

Biology and Systematics of the North
American *Phyllonorycter* Leafminers on
Salicaceae, with a Synoptic Catalog of
the Palearctic Species
(Lepidoptera: Gracillariidae)

DONALD R. DAVIS
and
GERFRIED DESCHKA

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ABSTRACT

Davis, Donald R., and Gerfried Deschka. Biology and Systematics of the North American *Phyllonorycter* Leafminers on Salicaceae, with a Synoptic Catalog of the Palearctic Species (Lepidoptera: Gracillariidae). *Smithsonian Contributions to Zoology*, number 614, 89 pages, 451 figures, 6 maps, 4 tables, 1 graph, 2001.—Eleven leaf-mining species of *Phyllonorycter* are recognized as being restricted to the host plant genera *Populus* and *Salix* in North America, including Mexico. Previously described species and their new synonyms include the following: *P. apicinigrella* (Braun); *P. apparella* (Herrick-Schäffer.) (= *P. atomariella* (Zeller), *P. tremuloidiella* (Braun), *P. ontario* (Freeman)); *P. nipigon* (Freeman); *P. populiella* (Chambers); *P. salicifoliella* (Chambers) (= *P. kenora* (Freeman)); and *P. scudderella* (Frey and Boll) (= *P. salicivorella* (Braun)). The following new species are proposed in this study: *P. acanthus*, *P. deserticola*, *P. erugatus*, *P. latus*, and *P. mildredae*. Only *P. acanthus* and *P. deserticola* are known to occur in Mexico. Three species groups are recognized primarily on the basis of their similar morphology and, to a lesser extent, on their host preference: the *apparella* group (including *P. apparella*, *P. deserticola*, *P. latus*, and *P. nipigon*), which are almost entirely restricted to *Populus*; the *salicifoliella* group (including *P. acanthus*, *P. erugatus*, *P. mildredae*, and *P. salicifoliella*), which feed mostly on *Salix* and secondarily on *Populus*; and the *hilarella* group (including *P. apicinigrella*, *P. populiella*, and *P. scudderella*), which feed primarily on *Salix* but with one species restricted to *Populus*. The known life stages of each species are fully illustrated and described, and their distributions are plotted on maps. A synoptic catalog of the 24 Old World species of *Phyllonorycter* reported from Salicaceae is also provided, wherein *P. eophanes* (Meyrick) is synonymized under *P. iteina* (Meyrick). Tentative association of the Palearctic species, based on male genital morphology, with the three proposed species groups is summarized in Table 1.

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Biology and Systematics of the North American *Phyllonorycter* Leafminers on Salicaceae, with a Synoptic Catalog of the Palearctic Species (Lepidoptera: Gracillariidae)

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Introduction

The leaf-mining genus *Phyllonorycter* constitutes one of the most successful lineages within the Holarctic Gracillariidae. Approximately 275 names have been proposed, including 82 currently recognized species for America north of Mexico. Nearly 20 plant families have been reported to include hosts, with the Fagaceae, Betulaceae, Leguminosae, and Salicaceae especially favored by *Phyllonorycter*, and the Caprifoliaceae, Ericaceae, and Rosaceae utilized to a slightly lesser extent. As summarized herein, 34 species of *Phyllonorycter* are known to feed on Salicaceae, and all are confined to the Holarctic region. All 34 species are restricted to this host family except two: *P. comparella*, which has been questionably associated with *Pyrus malus*; and *P. hilarella*, which normally feeds on *Salix* and less commonly on *Populus*, but which has been reported once from *Alnus*.

Within the North American *Phyllonorycter*, the species restricted to Salicaceae have presented probably the greatest taxonomic confusion, even though these taxa have been subjected to two previous separate studies (Braun, 1908b; Freeman,

1970) over the past century. Because of this confusion, some of the most detailed investigations involving members of this complex have been marred by the misidentification of the herbivore. For example, the most detailed life history and larval morphology studies of any member of this group actually focused on *P. apparella* (and possibly to a much lesser extent on *P. nipigon*) and not *P. salicifoliella* as stated (Martin, 1956; Watson, 1956). Fortunately, voucher specimens from these classic studies are still available and were examined by the senior author (DRD). Similarly, extensive studies on the biology and host relationships of what was thought to be *P. salicifoliella* (Alberts, 1989; Auerbach, 1991; Auerbach and Alberts, 1992; Auerbach and Fleicher, 1995) involved instead *P. apparella* and *P. nipigon*, as determined from voucher material kindly provided by Auerbach. Future research, especially on the Palearctic fauna, should show whether the conclusions reached in the current study will be in need of still further taxonomic change.

The Nearctic *Phyllonorycter* that mine Salicaceae comprise a polyphyletic assemblage of at least three distinct species groups, each with Old World components. With the possible exception of the *apparella* group, each group also contains allied species restricted to other plant families. These groups were only partially resolved in an early review of the evolution of the genus based on wing pattern (Braun, 1914). A preliminary alignment of the 24 Palearctic species known to feed on Salicaceae, together with the 11 Nearctic species, is proposed in Table 1. Affinities of the taxa were determined primarily on male genitalic characters (discussed below). Associations of some Palearctic species remain tentative pending examination of material currently unavailable. Three names, considered herein as nomina dubia, currently cannot be associated with any of the three groups. No type material is presently known to

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TABLE 1.—Species groups of *Phyllonorycter* leafminers on Salicaceae.

<i>apparella</i> group	<i>salicifoliella</i> group	<i>hilarella</i> group	nomina dubia
<i>apparella</i> (Herrick-Schäffer)	<i>armeniella</i> (Kuznetzov)	<i>dentifera</i> (Noreika)	<i>crocinella</i> (Sorhagen)
<i>latus</i> Davis and Deschka	<i>comparella</i> (Duponchel)	<i>quinqueguttella</i> (Stainton)	<i>graeseriella</i> (Sorhagen)
<i>nipigon</i> (Freeman)	<i>chiclanella</i> (Staudinger)	<i>connexella</i> (Zeller)	<i>salincolella</i> (Sorhagen)
<i>deserticola</i> Davis and Deschka	<i>populi</i> (Filipjev)	<i>populiella</i> (Chambers)	
	<i>populifoliella</i> (Treitscke)	<i>pruinoseella</i> (Gerasimov)	
	<i>sagitella</i> (Bjerkander)	<i>viminetorum</i> (Stainton)	
	<i>salicifoliella</i> (Chambers)	<i>apicinigrella</i> (Braun)	
	<i>acanthus</i> Davis and Deschka	<i>scudderella</i> (Frey and Boll)	
	<i>erugatus</i> Davis and Deschka	<i>hilarella</i> (Zetterstedt)	
	<i>mildredae</i> Davis and Deschka	<i>rolandi</i> (Svensson)	
	<i>pastorella</i> (Zeller)	<i>salicicolella</i> (Sircom)	
	<i>iteina</i> (Meyrick)	<i>dubitella</i> (Herrick-Schäffer)	
	<i>populicola</i> (Kuznetzov)	<i>salictella</i> (Zeller)	
	<i>populialbae</i> (Kuznetzov)		

exist of these names, and no additional material has been unquestionably associated with them since their original discovery. Designation of neotypes for these names eventually may be necessary in order to decide their proper status (see article 75 of the International Code of Zoological Nomenclature, 4th edition, 1999).

Much of the difficulty encountered within the Nearctic members of this complex involves those species most allied to *P. salicifoliella* (i.e., *P. acanthus*, *P. erugatus*, *P. mildredae*). Synapomorphies of the male genitalia defining this group include the following: (1) presence of a short, tubular process (AP, Figure 248) at the ventral apex of the cucullus, which bears a minute, apical/subapical pore (Figures 270–272, 274–276, 278–280, etc.), which is present in all three groups (Figures 337, 340); (2) presence of a subapical cluster or brush (SB, Figures 248, 270, 273, 277, etc.) of 4–30, elongate, spinose setae; and (3) elongate aedeagus (1.5–2.0× length of valva), which attains its greatest relative length in the Indian species, *P. iteina* (Figure 388). Some of the confusion within the *salicifoliella* complex has been fostered by the loss of critical type material (Freeman, 1970). Clemens (1861) proposed the name *P. salicifoliella* without describing the insect or its mine other than noting its host (*Salix vitellinae* var. *alba* (L.)) and the location of the mine. The species was not formerly described until Chambers (1871) provided a detailed account of adults reared from *Salix babylonica*. Because all material studied by both authors has disappeared, a neotype reared from *S. babylonica* has been proposed in this study. As discussed later in more detail, *P. salicifoliella* demonstrates a broad array of genital variation that approximates a comparable range shown within the newly proposed sister species, *P. erugatus*. Accurate identification of these species, as well as those of the *apparella* species group, on the basis of their similar, variable wing patterns is impossible without careful examination of genital characters. For example, a large series of *Phyllonorycter* identified as *P. salicifoliella* by Annette Braun, our foremost early worker on Gracillariidae, was discovered upon dissection to contain four other species in this complex and only a single specimen of *P. salicifoliella*.

Freeman (1970) recognized eight species in his review of the North American leaf-mining *Phyllonorycter* on Salicaceae, of which five are synonymized herein. One name was found to represent a more widely distributed holarctic species. He did not treat *P. salicifoliella*, except to mention under his description of *P. kenora* (herein synonymized under the foregoing name) that it was impossible for him to apply the name *salicifoliella* to any known species.

The *apparella* species group feeds on *Populus* and possesses elongate, slender valvae in the males (Figures 233, 236, 239, 242) and relatively short aedeagi (<0.75× the length of valva). Included Nearctic species are *P. apparella*, *P. deserticola*, *P. latus*, and *P. nipigon*. *Phyllonorycter apparella* is the only member of this group represented in the Palearctic region, and it is the only Salicaceae-mining *Phyllonorycter* species currently known to be Holarctic in distribution.

Males of the *hilarella* group (Figures 260–268, 394–422) are characterized by their asymmetrical valvae, with a large, often curved spine typically arising near the apex of the left, more enlarged valva. Two of the three Nearctic species (*P. apicinigrella*, *P. scudderella*) mine *Salix*, and the third (*P. populiella*) feeds on *Populus*. A complex of eight, almost exclusively *Salix*-feeding species, which exhibit similar to nearly identical male genital morphology, are currently recognized within the *hilarella* group. Included within this subgroup are *P. apicinigrella* and *P. scudderella* in North America, and *P. dubitella*, *P. hilarella*, *P. rolandi*, *P. salicicolella*, *P. salictella*, and *P. viminetorum* from the Holarctic region. The most notable genital character distinguishing these species involves the relative development of the male saccus (Svensson, 1997)—varying from indistinct in *P. apicinigrella* (Figure 266) and *P. viminetorum* (Figure 405) to elongate and slender in *P. salictella* (Figure 420). Although the morphology of the male genitalia of *P. dubitella*, *P. hilarella*, *P. rolandi*, and *P. scudderella* are particularly similar, their wing patterns are usually distinct (Fennell, 1970; Watkinson, 1985; Svensson, 1996, 1997). For example, the forewing of *P. hilarella* differs from its siblings in possessing a complete basal fascia (sometimes also evident in *P. salicicolella*), in lieu of a strongly oblique pair of costal and dorsal

strigulae variably present in the other three species. Although sometimes treated as a subspecies of the widespread, variably colored *P. salictella*, *P. viminella* of Great Britain is synonymized under the former on the basis of their identical genitalia (Karsholt and Skou, 1987; Buszko, 1992). More investigation on population variation among the members of this complex needs to be pursued, including the utilization of life history, molecular, and morphological data.

General Biology

Leaf-mining insects can be excellent subjects for examining interactions among three trophic levels involving the host plants, herbivores, and predators/parasitoids (Price et al., 1980; Faeth, 1985, 1986; Abrahamson, 1989; Auerbach, 1991; Ohgushi, 1997). The plant family Salicaceae, with their sometimes toxic concentrations of secondary chemicals (i.e., those not necessary for primary metabolism), have been particularly utilized in such investigations (Zucker, 1982; Smiley et al., 1985; Rowell-Rahier and Pasteels, 1992). Controversy still persists as to the relative effects of host-plant chemistry compared to other factors (e.g., plant anatomy or degree of enemy-free space) in determining the host-plant range of herbivorous insects (see Bernays and Graham, 1988, and associated responses; Auerbach and Alberts, 1992). Previous studies have involved a relatively limited assortment of herbivores with little reference to *Phyllonorycter* leafminers on Salicaceae. Tritrophic-level interactions involving *Phyllonorycter salicifoliella* have been investigated on two North American *Salix* hosts (*S. sericea* Marshall; *S. eriocephala* Michx.) and their interspecific hybrids (Fritz, 1995; Fritz et al., 1997; Fritz et al., 1998). These studies supported the prediction of tritrophic interaction theory that plant genotype can affect natural enemy impact. Significant variation in *P. salicifoliella* survival and eulophid parasitism was found over two years of observation among genotypes within taxa in the field and in common garden experiments.

The general components within the Nearctic Salicaceae-*Phyllonorycter* association are briefly summarized.

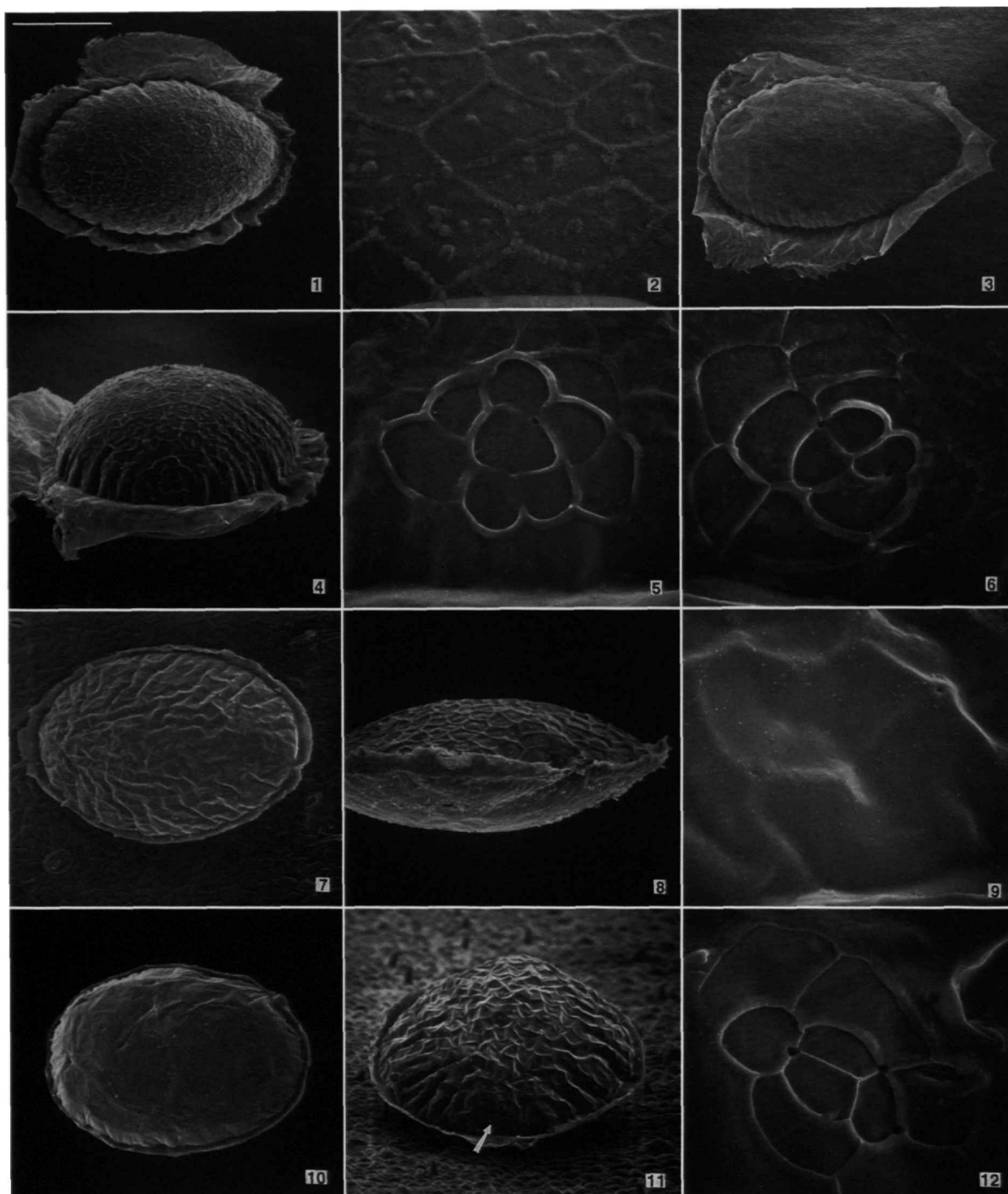
HOST PLANTS.—The Salicaceae are a predominantly north temperate, taxonomically isolated family of dioecious trees and shrubs, consisting of 350 species grouped into as many as four genera: *Populus*, *Salix*, *Chosenia*, and *Toisusu* (Heywood, 1993). It should be noted that one of the leading workers on *Salix* has estimated as many as 400 to 500 species in that genus alone (Argus, 1986). *Populus* and *Chosenia* are wind pollinated, and *Salix* and *Toisusu* are pollinated by insects. Chemically the family is characterized by the presence of phenolic glycosides in the bark of all species and in the leaves of some species (Rowell-Rahier and Pasteels, 1992). Salicin and, to a lesser extent, salicortin are particularly prevalent and are diagnostic for the family (Palo, 1984). Salireposide and tremulacin are largely characteristic of the genus *Populus*, although other phenoglycosides occur in this genus, some of which are shared with various species of *Salix* (Palo, 1984). No secondary me-

tabolites other than phenolics have been identified in the leaves of Salicaceae. Studies have shown that the concentration and composition of the different phenolic mixtures are species specific in *Salix* (Tahvanainen et al., 1985); however, the concentration of phenoglycosides can vary considerably within Salicaceae, not only between taxa, but also according to an individual's sex, age, season, altitude, among individual leaves, and even to the time of day (Palo, 1984; Horn, 1985).

