

# Comparative morphology of the larval mouthparts among six species of Notodontidae (Insecta, Lepidoptera), with discussions on their feeding habits and pupation sites

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## Abstract

Larval mouthparts are significant organs for the individual development, morphologically related with feeding habits, and providing valuable characters for taxonomy and phylogenetic analysis. In previous studies, larval mouthparts revealed two identifying characters of Notodontidae. However, the evolutionary driving force and exact definition of these structures remain unsatisfactory. In this study, the larval mouthparts of *Euhampsonia cristata* (Butler, 1877), *Fentonia ocypte* (Bremer, 1861), *Phalera assimilis* (Bremer & Grey, 1853), *Nerice davidi* Oberthür, 1881, *Cerura erminea* (Esper, 1783) and *Furcula furcula* (Clerck, 1759) are morphologically observed and compared using scanning electron microscopy (SEM). The larval mouthparts of the six species are commonly equipped with paired maxillary sacs, congruent with the previous descriptions. However, the larval mouthparts of *N. davidi* are peculiar for bearing toothed mandibles, providing an exception of Notodontidae. Otherwise, the mouthparts exhibit morphological differences on mandibles, spinnerets, labral notches, and setal arrangements among the six species. The morphological diversity and the related feeding and pupation habits are briefly discussed.

## Key Words

labral notch, mandible, maxillary sac, sensillum, spinneret

## Introduction

Larvae, the juveniles of holometabolous insects, are considered feeding devices that turn smaller embryos into larger individuals (Hart and Strathmann 1995). With respect to Lepidoptera, the larvae mainly feed on plant organs and are able to cause great losses to agriculture and forestry (van Emden 1957; Zacharuk and Shields 1991), or produce silk as a fiber resource for our textile industry (Stehr 1987; Wagner 2005). In fact, both of plant attacking and silk producing processes are inevitably undertaken by their feeding apparatus, which are commonly called mouthparts (Chapman 2013; Tong et al. 2021; Zhang et al. 2022).

Larval mouthparts are generally of the mandibulate type, representing a ground plan of biting and chewing mechanisms in insects (Chapman and de Boer 1995).

Mouthparts are usually structurally associated with feeding habits (Stehr 1987; Smith and Capinera 2005) and morphologically diverse among insect lineages (Grebennikov and Scholtz 2004; Beutel et al. 2008; Neugart et al. 2009; Beutel et al. 2010; Jiang and Hua 2015). Mouthpart characters have been utilized in previous phylogenetic analyses (McCabe 1988; Godfrey et al. 1989; Miller 1991). However, the detailed morphological comparisons are far less satisfactory in previous studies, especially in Notodontidae.

Notodontidae represent a large family of Lepidoptera, comprising approximately 3800 recognized species assigned to 734 genera across the world (Pan 2008; Schintlmeister 2013). Adults of Notodontidae are usually called trifold noctuid moths and are frequently considered serious pests because some of their larvae attack the leaves of

fruit trees. Larvae of Notodontidae are commonly called prominents for their remarkably larger head capsules and noticeably modified anal prolegs (Wagner 2005). Previously, larvae of Notodontidae were reported to be identified by two mouthpart modifications, which are shared by 154 species in 90 genera of Notodontidae (Godfrey et al. 1989). Later, counter-examples on mandibles were also discovered in two species of *Nerice* (Dolinskaya 2008). However, “Why these mandibles become morphologically different during development?” and “What exactly the stipital lobes really are?” still remain unanswered hitherto.

In this study, larval mouthparts of *Euhampsonia cristata* (Butler, 1877), *Fentonia ocypte* (Bremer, 1861), *Phalera assimilis* (Bremer & Grey, 1853), *Nerice davidi* Oberthür, 1881, *Cerura erminea* (Esper, 1783), *Furcula furcula* (Clerck, 1759) are morphologically observed and compared using scanning electron microscopy, in order to discover more morphological characters for larval taxonomy.

## Materials and methods

The female adults were collected under light traps, with the detailed collection information listed in Table 1. Fertilized eggs were obtained from a wild-captured female, confined in a paper box, at room temperature ( $26 \pm 1$  °C). The eggs were kept in plastic boxes with wet absorbent cotton to keep humidity. After emergence, the larvae were fed with fresh leaves of the specific host plant (Table 2). Photographs were taken with a Nikon D810 digital camera (Nikon, Tokyo, Japan). Voucher specimens were kept at the Entomological Museum of Shenyang Agricultural University (SYAU).

For scanning electron microscopy, the final instar larvae were fixed in Dietrich's solution (formalin: 95% ethanol: glacial acetic acid: distilled water = 6: 15: 1: 80, v/v), which was heated up to 70 °C and boiled for 1 min then left to stand for 12 h under hood before being preserved in 75% ethanol (Jiang and Hua 2015). Five individuals of each species were dissected under a Leica EZ4HD Stereoscopic Zoom Microscope, serially dehydrated in a graded ethanol, replaced by tertiary butanol, freeze-drying for 3 h, spotter-coated with gold, before examined under a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan) at 5 kV.

## Results

### Feeding habits and pupation sites

The larvae are all herbivorous, feeding on leaves of peculiar host plants (Table 2). The larvae of *E. cristata*, *F. ocypte*, *P. assimilis* feed on *Quercus mongolica* (Fig. 1A–C), while those of *N. davidi* feed on *U. pumila* (Fig. 1D), and the larvae of *C. erminea* and *F. furcula* feed on *Populus* sp. (Fig. 1E, F).

All first instar larvae prefer to chew on the ventral surface of host leaves, while the mature larvae usually bite

**Table 1.** Sample information of the larvae of Notodontidae.

Species	Localities	Dates
<i>Euhampsonia cristata</i> (Butler, 1877)	Sankuaishi Mountain (41°36'N, 124°16'E)	vii-30-2019
<i>Fentonia ocypte</i> (Bremer, 1861)	Sankuaishi Mountain (41°36'N, 124°16'E)	vii-30-2019
<i>Phalera assimilis</i> (Bremer & Grey, 1853)	Guanmen Mountain (40°49'N, 123°34'E)	vii-8-2019
<i>Nerice davidi</i> Oberthür, 1881	Houshi Mountain (41°40'N, 124°26'E)	vii-21-2020
<i>Cerura erminea</i> (Esper, 1783)	Hehuogou Mountain (41°11'N, 123°15'E)	viii-6-2020
<i>Furcula furcula</i> (Clerck, 1759)	Shenyang Agricultural University (40°48'N, 123°33'E)	viii-5-2021

on the edge of leaves (Fig. 1). The larvae of *P. assimilis* live gregariously, whereas the larvae of the other five species are solitary. The mature larvae usually hold on the twigs and leaves, and bite on the leaf edge (Fig. 1A–C).

