

A comparative survey of proboscis morphology and associated structures in fruit-piercing, tear-feeding, and blood-feeding moths in Calpinae (Lepidoptera: Erebidae)

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Abstract Functional feeding categories for adult species of Calpinae are described. Structures associated with the proboscis were examined using exemplar species in fruit-piercing, blood-feeding, and tear-feeding species using both light microscopy and SEM methods. At least three genera currently placed in Calpini, and several others in related groups lack specialized piercing structures. The proboscis of the tear-feeding species, *Hemiceratoides hieroglyphica*, is equipped with specialized cuticular hooks not yet observed in other tear-feeding species. Tearing hooks moveable by blood pressure are restricted to Calpini species, and little additional variation within this taxon exists, suggesting proboscis morphology may not be strongly correlated with feeding behavior (e.g., fruit piercing vs. blood feeding). A glossary of terms and character codings for proboscis structures is provided, and morphologies for all included calpine taxa are described.

We discuss the taxonomic significance of proboscis morphology in Calpinae and the evolutionary implications of their associated feeding behaviors. This survey indicates morphology provides powerful prediction, but not proof of lepidopteran adult food habits.

Keywords Calpinae · Lepidopteran mouthparts · Morphology · Evolution

Introduction

Morphological studies of the proboscis in Lepidoptera have played a significant role in framing our understanding of the evolutionary history of this megadiverse taxon (Davis 1986; Nielsen and Kristensen 1996; Kristensen 1968, 1984; Kristensen and Nielsen 1981). The structure and function of the lepidopteran proboscis has been examined for broad range of taxa across multiple subgroups (Bänziger 1971b, 1973; Büttiker et al. 1996; Krenn 1990, 1997, 2010; Speidel et al. 1996). Some studies selected higher-level exemplars from distantly related taxa (e.g., Erebidae, Noctuidae, Geometridae, and Pyralidae) based on adult feeding behavior (Bänziger 1973; Büttiker et al. 1996) to examine whether feeding structures and behaviors were correlated. Other studies were more taxonomically focused on related species that shared similar feeding behaviors (Bänziger 1970, 1986, Table 6) to related subfamilies (Speidel et al. 1996) or families (Krenn 1998; Krenn and Kristensen 2000; Krenn and Mühlberger 2002; Krenn and Penz 1998; Krenn et al. 2001) to establish morphological homologies among related taxa. This taxonomic diversity of studies has led to some inconsistent application of terminology for sensilla and other specialized feeding structures. The lack of explicit homology criteria for mouthpart microstructures hampers

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our ability to compare proboscides across the order and trace their evolution and associated feeding behaviors.

To address the lack of explicit homology criteria and examine the question of whether morphology and feeding behaviors are correlated, we focused on a putatively monophyletic group of noctuid moths, Calpinae, whose adults exhibit a variety of sensilla and specialized structures such as erectile barbs, eversible hooks, and cutting ridges. Further, different species engage in several types of feeding behaviors that include a variety of fruit-piercing capabilities (primary or secondary fruit piercers), tear feeding (lachrophagy), and mammalian skin piercing (facultative hematophagy) (Bänziger 1970, 1973, 1980; Breitenbach 1877; Hilgartner et al. 2007; Künckel 1875). Primary and secondary piercing refers to whether an adult can penetrate intact skin to obtain juice (primary piercer) or whether it can only enlarge an existing hole or wound in the skin made by another animal (secondary piercer) (Jack 1922; Norris 1935). In addition to these food habits, these moths have stereotypical feeding behaviors (modified from nectar feeding) that include concomitant stylet dynamics including anti-parallel or spindle movements of the proboscis and oscillatory torsion of the head during the piercing act (Bänziger 1970, 1973, 1980; Breitenbach 1877; Künckel 1875).

Aims of the study

This study builds upon prior light microscopy (Bänziger 1970, 1973, 1980; Hattori 1969) and scanning electron microscopy (SEM) studies (Büttiker et al. 1996; Cochereau 1977; Speidel et al. 1996). By comparing proboscides at several hierarchical levels (among species, among genera, and among tribes) in Calpinae with two different techniques, we can also examine whether one technology results in biased or inconsistent homology assessment due to magnification limitations (light microscopy) or preparation artifacts (SEM).

The first objective is to describe the diversity and to document the homology of proboscis structures in Calpinae. The surface microstructure and visible macrostructures of the proboscis are documented with light microscopy and SEM imaging. From these images, a glossary of proboscis terminology is generated that lists criteria that can be used to accurately homologize these structures within the subfamily. Character coding for the proboscides of species examined provides an example of the application of these homology criteria. We also examined whether these technologies are complimentary or whether one results in inconsistent homology assessment due to preparation artifacts or magnification limitations.

Another objective was to address whether proboscis morphology is a sufficient and accurate predictor of adult

feeding behavior as some have suggested (e.g., Büttiker et al. 1996). To facilitate behavior/morphology comparisons, we formally delineate five functional feeding categories, including subtypes for fruit piercing. We then examined species representing the diversity of feeding behaviors (primary, secondary fruit piercing and facultative hematophagy, lachryphagy) to determine whether proboscis structures can be used to diagnose feeding behavior. Three species with unknown feeding behavior are included to provide predictions for future behavioral studies.

Finally, to resolve the controversy over interpretation of proboscis morphology and associated structures of *Hemiceratoides hieroglyphica* (Saalmüller, 1891), we figure with SEM and re-describe them. We also figure and describe known lachryphagous species to establish a baseline of morphological variation for this behavior.

Overview of calpinae and adult feeding habits

Calpinae is cosmopolitan in its distribution; however, many genera have geographic distributions that are somewhat restricted. Calpinae presently consists of four subgroups traditionally classified as tribes, i.e., Anomini, Calpini, Phyllochini, and Scoliopterygini (Fibiger and Lafontaine 2005; Holloway 2005). Of these, only Calpini has been revised and demonstrated to be monophyletic (Zaspel 2008a, b). Calpinae is characterized by the tearing structures of the proboscis (Fibiger and Lafontaine 2005; Goater et al. 2003; Holloway et al. 2001; Holloway 2005; Kitching and Rawlins 1998). Species in this group exhibit a broad range of adult feeding behaviors including those that can be considered “piercers” of fruits or other hosts. Species of *Oraesia* cause damage to thick and soft-skinned fruit in India, Nepal (Fig. 1a), Thailand, Korea and Japan (Bänziger 1982, 1987; Hattori 1969; Ramakrishna Ayyar 1944; Yoon and Lee 1974). Species of *Anomis* commonly pierce soft-skinned fruits in tropical regions (Fig. 1b). In temperate Europe, several erebid species pierce fruit including members of *Plusiodonta*, *Calyptra*, *Scoliopteryx* (Fig. 1c), *Ophiusa*, and *Dysgonia* (Bänziger 1969, 2007). Species of *Eudocima* are common pests of a wide variety of fruits ranging from hard-skinned longan, to thick-skinned oranges, to soft or ripening fruits in cultivated Rosaceae [e.g., peaches, plums, and apples; (Fig. 1d)]. *Gonodonta* spp. have been documented piercing citrus fruits, including tangerines, grapefruits, and oranges, at times causing extensive losses (Todd 1959).

Species belonging to other calpine genera (sensu Fibiger and Lafontaine 2005) lack tearing hooks (e.g., *Hypsorophora* and *Phyprosopus*) and may be misplaced. The inclusion of tear-feeding *H. hieroglyphica* (Fig. 1e; Hilgartner et al. 2007) based upon its proboscis morphology (Hilgartner et al. 2007) is controversial. From their



Fig. 1 Feeding behaviors of adult moths in Calpinae. **a** *Oraesia rectistria* piercing plum in Nepal (photo J.M. Zaspel). **b** *Anomis fructusterebrans* Bänziger 1986 piercing yellow Himalayan raspberry (*Rubus ellipticus* Sm.) in N. Thailand (photo H. Bänziger). **c** *Scoliopteryx libatrix* piercing raspberry in Switzerland (photo H. Bänziger).

d *Eudocima tyrannus* piercing apple in Korea (photo H. Fay). **e** *Hemiceratoides hieroglyphica* with the proboscis tip inserted between the eyelids of a bird in Madagascar (photo R.D. Hilgartner). **f** *Calyptra thalictri* feeding on blood from human thumb in Far Eastern Russia (photo J.M. Zaspel)

studies of *H. hieroglyphica*, this study suggests that the tear-feeding habit evolved from the fruit-feeding habit (Hilgartner et al. 2007). Bänziger (2007) contests the placement of *H. hieroglyphica* and interpretation of morphological homologies asserting that these descriptive terms are applied incorrectly.

A pioneering series of papers on proboscis morphology and adult feeding behaviors in fruit-piercing and blood-feeding moths have been produced (see Bänziger 1969–2007). This work has spanned decades, continents, and a diversity of species. Bänziger (1982) commented on whether proboscis morphology could be used to predict

feeding behavior stating and proposed more precise characterization of moth fruit-piercing behaviors, further dividing primary and secondary piercers by the type of fruit skins. For convenience, Bänziger (1982) described four categories based on their increasing difficulty to be pierced by moths: 1. soft-skinned fruit (e.g., raspberry), 2. soft-skinned fruit (e.g., peach, grape), 3. thick-skinned fruit (citrus), and 4. hard-skinned fruit (longan, lichi). Moths were classified according to their ability to pierce the four fruit skin categories as primary piercers. For example, a moth like *Calyptra minuticornis* (Guenée, 1852) was classified as a primary piercer of thick-skinned fruits (oranges) and all softer-skinned fruit, but a secondary piercer of hard-skinned fruit (longan).

Calpinae are also notable for including facultative hematophages. Males of ten *Calyptra* species have been documented piercing mammalian skin and feeding on blood under either natural or experimental conditions (Fig. 1f; Bänziger 1971b, 1982, 1989; Zaspel et al. 2007; Zaspel 2008a). Bänziger (1986, pp. 122–123 and Table 6) gave detailed data on the proboscis length, width, number, and length of both tearing hooks and erectile barbs of *C. eustrigata* (Hampson, 1926), *C. minuticornis*, *C. orthograpta* (Butler, 1886), and *C. fasciata* (Moore, 1882). The rasping, piercing structures and hematophagous behaviors have attracted popular interest (e.g., Quammen 1985), but as these species do not vector disease, if mentioned, they are more of a footnote in scientific textbooks (e.g., Evans 1984, Grimaldi and Engel 2005).

Until recently, lachrophagy was not documented for the subfamily. Tear-feeding moths typically imbibe tears by placing the distal part of the proboscis onto the eyelid where it joins the eye and drinks tears from the host. Lachryphagous species, e.g., species of *Arcyophora* and *Lobocraspis griseifusa* Hampson 1895, and, like all other confirmed tear drinkers, are neither fruit piercing nor skin piercing (Bänziger 1973). Their proboscides lack piercing armature (Bänziger 1973). However, Hilgartner et al. (2007) reported *H. hieroglyphica* apparently drinking fluid from the eyes of a sleeping bird in Madagascar.

Materials and methods

Specimen preparation

*Microptics*TM imaging

Proboscis preparations were made of male and female individuals of 42 species from twelve genera representing the four tribes currently placed in Calpinae (Table 1).

Species were chosen to represent the diversity of adult feeding categories defined below. Dried proboscides were

removed at the base of the head from pinned specimens using fine-tip forceps. Proboscides were cleared by submerging in 10% cold KOH for 18–24 h, followed by a short heating treatment (30 min.). Structures were cleaned in several rinses of approximately 70% ethanol. Rinsed proboscides were then placed in a watch glass, positioned with K-Y jelly, and covered with 70% ETOH for digital imaging.

All digital images (96 total) were taken on a MicropticsTM (Visionary Digital) laboratory workstation with a Nikon D1 digital SLR camera, using a K2 microscope lens fitted with a CF-3 objective when photographing whole structures (proximal region proboscis images); the K2 lens fitted with a 10X objective was used for distal region proboscis images. Permanent slide mounts (Euparal [Bioquip, Garden City, CA]) were made of all proboscides (Table 2). Slides were placed on a slide warmer (approximately 59°C) for 24–48 h and then cured for 6 months at room temperature while stored horizontally in a slide cabinet.

SEM imaging

From the original twelve genera and 42 species, 17 species were selected to represent the diversity of proboscides based on the results of the light microscopy study. For these selected species, male and female proboscis preparations were prepared for scanning electron micrographs (Table 1). Proboscides were removed and cleared as for light microscopy. Once rinsed, structures were dehydrated overnight in 95% EtOH in watch glasses (minimum 12 h). Proboscides were transferred to a sample holder (Tousimis, Rockville, MD) and then fully dehydrated using a critical point dryer (Samdri 780A, Tousimis, Rockville, MD) according to manufacturer's directions. Dehydrated proboscides were positioned on SEM image tabs (PELCO, product number 16084-20, Ted Pella Inc., Redding, CA). Once mounted, the samples were sputter coated with a thin layer of gold using a Denton Vacuum Desk III LLC sputter coater (Moorestown, NJ) for 2–4 min. A total of 92 images were obtained using a JSM-5510LV scanning electron microscope (JOEL, USA).