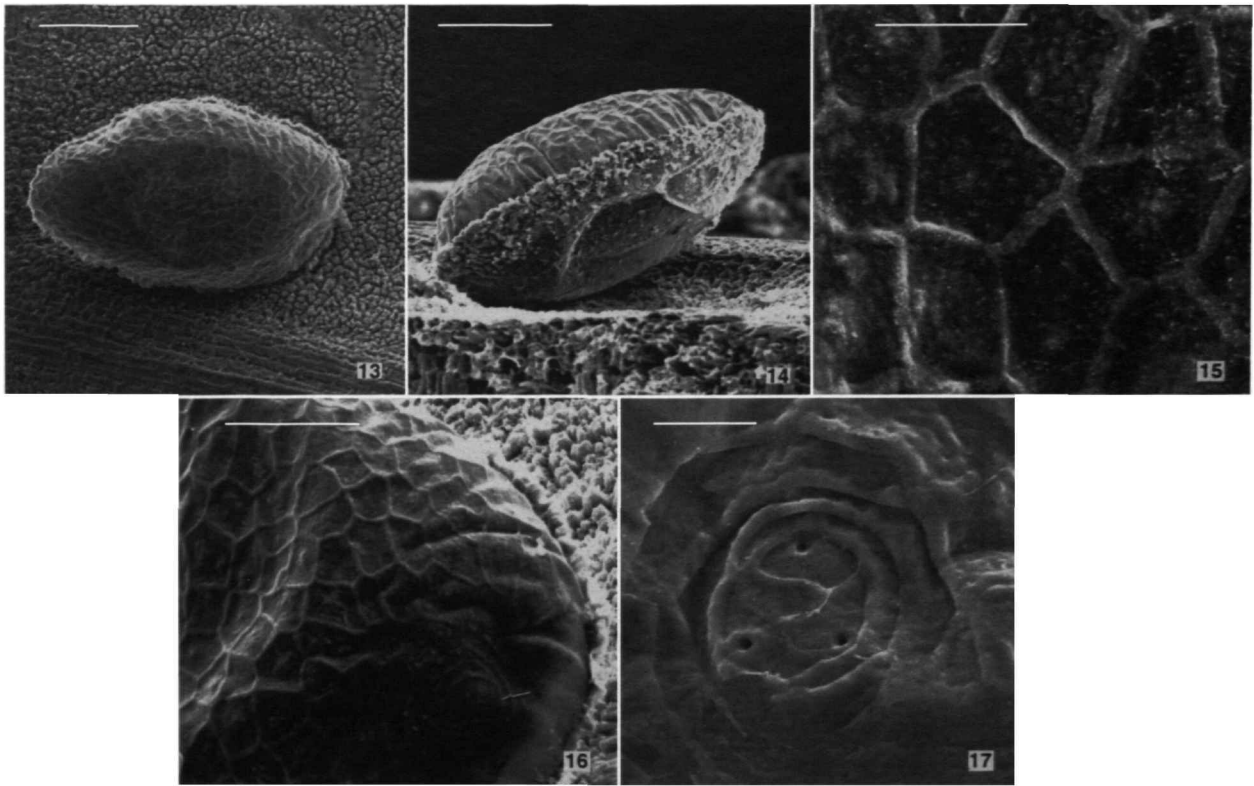
LEAFMINERS.—The general life history of all members of this complex is believed to be similar to that described for *P. apparella* (Martin, 1956), which also is typical for most *Phyllonorycter* (Needham et al., 1928; Miller, 1973; Davis, 1987; Landry and Wagner, 1995). The eggs are flat (with the micropylar axis parallel to the substratum), approximately 0.3 mm in length, 0.2 mm in width, and are lightly cemented to the lower leaf surface. Eggs of three species (*P. apparella*, *P. nipigon*, *P. salicifoliella*) have been examined in detail by DRD (Figures 1–17). These show specific differences, with the eggs of *P. apparella* being less flat, possessing the broadest circumferential fringe, and with the upper surface minutely papillate (Figure 2). Numerous aeropyles are present over the upper half above the fringe, usually at the intersections of a reticulum of low ridges (Figure 2). The lower half of the egg, which is mostly in contact with the leaf, is smooth. Two or three micropyles are present at the anterior pole and are surrounded by a network of 8–10 cellular partitions (Figures 5, 6). Eggs of *P. salicifoliella* essentially lack a circumferential fringe but do possess a sub-medial zone of rugose tissue that demarcates the upper and lower surfaces (Figures 13, 14).

All species are believed to possess three early sap-feeding and two later tissue-feeding instars. The apodal, prognathous, sap-feeding instar initiates a slender, serpentine to wedge-shaped, subepidermal tract on the underside of the leaf. The succeeding two instars continue feeding in the spongy parenchyma, which, by the third instar, is enlarged to form a blotch. The eruciform, hypognathous, tissue-feeding larvae typically do not enlarge the area of the mine, but they feed deeper into the leaf, removing most of the palisade tissue within the elongate blotch. Possessing a fully functional spinneret, this larval form lays a layer of silk across the lower epidermis of the mine, which, upon contracting, draws the edges of the mine closer together, resulting in a tentiform mine with a single (rarely 2 or 3) longitudinal, epidermal fold (Figures 18–26). By the fourth and fifth instars the larval frass appears granular and is typically collected at one end of the mine where it is secured by silk (Martin, 1956). Pupation occurs within the mine in a silken cocoon that is often located near the center.

An individual female of *P. apparella* normally deposits no more than one egg per leaf (Auerbach, 1991). During periods of high moth density, multiple oviposition by several females on preferred, younger leaves can result in several mines per leaf. As these mines enlarge, some will inevitably coalesce. Typically when this occurs, one intruding larva will kill the other by biting into the abdomen and partially ingesting the



FIGURES 1–12.—Egg morphology. *Phyllonorycter apparella*: 1, dorsal view (120 μm); 2, detail of dorsal surface (23.1 μm); 3, ventral view (120 μm); 4, anterior (micropylar) end (86 μm); 5, detail of micropyle in figure 4 (17.6 μm); 6, variation of micropylar ridges (15 μm). *Phyllonorycter nipigon*: 7, dorsal view (120 μm); 8, lateral view (86 μm); 9, detail of dorsal surface (17.6 μm); 10, ventral view (120 μm); 11, anterior (micropylar, see arrow) end (100 μm); 12, detail of micropyle in Figure 11 (12 μm). (Length of bar scale in parentheses.)



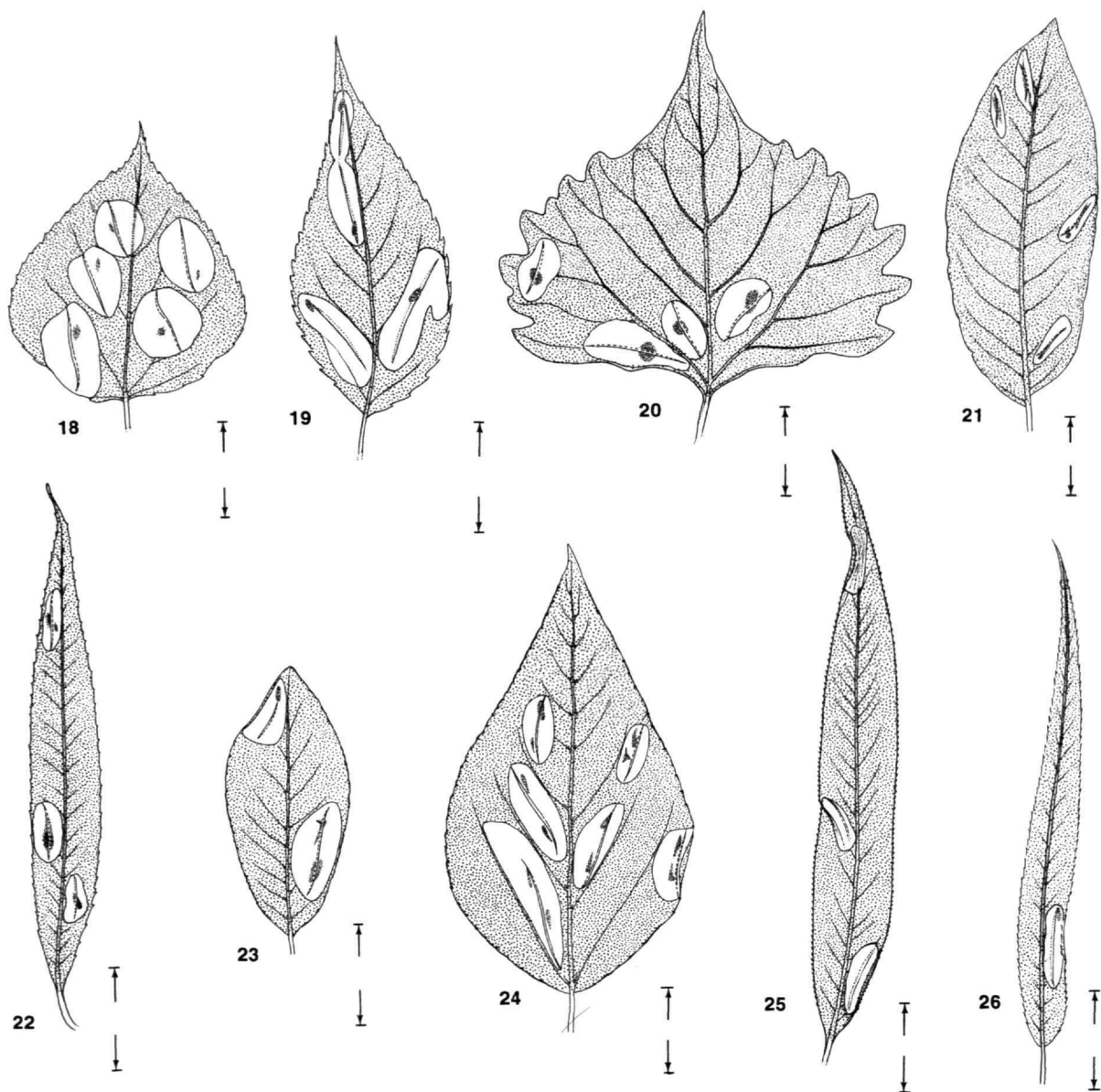
FIGURES 13–17.—Egg morphology. *Phyllonorycter salicifoliella*: 13, dorsal view (100 μ m); 14, lateral view (100 μ m); 15, detail of dorsal surface (20 μ m); 16, anterior (micropylar, see arrow) end (50 μ m); 17, detail of micropyle in Figure 16 (10 μ m). (Length of bar scale in parentheses.)

body fluids (Martin, 1956). Because only the third and possibly second instars actually enlarge the mine horizontally, only these stages display this aggression—a behavior Auerbach (1991) has termed larval interference. In heavy infestations, larval mortality to interference can reach as high as 58% in *P. apparella*, as compared to 36% mortality to parasitism within the same sample (Martin, 1956). Auerbach found in his study of *P. apparella* that larval interference, along with parasitism and unknown causes, were responsible for most mortality, and that the former was the only consistently spatially density-dependent source of mortality.

Although the larval mines of most *Phyllonorycter* develop on the underside of the leaf, some exceptions have been noted among those feeding on Salicaceae. *Phyllonorycter dentifera* mines only the upperside of the leaf (Noreika and Puplesis, 1992a); *P. pruinosa* most frequently mines the upperside (E.M. Hering, 1957); *P. populicola* mines both leaf surfaces (Kuznetsov, 1975); and *P. connexella*, *P. pastorella*, and *P. populifoliella* rarely mine the upper surface (Sorhagen, 1886; E.M. Hering, 1957). Because the larva is usually restricted in its mining by the midrib and larger veins, the relative dimensions

of the blotch mine typically varies according to the shape and venation of the leaf. The mines on *Populus* (Figures 18–20) tend to be broader and more oval to nearly circular (6–10 mm wide and 10–25 mm long) in contrast to the more slender and elongate mines on *Salix* (2.5–8 mm wide and 11–40 mm long; Figures 21–23, 25, 26). Because the edge of the mine frequently borders the edge of the leaf on *Salix*, these mines tend to cause the leaf edge to curl slightly under.

Both the sap-feeding and tissue-feeding instars of the *apparella* group studied (*P. apparella*, *P. deserticola*, *P. nipigon*) are similar in morphology to those of the *salicifoliella* group (*P. mildredae* and *P. salicifoliella* examined). No larvae of the *hilarella* group were available for comparison. The morphology of all five instars and pupa of *P. apparella* was studied in detail by Watson (1956). No conspicuous structural differences have been discovered to distinguish the forementioned species, although minor differences in setal positions have been noted. Some of these may later prove to be the result of normal within-species variation. Full chaetotaxal drawings of three of the most commonly encountered species are provided to show both the overall similarity between species within this complex



FIGURES 18–26.—Leafmines, ventral view: 18, *Phyllonorycter apparella* on *Populus tremuloides*; 19, *Phyllonorycter nipigon* on *Populus balsamifera*; 20, *Phyllonorycter deserticola* on *Populus fremontii*; 21, *Phyllonorycter salicifoliella* on *Salix bebbiana*; 22, *Phyllonorycter salicifoliella* on *Salix babylonica*; 23, *Phyllonorycter salicifoliella* on *Salix monticola*; 24, *Phyllonorycter erugatus* on *Populus balsamifera*; 25, *Phyllonorycter acanthus* on *Salix bonplandiana*; 26, *Phyllonorycter mildredae* on *Salix nigra*. (All scales = 2 cm.)

as well as possible characters for future analyses whenever more material becomes available.

In the flattened sap-feeding instars, the labrum is prominently bilobed, with the anterior margin serrated (Figures 44, 95, 138, 162). Three pairs of stemmata are present in a well-separated, lateral row (Figures 49, 166). The mandibles are flat, with elongate, acute cusps (Figures 95, 100, 101). The spin-

neret and labial palpi are absent. All legs, prolegs, and crochets are absent. Paired ambulatory callosities are present both dorsally and ventrally on all three thoracic segments (Figures 102, 103, 168, 169), ventrally on abdominal segments 3–5 (Figures 51, 104, 170), and ventrally on the tenth abdominal segment (Figure 172).