When fully grown, the larvae stop feeding, build a cocoon and finally step into a prepupal period. The sites of pupation and ways of cocoon spinning varied significantly among the six species. The mature larvae of *E. cristata*, *F. ocypte*, *N. davidi* and *P. assimilis* usually build cocoons in soil. The larvae of *C. erminea* and *F. furcula* secrete a thickened cocoon covering the bark.

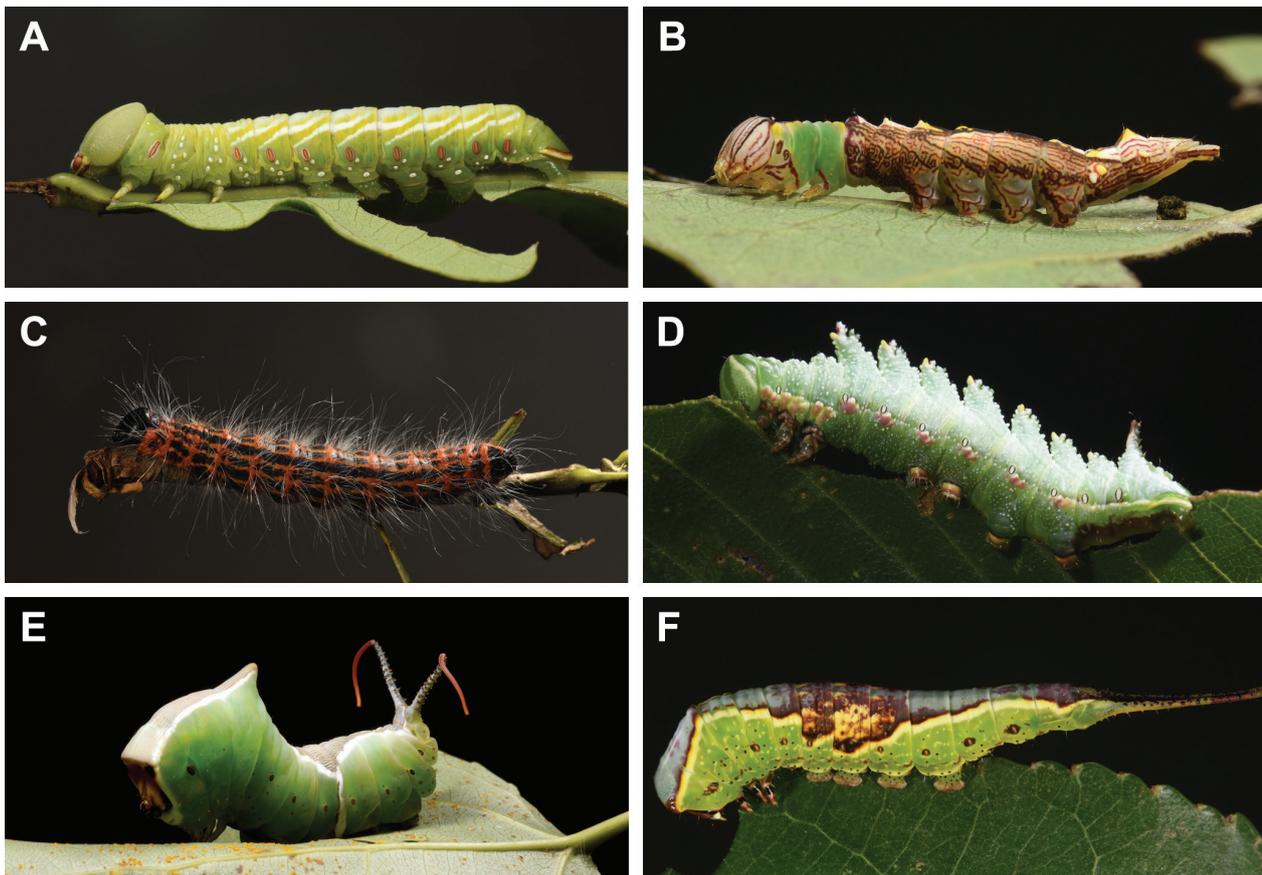
### Larval mouthparts of *Euhampsonia cristata* (Butler, 1877)

The mouthparts are of the mandibulate type, consisting of a labrum, a pair of mandibles, and a maxilla-labial complex (Fig. 2A–G).

The labrum is V-shaped, possessing six pairs of setae: three pairs of medial setae (MS1, MS2, MS3) and three pairs of lateral setae (LS1, LS2, LS3). Two lateral setae (LS1, LS2) are significantly longer than the mesal setae. The epipharynx is furnished with three pairs of sensilla chaetica (SC1, SC2, SC3) and a digitiform sensillum at the lateral area (Fig. 2B).

The paired mandibles are heavily sclerotized, almost spherical each with a smooth cutting edge but without incisor cusps (Fig. 2C–E). Each mandible bears two long setae on the external surface.

The maxilla-labial complex consists of paired maxillae, a pair of labial palps, and a spinneret (Fig. 2F, G). Each maxilla is composed of a cardo, stipes, galea, maxillae sac and a two-segmented maxillary palp. The cardo bears two long setae. The stipes bears a sensillum chaeticum. The maxilla is remarkably equipped with a protuberant maxillary sac on the inner surface of the galea (Fig. 2F). The labial palp is furnished with a prominent sensillum styloconicum and a short sensillum chaeticum (Fig. 2G). The spinneret is situated between the bases of the labial palps and is generally tubular, gradually tapering towards the apex, and longitudinally depressed on the dorsal surface of the distal end (Fig. 2G). The role of the spinneret is to release the silk secreted by the larval silk glands.



**Figure 1.** The mature larvae in habitus of the six species in Notodontidae. **A.** *Euhampsonia cristata*; **B.** *Fentonia ocypete*; **C.** *Phalera assimilis*; **D.** *Nerice davidi*; **E.** *Cerura erminea*; **F.** *Furcula furcula*.

#### Larval mouthparts of *Fentonia ocypete* (Bremer, 1861)

The larval mouthparts of *F. ocypete* are morphologically remarkable for the shape and setae of the labrum, the sensilla on the epipharynx, and the structure of the spinneret (Fig. 3A–G).

The labrum is longitudinally split, with a pair of lateral lobes overlapped in the middle (Fig. 3A). The labrum possesses six pairs of setae: three pairs of medial setae (MS1, MS2, MS3) and three pairs of lateral setae (LS1, LS2, LS3). The mesal setae (MS1) are located at the base, and the lateral setae (LS1, LS2) are more prominent than the mesal setae. The epipharynx possesses two pairs of sensilla chaetica similar in length (SC1, SC2). The epipharynx is also furnished with a semispherical sensillum digitiformium on the lateral area and an epipharyngeal sensillum at the basal part (Fig. 3B).