Terminology

Terminology for proboscis morphology follows Bänziger (1970, 1980), Büttiker et al. (1996), and Speidel et al. (1996). Sensilla terminology follows Altner and Altner (1986), Fauchaux (1985, 1991, 1995), Hallberg (1981), and Hallberg et al. (1994). These terms and their application in this study are presented in Results (Table 2).

Table 1 Sensilla and other structures associated with calpine proboscides and their proposed function

Structure (Abbreviation): Definition/Criterion	References
Sensory	
<i>Erectile Barbs Subtype 1 (eb)</i> : Modified sensilla styloconica, apical cone present, surrounded by endocuticular material. Mechanoreception; possibly contact chemoreception	Büttiker et al. (1996)
<i>Furcate Erectile Barbs (feb)</i> : Cuticular styloconic sensilla, often asymmetrical, branched with hairs or finger-like projections. May perceive mechanical distortions	
<i>Sensilla Basiconica (sb)</i> : Peg-shaped sensilla with minute pores. Olfactory structures, chemoreceptors	Altner and Altner (1986)
<i>Sensilla Styloconica (ss)</i> : Cuticular structures consisting of a basiconic peg elevated on a style or cone (sc). Contact chemo-mechanoreceptors	Altner and Altner (1986)
<i>Sensilla Trichodea (st)</i> : Cuticular, hair-like projection, aporous. Mechanoreceptors, function in food localization	Büttiker et al. (1996)
<i>Smooth Sensilla Styloconica Subtype 1 (sss₁)</i> : Flattened, feather-like with a basiconic sensillum but without distal cone. Contact chemo-mechanoreceptors	Altner and Altner (1986)
<i>Smooth Sensilla Styloconica Subtype 2 (sss₂)</i> : Flattened, rectangular with a basiconic sensillum but without distal cone. Contact chemo-mechanoreceptors	Altner and Altner (1986)
Structural	
<i>Cuticular Hooks (h)</i> : Fixed, deltoid-pyramid to wedge-like structures. Unknown	
<i>Dorsal Galeal Linkage (dgl)</i> : Zipper-like structure comprised of glossae and paraglossae. Holds tubes of the proboscis together	Büttiker et al. (1996)
<i>Legulae (l)</i> : Individual zipper-like structures comprised of glossae and paraglossae. Form dorsal and ventral galeal cross-linkages of proboscis	Davis (1986)
<i>Minute Triangular Spines (mts)</i> : Cuticular structures, membraneous. Possibly used in brushing eye of host to induce production of tears	
<i>Tearing Hooks (th)</i> : Aporous, cuticular structure attached to socket by elastic endocuticula, moveable by blood pressure. Involved in piercing through fruit or mammalian tissue, possible mechanoreception	Bänziger (1970)
<i>Rasping Spines (rs)</i> : Finger-like, flattened, aporous structures, without hairs or a sensory cone. Possibly contact chemoreceptors	Bänziger (2007)
<i>Serrate Ridge (sr)</i> : Ventrally serrated cuticular ridge located on ventral side of proboscis. Used for piercing hard-skinned fruit (e.g., longan, litchi)	Hattori (1969)

Characterization of functional feeding groups

Functional feeding categories were initially defined by Bänziger (1982). He distinguished between primary (moth penetrates intact skin) and secondary piercers (moth uses existing hole or wound) (Jack 1922; Norris 1935) and the types of substrates being pierced. For calpine species examined (Table 1), we provide their classification based on documented behaviors.

A. Non-piercing, fruit sucking Moths in this feeding group take up fruit juice from a wide variety of cracked or damaged fruits; no piercing is involved. While non-piercing, fruit sucking is a common trait within Lepidoptera; in our study, this generalist behavior was exhibited by only three species: *Goniapteryx servia* (Stoll, 1780), *Hypsorhpha hormos* Hübner 1880, and *Phyprosopus callitrichoides* Grote 1872.

A2. Primary piercing of soft-skinned fruit; secondary piercing of thick- or hard-skinned fruit Moths in this feeding category are capable of piercing soft-skinned fruits such as mandarins and figs. One species, *Scoliopteryx*

libatrix (Linnaeus, 1758) (*Scoliopterygini*) represents this category in our study. *Scoliopteryx libatrix* is a confirmed primary piercer of soft-skinned fruit (Bänziger 1969).

B. Primary piercing of thick-skinned fruit; secondary piercing of hard-skinned fruit Moths in this category are capable of piercing the intact rind of thick-skinned fruit (e.g., oranges, grapefruit) as well as all softer-skinned fruit. Typically, moths are not capable of piercing hard-skinned fruits such as longan and, by extension the related lichi.

Twenty-nine species representing four genera within Calpini (sensu Zaspel and Branham 2008) were selected for this category. Examined species were: *Calyptra albivirgata* (Hampson, 1926), *C. bicolor* (Moore, 1883), *C. eustrigata*, *C. fasciata*, *C. fletcheri* (Berio, 1956), *C. gruesa* (Draudt, 1950), *C. lata* (Butler, 1881), *C. minuticornis*, *C. ophideroides* (Guenée, 1952), *C. orthograpta*, *C. parva* Bänziger 1979, *C. pseudobicolor* Bänziger 1979, *C. subnubila* (Prout, 1928), *C. thalictri* (Borkhausen, 1790), *Gonodonta nutrix* (Cramer, 1780), *Plusiodonta coelonota* (Kollar, 1844), *P. compressipalpus* Guenée 1852, *P. incitans* (Walker, 1858), *Oraesia argyrosigna* Moore 1884,

Table 2 Specimens examined: Genus, species, author, feeding category, collection, country

Genus species author	Feeding group	Collection	Country	SEM	Light microscope
<i>Anomis mesogona</i> (Walker, 1858)	PTS	FLMNH (JMZ431)	Taiwan	X	X
<i>A. privata</i> (Walker, 1865)	PTS	FLMNH	Taiwan	X	X
<i>Calyptra albivirgata</i> (Hampson, 1926)	PTS	NMNH (JMZ359)	China		X
<i>C. bicolor</i> (Moore, 1883)	PTS/MSP	NMNH (JMZ348)	Nepal		X
<i>C. bicolor</i>	PTS/MSP	NMNH (JMZ349)	Nepal		X
<i>C. canadensis</i> (Bethune, 1865)	PTS	AMNH (JMZ374)	USA	X	X
<i>C. canadensis</i>	PTS	AMNH (JMZ375)	USA	X	X
<i>C. eustrigata</i> (Hampson, 1926)	PTS/MSP	NMNH (JMZ332)	Thailand	X	X
<i>C. eustrigata</i>	PTS/MSP	NMNH (JMZ331)	Malaysia	X	X
<i>C. fasciata</i> (Moore, 1882)	PTS/MSP	Fibiger (JMZ330)	Nepal		X
<i>C. fletcheri</i> (Berio, 1956)	PTS/MSP*	NMNH (JMZ352)	Nepal		X
<i>C. gruesa</i> (Draudt, 1950)	PTS	NMNH (JMZ357)	China		X
<i>C. lata</i> (Butler, 1881)	PTS	FLMNH (JMZ495)	Russia (RFE)	X	X
<i>C. lata</i>	PTS	NMMH (JMZ358)	Korea	X	X
<i>C. minuticornis</i> (Guenée, 1852)	PTS/MSP	NMNH (JMZ354)	Thailand		X
<i>C. minuticornis</i>	PTS/MSP	Fibiger (JMZ351)	Nepal		X
<i>C. ophideroides</i> (Guenée, 1852)	PTS/MSP	NMNH (JMZ335)	Himalaya		X
<i>C. orthograptia</i> (Butler, 1886)	PTS/MSP	NMNH (JMZ347)	China		X
<i>C. orthograptia</i>	PTS/MSP	NMNH (JMZ436)	Thailand		X
<i>C. parva</i> Bänziger, 1979	PTS/MSP	NMNH (JMZ344)	Thailand		X
<i>C. pseudobicolor</i> Bänziger, 1979	PTS/MSP	NMNH (JMZ341)	Nepal		X
<i>C. pseudobicolor</i>	PTS/MSP	NMNH (JMZ342)	Nepal		X
<i>C. subnubila</i> (Prout, 1928)	PTS	NMNH (JMZ350)	Indonesia		X
<i>C. thalictri</i> (Borkhausen, 1790)	PTS/MSP*	NMNM (JMZ334)	Slovakia	X	X
<i>C. thalictri</i>	PTS/MSP*	NMNH (JMZ360)	Russia (RFE)	X	X
<i>Eudocima homaena</i> (Hübner, 1823)	PHS	Fibiger (JMZ397)	Indonesia	X	X
<i>Eudocima salamina</i> (Cramer, 1777)	PHS	NMNH (JMZ396)	Papua New Guinea		X
<i>Ferenta castula</i> (Dognin, 1912)	UFG	NHM (JMZ497)	Colombia		X
<i>Goniapteryx servia</i> (Stoll, 1780)	NP	FLMNH (JMZ472)	USA	X	X
<i>Gonodonta nutrix</i> (Cramer, 1780)	PTS	FLMNH (JMZ446)	USA	X	X
<i>Graphigona regina</i> (Guenée, 1852)	UFG	NHM (JMZ510)	Costa Rica		X
<i>Hemiceratooides hieroglyphica</i> (Saalmüller, 1891)	TD	NMNH (JMZ61)	Malawi	X	X
<i>Hypsoropha hormos</i> Hübner, 1880	NP	FLMNH (JMZ476)	USA	X	X
<i>Oraesia argyrosigna</i> Moore, 1884	PTS	Fibiger (JMZ394)	Nepal		X
<i>O. emarginata</i> (Fabricius, 1794)	PTS	NMNH (JMZ388)	Malaysia		X
<i>O. emarginata</i>	PTS	NMNH (JMZ389)	Sri Lanka		X
<i>O. excavata</i> (Butler, 1878)	PTS	NMNH (JMZ365)	Japan		X
<i>O. excitans</i> Walker 1858	PTS	NMNH (JMZ366)	Mexico		X
<i>O. glaucochelia</i> (Hampson, 1926)	PTS	NMNH (JMZ378)	Bolivia		X
<i>O. honesta</i> Walker 1858	PTS	NMNH (JMZ372)	Mexico		X
<i>O. honesta</i>	PTS	NMNH (JMZ373)	Mexico		X
<i>O. nobilis</i> Felder and Rogenhofer 1874	PTS	NMNH (JMZ363)	Brazil		X
<i>O. provocans</i> Walker 1858	PTS	NMNH (JMZ369)	Malawi		X
<i>O. rectistria</i> Guenée 1852	PTS	NMNH (JMZ370)	India		X
<i>O. rectistria</i>	PTS	FLMNH (JMZ485)	Nepal	X	X
<i>O. serpens</i> Schaus 1898	PTS	NMNH (JMZ367)	Venezuela		X
<i>O. serpens</i>	PTS	NMNH (JMZ368)	Venezuela		X
<i>O. striolata</i> Schaus 1911	PTS	NMNH (JMZ377)	Peru		X

Table 2 continued

Genus species author	Feeding group	Collection	Country	SEM	Light microscope
<i>O. striolata</i>	PTS	NMNH (JMZ376)	Bolivia		X
<i>O. triobliqua</i> (Saalmüller, 1880)	PPTS	NMNH (JMZ337)	Rhodesia		X
<i>Phyllodes consobrina</i> Westwood 1848	PTS	FLMNH (JMZ469)	Assam	X	X
<i>Phyprosopus callitrichoides</i> Grote 1872	NP	FLMNH (JMZ484)	USA	X	X
<i>Plusiodonta coelonota</i> (Kollar, 1844)	PTS	NMNH (JMZ384)	Taiwan		X
<i>Plusiodonta compressipalpus</i> Guenée 1852	PTS	FLMNH (JMZ483)	USA	X	X
<i>Plusiodonta incitans</i> (Walker, 1858)	PTS	NMNH (JMZ386)	Mexico		X
<i>Plusiodonta incitans</i>	PTS	NMNH (JMZ387)	Argentina		X
<i>Scoliopteryx libatrix</i> (Linnaeus, 1758)	PTS	Fibiger (JMZ381)	Denmark	X	X
<i>S. libatrix</i>	PTS	FLMNH (JMZ327)	USA		X
<i>Tetrisia florigera</i> Walker 1867	UT	NHM (JMZ496)	Peru		X

Feeding categories NP Non-piercing, fruit sucking, *PTS* Primary piercing of thick-skinned fruits and secondary piercing of hard-skinned fruits, *PHS* Primary piercing of hard-skinned fruits, *MSP* Mammalian skin piercing (*under experimental conditions), *TD* Tear drinking, *UFG* Unknown feeding group, *Imaging* Scanning electron microscopy (SEM), Microoptics image

Four institutional and one private collection were consulted. The acronym of the collection is followed by the name of the individual that prepared the loan: *AMNH* American Museum of Natural History, New York (D. Grimaldi); *FLMNH* Florida Museum of Natural History, Florida (G. Austin, M. Thomas); *NHM* Natural History Museum, London (M. Honey); *MF* Personal collection of M. Fibiger, Denmark (Michael Fibiger); *NMNH* National Museum of Natural History, Washington D.C. (M. Pogue). Institutional acronyms follow Heppner and Lamas (1982)

O. emarginata (Fabricius, 1794), *O. excavata* (Butler, 1878), *O. excitans* Walker 1858, *O. glaucochelia* (Hampson, 1926), *O. honesta* Walker 1858, *O. nobilis* Felder and Rogenhofer 1874, *O. provocans* Walker 1858, *O. rectistria* Guenée 1852, *O. serpens* Schaus 1898, *O. striolata* Schaus 1911, and *O. triobliqua* (Saalmüller, 1880).