All last instar larvae examined agree in lacking setae AF1,

AF2, P2, S3, and SS3 on the head and in possessing only three pairs of stemmata. Setae P1, A1, and A2 arise nearer the ad-frontal area in *P. nipigon* and *P. mildredae* than in *P. apparella*, *P. deserticola*, and *P. salicifoliella*. As is true for several gracillariid genera, the labral seta M3 is lacking. The distal, dorsal half of the hypopharynx is densely spined, with the apex bearing several rows of longer, sinuately tipped spines. The relative development and distribution of these spines may differ between species, with those of *P. salicifoliella* (Figure 174) being among the longest examined and those of *P. nipigon* (Figure 106) and *P. deserticola* (Figure 146) being the shortest. The apical hypopharyngeal spines of *P. apparella* appear more intermediate in length (Figure 58). Only one mandibular seta is present, compared to the normal complement of two, as exists in Gracillariinae. Complete loss of the mandibular setae occurs in some genera (e.g., *Cameraria*) of Lithocolletinae. The spinneret terminates in a short, tubular, bifurcate lobe, with the furcations longest in *P. nipigon* (Figure 110). The prothorax lacks XD2 and SV2 setae, as well as L3 (possibly an apomorphy for *Phyllonorycter*). Seta D1 of the prothorax typically arises dorsal to D2 in *P. nipigon*, anterior to D2 in *P. apparella* and *P. deserticola*, and ventral in *P. mildredae* and *P. salicifoliella*. As is true for most Lithocolletinae, four pairs of thoracic coxal setae are present (Figure 175) compared to five pairs in Gracillariinae. Another characteristic for the Lithocolletinae is the loss of D1 on the ninth abdominal segment. The lateral setae are unisetose on abdominal segments 1–8 and bisetose on 9. The number of abdominal crochets was found to vary from a single anterior row of 3 and a caudal row of 1 or 2 in *P. mildredae* to 1 or 2 scattered anterior rows of 5–7 and usually a single caudal row of 5 or 6 in *P. nipigon* (Figure 113). Crochets of A10 range from the most numerous (>30) in *P. nipigon*, where they encircle the entire planta in 3 or 4 indefinite rows (Figure 117), to less than 25 in *P. apparella*, where they are largely absent caudally (Figure 64).

The pupae of the *apparella* species group also are generally similar to those of the *salicifoliella* group. The frons is projected at the vertex into a broadly acute process (cocoon-cutter, cocoon-piercer) bearing a minutely serrated, V-shaped ridge (Figures 69, 70) and a subapical pore (Figures 70, 87, 129, 187). The function of the pore is unknown, but it may serve as an outlet for a cocoon-softening, proteolytic fluid similar to that secreted by some newly emerged saturniid moths (Kafatos and Williams, 1964; Tuskes et al., 1996). The clypeal setae are paired, elongate, and arise nearly contiguous (Figures 126, 127, 215, 224). The abdominal terga are densely spinulose, with the spines evenly dispersed and tending to be slightly larger anteriorly (Figures 72, 88, 130, 152, 188). Sternum VII is smooth, except for a median, prominently raised, triangular ridge, developed in several species of *Phyllonorycter*, and bearing 1 or 2 pairs of laterally projecting spines (Figures 90, 126, 127, 132, 133). Different modifications of sternum VII have been observed in some species of North American *Cam-*

eraria. Because the senior author believes that the spines may function as a type of cremaster during adult eclosion, he has suggested the name “accessory cremaster” for this structure. The accessory cremaster of *P. ulmifoliella* (Hübner) was figured by Wilson (1985:302) and mentioned by Watkinson (1985:347), but they variably placed it on either the eighth or sixth abdominal sternum, respectively. The abdominal intersegmental membrane is minutely pustulate and typically forms a fine reticulate pattern (Figures 73, 89, 131, 153, 189). Abdominal segments IX and X are abruptly depressed ventrally (as viewed laterally), with segment X projecting as a flattened lobe, more so in some species than in others (Figures 74, 91, 127, 134, 157). The cremaster usually consists of a pair of variably curved, broad-based spines, with one pair situated more laterad and slightly more anterior to the other (Figures 135, 136, 158–160, 191–193, 202, 212–214). The cremasters of *P. apparella* and its sister species, *P. latus*, are atypical in having lost the more medial, caudal pair of spines (Figures 75, 76, 92, 93).

Pupae of the *hilarella* group differ from the forementioned in at least three major features: the seventh abdominal sternum lacks all trace of an accessory cremaster (Figure 219); the abdominal intersegmental membrane is smooth (Figure 228); and the terminal cremaster of segment X lacks the lateral pair of hooks (Figures 221–223, 230–232; Wilson, 1985:303). In addition, the tergal abdominal spines tend to be more reduced medially (Figures 218, 227).

Most species within the Salicaceae-mining *Phyllonorycter* tend to be univoltine across the northern parts of their range, with the adults emerging in August to September. After overwintering, possibly under old tree bark or in deep crevices, the adults appear again in early spring shortly after the flush of new leaves (Martin, 1956). Some species, such as *P. salicifoliella*, also undergo one and possibly two, earlier, summer generations in more southern latitudes (Maier and Davis, 1989). Ivinski (1993) has noted that *Phyllonorycter* feeding on *Populus*, along with the genus *Caloptilia*, are the only Gracillariidae to overwinter as adults. The senior author also has collected adult *Phyllocnistis vitegenella* Clemens overwintering under tree bark in and around Washington, D.C. Some members of this complex may overwinter as pupae, as do most *Phyllonorycter*.

Host Salicaceae for the Nearctic *Phyllonorycter* are summarized in Table 1. As a means of determining which hosts are most frequently utilized, rearing lots from all *Phyllonorycter* examined have been tallied for each host. Literature records, for which no specimens of *Phyllonorycter* were available, are indicated simply by “X.” Leaf mines, often accompanied by plant voucher specimens, also have been preserved for rearings by the authors (DD, GD). Hosts reported by other collectors usually could not be verified because of the absence or unavailability of voucher material. Many hosts, especially in the troublesome genus *Salix*, were not identified to species by previous collectors, so it is now often difficult to assess the specific host

range of the herbivore. This was particularly true for *P. salicifoliella* for which in a majority (58%) of the collections the host was not determined to species. Records tallied indicate that most of the Nearctic *Phyllonorycter* tend to restrict their feeding to one or two host species within a single genus of Salicaceae. Although compiling rearing frequency from host records may not be a true test for host preference (Thompson and Pellmyr, 1991; Auerbach and Alberts, 1992), this procedure can provide information not otherwise apparent. Based on the reported host listings alone without tallying collection frequency, one could conclude erroneously (as in the cases of *P. apparella* and *P. nipigon*) that their host range was relatively unrestricted, when in reality a particular host is usually selected.

In addition to differences of phytochemical attributes between hosts, different phenologies have been found to favor certain hosts in the case of *P. apparella*. Although pupal mass of *P. apparella* was observed by Auerbach and Alberts (1992) to be greater on *Populus tremuloides* Michx., early instar efficiency was found to be the highest and developmental time the shortest on *P. grandidentata* at the same study site. This apparent contradiction was explained by the later budbreak of *P. grandidentata*, resulting in *P. tremuloides* being more utilized by the overwintering moths. Later egg incubation and early instar feeding were more efficient because development on *P. grandidentata* occurred at warmer temperatures.

PARASITIDS.—Partially because of their more sessile and moderately exposed habits, leaf-mining insects generally support the greatest number of parasitoids compared to external feeders that feed in more exposed sites or endophagous species that feed in more concealed sites (Hawkins and Lawton, 1987; Memmott and Godfray, 1993). *Phyllonorycter* populations especially support parasitoid faunas that are both biologically varied and rich in species (Askew and Shaw, 1979a, 1979b). The parasites are typically polyphagous with broad host ranges. Representatives of four families of Hymenoptera (Braconidae, Eulophidae, Ichneumonidae, and Pteromalidae) have been reared from North American *Phyllonorycter* leafminers on Salicaceae (Table 2). Most of the parasitoids are members of the Eulophidae, with 10 genera and 22 species reported. As was true for many plant hosts, several parasitoids could be determined only to genus in this study. The majority are believed to be primary parasites, but some hyperparasitism undoubtedly occurs. Askew and Shaw (1979a) reported for the *Phyllonorycter* they studied that certain species of *Sympiesis* and *Pnigalio* tended to be ectoparasitic hyperparasitoids, which were more polyphagous and more active later in the season. *Phyllonorycter apparella*, probably the most frequently reared member of this complex in North America, is associated with the largest and most diverse assemblage of parasitoids (21). This exceeds the upper parasitoid species load of 10–20 for most *Phyllonorycter* leaf miners studied in a deciduous forest

site in Great Britain (Askew and Shaw, 1974; Memmott and Godfray, 1993). However, because several of the parasitoid records summarized in Table 3 for *P. apparella* are from Auerbach's work (1991), wherein both *P. apparella* and *P. nipigon* were confused with *P. salicifoliella*, a few of the records may pertain only to *P. nipigon*. No parasitoids have been reported or collected for the less often encountered *P. latus*, *P. acanthus*, *P. populiella*, and *P. apicinigrella*.

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TABLE 2.—Salicaceae hosts of North American *Phyllonorycter*. (Numbers represent frequency of separate rearing lots; X=unconfirmed literature records.)

Plant hosts	<i>Phyllonorycter</i>										
	<i>apparella</i>	<i>latus</i>	<i>nipigon</i>	<i>deserticola</i>	<i>salicifoliella</i>	<i>acanthus</i>	<i>erugatus</i>	<i>mildredae</i>	<i>populiella</i>	<i>scudderella</i>	<i>apicinigrella</i>
<i>Populus</i>											
<i>x acuminata</i>	-	-	1	-	-	-	-	-	-	-	-
<i>alba</i>	-	-	-	-	-	-	-	-	2	-	-
<i>angustifolia</i>	-	-	X	-	-	-	-	-	-	-	-
<i>balsamifera</i>	2	-	29	-	X	-	6	-	-	-	-
<i>ssp. trichocarpa</i>	2	-	5	-	-	-	-	-	-	-	-
<i>canescens</i>	2	-	-	-	-	-	-	-	1	-	-
<i>deltoides</i>	1	-	-	-	-	-	-	-	-	-	-
<i>ssp. wislizenii</i>	-	-	-	1	-	-	-	-	-	-	-
<i>dilata</i>	-	-	-	-	-	-	1	-	-	-	-
<i>fremontii</i>	-	-	-	12	-	-	-	-	-	-	-
<i>grandidentata</i>	5	-	-	-	-	-	-	-	1	-	-
<i>macdougalii</i>	-	-	-	2	-	-	-	-	-	-	-
<i>nigra</i>	-	-	1	-	-	-	-	-	-	-	-
<i>tremuloides</i>	46	3	6	-	1	-	-	-	-	-	-
<i>sp.</i>	4	-	4	6	2	-	1	-	1	-	-
<i>Salix</i>											
<i>alba</i>	-	-	-	-	X	-	-	-	-	-	-
<i>amydaloides</i>	-	-	-	-	1	-	-	-	-	-	-
<i>babylonica</i>	-	-	-	-	1	-	-	-	-	X	-
<i>bebbiana</i>	-	-	-	-	4	-	-	-	-	X	-
<i>bonplandiana</i>	-	-	-	-	6	4	-	-	-	-	-
<i>candida</i>	-	-	-	-	-	-	-	-	-	3	-
<i>caroliniana</i>	-	-	-	-	1	-	-	3	-	-	-
<i>discolor</i>	-	-	-	-	1	-	-	-	1	-	-
<i>eriocephala</i>	-	-	-	-	1	-	-	-	-	-	-
<i>?fluviatilis</i>	-	-	-	-	X	-	-	-	-	-	-
<i>lasiandra</i>	-	-	-	-	-	-	-	-	-	-	1
<i>lasiolepis</i>	-	-	-	-	1	-	-	-	-	-	-
<i>lutea</i>	-	-	-	-	5	-	-	-	-	-	-
<i>monticola</i>	-	-	-	-	2	-	-	-	-	-	-
<i>nigra</i>	-	-	-	-	-	-	-	1	-	-	-
<i>purpurea</i>	-	-	-	-	1	-	-	-	-	-	-
<i>x rubens</i>	-	-	-	-	1	-	-	-	-	-	-
<i>scouleriana</i>	-	-	-	-	1	-	-	-	-	-	-
<i>sericea</i>	-	-	-	-	1	-	-	-	-	1	-
<i>sitchensis</i>	-	-	-	-	-	-	-	-	-	-	1
<i>sp.</i>	2	-	1	-	37	-	-	-	1	24	5

The introduction and text for the North American *Phyllonorycter* were prepared by the senior author (DRD). The junior author (GD) was largely responsible for the synoptic catalog of the Palearctic fauna. We especially wish to thank Jaroslav Buszko, Remigijus Noreika, and Paolo Triberti for their reviews of the Palearctic catalog.

Finally we acknowledge the cooperation of the institutions listed below and list their acronyms as used in this study.

- AMNH The American Museum of Natural History, New York City, New York, USA
- ANSP The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA

- BMNH The Natural History Museum (formerly the British Museum (Natural History)), London, England
- CNC The Canadian National Collections, Agriculture Canada, Ottawa, Canada
- CSU Colorado State University, Fort Collins, Colorado, USA
- DLW Collection of David L. Wagner, Storrs, Connecticut
- FIDU Forest Insect and Disease Survey Unit, Great Lakes Forestry Centre, Sault Ste. Marie, Canada
- GD Collection of Gerfried Deschka, Steyr, Austria
- UCB Essig Museum of Entomology, University of California, Berkeley, California, USA
- USNM Collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA, which include collections of the former United States National Museum
- UWL University of Wyoming, Laramie, Wyoming, USA

TABLE 3.—Parasitoid hymenoptera reared from North American *Phyllonorycter* leafminers on Salicaceae.

Parasitoids	<i>Phyllonorycter</i>										
	<i>apparella</i>	<i>latus</i>	<i>nipigon</i>	<i>deserticola</i>	<i>salicifoliella</i>	<i>acanthus</i>	<i>erugatus</i>	<i>mildredae</i>	<i>populiella</i>	<i>scudderella</i>	<i>apicinigrella</i>
BRACONIDAE											
<i>Apanteles ornigis</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Apanteles</i> sp.	X	-	-	-	-	-	-	-	-	-	-
<i>Mirax minuta</i>	-	-	-	-	X	-	-	-	-	-	-
<i>Parahormius pallidipes</i>	-	-	-	-	X	-	-	-	-	-	-
<i>Pholetesor</i> sp., probably <i>salicifoliella</i>	X	-	-	-	-	-	-	-	-	-	-
EULOPHIDAE											
<i>Aprostocetus</i> sp.	-	-	-	-	X	-	-	-	-	-	-
<i>Chrysocharis boriquenensis</i>	-	-	-	-	X	-	-	-	-	-	-
<i>Chrysocharis</i> sp.	X	-	X	-	X	-	-	-	-	-	-
<i>Cirrospilus cinctithorax</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Cirrospilus</i> sp.	X	-	-	-	-	-	-	-	-	-	-
<i>Closterocerus tricinctus</i>	X	-	X	-	-	-	-	-	-	-	-
<i>Closterocerus</i> sp., near <i>trifasciatus</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Dialyphus</i> sp.	-	-	-	-	X	-	-	-	-	-	-
<i>Horismenus fraternus</i>	X	-	X	-	-	-	-	-	-	-	-
<i>Horismenus</i> sp.	-	-	-	-	X	-	X	-	-	-	-
<i>Pediobius</i> sp.	X	-	-	X	-	-	-	-	-	-	-
<i>Pnigalio flavipes</i>	X	-	X	X	-	-	-	-	-	-	-
<i>Pnigalio tischeriae</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Pnigalio</i> sp., near <i>proximus</i>	-	-	-	-	-	-	-	-	-	-	-
<i>Pnigalio</i> sp.	X	-	X	-	-	-	-	-	-	-	-
<i>Sympiesis conica</i>	X	-	-	-	-	-	X	-	-	-	-
<i>Sympiesis marylandensis</i>	-	-	-	X	X	-	X	-	-	-	-
<i>Sympiesis stigmata</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Sympiesis</i> sp.	X	-	-	X	X	-	-	-	-	X	-
<i>Tetrastichus</i> sp.	X	-	-	-	-	-	-	-	-	-	-
<i>Zagrammosoma americanum</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Zagrammosoma multilineatum</i>	-	-	X	-	-	-	-	-	-	-	-
ICHNEUMONIDAE											
<i>Allophosternum foliicola</i>	X	-	X	-	-	-	-	-	-	-	-
<i>Diadegma</i> sp.	X	-	-	-	-	-	-	-	-	-	-
<i>stenosomus</i> complex	-	-	X	-	-	-	-	-	-	-	-
<i>Scambus decorus</i>	X	-	X	-	-	-	-	-	-	-	-
PTEROMALIDAE											
<i>Pteromalus</i> sp.	X	-	-	-	-	-	-	-	-	-	-

