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Systematics, phylogeny and biology of a new genus of Lithocolletinae (Lepidoptera: Gracillariidae) associated with Cistaceae

JURATE DE PRINS[1,4], DONALD R. DAVIS[2], ELIANE DE CONINCK[1], JAE-CHEON SOHN[2] &
PAOLO TRIBERTI[3]
[1]*Royal Museum for Central Africa, Tervuren, Belgium*
[2]*National Museum of Natural History, Smithsonian Institution, USA*
[3]*Museo di Storia Naturale, Verona, Italy*
[4]*Corresponding author. E-mail: jurate.de.prins@africamuseum.be*

Abstract

The gracillariid genus ***Triberta* gen. nov**. (Lepidoptera: Gracillariidae: Lithocolletinae Stainton, 1854) is described to accommodate two species formerly assigned to the genus *Phyllonorycter* Hübner, 1822: *Triberta helianthemella* (Herrich-Schäffer, 1861) **comb. nov**. and *T. cistifoliella* (Groschke, 1944) **comb. nov.** *Triberta cistifoliella* **bona sp**. is restored from synonymy based on morphological characters. The new genus is biologically associated with the plant family Cistaceae of the order Malvales and is endemic to the Palaearctics. Our molecular analysis of eleven nuclear genes failed to unambiguously place *Triberta* in the lithocolletine phylogeny, but revealed that this genus is distinct from either clade *Phyllonorycter* + *Cremastobombycia* and *Cameraria*. The distinctiveness of *Triberta* is also supported by inferred traits in wing venation, micro morphology of the last instar larva, pupa, genital morphology of the adult and life history. A key to the species of *Triberta* is provided. The interspecific homogeneity in external morphology, coupled with minor differences in genital traits, an apparent narrow specialization on Cistaceae host plants, restricted geographical range and molecular evidence based on multi-nuclear genes jointly suggest that the generic diversification of *Triberta* is a relatively old phenomenon and driven strongly by host selection.

Key words: evolution, host specificity, leaf mining, morphology, taxonomy

Introduction

This contribution presents another step towards understanding the systematics and evolutionary history of the subfamily Lithocolletinae Stainton, 1854 following the publication of the taxonomic-revisionary study about the Afrotropical Lithocolletinae (De Prins & Kawahara 2012). These tiny, attractive, distinctively ornate moths represent a highly successful lineage of Gracillariidae (Kawahara *et al*. 2011) and are placed phylogenetically among the ditrysian moths within the complex clade of the superfamilies Yponomeutoidea + Gracillarioidea (Mutanen *et al*. 2010; Sohn *et al*. 2013; Regier *et al*. 2013). The great majority of taxa within this complex possess diverse plant mining life histories (Grimaldi & Engel 2005; Sohn *et al*. 2013). Currently the monophyletic group Lithocolletinae comprises 552 species of leaf miners, with the Afrotropical *loxozona* species group as an exception in possessing a gall-forming life history. The presently known Lithocolletinae species are grouped into 10 genera (De Prins & Kawahara 2012; De Prins & De Prins 2013); nevertheless, many additional underscribed taxa can still be found in tropical regions, and many of these are already present in various research collections.

Species of Lithocolletinae have an intimate and often highly specialized feeding and reproductive interaction with a great variety of plants: no less than 771 plant species belonging to 38 families are recorded as host plants of these leaf miners (Lopez-Vaamonde *et al*. 2003, 2006; De Prins & Kawahara 2012; De Prins & De Prins 2005, 2013). However, the successful ecological colonization of congeneric lithocolletine moths which utilize the diverse variety of plant families occurred rather seldom during evolution. Six lithocolletine genera out of ten, including *Chrysaster* Kumata, 1961, *Hyloconis* Kumata, 1963, *Macrosaccus* Davis & De Prins, 2011, *Neolithocolletis,*

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Kumata, 1963, *Porphyrosela* Braun, 1908 and *Protolithocolletis* Braun, 1929, are trophically and reproductively associated with the plants assigned exclusively to one family Fabaceae (De Prins & Kawahara 2012). Moths belonging to the New World genus *Cremastobombycia* Braun, 1908 also mostly mine the leaves of one plant family, Asteraceae (Chambers 1871; Frey & Boll 1873, 1876; Davis *et al*. 2013). Exceptionally, the single *Cremastobombycia* species *C. lantanella* Busck, 1910 is associated with Verbenaceae plants feeding on *Lantana* spp. (Busck 1910; Davis *et al*. 2013), a decorative, ornamental bush planted worldwide, which explains the disrupted distribution of this gracillariid species (Busck 1910; Swezey 1910, 1913, 1928; Walsingham 1914; Zimmerman 1978; Palmer & Pullen 1995; De Prins & De Prins 2005, 2013; Davis *et al*. 2013). Another small New World genus, *Leucanthiza* Clemens, 1859, consisting of only three species, utilizes plants within Convolvulaceae and Thymelaeaceae in addition to Fabaceae (Braun 1914; Bourquin 1962; De Prins & De Prins 2005, 2013). Thus, the recorded monophagy or narrow oligophagy of different genera within the subfamily Lithocolletinae is considered more as a rule than as an exception.

The plant family Cistaceae comprises ca. 180 species and eight genera (Guzmán & Vargas 2005). The circumscription of species within Cistaceae remains problematic, which has resulted in multiple combinations of the same taxon under different generic names, especially for species now assigned to *Helianthemum* Mill. and *Halimium* Dunal (Spach) (Arrington & Kubitzki 2003; The Plant List 2010). The type genus *Cistus* L. is probably one of the most characteristic genera of the Mediterranean flora (Polunin & Huxley 1974; Schönfelder & Schönfelder 1994; Polunin 1997). Cistaceae plants are self-incompatible, leading to crossing between species (Bosch 1992; Falchi *et al.* 2009). Consequently, natural hybridization is common. However, the hybrids are not allopolyploidic (Ellul *et al*. 2002) and moreover, a long history of human activities in this region favoured the abundance and distribution of this family of plants (Thompson 2005). The evolutionary mechanisms responsible for the explosive morphological diversity within Cistaceae remain poorly understood. However, the published molecular evidence proposes that the early differentiation of Cistaceae may have occurred in the western Mediterranean with the major center of species diversity on both sides of the Strait of Gibraltar, Andalusia and northern Morocco (Guzmán & Vargas 2005; Falchi *et al*. 2009; Stevens 2012). It is an intriguing fact that the oldest pollen for Cistaceae (*Cistacearumpollenites*) dates from the Lower Miocene from Czechia (Bohemia) (Konzalova 1967). Fruits of *Cistus* were found in sedimentary rocks of Germany (Montbauer) and in amber-bearing sand of the Baltic Sea (Zemland) from the middle Eocene (Palibin 1909; Sohn *et al*. 2012).

The fossil leaf mines of gracillariids are among the oldest known fossils of ditrysian Lepidoptera dating back to the late Cretaceous (Labandeira *et al.* 1994; Sohn *et al*. 2012). Some gracillariids are associated with ancient angiosperms, which originated in the Cretaceous. However, the question remains whether these associations with ancient plants can serve as an evidence of an old origin, or are the result of recent colonization of archaic host plants (Davis & Wagner 2011; Brito *et al*. 2012). The age of the subfamily Lithocolletinae still remains unknown, but the phylogenetic results already obtained (Kawahara *et al*. 2011; De Prins & Kawahara 2012; Regier *et al*. 2013) suggest different geological ages of some genera, caused by different geological events and/or ecological adaptations. Based on the ribosomal 28S rDNA evidence of 100 *Phyllonorycter* species it has been suggested that the genus *Phyllonorycter* originated during the early Palaeocene, ca. 62.3 million years ago (Mya) within the limits 50.3–73.3 Mya (Lopez-Vaamonde *et al*. 2006). Our best Maximum Likelihood (ML) tree indicates a divergence of *Triberta* which pre-dates the origin of *Phyllonorycter*. Differing from this proposal, our bootstrap (BP) consensus tree (data not shown) placed *Triberta* as a sister to (*Phyllonorycter*+*Cremastobombycia*)+*Cameraria*, likewise suggesting an earlier split of the genus than *Phyllonorycter*.

With the phylogeny obtained (Kawahara *et al*. 2011; De Prins & Kawahara 2012; Regier *et al*. 2013) we are beginning to understand the evolutionary diversification and patterns that suggest certain taxonomic changes within the Lithocolletinae clade. The emphasis is on genera because they are considered as monophyletic groups around which we can organize our understanding about Lithocolletinae diversity. We consider the generic rank within Lithocolletinae as having little meaning other than signifying the monophyletic group that includes other monophyletic groups circumscribing the appropriate subordinate rank taxa (Kitching *et al*. 2005). Here we propose the eleventh known genus of Lithocolletinae which is endemic to the Palaearctic and which shares striking external similarities with *Phyllonorycter*, but is nevertheless genetically, morphologically and behaviourally distinct. Members of this new genus were referred to in previous publications as *Lithocolletis helianthemella* Herrich-Schäffer, 1861 and *L. cistifoliella* Groschke, 1944 (De Prins & De Prins 2013 and the references therein). We provide a detailed, illustrated diagnoses and description of the genus and its two constituent species, (one of which is restored from synonymy), distributional and natural history data, a molecular phylogenetic analysis, and a comparison of the observed inferred evolutionary patterns of the new genus with other phylogenetic lineages.

Material and methods

Morphological studies. The morphological terminology of adults, male and female genitalia follows Vári (1961), Klots (1970), Kumata (1963; 1993, 1995), Kuznetzov (1981) and the Handbook of Zoology (Kristensen 2003). In addition specific larval and pupal structures are described using the terminology of Stehr (1987), Davis & Deschka (2001), Davis & De Prins (2011) and Davis *et al*. (2013). Although Kristensen (2003: 103) suggested the use of the term 'phallus', we follow Vári (1961) and Kumata (1963; 1993; 1995) to ensure the continuous stability in the terminology of Lithocolletinae. Abbreviations of wing veins follow Kumata (1993, 1995). Observations of morphological structures were carried out with Wild and Leica MZ12.5 stereomicroscopes (magnification 10–95×) and with a Leica DMLB microscope under magnifications of 150×, 200×, and 400× each equipped with a digital micrometer for measurement of lengths. Genitalia were prepared following the methods of Robinson (1976) with some modifications (Triberti 2007). Genital morphology was examined using a Leica DMLB microscope under magnifications of 75× and 100×. Drawings of internal structures were prepared using digital photographs taken with a camera connected to a light microscope. A composite genitalia image was created using Auto-Montage Syncroscopy. Wing venation slides were prepared following Vári (1961) and applying modifications suggested by Hoare (2000). Scanning Electron Microscopy (SEM) imaging was used on some larvae and male genitalia which were dried in HMDS, gold coated using a Jeol JFC-1300 Auto fine Coater and examined with a Jeol 6480 LV electron scanning microscope.

Taxonomic material. We designate the primary types and indicate different labels by numbers in square brackets (e.g., [1], [2]). The first record for host plant, parasitoid and distribution is provided. The institutional insect collection codes are in accordance with Evenhuis (2013), as follows:

BMNH	Natural History Museum, London, UK;
FSMC	Florida Museum of Natural History, Gainesville, USA;
MSNV	Museo Civico di Storia Naturale, Verona, Italy;
RMNH	Netherlands Biodiversity Centre Naturalis, Leiden, the Netherlands;
WJDP	Collection of Willy and Jurate De Prins, Leefdaal, Belgium;
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany;
ZSM	Zoologische Staatssammlung, Munich, Germany.

Phylogenetic analysis. For a molecular phylogeny of Lithocolletiinae, a total of 27 species were included as in-group taxa. These represent eight genera from the ten (except *Porphyrosela* and the monobasic *Protolithocolletis*) which are currently known. A monophyly of Gracillariidae was well documented by Kawahara *et al*. (2011). Therefore, our outgroup sampling was restricted within Gracillariidae. Six outgroups chosen for our analyses represent two other gracillariid subfamilies: Gracillariinae (4 spp.) and Phyllocnistinae (2 spp.). For 19 of the included species, their sequence data came from Kawahara *et al*. (2012). For the remaining taxa (14 spp.), the specimens were processed for DNA extraction at Akito Kawahara's Lab, Florida Museum of Natural History, University of Florida, Gainesville, following Regier's *et al*. (2008) protocol.

