

The morphology of galerucine and alticine larvae (Coleoptera: Chrysomelidae) and its phylogenetic implications

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Abstract

External characters of alticine and galerucine larvae were examined. Larvae with distinctly different feeding habits were described in detail and their external features were illustrated, mainly using SEM. The morphological descriptions and the used nomenclature may be used as a template for future studies on chrysomelid larvae to facilitate the phylogenetic evaluation of morphological characters of immature stages. Features potentially useful for phylogenetic reconstruction were compiled and arranged in a character state matrix. The usefulness of larval characters was critically evaluated. A larval groundplan of the galerucine-alticine lineage was reconstructed. Supported conventional groups are the Galerucinae s.l. (i.e. incl. alticines), the galerucine Luperini, Hylaspini, and Oidini, and the alticine *Blepharida*-group, placed as sister group of the *Oides* species. A large monophyletic unit is formed by *Altica*, the alticine leaf-miners *Podagricomela* and *Argopistes*, the alticine root feeders *Phygasia* and *Longitarsus*, and the galerucine genera *Monolepta*, *Exosoma* and *Diabrotica*. The phylogenetic results and the effects of different life and feeding habits are discussed. Surface-feeding is ancestral for the galerucine-alticine clade. Leaf-mining has distinct effects on the morphology.

Key words

Chrysomelidae, galerucines, alticines, larvae, morphology, feeding, phylogeny.

1. Introduction

In traditional concepts (e.g. SEENO & WILCOX 1982) Galerucinae and Alticinae are species-rich subfamilies of the megadiverse leaf beetles (Chrysomelidae). Both of them have a worldwide distribution. The former comprises more than 6,500 described species placed in ca. 600 genera, the latter ca. 8,000 species in more than 534 genera (NADEIN & BEZDĚK 2014). The two taxa together are strongly supported as a clade, which is probably either the sister group of the rest of Chrysomelinae or subordinate within this subfamily (REID 1995; FARRELL 1998; DUCKETT et al. 2004; GÓMEZ-ZURITA et al. 2008; HÜBLER & KLASS 2013).

The taxonomic status of the two groups is still discussed controversially (see e.g., NADEIN & BEZDĚK 2014). Some chrysomelid taxonomists treated flea beetles as an independent subfamily (DOGUET 1994; FURTH & SUZUKI 1994; KONSTANTINOV & VANDENBERG 1996; FARRELL 1998; GÓMEZ-ZURITA et al. 2008; HUNT et al. 2007; GE et al. 2011, 2012), whereas others considered alticines as a subordinate tribe of Galerucinae (BÖVING & CRAIGHEAD 1931; LAWRENCE & BRITTON 1994; CROWSON & CROWSON 1996; REID 1995, 2000; LINGAFELTER & KONSTANTINOV 1999; NADEIN & BEZDĚK 2014). The phylogenetic relationships of high-ranking subgroups of Chrysomelidae

were addressed in several recent contributions. In some studies the issue of galerucine-alticine relationships was specifically addressed, for instance by CROWSON & CROWSON (1996), LINGAFELTER & KONSTANTINOV (1999), KIM et al. (2003), GILLESPIE (2003, 2004, 2008), BÜNNIGE et al. (2008), and GE et al. (2011, 2012). Three different concepts are presently discussed. In the first alticines are paraphyletic with monophyletic galerucines nested within them (= MG concept) (REID 1995; CROWSON & CROWSON 1996; KIM et al. 2003; GILLESPIE et al. 2003, 2004, 2008; DUCKETT et al. 2004; BÜNNIGE et al. 2008). The second is monophyletic galerucines and alticines together forming a clade (= MGA concept) (SAMUELSON 1996; FARRELL 1998; GÓMEZ-ZURITA et al. 2008; HUNT et al. 2007; GE et al. 2011, 2012). In the third monophyletic alticines are nested within the galerucine Luperina (= MA concept) (LINGAFELTER & KONSTANTINOV 1999).

Adult morphology was used by SAMUELSON (1996), SUZUKI (1996) and LINGAFELTER & KONSTANTINOV (1999) to address the phylogenetic relationships. Molecular data were analysed by HSIAO (1994), HUNT et al. (2007), GILLESPIE (2003; 2004; 2008), BÜNNIGE et al. (2008) and GE et al. (2011; 2012), and combined data sets also including morphological characters by FARRELL (1998), KIM et al. (2003), DUCKETT et al. (2004) and GÓMEZ-ZURITA et al. (2008). Larval characters were used by LEE (1993). REID (1995, 2000), and CROWSON & CROWSON (1996) combined both adult and larval morphology. The larval morphology of Galerucinae and Alticinae was treated in a number of older and more recent studies. BÖVING (1929) studied external larval characters of species assigned to Galerucinae. TAKIZAWA (1972) subdivided Galerucinae mainly based on the arrangement of tubercles and the defensive glands of larvae. COX (1981) studied the larval morphology of British chrysomelids. The egg bursters of first instar larvae of Chrysomeloidea and Curculionoidea were described in COX (1988, 1994). KIMOTO & TAKIZAWA (1997) described larvae of Taiwanese chrysomelid species and provided keys. STEINHAUSEN (1997) described chrysomelid larvae of Central Europe. In TAKIZAWA (2005) Alticinae were subdivided mainly based on larval tubercular patterns. Even though the knowledge of the larval morphology increased over the last decades, the available information is still fragmentary and the documentation of structural features unsatisfying in most cases.

The main aim of our study is a detailed documentation of galerucine and alticine larval features and to provide a set of characters for a representative taxon sampling. A template for future larval studies is suggested to facilitate the phylogenetic evaluation of morphological features of immature stages. External features of larvae of three species, each representing one of the main feeding types, were described and illustrated in detail. We present a list of coded characters and a data matrix. The characters were evaluated to assess the phylogenetic information contained in the examined features and to reconstruct larval groundplan features. It was predicted by CROWSON & CROWSON (1996) that larval features are

essential for the reconstruction of the relationships within the galerucine-alticine lineage. It is one aim of this study to critically evaluate this statement made by the most prominent coleopterist of the 20th century.

2. Material and methods

2.1. List of taxa examined

Alticinae: *Altica caerulescens* (Baly, 1874), *Philopona vibex* (Erichson, 1834), *Ophrida xanthospilota* (Baly, 1881), *Podontia lutea* (Olivier, 1790), *Blepharida rhois* (Forster, 1771), *Podagricomela shirahatai* (Chûjô, 1957), *Argopistes scyrtoides* Leconte, 1878, *Phygasia fulvipennis* (Baly, 1874), *Longitarsus jacobaeae* (Waterhouse, 1858).

Galerucinae: Galerucini, *Monoxia minuta* Blake, 1939, *Diorhabda carinulata* (Desbrochers, 1870), *Pyrrhalta aenescens* (Fairmaire, 1878), *Pyrrhalta maculicollis* (Motschulsky, 1853), *Menippus cervinus* (Hope, 1831), *Pallasiola absinthii* (Pallas, 1773), *Galeruca daurica* (Joannis, 1866), *Galerucella grisescens* (Joannis, 1865), *Galerucella nipponensis* (Laboissiere, 1922); Oidini, *Oides decempunctatus* (Billberg, 1808), *Oides maculatus* (Olivier, 1807); Luperini, *Exosoma lusitanica* (Linnaeus, 1767), *Diabrotica* sp., *Monolepta hieroglyphica* (Motschulsky, 1858); Hylaspini, *Morphosphaera chrysomeloides* (Bates, 1866), *Gallerucida lutea* Gressitt & Kimoto, 1969, *Gallerucida singularis* (Harold, 1880), *Gallerucida bifasciata* Motschulsky 1860, *Gallerucida gloriosa* (Baly, 1861), *Agelastica alni orientalis* Baly, 1878.

Chrysomelinae (outgroup taxa): *Chrysomela populi* Linnaeus, 1758, *Chrysolina aeruginosa* (Faldermann, 1835), *Timarcha espanoli* Bechyně 1948.

2.2. Morphological examination

All examined specimens were fixed in 75% ethanol. Entire larvae were dissected and examined under a stereoscope. Color pictures were taken with a camera connected to the stereoscope (Zeiss SteREO Discovery V12). For scanning electron microscopy (SEM), specimens were dried at the critical point (Emitech K850 critical point dryer) and sputter-coated with gold (Emitech K500 sputter coater). Pictures were taken with a Philips XL30 ESEM and Scandium software. Sensilla basiconica on apical maxillary and labial palpomere were examined using a JSM-6700F field emission scanning electron microscope in Institute of Process Engineering, Chinese Academy of Sciences. All pictures were evaluated and assembled with Adobe Photoshop® CS 8.0 and Illustrator® CS software.

2.3. Phylogenetic analysis

We analysed 30 characters of 29 in-group terminals and three out-group taxa. Inapplicable characters were coded as ‘-’. WinClada 1.00.08 (NIXON 1999) was used to enter the data in a matrix, and NONA (GOLOBOFF 1999) for calculating minimum length trees (search settings: 1000 replicates, characters non-additive, with equal weight). Bremer support values (BREMER 1994) were calculated with the function implemented in TNT (GOLOBOFF et al. 2008). Ancestral character states were reconstructed with Mesquite 2.71 (MADDISON & MADDISON 2009).

2.4. Abbreviations

bs: basiconic sensillum; **ch:** chelonium; **cl:** claw; **cly:** clypeus; **cx:** coxa; **ds:** digitiform sensillum; **ec:** endocarina; **fm:** femur; **fs:** frontal suture; **ga:** galea; **lbs:** long basiconic sensillum; **lc:** lacinia; **lr:** labrum; **lp:** labium palpi; **mxp:** maxillary palpi; **pe:** penicillus; **px:** prothorax; **py:** anal plate (“pygidium”); **sbs:** short basiconic sensillum; **sp:** sensory papilla; **st:** seta; **tib-tar:** tibiotarsus; **tr:** trochanter.

3. Results

3.1. Description of larvae

3.1.1. *Podagricomela shirahatai* (leaf miner)

Mature larva (Figs. 1–15).

Body length: 6.0–7.2 mm.