Key to the North American Species of *Phyllonorycter* Leafminers on Salicaceae, Based Primarily on the Male Genitalia

1. Male genitalia with symmetrical valvae 2
 - Male genitalia with asymmetrical valvae 9
 2. Valvae elongate, 1.3× or more the length of aedeagus, gradually tapering to a slender, simple, often sinuate apex 3
 - Valvae shorter, 0.75× or less the length of aedeagus, abruptly narrowing near apex to form a small, porate apical process, often accompanied by a more subapical cluster of spines [Figure 248] 6
 3. Vinculum V-shaped, tapering gradually to anterior apex [Figures 233, 236] 4
 - Vinculum Y-shaped, abruptly tapering to more attenuate apex [Figure 239]
- *P. nipigon*

4. Valvae elongate (1.8× or more the length of aedoeagus) and slender (length 6.5× or more the maximum width) [Figures 233, 236] 5
Valvae relatively shorter (1.4× or less the length of aedoeagus) and broader (length less than 5× the maximum width) [Figure 242] *P. deserticola*, new species
5. Valvae extremely long (length more than 2.2× the length of aedoeagus), slender (length more than 9× maximum width), and straight [Figure 236]
..... *P. latus*, new species
Valvae relatively shorter (length less than 1.9× the length of aedoeagus) and broader (length less than 7× the maximum width), with a sinuate apex [Figure 233]
..... *P. apparella*
6. Subapical brush of spines (SB) of valva arising as a compact, cylindrical mass usually from a slightly raised tubercle [Figures 248, 271, 275, 279, 295, 304, 315, 319] ... 7
Subapical spines more scattered or reduced in number [Figures 310, 330] 8
7. Subapical spines usually arising well separated from base of apical process (AP) [Figures 248, 271, 275, 279, 304]. Apical process with longitudinal ridges [Figures 272, 276]. Female genitalia with antrum 1.2× or less the length of posterior apophyses [Figure 431]. Larva feeding predominantly on *Salix* *P. salicifoliella*
Subapical spines arising from base of apical process [Figures 315, 319]. Apical process with smooth walls [Figures 316, 320]. Antrum of female more elongate, 1.5× or more the length of posterior apophyses [Figure 435]. Larva feeding on *Populus*
..... *P. erugatus*, new species
8. Apical one-third of valva gradually narrowing, with a dense concentration of short, stout spines near mesal, ventral margin [Figures 309, 310] *P. acanthus*, new species
Apical one-third of valva broad, abruptly terminating in a relatively truncate apex; subapical setal cluster reduced to 3–6 short, spinose setae [Figures 329, 330]
..... *P. mildredae*, new species
9. Right valva broad to apex [Figure 260]. Larva feeding on *Populus* ... *P. populiella*
Right valva tapering to slender apex [Figures 263, 266]. Larva feeding on *Salix* 10
10. Forewing distinctly marked with four white costal striae and three white dorsal striae [Figure 40] *P. scudderella*
Forewing without white striae; instead yellow, edged with fuscous along termen and base of costa [Figure 41] *P. apicinigrella*

Phyllonorycter apparella (Herrich-Schäffer)

FIGURES 1–6, 18, 27, 42–84, 233–235, 335–337, 341, 342, 359–361, 423, 424; MAP 1

Tinea apparella Herrich-Schäffer, 1855:334.

Lithocolletis atomariella Zeller, 1875:350.—Walsingham, 1889:54.—Riley, 1891:108 [*Lithocolletes* (sic)].—Dyar, 1903:556 [*Lithocolletes* (sic)].—Freeman, 1970:272. [New synonymy.]

Lithocolletis apparella (Herrich-Schäffer).—Heinemann and Wocke, 1877:694.—Staudinger and Rebel, 1901:216.—Spuler, 1910:418.—Meyrick, 1912a:38; 1912b:9.—Petersen, 1927:172.—Lhomme, 1963:1032.—Szöcs, 1977:253.—Kuznetsov, 1981:288.

Lithocolletis populiella Busck, 1903:770 [not Braun, 1908].—Dyar, 1904:937.

Lithocolletis tremuloidiella Braun, 1908a:102; 1908b:317; 1914:115, 153.—Meyrick, 1912a:9; 1912b:37.—Barnes and McDunnough, 1917:187.—Ely, 1918:64.—McDunnough, 1939:96.—Freeman, 1970:275.—Brower, 1984:41. [New synonymy.]

Lithocolletis salicifoliella Martin, 1956:155 [in part, not Chambers, 1871].—Watson, 1956:168.—Alberts, 1989:1.—Auerbach, 1991:1599.—Auerbach and Alberts, 1992:1.—Auerbach and Fleischer, 1992:201.

Phyllonorycter apparella (Herrich-Schäffer).—Bradley et al., 1969:31.—Buhl et al., 1984:6.—Buszko, 1987:640; 1996:51.—Kuznetsov and Baryshnikova, 1998:29.

Lithocolletis ontario Freeman, 1970:273. [New synonymy.]

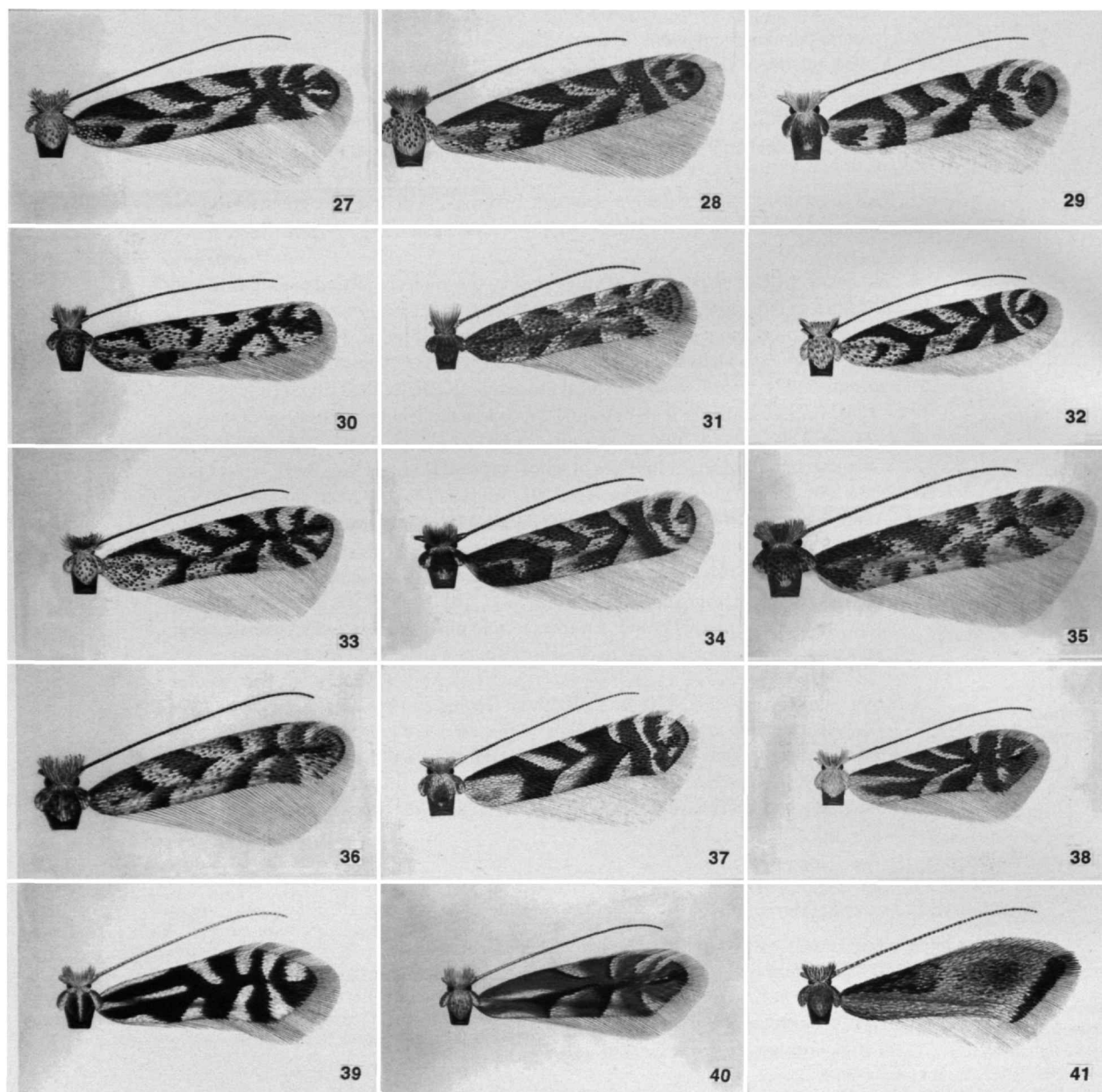
Phyllonorycter atomariella (Zeller).—Davis, 1983:10.

Phyllonorycter ontario (Freeman).—Davis, 1983:10.

Phyllonorycter tremuloidiella (Braun).—Davis, 1983:10.—Maier and Davis, 1989:17.

ADULT (Figure 27).—Length of forewing: 3.6–4.8 mm. Small, slender wing moths with bronzy brown forewings partially traversed by usually five, rarely four, mostly oblique white costal bands and usually five, highly variable, white dorsal bands. Valvae of male genitalia symmetrical, tapering to an acute, sinuate apex.

Head: Vertex rough, usually with equal mixture of white and brown piliform scales, sometimes entirely white; frons smooth, with broad, lustrous white scales often lightly suffused with brown. Antenna light brown to gray; each scale dark at apex fading to nearly white at base; a single row of



FIGURES 27-41.—Adults: 27, *Phyllonorycter apparella* (4.5 mm); 28, *P. latus* (4.3 mm); 29, *P. deserticola* (3.5 mm); 30, *P. nipigon* (4.3 mm); 31, *P. nipigon* (3.7 mm). *P. salicifoliella*: 32 (= *kenora*) (4.0 mm); 33 (3.6 mm); 34 (4.0 mm). *P. erugatus*: 35 (4.5 mm); 36 (5.0 mm). 37, *P. acanthus* (3.4 mm). 38, *P. mildredae* (3.1 mm). 39, *P. populiella* (3.5 mm). 40, *P. scudderella* (3.1 mm). 41, *P. apicinigrella* (3.8 μ m). (Forewing length in parentheses.)

scales encircling each segment; length three-fourths to four-fifths that of forewing. Labial palpus same color as frons.

Thorax: Dorsum usually white, irrorated with dark brownish tipped scales, occasionally entirely white. Venter white. Forewing variable, pale reddish to bronzy brown with typically five, rarely four, white costal bands and four to five dorsal

bands extending mostly obliquely midway across wing as in Figure 27; all white bands edged internally by dark brown scales except slender tornal band that possesses a dark costal margin that forms an elongate apical spot; basal transverse white band highly variable, often confluent with basal two dorsal bands, white bands frequently irrorated slightly with dark

brown scales. Fringe pale gray. Hindwing and fringe uniformly pale gray. Legs grayish brown dorsally, white ventrally; apices of tibial and tarsal segments slightly paler.

Abdomen: Grayish brown dorsally, white ventrally; conspicuous sex-scaling absent. Female with A7 moderately well sclerotized and tubular. Eighth sternum (Figure 235) of male elongate with mostly parallel margins then abruptly narrowing to minutely bidentate caudal apex.

Male Genitalia (Figures 233, 234, 335–337): Vinculum broadly V-shaped. Transtilla relatively slender. Valva symmetrical, elongate and very slender, tapering to an acute, sinuate apex; apical process with a minute, slit-like, subapical pore (Figure 337). Anellus completely membranous. Aedeagus slender, relatively short, approximately 0.7× the length of the eighth sternum.

Female Genitalia (Figures 423, 424): Accessory bursa with relatively short duct (approximately 0.33× the length of ductus bursae), arising from a short, enlarged, unsclerotized common duct (antrum) immediately anterior to ostium. Signum a single, elliptical, lightly sclerotized disk bearing a symmetrical pair of minute papillae.

EGG (Figures 1–6).—Flat type, approximately 0.3 mm long (excluding fringe), 0.19 mm wide, and 0.14 mm deep. Upper-side chorion finely reticulate and papillate (Figure 2). Aeropyles usually present at intersections of low ridges. Underside smooth (Figure 3), lightly cemented to host leaf. Division of upper and lower chorion surfaces sharply defined by broad, circumferential fringe of thin, irregular tissue (Figures 1, 3); maximum width of fringe 0.06 mm. Two micropyles present at anterior pole immediately above fringe (Figures 4–6), located on ridges of sharply defined network of ~8–10 irregular, cellular partitions (Figures 5, 6).

LARVA (Figures 42–84).—Similar to *P. nipigon*. Length of largest third instar 3.3 mm; head width 0.31 mm. Fifth instar: Length of largest larva 6.4 mm; head width 0.41 mm. A1, A2, and P1 arising distant from adfrontal suture (Figure 79). Apical spines of hypopharynx (Figure 58) reduced. Prothorax with D1 anterior to D2. Crochets on A3–A5 with 4–6 hooks in caudal row and 5–7 hooks in a sinuate anterior row.

LARVAL MINE (Figure 18).—As illustrated.

PUPA (Figures 69–77).—Maximum length 4.5 mm; width 1.0 mm. Vertex with triangular, dorsally flattened cocoon cutter with minutely serrated, lateral ridges (Figures 69, 70). Forewing extending to caudal margin of A6. Hindleg extending to anterior margin of A8. Dorsum of A2–A8 almost completely covered with dense concentration of short, scattered spines (Figures 72); intersegmental surfaces as in Figure 73. Caudal half of sternum A7 with a median, triangular raised area bearing usually 4 small, stout spines laterally (accessory cremaster; Figure 71). Cremaster consisting of a terminal, widely separated pair of short, broad-based spines (Figures 75–77). A9 with sternum sharply indented to A10 (Figure 74).

TYPES.—Not examined, Frankfurt a. M., Germany, deposition unknown (*apparella* H.-S.). Lectotype, ♂ (referred to as

type by Freeman, 1970:275), Kaslo, B.C., Canada, USNM (*tremuloidiella* Braun). Lectotype (referred to as type by Freeman, 1970:272), ♂, Cambridge, Massachusetts, USA, USNM (*atomariella* Zeller). Holotype, ♂, Simcoe, Ont., Canada, CNC (*ontario* Freeman).