This category was also represented by two additional species from Anomini, *Anomis mesogona* (Walker, 1858) and *A. privata* (Walker, 1865).

C. Primary piercing of hard-skinned fruit This feeding group includes moths that pierce intact skin of longan and lichi, as well as all soft-skinned fruit. The following taxa represented this feeding category: *Eudocima homaena* (Hübner, 1823) and *E. salamina* (Cramer, 1777).

D. Mammalian skin piercing Moths in this category use their proboscis to pierce mammalian skin and imbibe blood. This facultative behavior has only been documented in males. All the species that facultatively imbibe blood also are primary piercers of thick-skinned fruit (type B). In this study, ten species were classified in this D group, although some species exhibit different adult behaviors in parts of their geographic range: *Calyptra bicolor*, *C. eustrigata*, *C. fasciata*, *C. fletcheri*, *C. minuticornis*, *C. ophideroides*, *C. orthograptia*, *C. parva*, *C. pseudobicolor*, and *C. thalictri*.

Of these ten, three exhibit polytypic or have incompletely documented behaviors. *Calyptra fasciata* exhibits differential feeding behavior depending on geographic region (Bänziger 1989). *Calyptra fletcheri* has only been

hematophagous under experimental conditions (Bänziger 1989). *Calyptra thalictri* is an obligate fruit piercer in southern Europe (refusing blood meals) and was found to be hematophagous under experimental conditions in Far Eastern Russia (Zaspel et al. 2007). The remaining seven species (*Calyptra bicolor*, *C. eustrigata*, *C. minuticornis*, *C. ophideroides*, *C. orthograptia*, *C. parva*, and *C. pseudobicolor*) have been recorded feeding on blood in nature (Bänziger 2007).

E. Tear drinking Moths in this category imbibe tears by placing the distal part of the proboscis onto the eyelid where it joins the eye and drinks tears from the host (Bänziger 1973). A typical “exclusively lachrophagous” species, *Lobocraspis griseifusa* (Nolinae) is included (Büttiker et al. 1996) to illustrate the armature of the proboscides. This proboscis is compared with that of *H. hieroglyphica*. Placement of *H. hieroglyphica* in Calpinae is controversial and represents a unique example of this feeding category for the subfamily.

F. Adult feeding poorly documented or unknown Three additional calpine species *Ferenta castula* (Dognin, 1912), *Graphigona regina* (Guenée, 1852), and *Tetrisia florigera* Walker 1867 were examined because preliminary observations suggested that their proboscides were superficially similar to those of *Eudocima* species, and they may represent additional examples of feeding group C (primary piercing hard-skinned fruits). *Calyptra canadensis* (Bethune) is also included here because its adult feeding behavior is unknown. Piercing capabilities for all four

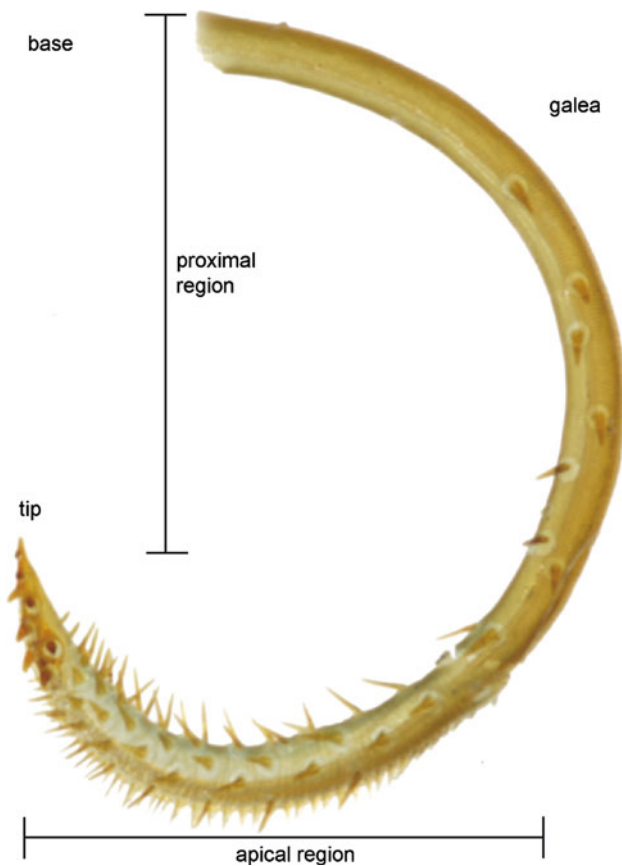


Fig. 2 Description of proboscis regions; *Oraesia rectistria*. Arrow indicates “bend region” dividing regions of the proboscis into proximal and apical regions

species have not yet been reported or tested. A fifth genus, *Phyllodes*, is included here even though initial observations suggest that it may belong to the A2 (thin-skinned) or B (thick-skinned) feeding group. Bänziger (1982) found *Phyllodes consobrina* Westwood 1848 and *P. eyndhovii* Vollenhoven 1858 feeding upon figs, mandarin, and rambutan. He could not determine whether they were primary or secondary piercers.

Results

Overview of calpinae proboscis morphology

Basic characteristics of surface microstructure and most other structures of the proboscis were adequately visualized using a light microscope. For example, the presence of tearing hooks, rasping spines, and shape of dorsal legulae were easily visualized using light microscopy (Figs. 2, 3). The endocuticula that joins the tearing hooks with the sclerotized socket and also surrounds the erectile barbs were evident by light microscopy and were not visible by

SEM. However, without SEM images, surface microstructure, minor structural differences in the shape of tearing hooks, and the presence of furcate erectile barbs were difficult to detect (e.g., Figs. 4, 5, 6, 7, 8, 9, 10, 11, 12). We confirmed Bänziger’s observation (Bänziger 1971a, 2007) that dehydration generated unequal shrinking of the proboscis. This deformation was slight in sclerotized, piercing proboscides, but soft, non-piercing proboscides were greatly deformed (Fig. 4). While this deformation seriously impairs a correct understanding of how a proboscis and its armature work in a live insect, the shape of the sensilla, barbs, hooks, and other proboscis ornaments were not affected by dehydration.

A diagram of the proboscis of *Oraesia rectistria* illustrates proximal versus apical regions as seen in all for calpine moths (Fig. 2). The proximal region is defined as the area from the basal proboscis joint to the “bend region” (Bänziger 1971a); the apical region is demarcated by this

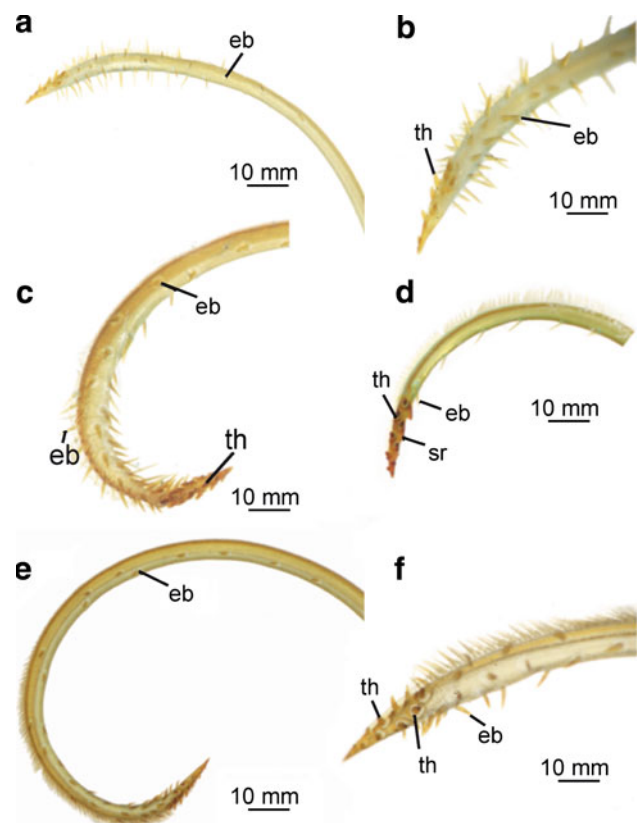


Fig. 3 Examples of proboscis structures visible by light microscopy in primary piercing of thick-skinned fruit, feeding group (a–c), Primary piercing of hard- and thick-skinned fruit group (d) and Mammalian skin-piercing group (e, f) a *Oraesia serpens*; Proximal proboscis region. b *O. serpens*; Apical proboscis region. c *Gonodonta nutrix*; Proximal proboscis region. d *Eudocima homanea*; Proximal proboscis region. e *Calyptra fasciata*; Proximal proboscis region. f *Calyptra fasciata*; Apical proboscis region. *dgl* dorsal galeal linkage, *eb* erectile barbs, *sr* serrated ridges, *th* tearing hooks

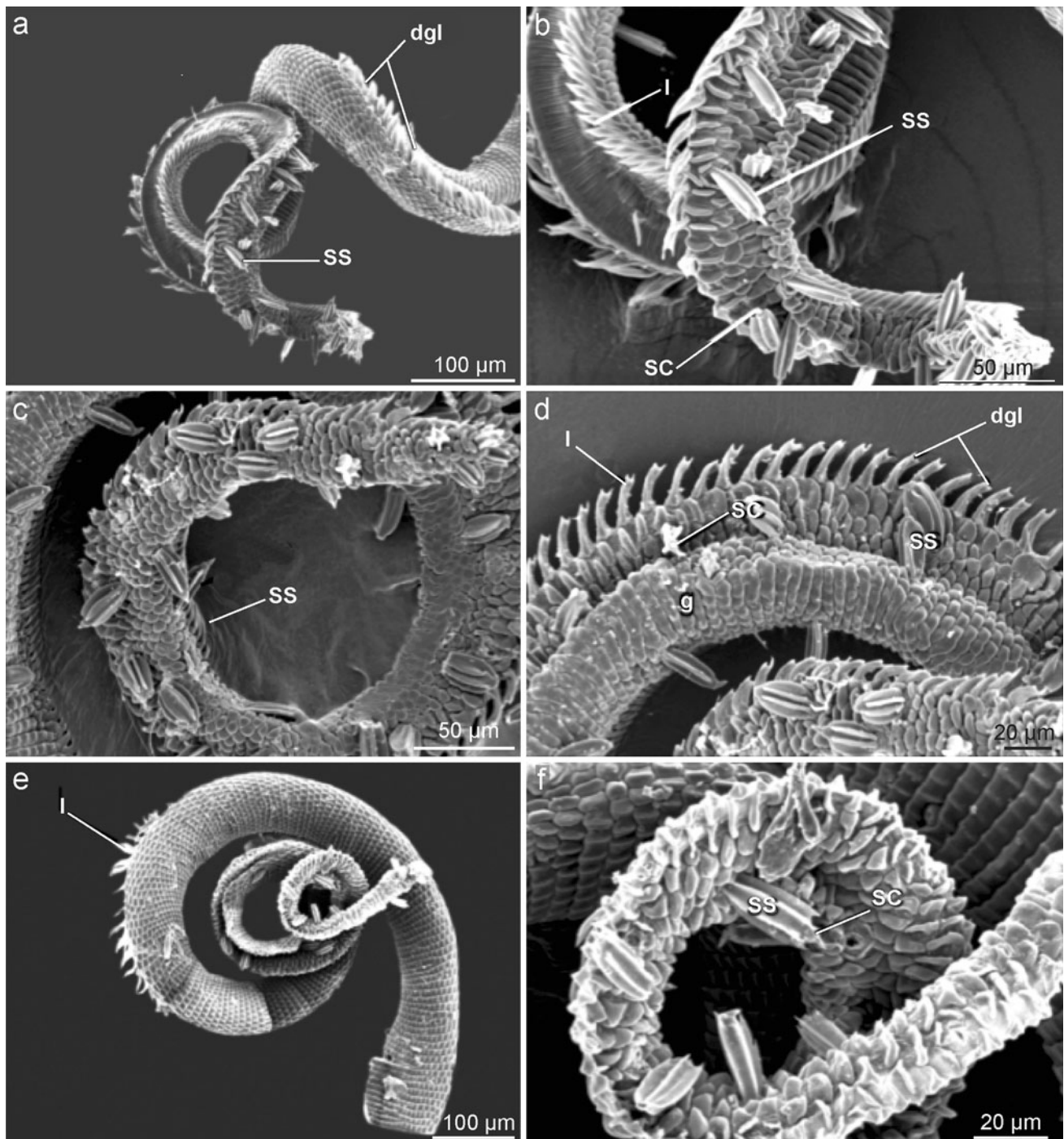


Fig. 4 Examples of proboscis structures visible by scanning electron microscopy in *non-piercing, fruit-sucking* feeding group. **a** *Goniapteryx servia*; Proximal proboscis region. **b** *G. servia*; Apical proboscis region. **c** *Hypsoropha hormos*; Apical proboscis region. **d** *H. hormos*;

Proximal proboscis region. **e** *Phylloscopus callitrichoides*; Proximal proboscis region. **f** *P. callitrichoides*; Apical proboscis region. *dgl* dorsal galeal linkage, *g* galea, *l* legula, *sc* sensory cone, *ss* sensilla styloconica

point of flexion and extends to the tip or apex. An additional six proboscis images taken using the Microptics™ system were selected from the 96 total images and used to describe associated structures (Fig. 3a–f).