The sequences considered for our study consisted of eleven nuclear genes, totaling 8,838 bp: *Gelsolin* (552 bp), *Histidyl tRNA synthetase* (447 bp), *AMP deaminase* (768 bp), *Glucose phosphate dehydrogenase* (621 bp), *Acetyl-coA carboxylase* (501 bp), *Pyrimidine biosynthesis* (*CAD*: 2,913 bp), *Dopa-decarboxylase* (708 bp), *Enolase* (1,134 bp), *Elongation factor-1 alpha* (519 bp), *Histone 3* (273 bp), and *Wingless* (402 bp). These are the same as the ten gene set plus *Wingless* chosen by Kawahara *et al*. (2012) on the basis of their high amplification success rate and phylogenetic utility. The primers for these genes are provided in Regier *et al*. (2008). The prepared sequences for each gene were translation-aligned, edited, assembled, and concatenated using Geneious 6.1.6 (Biomatters Ltd.). The final dataset included 21.3% of missing data. GenBank accession numbers are listed in Appendix 1.

Phylogenetic analyses were conducted under Maximum Likelihood (ML) criterion as implemented in GARLI

2.0 (Zwickl 2011). We used jModelTest (Posada 2008) to determine the best substitution model for our dataset which was identified as GTR+G+I, i.e., the General-Time-Reversible model with among-site rate variation accommodated using a gamma distribution plus separate estimation of a proportion of invariable sites. Default settings from the NCBI web resources (available at www.molecularevolution.org) were used for the tree-searching and bootstrapping with GARLI. The best ML tree from 150 independent search replicates was saved and visualized using FigTree v.1.3.1 (Rambaut 2009). To evaluate nodal supports, bootstrap (BP) values were calculated from 800 and 500 pseudoreplicates for the concatenated and single-gene datasets respectively. For purposes of discussion, we will refer to BP values of 70–79% as "moderate", 80–89% as "strong", and 90% as "very strong" support.

Systematics

Triberta De Prins gen. nov.

Type species: *Lithocolletis cistifoliella* Groschke, 1944, by present designation.

Triberta is assigned to the subfamily Lithocolletinae on the basis of eleven nuclear genes and the following putative morphological synapomorphies: hindwing vein Rs parallel to vein M at the basal half of wing; adults rest parallel to surface, adult head with occipital tuft; internal feeding of all larval instars within the mine.

Diagnosis. According to the phenotypic, biological and ecological characters *Triberta* resembles other genera of Lithocolletinae, but according to the wing venation it is the closest to the monotypical Nearctic genus *Protolithocolletis* Braun, 1929. We define *Triberta* as a genus-group taxon of the clade *Triberta* + *Macrosaccus* + (*Leucanthiza* + *Chrysaster*) (Fig. 01). The ecological trait defining *Triberta* is that pupation occurs outside the mine (a trait shared with *Chrysaster* and *Leucanthiza*) in a transparent oval-shaped and slightly raised cocoon (Fig. 59). In contrast the pupation of *Cameraria* occurs within an upperside blotch mine under a flat circular cocoon while in *Protolithocolletis* "the pupa and its cocoon are invariably found within the mine" (Braun 1929: 39). The last instar larva of *Chrysaster* spins an ellipsoid silken cocoon at the edge of a contracted leaf (Kumata 1961) and the larva of *Leucanthiza* weaves its cocoon on some substance on the surface of the ground (Clemens 1859). The shape and structure of this cocoon spinning clearly separates the new genus *Triberta* from the latter two genera *Chrysaster* and *Leucanthiza*. In addition to the ecological and molecular characters, *Triberta* may be distinguished from all remaining lithocolletine genera by the combination of the following morphological diagnostic traits: the forewing pattern with three white fasciae or chevrons strongly angulated at midline, or rows edged basally and apically (a trait easily differentiating *Triberta* from *Cameraria* and *Cremastobombycia*, where fasciae typically are black margined distally); occipital tuft developed like in most Lithocolletinae genera but different from *Chrysaster* and *Leucanthiza* where vertex is smooth (Figs 60, 61). Wing venation is similar in that of *Protolithocolletis* in retaining 7 apical veins in forewing: R_2, R_3, R_4, R_5, M_1, M_{2+3}, Cu_1 (R_1 rudimentary), the cell between R_5 and M_1 open, but different from *Cameraria*, *Phyllonorycter* and *Porphyrosela* which have only five or four apical veins. The hindwing venation is similar to *Cremastobombycia*, *Hyloconis*, *Porphyrosela* and *Protolithocolletis* in the presence of $M_{2+3;}$ this vein is lost in *Cameraria*, *Chrysaster*, *Leucanthiza, Macrosaccus, Neolithocolletis* and *Phyllonorycter* (Fig. 03). Sternum VIII in males forms a characteristic flap, laying under the valvae like in many Lithocolletinae genera except *Chrysaster, Leucanthiza*, *Macrosaccus* and *Protolithocolletis,* a trait easily differentiating *Triberta* from the latter genera. In *Cameraria* sternum VIII often bifid caudally, while in *Triberta* it is shaped like a broad triangle (Figs 04, 06, 21). Uncus fused with tegumen to form a single sclerite (Kuznetzov 1981) (Fig. 08). The apical part of tegumen in the male genitalia with two apical setae like in *Cameraria* (Figs 05, 09). Apex of tegumen is setose in remaining nine lithocolletine genera except *Phyllonorycter*. Ventral surface of valvae in *Triberta* covered with long hair-like setae (Fig. 06), anellus strongly developed, tubular in many species of *Cameraria*, however differently from *Cameraria*, *Macrosaccus*, *Leucanthiza* and *Protolithocolletis* saccus in being simple, not prominent; aedoeagus is rather short, ca. 2/3 of valval length, bifurcate at coecum, a trait easily differentiating *Triberta* from all remaining lithocolletine genera; transtilla in *Triberta* incomplete like in the great majority of *Cameraria* species and *Hyloconis* (Figs 06–09, 16–19). In the female genitalia (Figs 22–25), papillae anales are semi-circular, not flattened like as in *Cameraria* and *Porphyrosela*, with the clearly visible separation of papillae caudally; two pairs of apophyses present, the trait evidently separating the new genus from *Porphyrosela.* The latter genus has only one pair of apophyses. Ostium bursae opens at subanterior area of segment VIII, the trait differentiating the new genus from *Cameraria*, *Cremastobombycia*, *Phyllonorycter* and *Porphyrosela*; in most species of the latter genera the ostium bursae opens at the posterior margin of segment VII (*Cameraria*, *Cremastobombycia*, *Porphyrosela*) or in different locations within segment VII (*Phyllonorycter*); ductus bursae long, narrow, corpus bursae spherical, signa confined to 1–2 moderately sclerotized oval areas—these traits are shared with many lithocolletine genera but not with *Porphyrosela*, which has no signum, and not with *Macrosaccus* and *Neolithocolletis*, where the signum area consists of numerous microscopic spicules scattered on the wall of corpus bursae or arranged in linear series on subcaudal part of corpus bursae. Larva constructs an abaxial mine (Figs 56–58). Larva of *Triberta* is of 'cylindrical'-type like that in *Phyllonorycter* and clearly different from *Cameraria,* the genus whose larva belongs to the 'flat'-type group (Chambers 1878; Chapman 1902; Braun 1908). As was noted by Stehr (1987) in lepidopteran leaf miners the mandibles and hypopharynx provide diagnostic structures that are useful for generic diagnoses. Davis *et al*. (2013) indicated that in tissue feeding gracillariid larvae the anterior margin and dorsal surface of hypopharynx are highly diagnostic: the hypopharynx of larval *Cremastobombycia* bears a transverse series of six, relatively large, spinose, digitate lobes (Davis *et al*. 2013: Figs 13–15). The hypopharynx of tissue-feeding *Phyllonorycter* larvae possesses a series of over 20 much smaller, curved, smooth spines (Davis & Deschka 2001: Figs 56–58). The hypopharynx of the two non-feeding larval instars in *Cameraria* is mostly smooth and without anterior spines (De Prins *et al*. 2003: Fig. 10; Davis *et al*. 2013). The ventral surface of the last instar larva of *Triberta* is covered with hypopharyngeal striations, which differentiates the latter genus from *Cameraria*, *Cremastobombycia* and *Phyllonorycter*. Pupa without cremaster in *Triberta* and remaining eight lithocolletine genera, except in *Phyllonorycter* and *Porphyrosela*. The cremaster is well-defined in *Phyllonorycter* and reduced, consisting of four little hooks, in *Porphyrosela* (Bentancourt & Scatoni 2007). A thickened sclerotized ridge present along the lateral sides of pupal A1–8, in *Triberta,* which differentiates the new genus from *Phyllonorycter* and *Cameraria*. In the latter genera this lateral cuticle sclerotization is absent. Pupation occurs outside the mine, an ecological trait shared only with *Chrysaster* and *Leucanthiza;* and in a transparent oval-shaped and slightly raised cocoon. Members of the new genus *Triberta* are known to feed exclusively on Cistaceae. *Triberta* also differs from *Phyllonorycter* and *Cameraria* in a concatenated dataset of eleven nuclear gene sequences.

To facilitate the assignment of lithocolletine moths to *Triberta*, a summary of the foregoing diagnoses is provided: **Adult**: 1) wing venation: presence of 7 terminal veins in forewing, presence M_1 and M_2 in hind wing like in *Protolithocolletis;* 2) male genitalia: sternum VIII developed, saccus undeveloped, a pair of setae on apex of tegumen, aedoeagus bifurcate at coecum; 3) female genitalia: ostium bursae opens in subanterior area of segment VIII; compact signum on corpus bursae present. **Larva**: 4) feeds on Cistaceae, differing from all other genera of Lithocolletinae; hypopharynx of last instar larva covered with striations. **Pupa**: 5) pupation outside the mine; pupa with lateral cuticle sclerotization and without cremaster. **Molecular**: 6) *Triberta* is not nested within two well-supported clades *Phyllonorycter*+*Cremastobombycia* and *Cameraria*.

Description. *Adult* (Figs 02, 06–25). Small moths, forewing length ca**.** 2.5–4.5 mm.

Head. Vertex plate joined with frontoclypeus, head tufted with erect long piliform scales, whitish posteriorly, ochreous anteriorly; frons covered with appressed, smooth, shiny white scales with ochreous apices; eyes large, ocular index ca. 0.6–0.7, interocular index ca. 1.0. Antenna ca. 20% shorter than forewing, smooth scaled, filiform; scape short, thickened, bearing pecten of different lengths, flagellomere 1 ca. 1.6× shorter than scape, flagellomere 2 ca. 10% longer than flagellomere 1. Proboscis developed, naked, of medium length, ca. 1.7× length of labial palpus. Maxillary palpus small, rudimentary, two-segmented, apical maxillary palpomere almost globular. Labial palpus moderate, porrect, filiform, drooping, straight, with ratio of labial palpomeres from base 1.0:1.8:2.0(Fig. 02).

Thorax: Forewing length 2.5–4.5 mm; forewing ground colour beige-ochreous with intermixture of dark brown and white fasciae or chevrons which are highly variable in angulation and width; white markings are edged on both sides basally and apically; fringe very long, particularly at dorsal margin, reaching width of wing in forewing and ca. 3× width of wing in hindwing; fringe of hindwing very long, exceeding 4× width of hindwing. Descaled forewing lanceolate, slender, and with strongly acute apex. Venation with 10 veins, distal margin with 7 veins R_2, R_3, R_4, R_5, M_1, M_{2+3}, $Cu_{1;}$ R_1 is rudimentary, M is forked to form M_1 and M_{2+3}, Cu_1 separate, CuP indistinct (fold) over entire length, A_1 strong, separate; discal cell is open with absence of crossvein between R_5 and M_1 and with weak connection between R_2 and R_3. Hindwing lanceolate, maximum width/hindwing length is 0.15, venation

5 veined; Sc very short, terminating near base of costa; Rs very long, extending almost to apex of hindwing; M_1 and M_2 stalked; basal 2/3 of M_{1+2} indistinct, parallel to Rs; distal part of M_1 terminates at 0.7 the distance to dorsal margin; M_2 terminates at 0.6 of dorsal margin, Cu_1 strong, ending at 0.4 of dorsal margin; A_1 vestigial (Fig. 03). Frenulum in male is a single stout bristle; frenula in female are two tightly appressed bristles. Legs slender, with darker rings; epiphysis on foreleg absent, mid-tibia bearing a pair of tibial spurs; hind tibia thickened, with long fine loose hairs, long medial and short apical spurs; hind tarsus smooth, slender, ca. 1.5× as long as tibia.