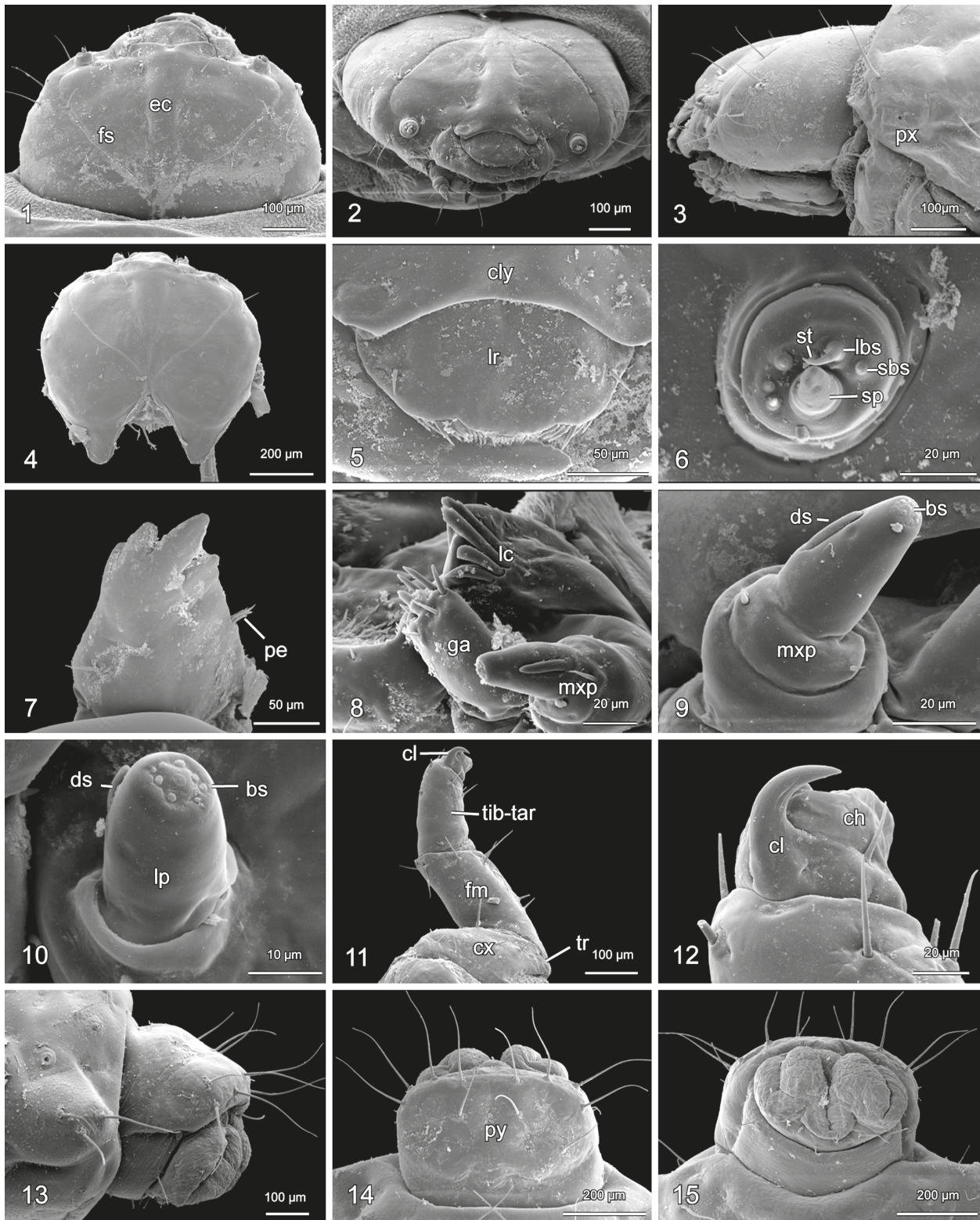
General body shape: Elongate, flattened, slightly curved after fixation in ethanol. Body surface with small tubercles. Setae long and thin, whitish.

Coloration: Body mostly pale yellow, with head, legs, small tubercles and anal plate (“pygidium”) dark brown.

Head: Prognathous, flattened, narrower than prothorax, partly retracted into prothorax; posterior emargination of head capsule deeply V-shaped (Figs. 1–4). Coronal suture absent; frontal suture V-shaped, reaching antennal sockets; median endocarina solid, extending from base of frontal sutures to clypeus (Fig. 1). Frons with two pairs of long setae anteriorly and three pairs of microsetae medially; dorsal region of each epicranial half bearing four long setae (two inserted along frontal suture); anterolateral region bearing four long setae (Figs.

2–3). Typical stemmata and cornea lenses absent, but dark eye spot present behind antenna (not visible on SEM micrographs). Clypeus transverse, with rounded lateral edges, bearing two pairs of setae. Labrum transverse, slightly sclerotized; lateral edges rounded, anteromedially not notched; dorsal surface bearing two pairs of setae; posterior margin convex (Fig. 5). Anterior epipharynx with patch of microtrichia grouped in short transverse row close to anteromedian margin. Antenna with membranous articulating area; located at ends of frontal sutures; two-segmented; first antennomere with large conical sensory papilla and four basiconic sensilla; second antennomere with one elongate basiconic sensillum and two setae (Fig. 6) (the terminology of antenna sensilla follows LESAGE & ZMUDZINSKA-KRZESINSKA 2004). Mandible strongly sclerotized, symmetrical, palmate, with four teeth; second tooth larger than others; external face bearing two setae; penicillus present, formed by seven stout setae (Fig. 7). Maxillae elongate; cardo indistinct, bearing seta; stipes elongate, with two pairs of ventrolateral setae; palpiger indistinct, bearing two setae (one long and one short); mala distinctly divided into two parts; external lobe (“galea”) with seven setae arranged in circle around stout pedunculate seta; inner lobe (“lacinia”) with straight longitudinal row of four long and thick setae (Fig. 8); maxillary palpi with three palpomeres; basal palpomere wider than long, bearing seta; median palpomere smaller than basal palpomere, with two setae; distal palpomere elongate, with large digitiform sensillum on lateral side and 12 basiconic sensilla on apex (Fig. 9). Labium with large trapezoid and slightly sclerotized postmentum bearing two pairs of setae; praementum short, with one median semi-elliptical sclerotized band, bearing two pairs of setae (one close to the base of the labial palpi and one ventrally); ligula with three pairs of short setae arranged in longitudinal rows; labial palpi two-segmented; basal palpomere indistinct; distal palpomere elongate, with large digitiform sensillum on lateral side and nine basiconic sensilla on apex (Fig. 10). Hypopharynx forming subparallel steep structure, with dense vestiture of hairs at lateral edges.

Thorax: Prothorax slightly narrower than the other thoracic segments; with one large dorsal sclerotized, plate-like pronotum, divided by median zone of weakness; with four pairs of setae anteriorly, two pairs laterally, and two pairs posteriorly; prosternum with distinct sclerotized area and pair of setae in central region. Meso- and metathorax subequal, wider than prothorax; meso- and metanotum bearing pair of setae anteriorly and three pairs posteriorly; lateral region with distinct sclerotized tubercles, bearing three pairs of normally sized setae and three pairs of smaller setae; meso- and metasterna with a sclerotized area, but smaller than prosternal sclerite; bearing pair of setae anteriorly. Mesothoracic spiracle annuliform, situated on anterior pleural region close to mesocoxal articulation. Legs increasing in size from pro- to metathorax, widely separated at their base, five-seg-



Figs. 1–15. Mature larva, *Podagricomela shirahatai*, SEM. 1: dorsal view of head; 2: frontal view of head; 3: lateral view of head; 4: dorsal view of head capsule with thorax removed; 5: labrum, frontal view; 6: antenna; 7: mandible, dorsal view; 8: mala; 9: maxillary palp, ventral view; 10: labial palp, ventral view; 11: hind right leg; 12: claw of hind right leg; 13: abdomen segments IX and X, lateral view; 14: abdomen segments IX and X, dorsal view; 15: abdomen segments IX and X, ventral view.

mented; coxa approximately trapezoid, bearing six setae; trochanter triangular, with three setae; femur sclerotized dorsally, membranous ventrally, bearing five pairs of setae; tibia-tarsus slightly narrower than femur, bearing

six pairs of setae; claw sclerotized, falciform, bearing one seta on inner margin; pad-like attachment structure (“chelonium”) present (Figs. 11–12).

Abdomen: Segments I–VIII dorsally indistinctly divided into three transverse plicae by transverse grooves; first plica bearing two pairs of setae, second plica two pairs, last plica three pairs; lateral region with spiracle and pair of setae anterior to it; ventro-lateral region with small globular projection bearing three setae; ventral region bearing three pairs of setae anteriorly and one pair posteriorly. Segment IX narrower than VIII, dorsally forming undivided semicircular anal sclerite (“pygidium”) with six pairs of setae; ventral sclerites fused, forming narrow transverse band with two pairs of setae (Figs. 13–14). Segment X not visible in dorsal view, bearing pygopod; ventral side bearing three pairs of short setae (Fig. 15). Spiracles annuliform, present on segments I–VIII, similar to mesothoracic spiracles but smaller.

Material examined: About 20 mature larvae (final instar) and 10 adults collected on *Zanthoxylum bungeanum* (Rutaceae) in May 2013 in Gansu, China, by Hong-Jian Wang. This species was identified by Shu-Yong Wang, Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

3.1.2. *Longitarsus jacobaeae* (root feeder)

Mature larva (Figs. 16–30).

Body length: 6.2–8.0 mm.

General body shape: Elongate, subcylindrical, slightly curved after fixation in ethanol.

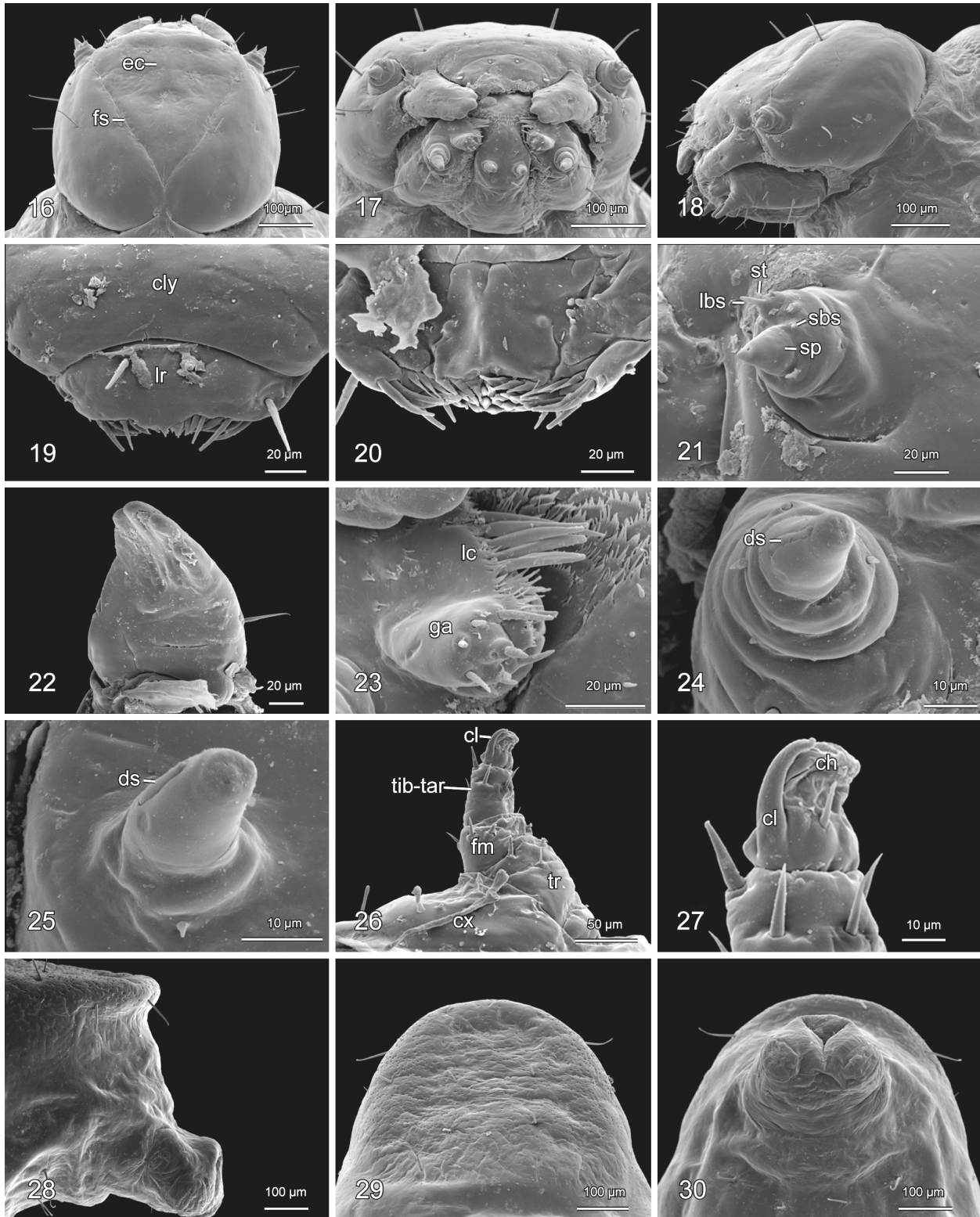
Coloration: Body mostly white, weakly sclerotized, surface with sparse vestiture of whitish setae.