From these observations, a glossary of proboscis structures was compiled for Calpinae that is reconciled with established terminology for Lepidoptera (Table 2). The exact function(s) of some structures still needs experimental

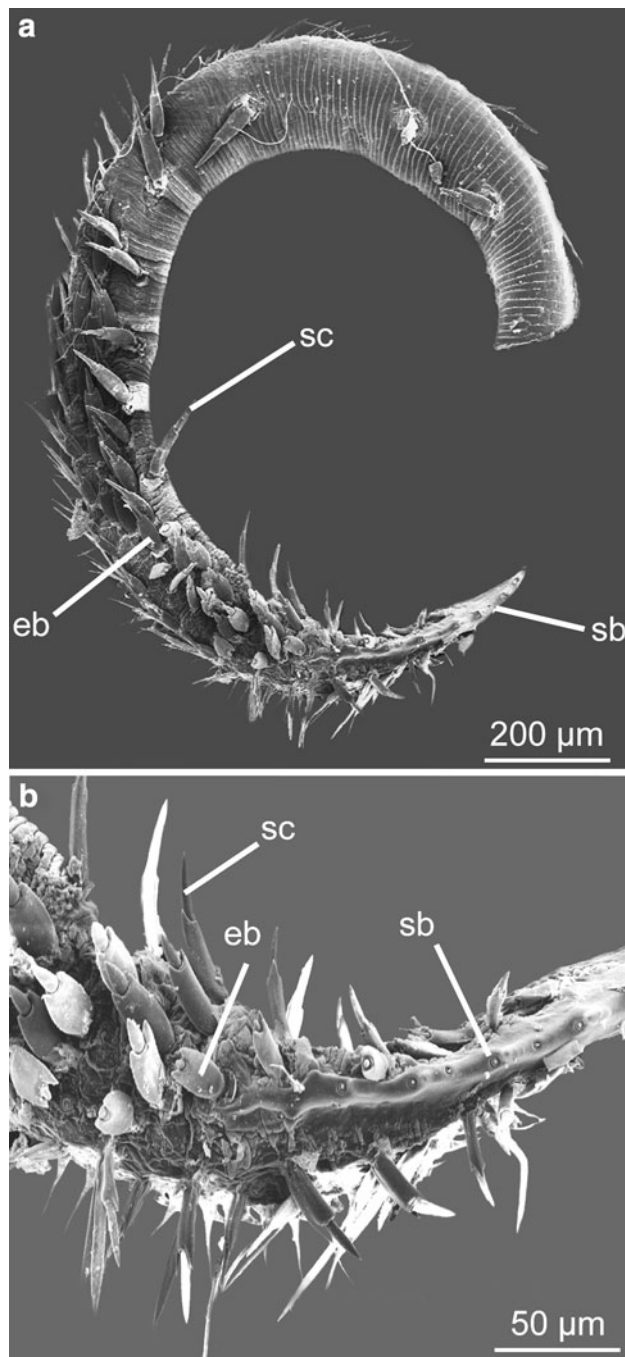


Fig. 5 Examples of proboscis structures visible by scanning electron microscopy in *primary piercing of soft-skinned fruits; secondary piercing of thick- or hard-skinned fruit feeding groups*, **a** *Scoliopteryx libatrix*; Proximal proboscis region. **b** *S. libatrix*; Apical proboscis region. *eb* erectile barbs, *feb* furcate erectile barbs, *sb* sensilla basiconica, *sc* sensory cone

confirmation (e.g., furcate erectile barbs), but proposed function based on the primary literature is provided. This study revealed thirteen new characters of importance to the systematics of Calpinae. Descriptions of proboscis

characters for calpine and other genera are listed in the “Character Summary” section.

Little structural variation was observed within genera (data not shown except for *Calyptra* (compare Figs. 6c, 9a–c, 10a–c)). Therefore, feeding groups are represented by one or more species selected to represent the variation as needed. For these selected species, proboscis morphology is described in detail for either light microscopy or SEM. Proboscides descriptions are organized according to their placement in functional feeding groups rather than the species’ phylogenetic affinities, including the “undocumented” feeding group.

Non-piercing, fruit-sucking feeding (group A)

These proboscides are characterized by an equal or almost equal distribution of sensilla styloconica (*ss*) throughout the length of the proboscis. Some details differ at the microstructural level.

Goniapteryx servia of tribe Calpini (sensu Fibiger and Lafontaine 2005). The surface of the proximal region of the proboscis is fluted with circular ribs and distinct longitudinal depressions throughout (Fig. 4a). Cuticular processes are absent from the ribs. Sensilla styloconica (*ss*) are absent from the proximal region (Fig. 4a). The apical region is densely nodulose with asymmetrical nodules throughout (Fig. 4b). The nodules near the legulae of the dorsal galeal cross-linkage are with septa (Fig. 4b). Sensilla styloconica are present in the apical portion of the proboscis, with each sensillum consisting of a stylus with longitudinal ridges and an apical sensory cone (*sc*); proximal and apical regions are without visible sensilla basiconica, sensilla trichodea, or cuticular processes. The legulae (*l*) of the dorsal galeal linkage (*dgl*) are primarily triangular, with most terminal legula slightly twisted, with two lateral prominences (Fig. 4a, b).

Hypsoropha hormos of tribe Calpini (sensu Fibiger and Lafontaine 2005). Proximal region is smooth in appearance and without visible sensory structures. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are rectangular. The surface of the proximal region of the proboscis is fluted, and nodulose with longitudinal depressions faintly present in most proximal circular ribs (1/4 entire length of proboscis) (Fig. 4c). Sensilla trichoidea or other cuticular processes are absent from the ribs. The apical region is densely nodulose with the nodules of the apical region asymmetrical and with septa toward the apex (Fig. 4c, d). Sensilla styloconica (*ss*) are distributed throughout the proximal and apical portions of the proboscis, with each sensillum consisting of a stylus with longitudinal ridges and an apical sensory cone (*sc*); proximal and apical regions are without visible sensilla trichodea or cuticular processes (Fig. 4c, d). The legulae (*l*) of the dorsal galeal

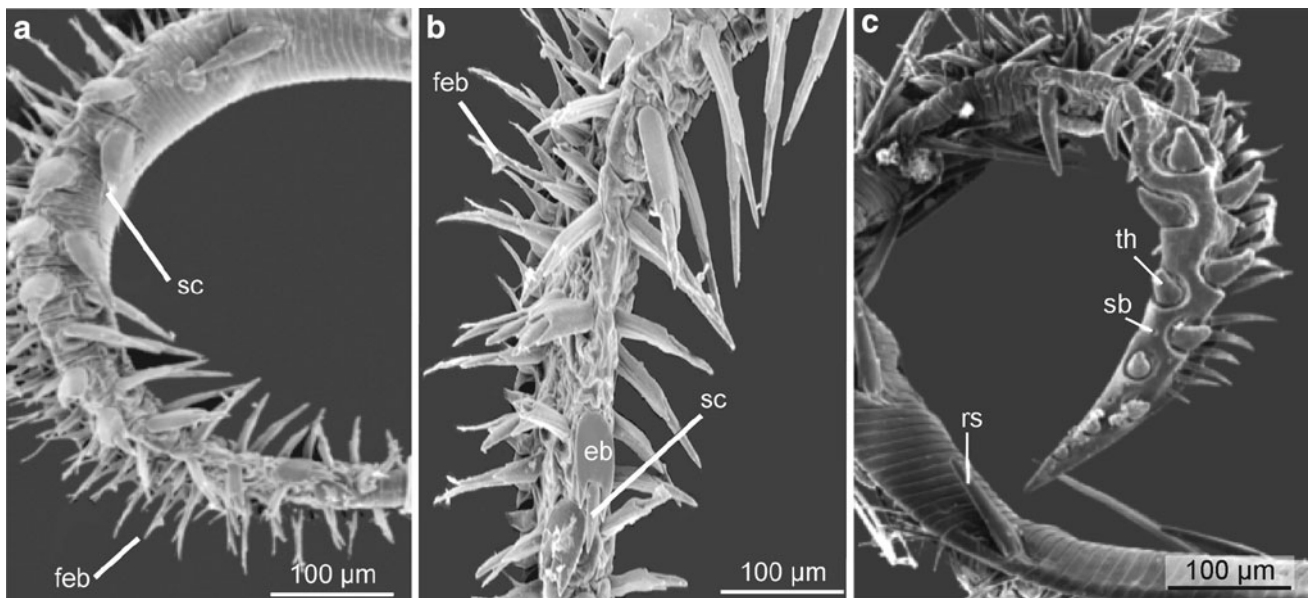


Fig. 6 Examples of proboscis structures visible by scanning electron microscopy in *primary piercing of thick-skinned fruit feeding groups*, **a** *Anomis mesogona*; Proximal proboscis region. **b** *A. mesogona*; Apical proboscis region. **c** *Calyptra lata*; Proximal proboscis region,

rs rasping spines, Apical region, *sb* sensilla basiconica, *th* tearing hooks. *eb* erectile barbs, *feb* furcate erectile barbs, *rs* rasping spines, *sb* sensilla basiconica, *sc* sensory cone, *th* tearing hooks

cross-linkage (*dgl*) are rectangular, slightly twisted, terminating in two lateral prominences (Fig. 4c).

Phyprosopus callitrichoides of tribe Calpini (sensu Fibiger and Lafontaine 2005). The surface of the proximal region of the proboscis is fluted with circular ribs and distinct longitudinal depressions throughout (Fig. 4e). Cuticular processes are absent from the ribs. Sensilla styloconica (*ss*) are absent from the proximal region (Fig. 4e). The apical region is sparsely nodulose becoming densely nodulose toward the apex of the proboscis (Fig. 4f). Nodules of the apical region are asymmetrical and are separated (Fig. 4f). Sensilla styloconica are present in the apical portion of the proboscis, with each sensillum consisting of a stylus with longitudinal ridges and an apical sensory cone (*sc*); proximal and apical regions are without visible sensilla trichoidea or cuticular processes. The legulae (*l*) of the dorsal galeal cross-linkage are triangular and are restricted to the middle portion of the galea (Fig. 4e).

Primary piercing of soft-skinned fruit; secondary piercing of thick- or hard-skinned fruit (group A2)

A single species with confirmed feeding behaviors represents this category. *Phyllodes consobrina* and *C. canadensis* are discussed under “unknown,” but their proboscides’ morphologies share some of the features detailed here.

Scoliopteryx libatrix of tribe Scoliopterygini (sensu Fibiger and Lafontaine 2005, Holloway 2005). The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 5a);

depressions and cuticular processes are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*) with two lateral prominences and a triangular distal cone (Fig. 5a). The erectile barbs of the proximal galea are singular and sparsely positioned along the lateral side of the proboscis (Fig. 5a). Erectile barbs are abundant in the apical region of the proboscis and are arranged on both lateral and ventrolateral sides (Fig. 5b). The surface of the apical region is heterogeneous with both nodulose and smooth regions (Fig. 5b). The nodulose area at the tip of the proboscis consists of areas with and without septa (Fig. 5b). The tip of the proboscis is smooth with a thin band of cuticle with slight ridges extending into the nodulose portion (Fig. 5b). Sensilla basiconica are situated beneath the ridges at the tip of the proboscis (Fig. 5b). Furcate erectile barbs (*feb*) are present in the apical portion of the proboscis, with each sensillum consisting of short and long triangular branches, some secondarily bifurcated with setose distal processes. Proximal and apical regions are without visible sensilla trichoidea. The legulae of the dorsal galeal cross-linkage are thin and triangular (Fig. 5a).