The paired mandibles have a smooth cutting edge and a ridge on the inner side (Fig. 3C–E). Each mandible bears two long setae situated on the basal part of the outer surface.

The maxilla-labial complex is morphologically similar to those of *E. cristata* (Fig. 3F, G) with paired maxillae, a pair of labial palps, except for the structure of spinneret (Fig. 3G). The spinneret is dorsal-ventrally depressed, with the distal opening slightly separated (Fig. 3G).

#### Larval mouthparts of *Phalera assimilis* (Bremer & Grey, 1853)

The mouthparts of *P. assimilis* are morphologically similar to those of *E. cristata* except for the detailed characters on epipharynx, mandibles and spinneret (Fig. 4A–G).

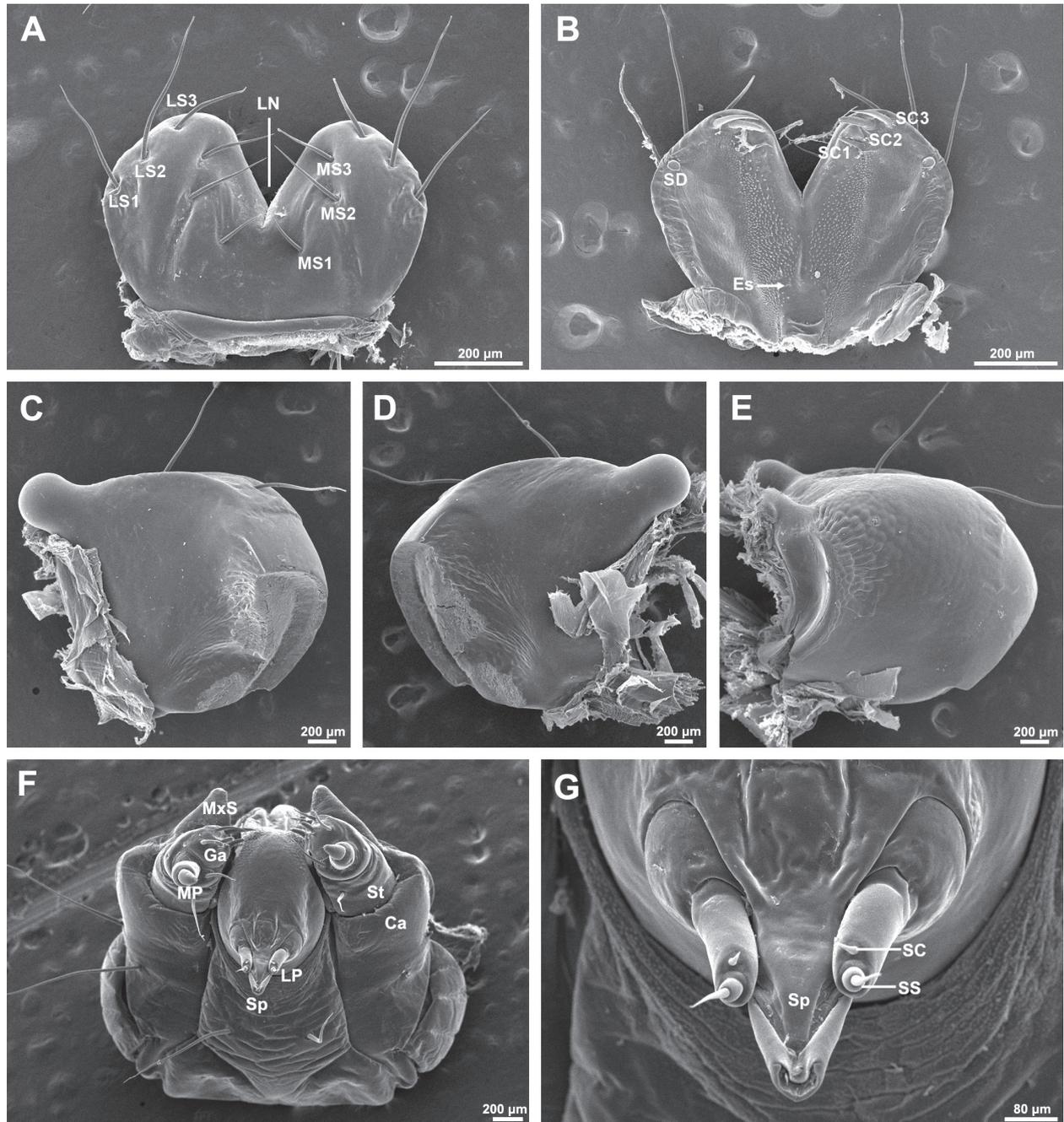
The labrum is V-shaped and bears six pairs of setae, with LS1 and LS2 slightly longer than the others (Fig. 4A). The epipharynx is equipped with three sensilla chaetica along the mesal notch (SC1, SC2, SC3), a sensillum digitiformium at the lateral margin (SD), and an epipharyngeal sensillum arranged on the central region (Fig. 4B).

The paired mandibles also have a smooth cutting edge and a ridge on the inner side (Fig. 4C–E). Each mandible also bears two long setae situated on the external surface.

The maxillary sac is also elongate and hirsute (Fig. 4F). The spinneret is comparative short, with the distal opening dorsal-ventrally depressed (Fig. 4G).

#### Larval mouthparts of *Nerice davidi* Oberthür, 1881

The mouthparts of *N. davidi* differ significantly from those of the other species in terms of the shape of the labrum, setal length, sensilla on the epipharynx, structure of the spinneret (Fig. 5A–G), and especially the teeth on the mandibles.



**Figure 2.** Larval mouthparts of *Euhampsonia cristata* (Butler, 1877). **A.** Labrum; **B.** Epipharynx; **C.** Left mandible, inner view; **D.** Right mandible, inner view; **E.** Left mandible external view; **F.** Maxilla-labial complex; **G.** Magnification of the spinneret. **Ca**, cardo; **Es**, epipharyngeal sensillum; **Ga**, galea; **LN**, labral notch; **LP**, labial palp; **LS1–3**, lateral seta; **MS1–3**, median seta; **MP**, maxillary palp; **MxS**, maxillary sac; **SC**, sensillum chaeticum; **SD**, sensillum digitiformium; **SS**, sensillum styloconicum; **Sp**, spinneret; **St**, stipes.