Head: Elongate-oval, orthognathous (referred to as hypognathous in LEE et al. 1998), narrower than pronotum, with weakly emarginated hind margin (Figs. 16–18). Epicranial suture Y-shaped; coronal suture short; frontal suture V-shaped, reaching antennal sockets; median endocarina solid, extending from base of frontal sutures to clypeus (Fig. 16). Frons with three pairs of long setae and one pair of frontal campaniform sensilla. Vertex convex; each epicranial half bearing four setae dorsally (two inserted along frontal suture) and four setae anterolaterally (Fig. 18). Stemmata absent. Clypeus transverse, with rounded lateral edges, bearing two pairs of small setae. Labrum transverse, slightly sclerotized; with rounded lateral edges, anteromedially not notched; dorsal surface bearing two pairs of setae; posterior margin nearly straight (Fig. 19). Anterior epipharynx with patch of microtrichia grouped in short transverse row close to anteromedian margin (Fig. 20). Antenna with membranous articulating area strongly convex; located at ends of frontal sutures; two-segmented; first antennomere with large conical sensory papilla and four basiconic sensilla; second antennomere slightly sclerotized basally, bearing one elongate basiconic sensilla and two setae (Fig. 21). Mandible symmetrical, palmate, sclerotized,

with four indistinct teeth; external face bearing two setae; penicillus absent (Fig. 22). Maxillae with indistinct cardo; stipes elongate, with three pairs of ventrolateral setae; palpiger bearing two pairs of setae; external lobe of mala with straight longitudinal row of long five stout setae; inner lobe of mala with eight setae arranged in circle around stout pedunculate seta (Fig. 23); palpi with three palpomeres; basal palpomere wider than long, bearing seta; median palpomere similar to basal palpomere, bearing three pairs of setae; distal palpomere elongate, with distinct digitiform sensillum on lateral side (Fig. 24). Labium with large trapezoid membranous postmentum bearing three pairs of setae; praementum short, with one median semi-elliptical sclerotized band, bearing two pairs of setae (one close to base of labial palpi and one ventrally); ligula bearing three pairs of short setae arranged in longitudinal rows; labial palpi two-segmented; basal palpomere small, bearing one short seta; distal palpomere elongate, narrowed towards apex, with large digitiform sensillum on lateral side (Fig. 25).

Thorax: Prothorax slightly narrower than other thoracic segments; slightly sclerotized, with three pairs of setae anteriorly, three pairs posteriorly, two pairs laterally, and a sparse vestiture of microsetae; prosternum with four setae. Meso- and metathorax subequal in size, wider than prothorax; both with a transverse median groove separating two indistinct plicae; both plicae with slightly sclerotized bisetose median tubercle and two pairs of slightly sclerotized unisetose tubercles laterally; lateral region with tubercle bearing three pairs of setae; meso- and metasterna both with four setae. Mesothoracic spiracle annuliform, situated on anterior pleural region close to mesocoxal articulation. Legs increasing in size from pro- to metathorax, five-segmented; coxa approximately trapezoidal, bearing four long setae and three short setae; trochanter triangular, with three setae; femur sub-rectangular, sclerotized dorsally, membranous ventrally, bearing six setae; tibiotarsus slightly narrower than femur, elongate, with seven setae; claw sclerotized, curved, bearing one seta on inner margin; pad-like attachment structure (“chelonium”) present (Figs. 26–27).

Abdomen: Segments I–VIII weakly sclerotized, with sparse vestiture of whitish setae; dorsal region with two transverse median grooves separating three indistinct plicae; each plica bearing five setae in most specimens; ventral region usually with four setae. Segment IX dorsally forming undivided subtriangular sclerite (“pygidium”), longer than wide, bearing four pairs of small setae dorsally and two pairs on the lateral and posterior margins, respectively; ventral sclerites fused, forming narrow transverse band with two pairs of setae (Figs. 28–29). Segment X not visible in dorsal view, bearing pygopod; ventral side bearing three pairs of small setae (Fig. 30). Spiracles annuliform, present on segments I–VIII, similar to mesothoracic spiracles but smaller.



Figs. 16–30. Mature larva, *Longitarsus jacobaeae*, SEM. **16:** dorsal view of head; **17:** frontal view of head; **18:** lateral view of head; **19:** labrum, dorsal view; **20:** epipharynx, ventral view; **21:** antenna; **22:** mandible, ventral view; **23:** mala; **24:** maxillary palp, ventral view; **25:** labial palp, ventral view; **26:** hind right leg, lateral view; **27:** claw of hind right leg, lateral view; **28:** abdomen segments IX and X, lateral view; **29:** abdomen segments IX and X, dorsal view; **30:** abdomen segments IX and X, ventral view.

Material examined: Adults were collected on *Senecio jacobae* (Asteraceae) in southern France by Dr. Jim Cullen, CSIRO Entomology, Australia. About 30 lar-

vae of various instars and 10 pupae were reared from these adults from June to July 1979 in Canberra, Australia.

3.1.3. *Philopona vibex* (external leaf feeder)

Mature larva (Figs. 31–45).

Body length: 4.0–4.5 mm.

General body shape: Eruciform, slightly curved after fixation in ethanol. Body surface with prominent tubercles; setae whitish, capitate; cuticular surface structure somewhat asperate (Fig. 33).

Coloration: Body mostly yellow; head, legs and tubercles moderately pigmented.

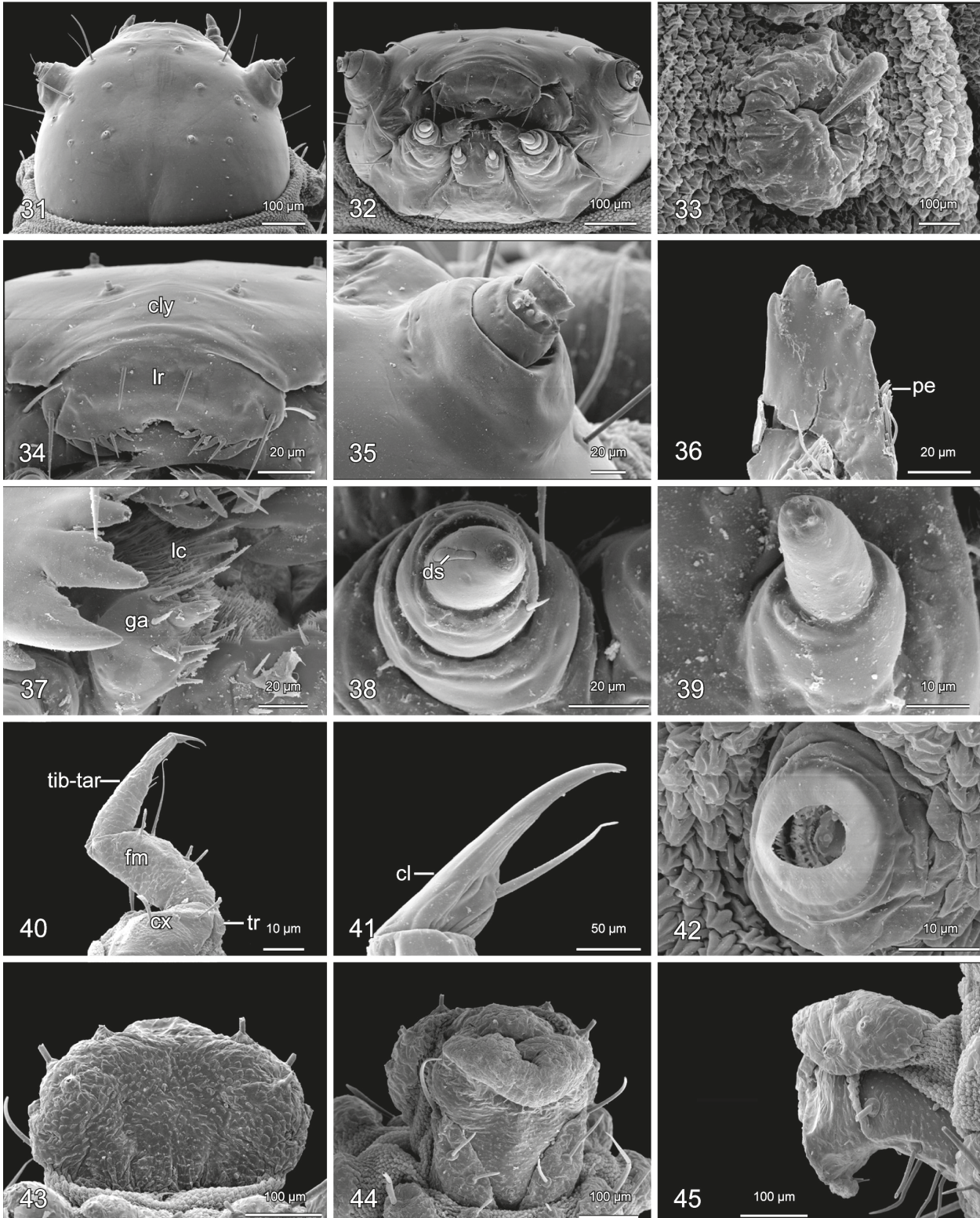
Head: Moderately sclerotized, globular, orthognathous, narrower than pronotum (Figs. 31–32). Epicranial suture Y-shaped; coronal suture short; frontal suture V-shaped, slightly arched, reaching antennal sockets; median endocarina solid, extending from base of frontal sutures to clypeus (Fig. 31). Frons with three pairs of long setae; vertex convex; dorsal region of each epicranial half bearing four long setae (two inserted along frontal suture), anterolateral region with four setae (Figs. 31–32). Stemmata absent. Clypeus transverse, with rounded lateral edges, bearing three pairs of small setae. Labrum transverse, slightly sclerotized; lateral edges rounded, with shallow anteromedial notch; dorsal surface bearing four pairs of setae; posterior margin nearly straight (Fig. 34). Antenna with membranous articulating area strongly convex; located at ends of frontal sutures; two-segmented (small distal segment and tip of large conical sensory papilla broken off in specimen examined with SEM); antennomere one with seven basiconic sensilla and large conical sensory papilla (Fig. 35). Mandible strongly sclerotized, symmetrical, palmate, with five teeth with serrate lateral edge; second and third teeth larger than others; external face bearing two setae; penicillus present, formed by nine stout setae (Fig. 36). Maxillae with transverse cardo, bearing seta; stipes elongate, bearing two pairs of ventrolateral setae; palpiger with two setae; mala distinctly divided into two parts; external lobe with seven setae arranged in circle around stout pedunculate seta; inner lobe with straight longitudinal row of long and thick setae (Fig. 37); maxillary palpi three-segmented: basal palpomere wider than long, bearing one seta; second palpomere similar to basal palpomere, bearing two setae; distal palpomere elongate, with large digitiform sensillum on lateral side (Fig. 38). Labium with large trapezoid postmentum bearing two pairs of setae; praementum with one median semi-elliptical sclerotized band, bearing two pairs of setae (one close to base of labial palpi and one ventrally); ligula with three pairs of setae arranged in longitudinal rows; labial palpi two-segmented; basal palpomere with seta; distal palpomere elongate (Fig. 35). Hypopharynx forming subparallel steep structure, with dense vestiture of hairs at lateral edges.

