxilla has a short cardo (Fig. 10A) that causes a limited movability which could be noticed during the preparation. Galea and lacinia can clearly be distinguished, none of them is reduced (Fig. 10A). On the distal margin the galea bears several sclerotized teeth on the ventral side and numerous bristles on the dorsal side (Figs. 10A-C). Those bristles are neither hooked nor curled (Fig. 10C). The lacinia is a lobe located on the distal margin of the galea on the median side of the stipes. The lacinia bears numerous short bristles pointing forward (Fig. 10A).

Labium (Figs. 10D–F)

The labium is almost rectangular, strongly sclerotized and covered with numerous bristles on the ventral side and (Fig. 10D). The hypopharynx is a v-shaped bristle crest of numerous and dense setae (Fig. 10E). Both the bristles of maxilla and labium are pointing forward (Fig. 10F).

Gut content and pollen grains and fluid on mouthparts

In the dissected guts of *H. pickeri* no pollen grains could be found. Most of the guts were completely empty while on the mouthparts some dried up substance could be identified (e.g. Figs. 9I, 10C).

3.6. Feeding group 6

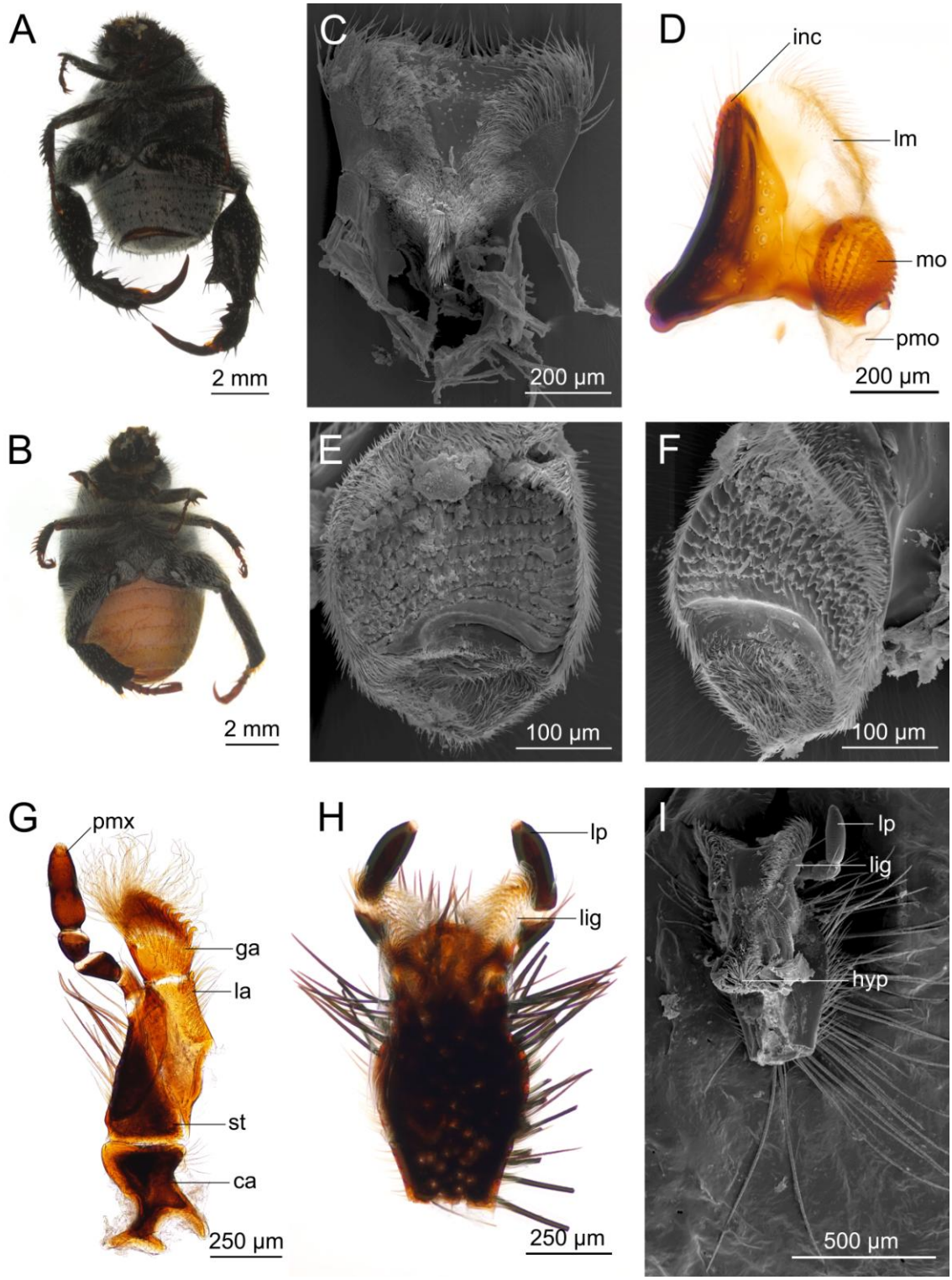

Fig. 11: Body and mouthparts of *P. flavolineata* in light microscopy (LM) and scanning electron microscopy (SEM). **A** Male of *P. flavolineata* (LM). **B** Female of *P. flavolineata* (LM). **C** Labrum ventral view (SEM). **D** Right mandible ventral view (LM). **E** Detail mola medial view (SEM). **F** Detail mola (SEM). **G** Left maxilla dorsal view (LM). **H** Labium dorsal view (LM). **I** Labium dorsal view (SEM).
ca cardo, *ga* galea, *hyp* hypopharynx, *inc* incisor, *la* lacinia, *lm* lacinia mobilis, *lig* ligula, *lp* palpus labialis, *mo* mola, *pm* postmola, *pmx* palpus maxillaris, *st* stipes

The feeding group 6 is composed by individuals of *P. flavolineata* (Tab. 1). Their maxillae do not differ in size and shape from those of feeding group 5, while the other mouthparts are similar to those of feeding group 2. The characteristic mouthpart morphology is summarized in Table 7.

Tab. 7: Characteristics of the mouthpart morphology of feeding group 6.

Labrum	distal margin straight and covered with few, short bristles