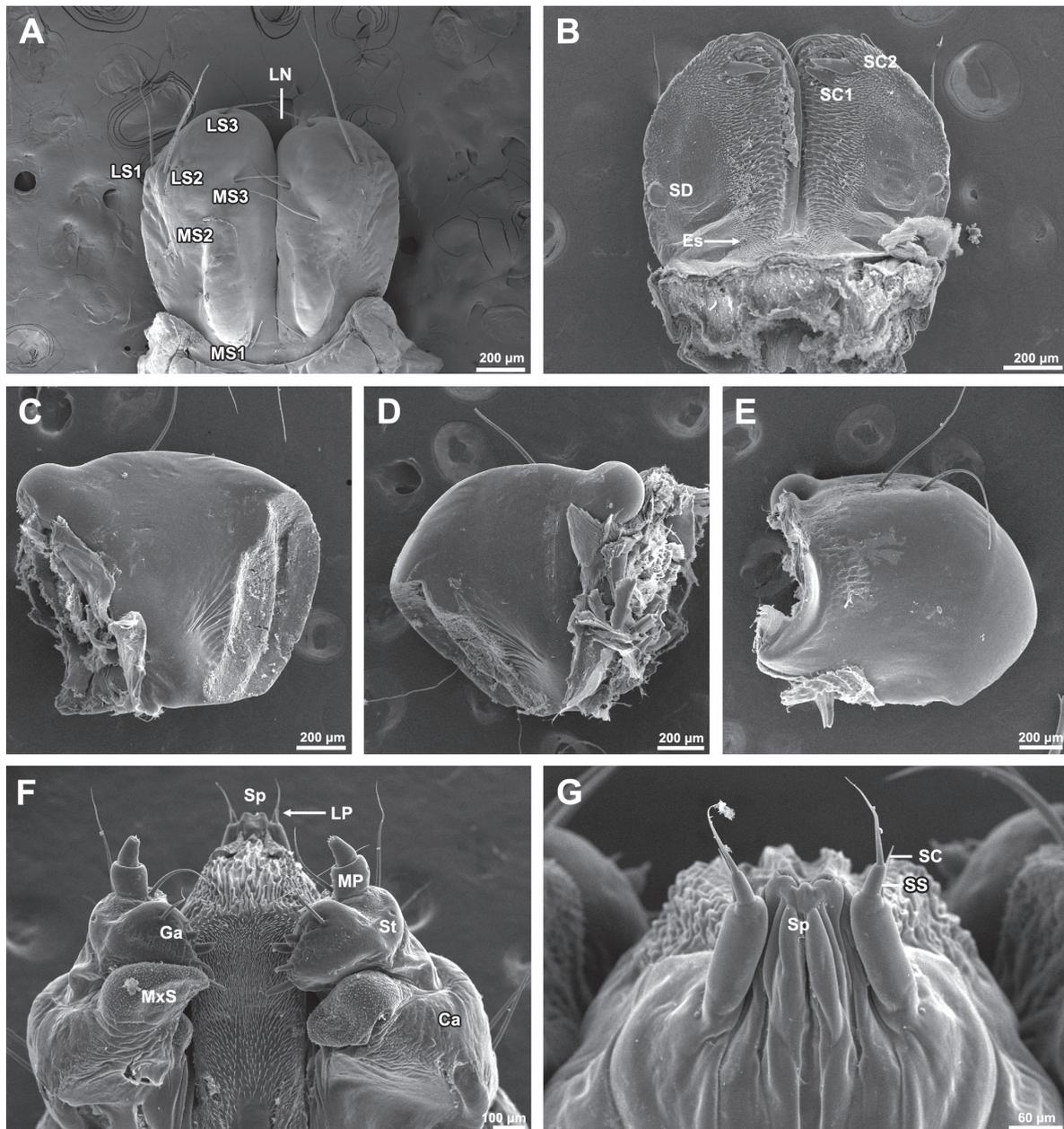
The labrum is equipped with a shallow notch, which is not extended to the center (Fig. 5A). The labrum also possesses six pairs of setae with LS2 slightly longer than others. The epipharynx bears three pairs of sensilla chaetica (SC1, SC2, SC3) on each ventrolateral margin, a sensillum digitiformium along the lateral margin, and an epipharyngeal sensillum in the central area (Fig. 5B).

The paired mandibles are heavily sclerotized and peculiar for bearing six blunt dentitions (T1–T6) on the distal margin (Fig. 5C–E). Each mandible bears two prominent setae on the external surface.

The maxilla-labial complex also has a pair of maxillary sacs (Fig. 5F). The labial palp has a sensillum styloconicum and a sensillum chaeticum that are generally similar in length (Fig. 5G). The spinneret situated between the bases of the labial palps is dorsal-ventrally depressed (Fig. 5G).

#### Larval mouthparts of *Cerura erminea* (Esper, 1783)

The mouthparts of *C. erminea* are morphologically similar to those of *E. cristata* with the exception of the setal



**Figure 3.** Larval mouthparts of *Fentonia ocypete* (Bremer, 1861). **A.** Labrum; **B.** Epipharynx; **C.** Left mandible, inner view; **D.** Right mandible, inner view; **E.** Left mandible external view; **F.** Maxilla-labial complex; **G.** Magnification of the spinneret. **Ca**, cardo; **Es**, epipharyngeal sensillum; **Ga**, galea; **LN**, labral notch; **LP**, labial palp; **LS1–3**, lateral seta; **MS1–2**; median seta; **MP**, maxillary palp; **MxS**, maxillary sac; **SC**, sensillum chaeticum; **SD**, sensillum digitiformum; **SS**, sensillum styloconicum; **Sp**, spinneret; **St**, stipes.

length, sensilla on the epipharynx, and the structure of the spinneret (Fig. 6A–G).

The labrum is furnished with a longitudinal notch in the middle (Fig. 6A) and six pairs of setae on the external surface. The lateral setae (LS2) and mesal setae (MS2) are slightly longer than the others. The epipharynx bears three sensilla chaetica (SC1, SC2, SC3), which are gradually shorter from distal pairs to basal pairs. The epipharynx is also equipped with a small sensillum digitiformum and an epipharyngeal sensillum (Fig. 6B).