Thorax: Prothorax slightly narrower than other thoracic segments; with one large sclerotized dorsal pronotum, divided by median zone of weakness; with five pairs of

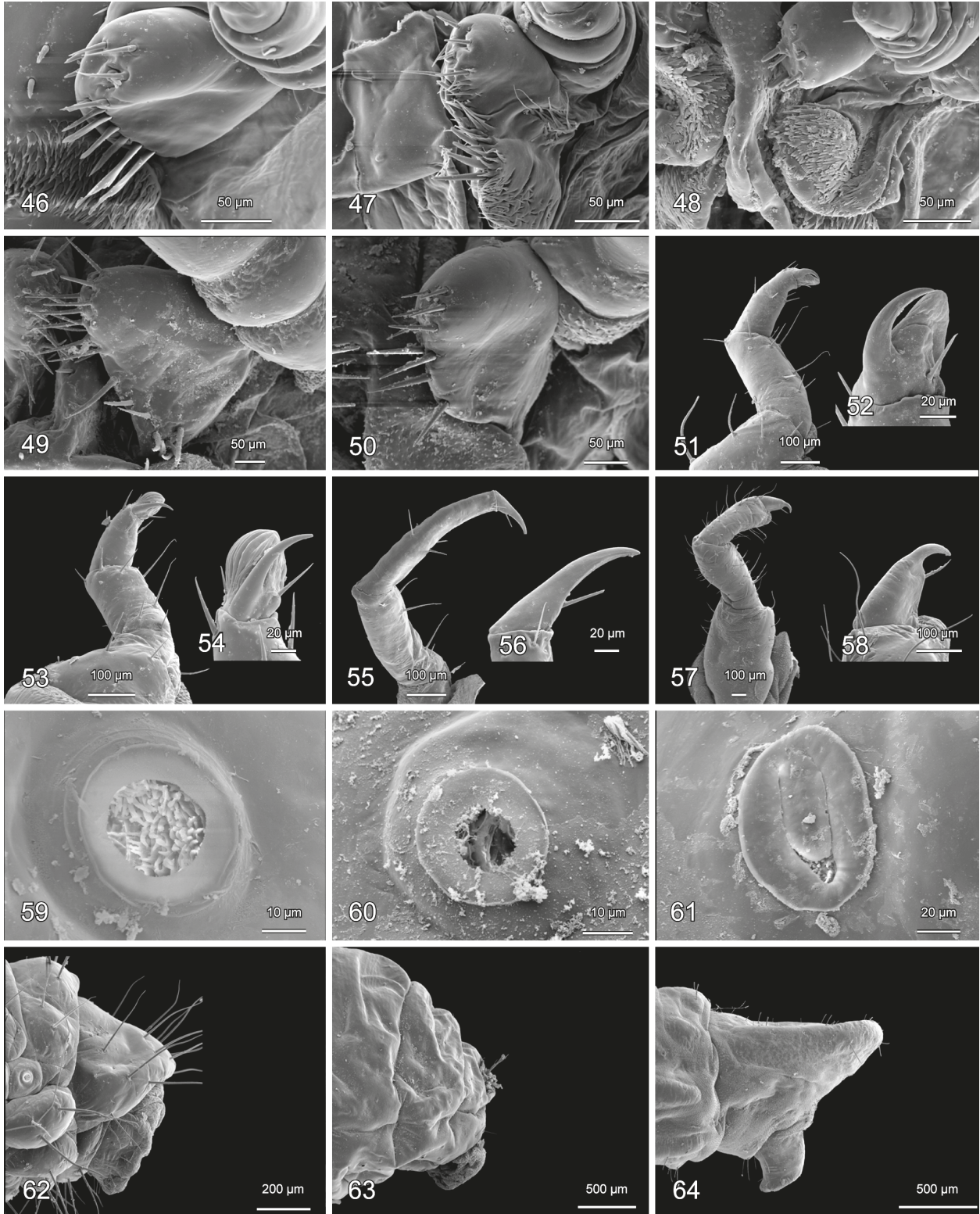
setae inserted anteriorly and three pairs of setae posteriorly; two unisetose tubercles present on ventro-lateral pleural region very close to coxal articulation; prosternum with two pairs of paramedian setae. Meso- and metathorax subequal in size, wider than prothorax; both with a transverse median groove separating two plicae; first plica with median bisetose tubercle; second plica with two pairs of unisetose tubercles (external ones larger than internal ones); lateral region with one pair of bisetose tubercle and pair of unisetose tubercles anterior to coxae; meso- and metasterna with two pairs of paramedian setae. Mesothoracic spiracle annuliform, situated on anterior pleural region close to mesocoxal articulation. Legs: increasing in size from pro- to metathorax, five-segmented; coxa largely trapezoidal, bearing four club-like setae (three long and one short); trochanter triangular bearing four setae; femur sclerotized dorsally, membranous ventrally, bearing four setae on inner margin (one of them extremely long); tibiotarsus elongate, strongly narrowing towards apex, bearing four setae; claw sclerotized, curved, bearing one seta on inner margin; pad-like attachment structure (“chelonium”) absent (Figs. 40–41).

Abdomen: Segments I–VII bearing well defined dorsal sclerites arranged in two transverse plicae; first plica with bisetose median tubercle; second plica with two pairs of unisetose tubercles; lateral region with pair of unisetose tubercles; ventro-lateral region with pair of bisetose tubercles, almost adjacent with spiracle postero-ventrally; ventral side with large anteromedian bisetose tubercle and two pairs of posterior bisetose tubercles. Segment VIII similar to preceding abdominal segments, except for fusion of two pairs of dorsal posterior unisetose tubercles to pair of bisetose tubercles. Segment IX dorsally forming an undivided semicircular sclerite (“pygidium”) with four pairs of setae; ventral sclerites fused, forming two oblique bands, each with three setae (Figs. 43–45). Segment X not visible in dorsal view, bearing pygopod; sternite medially broadly interrupted with edges diverging posteriorly, bearing four pairs of small setae (Fig. 44). Spiracles annuliform, present on segments I–VIII, similar to mesothoracic spiracles but smaller (Fig. 42).

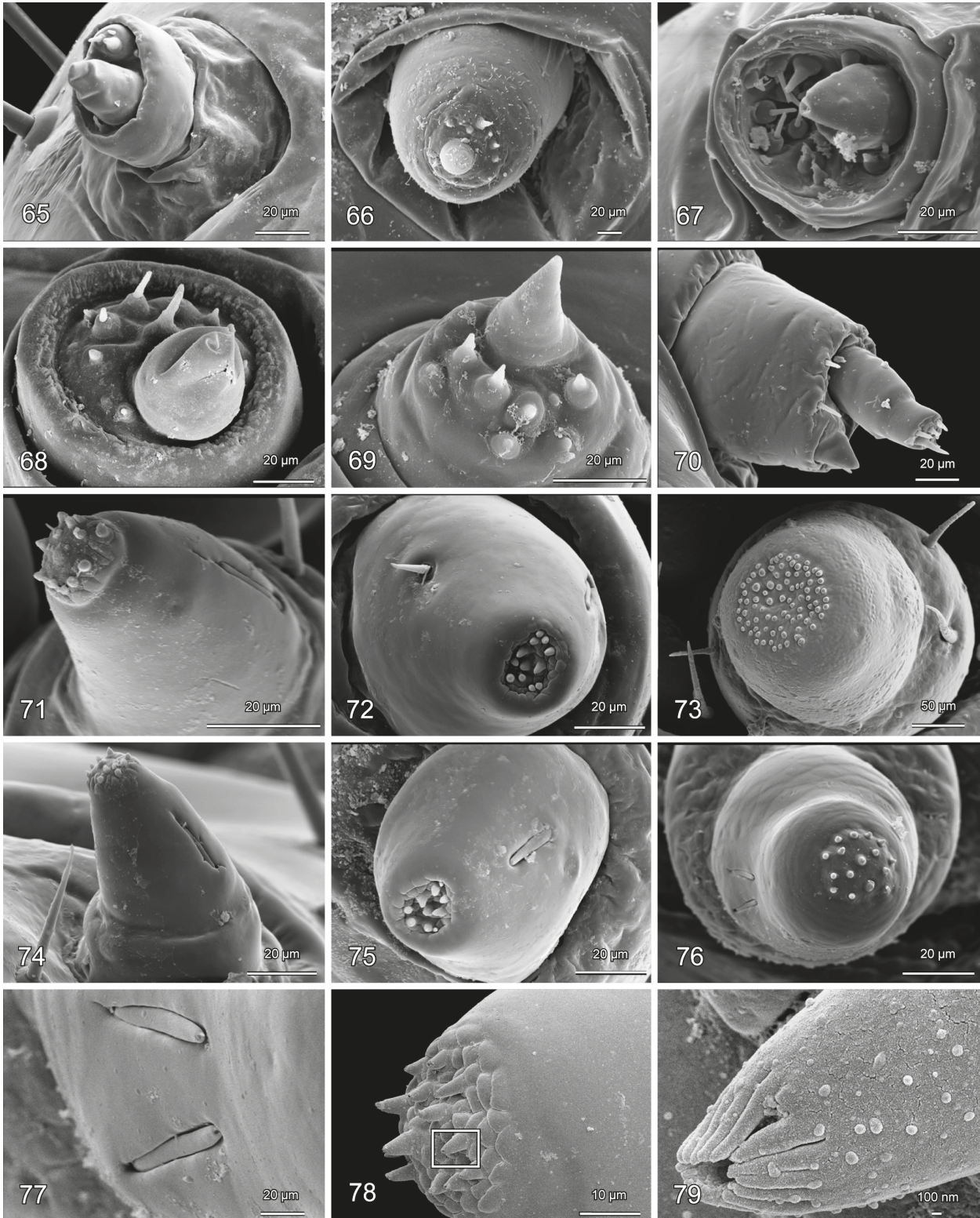
Material examined: Five mature larvae and eight other instars, reared from adults collected on leaves of *Vitex negundo* (Lamiaceae) in May 2004, in Beijing, China, by Huai-Jun Xue and Wen-Zhu Li. This species was identified by Shu-Yong Wang, Institute of Zoology, Chinese Academy of Sciences, Beijing, China.