Mandible	postmola normal-sized, incisor smooth and without cutting edges, lacinia mobilis possesses no sclerotized tooth
Maxilla	galea bears one row of small teeth on the distal margin and is covered with numerous bristles, lacinia bears numerous bristles
Labium	ligula elongated

Specimens of *P. flavolineata* show a marked sexual dimorphism (Fig. 11A, B). The body size does not differ between sexes while a difference in the shape of the hind legs can be seen. Like various other monkey beetles the males of *P. flavolineata* have long hind legs (Fig. 11A).

The shape and structures of the labrum (Fig. 11C) shows none difference from the other two species of *Pachycnema*. The mandible is composed of an incisor part on the distal edge, a lacinia mobilis, a mola and a postmola in the proximal part (Fig. 11D). Unlike the other studied species the left and right mola of *P. flavolineata* is not entirely symmetric and the structure of the numerous teeth can differ between individuals in small dimensions (Figs. 11E, F).
The maxilla appears to be similar to those of *H. pickeri* (Fig. 11G) with the same shaped teeth and bristles on the galea.
The labium equals those of *P. calcarata* and *P. crassipes* (Figs. 11H, I).

Gut content and pollen grains and fluid on mouthparts

In the guts of *P. flavolineata* numerous intact Asteracea pollen grains and brown-orange substance could be found. On the mouthparts were no pollen grains but some dried up substance, especially on the tip of the galea bristles.

4. Discussion

Monkey beetles have a wide distribution and feed on different food sources. They are reported to visit flowers for multiple reasons: feeding on the flowers, using them for shelter and as mating sites (Johnson, 2004; Nicolson et al., 2007). Most of the adult beetles feed on flowers, including nectar and pollen. Some are reported to feed on petals, young leafs and fruits (Nel & Scholtz, 1990). Beetles feeding on floral tissue are often destructive to their host plant and leave the flowers damaged (Picker & Midgley, 1996). Characteristic mouthpart adaptations for pollen feeding can be seen in several modifications of the mandible and the maxilla. The present study reveals different mouthpart modifications in monkey beetles according to their food source.