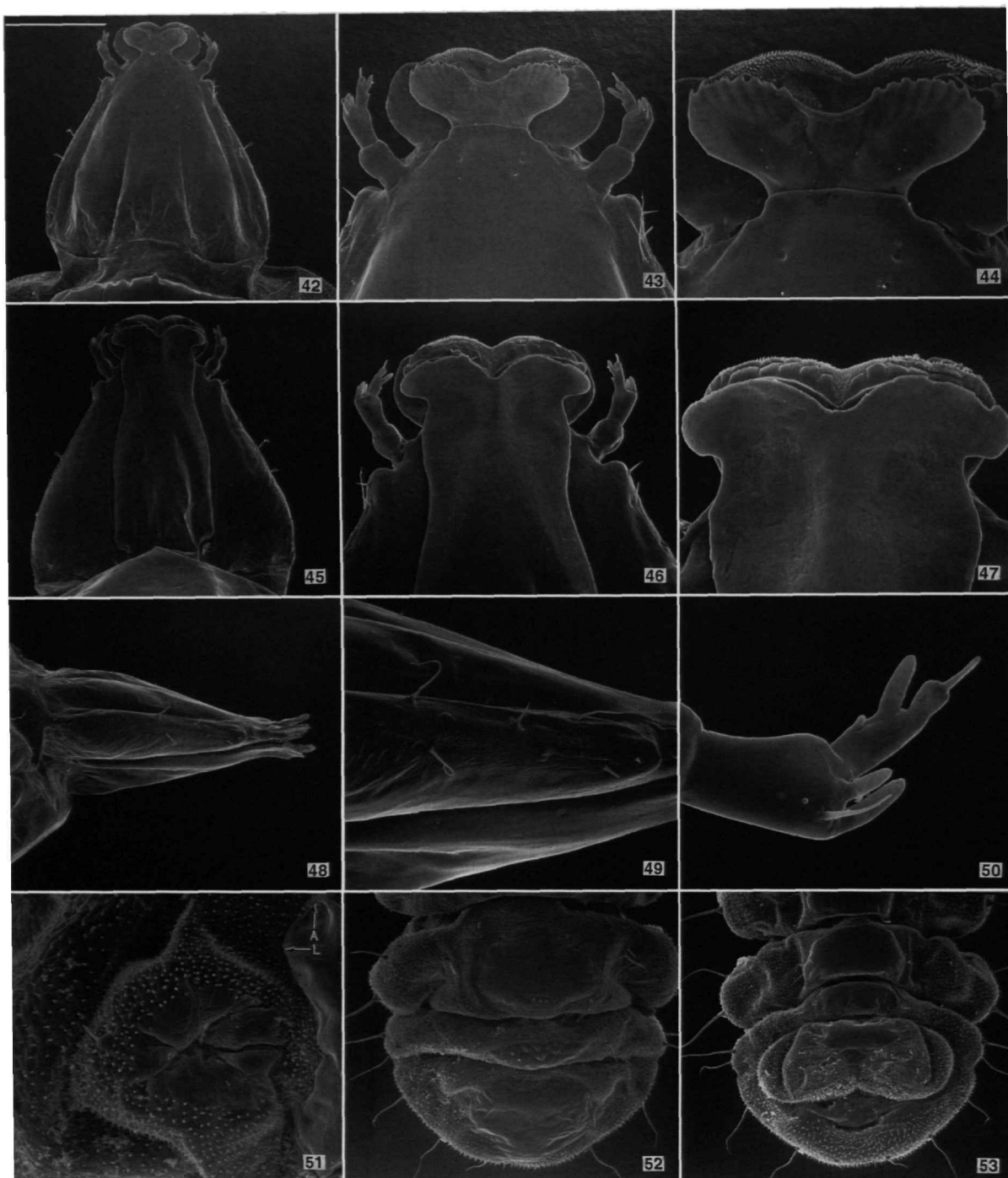
HOSTS (Table 1).—In North America, *Populus tremuloides* Michx., is the most frequently encountered host, with *P. grandidentata* Michx., and *P. canescens* (Alt.) J.E. Smith also being mined (Braun, 1908a). *Populus balsamifera* L., *P. deltoides* Marsh., and *Salix* sp. serve as hosts much less frequently. In the Palearctic region, *Populus alba* L., *P. nigra* L., *P. tremula* L., and *Salix* species have been reported as foodplants.

PARASITIDS (Table 2).—Braconidae: *Apanteles ornigis* Weed, *Apanteles* sp., *Pholetesor* sp., probably *salicifoliella* (Mason); Eulophidae: *Chrysocharis* sp., *Cirrospilus cinctithorax* (Girault), *Cirrospilus* sp. near *trifasciatus* (Ashmead), *Closterocerus* sp. near *trifasciatus*, *Horismenus fraternus* (Fitch), *Pediobius* sp., *Pnigalio flavipes* (Ashmead), *Pnigalio tischeriae* (Ashmead) (regarded by some as a junior synonym of *Pnigalio flavipes*), *Pnigalio* near *proximus* (Ashmead), *Pnigalio* sp., *Sympiesis conica* (Provancher), *Sympiesis* sp., *Tetrastichus* sp.; Ichneumonidae: *Alophosternum foliicola* (Cushman), *Diadegma* sp., *stenosomus* complex, *Scambus decorus* (Whalley); Pteromalidae: *Pteromalus* sp. (most records from Auerbach (1991), in which a few records may pertain only to *Phyllonorycter nipigon*).

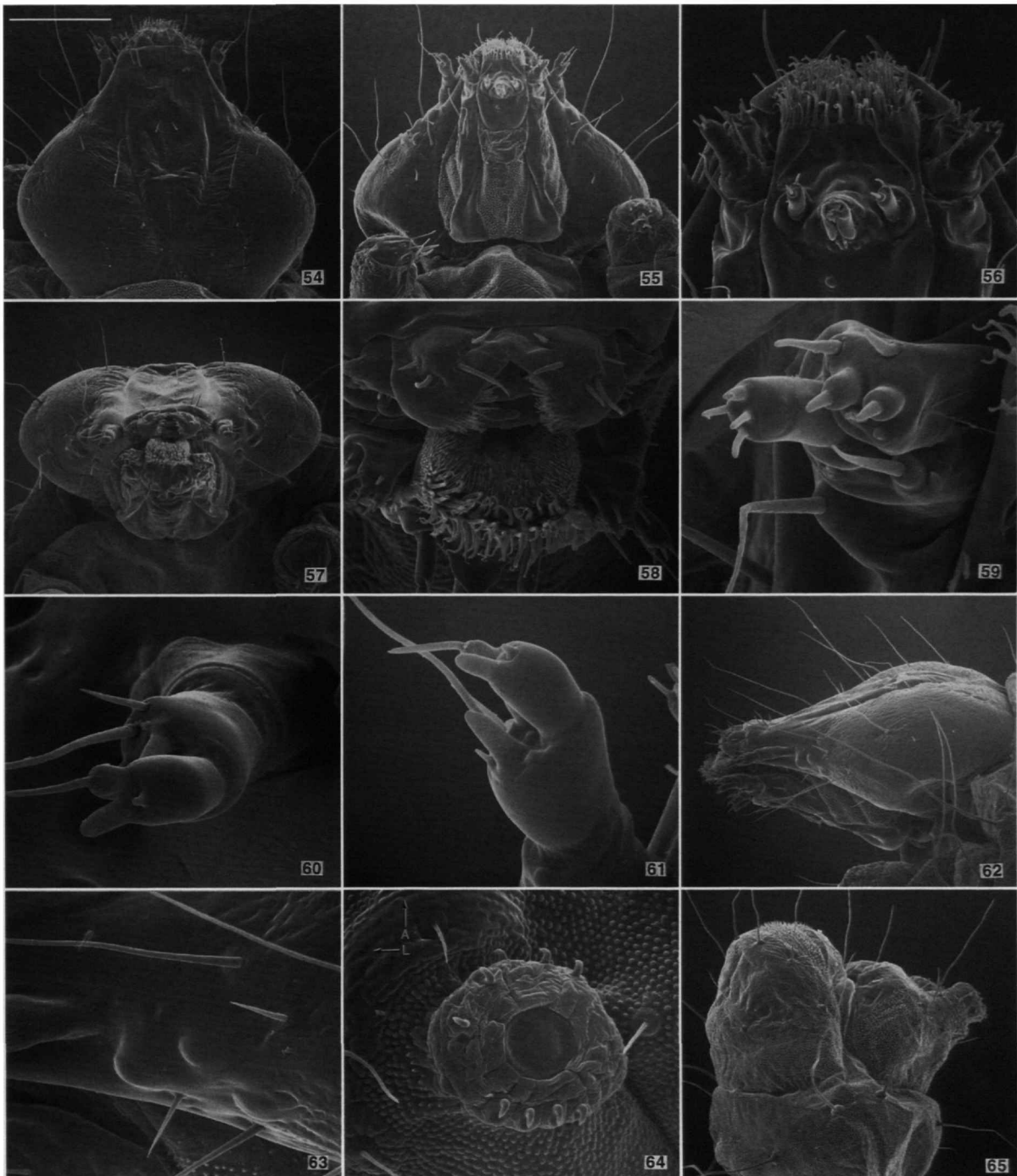
FLIGHT PERIOD.—Mid-July to late November; bivoltine (Maier and Davis, 1989).

DISTRIBUTION (Map 1).—Generally holarctic, from western Europe (but absent from Great Britain) to the Balkans, north to Finland and west to central Asia. Widely distributed in North America, from New Mexico, Ohio, and southern Maryland, north to central Alaska and Ontario.

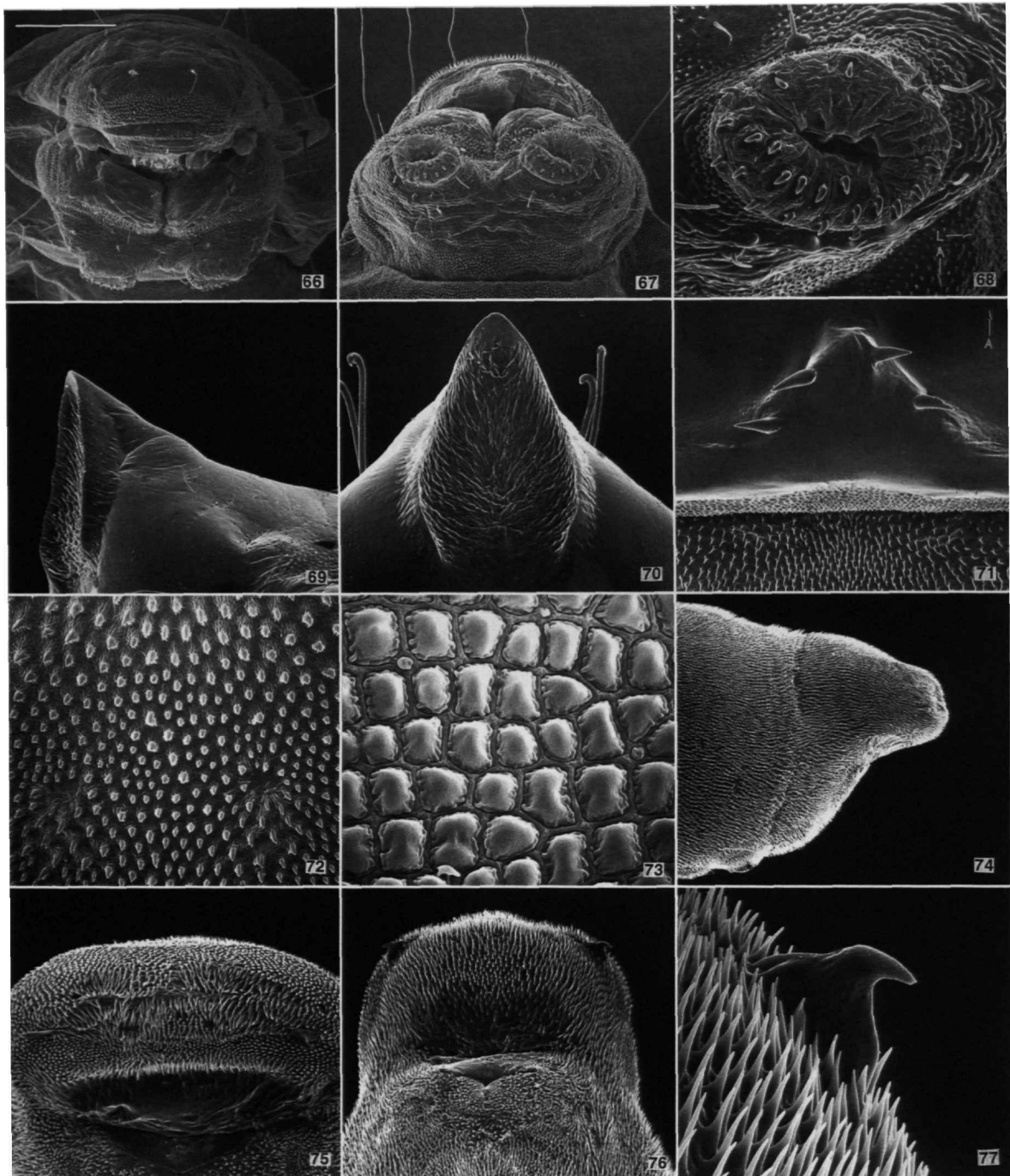
MATERIAL EXAMINED.—CANADA: ALBERTA: Bruderheim: 1♂, 1♀, 22–25 Aug 1986, *Populus tremuloides* (CNC). Drumheller, 2361 ft (726 m): 2♂, 3♀, mine: 24 Aug 1982, e. 29 Aug–3 Sep 1982 [e.=emerged], G. Deschka, mine in *Populus tremuloides*, zucht nr. 1694 (GD). Edmonton, Winterburn Road: 8♂, 15♀, 17 Apr–9 May 1983, G. Braybrook (CNC); 1♂, 17 Apr 1983, slide 31133 (USNM). Elk Island Nat. Park: 3♂, 11♀, mine: 30–31 Aug 1982, e. 2–10 Sep 1982, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1702, slide GD 1770 (GD). Red Deer, 853 m: 12♂, 13♀, mine: 27 Aug 1982, e. 29 Aug–11 Sep 1982, mine in *Populus tremuloides*, zucht nr. 1696, slide GD 1767A (GD). Sturgeon Lake: 2♂, 4♀, mine 16 Jul 1982, e. 24 Jul–2 Aug 1982, G. Deschke, mine in *Populus tremuloides*, zucht nr. 1657 (GD). BRITISH COLUMBIA: Clinton, 887 m: 8♂, 6♀, mine: 11 Aug 1982, e. 2–10 Aug 1982, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1678, slide GD 1761 (GD). Golden, 784 m: 2♂, 2♀, mine: 17 Aug 1982, e. 20–29 Aug 1982, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1684, slide GD 1763 (GD). Hazelton, 320 m: 26♂, 35♀, mine: 16 Jul 1979, e. 9–17 Aug 1979, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1438, slide GD 1517 (GD).



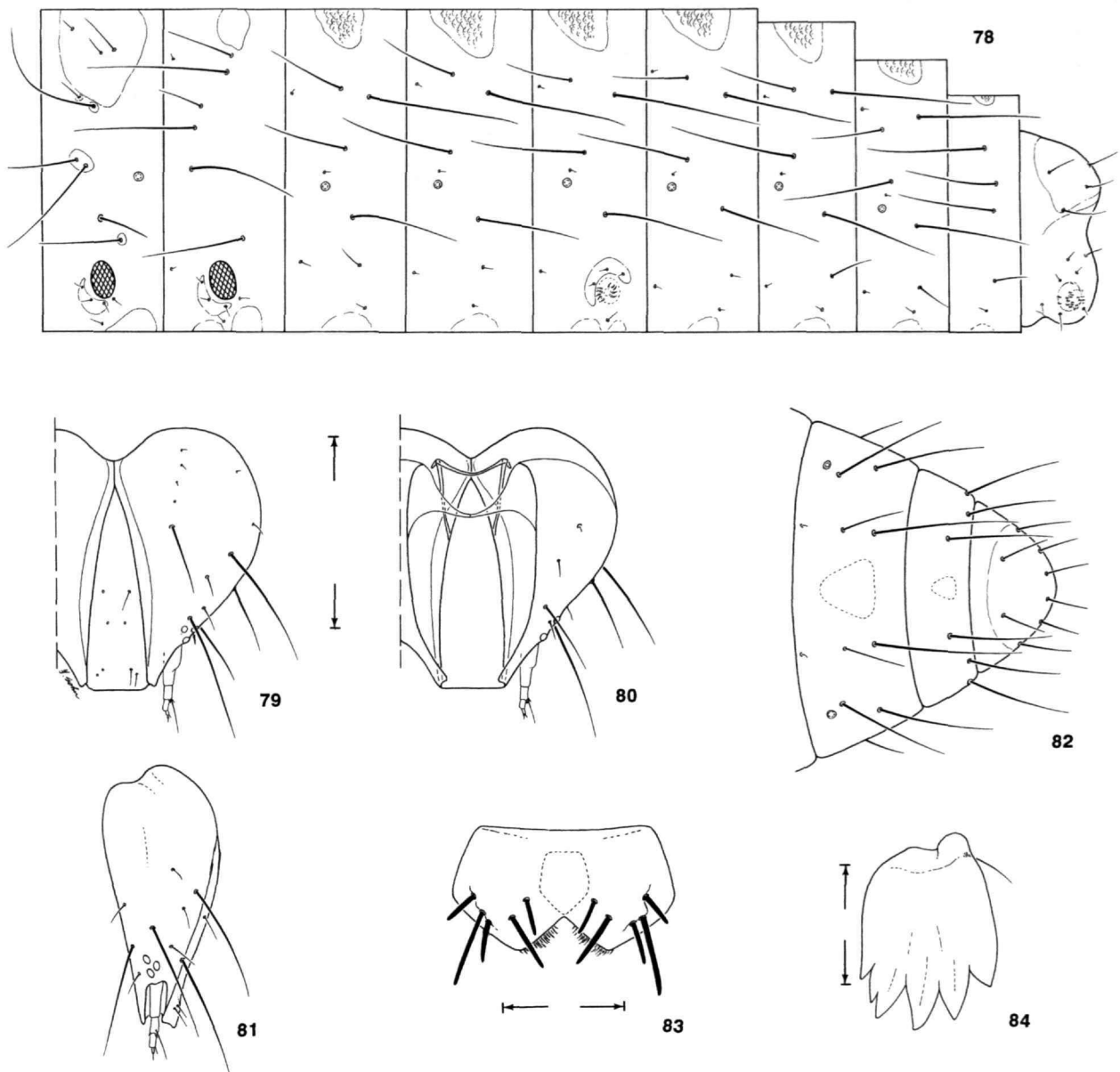
FIGURES 42–53.—*Phyllonorycter apparella*, third instar (sap-feeding) larva: 42, head, dorsal view (136 μm); 43, head, dorsal view (55 μm); 44, labrum, dorsal view (30 μm); 45, head, ventral view (120 μm); 46, head, ventral view (60 μm); 47, labium, ventral view (33 μm); 48, head, lateral view (120 μm); 49, stemmata area, lateral view (43 μm); 50, antenna, dorsal view (13.6 μm); 51, ambulatory callosity, abdominal segment 4, ventral view (30 μm); 52, abdominal terga 8–10 (107 μm); 53, abdominal sterna 8–10 (120 μm). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 42.)