Figs. 31–45. Mature larva, *Philopona vibex*, SEM. **31:** dorsal view of head; **32:** frontal view of head; **33:** capitate seta and asperate cuticular surface; **34:** labrum, frontal view; **35:** antenna, lateral view; **36:** mandible, ventral view; **37:** mala; **38:** maxillary palp, ventral view; **39:** labial palp, ventral view; **40:** hind right leg, lateral view; **41:** claw of hind right leg, lateral view; **42:** spiracle of abdomen segment VIII; **43:** abdomen segments IX, dorsal view; **44:** abdomen segments IX and X, ventral view; **45:** abdomen segments IX and X, lateral view.



Figs. 46–50. Mala, SEM. 46: *Gallerucida bifasciata*; 47: *Ophrida xanthospilota*; 48: *Pyrrhalta maculicollis*; 49: *Timarcha espanoli*; 50: *Ambrostoma superbum*. — **Figs. 51–58.** Hind leg and claw, lateral view, SEM. 51–52: *Altica caerulescens*; 53–54: *Phygasia fulvipennis*; 55–56: *Diorhabda carinulata*; 57–58: *Ambrostoma superbum*. — **Figs. 59–61.** Abdomen VIII spiracle, SEM. 59: *Gallerucida bifasciata*; 60: *Podagricomela shirahatai*; 61: *Exosoma lusitanica*. — **Figs. 62–64.** Abdomen segments IX and X, lateral view, SEM. 62: *Gallerucida bifasciata*; 63: *Ophrida xanthospilota*; 64: *Phygasia fulvipennis*.



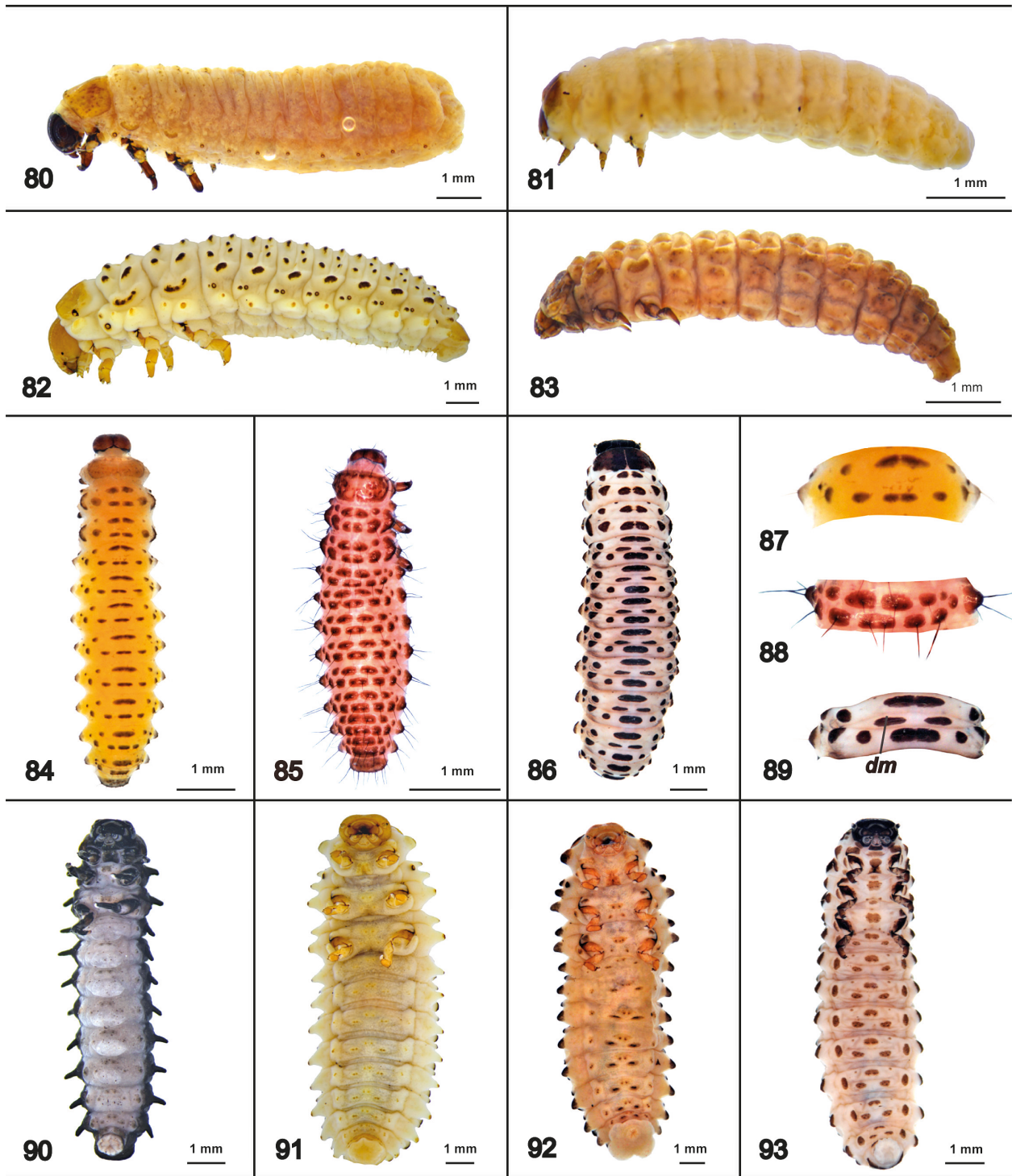
Figs. 65–70. Antenna, SEM. 65: *Altica caerulescens*; 66: *Podontia lutea*; 67: *Gallerucida bifasciata*; 68: *Oides decempunctatus*; 69: *Pyrrhalta maculicollis*; 70: *Gastrophysa atrocyanea*. — **Figs. 71–73.** Maxillary palp, SEM. 71: *Pyrrhalta maculicollis*; 72: *Podontia lutea*; 73: *Timarcha espanoli*. — **Figs. 74–76.** Labium palp, SEM. 74: *Pyrrhalta maculicollis*; 75: *Podontia lutea*; 76: *Timarcha espanoli*. — **Fig. 77.** Digitiform sensilla at higher magnification. — **Figs. 78–79.** FE-SEM. 78: *Ambrostoma superbum* maxillary palp; 79: Basiconic sensillum in Fig. 78 at higher magnification.

3.2. Character list and notes

The following characters 1–30 are included in the matrix (Table 1) and in the phylogenetic analysis. All characters except for 9 and 27 are phylogenetically informative.

1. **Association with plants:** (0) external leaf feeder; (1) leaf miner; (2) root feeder; (3) feeding in bulbs. — External leaf feeders, leaf miners and root borers occur within the galerucine-alticine lineage. An unusual specialization is feeding in bulbs, which is characteristic for larvae of *Exosoma* spp. (CROWSON & CROWSON 1996). Species of *Phyllostreta* can be leaf miners or root feeders (NEEDHAM et al. 1928) and all three main feeding types occur in *Psylliodes* (COX 1998).
2. **Head:** (0) prognathous; (1) orthognathous (often referred to as hypognathous). — The head of external leaf feeders and root feeders is orthognathous, i.e. the mouthparts are ventrally directed, a condition also found in other chrysomelid lineages. In leaf-mining larvae, the head is moderately flattened and prognathous, with the posterior portion slightly retracted into the prothorax (Fig. 3).
3. **Posterior emargination of head capsule:** (0) deep; (1) shallow; (2) absent. — The posterior emargination of the head capsule is deep and V-shaped in leaf-miners (Fig. 4). Due to the retraction of the posterior cephalic region the emargination is largely concealed within the prothorax. In other galerucine and alticine larvae the emargination is shallow or lacking.
4. **Numbers of stemmata or eye spots:** (0) 0; (1) 1; (2) 6. — Galerucine and alticine larvae either lack stemmata or a single stemma is present on each side of the head. External feeders usually have one pair of larval eyes. However, they can be reduced in some external feeding alticines, like in *Alagoasa*, *Altica*, *Syphrea* and *Walterianella* (CASARI & TEIXEIRA 2011; DUCKETT & CASARI 2002; HUA et al. 2013). Eye spots lacking a cornea lens occur in some leaf miners and root feeders, such as *Candezea palmerstoni*, *Febra insularis* and *Monolepta australis* (BRYANT & GRESSITT 1957; HOUSTON 1982). Almost all chrysomeline larvae have 6 pairs of stemmata.
5. **Antennal socket membrane:** (0) scarcely wider than antennomere 1; (1) 2–5 times wider than antennomere 1. — The antennal socket membrane is scarcely wider than the first antennal segment in Galerucini, but 2–5 times wider than antennomere 1 in other galerucine and alticine larvae (LAWSON 1991).
6. **Number of antennomeres:** (0) 1; (1) 2; (2) 3. — The number of antennomeres is one or two in the galerucine-alticine lineage. In alticines, all known larvae of the *Blepharida*-group have one antennomere, whereas two are present in the others. In galerucines two occur in the tribe Hylaspini and only one in the others. The number of antennomeres is three in Chrysomelinae.
7. **Coronal suture:** (0) absent; (1) short and indistinct, less than 1/3 of the length of the dorsal head capsule; (2) well developed, 1/3–1/2 of the length of the head. — The coronal suture is absent in leaf miners. Root feeding alticine larvae always have a short coronal suture, but it is long in galerucine root feeders (Luperini). The coronal suture of larvae of the alticine *Blepharida*-group is well-developed (FURTH & LEE 2000).
8. **Shape of frontal suture:** (0) V-shaped; (1) slightly arched; (2) U-shaped. — The frontal suture is V-shaped in leaf miners and U-shaped in *Monoxia* and *Lysanthia occidentalis* (CASARI & TEIXEIRA 2011). In other larvae they are either V-shaped or slightly arched.
9. **Endocarina:** (0) absent; (1) present. — The median internal ridges or endocarinae of most galerucine and alticine larvae are distinct, but they are weakly developed or absent in *Exosoma* and some root feeders like *Luperus* and *Systema blanda* (CROWSON & CROWSON 1996; LEE et al. 1998).
10. **Contact between endocarina and transverse frontoclypeal sutures:** (0) absent; (1) present. — The anterior or middle part of the endocarina can be indistinct and the contact with the transverse frontoclypeal ridge is absent in the genus *Oides*.
11. **Anterior part of endocarina:** (0) divided into two parts; (1) undivided. — The endocarina usually extends from the junction of the coronal and frontal sutures to the clypeus, both forming a blackish T-shaped structure. In some species, such as *Chrysomela populi*, *Galerucella griseescens* and *Monoxia minuta*, the anterior part of endocarina is divided into two parts.
12. **Pale area of anterior margin of labrum:** (0) present; (1) absent. — The labrum of galerucine and alticine larvae is transverse and heavily sclerotized. A pale triangular area is present near the anterior margin in *Galeruca daurica*, *Galerucella griseescens*, *Oides decempunctatus*, *Pallasiola absinthii* and so on. This character is unstable in some genera. For example, the pale triangular area is present in *Gallerucida lutea* and *G. gloriosa*, but absent in *G. singularis* and *G. bifasciata*.
13. **Notch of anterior margin of labrum:** (0) distinct; (1) shallow; (2) absent. — The anterior labral margin is usually distinctly notched or not notched at all. A shallow notch occurs only in few species, like *Monoxia minuta* and *Galeruca daurica*.
14. **Posterior margin of labrum:** (0) straight or nearly straight; (1) posteriorly convex. — The posterior labral margin is either convex or straight. It is straight or nearly so in larvae of *Philopona vibex*, *Argopistes scyrtoides* and *Blepharida*-group of Alticinae, and also in *Agelastica alni orientalis*, *Exosoma lusitanica*, *Gallerucida lutea*, *Menippus cervinus* and *Oides* of Galerucinae.