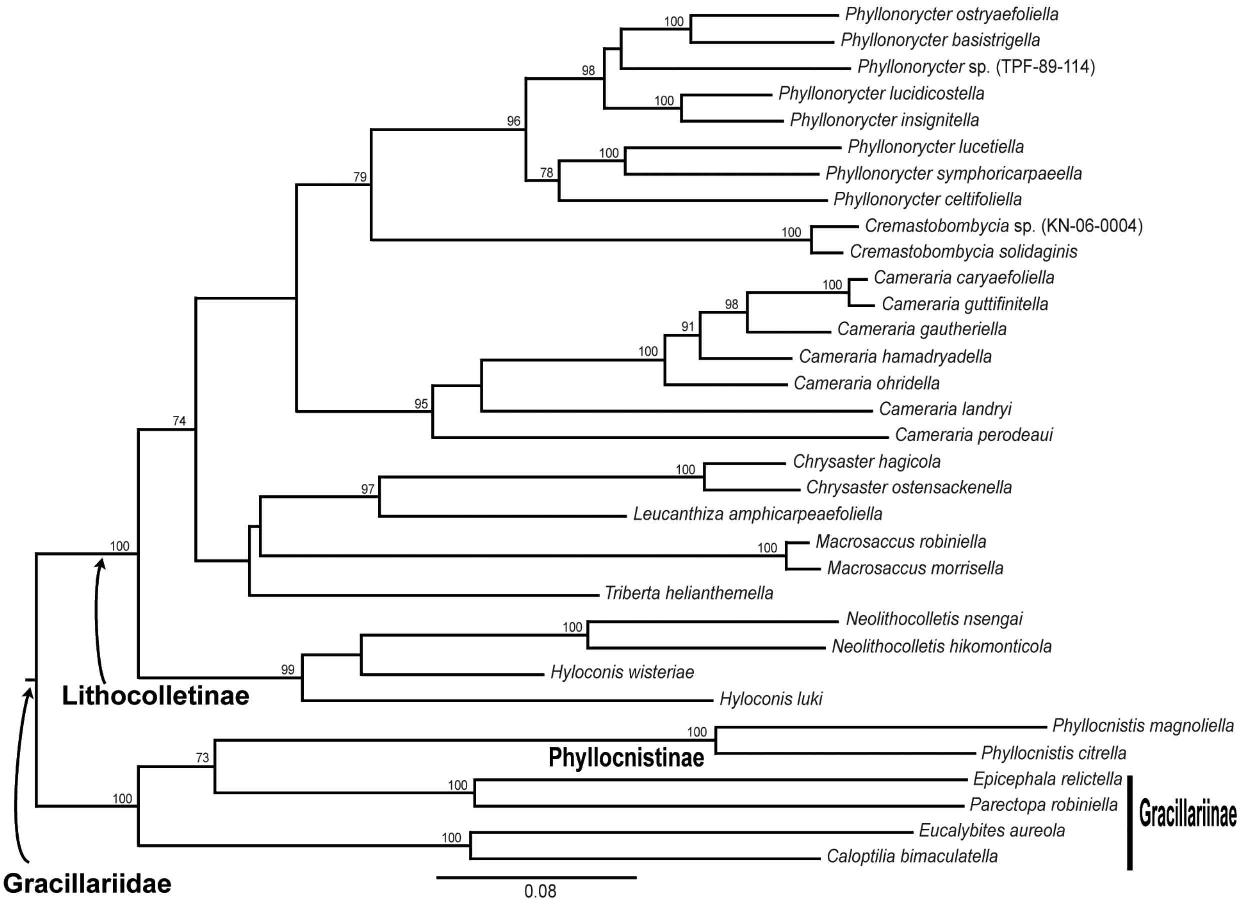
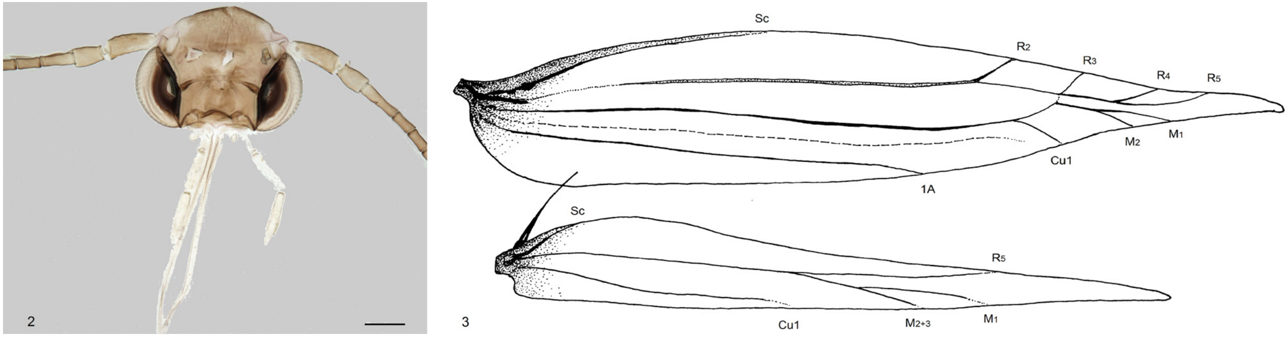
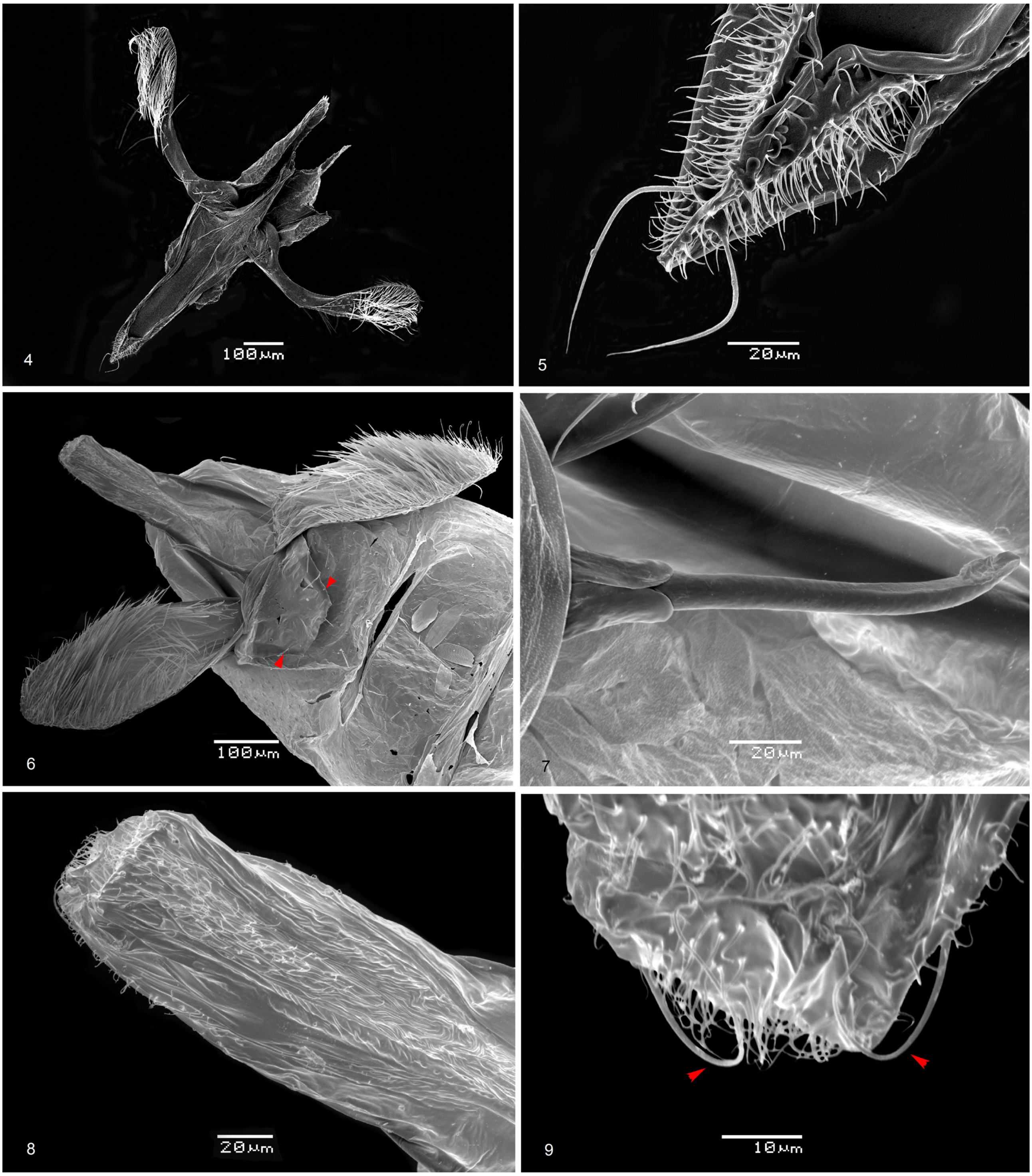


FIGURE 01. Maximum Likelihood tree of Lithocolletiinae. The numbers above nodes denote the bootstrap nodal supports. Only the bootstrap values > 70% are shown.



FIGURES 02–03. Adult morphology of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 02, descaled head prep. DP 3797♀. Scale bar 100 µm. 03, wing morphology, descaled wing prep. DP 3809♀. Scale bar 1 mm.

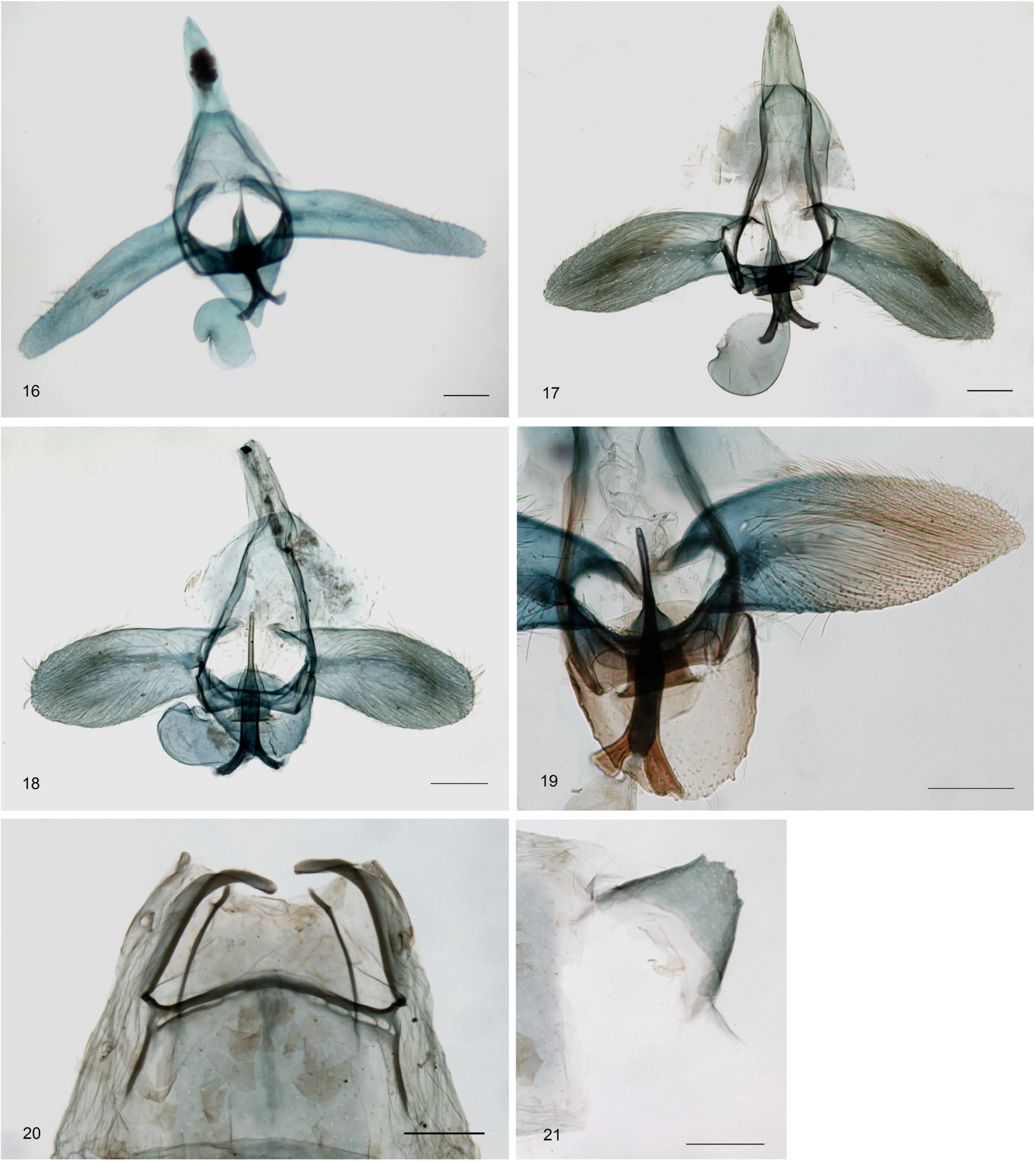


FIGURES 04–09. Male genitalia of *Cameraria* and *Triberta*. 04, Male genitalia of *Cameraria ohridella*, Belgium, Tervuren, 11.v. 2012, leg. E. De Coninck. Scale bar as indicated. 05, same preparation, tegumen with a pair of apical setae. Scale bar as indicated. 06, male genitalia of *Triberta helianthemella*, Austria, North Tirol, 07.xi.1964; prep. DP 3826♂; arrows indicate the modified sternum VIII. 07, same preparation, aedoeagus. 08, same preparation, tegumen. 09, same preparation, apex of tegumen; arrows indicate a pair of apical setae. Scale bar as indicated.