FIGURES 54–65.—*Phyllonorycter apparella*, fifth instar (tissue-feeding) larva: 54, head, dorsal view (136 μm); 55, head, ventral view (136 μm); 56, labium, ventral view (43 μm); 57, head, anterior view (136 μm); 58, labrum, hypopharynx, anterodorsal view (38 μm); 59, maxilla, anterior view (12 μm); 60, antenna, anterior view (13.6 μm); 61, antenna, ventral view (15 μm); 62, head, lateral view (136 μm); 63, stemmatal area, lateral view (30 μm); 64, proleg, abdominal segment 4 (33 μm); 65, abdominal segments 9, 10, lateral view (150 μm). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 54.)



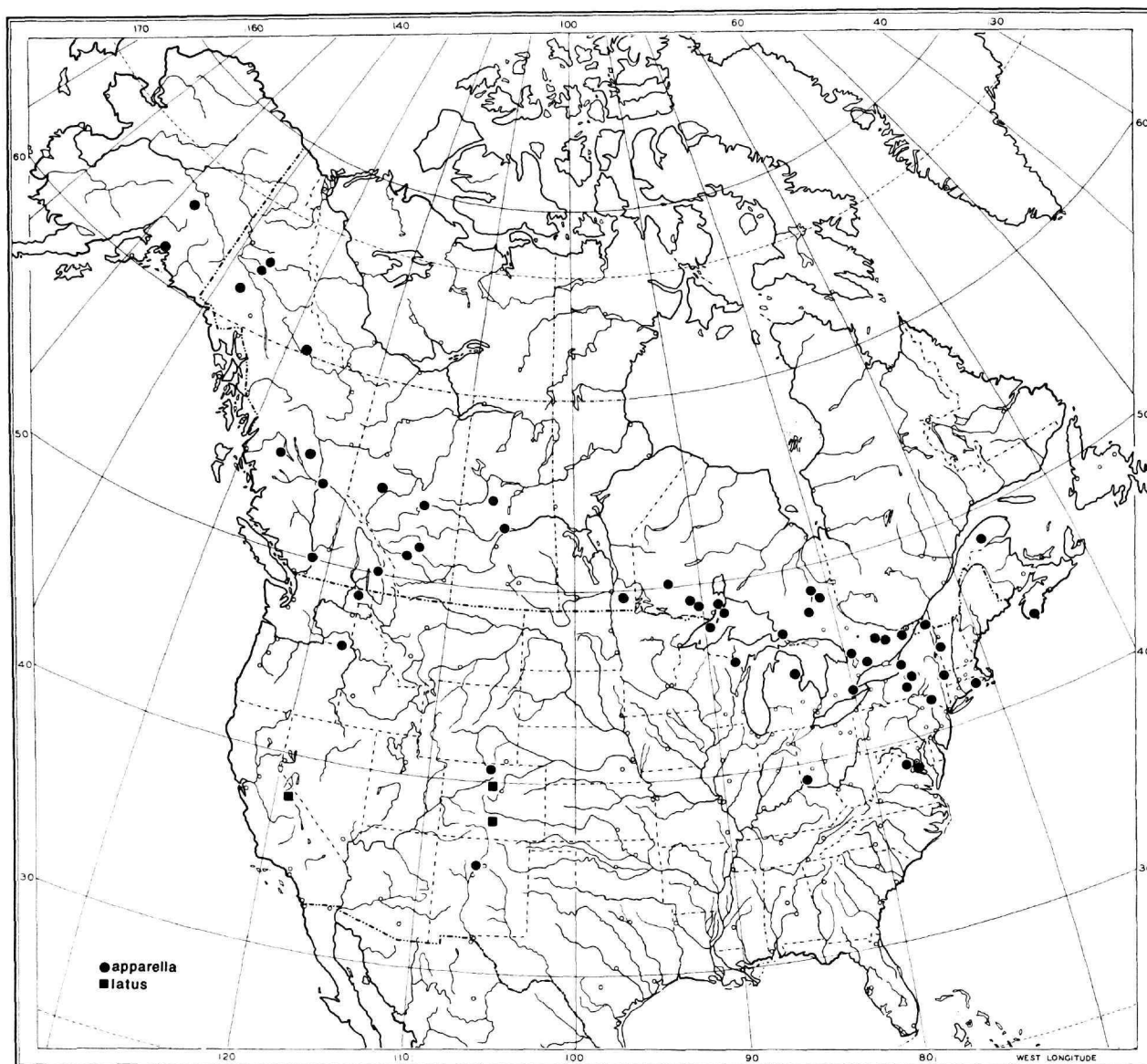
FIGURES 66–77.—*Phyllonorycter apparella*, fifth instar larva: 66, abdominal segment 10, caudal view (150 μ m); 67, ventral view of Figure 66 (120 μ m); 68, anal proleg (38 μ m); 69, pupa: frontal process (cocoon-cutter), lateral view (86 μ m); 70, anterior view of Figure 69 (86 μ m); 71, accessory cremaster, abdominal sternum 7 (86 μ m); 72, tergal spines, abdominal segment 4 (86 μ m); 73, interssegmental area, abdominal terga 4–5 (10 μ m); 74, abdominal segments 8–10, lateral view (150 μ m); 75, caudal view abdominal segment 10 (75 μ m); 76, ventral view of Figure 75 (86 μ m); 77, detail of cremasteral hook in Figure 75 (13.6 μ m). (A=anterior; scale lengths in parentheses; bar scale for all photographs shown in Figure 66.)



FIGURES 78–84.—*Phyllonorycter apparella*, chaetotaxy of fifth instar larva: 78, lateral schematic of prothorax, mesothorax, and abdominal segments 1, 2, 5–10; 79, dorsal view of head (0.3 mm); 80, ventral view; 81, lateral view; 82, dorsal view of abdominal segments 8–10; 83, labrum, dorsal view (0.05 mm); 84, mandible (0.05 mm). (Scale lengths in parentheses.)

Iskut: 1♂, 2♀, 22 Aug 1994, *Populus trichocarpa* Torr. and A. Gray (CNC, USNM). Kalso: 1♂ (holotype, slide USNM 17098), 3♂, 4♀ (paralectotypes, slides 17098, 17466, 18038, 20485, 22736, 30395, 30396), J.W. Cockle, 3♂, 16 Aug 1903, slide USNM 22737 (USNM). Kamloops: 1♂, 2♀, 27–30 Aug 1937, J. Jacob, on *Populus tremuloides*, CNC slide MIC 2248 (CNC). Manson Creek: 1♂, 4 Aug 1967, 2♂, 8 Aug 1967, Free-

man and Lewis, trembling aspen, slides CNC 2886, GD 1321 (CNC, GD). Muncho Lake, 817 m: 1♂, mine: 3 Aug 1982, e. 14 Aug 1982, G. Deschka, mine in *Salix*, zucht nr. 1671, slide GD 1759 (GD). Narcasli: 1♀, 31 Jul 1967, Freeman and Lewis, trembling aspen (GD). Pentiction, Shingle Creek: 1♂, 1♀, 7–20 Sep 1934, A. Gartrell, *Populus*, CNC slide MIC 2247 (CNC). Prince George, 567 m: 3♂, 1♀, mine: 8 Aug 1982, G. Deschka,



MAP 1.—Distribution of *Phyllonorycter apparella* and *P. latus*.

mine in *Populus tremuloides*, zucht nr. 1674, slide GD 1760 (GD). MANITOBA: Aweme: 1♂, 30 Aug 1920, N. Criddle, slide DRD 3830 (CNC). 8.5 mi [13.6 km] west of Jct. 1 and 11: 1♂, 26 Jul 1989, e. 9 Aug 1989, S. Passoa, *Populus tremuloides*, slide USNM 30764 (USNM). NOVA SCOTIA: Barrington: 2♂, 1 Sep 1973, G. Lewis, *Populus tremuloides*, 73-20 (CNC). ONTARIO: Ackray: 1♀, 9 Jul 1954, trembling aspen (GLFC); 1♂, 1♀, 9 Aug 1954, trembling aspen (USNM). Bells Corners: 1♀, 22 Jul 1955, G. Lewis, *Populus tremuloides*, 55-78, CNC slide MIC 2226 (CNC). Cochrane: 2♂, 5♀, 8-9 Aug 1967, G. Lewis,

Populus tremuloides, 67-44, CNC slides MIC 2238, 2239 (CNC). Deux Rivieres: 1♂, 8 Aug 1967, G. Lewis, *Populus tremuloides*, 67-49, CNC slide MIC 2240 (CNC). Foleyet: 1♂, 25 Aug 1965, *Populus tremuloides*, CNC slide MIC 2296 (CNC). Ft. William: 1♀, 11 Aug 1963, *Populus*, CNC slide MIC 2241 (CNC). Kapuskasing: 2♂, Farquier, *Populus tremuloides* (CNC); 3♂, 5♀, 25-29 Aug 1965, C. Miller, *Populus tremuloides*, CNC slides MIC 2234-2236 (CNC). Kaweme: 1♂, 3♀, 17 Jul 1954, trembling aspen (GLFC). Peterboro[ugh]: 1♂, 2 Oct 1967, T. Freeman, *Populus tremuloides*, slide CNC

2875 (CNC). Raith: 6♂, 9♀, 26–31 Jul 1955, A. Klots, mine on *Populus tremuloides* (AMNH, USNM). Sault Ste. Marie: 5♀, 10–12 Jul 1954, J. Martin, trembling aspen (GLFC); 2♂, 2♀, 17 Jul 1954, J. Martin, trembling aspen, slides USNM 31160, 31161 (USNM). Shebandowan: 1♀, 4 Aug 1967, G. Lewis, *Populus tremuloides* (CNC). Simcoe: 1♂, 1♀, 14–15 Sep 1965, T. Freeman, *Populus tremuloides*, 65-83, slide CNC 2878 (CNC). Sioux Lookout: 2♀, T. Freeman, *Populus tremuloides*, 67-48 (CNC). Sparrow Lake: 3♂, e. 22 Jul 1926, *Populus tremuloides*, A. Braun, B.1251, slide DRD 3822 (ANSP). Thunder Bay, Hills Block Cons. Forest: 3♂, 2♀, 27–30 Aug 1981, J. Wales (CNC). Thunder Bay, Sibley Prov. Park: 9♂, 11♀, 20–25 Aug 1982, J. Landry, *Populus tremuloides* leaf mines (CNC); 1♂, same data, slide USNM 31134 (USNM). QUEBEC: Gaspé Peninsula, Routhierville: 2♀, e. 2 Sep 1956, A. Braun, *Salix* sp., B.2243, slide DRD 3824 (ANSP). SASKATCHEWAN: Dore Lake: 21♂, 22♀, 25 Aug 1967, Freeman and Lewis, *Populus tremuloides*, 67-59, CNC 2879–2882 (CNC). Prince Albert: 1♂, 1 Aug 1967, Freeman and Lewis, *Populus tremuloides*, 67-25, CNC slide MIC 2245 (CNC). YUKON: Stewart Crossing: 7♂, 31♀, 30 Jul 1982, e. 18–26 Aug 1982, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1664, slides GD 1750, 1753 (GD). Stewart River banks, near Stewart Crossing: 1♂, 5♀, mine: 30 Jul 1982, e. 11–22 Jul 1982, G. Deschka, mine in *Salix* sp., zucht nr. 1668, slide GD 1754 (GD). 8 km east of Watson Lake, 685 m: 20♂, 21♀, mine: 20 Jul 1982, e. 2–8 Aug 1982, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1664, slide GD 1754 (GD). UNITED STATES: ALASKA: Cooper Landing: 1♂, 11 May 1994, K. Zogas, *Populus glauca* Haines, slide USNM 31583 (USNM). Destruction Bay, Kluane Lake: 3♂, 6♀, mine: 11 Jul 1979, e. 23 Aug–3 Sep 1979, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1459, slide GD 1527 (GD). 12 mi [19.2 km] SW of Fairbanks: 3♀, mine: 31 Jul 1979, e. 11 Aug 1979, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1452, slide GD 1523. Talmeta Pass, 3000 ft [915 m], east of Chikaloon: 2♂, 4♀, mine: 8 Aug 1979, e. 19–27 Aug 1979, G. Deschka, mine, *Populus tremuloides*, zucht nr. 1657 (GD). COLORADO: Long Peaks, 9000 ft [2744 m]: 4♂, 5♀, e. 1 Aug–27 Sep 1919, A. Braun, *Populus tremuloides*, B.102.2 (ANSP); 2♂, e. 28–31 Aug 1919, A. Braun, B.102.2 (CNC); 4♂, 8♀, e. 31 Aug 1919, A. Braun, slides USNM 18048, 28931 (USNM). CONNECTICUT: Hartford Co., Southington: 1♂, 8 Jul 1980, C. Maier, *Populus tremuloides*, slide DRD 3565 (CTM). Litchfield Co., Goshen: 8♂, 1♀, 26 Aug 1981, C. Maier, *Populus tremuloides* (CTM); 1♂, 26 Aug 1981, C. Maier, slide USNM 30817 (USNM). DISTRICT OF COLUMBIA [Washington]: 2♂, 1♀, 1894, C.V. Riley, *Populus tremuloides* (BMNH). IDAHO: Kootenai Co., Coeur d'Alene: 13♂, 15♀, 27 Aug 1919, J. Everden, e. 9 Sep 1919, *Populus trichocarpa*, USNM slide 31703 (USNM). Latah Co., Moscow: 4♂, 7♀, 10 Jul 1985, M. Furniss, *Populus tremuloides*, slide 28498 (USNM). MAINE: York Co., near Kittery: 2♂, mine: 20 Sep 1986, *Populus tremuloides*, lab reared (CTM). MARYLAND: Prince Georges Co., Cedarville State Forest, vicinity of