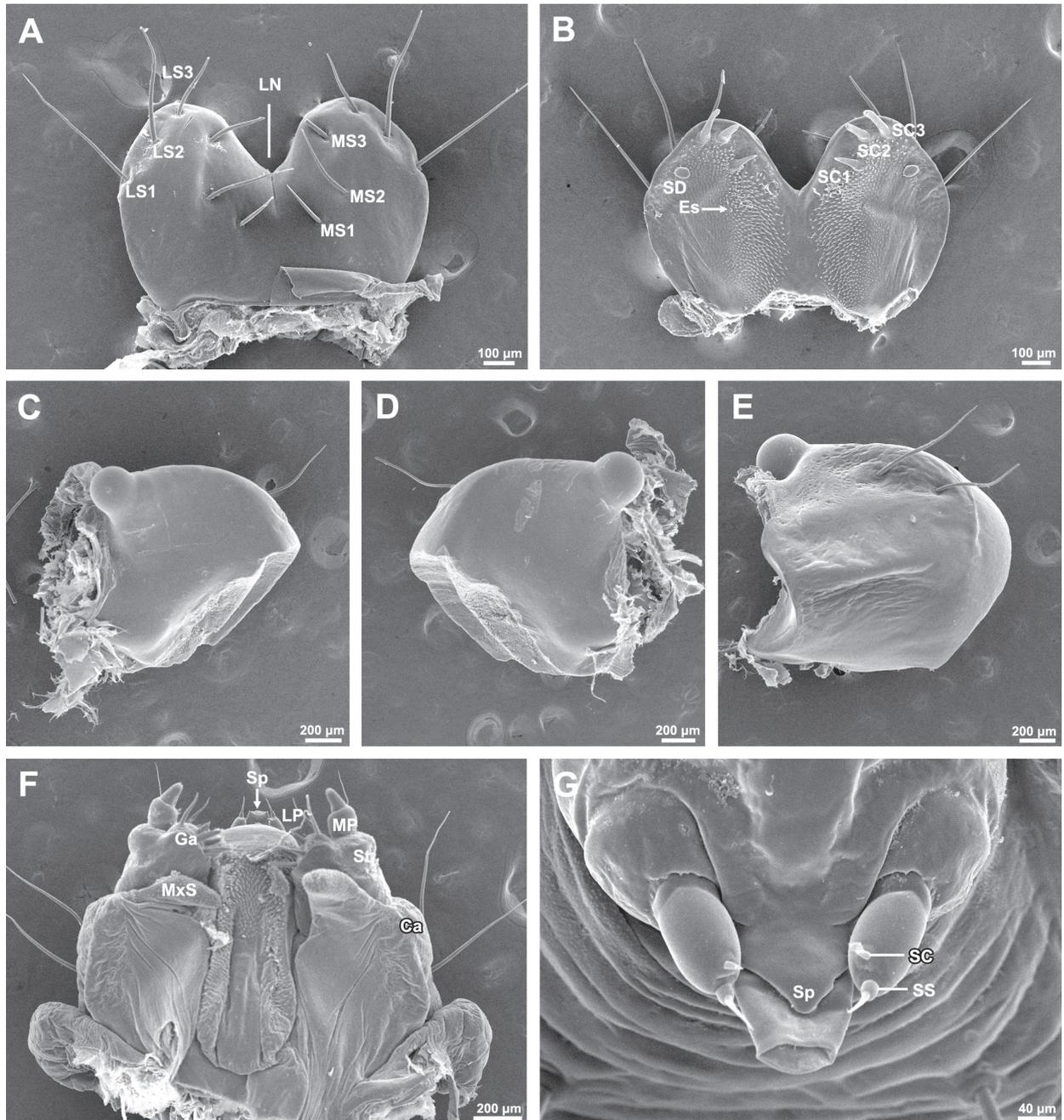
The paired mandibles are heavily sclerotized and furnished with a smooth cutting edge (Fig. 6C–E). Each mandible also bears two prominent setae on the exterior surface.

The maxillary sacs are certified to be hollow and occasionally cut open (Fig. 6F). The spinneret is short, dorsal-ventrally depressed, with the distal opening widely separated (Fig. 6G).

#### Larval mouthparts of *Furcula furcula* (Clerck, 1759)

The mouthparts of *F. furcula* are morphologically similar to those of *C. erminea* with the structure of spinneret (Fig. 7A–G).

The labrum is V-shaped and furnished with six pairs of setae, with the medial setae (MS1, MS3) noticeably



**Figure 4.** Larval mouthparts of *Phalera assimilis* (Bremer & Grey, 1853). **A.** Labrum; **B.** Epipharynx; **C.** Left mandible, inner view; **D.** Right mandible, inner view; **E.** Left mandible external view; **F.** Maxilla-labial complex; **G.** Magnification of the spinneret. **Ca**, cardo; **Es**, epipharyngeal sensillum; **Ga**, galea; **LN**, labral notch; **LP**, labial palp; **LS1–3**, lateral seta; **MS1–3**; median seta; **MP**, maxillary palp; **MxS**, maxillary sac; **SC**, sensillum chaeticum; **SD**, sensillum digitiformum; **SS**, sensillum styloconicum; **Sp**, spinneret; **St**, stipes.

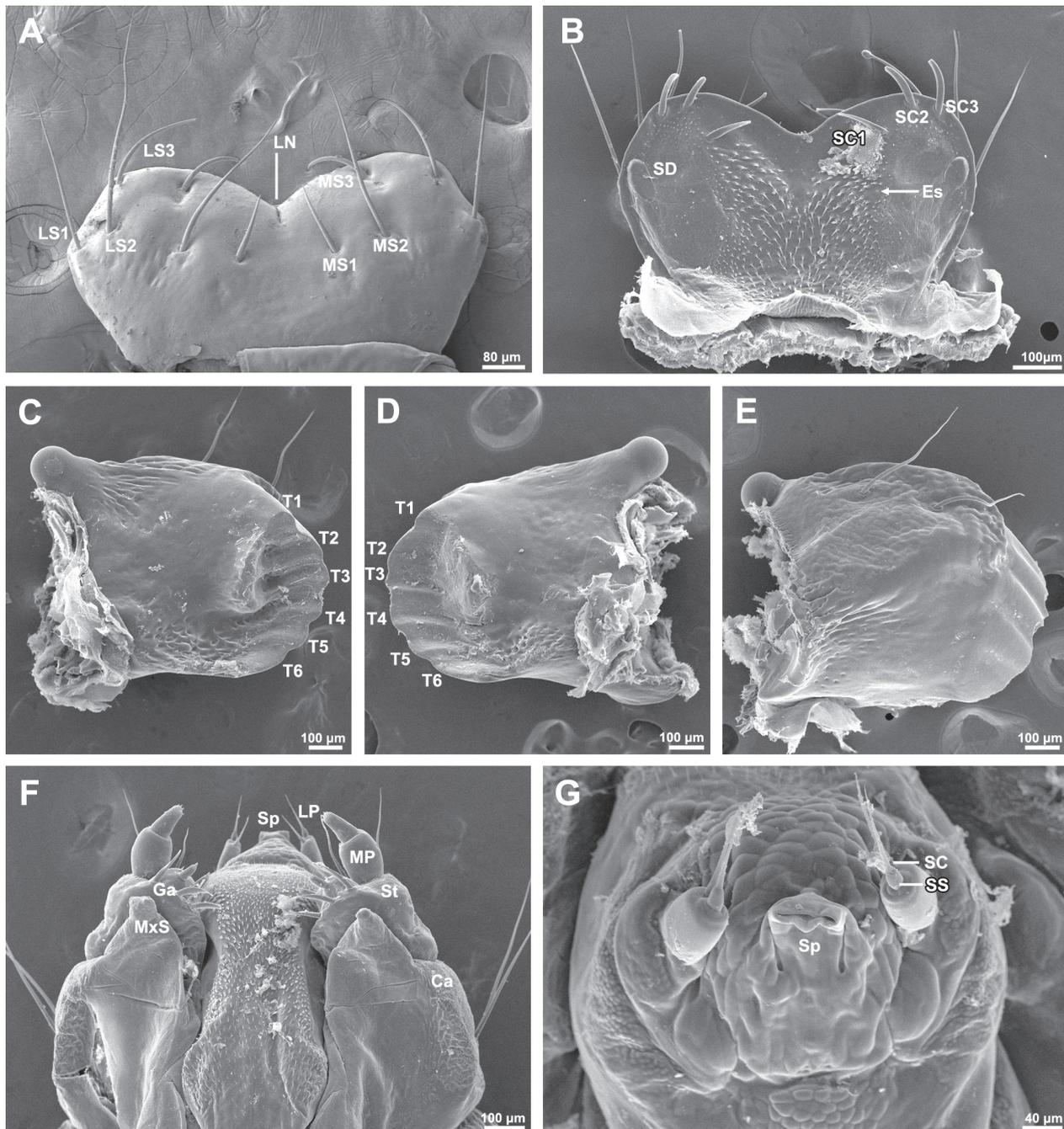
shorter than the others (LS1, LS2, LS3, MS2). The epipharynx also possesses three pairs of sensilla chaetica (SC1, SC2, SC3), all of which are similar in length. A digitiform and an epipharyngeal sensillum are present at the lateral margin and central region. (Fig. 7B).