FIGURES 10–15. The primary types of *Triberta* species. 10, the neotype of *Lithocolletis cistifoliella* Groschke, 1944, male, in ZSM. 11, the lectotype of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, in ZMHB. 12, the paralectotype 1 of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, in ZMHB. 13, the paralectotype 2 of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, in ZMHB. 14, the paralectotype 3 of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, female, in ZMHB. 15, the paralectotype 4 of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, female, in ZMHB. Scale bar 1 mm.

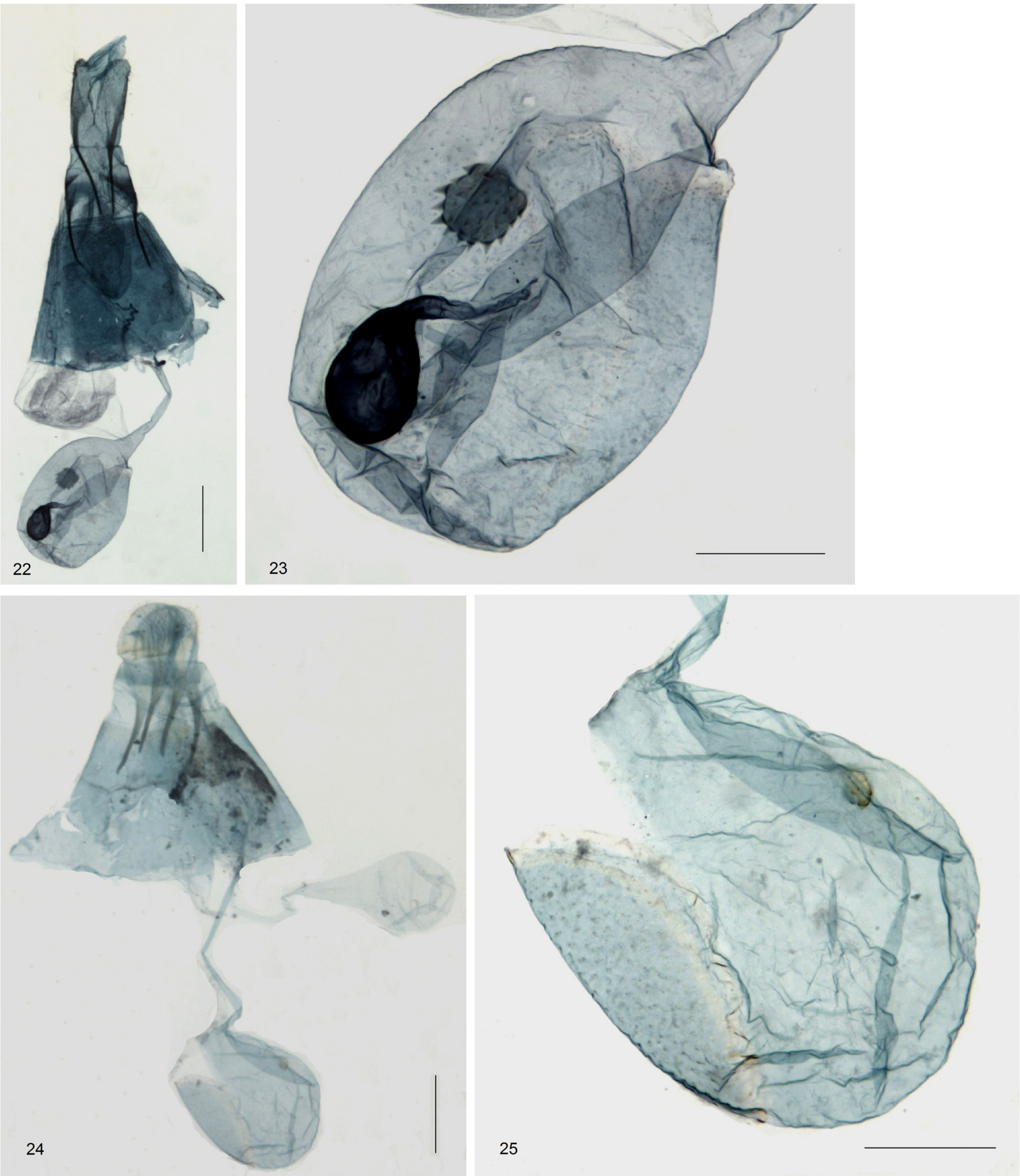
Abdomen. Anterior margins of abdomen with narrow opening and sclerotized, becoming slightly broader towards S2; the sclerotized anterior margin of the abdomen well connected on T2 and unconnected on S2 or weakly joined by V-shaped narrow sclerotized connection; S2 apodemes of median length, ending well beyond the abdominal opening, slender, with barbed bases, very slender distally; a pair of sclerotized T2 apodemes initiate at the lateral connection corner of abdominal opening, with broad sclerotized bases, slightly shorter than S2 apodemes. A pair of tiny sublateral-medial spicules present on each abdominal sternum. Sternum VIII in adult males developed, flap-like, extended, more or less triangular caudally (Figs 06, 16, 19, 21).

Male genitalia (Figs 16–19). Tegumen rather long, with a pair of subapical setae. Tuba analis sometimes significantly protruded. Valvae symmetrical, setose. Transtilla incomplete. Vinculum developed, crescent or trapezium shaped, without prominent saccus. Anellus developed, strongly sclerotized, tubular, broader at base; juxta present. Aedoeagus ca. ¼ shorter than valva, relatively complex, with bifurcated coecal end and gradually tapering towards slender apex; cornuti absent.

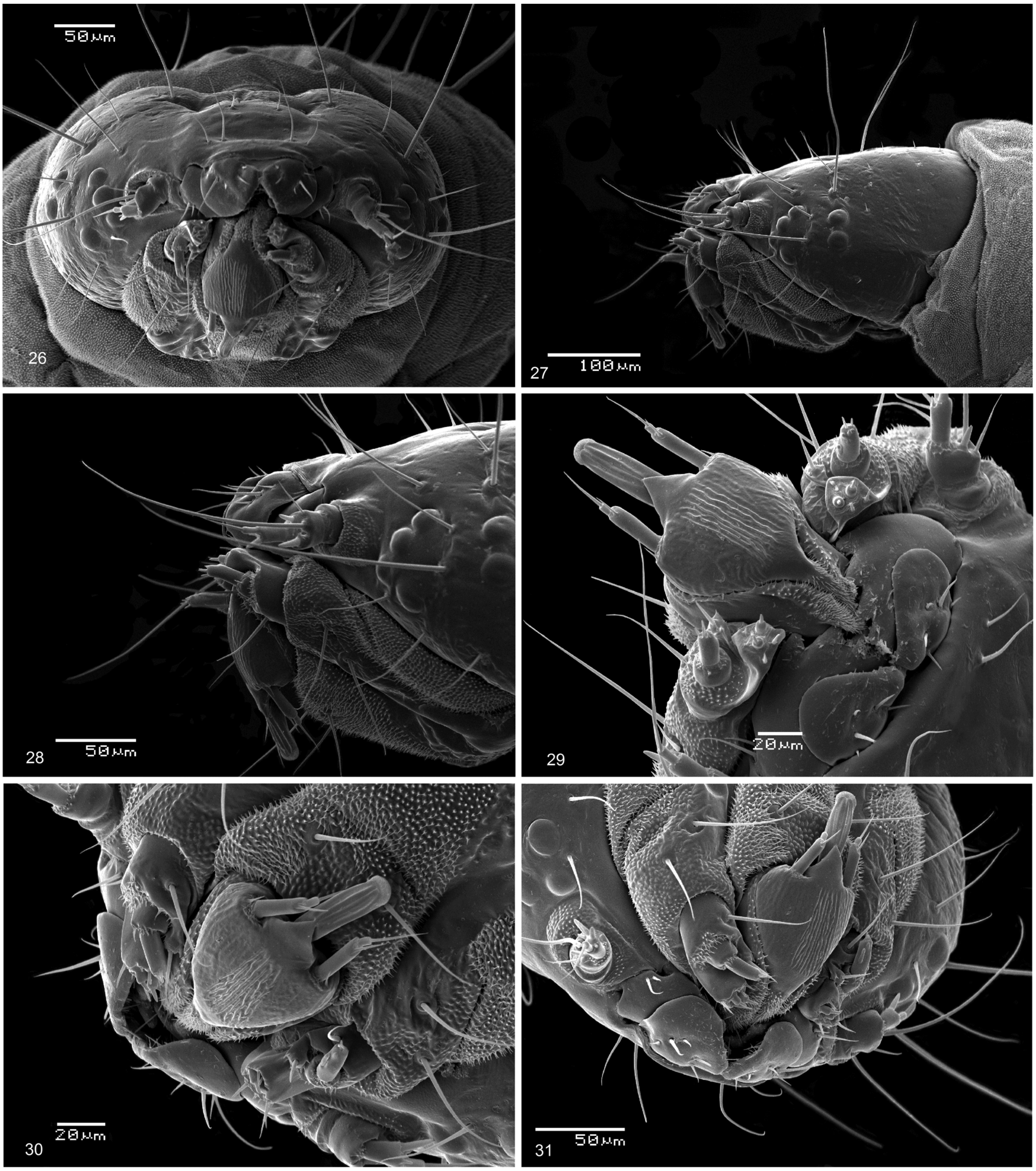


FIGURES 16–21. Male genitalia of *Triberta* species. 16, *Lithocolletis cistifoliella* Groschke, 1944, male, neotype, prep. TRB3554♂, in ZSM. 17, *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, lectotype, prep. TRB3935♂, in ZMHB. 18, *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, paralectotype, prep. TRB3945♂, in ZMHB. 19, Valva of *Triberta helianthemella*, male, Italy, Verona, 25/30.vi.2010, leg. P. Triberti, prep. TRB3552♂, in MSNV. Scale bar 100 µm. 20, abdomen opening of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, lectotype, prep. TRB3935♂, in ZMHB. Scale bar 200 µm. 21, sternum VIII of *Lithocolletis helianthemella* Herrich-Schäffer, 1861, male, lectotype, prep. TRB3935♂, in ZMHB. Scale bar 100 µm.

Female genitalia (Figs 22–25). Papillae anales rounded caudally, not connected laterally. Segment VIII short, well connected to segment VII. Posterior apophyses without basal plate, but thickened basally and gradually acute apically; anterior apophyses originating from sclerotized basal plate of segment VIII, similar in form to posterior apophyses. Ostium bursae opens at the subanterior region of segment VIII. Ductus bursae very narrow, long with sclerotized antrum; ductus seminalis arises ca. midway along ductus bursae (Figs 22, 24). Corpus bursae distinct from ductus bursae, globular, with two signa regions: a relatively large speculate-sculptured disc along lateral wall of corpus bursae and a strongly sclerotized stellate signum covered with small sharp barbs about midway along the opposite wall of corpus bursae (Figs 23, 25).