Cedarville Lake: 4♂, 5♀, 11 Sep 1994, e. 20–27 Sep 1994, D.R. Davis, *Populus grandidentata*, DRD 1516 (USNM). MASSACHUSETTS: Barnstable Co., Barnstable: 1♀, 19 Aug 1952, C. Kimball, slide 28439 (USNM). Middlesex Co., Cambridge: 1♂ (lectotype, *L. atomariella*), slide USNM 32139 (CNC 2601) (USNM). MICHIGAN: Gogebic Co., Watersmeet: 1♂, 5 Aug 1963, aspen (USNM). Iron Co., Iron River: 1♂, 5 Aug 1963, aspen (USNM). Oakland Co., Clarkston, 4920 Pelton Road: 1♂, 3♀, mine: 15 Jul 1990, C. Maier, *Populus tremuloides*, lab reared (CTM, USNM). MINNESOTA: Clearwater Co., Itasca State Park: 3♂, 3♀, e. Aug 1992, M. Auerbach, ex *Populus grandidentata*, slide 31181 (USNM); 3♂, 3♀, e. Aug 1992, M. Auerbach, ex *Populus tremuloides*, slide 31183 (USNM). NEW MEXICO: Los Alamos Co., Bandelier National Monument, 7500 ft [2287 m]: 5♂, 7♀, 53 larvae, 3 pupae 18 Jul 1980, e. 1–8 Aug 1980, 2♂, 2♀, Aug 1979, W. Pippin, aspen, slides USNM 21367, 30474–30476 (USNM). NEW YORK: Essex Co., Saramac Lake: 1♂, 12 Jul 1988, e. 17 Jul 1988, DLW 88 H 25, *Populus tremuloides* (DLW). Madison Co., Tuscarora Lake: 5♂, 5♀, 3–9 Jul 1975, E. Jäckh, *Populus tremuloides* (GD, USNM). Monroe Co.: 1♀, 5 May 1949, C. Kimball, slide 28438 (USNM). Onondaga Co., Radisson: 8♂, 10♀, 3–14 Jul 1977, E. Jäckh, *Populus tremuloides* (GD, USNM). St. Lawrence Co., Oak Point: 1♂, 3♀, 1–2 Aug 1983, e. 8–9 Aug 1983, D. Wagner, JAP No. 83H25, *Populus* sp., slide DRD 3736 (DLW). Tompkins Co., Dryden: 2♂, 3 Oct 1960, R. Hodges, slide USNM 17025 (USNM). OHIO: Hamilton Co., Cincinnati: 2♀, 13 Apr–3 May 1906, A. Braun (ANSP); 2♂, 2♀, e. 2–4 Jul 1907, A. Braun, *Populus balsamifera candicans* Aiton (ANSP); 2♀, e. 13–14 Jul 1917, A. Braun, on *Populus canescens* (ANSP); 1♀, 27 Jul 1911, A. Braun (ANSP); 1♂, 27 Jul 1911, A. Braun, slide DRD 3823 (ULK); 1♂, e. 16 Aug 1917, A. Braun, on *Populus canescens*, slide CNC 2 (CNC); 2♂, 1♀, 16 Sep 1906, A. Braun, on *Populus* (ANSP); 1♂, 1♀, 8 Oct 1904, A. Braun, slide DRD 3823 (ANSP); 1♂, 2♀, 1–15 Nov 1903, A. Braun (ANSP); 1♀, 4 Aug 1907, on *Populus canescens*; 1♂, 2♀, e. 14 Aug 1917; 1♂, 2♀, 16 Aug 1917; 1♀, 27 Aug 1911; 3♂, 1♀, 2 Oct 1909; 1♂, 9 Oct 1906; 1♂, 15 Nov 1903; 1♂, 20 Nov 1904; 1♂, 22 Nov 1916, A. Braun, slides USNM 30377, 30378, 30398, 30399 (USNM). Highland Co., Ft. Hill: 1♀, e. 22 Sep 1965, A. Braun, *Populus grandidentata*, B.2411, slide DRD 3826 (ANSP). VERMONT: Chittenden Co., South Burlington: 1♂, 1/6 Jun 1987, e. DOA 7 Jul 1987, DLW 87F27, *Populus tremuloides*, slide 3774 (DLW); 1♂, 1♀, 25/30 Jun 1987, e. 7/8 Jul 1987, DLW 87F110, *Populus grandidentata*, slide 3781 (DLW); 2♀, 27 Jul 1988, e. 20 Sep 1988, DLW 88H94, *Populus deltoides*, slide 3780 (DLW). VIRGINIA: Fairfax Co., Springfield, Accotink Creek: 1♂, 7♀, mine: 22 Jul 1975, e. 23 Jul–2 Aug 1975, G. Deschka, mine in *Populus grandidentata*, zucht nr. 1097 (GD).

REMARKS.—The wing markings of this species are variable over its broad distribution and between the two generations encountered in the southern part of its range. The observed variation is sufficient to include *Phyllonorycter atomariella* (Zeller)

(or at least the lectotype), *P. tremuloidiella* (Braun), and *P. ontario* (Freeman) among the Old World *P. apparella* (Herrich-Schäffer), all of which share the same genital morphology. The type series of *Phyllonorycter atomariella* apparently represented a mixed series. Braun (1908b) synonymized Zeller's name under *P. salicifoliella* based on the two syntypes in the collections of the Museum of Comparative Zoology (MCZ) as well as the syntype at the Smithsonian Institution (USNM), which she observed possessed less dusting on the forewings and more white markings than did the MCZ material. Freeman (1970) recognized *P. atomariella* as a valid species based on the male in the USNM and figured its genitalia. His reference to this specimen as the "type" probably can be interpreted as a lectotype designation, although Braun had earlier referred to all three specimens as "types." The senior author has examined all known syntypes, including four specimens collected from Cambridge, Massachusetts (including a female labeled as type), now deposited in The Natural History Museum, London (BMNH). Only the male illustrated by Freeman represents *P. apparella*; all of the others are believed to be examples of *P. salicifoliella*. The presence of a Zeller type in the USNM is unusual, if not questionable. The "type" microslide (CNC 2601 [USNM 32139]) that Freeman (1970, fig. 9) photographed still resides in the USNM, but the present whereabouts of the moth is unknown.

Several important references pertaining to *Phyllonorycter apparella* have appeared in the literature over the last 50 years mistakenly under the name *P. salicifoliella* (Martin, 1956; Watson, 1956; Alberts, 1989; Auerbach, 1991; Auerbach and Alberts, 1992; Auerbach and Fleicher, 1992). North American references of *Phyllonorycter* mining the leaves of *Populus tremuloides*, and, to a lesser extent *Populus grandidentata*, usually pertain to this moth. Data in the foregoing references involving *Phyllonorycter* mining *Populus balsamifera* likewise pertain most probably to *Phyllonorycter nipigon*.

Phyllonorycter apparella can be recognized most easily by the male genitalia, particularly by the attenuated, sinuate apex of the valva. In North America, this species is most allied to another *Populus tremuloides* feeder, *Phyllonorycter latus*, especially as shown by their similar genitalia, pupal cremaster, and host preference. Criteria for distinguishing the two species are provided in the key to species and are discussed under *P. latus*. The pupal cremaster of European *P. apparella* agrees with North American *P. apparella* (and *P. latus*) in having lost the inner-most pair of spines present in other North American members of the *apparella* and *salicifoliella* groups.

Phyllonorycter latus, new species

FIGURES 28, 85–93, 236–238, 425, 426; MAP 1

ADULT (Figure 28).—Length of forewing: 3.7–4.4 mm. Small moths, with slender reddish brown forewings largely traversed by 5 irregularly oblique white bands. Valvae of male

genitalia symmetrical, gradually tapering to a slightly curved acuminate apex; vinculum broad.

Head: Vertex rough, with a variable mixture of mostly white and light brown, piliform scales; frons smooth, with broad white scales rarely suffused with pale brown. Antenna gray, a single row of dark-tipped scales encircling each segment; length of antenna approximately 0.8× that of forewing. Labial palpus mostly white, light to dark brown laterally.

Thorax: Pronotum mostly white, irrorated with dark brownish tipped scales. Venter white. Forewing variable, pale reddish to bronzy brown with usually five white bands extending across wing; basal two bands strongly slanted distad; distal band the smallest and interrupted by dark fuscous subapical spot; a large, highly variable streak or spot present at dorsal (anal) half of wing base; reddish bands mostly margined distally with dark brown; basal two dorsal bands dark margined along dorsal (caudal) margin of wing. Fringe pale gray. Hindwing and fringe uniformly pale gray. Legs mostly dark brown or fuscous dorsally, white ventrally, with apices of tibial and tarsal segments white; hindleg much paler dorsally, pale gray.

Abdomen: Dark brown dorsally, white ventrally; conspicuous sex-scaling absent. Eighth sternum of male elongate, gradually tapering caudally to a narrow, truncate apex (Figure 238).

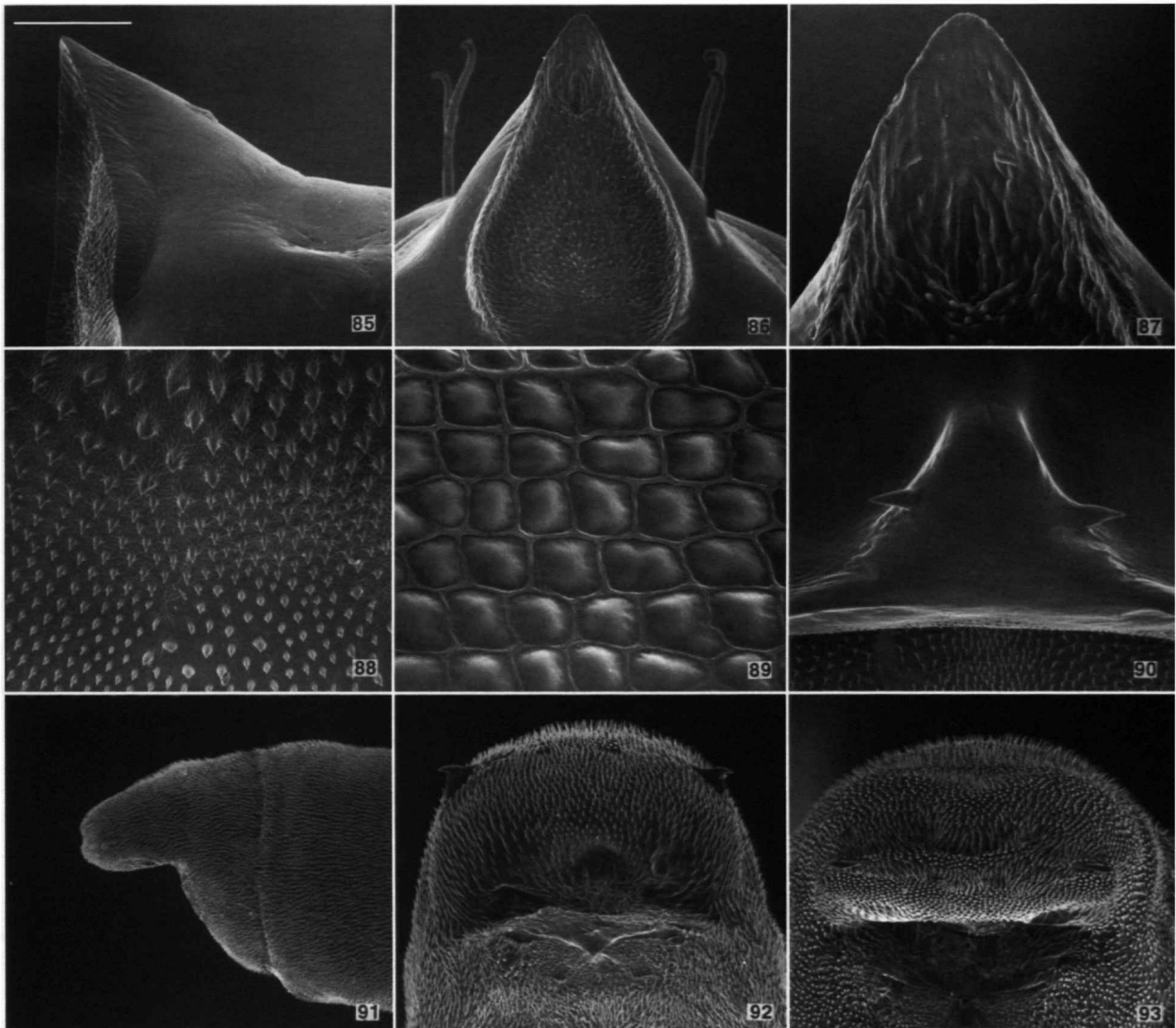
Male Genitalia (Figures 236, 237): Vinculum broadly V-shaped. Transtilla thickened, quadrate. Valva symmetrical, elongate, and very slender, tapering to a slightly curved, acuminate apex. Anellar membrane scabrous. Aedoeagus slender, with a minute, subapical lobe, relatively short, approximately 0.55× the length of eighth sternum.

Female Genitalia (Figures 425, 426): Accessory bursa with relatively long duct, nearly equalling length of ductus bursae, and arising from posterior end of latter from a short common duct. Signum a single, elliptical, lightly sclerotized disk bearing a pair of minute spinose papillae.

PUPA (Figures 85–93).—Maximum length 4.8 mm; width 0.8 mm. Vertex with triangular cocoon cutter similar to *P. apparella*. Forewing and antenna extending to caudal margin of A7. Hindleg extending to A8. Dorsum of A2 to anterior half of A8 almost completely covered with dense concentration of moderately large to small spines, with the largest spines situated cephalad; intersegmental surfaces as in Figure 89. Caudal half of sternum A7 with slightly raised triangular area bearing bilateral pair of small stout spines (Figure 90). Cremaster consisting of single pair of widely spaced, broad-based, curved spines (Figures 92, 93) on caudal margin of A10. A9 with sternum abruptly constricting ventrally (viewed laterally, Figure 91) to A10.

HOLOTYPE.—Colorado: Grand Co., Grand Lake, 2450 m, ♂; e. larva 14–21 Aug 1978 [e.=emerged], G. Deschka, mine in *Populus tremuloides* Michx., zucht nr. 1346, mine: 30 Jul 1978, slide USNM 30776 (GD 1549), USNM.

PARATYPES.—CALIFORNIA: Inyo Co., Sentinel Meadow, Inyo National Forest: 1♂, 4♀, 30 Aug 1957, G.R. Struble, *Populus tremuloides*, Hopk. US. 34091A, slides USNM 28427,



FIGURES 85–93.—*Phyllonorycter latus*, pupa: 85, frontal process (cocoon-cutter), lateral view (86 μm); 86, dorsal view of Figure 85 (86 μm); 87, detail of subapical pore in Figure 85 (30 μm); 88, tergal spines of abdominal segment 6 (75 μm); 89, dorsal intersegmental area between segments 4–5 (10 μm); 90, accessory cremaster, abdominal segment 7, ventral view (86 μm); 91, abdominal segments 8–10, lateral view (150 μm); 92, ventral view of Figure 91 (75 μm); 93, caudal view of abdominal segment 10 (75 μm). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 85.)

30441. COLORADO: Alamosa Co., Great Sand Hills, 2450 m: 5 σ , e. larva 9–13 Aug 1978, G. Deschka, mine in *Populus tremuloides* Michx., zucht nr. 1343, mine: 25 Jul 1978, slides GD 1559, USNM 21738. Grand Co., Grand Lake, 2450 m: 19 σ , 19 f , e. larva 14–21 Aug 1978, G. Deschka, mine in *Populus tremuloides* Michx., zucht nr. 1346, mine: 30 Jul 1978, slide 1549. Paratypes in DLW, GD, and USNM.

HOST (Table 1).—*Populus tremuloides* Michx.

FLIGHT PERIOD.—August; univoltine.

DISTRIBUTION (Map 1).—Probably widespread through the western United States but currently known only from Inyo County in California and Grand and Alamosa Counties in Colorado.

ETYMOLOGY.—The specific name is derived from the Latin *latus* (broad) in reference to relatively broad vinculum, the most diagnostic feature of this species.

REMARKS.—*Phyllonorycter latus* represents a western derivative of *P. apparella*, with both species primarily restricted to

Populus tremuloides in North America. Their male genitalia agree in possessing a broad vinculum and curved apex to the valva, but the latter is shorter and less sinuate in *P. latus*. Their pupae are quite similar in retaining only the lateral pair of cremasteral spines, having lost the inner-most pair present in *P. nipigon* and in most other species examined in this study. The male genitalia of *P. latus* superficially resemble that of *P. nipigon*, but the two species are easily separated by the broader vinculum of *P. latus*.

Phyllonorycter nipigon (Freeman)

FIGURES 7–12, 19, 30, 31, 94–136, 239–241, 427, 428; MAP 2

Lithocolletis nipigon Freeman, 1970:276.

Phyllonorycter nipigon (Freeman).—Davis, 1983:10.

Lithocolletis salicifoliella Martin, 1956:155 [in part; not Chambers, 1871].—Watson, 1956:168.—Alberts, 1989:1.—Auerbach, 1991:1599.—Auerbach and Alberts, 1992:1.—Auerbach and Fleicher, 1992:201.