The paired mandibles are heavily sclerotized, with a smooth cutting edge and two long setae on the external surface of each mandible (Fig. 7C–E).

The maxilla-labial complex also has a pair of maxillary sacs (Fig. 7F). The spinneret is unique and different from others, it is lamellar and broad-flat. (Fig. 7G).

## Discussion

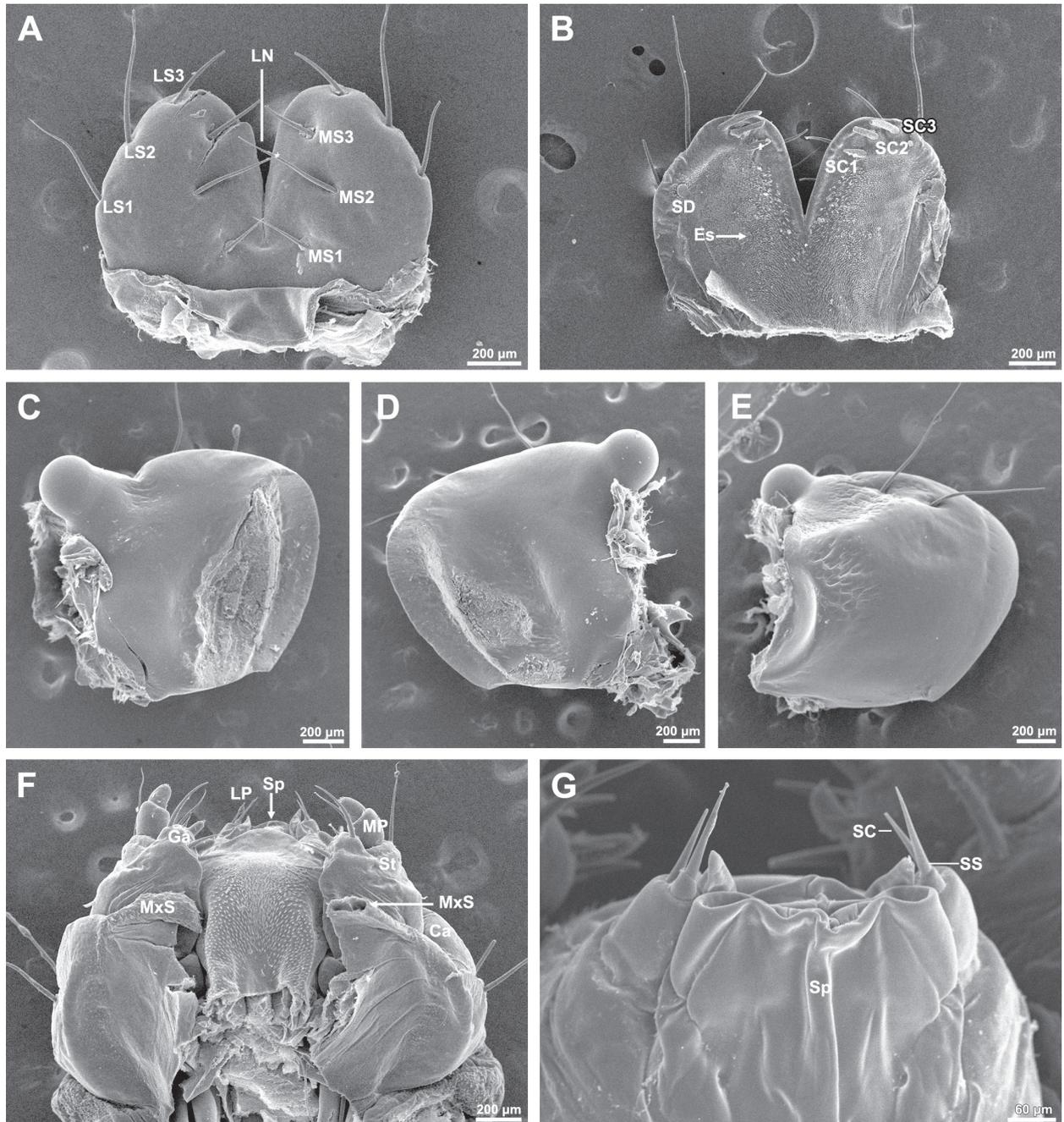
Mouthpart apparatuses of the final instar larvae of *E. cristata*, *F. ocypete*, *P. assimilis*, *N. davidi*, *C. erminea*, and *F. furcula* were morphologically compared for the first time, using scanning electron microscopy. Based on our morphological comparison, the larval maxillary sac is confirmed to be shared by all the six species. The labral notches, setal arrangements, and spinnerets exhibit morphological diversity among the six species. The toothed mandibles were also confirmed in the mature larvae of *N. davidi*.



**Figure 5.** Larval mouthparts of *Nerice davidi* Oberthür, 1881. **A.** Labrum; **B.** Epipharynx; **C.** Left mandible, inner view; **D.** Right mandible, inner view; **E.** Left mandible external view; **F.** Maxilla-labial complex; **G.** Magnification of the spinneret. **Ca**, cardo; **Es**, epipharyngeal sensillum; **Ga**, galea; **LN**, labral notch; **LP**, labial palp; **LS1–3**, lateral seta; **MS1–3**, median seta; **MP**, maxillary palp; **MxS**, maxillary sac; **SC**, sensillum chaeticum; **SD**, sensillum digitiformium; **SS**, sensillum styloconicum; **Sp**, spinneret; **St**, stipes; **T1–6**, tooth.