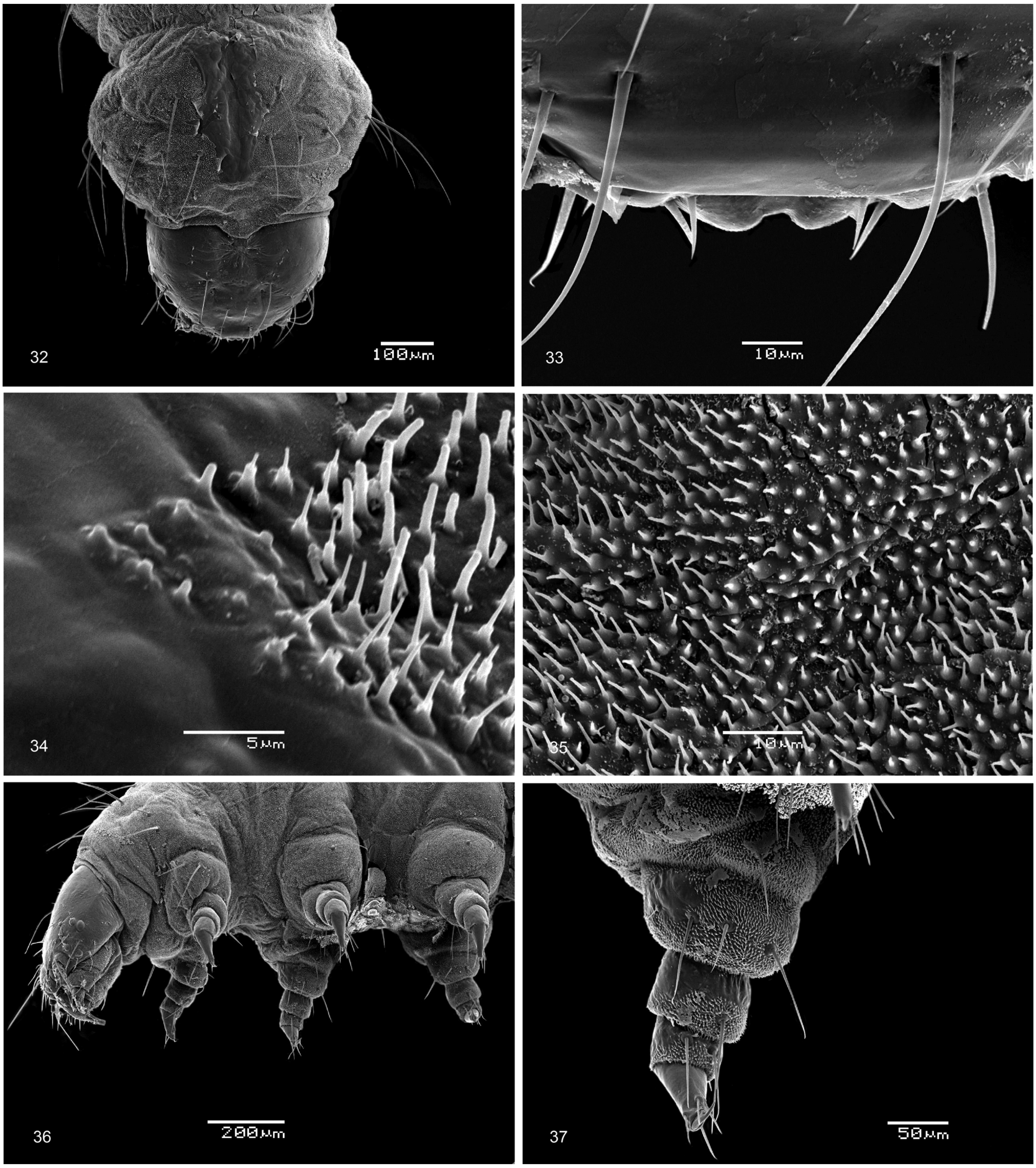


FIGURES 22–25. Female genitalia of *Triberta* species. 22, *Triberta cistifoliella*, Greece, prep. TRB3559♀. Scale bar 200 µm. 23, same preparation, signum on corpus bursae, prep. TRB3559♀. Scale bar 100 µm. 24, *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti, prep. DP3807♀. Scale bar 200 µm. 25, same preparation, signum on corpus bursae, prep. DP3807♀. Scale bar 100 µm.

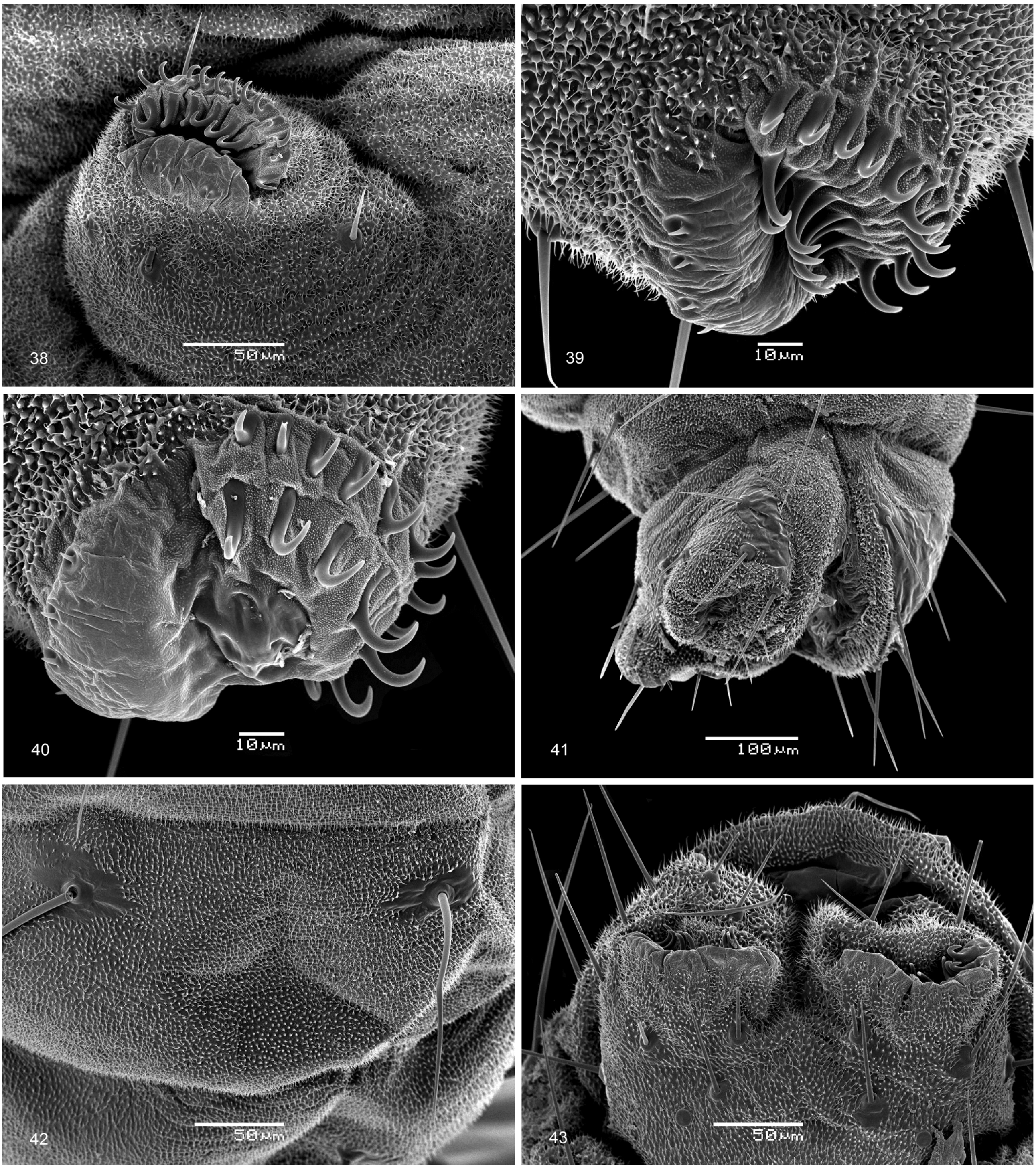


FIGURES 26–31. Head of late instar larva of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 26, frontal view. 27, lateral view. 28, mouthparts. 29, mandibles and hypopharynx, ventral view. 30, ventral surface of head. 31, maxillary palpus. Scale bar as indicated.

Larva. Last instar larva ca. 3.6 mm long. Head of late instars approximately round with full complement of mouthparts (Fig. 26, 29–31); 3 pairs of stemmata arranged per pair: stemmata 1 and 2 in a horizontal row distant from each other; stemmata 3 and 4 close to antenna in a vertical row at short distance close to each other; stemmata 5 and 6 in a vertical row touching each other (Figs 27, 28). Nine setae surround the stemmata of which S3 is very short; antenna 3-segmented with second segment moderately long; sensilla as shown in Fig. 31; labrum strongly bilobed with raised median part (Fig. 33); M_1 and M_4 present; inner perimeter of labrum without spines; the dorsal surface of the hypopharynx of the last tissue feeding larval instar is covered with hypopharyngeal striations (Figs 29–31); ventral surface of head covered with numerous short rough spines; maxillary palpus as shown in Figs 29–31; median lobe of the maxilla with numerous sensory setae of different lengths. Labial palpus bears two sensory setae: one short seta, ca. 2× longer than apical palpomere and one long seta ca. 4x length of apical palpomere. Spinneret a relatively long striate tube (Fig. 29). Thorax with setae XD_1 and XD_2, SD_1 long, immediately ventral to $XD_{2;}$ SD_2 absent on T1; L group of setae long, L_2 longer than L_1; dorsal surface of T1 covered with both longer and shorter protrubances (Fig. 34); T2 and T3 with long D_1 and shorter $D_{2;}$ dorsal surface of thoracic segments covered with tiny spines (Fig. 35). Legs fully developed, coxae with 4 coxal setae; femur and tibia with very long setae; tarsal claw with a sharp spine (Figs 36, 37). Abdomen with bisetose D group on A1–8, unisetose on A9 (Fig. 42). Prolegs present on A3–5, 10; crochets consisting of 16 larger hooks arranged in biordinal semicircle and four small spines arranged in a row opposite the larger hooks (Figs 38–40); anal prolegs with crochets consisting of ca. 10–12 rather large hooks arranged in a uniordinal semicircle (Fig. 43). Anal plate with three pairs of setae (Fig. 41).

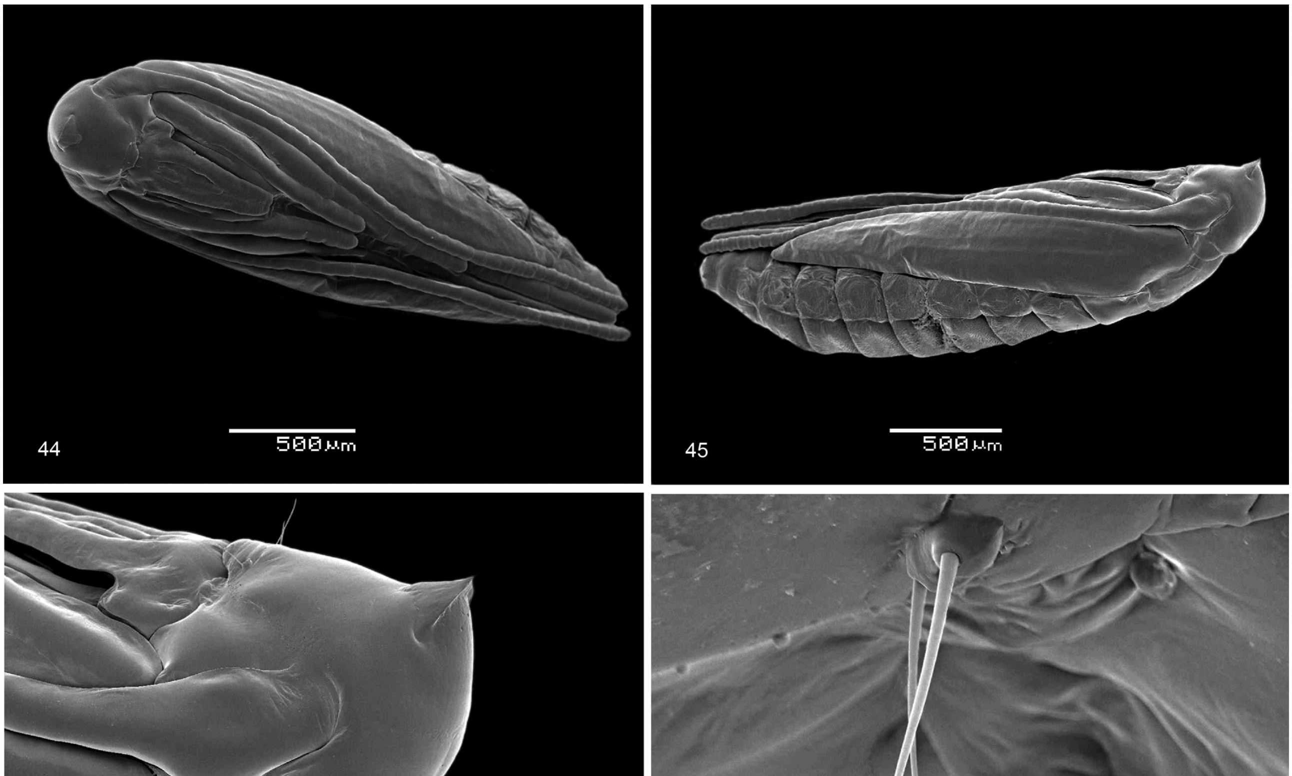


FIGURES 32–37. Late instar larva of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 32, head and 1st thoracic segment of last instar larva, dorsal view. 33, same preparation, proximal part of head. 34, dorsal surface of T1. 35, dorsal surface of T3. 36, legs of late instar larva, latero-ventral view. 37, median thoracic leg, lateral view. Scale bar as indicated.