- 15. Mandibular penicillus:** (0) absent; (1) present. — A group of approximately 10 closely packed setae on the mesal mandibular edge is commonly referred to as penicillus. It is present in most galerucine and alticine genera, but absent in all known *Blepharida*-group larvae of Alticinae (FURTH & LEE 2000; JEREZ 1999; LEE 1999; ZHANG & YANG 2008). In Chrysomelinae, a penicillus is present in *Geomela* (REID 1995).
- 16. Inner lobe of mala (lacinia):** (0) reduced; (1) well developed. — The apical lobe (mala) of the maxilla is divided into two lobes in most galerucine and alticine larvae (Figs. 46–47). This feature is not recorded in any other chrysomelid group (JOLIVET et al. 1994). Even though the presence of a separate larval lacinia and galea is a groundplan feature of Coleoptera and Polyphaga, a divided mala is apparently an apomorphic feature in Chrysomelidae and the galerucine-alticine lineage (CROWSON & CROWSON 1996). It is unclear whether the lobes are homologous to the lacinia and galea or whether the bifurcation is a de novo formation. An undivided mala is likely a groundplan apomorphy of Cucujiformia excl. Lymexylidae (e.g., BEUTEL & ŚLIPŃSKI 2001). A group of setae on the external lobe is irregularly arranged in a circle at the inner margin. A longitudinal row of fixed long setae is usually present on the apical margin of the inner lobe, but in *Pyrhhalta* the inner lobe bears very densely arranged scale-like serrate surface structures, probably modified setae (Fig. 48). The undivided mala of Chrysomelinae usually bears 10–15 setae on its mesal margin (Figs. 49–50).
- 17. Praementum:** (0) not curved medially; (1) curved medially. — The labium is composed of an apical praementum and a basal undivided postmentum. The former is usually present as a semicircular sclerite embracing the large membranous articulatory areas for the labial palpi. In some species the praementum is curved medially. This character can be unstable within a genus, praementum curved medially in *Galerucella nipponensis*, but not curved in *G. griseascens*.
- 18. Postmentum:** (0) membranous; (1) sclerotized. — The postmentum is usually trapezoid and sclerotized in chrysomelid larvae.
- 19. Shape of legs:** (0) short and stout, tibiotarsus as long as femur; (1) long and slender, tibiotarsus nearly twice as long as femur. — The number of leg segments of galerucine and alticine larvae is five like in almost all other polyphagan larvae (different degrees of leg reduction occur in some groups of beetles such as Buprestidae, Lamiinae and Curculionoidea), i.e. coxa, trochanter, femur, tibiotarsus, and pretarsal claw (e.g., LAWRENCE et al. 2010), the last two elements corresponding with the tibia and tarsungulus of some authors (e.g., BÖVING & CRAIGHEAD 1931; FURTH & LEE 2000; LESAGE & ZMUDZINSKA-KRZESINSKA 2004). Occasionally the leg is 4-segmented in chrysomelid larvae e.g., in *Pseudolampsis darwini* and *P. guttata* (CASARI & DUCKETT 1997). Legs of external leaf feeders are usually stout (Fig. 52). In some cases they become very long and slender, for instance in *Philopona* and *Diorhabda* (Fig. 55). The legs of some leaf miners and root feeders are slightly shortened compared to those of external leaf feeders.
- 20. Pad-like chelonium at distal part of leg:** (0) absent; (1) present. — An unpaired, membranous pad-like structure at the base of the claw of chrysomelid larvae (Figs. 52, 54) is often referred to as pulvillus. As it is obviously not homologous to paired pulvilli occurring in adults of other insect lineages (BEUTEL & GORB 2001) the term chelonium (BIENKOWSKI 2010; NESTEROVA 2008) or claw pad should be used. The presence of this adhesive structure suggests that galerucine and alticine larvae were originally adapted to feeding externally on foliage, rather than being subterranean (JOLIVET et al. 1994). The chelonium improves adhesion on smooth surfaces (GORB & GORB 2004). It is lacking in *Diorhabda* of Galerucinae and some Oedionychina genera (such as *Alagoasa*, *Philopona*, *Wanderbiltiana* and *Omophoita*) of alticines (Figs. 41, 56) (DUCKETT & CASARI 2002; DUCKETT & SWIGOŃOVÁ 2002; TAKIZAWA 2005).
- 21. Tubercles of postcephalic body:** (0) indistinct or absent; (1) distinctly developed. — Distinct tubercles are usually present in alticine and galerucine larvae (Figs. 82, 84–86). Genera of Oedionychina are characterized by their conically produced tubercles. However, they are indistinct or vestigial in larvae living under ground, in leaf miners, and in the alticine *Blepharida*-group (Figs. 80–81, 83).
- 22. Dorsal tubercle of prothorax:** (0) D-DL; (1) D-DL-EPa; (2) D-DL-EP. — KIMOTO (1962) named tubercles according to their position: dorsal tubercle (D), dorso-lateral tubercle (DL), epipleural tubercle (EP), pleural tubercle (P) and sternal tubercle (S). The prothoracic dorsum always bears a large sclerotized plate, which is formed by combining smaller tubercles. In the (D-DL) type, the prothoracic plate is formed by (D) and (DL), and the tubercle (EP) is located at the epipleural region. In the (D-DL-EPa) type, the epipleural tubercle (EP) is divided into two subunits named as EPa and EPp. The prothoracic plate is formed by (D), (DL) and (EPa), and the small tubercle (EPp) remains at the epipleural region. The (D-DL-EPa) type occurs in all alticine larvae and some galerucine larvae, whereas other larvae of galerucines display the type (D-DL). In Chrysomelinae the types (D-DL-EP) and (D-DL-EPa) occur.
- 23. Dorsal region of abdominal segments I–VII:** (0) with one row of tubercles; (1) with two rows; (2) with three rows. — In the galerucine tribes Galerucini and Oidini the dorsal region of the abdominal segments is composed of two rows of tubercles



Figs. 80–83. Lateral view of mature larvae. **80:** *Blepharida rhois*; **81:** *Argopistes scyrtoides*; **82:** *Oides decempunctatus*; **83:** *Monoxia minuta*. — **Figs. 84–86.** Dorsal view of mature larvae. **84:** *Galerucella grisescens*; **85:** *Galerucella birmanica*; **86:** *Gallerucida bifasciata*. — **Figs. 87–89.** Tubercles on dorsal region of first abdomen segment. **87:** *Galerucella grisescens*; **88:** *Galerucella birmanica*; **89:** *Gallerucida bifasciata*. — **Figs. 90–93.** Ventral view of mature larvae. **90:** *Menippus cervinus*; **91:** *Oides decempunctatus*; **92:** *Oides maculatus*; **93:** *Gallerucida bifasciata*.

(Figs. 84–85, 87–88), whereas three rows are present in Hylaspini, with the additional tubercle named Dm in TAKIZAWA (1972) (Figs. 86, 89), one row is present in some Chrysomelinae larvae, like *Chrysomela populi*. In alticines, most leaf feeders display two rows of tubercles on the dorsum of the

abdominal segments. This character is not applicable in cases when the tubercles are strongly reduced, like in some root feeders and leaf miners.

24. Sternal tubercles: (0) small; (1) large. — Two tubercles are present on the sternal region, the eusternal tubercle (ES) and the sternellar-parasternal

tubercle (SS-PS). In some groups, the sternal tubercles are reduced in size and less sclerotized (Figs. 90–91).