Mandibles, the essential components of mandibulate mouthparts, varied morphologically among lineages that have diverse feeding habits (Chapman and de Boer 1995; Chapman 2013). The mandibles usually possess sharp apical cusps in predacious larvae (Michat 2010; Lawrence et al. 2011; Cao and Liu 2013), or bear morphologically diverse molar regions for filtering or grinding in saprophagous larvae (Jiang and Hua 2015). With respect to the phytophagous larvae, the mandibles are equipped with smooth cutting edges in the leaf-feeding

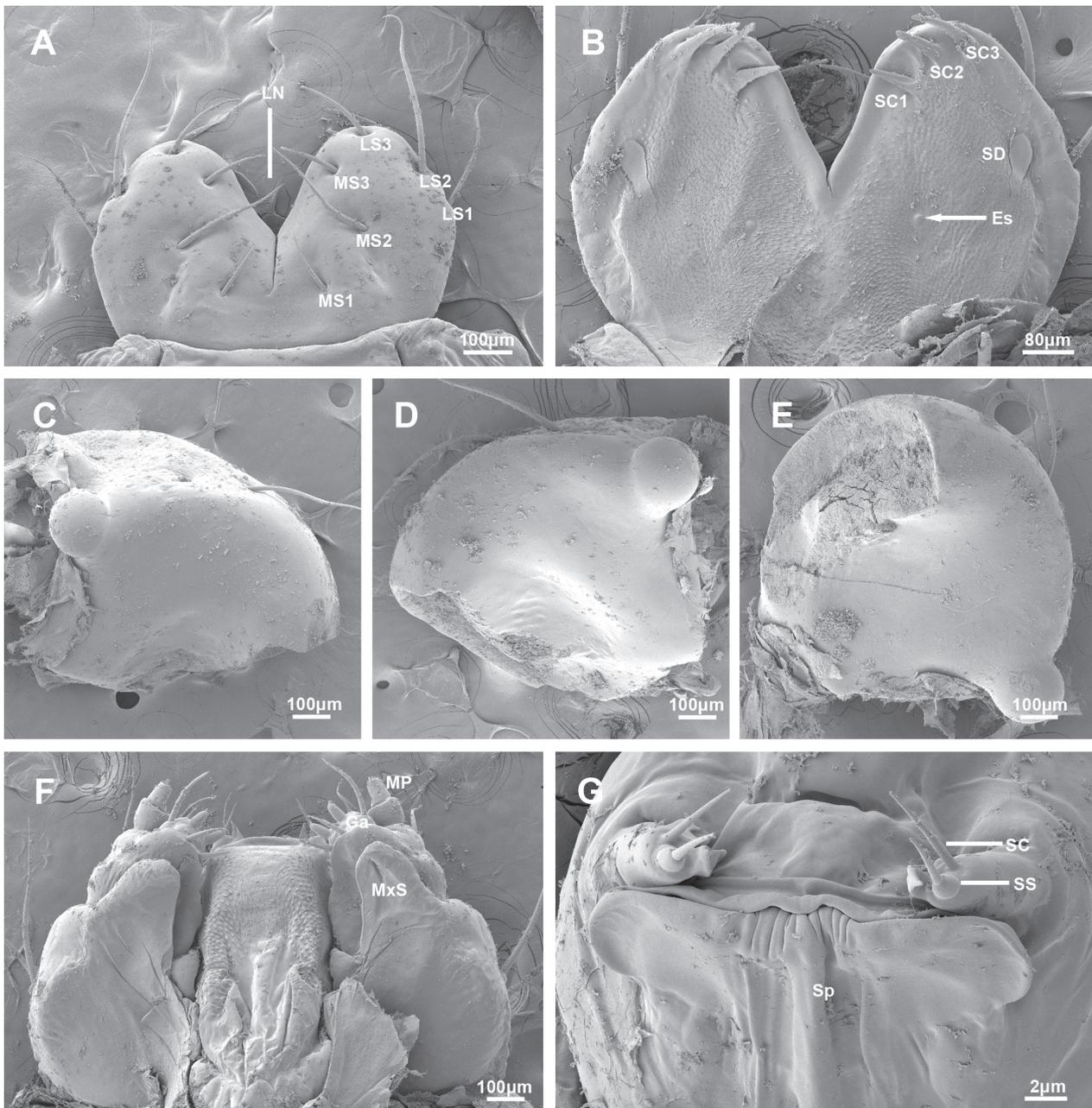
caterpillars in some Saturniidae (Bernays and Janzen 1988), furnished with dentate cusps in the concealed feeding larvae in Lycaenidae, Gelechiidae, Cossidae, Carposinidae, or Tortricidae (Liu et al. 2011; Song et al. 2014; Abd El-Ghany and Faucheux 2021), or combined cutting edges and dentate cusps in some Saturniidae (Zhang et al. 2022). In Notodontidae, the larval mandibles are peculiar for being serrate in the first instar but smooth in the later stages (Miller 1991; Dolinskaya 2008). The morphological differences are helpful for



**Figure 6.** Larval mouthparts of *Cerura erminea* (Esper, 1783). **A.** Labrum; **B.** Epipharynx; **C.** Left mandible, inner view; **D.** Right mandible, inner view; **E.** Left mandible external view; **F.** Maxilla-labial complex; **G.** Magnification of the spinneret. **Ca**, cardo; **Es**, epipharyngeal sensillum; **Ga**, galea; **LN**, labral notch; **LP**, labial palp; **LS1–3**, lateral seta; **MS1–3**, median seta; **MP**, maxillary palp; **MxS**, maxillary sac; **OB**, An occasional broken of the sac; **SC**, sensillum chaeticum; **SD**, sensillum digitiformium; **SS**, sensillum styloconicum; **Sp**, spinneret; **St**, stipes.

the first-instar larvae chewing on leaf surfaces, and more suitable for the mature larvae cutting and biting on leaf edges (Liu et al. 2023). In this study, the serrated mandibles of the mature larvae of *N. davidi* are quite different from all the other known larvae in Notodontidae (Miller 1991; Dolinskaya 2008), but very similar to the stem chewing larvae of *Sericinus montela* (Wang and Jiang 2023) or to the polyphagous larvae of *Spodoptera exigua* (Li et al. 2008). The atypical morphological differences on larval mandibles may imply potential enigmatic feeding strategy of *N. davidi*.