Primary piercing of thick-skinned fruit but secondary piercing of hard-skinned fruit (group B)

The proboscides of moths in this category typically have a smooth surface with circular or semi-circular ribs. Sensilla styloconica are typically modified into dorsoventrally flattened, erectile barbs (*eb*), although species-specific differences in shape or position occur. In all four genera

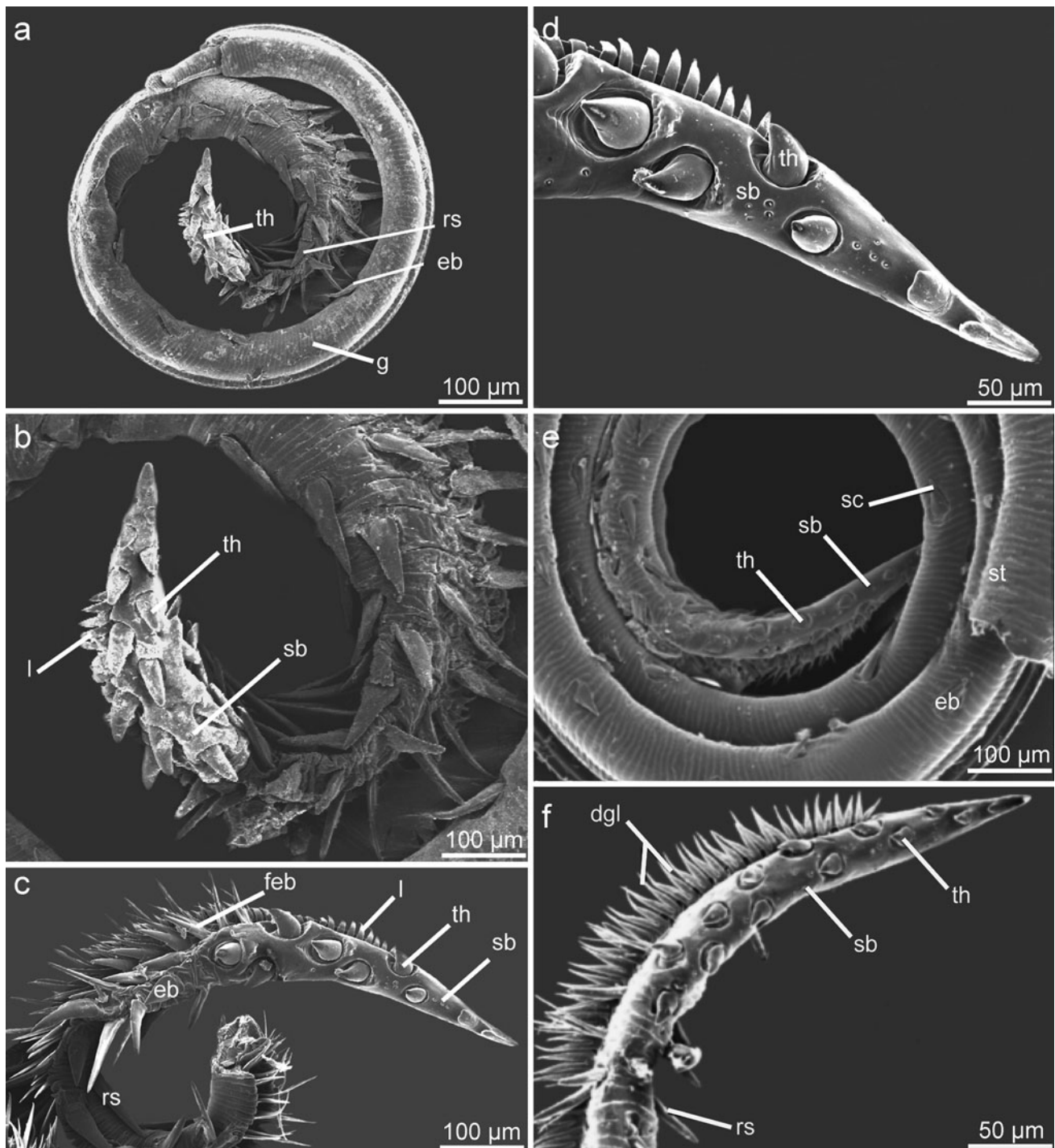


Fig. 7 Examples of proboscis structures visible by scanning electron microscopy in *primary piercing of thick-skinned fruit feeding groups*, **a** *Gonodonta nutrix*; Proximal proboscis region. **b** *G. indentata*; Apical proboscis region. **c** *Oraesia rectistria*; Apical proboscis region. **d** *O. rectistria*; Apical proboscis region. **e** *Plusiodonta*

compressipalpus; Proximal proboscis region. **f** *P. compressipalpus*; Apical proboscis region. *dgl* dorsal galeal linkage, *g* galea, *eb* erectile barbs, *feb* furcate erectile barbs, *l* legula, *rs* rasping spines, *sb* sensilla basiconica, *sc* sensory cone, *st* sensilla trichoidea, *th* tearing hooks

(and species), the surface of the apical region is smooth and the tip has tear-shaped, tearing hooks. Sensilla trichoidea are absent in all four species, and sensilla basiconica are visible in only species of *Anomis* and *Calpytra*. Many of

these features are shared by the facultative hematophagous species (Group D).

Calpine species *Oraesia serpens*. The surface of the proximal region of the proboscis is simple and smooth with

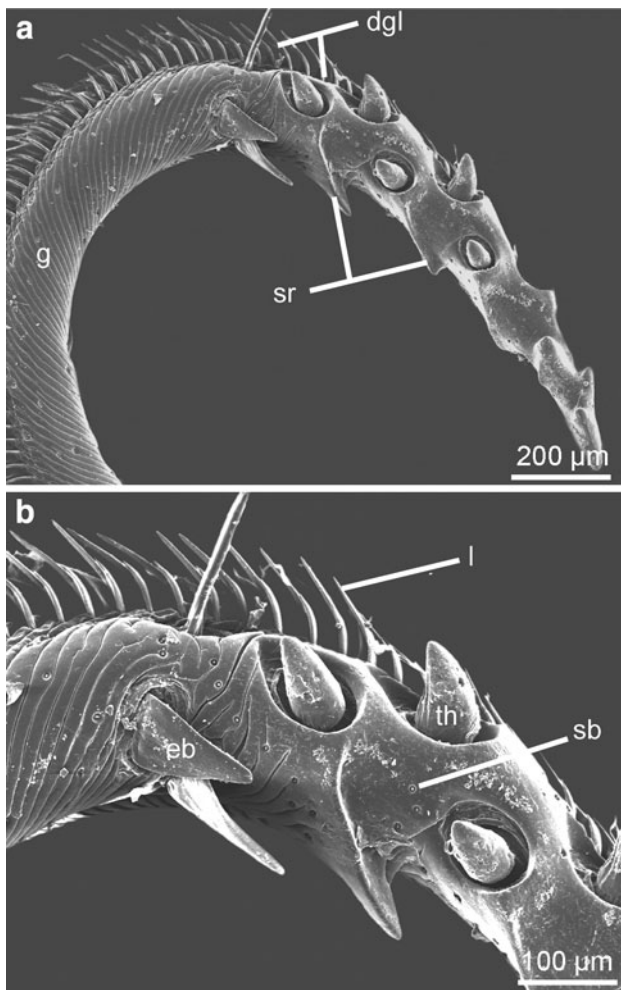


Fig. 8 Proboscis of taxa in the *primary piercing of hard- and thick-skinned fruits* feeding group, **a** *Eudocima homaena*; Apical proboscis region. **b** *E. homaena*; Apical proboscis region. *dgl* dorsal galeal linkage, *g* galea, *eb* erectile barbs, *l* legula, *sb* sensilla basiconica, *sr* serrated ridges, *th* tearing hooks

circular or semi-circular ribs. Chaetiform sensilla and other cuticular processes are not visible or are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*) (Fig. 3a). The erectile barbs are abundant in the apical region of the proboscis especially along the lateral margin of the dorsal galeal cross-linkage where they are furcated (Fig. 3b). The ventral surface of the apical region is smooth, and the tip is fully sclerotized with curved, tear-shaped, socketted, tearing hooks (*th*) (Fig. 3b). Proximal and apical regions are without visible sensilla basiconica or sensilla trichoidea. The legulae of the dorsal galeal cross-linkage are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side (although not visible in Fig. 3b). The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs; depressions and

cuticular processes are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*), with a distal cone (Fig. 7c). Erectile barbs are abundant in the apical region of the proboscis, along with distinct rasping spine-like (*rs*) structures. The rasping spines are triangular and without a distal cone. The surface of the apical region is smooth, and the tip has tear-shaped, socketted tearing hooks (*th*, Fig. 7d). Furcate erectile barbs are present along the lateral margin of the dorsal galeal cross-linkage (Fig. 7c). The furcate erectile barbs are asymmetrical, consisting of one short and one long lateral prominence, with a large sensory cone set in between (Fig. 7c). Sensilla basiconica are positioned throughout the tip of the proboscis, typically arranged in groups of two or three (Fig. 7d). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are flattened and triangular (Fig. 7d).

Calpine species *Gonodonta nutrix*. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 3c). Chaetiform sensilla and other cuticular processes are not visible or are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*) (Fig. 3c). The erectile barbs are abundant in the apical region of the proboscis, along with distinct rasping spine-like structures. The ventral surface of the apical region is smooth, and the tip is fully sclerotized with cone-shaped, socketted tearing hooks (*th*) (Fig. 3c). Furcate erectile barbs are present along the lateral margin of the dorsal galeal cross-linkage. Sensilla basiconica or sensilla trichoidea are not visible in either proximal or apical regions. The legulae of the dorsal galeal cross-linkage are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs; depressions are absent. Cuticular processes are absent from the ribs. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*), without a distinct distal cone (Fig. 7a). Individual erectile barbs are positioned in a single row along the lateral side of the proboscis and are abundant in the apical region. Rasping spines (*rs*) are present along the lateral margin of the dorsal galeal cross-linkage (Fig. 7a, b). The surface of the apical region is smooth, and the tip is has cone-shaped, socketted tearing hooks (*th*, Fig. 7b); furcate erectile barbs are absent. Sensilla basiconica (*sb*) are positioned throughout the tip of the proboscis, typically arranged in groups of two or three (Fig. 7b). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are short and conical (Fig. 7b).

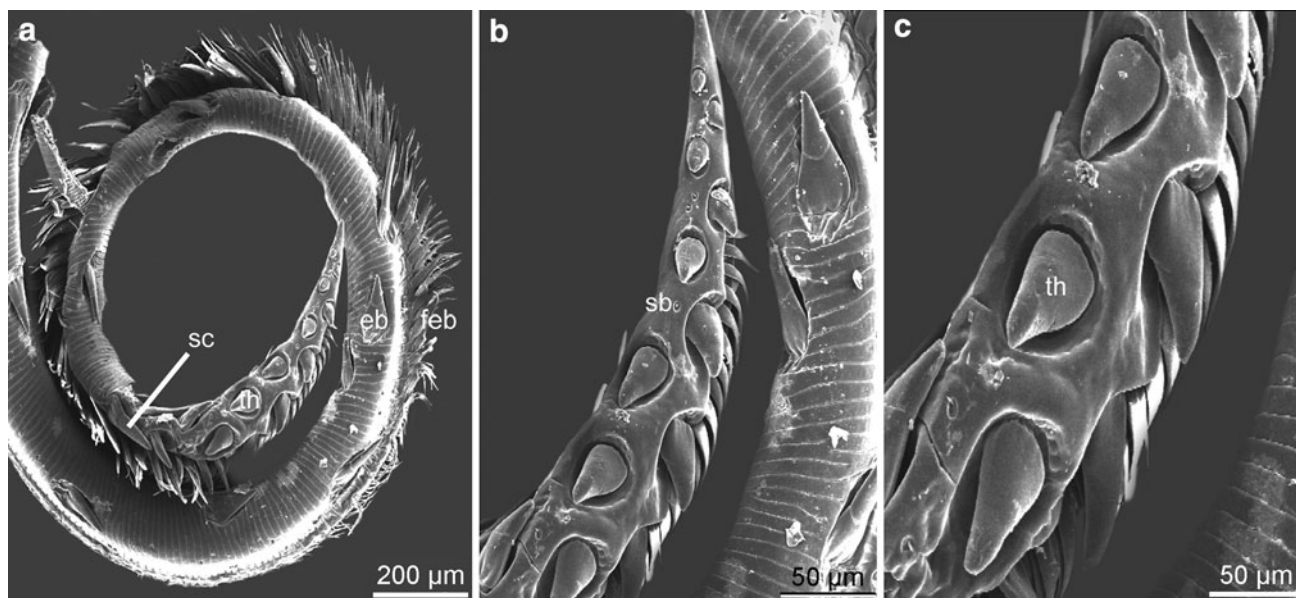


Fig. 9 Proboscides of taxa in the *mammalian skin-piercing* feeding group, **a** *Calyptra eustrigata*; Proximal proboscis region. **b** *C. eustrigata*; Apical proboscis region. **c** *C. eustrigata*. *eb* erectile barbs,

feb furcate erectile barbs, *l* legula, *sb* sensilla basiconica, *sc* sensory cone, *th* tearing hooks

Anomis mesogona of tribe Anomini (sensu Fibiger and Lafontaine 2005, Holloway 2005). The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 6a); depressions and cuticular processes are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*), each with two lateral prominences and a triangular distal cone (Fig. 6a). The erectile barbs are singular and sparsely positioned along the lateral side of the proximal galea (Fig. 6a). Erectile barbs are typically more abundant toward the apical region of the proboscis and are arranged on both lateral and ventrolateral sides (Fig. 6b). The apical region is nodulose with asymmetrical nodules throughout (Fig. 6b). The nodulose area at the tip of the proboscis is without septa (Fig. 6b). Furcate erectile barbs (*feb*) are also present in the apical portion of the proboscis, with each sensillum consisting of short and long triangular branches, some secondarily bifurcated. Sensilla basiconica are present only in apical region; proximal and apical regions are without visible sensilla trichoidea, or cuticular processes. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side. (Fig. 6a).