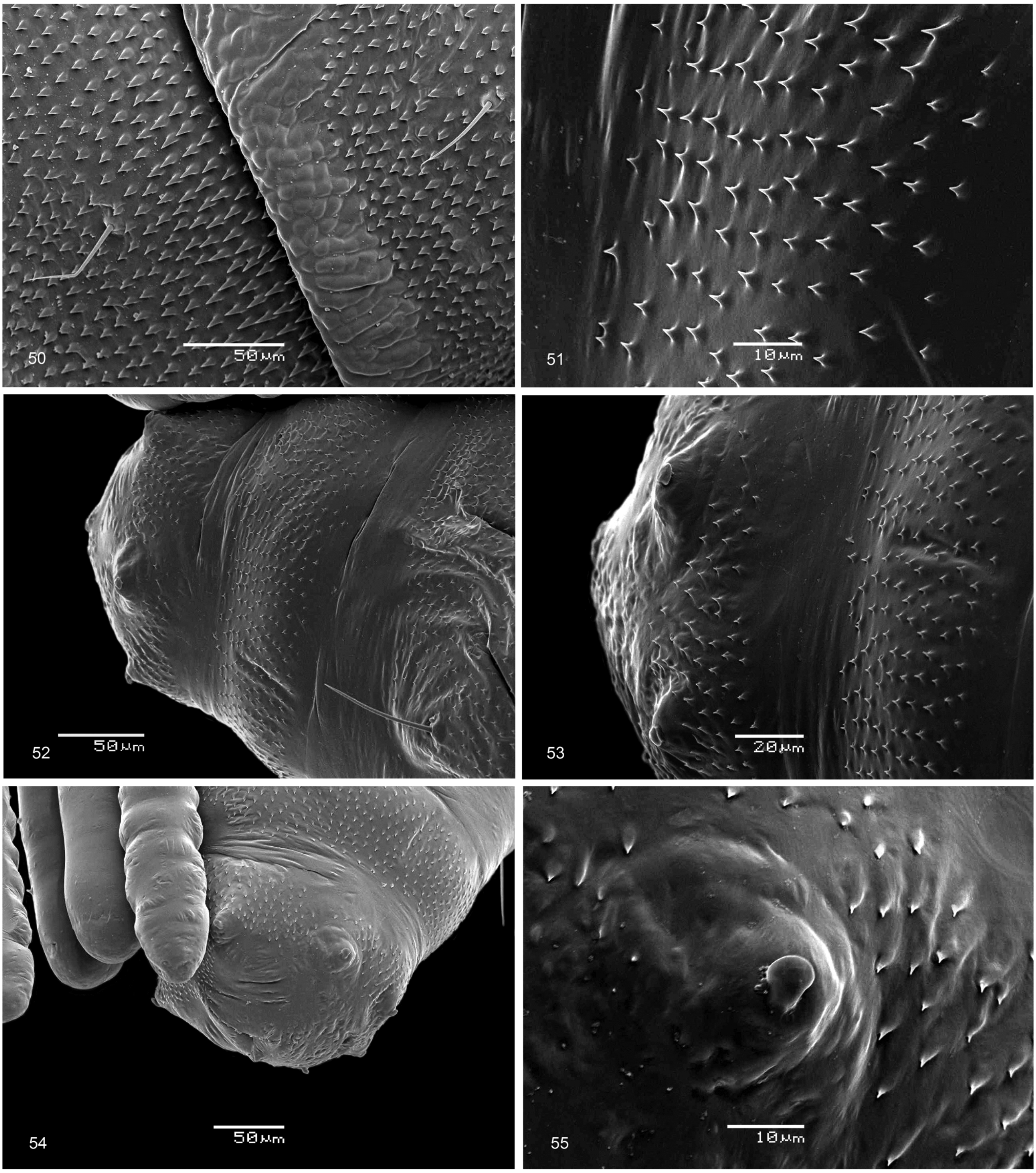


FIGURES 38–43. Prolegs of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 38, ventral view. 39, crochets in rest position, ventral view. 40, crochets in open position, ventral view. 41, caudal segments. 42, abdominal segment A9, dorsal view. 43, caudal prolegs, ventral view. Scale bar as indicated.

Pupa. Maximum length ca. 2.5 mm, width ca. 0.8 mm; body elongate, compact, relatively flat, narrower over last 4 segments (Figs 44–45); color a bright shade of brown. A thickened sclerotized ridge present along the lateral sides of A1–8. Head smooth, with two pairs of sockets bearing sensillae (Fig. 46, 47). Vertex furnished with a frontal process (cocoon cutter), which is relatively short, broadly triangular, with slightly wrinkled median surface (Fig. 46). Forewings long, extending to the posterior margin of abdominal segment A6, and contiguous at their distal ends (Figs 44, 54). The appendages of antennae longer than forewings and extend up to caudal end of pupa. Labium rather long, ca. 1.7× shorter than proboscis. The hind leg sheaths are slightly shorter than antennal appendages (Fig. 54). The distance between the apices of the mesothoracic and metathoracic legs is approximately 1.46× the distance between the apices of the prothoracic and mesothoracic legs. One pair of dorsal setae is present on segments TII–TIII. Abdominal segments A1–5 of more or less equal size, A6–8 strongly decreasing in size. Abdominal segments A3–8 covered with dense, minute spines dorsally (Fig. 51); the posterior margin of A1 with a wrinkled band (Fig. 50); dorsal surface of each abdominal segment carries a pair of setae, except segment A9 which lacks setae (Fig. 52). Terminal segment A10 fully covered with small spinaculae (Figs 53, 54); caudal surface of A10 without cremaster but with eight tiny protuberances each carrying a tiny nodule (Fig. 55) (Gregor & Patočka 2001: 34; Patočka & Turčáni 2005).



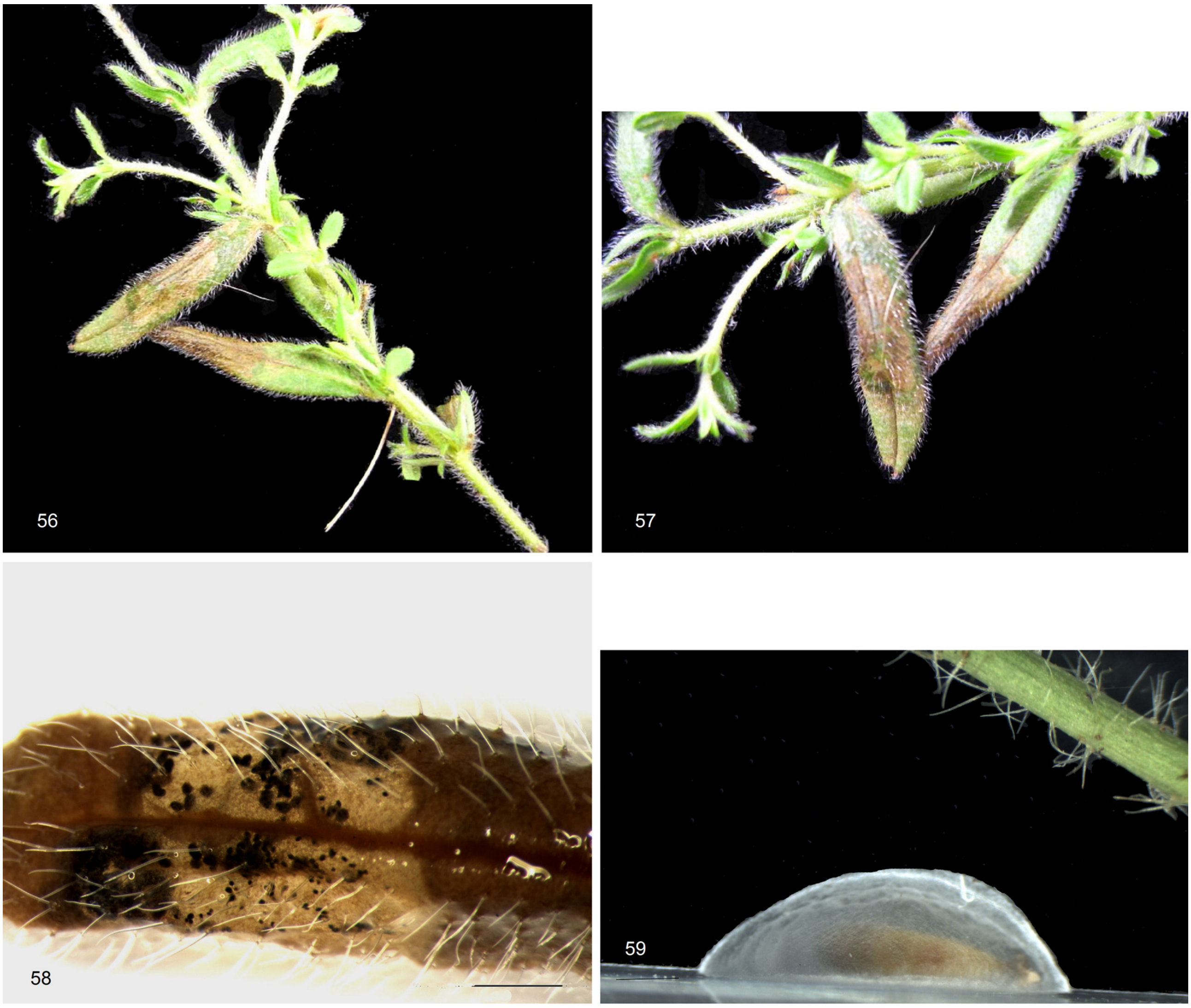
FIGURES 44–49. Pupa of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 44, ventral view. 45, lateral view. 46, pupal head. 47, A pair of frontal sensillae on pupal head. 48, sclerotized ridge on pupal segments A2. 49, sclerotized ridge on pupal segments A6-8. Scale bar as indicated.



FIGURES 50–55. **P**upa of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 50, dorsal surface of segment A1. 51, dorsal surface of segment A8. 52, segments A8-9, lateral view. 53, caudal segment, dorsal view. 54, A10, caudal view. 55, nodule on caudal protuberance. Scale bar as indicated.

Biology. Larva solitary, feeding exclusively on Cistaceae. Abaxial mine begins as a small corridor that closely follows a thick vein of the plant. It continues into a contracted blotch mine that may occupy the entire leaf; mine becomes transparent when it is fully grown. The tissue-feeding instars remove mesophyll layers of the leaf, and though the mine is formed under the abaxial epidermial layer, from adaxial leaf surface it is visible as a large, contiguous brownish blotch (Figs 57, 58). However, in some cases the mine can be formed on adaxial surface (see the original description of *Lithocolletis cistifoliella* here below). Frass distributed either in a row while larva crosses the vein or loose in small accumulations. Pupation occurs outside the mine in a transparent cocoon on a clean background without excrements (Fig. 59). Biology bivoltine with hibernation as adults is reported.