Maxillae of Notodontidae are peculiar for bearing paired “stipital lobes” on the maxillary complex, which represents another identifying character for the family (Godfrey et al. 1989). These characters were reported to be shared by more than 143 species of Notodontidae (Miller 1991; Dolinskaya 2008), but were never reported in the other larvae in Lepidoptera (Albert 1980; Grimes and Neunzig 1986; Godfrey et al. 1989; Li et al. 2018). Based on our morphological investigation under electron microscopy, the so-called “stipital lobes” are internally hollow. From a perspective of location, it is difficult to



**Figure 7.** Larval mouthparts of *Furcula furcula* (Clerck, 1759). **A.** Labrum; **B.** Epipharynx; **C.** Left mandible, inner view; **D.** Right mandible, inner view; **E.** Left mandible external view; **F.** Maxilla-labial complex; **G.** Magnification of the spinneret. **Ca**, cardo; **Es**, epipharyngeal sensillum; **Ga**, galea; **LN**, labral notch; **LP**, labial palp; **LS1–3**, lateral seta; **MS1–3**; median seta; **MP**, maxillary palp; **MxS**, maxillary sac; **SC**, sensillum chaeticum; **SD**, sensillum digitiformium; **SS**, sensillum styloconicum; **Sp**, spinneret; **St**, stipes.

**Table 2.** Relationships between larval mouthparts and habits.

Species name	mandibles	Labral notch	Type of spinnerets	Host plants	Pupation sites
<i>Euhampsonia cristata</i> (Butler, 1877)	smooth	V-shape	Longitudinal depressed	<i>Quercus mongolica</i> (Fagaceae)	In soil
<i>Fentonia ocypete</i> (Bremer, 1861)	smooth	Deep	Longitudinal depressed	<i>Quercus mongolica</i> (Fagaceae)	In soil
<i>Phalera assimilis</i> (Bremer & Grey, 1853)	smooth	V-shape	Depressed tupular	<i>Quercus mongolica</i> (Fagaceae)	In soil
<i>Nerice davidi</i> Oberthür, 1881	toothed	Shallow	Depressed tupular	<i>Ulmus pumila</i> (Ulmaceae)	In soil
<i>Cerura erminea</i> (Esper, 1783)	smooth	V-shape	Broadly depressed	<i>Populus</i> sp. (Salicaceae)	Cocoon on bark
<i>Furcula furcula</i> (Clerck, 1759)	smooth	V-shape	Broadly depressed	<i>Populus</i> sp. (Salicaceae)	Cocoon on bark

say that these structures are located on the stipes. For these reasons, the structures should be defined as “maxillary sac” rather than “stipital lobe”. These sacs seem to form seals between the mandibles and maxillae, assisting

to hold leaf tissue within the oral cavity while the mandibles are acting (Godfrey et al. 1989; Miller 1991).

Spinneret usually form into a tube-like structure that produces silk in immature insects (Capinera 2008), and

varies in shapes among insect lineages (Grimes and Neunzig 1986; Lin 2002; Li et al. 2008; Liu et al. 2011; Chen and Hua 2014; Zhang et al. 2014; Zhou et al. 2015; Liu et al. 2018). In Lepidoptera, the spinnerets are normally tubular in Cossidae, Gelechiidae, Carposinidae, Tortricidae and Lasiocampidae (Liu et al. 2011; Men and Wu 2016; Rana and Mohankumar 2017; Xu et al. 2017; Song et al. 2018; Abd El-Ghany and Faucheux 2021), rudimentary but bearing paired flake lobes in some Saturniidae (Zhang et al. 2022). In this study, the larval spinnerets of Notodontidae are longitudinally depressed in *E. cristata*, *F. ocypete*, *P. assimilis* and *N. davidi* that usually pupate in the soil (Pei 1988; Li et al. 2003; Zeng and Ji 2018), broadly depressed in *C. erminea* and *F. furcula*, which usually built thickened cocoons covering the bark (Pan 2013) (Table 2). The structural differences among the six species are very likely related to silk secreting or cocoon spinning behaviors (Craig 1997; Zalucki et al. 2002; Sorensen et al. 2006).

The labral notches of phytophagous insects are usually morphologically adapted to peculiar food resources (Chapman and de Boer 1995). The labral notches are shallow in the tunneling species in some Cossidae, Gelechiidae and Carposinidae (Liu et al. 2011; Song et al. 2014; Xu et al. 2017; Abd El-Ghany and Faucheux 2021), deeply split in the leaf biting larvae of Sphingidae, Noctuidae, Saturniidae, and some Notodontidae (Cardoso et al. 2017; Rana and Mohankumar 2017; Venancio et al. 2020), or even diverse among congeneric larvae of Saturniidae that exhibit divergent feeding habits (Zhang et al. 2022). In this study, the labral notches are morphologically similar between larvae of *C. erminea* and *F. furcula* attacking *Populus* sp. (Table 2), and *E. cristata* and *P. assimilis* consuming leaves of *Quercus mongolica* (Table 2). The labral notch of *F. ocypete*, however, is much deeper than those of all the other species in Notodontidae (Miller 1991; Dolinskaya 2008).

In fact, larvae of *F. ocypete* are quite peculiar not only for the deep split labral notches, but also for the setae on the labrum and the sensilla on the epipharynx. In general, the lepidopterous larvae usually possess six pairs of setae on the labrum (Lin 1997, 2002; Li et al. 2008; Chen and Hua 2014; Men and Wu 2016; Chen et al. 2018; Li et al. 2018), and three pairs of sensilla chaetica on the epipharynx (Liu et al. 2011; Men and Wu 2016; Chen et al. 2018; Li et al. 2018). The larvae of *F. ocypete* also have six pairs of setae on the labrum but the MS1 are shorter than others and located on the base, and two pairs of sensilla chaetica on the apex of epipharynx. The atypical morphological features of *F. ocypete* imply its peculiar taxonomic status or enigmatic living habits, which still need further observations.

Different from other agricultural pest species, larvae of Notodontidae are more frequently discovered on trees in forest ecosystems (Pei 1988; Wu and Fang 2003; Wang 2005; Xue et al. 2005; Liu et al. 2011; Pan 2013; Zeng and Ji 2018). For better inhabiting the relatively complicated

ecosystem, larvae of Notodontidae not only employ dramatically diverse defensive strategies to avoid being attacked (Ruxton et al. 2005; Liu et al. 2023), but also possess structurally specialized mouthparts for feeding more efficiently, similar to other forest-dwelling larvae in Saturniidae (Zhang et al. 2022). Based on our previous observations, the serrate mandibles are more valuable for the first-instar larvae chewing on the leaf surface (Liu et al. 2023). On the other hand, the mesally smooth mandibles are more suitable for the mature larvae cutting the hardened leaf edges of woody plants (Fig. 1). Moreover, the toothed mandibles of mature larvae in *N. davidi*, as an exception of Notodontidae, are very likely adapted to the rough and wrinkled leaves or other tissues of their host plant *U. pumila*.

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