Calpine species *Calyptra lata*. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs; depressions and cuticular processes are absent (Fig. 6f). Rasping spines (*rs*) are sparsely positioned along the lateral margin of the dorsal galeal cross-linkage and on the ventrolateral sides of the

proboscis and are without a distal cone. The surface of the apical region is smooth, and the tip is with curved, tear-shaped, socketted tearing hooks (Fig. 6f). Sensilla basiconica (*sb*) are positioned throughout the tip of the proboscis, typically arranged in groups of two or three (Fig. 6f). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side (Fig. 6f).

Calpine species *Plusiodonta compressipalpus*. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 7e); depressions are absent. Cuticular processes or chaetiform sensilla (*cs*) are present at the base (Fig. 7e). Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*), occasionally with a distinct distal cone (Fig. 7e). Individual erectile barbs are positioned in a single row along the lateral side of the proboscis and are more abundant in the apical region of the proboscis (Fig. 7e, f). Rasping spines (*rs*) are sparsely positioned along the lateral margin of the dorsal galeal cross-linkage and are without a distal cone (Fig. 7f). The surface of the apical region is smooth, and the tip has curved, tear-shaped, socketted tearing hooks (Fig. 7f). Sensilla basiconica (*sb*) are positioned throughout the tip of the proboscis, typically arranged in groups of two or three (Fig. 7f). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are forked and triangular (Fig. 7f).

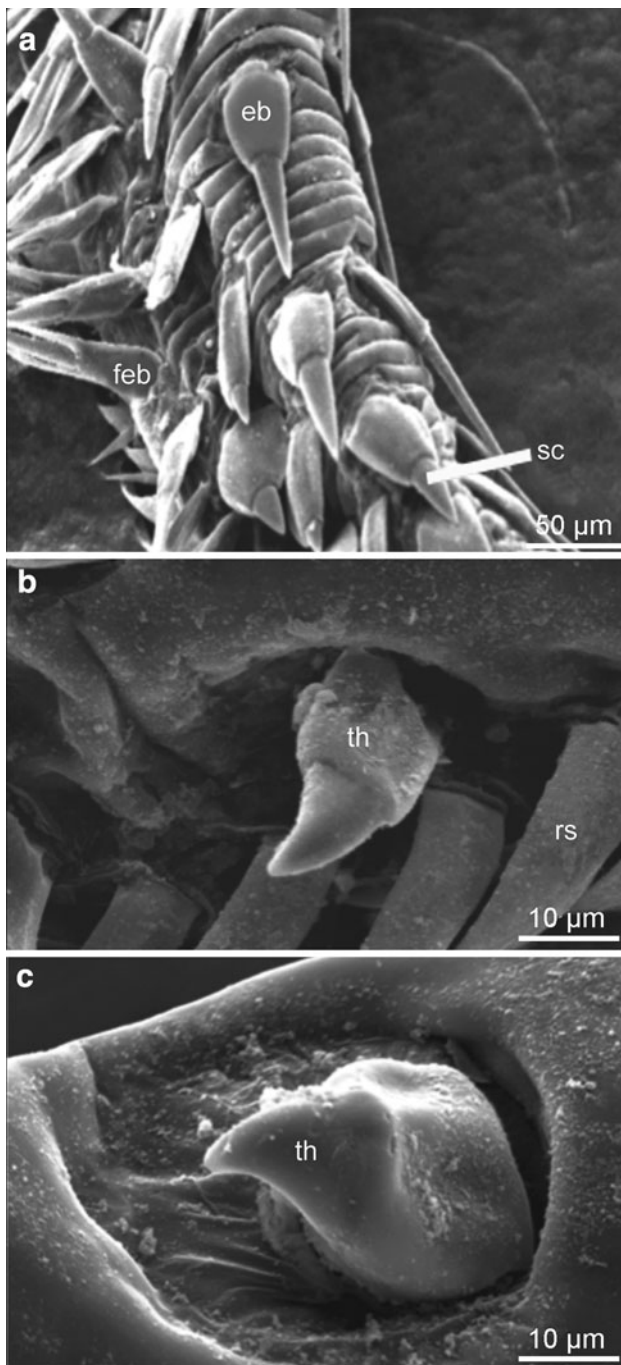


Fig. 10 Proboscides of taxa in the *mammalian skin-piercing* feeding group. **a** *Calyptra thalictri*; Apical proboscis region. **b** *C. thalictri*; Apical proboscis region. **c** *C. thalictri*; Apical proboscis region. *eb* erectile barbs, *feb* furcate erectile barbs, *l* legula, *sc* sensory cone, *th* tearing hooks

Primary piercing of hard-skinned fruit (group C)

Here, one species represents the genus whose species are documented globally as pests on fruits (Todd 1959). Three species discussed under “unknown” share many of the

proboscides’ features of this primary piercer of hard-skinned fruit.

Calpine species *Eudocima homaena*. The surface of the proximal region of the proboscis is simple and smooth with diagonal circular or semi-circular ribs. Two or three dorsoventrally flattened erectile barbs (*eb*) in depressions linked by endocuticula occur just below the junction of the ribbed and smooth areas of the apical region. The surface of the apical region is smooth and fully sclerotized with serrated ridges (*sr*). The ventral surface of the apical region is smooth, and the tip is with tearing hooks (*th*) linked by pale, elastic endocuticula (Fig. 3d). The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are long and spike like (Fig. 3d). The ventral surface of the proximal region of the proboscis is simple and smooth with diagonal circular or semi-circular ribs; depressions are absent. Chaetiform sensilla and other cuticular processes are not visible or are absent from the ribs. Two or three dorsoventrally flattened erectile barbs occur just below the junction of the ribbed and smooth areas of the apical region and are without a distinct distal cone (Fig. 8a, b). The surface of the apical region is smooth with serrated ridges (*sr*); the tip is cone-shaped, with socketted tearing hooks (*th*, Fig. 8a). Rasping spines and furcate erectile barbs are absent. Sensilla basiconica are positioned throughout the tip of the proboscis and on the tearing hooks, typically arranged in groups of two or three (Fig. 8b). Proximal and apical regions are without visible sensilla trichodea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are long and spike like (Fig. 8b).

Mammalian skin piercing (group D)

Three *Calyptra* species are illustrated here. One, *C. fasciata* was examined only with light microscopy. Two, *C. eustrigata* and *C. thalictri* were examined only with SEM. The ability to visualize structures under the two different preparation techniques was comparable except for the details of the sensilla. The distal cone of sensilla styloconica is visible with SEM but not with light microscopy. Also, the relative positions of the sensilla are deformed during dehydration for SEM (compare Figs. 3e, f, 10a–c, 11a–c). Specialized structures for blood feeding were not found in hematophagous *Calyptra* species, and the presence/absence, type and distribution of sensilla trichodea, sensilla basiconica are comparable with the feeding group B species. Sensilla trichodea are lacking (not visible) in all species, whereas the sensilla basiconica are absent in *C. fasciata* and *C. thalictri*, and present in *C. eustrigata*.

Calpine species *Calyptra fasciata*. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 3e). Chaetiform sensilla and other cuticular processes are not visible or are absent.

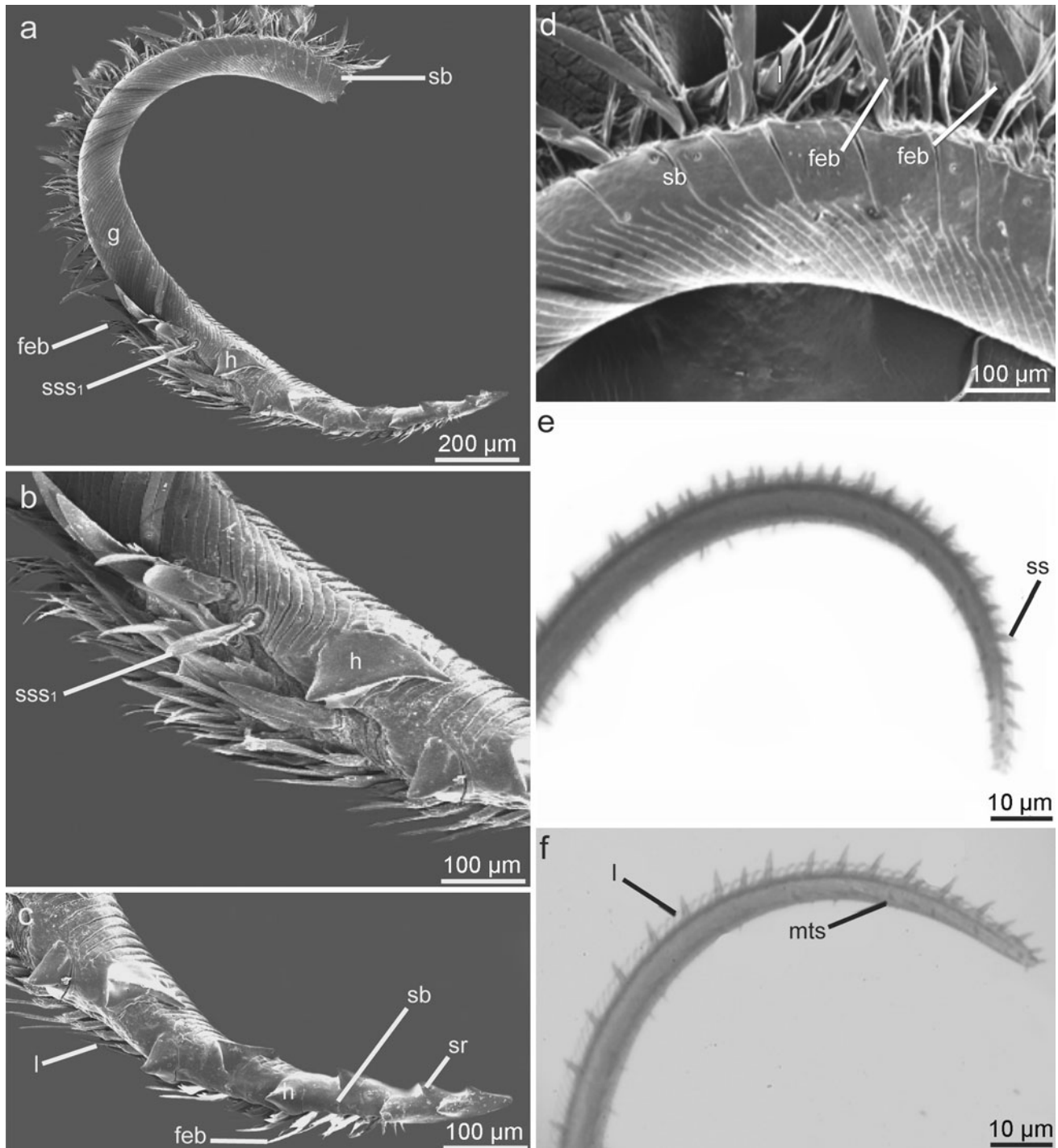


Fig. 11 Proboscis of, tear-feeding taxa, **a** *Hemiceratoides hieroglyphica*; Proximal proboscis region. **b** *H. hieroglyphica*; Apical proboscis region. **c** *H. hieroglyphica*; Apical proboscis region. **d** *H. hieroglyphica*; Apical proboscis region. **e** *Lobocraspis griseifusa*; Apical proboscis region. **f** *L. griseifusa*; Apical proboscis region. *dgl*

dorsal galeal linkage, *feb* furcate erectile barbs, *g* galea, *h* cuticular hook, *l* legula, *mts* minute triangular spine, *sb* sensilla basiconica, *sr* serrated ridge, *ss* sensilla styloconica, *sss₁* smooth sensilla styloconica subtype 1

Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*) (Fig. 3e). Individual erectile barbs are positioned in a single row along the lateral side of the proboscis, but in the apical region, they are

present on all sides, lacking only in the tip region (Fig. 3e). They are distally inclined and set in endocuticular depressions when at rest but, for piercing, they are everted by blood pressure (Bänziger 1980), and Furcate erectile