Host plants: Cistaceae: *Cistus creticus* L. (= *C. villosus* L.) (Klimesch 1956: 215); *C. incanus* L. (Klimesch 1956: 215), *C. monspeliensis* L. (Walsingham 1908: 976), *C. salviifolius* L. (Groschke 1944: 122). *Helianthemum chamaecistus* Mill. (Hartig 1964: 177), *H. nummularium* (Cav.) Losa & Rivas Goday (Gregor 1986: 229), *H.* sp. (Eckstein 1933: 163; Weber 1945: 389; Gregor & Povolný 1950: 135; Hartig 1964: 177; Szöcs 1981: 216), *H. vulgare* Gaertn. (Herrich-Schaffer 1861: 20), *Tuberaria guttata* (L.) Fourr. (Roüast 1884: 138).



FIGURES 56–59. Biology of *Triberta helianthemella*, Italy, Verona, 25/30.vi.2010, leg. P. Triberti. 56, host plant *Helianthemum nummularium*. 57, mine, adaxial view. 58, excrements of larva in mine, adaxial view. 59, transparent cocoon outside the mine. Scale bar 1 mm.

Natural enemies. Eulophidae: *Chrysocharis phryne* (Walker, 1839) (Noyes 2012), *Cirrospilus staryi* Bouček, 1958 (Bouček 1959: 180), *Hemiptarsenus ornatus* (Nees, 1834) (Noyes 2012), *Sympiesis gregori* Bouček, 1958 (Bouček 1959: 131).

Distribution. *Triberta* is a genus of xerothermic habitats in central and southern Europe, the Mediterranean region, and the Canary Islands.

Austria (Knitschke 1927: 97); Canary Islands: La Palma (Hering 1927), Tenerife (Walsingham 1908: 976); Croatia (Wocke 1871: 329); Czech Republic (Nickerl 1894: 29); France (Jourdheuille 1870: 133, 254); Germany (Herrich-Schaffer 1861: 20); Greece (Klimesch 1968: 176); Hungary (Szöcs 1981: 216); Italy (Mann 1867: 841), Sicily (Amsel 1951: 422), Macedonia (Klimesch 1942: 387); Moldova (Bouček 1961: 21); Serbia (Amsel 1951: 422); Slovakia (Gregor 1986: 229); Spain (Vives Moreno 1994: 54, 557); Switzerland (Weber 1945: 389); Turkey (Stainton 1867: 35).

FIGURES 60–61. Diagnostic characters in *Triberta* head vestiture of adults. 60, vertex of the neotype of *Lithocolletis cistifoliella* Groschke, 1944. 61, vertex of the lectotype of *Lithocolletis helianthemella* Herrich-Schäffer, 1861. Scale bar 100 µm.

Generic relationships and species diversity. Based on taxa included in our phylogenetic analysis *Triberta* is the sister lineage to the clade *Macrosaccus+(Leucanthiza + Chrysaster)*. The ecological / morphological traits shared by these latter genera are as follows: *Triberta, Leucanthiza* and *Chrysaster* pupate outside the mine, the mine of *Triberta* and *Macrosaccus* is blotch abaxial, while *Leucanthiza* and *Chrysaster* construct adaxial mines; pupa in *Triberta* without cremaster like in other members of the clade; in the male genitalia, apex of tegumen carries one pair of setae, valvae symmetrical, densely setose; sternum VIII in *Triberta* is caudally extended, the character that separates *Triberta* from the other genera of the clade *Chrysaster*, *Leucanthiza* and *Macrosaccus*; in the female genitalia, ductus bursae very slender and long extending to segment V, corpus bursae in most cases distinct from ductus bursae and bears a compact signum (signa).

In addition to the morphological characters mentioned above, a molecular phylogeny based on eleven nuclear genes places *Triberta* apart from *Phyllonorycter*, *Cremastobombycia*, and *Cameraria* (Fig. 01).

Two species, both Palaearctic, are currently recognized in the new genus *Triberta*. The circumscription, delimitation and delineation of *Triberta* species will be presented in a separate study.

Etymology. The name *Triberta* is used as a noun in the nominative singular and feminine gender. This name is a patronym in honour of Paolo Triberti, a lepidopterist from the Museo Civico di Storia Naturale, Verona, Italy, who revised and studied many groups of Gracillariidae, the lepidopteran family to which the new genus belongs.

Taxonomic account

Triberta cistifoliella (Groschke, 1944), comb. nov.

Lithocolletis cistifoliella—Groschke (1944: 122–124, figs 7, 9) [original description]; Amsel (1951: 422).

Lithocolletis helianthemella—Walsingham 1908: 976 [misidentification of *L. cistifoliella*], Klimesch 1942: 387 [misidentification of *L. cistifoliella* (Klimesch 1956: 215)], 1968: 176; Kuznetzov 1981: 296 [synonymization of *L. cistifoliella* Groschke with *L. helianthemella* Herrich-Schäffer, the illustration Fig. 272/1 on p. 297 as *L. helianthemella* is a misidentification of *L. cistifoliella*].

Lithocolletis cisticolella—Hering 1957: 304 [an incorrect subsequent spelling of *L. cistifoliella* Groschke, 1944 (Klimesch 1979: 155)].

Phyllonorycter cistifoliella—Klimesch 1979: 155; Vives Moreno 1994: 54; Gaedike *et al*. 1995: 18; De Prins & De Prins 2005: 300.

Translation of the original description:

[As in the case of *Weberina lentiscella* spec. nov. where the mine was known years before the insect could be identified, a *Lithocolletis*-mine was known for years to occur on *Cistus salvifolius* [sic], of which I now describe the insect as ***Lithocolletis cistifoliella*** spec. n. (fig. 7).

The colour and pattern of the forewing show that the new species is very closely related to *Lithocolletis helianthemella* H.-S. (fig. 8). The forewing is dark golden brown. Forewing with white base, with a sharply broken transverse band, and with 3 strongly curved and 1 almost straight, pure white uncinate markings at costa and dorsum which are connected to form transverse bands. All white markings and the outer margins are edged with blackish brown, basally stronger than distally. A black longitudinal line present distally. Inside the golden brown area, near the corners of the transverse bands, not as clearly edged with white and touching the white markings.

Forewing fringes golden brown, externally white.

Hind wings grey, as are the fringes which possess a golden brown luster at their bases.

Head and thorax white with contrasting dark brown tegulae and patagia. Abdomen grey.

Antennae whitish to brownish, not strongly ringed.

Legs white with very strong, brownish black rings.

J. Klimesch, Linz, kindly sent me a drawing of the forewing of *Lithocolletis helianthemella* H.-S., and this allows me to show more easily and clearly the differences between both species. The pure white bases, the more oblique and connected white strigulae, and the characteristic apical part, in my opinion, differentiate clearly this *Lithocolletis cistifoliella* from *L. helianthemella* H.-S., so that captured specimens can also be identified unquestionably to belong to one or the other species.

I reared 8 specimens which belong to two separate generations: 5 specimens from 4.xii.1942 to 9.i.1943 and 3 specimens from 23.vi to 15.vii.1943, and furthermore I caught one specimen flying on Monte Poretta near Taormina on 2.ix.1942, which is certainly a late specimen of the summer generation.

At the same locality I also found caterpillars of the bred specimens in November–December and in June. They made mines (fig. 9) on the underside of the leaves, except in two instances where the mines were on the upperside, without any preference of a particular place on the leaf. As typical for this genus, the initial epidermal mines grew to tentiform mines, which followed the strong side nerve of the *Cistus*-leaf. The frass is gathered into a smooth ball. In order to pupate, the caterpillar leaves the mine and makes a white, shiny cocoon similar to those in the genus *Caloptilia*.

This last fact is, apart from the systematic characters, a further biological character that demonstates a relationship of the new species with *Lith. helianthemella*.

The pupal period of both generations is 3–4 weeks.]

Neotype designation. The German lepidopterist Franz Groschke (1914–1956) worked at (or was associated with) the Zoological Institute in Tharandt (possibly part of the "Forstliche Hochschule Tharandt"), next to Dresden during the war years of his military service in 1940–1944. However his collection was not transferred to the State Museum of Zoology (Staatliches Museum für Tierkunde) in Dresden (Matthias Nuss, pers. corr.). The type specimens of *Lithocolletis cistifoliella* are also absent in Stuttgart (Staatliches Museum für Naturkunde Stuttgart) where Franz Groschke worked before his death in 1956 (Andreas Zwick, pers. corr.). There is no publication except the original description which refers to the type specimens of *L. cistifoliella*, though significant efforts were made to find them by Jozef Wilhelm Klimesch during the preparation of his study "Beiträge zur Kenntnis der Microlepidopteren-Fauna des Kanarischen Archipels" (1979). We believe that the type specimens of *Lithocolletis cistifoliella* Groschke 1944 were lost during the last years of the second world war or the years after the war, and could not be traced despite the efforts of the curators from Staatliches Museum für Tierkunde in Dresden and Staatliches Museum für Naturkunde in Stuttgart. There is an exceptional need to designate the name bearing type under the conditions specified by the ICZN Art. 75: (1) the neotype is designated with the express purpose to clarify the taxonomic status of closely related species within the new genus *Triberta* and to restore the species *Lithocolletis cistifoliella* Groschke 1944 from synonymy; (2) we present the diagnosis of the valid species *L. cistifoliella* and its bibliographic references; (3) label data are presented to ensure the recognition of the specimen designated; (4) we state that the neotype is consistent with what it is known of *Lithocolletis cistifoliella* Groschke, 1944 from the original description and the original illustrations (Groschke 1944: 122–124, figs. 7, 9); (5) the neotype originates near to the original type locality (ICZN Art. 76.1); (6) we designate as the neotype of *Lithocolletis cistifoliella* Groschke, 1944 the historic male specimen collected and studied by Josef Wilhelm Klimesch, who labelled it in the collection as 'a paralectotypus', but did not officially designate it as the neotype; (7) the deposition of the neotype is the ZSM, a publically recognized scientific institution, that has managed to preserve historic Lepidoptera specimens, has proper facilities for preserving this particular name-bearing type for future generations, and assures the accessibility of the neotype of *Lithocolletis cistifoliella* Groschke, 1944 for further studies.

Here we designate the following male specimen as the neotype of *Lithocolletis cistifoliella* Groschke, 1944:

♂, [1] 'Sicilia, Palermo, S. Martino d. Scale, 1–12.vi.1954, J. Klimesch'; [2] 'genitalia slide TRB3554♂', in the ZSM (Figs 10, 16).
Additional specimen from the same series:
♀, 'Sicilia, Mistretta, Mercuore, 700 m, 21–30.VI.52, J. Klimesch', in the ZSM.
Remarks: the abdomen of this female specimen is damaged and genitalia are not in condition to be examined.

Triberta helianthemella **(Herrich-Schäffer, 1861), comb. nov.**

Lithocoiletis helianthemella—Herrich-Schäffer (1860–1862: 20, nr. 89; pl. 18, fig. 115) [an incorrect subsequent spelling of the generic name].

Lithocolletis helianthemella—Wocke 1861:127; 1871: 329; Walker 1864: 908; Mann 1867: 841; Stainton 1867: 35; Jourdheuille 1870: 133, 254; Chambers 1877: 84; 1878: 150; Staudinger 1880: 412; Steudel & Hofmann 1882: 230; Roüast 1884: 138; Nickerl 1894: 29; Disqué 1908: 82; Hering 1927: 463 [mines only], Knitschke 1927: 97; Le Marchand 1932: 41; 1936: 111; 1939: 258; Eckstein 1933: 163; Klimesch 1942: 387 [a misidentification of *L. cistifoliella* Groschke, see Klimesch 1956: 215); Groschke 1944: 122; Weber 1945: 389; Gregor & Povolný 1950: 135, 140; Amsel 1951: 422; Osthelder 1951: 217; Hartig 1956: 136; 1964: 177; Hartwieg 1958: 117; Bouček 1959: 131, 180; 1961: 21; Bradley *et al.* 1969: 28; Kuznetzov 1981: 170, 173, 234, 296, 301 (the illustration Fig. 272/1 on p. 297 is a misidentification of *L. cistifoliella*); Szöcs 1981: 216.