Labrum and labium showed lesser modifications among the feeding groups than maxilla and mandible. Nectar feeding species possess an elongated ligula on the labium, equipped with numerous bristles to transport the nectar into the epipharynx, while the labium of pollen feeders is strongly sclerotized with a small and barely forward pointing ligula.

The descriptions of the first pollination guild defined by Picker & Midgley (1996) are for the most part conforming to the first feeding group of the present study. Species of the first feeding group are densely covered with hair, possess elongated mouthparts and may play a vital role as pollinator. They cannot damage their host plants because they do not have any structures that could be used for biting off floral tissue. In the guts of the investigated species of the first feeding group no foliage could be found. On the galea of *A. ursus* a dried substance could be examined using the scanning electron microscope that showed imprints of the labrum surface. Those two structures, labrum and maxillae, must be in direct contact with each other during the feeding process. Due to the position of the mandible, labrum and maxilla are not separated and lay against each other. Those two structures could be used to transport food into the epipharynx during the feeding process.
They do not correspond with the colour and the sexual dimorphism described by Picker & Midgley (1996). Beetles of the genus *Anisonyx* are in the first pollination guild as well as in the first feeding group and show no sexual dimorphism and are darkly coloured. Species of *Pachycnema* belonged to the second pollination guild by

Picker & Midgley (1996) while *P. calcarata* and *P. crassipes* became reassigned to the first feeding group because of their mouthpart morphology, even though they are not darkly coloured and show a distinct sexual dimorphism. *P. flavolineata* was not assigned to this feeding group because of its maxilla.

Species of the second and the third feeding group could be destructive to their host plants as described in the second pollination guild by Picker & Midgley (1996) because their mandible and maxillae are strongly sclerotized and bear numerous teeth that could be used to feed on floral tissue. The second and the third feeding group showed similar characteristics of their mouthpart morphology, because of the different shape of their incisor they were separated into two groups. Although not all specimens of the second and the third group contained foliage in their guts, they could still feed on flowers because their mouthparts possess cutting structures which are used to feed on foliage in other species. They possess a small lacinia while the galea bears numerous teeth and a few bristles. Those teeth in combination with the cutting edge of the mandible's incisor may be used to feed on floral tissue. The specimen that became characterized as beetles that could destroy flowers by the look of their mouthpart anatomy has been the only ones with floral tissue in their gut.

As members of the third pollination guild by Picker & Midgley (1996) species of *Lepithrix* were mentioned and were assigned to the fourth feeding group, as well as *C. decora*. The mouthparts of this feeding group are similar to those of the first group, except for the mandible. The mandible of this group has a very broad mola with numerous rows of small teeth. In the guts intact pollen grains could be found which suggest that the mola is not used to crack pollen grains.

Two species could not clearly be categorized into a feeding group because their mouthparts possess dissimilar modifications therefore they are forming the fifth and the sixth feeding group. *H. pickeri* cannot be characterized as member of any of the four feeding groups therefore the feeding group five was designed. The mouthpart morphology, especially those of the mandible, could lead to the expectation that this species feeds on nectar or pollen. Unfortunately the dissected guts had been empty and no proof of this speculation could be found.

Picker and Midgley (1996) described species of the genus *Heterochelus* as beetles that are destructive to their host plants. The examination of the mouthparts of *H. pickeri* revealed that it is unlikely that these beetles damage flowers. The mandible has not got any cutting edges and the mola is reduced to a small and toothless structure, while the galea has both, hooked teeth and curled setae. From its position in the head capsule those teeth may be used to comb pollen grains and may be unable to feed on floral tissue. Because of the empty guts within the studied specimens of *H. pickeri* it cannot be said for certain what the regular food is. The different classification of this species between the pollinator guild by Picker & Midgley (1996) and the feeding groups may derive from the distinct identification level between the studies. The pollinator guilds were defined for genera while the feeding groups were constructed for different species. Of the genus *Lepisia* three species were investigated and characterized in different feeding groups regarding to their different mouthpart adaptations and gut contents.
With the exception of *H. pickeri* all studied species possess a toothed mola with numerous rows of teeth. Even though it has lost its biting capacity it may be useful to knead and transport nectar and pollen.