25. **Thoracic defensive glands:** (0) absent; (1) mesothorax and metathorax; (2) prothorax, mesothorax and metathorax. — Within alticines defensive glands are present on the thorax and abdominal segments I–VIII of larvae of *Nonarthra* and on abdominal segments I–VIII of larvae of *Pseudolampsis* (CASARI & DUCKETT 1997; TAKIZAWA 2005). In galerucines, defensive glands occur in species of the tribe Hylaspini. Three different configurations occur, with glands present on all thoracic and abdominal segments I–VIII or I–IX, on the meso- and metathorax and abdominal segments I–VIII, or on abdominal segments I–VIII (TAKIZAWA 1972).
26. **Defensive glands of abdominal segments:** (0) absent; (1) present. — See previous character.
27. **Type of spiracles:** (0) biforous; (1) annular. — Spiracles are present on the mesothorax and abdominal segments I–VIII in galerucine and alticine larvae. Generalized groups usually have annular spiracles (Figs. 59–60), but they are biforous in *Exosoma* (Fig. 61) (BÖVING & CRAIGHEAD 1931).
28. **Anal plate (“pygidium”):** (0) absent; (1) present. — An anal plate, a well sclerotized dorsal plate-like sclerite on segment IX (often referred to as pygidium in Chrysomelidae), is usually present in galerucine and alticine larvae also including leaf-feeders and root-feeders (Figs. 62, 64). However, larvae of the *Blepharida*-group and most leaf-miners lack this structure (Fig. 63).
29. **Anal opening:** (0) dorsal; (1) ventral. — The anal opening is usually located ventrally on segment X, but this is not the case in larvae of six alticine genera belonging to the *Blepharida*-group, where the anus opens dorsally on segment IX (Fig. 63). In these species, a fecal shield covers the dorsal side of the body and can deter attacking enemies (PRATHAPAN & CHABOO 2011).
30. **Shape of anal plate (“pygidium”):** (0) semicircular or sub-rectangular; (1) subtriangular. — The anal plate of root feeders is subtriangular and longer than wide (Fig. 64). In the other larvae considered here it is semicircular or sub-rectangular, with similar width and length or slightly wider than long.

Urogomphi (char. 31) and ambulatory warts (char. 32) occur very rarely in galerucine and alticine larvae; they are apparently not useful as phylogenetic characters and are thus not included in the matrix and in the phylogenetic analysis.

31. **Urogomphi:** Urogomphi are prominences or appendages of tergum IX of beetle larvae (e.g., LAWRENCE et al. 2010). In some alticine (e.g., *Chaetocnema* and *Psylliodes*) and galerucine larvae (e.g., *Diabrotica duodecimpunctata*, *D. vittata*) a pair of simple curved urogomphi is present. A single me-

dian terminal process occurs in larvae of *Phyllotreta cruciferae*, *P. atra*, and *P. vittula* (BÖVING 1930; COX 1988; COX 1981). The absence in the vast majority of chrysomelid larvae suggests that they evolved secondarily in these species. The presence or absence of urogomphi is not associated with any particular feeding habit. Their condition can differ within one genus according to BÖVING (1927) and COX (1998).

32. **Ambulatory warts:** The presence of ambulatory warts is an uncommon feature in galerucine and alticine larvae. They are only known in *Homichloda barkeri*, where they insert medioventrally on abdominal segments I–VIII. It is likely that they improve the adhesion to the leaf surface (COX 1997).

The following characters of sensilla of the antennae (char. 33) and palps (char. 34) are based on SEM micrographs of eight galerucine and alticine species and three species of Chrysomelinae. As the taxon sampling is limited and the definition of discrete character states difficult, these features are also not included in the matrix.

33. **Antennal sensilla:** The basal antennomere of the 2-segmented antennae is partly membranous and bears 4–5 small basiconic sensilla and a conical sensory papilla which is larger than antennomere 2. Antennomere 2 is very small and slightly sclerotized basally, equipped with one elongate basiconic sensillum and with two setae (Fig. 65). A cone-shaped sensory papilla and 6–8 sensilla basiconica (two additional sensilla trichodea occur in some species) are distributed on the membranous part of the distal antennomere (Figs. 68–69). In Chrysomelinae antennomere 2 bears a cone-shaped sensory papilla and antennomere 3 several small sensilla basiconica (Fig. 70).
34. **Sensilla of the maxillary and labial palpomeres:** The apical maxillary and labial palpomeres of chrysomelid larvae bear a very similar set of sensilla, usually a group of sensilla basiconica at the apex and one digitiform sensillum on the lateral side. The usual number of sensilla basiconica on the apical maxillary palpomere is 11–15 (Figs. 71–72), but the number is greatly increased (ca. 83) in *Timarcha*, possibly related to large size (Fig. 73). The number on the apical labial palpomere is 10–16 (Figs. 74–76). The apical part of the sensilla basiconica consists of many finger-like projections, which surround the terminal pore (Fig. 79). It is likely that these sensilla function as gustatory receptors (FARAZMAND & CHAIKA 2008). The digitiform sensillum lies in a longitudinal groove. The usual number on the lateral side of maxillary and labial palpomere is one, but *Timarcha* has two on the lateral region of the labial palpomere (Fig. 77). The function is more or less unclear. It may be a hygro-/thermoreceptor (EILERS et al. 2012), a receptor of CO₂ (HONOMICHL & GUSE 1981), or a mechanoreceptor (FARAZMAND & CHAIKA 2008).

Table 1. Character state matrix. (-) refer to inapplicable characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		
Chrysomelinae (outgroup)	<i>Chrysomela populi</i>	0	1	2	2	0	2	2	0	1	1	0	1	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1	1	0		
	<i>Chrysolina aeruginosa</i>	0	1	2	2	1	2	2	0	1	1	1	1	0	0	0	0	0	1	0	0	1	2	1	1	0	0	1	1	0		
	<i>Timarcha espanoli</i>	0	1	2	2	1	2	1	0	1	1	1	1	2	0	0	0	1	1	0	0	1	2	1	0	0	0	1	1	1	0	
Galerucinae: alticines	<i>Altica caerulescens</i>	0	1	1	0	1	1	0	1	1	1	0	2	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	
	<i>Philopona vibex</i>	0	1	2	0	1	1	1	1	1	1	1	0	2	0	1	1	0	1	1	0	1	1	1	1	0	0	1	1	1	0	
	<i>Ophrida xanthospilota</i>	0	1	1	1	1	0	2	0	1	1	1	0	0	0	0	1	0	1	0	1	0	1	2	0	0	0	1	0	0	-	
	<i>Podontia lutea</i>	0	1	2	1	1	0	2	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	2	0	0	0	1	0	0	-	
	<i>Blepharida rhois</i>	0	1	1	1	1	0	2	0	1	1	1	0	0	0	0	1	1	1	0	1	0	1	2	0	0	0	1	0	0	-	
	<i>Podagricomela shirahatai</i>	1	0	0	1	1	1	0	0	1	1	1	0	2	1	1	1	0	1	0	1	0	1	-	0	0	0	1	1	1	0	
	<i>Argopistes scyrtoides</i>	1	0	0	0	1	1	0	0	1	1	1	0	2	0	0	1	0	0	0	1	0	1	-	0	0	0	0	1	1	-	
	<i>Phygasia fulvipennis</i>	2	1	1	0	1	1	1	0	1	0	1	0	2	1	1	1	0	0	0	1	0	1	-	0	0	0	1	1	1	1	
	<i>Longitarsus jacobaeae</i>	2	1	1	0	1	1	1	0	1	1	1	0	2	1	0	1	0	0	0	1	0	1	-	0	0	0	1	1	1	1	
	Galerucinae: galerucines	<i>Monoxia minuta</i>	1	0	0	1	0	2	1	1	1	0	0	1	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	
		<i>Diorhabda carinulata</i>	0	1	2	1	0	0	2	0	1	1	1	0	2	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	1	0
		<i>Pyrrhalta aenescens</i>	0	1	2	1	0	0	2	0	1	1	1	0	2	1	1	0	0	1	0	1	1	0	1	0	0	0	1	1	1	0
		<i>Pyrrhalta maculicollis</i>	0	1	2	1	0	0	2	0	1	1	1	0	2	1	1	0	0	1	0	1	1	0	1	1	0	0	1	1	1	0
<i>Menippus cervinus</i>		0	1	1	1	0	0	1	1	1	1	1	0	2	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	1	0	
<i>Pallasiola absinthii</i>		0	1	2	1	0	0	2	0	1	1	1	1	0	1	0	1	0	1	0	1	1	0	1	1	0	0	1	1	1	0	
<i>Galeruca daurica</i>		0	1	1	1	0	0	2	0	1	1	1	1	1	1	0	1	0	1	0	1	1	0	1	1	0	0	1	1	1	0	
<i>Galerucella griseescens</i>		0	1	1	1	0	0	2	0	1	1	0	1	2	1	1	1	0	1	0	1	1	0	1	0	0	0	1	1	1	0	
<i>Galerucella nipponensis</i>		0	1	1	1	0	0	2	0	1	1	1	1	2	1	0	1	1	1	0	1	1	0	1	0	0	0	1	1	1	0	
<i>Oides decempunctatus</i>		0	1	1	1	1	0	2	1	1	0	-	1	0	0	0	1	0	1	0	1	1	0	1	0	0	0	1	1	1	0	
<i>Oides maculatus</i>		0	1	1	1	1	0	2	1	1	0	-	1	0	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	1	0	
Luperini		<i>Exosoma lusitanica</i>	3	1	1	0	1	0	2	0	0	-	0	2	0	0	1	0	0	0	1	0	1	-	0	0	0	0	1	1	1	
		<i>Diabrotica</i> sp.	2	1	1	0	1	0	2	0	1	1	0	2	1	1	1	1	0	0	1	0	1	-	0	0	0	0	1	1	1	
Hylaspini	<i>Monolepta hieroglyphica</i>	2	1	1	1	1	0	1	-	1	0	-	0	2	1	0	1	0	0	1	0	1	-	0	0	0	0	1	1	1		
	<i>Morphosphaera chrysomeloides</i>	0	1	2	1	1	1	1	1	1	1	1	2	1	0	1	0	1	0	1	1	1	2	1	0	1	0	1	1	1	0	
	<i>Gallerucida lutea</i>	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0	1	1	2	1	1	2	1	1	1	1	0	
	<i>Gallerucida singularis</i>	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	1	0	1	1	2	1	2	1	1	1	1	1	0	
	<i>Gallerucida bifasciata</i>	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	1	1	2	1	2	1	2	1	1	1	0	
<i>Gallerucida gloriosa</i>	0	1	1	1	0	1	1	1	1	1	1	1	0	1	0	1	1	1	0	1	1	2	1	2	1	2	1	1	1	0		
<i>Agelastica alni orientalis</i>	0	1	2	1	1	1	2	0	1	1	1	0	2	0	0	1	0	1	0	1	1	2	0	0	1	1	1	1	1	0		

4. Discussion

The main aim of this study was to improve the knowledge of external features of larvae of the galerucine-alticine lineage, which is presently still very fragmentary. In our descriptions accompanied by a detailed documentation (mainly using SEM micrographs) we use a nomenclature consistent with a general terminology for beetle larvae suggested by LAWRENCE et al. (2010). This approach and standardized descriptions with a comparable coverage of structures and sets of illustrations will likely increase the efficiency and usefulness of studies on chrysomelid larval morphology aiming at phylogenetic reconstruction. It will also facilitate comparisons with other coleopteran groups in broader scale systematic and evolutionary investigations (see e.g., LAWRENCE et al. 2011).