Phyllonorycter helianthemella—Klimesch 1979: 155, 156; Leraut 1980: 62; 1997: 96; Derra 1985: 367; Gregor 1986: 229; Laštůvka & Marek 1992: 62; Huemer & Tarmann 1993: 30; Vives Moreno 1994: 54, 557; Gaedike *et al.* 1995: 18; Buszko 1996: 52; Gregor & Patočka 2001: 34; Fazekas 2002: 297; Szabóky *et al.* 2002: 29; Huemer & Triberti 2004: 180; Biesenbaum 2005: 23, 140, 141; De Prins & De Prins 2005: 300; Laštůvka & Liška 2005: 6; Huemer & Erlebach 2007: 272; Pastorális 2008: 95, 101; Patočka & Kulfan 2009: 56; SwissLepTeam 2010: 49; Huemer 2013: 53.

Translation of the original description:

89. *Lithocoiletis* [sic] *helianthemella* m.—f. 115.

[According to my analytical table it is near *L. acerifoliella*, but certainly different from it. The pattern on the forewing does not consist of 3 golden, "broken" transverse bands, edged on both sides with black and basally coloured golden, but of 4 black chevrons which do not reach either the costa nor the dorsum; in the apex a black transverse line and a black dot.

The larva mines in September and early October on the underside of *Helianthemum vulgare*, mainly the larger leaves, in rocky, shadow-rich localities near Regensburg. It is 2" long; yellow, with faint green transparent gut; with single, fine hairs; head and first 3 legs brownish; head black, last abdominal segments brown; ventral side yellow with central row of brown dots (shining gut canal). In mid-September or October it makes an oval, flat, whitish spinning on a leaf in which it pupates after a few days before hibernating; from 29 larvae only 1 made its cocoon inside the mine.

The larva of the summer generation is full-grown at the end of June and the adult emerges mid-July; only this have we reared thus far, and moreover just 1 specimen, but we await more in springtime (Ottm. Hofmann).]

Lectotype designation. Gottlieb August Wilhelm Herrich-Schäffer (1799–1874) was an occasional insect dealer of mainly Lepidoptera, who sold insects either directly or sometimes via Zoologische-Mineralogische Verein Regensburg. His private collection via Otto Staudinger and Andreas Bang-Haas was sold in parts and can be found in the following museums: 1) via the collection of O. Staudinger to the Museum für Naturkunde der Humboldt-Universität, Berlin; 2) via the collection of M. J. Bastelberger to the Zoologische Staatssammlung, Munich; 3) via the collections of O. Hofmann and Th. Walsingham to the Natural History Museum, London (Horn & Kahle 1935–1937). Five specimens (3 males and 2 females) were found in the collection of ZMHB which belonged to the collection of Staudinger, and were identified as '*helianthemella*' and were collected and reared in Regensburg without indication which specimen is the name bearing type. We believe that these five specimens were originally collected by Gottlieb August Wilhelm Herrich-Schäffer and sold to Otto Staudinger (Figs 11–15). The phenotype of the male specimen bearing the label of the genitalia slide TRB3935♂ most closely resembles the original description. Therefore, we designate it as the lectotype (Fig. 11).

Here we designate the following male specimen as the lectotype of *Lithocolletis helianthemella* Herrich-Schäffer, 1861:

♂, [1]‘Rgsbg.’[handwritten]; [2]‘ex coll. Staudinger’; [3] genitalia slide TRB3935♂, in ZMHB (Figs 11, 17).
Paralectotypes: 2♂, 2♀:
♂, [1] ‘Regensburg’ [handwritten]; [2] ‘ex coll. Staudinger’; [3] genitalia slide TRB3945♂, in ZMHB (Figs 12, 18)
♂, [1] ‘Regensb’. [handwritten]; [2] ‘ex coll. Staudinger’, in ZMHB (Fig. 13).
Remarks: the sub-triangular shape of the distal half of valva in the male genitalia is variable within the type series (Figs 17, 18).
♀, [1] ‘Regensburg’ [handwritten]; [2] ‘ex coll. Staudinger’, in ZMHB (Fig. 14).
♀, [1] ‘Regensburg’ [handwritten]; [2] ‘ex coll. Staudinger’, [3] ‘Coll. Led.’, in ZMHB (Fig. 15).

Key to the species of *Triberta* based primarily on phenotypic characters of adults, male and female genitalia and on larval host plants

1. Vertex of head whitish with slight brownish suffusion posteriorly; in the male genitalia, valva slender, bar-shaped, its median width never greater than a quarter of its length; caudal part of sternum VIII sharply triangular; in the female genitalia, signum of corpus bursae round, as big as ca. 63×56 µm; host *Cistus* sp. (Figs 16, 22, 23, 60) .... ***T. cistifoliella***

\- Vertex of head brown anteriorly and whitish posteriorly; in the male genitalia, valva with central part enlarged, its median width never less than one third of its length; caudal part of sternum VIII broadly roundish; in the female genitalia, signum of corpus bursae not round, as big as ca. 32×21 µm; host *Helianthemum* sp. (Figs 17–19, 21; 24, 25, 61)..... ***T. helianthemella***

Discussion

The position of *Triberta helianthemella* within Lithocolletinae was not strongly supported in our ML phylogenetic tree. We think that this problem is due to the insufficient phylogenetic signals from the sampled 11 genes. Our single gene trees showed no meaningful supports (>70% BP) except CAD and also no significant signal conflict regarding the placement of *Triberta* among the trees. Our molecular phylogeny, however, supported the distinctiveness of *Triberta* from *Phyllonorycter*. A larger dataset than ours would be necessary to resolve the relationships of *Triberta* with other lithocolletine genera.

The especially diverse genus *Phyllonorycter* Hübner, 1822, presently including 428 species among its numerous and well-defined species groups (Pierce & Metcalfe 1935; Kumata 1963, 1973; Deschka 1975; Davis & Deschka 2001; Kuznetzov & Baryshnikova 2004, 2006; Triberti 2007; De Prins & Kawahara 2012), has traditionally harboured several previously described lithocolletine species with disputable taxonomic affinities or life histories. The first division of the genus *Phyllonorycter* was suggested by Chapman (1902) based on observations of the morphology of larvae made by the American lepidopterist Chambers, who discovered two types of larvae within the then known lithocolletine species: a ‘cylindrical-larva group’ (group I), and a ‘flat-larva group’ (group II). For the latter taxon the generic rank *Cameraria* Chapman, 1902 was proposed. The search and discovery of diagnostic differences in the morphology of pre-imaginal stages became important for the systematics of Lithocolletinae, and diagnoses based on pre-imaginal stages have remained the key-argument for generic delineation within this subfamily for more than a hundred years later. Referring to an apomorphy found on the pupal sternum 7, Davis & De Prins (2011) proposed the new genus *Macrosaccus* and transferred to this new genus the Nearctic *M. robiniella* (Clemens, 1859), an invasive species to Europe, and two other New World species *M. morrisella* (Fitch, 1859) and *M. uhlerella* (Fitch, 1859), which were formerly assigned to *Phyllonorycter*. In the hundred years of taxonomic history following the first separation of the genus *Cameraria* Chapman, 1902 from *Phyllonorycter* Hübner, 1822, the subsequent erections of several new lithocolletine genera: *Cremastobombycia* Braun, 1908, *Porphyrosela* Braun, 1908, *Protolithocolletis* Braun, 1929, *Chrysaster* Kumata, 1961, *Hyloconis* Kumata, 1963, *Neolithocolletis* Kumata, 1963 and *Macrosaccus* Davis & De Prins, 2011, were based on the combined data of adult morphology, pre-imaginal stages, and life history obtained from many rearing experiments and meticulous observations.

Host specificity within the Lithocolletinae genera differs greatly: members of *Phyllonorycter* and *Cameraria* exploit a wide range of host plants worldwide, while species belonging to the remaining lithocolletine genera, including *Triberta*, are specialized to feed on plants belonging only to a single family and, furthermore, occur in biotopes which are biogeographically restricted. Interspecific differences of microstructures within the adult genitalia can be observed in most lithocolletine genera (Opler & Davis 1981; Kumata 1993, 1995; Davis & Deschka 2001; Kuznetzov & Baryshnikova 2004, 2006; Davis & De Prins 2011; Davis *et al*. 2013; De Prins & Kawahara 2012). However, within *Porphyrosela* the species are most readily detectable based on wing pattern (De Prins & Kawahara 2012). The intraspecific phenotypic characters are variable in *Triberta* while the micro-morphological design of genitalia is stable and shows a 'primitive' morphology (Gregor & Povolný 1950). Therefore, we follow the historic approach of species delimitation within this new genus of Lithocolletinae, thereby attempting to avoid taxonomic inflation (Braby *et al*. 2012). The interspecific differences presented here are based on morphology, ecology and biogeography. Although a closer examination of the species of *Triberta* revealed previously unrecognized morphological and ecological differences, future identification on species level will probably have to rely on the combination of diagnostic ecology, micro-morphological characters, and molecular-based DNA technology, which will possibly speed up the process of species recognition and delineation.

Morphology has provided the basis for the classification of the subfamily Lithocolletinae (Davis & Robinson 1998), but the use of morphologic characters is complex and encompasses many difficulties: (i) few unambiguous synapomorphies; (ii) questionable character homology; (iii) paucity of characters; (iv) intraspecific polymorphism and phenotypic plasticity. The approach to compare and integrate morphological and molecular data sets including multi-gene sets and micromorphological and microstructural characters (Davis & De Prins 2011; De Prins & Kawahara 2012) may provide a solution to the problem and should help to clarify the obscure inter-relationships of the Lithocolletinae genera. For example, until recently, the genus *Leucanthiza* has been considered as belonging to Gracillariinae (De Prins & De Prins 2005), but following the genetic markers, wing venation characters and genital micromorphology it has now been firmly placed within Lithocolletinae (Kawahara *et al*. 2011). All 11 known lithocolletine genera are characterized by vein Rs running nearly parallel to vein M_1 or M_{1+2} in the basal half of the hindwing (Kumata 1993; Davis & Robinson 1998). The present study shows that ecology, morphology and molecular approaches should be very cautiously applied for the delimitation of lithocolletine species / species complexes in cases of rapid radiation of host plants (Guzmán & Vargas 2005; Stevens 2012). Once lithocolletine species have been circumscribed, only then can clearly redefined diagnostic characters involving morphological, ecological and / or molecular (full mitochondrial genomes or COI barcode as a marker tool for species ID) data be applied for detecting and resolving *Triberta* species among the available vouchers of Lepidoptera.

Conclusions

Our study provides three main contributions towards a more effective classification of the lithocolletine moths: (i) the robust molecular analysis presented here clearly separates the genus *Triberta* from *Phyllonorycter*, increasing the total number of genera within the subfamily of Lithocolletinae to eleven; (ii) the molecular data are corroborated with morphologically diagnostic generic characters representing different stages of ontogenetic development of the moths and strengthened by information on their biology; (iii) the taxonomy of the species assigned to the new genus is clarified and the primary name bearing types are designated. The new genus *Triberta* has probably originated from Palaearctic ancestors, but more thorough search, particularly in North and Central America and in the fragmented Cistaceae rich islands in the Andes, the African Horn and Central Asia could reveal a different evolutionary history. Samples from all the available Cistaceae host plants over their vast distribution would contribute greatly towards a more complete picture of the inter-/ intraspecific diversity within this Cistaceae-associated genus.

Mitochondrial genes and especially the COI gene are often suggested for species identification and delimitation. Most of these studies dealt with specimens collected within the last decade. However, the historic collections of most museums often possess great amounts of voucher specimens of new or taxonomically very important taxa which were collected by former generations of lepidopterists dating back sometimes more than a hundred years. These specimens play a significant role in fine tuning-species delimitation approaches and provide the information for filling major gaps in our knowledge. In this study we have tried to combine the evidences of generic traits with those of historic voucher specimens. In order to accurately circumscribe the species, we have designated primary types from specimens collected as long ago as 150 years.

Remarks. This paper echoes the findings of V. T. Chambers (1877, 1878) published in the second volume of *Psyche*, *a journal of Entomology*, in which Chambers, based on his detailed study of larval morphology of the then known American lithocolletine species, for the first time suggested the possible division of the lithocolletine genus *Phyllonorycter*. V. T. Chambers, unfortunately, did not officially formulate his findings according to the rules of the ICZN, and therefore, following the Principle of Priority (Art. 23) the lithocolletine genus *Cameraria*, which in fact was discovered and studied by Chambers, was attributed officially to Chapman (1902). One hundred and thirty six years later, in the present publication, we delineate one more lithocolletine genus *Triberta* and remove both of its constituent species from the genus *Phyllonorycter*.

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