P. flavolineata is the only member of the sixth feeding group. It would probably fit into the third feeding group with no cutting edges on the incisor part of the mandible. That would also be confirming with the gut content analysis because individuals of this species had eaten numerous Asteracean pollen grains such as individuals of *Lepithrix.* The maxillae of the feeding group six bore a row of teeth that didn’t exist in members of the third group but in the fifth feeding group.

Characteristic modifications of the mandible are reported for beetles feeding on pollen and nectar, such as hairiness, a soft lacinia mobilis and postmola and a strongly sclerotized mola to squeeze and transport the pollen (Krenn et al., 2005). The mandible may have lost their biting capacity and may not be able to crack the pollen wall (Miller, 1961). Most of the pollen grains found in the fore- and midgut were intact; therefore beetles may use other methods to open the pollen grains, e.g. osmotic shock (Johnson & Nicolson, 2001).

Péringuey (1902) characterizes the maxilla of Hopliini as bi-lobated, whereby the inner lobe is often indistinct or lacking and always immovable. They are described as robust mouthparts often toothed or hooked. This description of the maxilla coincides with those found in the present study. The inner lobe, the lacinia, which usually represents the sclerotized and robust part of the maxilla, appeared to be reduced and covered with bristles in those feeding groups that feed on nectar and pollen. Those pads and tufts of bristles are used to mop up nectar and sweep up pollen and the elongated cardo allows an advanced movability to gather the pollen and transport it to the mouth (Fuchs, 1974; Johnson & Nicolson 2001; Krenn et al., 2005; Schremmer, 1961).

In the present study the term mala was not used to characterize the maxilla. Mala describes a one-lobed maxilla where galea and lacinia are fused together forming that single lobe (Betz et al., 2003; Wiliams, 1938). Though all investigated species possess only a small lobe located on the distal margin of the galea with sclerotized setae the two lobes could be distinguished. In *H. pickeri* and *A. ursus* a noticeable sized lacinia could be seen and clearly distinguished from the galea whereas the other species bear a small and unsuspicious lacinia. The maxillae are the main organs used for nectar uptake, equipped with dense bushes of setae (Barth, 1985; Johnson & Nicolson 2001, Wilhelmi & Krenn, 2012). Since the lacinia is reduced even in species that feed on nectar and pollen it seems that the galea takes the function as pollen broom.

Hopliini form a diverse group of beetles with almost worldwide distribution, showing their greatest morphological diversity in South Africa (Ahrens et al., 2011; Péringuey, 1902). While their phylogenetical relationships are not entirely clarified (Carillo-Ruiz & Morón, 2006), their importance as pollinators, especially for Asteracean, has been reported in numerous studies (Colville et al., 2002; Johnson & Nicolson, 2001; Picker & Midgley, 1996). The examination of the mouthparts and the gut contents allows concluding which feeding preference the species may have. Further morphological and behavioural investigations are necessary to identify the host plants of all studied species. A combination between the methods of the study made by Picker & Midgley (1996) and the present one would probably lead to further knowledge of the feeding preferences.

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6. Abstract

Monkey beetles appear to be one of the most important pollinating insects in the Cape Province of South Africa. This region contains the majority of the world´s monkey beetle species which feed on petals of flowers, pollen and nectar. They play a vital role in the pollination of Asteraceae and Aizoaceae, using the flowers as food source and as mating sites in addition. The purpose of this study is to describe the mouthpart morphology and examine the gut content of representatives of the pollinator guilds. The studied monkey beetle species were grouped into six feeding groups by their mouthpart morphology and their gut content. Mouthparts were dissected and examined using a light microscope as well as using a SEM. The first feeding group contains three species and feed probably on nectar. Those beetles have elongated mouthparts equipped with brushes of dense setae. The second and the third group, which contain the majority of the investigated species, were divided into two different groups, even though they had similar mouthpart modifications but these two groups had different incisor parts on their mandible. Both feed on nectar and pollen and could be destructive to the plants they visit. Members of the third group had foliage material in their gut which confirms that they actual feed on floral tissue. The fourth group contains species that feed mainly on pollen and maybe additionally on nectar. These species possess a broad mola and postmola to knead the pollen grains. Two species were not suitable for the existing feeding groups because of their uncommon modifications of maxilla and mandible, therefore the fifth and the sixth group were designed. Both feeding groups possess a galea with one row of teeth on the distal margin. The fifth feeding group possesses an uncommon mola, with a small surface without teeth while the sixth group forms an intermediate group between the second and the fifth group, with similar mouthpart modifications of both groups. In the dissected guts only intact pollen grains could be found. This leads to the presumption, that the toothed mola has lost its biting capacity and the pollen grains are swallowed intact. The modification of the maxillae with a sclerotized galea and a reduced lacinia mobilis suggests that the main structure for nectar and pollen uptake in Hopliini is formed by the galea.