As pointed out above, the relationships within the galerucine-alticine lineage are still discussed controversially. Our investigation of the external larval morphology yielded only a relatively low number of 30 characters that we considered phylogenetically relevant. It is therefore conceivable that the statement of CROWSON & CROWSON (1996) (and BÖVING 1931) concerning the phylogenetic usefulness of larval features was overoptimistic. Nevertheless, it is evident that characters of the immature stages do not only distinctly reflect the specific life habits (see below), but also contain phylogenetic information. One important result of our analysis (see Fig. 94) was the reconstructed larval groundplan of the monophyletic galerucine-alticine lineage (Table 2). Ancestral larvae were probably external leaf feeders with an orthognathous head with V-shaped frontal sutures, a short coronal suture, and a median endocarina. The labrum was posteriorly convex and lacking an anteromedian notch, the antenna two-segmented, the mandibular penicillum was missing, and a distinct inner maxillary lobe was present. The legs were stout and a distal attachment pad was present (“chelonium”). The body surface was characterized by distinct tubercles, with enlarged tubercles on the ventral side. The dorsal region of abdominal segments I–VII displays two rows. Thoracic and abdominal defensive glands were absent. The spiracles were annular. A semicircular or subrectangular anal plate (“pygidium”) was present and the anal opening was ventrally directed. In the analysis, the absence of eyes was assigned to the basal node of the group. We consider this as an artifact. Parallel loss of the light sense organs in different subgroups appears more likely than the assumption that a single eyespot has re-evolved in the group.

Considering the relatively low number of potentially useful larval characters, the resolution of our tree is surprisingly good. That both traditional subfamilies turned out as non-monophyletic is in contrast to previously suggested hypotheses (REID 1995; CROWSON & CROWSON 1996; FARRELL 1998; LINGAFELTER & KONSTANTINOV 2000; KIM et al. 2003; NADEIN & BEZDĚK 2014) and arguably an artifact resulting from the limited taxon sampling and the

Table 2. Larval groundplan of the monophyletic galerucine-alticine lineage.

1.	Association with plants: (0) external leaf feeder;
2.	Orientation of mouthparts: (1) orthognathous
3.	Posterior emargination of head capsule: (2) absent
4.	Numbers of stemmata or eye spots: (0) 0
5.	Antennal socket membrane: (1) 2–5 times wider than antennomere 1
6.	Number of antennal segments: (1) 2
7.	Coronal suture: (1) short and indistinct, less than 1/3 of the length of the dorsal head capsule
8.	Shape of frontal suture shape: (0) V-shaped
9.	Endocarina: (1) present
10.	Contact between endocarina and transverse frontoclypeal sutures: (1) present
11.	Anterior part of endocarina: (1) not separate into two parts
12.	Pale area of anterior labral margin of labrum: (0) present
13.	Anterior margin of labrum: (2) notch missing
14.	Posterior margin of labrum: (1) convex
15.	Mandibular penicillus: (0) absent
16.	Inner lobe of mala (lacinia): (1) well developed
17.	Praementum: (0) not curved medially
18.	Postmentum: (1) sclerotized
19.	Shape of legs: (0) short and stout, tibiotarsus as long as femur
20.	Pad-like chelonium at distal part of leg: (1) present
21.	Tubercles of body: (1) tubercles distinctly developed
22.	Dorsal tubercle of prothorax: (1) D-DL-EPa
23.	Dorsal region of abdominal I–VII segments: (1) composed of two rows
24.	Sternal tubercles: (1) large
25.	Defensive glands of thorax: (0) absent
26.	Defensive glands of abdominal segments: (0) absent
27.	Type of spiracles: (1) annular
28.	Anal plate: (1) present
29.	Anal opening: (1) ventral
30.	Shape of anal plate: (0) semicircular or sub-rectangular, width similar with length or little wider than length

limited size of the character set. Supported conventional groups are the Galerucinae s.l. (i.e. including alticines), the galerucine Luperini, Hylaspini, and Oidini, and the alticine *Blepharida*-group, which forms the sister group of the two included *Oides* species. Only few subordinate clades such as Oidini and the *Blepharida*-group are supported by a Bremer support above 1 (see Fig. 94). A large clade is formed by *Altica*, the alticine leaf-miners *Podagricomela* and *Argopistes*, the alticine root feeders *Phygasia* and *Longitarsus*, and the species of the galerucine genera *Monolepta*, *Exosoma* and *Diabrotica* (Lupe-rini).

External leaf feeders, root feeders, and leaf miners are the three main larval feeding types in the galerucine-alticine clade. Other habits occurring in the group are drilling in stems and roots or feeding on bulbs (NADEIN & BEZDĚK 2014). Our analysis suggests that surface feeding on leaves is ancestral (see above). Larvae of the

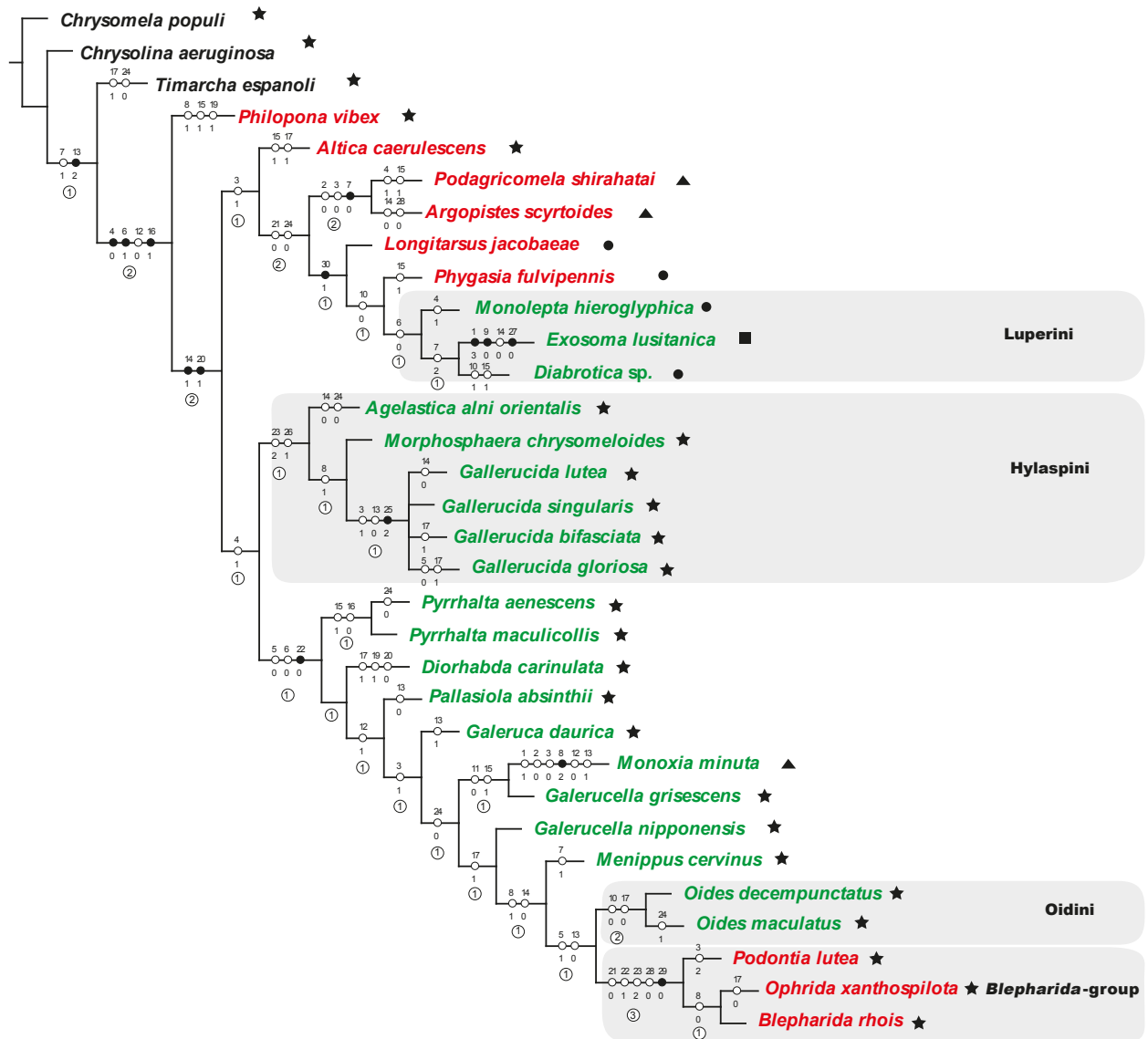


Fig. 94. Strict consensus cladogram representing 6 minimum length trees, obtained with 30 larval characters (minimum length tree 107 steps, CI: 38, RI: 67). Black circles indicate non-homoplasious apomorphies, white circles homoplasious ones. Encircled numbers indicate Bremer Support values calculated using TNT. Galerucine species names in green, alticine species in red. Feeding habits are also mapped on the tree; black star: the larva is an external leaf feeder; black triangle: leaf miner; black circle: root feeder; square: larva feeding in bulbs.

galerucine Luperini and of twelve alticine genera have been reported as root feeders. Root feeders are easily distinguished by the relatively long and slender body, the depigmentation, i.e. light coloration of the postcephalic segments, and the lack of distinct tubercles on the body surface. The legs of most root feeders are normally developed as in the leaf feeders. External leaf feeding flea beetle larvae of the *Blepharida*-group (except for *Asiophrida marmorea*) are characterized by the habit of covering their dorsal side with their excrements (PRATHAPAN & CHABOO 2011). Members of this clade share a considerably number of potential larval synapomorphies, such as one-segmented antennae, the loss of the mandibular penicillus, an incised anterior labral margin, and an anal opening dorsally on abdominal segment IX (FURTH & LEE 2000).

The galerucine genus *Monoxia* and nineteen alticine genera are reported as leaf miners in the larval stages (SANTIAGO-BLAY 2004). The postcephalic body of these larvae is slightly flattened dorsoventrally, the head is flattened and prognathous, and the posterior emargination of the head capsule is deep and V-shaped. The posterior part of the head is deeply retracted into the prothorax and powerful muscles are attached to it, supporting the penetration of fresh leaf tissue in the mine (NEEDHAM et al. 1928; PARRY 1974). Further features are the absence of the coronal suture (apomorphic) and a V-shaped frontal suture (presumably plesiomorphic). The stemma is either represented by a single eyespot without a cornea lens or completely absent. The basal labial palpomere is extremely reduced. The thoracic legs are not reduced but widely separated at their base.

Larval characters alone are apparently insufficient for a robust reconstruction of the relationships. Considering the low support values and the limited number of characters, our result should be treated with caution. It is apparent that our larval data set has its limitation with respect to systematics, adding one more insufficiently supported hypothesis to the conflicting concepts suggested by other authors (see above: MGA versus MG versus MA). Nevertheless, larval features will contribute to the clarification of the relationships and are clearly important in an evolutionary context. It is evident that for a reliable clarification of galerucine-alticine relationships not only a much denser taxon sampling is required, but also an extensive combined data set containing several suitable molecular markers and also well-documented larval and adult morphological data. This would have been clearly beyond the scope of this contribution, but will be the target in follow up studies.

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