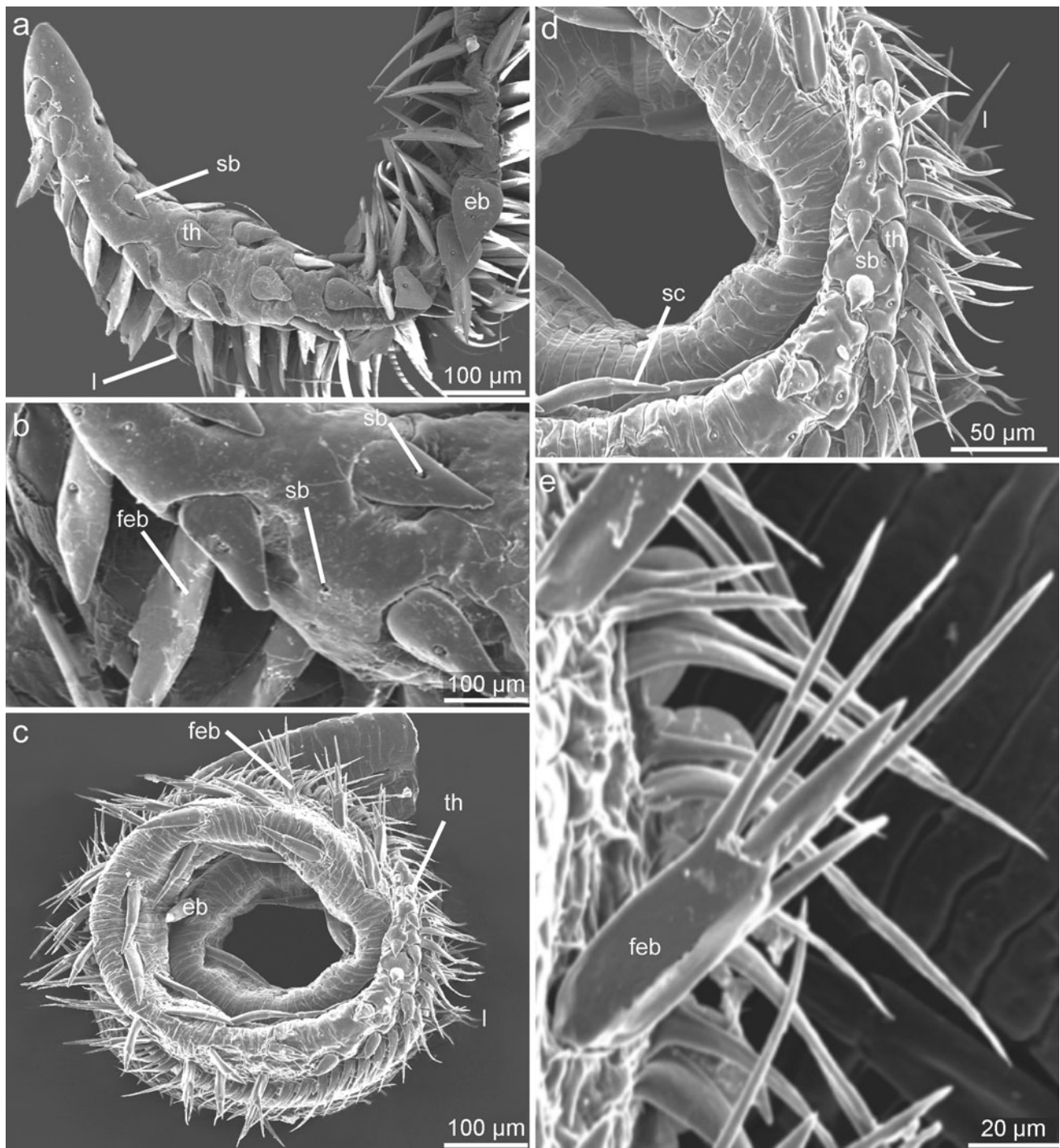


Fig. 12 Uncertain feeding types, **a** *Phylloides consobrina*; Apical proboscis region. **b** *P. consobrina*; Apical proboscis region. **c** *Calyptra canadensis*; Apical proboscis region. **d** *C. canadensis*; Apical proboscis region. **e** *C. canadensis*; Apical proboscis region. *dgl*

dorsal galeal linkage, *eb* erectile barbs, *feb* furcate erectile barbs, *l* legula, *sb* = sensilla basiconica, *sc* sensory cone, *sss*₂ smooth sensilla styloconica subtype 2, *th* tearing hooks

barbs are present along the lateral margin of the dorsal galeal cross-linkage (Fig. 3e). The apical section is lance-like and fully sclerotized. The ventral surface of the apical region is smooth and dorsolaterally, and the tip bears curved tear-shaped, tearing hooks (*th*) (Fig. 3f). These

hooks are surrounded by (*pale*) elastic endocuticula and set in a circular sclerotized socket. This socket is protruded distally to form a collar that prevents overturning of the tearing hooks. Sensilla basiconica or sensilla trichoidea are not visible in either proximal or apical regions. The legulae

of the dorsal galeal cross-linkage are curved and triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side.

Calpine species *Calyptra eustrigata*. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 9a, b); depressions and cuticular processes are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*), with a distinct distal cone (Fig. 9a). Individual erectile barbs are positioned in a single row along the lateral side of the proboscis and are positioned on ventrolateral sides in the apical region (Fig. 9a). Furcate erectile barbs (*feb*) are present along the lateral margin of the dorsal galeal cross-linkage (Fig. 9b). The furcate erectile barbs are symmetrical, consisting of two long lateral prominences, with a longer sensory cone set in between (Fig. 9b). The surface of the apical region is smooth, and the tip is with curved, tear-shaped, socketted tearing hooks (*th*) (Fig. 9a–c). Sensilla basiconica (*sb*) are positioned throughout the tip of the proboscis, typically arranged in groups of two or three (Fig. 9b). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal linkage (*dgl*) are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side (Fig. 9b).

Calyptra thalictri of Calpini. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 10a); depressions and cuticular processes are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs (*eb*), with a distinct distal cone (Fig. 10a). The surface of the apical region is smooth, and the tip is with sharp tear-shaped, socketted tearing hooks (*th*) (Fig. 10b, c). Proximal and apical regions lack visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal linkage (*dgl*) are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side (Fig. 10b).

Tear drinking (group E)

The two tear-feeding species illustrated here have different proboscides' morphologies. *Lobocraspis griseifusa* (Nolinae) has a lightly ornamented proboscis. In contrast, *H. hieroglyphica*, whose placement in Calpinae is controversial, has modified erectile barbs, but the modifications differ from those found in other members of the Calpinae. Also, the hook-like structures on the apical region are not like the tearing hooks in other calpine species.

Hemiceratooides hieroglyphica of Calpini (sensu Hilgartner et al. 2007). Placement of this species in this group

at present is tentative because nothing certain is known about its feeding habits. The most likely assumption is that it may pierce fruit and occasionally suck tears. The surface of the proximal region of the proboscis is simple and smooth with diagonal semi-circular ribs (Fig. 11a). The ribs of the proximal region terminate into lateral plates with shallow cuticular depressions (Fig. 11d). Furcate erectile barbs (*feb*) are present in the proximal and apical regions and occur along the lateral margin of the dorsal galeal cross-linkage (Fig. 11a, b, d). The furcate erectile barbs are of two types (*feb1* and *feb2*), both seemingly symmetrical: one consisting of a long, thin, feather-like plate with three small lateral prominences at the base, and the other with four prongs (two short and two long) (Fig. 11d). Smooth sensilla styloconica (subtype 1, *sss1*) are present in the apical region and are feather-like (Fig. 11a, b, d). The apical region is with fixed, deltoid-pyramidal hooks (*h*), without a distal cone (Fig. 11a–c). The surface of the apical region is smooth, and the tip is with sclerotized ridges (*sr*) (Fig. 11c). Sensilla basiconica (*sb*) are positioned throughout the length of the galea (*g*), typically arranged in the center of the plates along the lateral margins of the dorsal galeal cross-linkage (Fig. 11d). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side (Fig. 11d).

Lobocraspis griseifusa (Nolinae). The surface of the proximal region of the proboscis is simple and smooth (Fig. 11e) with minute triangular spines present (*mts*). Sensilla styloconica (*ss*) are present and with a distal cone (Fig. 11e, f). Sensilla basiconica or sensilla trichoidea are not visible in either proximal or apical regions. The legulae of the dorsal galeal linkage (*dgl*) are triangular and are incurved (Fig. 11e). The apex of the proboscis is pale in appearance, membranous, and blunt (Fig. 11f).

Adult feeding poorly documented or unknown (group F)

Of the five species discussed here, three share the proboscides' morphology of *Eudocima* spp. (group C, primary piercer hard-skinned fruit) based on superficial examination. The minor variation between *F. castula*, *G. regina*, and *T. florigera*, is described here.

The remaining two species *P. consobrina* and *C. canadensis* are predicted to share the group A2 or B feeding morphologies. They are figured because of the variation present in the B feeding group. For example, the sensilla styloconica can be absent or present in B feeding group species, and if present, the sensilla styloconica may or may not possess a distal cone.

Ferenta castula of Calpini (sensu Zaspel and Branham 2008). The surface of the proximal region is simple and smooth with diagonal semi-circular ribs. Several dorsoventrally flattened erectile barbs (*eb*) in depressions linked by endocuticula occur just below the junction of the ribbed and smooth areas of the apical region. The apical region is heavily sclerotized with serrated ridges present, originating from sockets of tearing hooks (*th*). The tip of the proboscis is short and blunt.

Graphigona regina of Calpini (sensu Zaspel and Branham 2008). The surface of the proximal region of the proboscis is simple and smooth with diagonal circular or semi-circular ribs. Several dorsoventrally flattened erectile barbs (*eb*) in depressions linked by endocuticula occur just below the junction of the ribbed and smooth areas of the apical region. The surface of the apical region is smooth and fully sclerotized with serrated ridges (*sr*). The ventral surface of the apical region is smooth, and the tip is with tearing hooks (*th*).

Tetrisia florigera of Calpini (sensu Zaspel and Branham 2008). The surface of the proximal region is simple and smooth with diagonal semi-circular ribs. Some microtrichia are present. Several dorsoventrally flattened erectile barbs (*eb*) in depressions linked by endocuticula occur just below the junction of the ribbed and smooth areas of the apical region. The apical region is heavily sclerotized with serrated ridges present, originating from sockets of tearing hooks (*th*). The tip of the proboscis is long and sharp.

Phyllodes consobrina of Calpini (sensu Zaspel and Branham 2008). The surface of the proximal region (*pr*) of the proboscis is simple and smooth with diagonal circular or semi-circular ribs; depressions and cuticular processes are absent. Sensilla styloconica are modified into thin, highly flattened, tear-shaped erectile barbs (sensilla styloconica subtype 1, *eb*; Fig. 12a), without a distal cone. Other sensilla styloconica are modified into a smooth, flattened rectangular shape (subtype 2, *sss*₂), are abundant in the apical region of the proboscis, and are overlain along the lateral margin of the galea (Fig. 12a). The surface of the apical region is smooth, and the tip is with socketted tearing hooks and compressed furcate erectile barbs (*feb*) with asymmetrical edges. Sensilla basiconica are positioned throughout the tip of the proboscis and are located in the center of the smooth sensilla styloconica (subtype 2, *sss*₂), furcate erectile barbs, and tearing hooks (Fig. 12a, b). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are thin and triangular (Fig. 12a).

Calpine species *Calyptra canadensis*. The surface of the proximal region of the proboscis is simple and smooth with circular or semi-circular ribs (Fig. 12c, d); depressions and cuticular processes are absent. Sensilla styloconica are modified into dorsoventrally flattened, ovate erectile barbs

(*eb*), with a distinct distal cone (Fig. 12c, d). Individual erectile barbs are positioned in a single row along the lateral side of the proboscis and are positioned on ventrolateral sides in the apical region (Fig. 12c). Furcate erectile (*feb*) are present along the lateral margin of the dorsal galeal cross-linkage (Fig. 12e). The furcate erectile barbs are four-pronged and asymmetrical, consisting of two short and two long prongs, with a large sensory cone set in between (Fig. 12e). The surface of the apical region is smooth, and the tip is with tear-shaped, socketted tearing hooks (Fig. 12d). Sensilla basiconica are positioned throughout the tip of the proboscis, typically arranged in groups of two or three (Fig. 12d). Proximal and apical regions are without visible sensilla trichoidea. The legulae (*l*) of the dorsal galeal cross-linkage (*dgl*) are triangular and connected to elongate rasping spines which are oriented obliquely basally so as to become interlaced with the spines of the opposite side (Fig. 12d).

Character summary

From this comparative morphological study, a glossary of terms was generated and thirteen characters were defined. These characters and their distribution in our study taxa are described here. A cladistic analysis that includes these characters for a similar, but not identical, set of taxa is available elsewhere (Zaspel 2008b, Zaspel in prep.).

- (1) *Surface microstructure of proximal region of proboscis* (0) fluted; (1) simple and smooth.