7. Zusammenfassung

Die in Südafrika lebenden „Monkey Beetles“ (Scarabaeidae: Hopliini) sind wichtige Bestäuber von den dort beheimateten Blütenpflanzen. Die Käfer verwenden die Pflanzen nicht nur als Nahrungsquelle sondern auch als Schutz oder als Balz- und Paarungsplätze. Einige „Monkey Beetles“ ernähren sich nicht nur von Nektar und Pollen sondern fressen auch Teile der Blüte und zerstören so die Pflanze. In einer früheren Studie wurden verschiedene Arten von südafrikanischen Hopliini anhand ihres Verhaltens bei den Blüten und der Präferenz für bestimmte Blütenfarben in Bestäubungsgilden eingeteilt.

In der vorliegenden Studie wurden die Mundwerkzeuge und die Köpfe verschiedener Arten unter dem Licht- und dem Elektronenmikroskop untersucht und anhand von Ähnlichkeiten in sechs Gruppen zusammengefasst. Die Einteilung anhand der Morphologie der Mundwerkzeuge und anhand des Inhalts des Vorderdarmes haben Rückschlüsse über die Nahrungspräferenzen der verschiedenen Nahrungsgruppen ermöglicht. Käfer der ersten Gruppe ernähren sich vorwiegend von Nektar, dazu besitzen sie verlängerte Mundwerkzeuge mit zahlreichen Borsten, die ihnen vermutlich Aufsaugen des Nektars ermöglichen. Die zweite und die dritte Gruppe enthalten die meisten der untersuchten Arten. Diese beiden Gruppen unterscheiden sich nur in der Morphologie der Mandibel, während die anderen Strukturen keine Unterschiede zeigen. Bei der Mandibel der einen Gruppe ist der Incisiviteil als eckiger Zahn ausgebildet während er bei der anderen Gruppe abgerundet und von der weichhäutigen Lacinia mobilis umgeben ist. Beide Gruppen haben eine Maxille bei der nicht die Lacinia, sondern die Galea stark sklerotisiert ist und Zähne bildet und zusätzlich mit Borsten ausgestattet ist, während die Lacinia nur in reduzierter Form vorhanden ist. Käfer aus der zweiten und dritten Ernährungsgruppe fressen sowohl Nektar und Pollen als auch Teile der Pflanze, wie sich bei der Untersuchung des Vorderdarmes zeigte. Die vierte Gruppe, die der dritten Bestäubungsgilde von Picker & Midgley (1996) entspricht, hatte sowohl auf den Mundwerkzeugen als auch im Darm große Mengen intakter Pollenkörner. Obwohl diese Gruppe eine sehr große und stark bezahnte Mola besitzt, werden die Pollenkörner intakt geschluckt. Zwei Arten konnten anhand der Modifikationen ihrer Mundwerkzeuge zu keiner der vier Ernährungsgruppen zugeteilt werden, da sie sich zu sehr von den anderen Arten unterschieden, darum wurde eine fünfte und eine sechste Gruppe für diese beiden

Arten konstruiert. Bei beiden besitzt die Galea eine Reihe kleiner Zähne an der distalen Kante und ist mit zahlreichen Borsten besetzt. Bis auf die fünfte Ernährungsgruppe besitzen alle eine Mandibel mit stark bezahnter Mola.
Bei allen untersuchten Tieren waren die im Vorderdarm gefundenen Pollenkörner intakt was darauf hindeutet, dass die Mola nicht dazu verwendet werden kann um die Pollenkörner aufzubrechen, sondern um den Pollen lediglich weiter unten in den Epipharynx zu transportieren. Bei der Maxille, bei der die Lacinia stark reduziert war, kann vermutet werden, dass die Galea die Funktion des Pollen- und Nektareinsammelns übernimmt.

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