The proximal proboscis surface can be characterized as fluted (Fig. 4a, e) for the non-piercing species included in the study (*Goniapteryx servia*, *Hypsoropha hormos*, and *Phyprosopus callitrichoides*). Piercing species of soft, thick, or hard-skinned fruits have a simple and smooth proximal proboscis region (e.g., Fig. 7a). Features of the proximal proboscis region tend to be modified repeatedly within Noctuoidea (Speidel et al. 1996). The fluted condition can be considered symplesiomorphic.

- (2) *Surface microstructure of proximal region of proboscis* (0) without circular ribs; (1) with circular ribs and longitudinal depressions; (2) with circular and semi-circular ribs but without longitudinal depressions; and (3) with semi-circular ribs and shallow longitudinal depressions.

Circular ribs are present in all taxa except for the tear-feeder *Lobocraspis griseifusa* (Fig. 11f). The putative tear feeder, *H. hieroglyphica*, has diagonal semi-circular ribs that terminate in lateral plates with shallow depressions (Fig. 11d). Non-piercing species *Goniapteryx servia*, *Hypsoropha hormos*, and *Phyprosopus callitrichoides* have cuticular ribs with longitudinal depressions (Fig. 4a),

although these ribs are faint in *H. hormos* (Fig. 4c). Piercing species possess circular and semi-circular ribs but lack longitudinal depressions (e.g., Figs. 5a, 6a); the ribs are diagonal in *Eudocima homaena* (e.g., Fig. 8a, b), *Ferenta castula*, *Graphogona regina*, *Tetrisis florigera*, and *Phyllodes consobrina*. Diagonal semi-circular ribs seem to be characteristic of species that pierce hard-skinned fruits (e.g., *Eudocima* spp.), but the distribution of this trait needs further examination.

- (3) *Circular ribs with cuticular processes* (0) absent; (1) present.

Cuticular processes are present in *Plusiodonta compressipalpus* (Fig. 7e) and *Tetrisia florigera* (proximal region only, not figured). Cuticular processes were absent in the other species examined.

- (4) *Surface microstructure of apical region of proboscis* (0) densely nodulose; (1) smooth.

The apical region of the proboscis is densely nodulose in non-piercing species (e.g., *Goniapteryx servia*, Fig. 4b) and one piercing species, *Anomis mesogona* (Fig. 6b). The apical region of the proboscis in *Phyprosopus callitrichoides* is sparsely nodulose but becomes more densely nodulose toward the tip (Fig. 4e, f). The nodulose condition is common within Noctuoidea (Speidel et al. 1996). Thus, this character can be considered symplesiomorphic for the taxa in this study.

- (5) *Apex of proboscis* (0) smooth; (1) nodulose; (2) serrate; (3) heterogeneous, both smooth and nodulose.

This character refers to the condition of the proboscis tip. In non-piercing taxa, the apex is nodulose (Fig. 4a–f). The proboscis apices in piercing species are variable, but some general trends can be discerned. The soft-skinned fruit piercer *Scoliopteryx libatrix* has a proboscis tip with both smooth and nodulose regions (Fig. 5b). *Anomis mesogona*, commonly a piercer of soft-skinned fruit but also thick-skinned fruits has a nodulose proboscis apex (Fig. 6b). The remaining taxa in the category of “piercers of thick-skinned fruits” have a smooth proboscis tip (e.g., *Calyptra lata*, Fig. 6c). *Eudocima homaena* has a serrate proboscis apex (Fig. 8a); the serrate condition is also present in some of the species with unknown feeding behaviors (e.g., *Ferenta castula* and *Graphigona regina*, not figured). The proboscis apex of *H. hieroglyphica* has sclerotized ridges, but lacks serrations (Fig. 11c).

- (6) *Nodules near the dorsal galeal cross-linkage* (0) contiguous; (1) well-defined by septa.

In taxa with nodules near the galeal cross-linkage, some nodules are clearly separated by septa (e.g., *Phyprosopus callitrichoides*; Fig. 4f) while in other taxa, nodules appear

contiguous (e.g., *Anomis mesogona*; Fig. 6b). In *Hypsoropha hormos*, the apical nodules are more defined with septa toward the proboscis apex (Fig. 4c).

- (7) *Erectile barbs occurring along exterior lateral margin of proboscis* (0) absent; (1) present.

Erectile barbs are modified sensilla styloconica that possess an apical cone. These structures are present in piercing taxa including those that commonly pierce soft-skinned fruits (*Scoliopteryx libatrix* and *Anomis mesogona*, Figs. 5b, 6b). Erectile barbs are typically abundant in the apical region and can be found on both lateral and ventrolateral sides. The lack of erectile barbs is the symplesiomorphic condition. Erectile barbs are also present in the included species with unknown feeding behaviors.

- (8) *Furcate erectile barbs* (0) absent; (1) present, symmetrical; (2) present, asymmetrical.

Furcate erectile barbs are restricted to piercing taxa. They vary in their distribution and shape. For example, in *Scoliopteryx libatrix*, the barbs are a long, triangular shape and some bifurcate distally (Fig. 5b). In *Anomis mesogona*, some secondary bifurcations are also present (Fig. 6a, b). In *Oraesia serpens*, the barbs are asymmetrical (Fig. 7c) but are of two symmetrical types in *Hemiceratoides hieroglyphica* (Fig. 11d). Furcated erectile barbs may be diagnostic at the generic level. Furcate erectile barbs were absent or not visible in the species of *Gonodonta*, *Plusiodonta*, and *Eudocima* examined.

- (9) *Rasping spines occurring along lateral margin of proboscis* (0) absent; (1) present.

Rasping spines are absent in all non-piercing “calpines” yet are common in piercing moths regardless of host (plant or animal). These structures can be cylindrical as in *Calyptra lata* (Fig. 6c) or dorsoventrally flattened as in *Oraesia serpens* (Fig. 7c) and *Phyllodes consobrina* (Fig. 12a). A broader taxon sampling is needed to determine the phylogenetic usefulness of this character.

- (10) *Two or three rasping spines below junction of ribbed and smooth region of apical region of the proboscis* (0) absent; (1) present.

This character was found in *Eudocima* spp. and also species of unknown feeding habits (*F. castula*, *G. regina*, and *T. florigera*). This character could be a synapomorphy uniting the species of *Eudocima* or a larger clade of *Eudocima*, *Ferenta*, *Graphigona*, and *Tetrisia*.

- (11) *Shape of dorsal legulae* (0) flattened and triangular; (1) conical; (2) forked and triangular; (3) spike like; (4) curved and triangular; (5) rectangular.

Dorsal legulae exhibit considerable morphological variation. In the non-piercing *Goniapteryx servia* and *Phyprosopus callitrichoides*, the dorsal legulae are triangular (Fig. 4b, e) and are triangular and flattened in *Oraesia serpens* (Fig. 7c). Dorsal legulae are rectangular in *Hypsoropha hormos* (Fig. 4c) and conical in *Gonodonta nutrix* (Fig. 7b). In species of *Eudocima*, the dorsal legulae are long and spike like (Fig. 8b). *Calyptra* spp. have triangular legulae that end in elongate rasping spines (Fig. 9b). Shape of legulae may be synapomorphic for the groups of species or define genera.

- (12) *Tearing hooks in the apical region of the proboscis* (0) absent; (1) present.

Tearing hooks are absent in the non-piercing groups included in this survey (e.g., *Hypsoropha hormos*, Fig. 4c). Tearing hooks are present in some, but not all piercing taxa included in the study. *Scoliopteryx libatrix* and *Anomis mesogona* lack tearing hooks (Figs. 5a, 6b). The remaining taxa have tearing hooks. The shape of the hooks can vary among congeneric species (compare Figs. 9c, 10c). The presence of tearing hooks is an apomorphy for the tribe Calpini (sensu Zaspel and Branham 2008).

- (13) *Tearing hooks with basiconic sensilla* (0) absent; (1) present.

This condition is represented by *Phyllodes consobrina*. SEM is required to assess whether the basiconic sensilla are present, and further study is needed to determine their function.

Discussion

Proboscides diversity and homology assessment

This survey is the first to describe the diversity of proboscis structures in species of Calpinae with a focus on the facultatively hematophagous *Calyptra* species. The resulting glossary documents terms for these structures, typically sensory structures, and their commonly assumed function. These homology assessments were used to generate character descriptions and codings for use in phylogenetic analyses.

We examined whether one technology was biased or inconsistent. The survey includes a number of light microscopy and SEM images of the same species such that a direct comparison of the two techniques is facilitated. In general, light microscopy is adequate for documenting the presence and type of armature present on a proboscis; however, the presence and details of the sensilla (distal cone present or absent) and other microstructures are difficult to ascertain without SEM images to confirm. SEM

dehydration results in distortion of relative positions that precludes its use for any character coding involving relative distance metrics.

Reassessment of *H. hieroglyphica* proboscis morphology

This survey indicates that the tear-shaped, tearing hooks of the proboscis are likely restricted to Calpini (sensu Zaspel and Branham 2008), although non-, triangular hooks were found in *H. hieroglyphica*. Other details of the proboscides of species of *Calyptra* and *H. hieroglyphica* differ, especially the placement and shape of the furcated erectile barbs. Scanning electron micrographs (SEM) of the proboscis of *H. hieroglyphica* clearly depicts numerous strong differences in microstructure when compared to those the SEMs of typical the tear-feeding moths (Büttiker et al. 1996; this report Figs. 11, 12); the armature is similar to that found in piercing proboscides. Although *H. hieroglyphica* possess modifications of the proboscis similar to those found in fruit-piercing moths, its proboscis differs in that the sensilla basiconica are modified into hooks fused to the proboscis, and the sensilla styloconica are modified into fixed erectile barbs; both are not movable by blood pressure. Placement of this species in Calpini based on its mouthparts is not supported by our data; other morphological data will be needed to maintain its assignment to the subfamily Calpinae.

Given that the placement of *H. hieroglyphica* in Calpini is unsupported, and its placement in Calpinae is suspect, the assertion that blood feeding arose from tear feeding (Hilgartner et al. 2007) needs to be re-examined. Lachrymal fluid feeding occurs in at least seven lepidopteran families: Erebidae, Geometridae, Notodontidae, Noctuidae, Pyralidae, Sphingidae, and Thyatiridae (Fig. 11; *Lobocraspis griseifusa* at batend eye: Bänziger 1972, 1992; Büttiker 1973; Büttiker et al. 1996; Norris 1935). Despite their modified behavior, tear feeders essentially imbibe fluid from a pool of liquid—not unlike puddling Lepidoptera, for which little morphological adaptation is required. The relatively unornamented proboscis of *Lobocraspis griseifusa* supports this hypothesis. Given that tear-feeding behavior is found in females as well as males (whereas only males are hematophagous), several other reservations (see Bänziger 2007), and the lack of a close evolutionary relationship, the tear to blood-feeding pathway does not seem likely. Our survey does suggest that the proboscis morphology of lachryphagous moths needs reassessment.

Proboscides morphology and feeding behaviors

Our study supports Bänziger (1982) contention that mouthpart structure alone is not sufficiently indicative of

what fruit type a moth will or can pierce, but that it “nevertheless provides important clues.” A comparison of *Eudocima* spp. and the three species with unknown behaviors (*F. castula*, *G. regina*, *T. florigera*) results in the prediction that these species should be capable of piercing hard-skinned fruits (Category C morphology) because they possess the serrated edged proboscides, reinforced tearing hooks and heavily sclerotized, lance-like apical area.

In contrast, it is more difficult to predict definitively whether a moth pierces thin-skinned (group A2) or thick-skinned fruits (group B) and whether moths are facultative hematophages (group D). A comparison of the proboscides of representatives of our feeding groups A2 (thin-skinned fruits), B (thick-skinned fruits) and D (mammal skin) feeding types reveals that the one major difference between group A2 and B is that group B species possess tearing hooks whereas group A2 species do not. No differences exist between groups B and D—that is, there are no specialized structures on the proboscides of male hematophagous species of *Calyptra*. In all three feeding groups, variation occurs in the type of ornamentation and their placement on the proboscis (presence of sensilla trichodea, sensilla basiconica, and sensilla styloconica). Also, the presence or absence of the distal cone of sensilla styloconica appears to be species specific among our B and D group species. Whether these microstructural differences have biological relevance will need to be examined further.

In general, our survey results refute the assertions of Buttiker et al. (1996) that feeding behavior can be deduced directly from observations of morphology. Some piercing noctuid taxa not included in the survey such as species of *Ercheia*, *Pericyma*, and *Serrododes* have proboscis armatures that are in some respects superficially similar to Calpinae (Hattori 1969). In contrast, others [e.g., *Facidina suffumata* Guenée 1852, *Saroba albopunctata* (Semper, 1901), and species of *Platyja*] lack “normal armature (teeth, hooks, barbs, serrations, and ridges)” altogether but pierce with a pointed, fully sclerotized terminal section of the proboscis (Bänziger 1982). Clearly, adult fruit-piercing and lachryphagous behaviors have evolved multiple times within Noctuoidea and Lepidoptera, more generally. We conclude that proboscis morphology when carefully examined provides powerful prediction, but not proof of lepidopteran adult food habits.

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