ADULT (Figures 30, 31).—Length of forewing: 3.4–4.4 mm. Small, slender wing moths with reddish brown forewings mostly traversed by 4 or 5 highly variable white bands. Valvae of male genitalia symmetrical, gradually tapering to a nearly straight, slightly down-curved, acuminate apex; vinculum slender.

Head: Vertex rough, with a variable mixture of white and light to dark brown piliform scales; frons smooth, with broad white scales heavily suffused with brown dorsally. Antenna gray; a single row of scales encircling each segment, which are darker at their apex; length of antenna approximately 0.8× that of forewing. Labial palpus mostly white, light to dark brown laterally.

Thorax: Dorsum mostly white, irrorated with dark brownish tipped scales. Venter white. Forewing variable, pale reddish to bronzy brown with usually five white costal bands extending across wing to fuse with usually four broader white dorsal bands; distal two costal and dorsal bands reduced and normally separated by reddish brown bands; white bands usually irrorated with dark brown; reddish bands typically margined distally by dark brown. Fringe pale gray. Hindwing and fringe uniformly pale gray. Legs usually dark grayish brown dorsally, white ventrally; apices of tibial and tarsal segments slightly paler; hindleg with dorsum pale gray.

Abdomen: Grayish brown dorsally, white ventrally; conspicuous sex-scaling absent. Female with A7 lightly sclerotized. Eighth sternum of male elongate, gradually tapering caudally to acute apex (Figure 241).

Male Genitalia (Figures 239, 240): Vinculum slender, tapering to a moderately elongate saccus. Transtilla slender. Valva symmetrical, elongate and very slender, tapering to a nearly straight, slightly downcurved, acuminate apex. Anellar membrane not smooth but finely wrinkled. Aedoeagus slender, with a minute, subapical lobe, relatively short, approximately 0.65–0.7× the length of eighth sternum.

Female Genitalia (Figures 427, 428): Accessory bursa

with elongate duct, equalling length of ductus bursae, arising from a short, slightly enlarged common duct (antrum) immediately anterior to ostium; common duct with a small narrow, sclerotized ring. Signum a single, elliptical to pyriform, lightly sclerotized disk bearing a pair of minute papillae.

EGG (Figures 7–12).—Similar to that of *P. apparella* except slightly larger, up to 0.324 mm long, 0.228 mm wide, and more depressed (0.12 mm deep). Upper surface reticulate as in *P. apparella* but apparently without micropapillae (Figure 9). Circumferential fringe less developed; maximum width ~0.28 mm. Micropyles 2–4, surrounded by 9 or 10 cellular partitions.

LARVA (Figures 94–124).—Hypermetamorphic; earliest instars (1–3) highly modified sapfeeders with strongly depressed bodies and reduced chaetotaxy; maximum length: 3.4 mm, width (T1): 0.6 mm. Later instars (4 and 5) tissue feeders, with typical cylindrical bodies; maximum length: 6.4 mm, width: 0.9 mm; body color pale green to white.

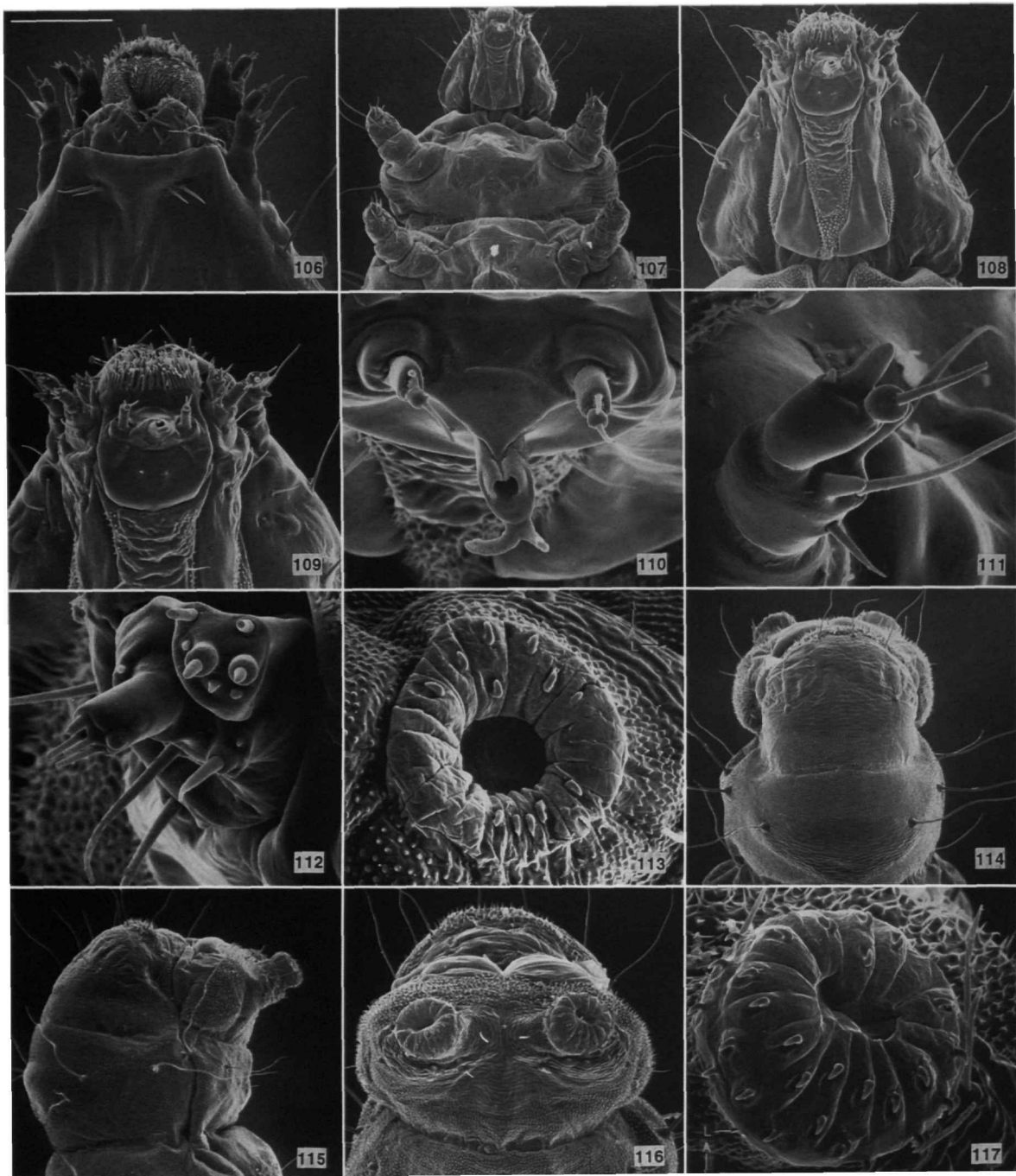
SAP-FEEDING INSTARS.—**Head:** Maximum width (third instar): 0.3 mm. Greatly depressed, triangular. Most setae lost or reduced; 3 pairs of stemma arranged in a widely spaced, lateral row; only 6 pairs of cranial setae preserved, a single pair (MD1) dorsally and 5 pairs laterally (probably A3 and L1 caudad to 3rd stemmata, S2 dorsad to 3rd stemmata, S1 dorsal to and SS2 ventral to median stemmata, and SS1 between 1st and 2nd stemma). Labrum broadly bilobed, less than 0.4 the width of head, with serrated (7–9 serrations per lobe) anterior margin; labral setae absent; venter of labrum smooth except for curved, longitudinal grooves from marginal serrations. Mandibles large, flat, with three relatively elongate, acute cusps and one small cusp. Labium smooth, with anterior margin excavate at middle; spinneret absent. Maxillary and labial palpi absent. Hypopharynx broad, densely covered with minute spines along anterior margin, with margin slightly incised at middle. Antenna reduced, 3-segmented, with numerous, short basiconic sensilla as shown (Figures 111).

Body: Setae generally absent or reduced except lateral to dorsal and ventral plates. Legs, prolegs, and crochets absent. Paired ambulatory callosities present both dorsally and ventrally on T1–3 and ventrally on A3–A5, A10 (Figures 102–104).

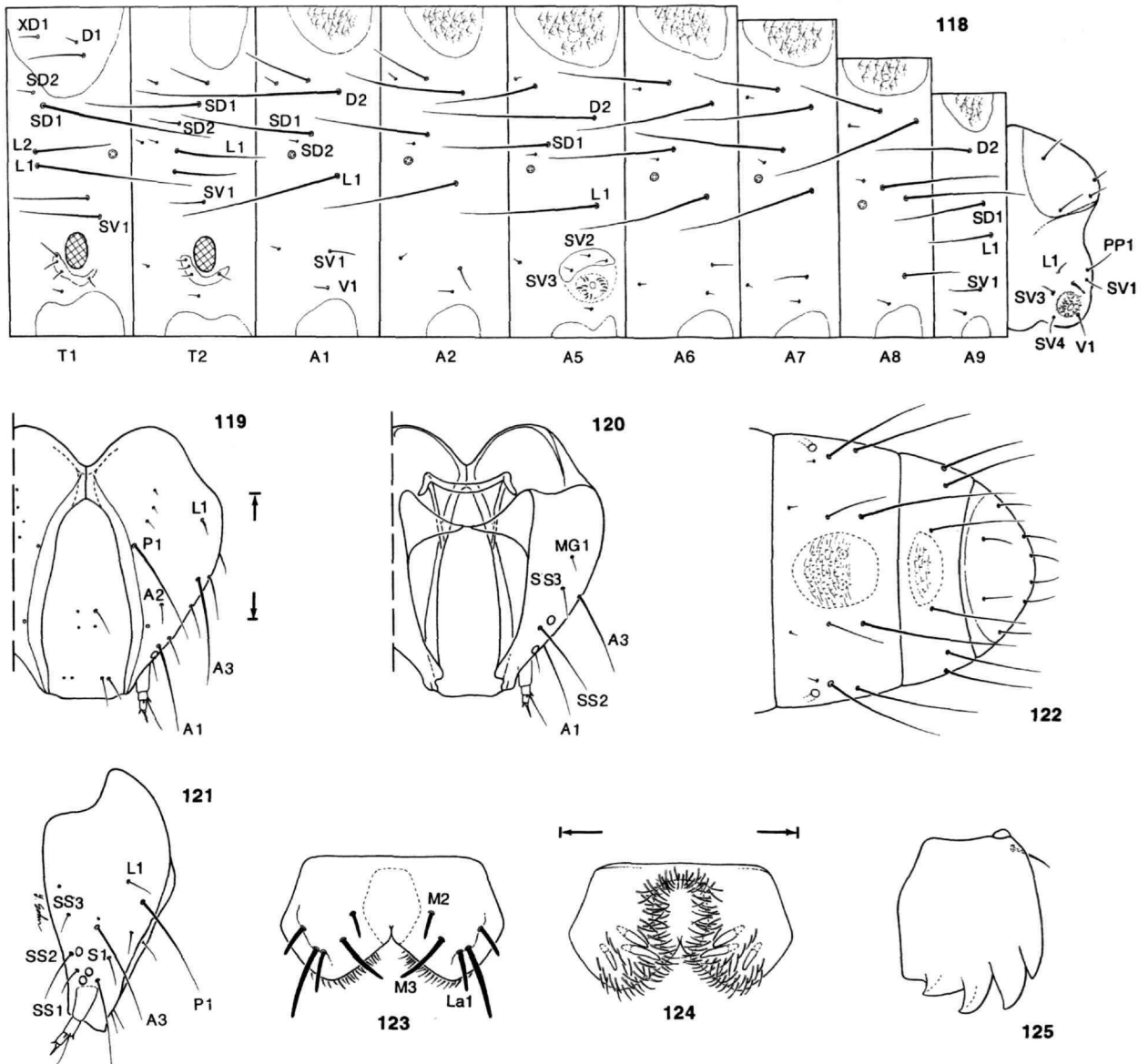
TISSUE-FEEDING INSTARS.—**Head:** Approximately round with full complement of mouthparts; dark reddish brown; maximum width (fifth instar) 0.4 mm. Frons (Figure 119) elongate, ~0.85× the distance to epicranial notch. Ecdysial line terminating near epicranial notch. Chaetotaxy relatively complete; all three MD setae present, arising caudad to P1 and Pa. P1 arising adjacent to ecdysial line. L1 reduced, arising laterad and widely separated from P1 (Figure 119). Setae AF1 and AF2, P2 absent. A2 arising about midway and almost in a line between A1 and P1. A3 arising anterior to stemma 1. C1 and C2 closely adjacent to each other. Three stemmata present; 1, 2, and 3 absent (Figures 120). S2, S3 absent. Antenna moderately long; sensilla as in Figure 111. Labrum (Figures 106, 123, 124) with M1 absent; three pairs of epipharyngeal spines present, the lat-



FIGURES 94–105.—*Phyllonorycter nipigon*, third instar (sap-feeding) larva: 94, head, dorsal view (60 μ m); 95, labrum, dorsal view (38 μ m); 96, head, ventral view (60 μ m); 97, labium, ventral view (38 μ m); 98, antenna, ventral view (20 μ m); 99, antenna, dorsal view (8.6 μ m); 100, anteroventral view of mouthparts (38 μ m); 101, anterior view of mouthparts (38 μ m); 102, dorsal ambulatory callosity of prothorax (30 μ m); 103, ventral ambulatory callosity of prothorax (27 μ m); 104, ambulatory callosity of abdominal sternum 4 (17.6 μ m); 105, abdominal segments 9, 10, dorsal view (86 μ m). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 94.)



FIGURES 106–117.—*Phyllonorycter nipigon*, fifth instar larva: 106, head, dorsal view (75 μ m); 107, ventral view of head, thoracic segments 1, 2 (0.27 mm); 108, head, ventral view (120 μ m); 109, detail of labium and hypopharyngeal spines in Figure 108 (75 μ m); 110, labial palpi and spinneret (25 μ m); 111, antenna, anterodorsal view (13.6 μ m); 112, maxilla, anteroventral view (15 μ m); 113, proleg of abdominal segment 4 (30 μ m); 114, abdominal segments 9, 10, dorsal view (176 μ m); 115, lateral view of Figure 114 (200 μ m); 116, ventral view of Figure 114 (120 μ m); 117, anal proleg (30 μ m). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 106.)

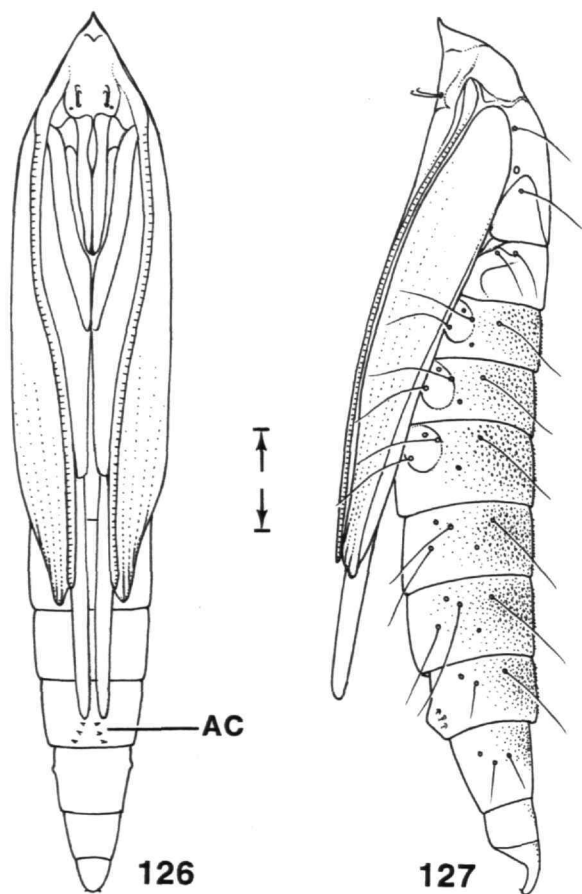


FIGURES 118–125.—*Phyllonorycter nipigon*, chaetotaxy of fifth instar larva: 118, lateral schematic of prothorax, mesothorax, and abdominal segments 1, 2, 5–10; 119, dorsal view of head (0.3 mm); 120, lateral view; 121, ventral view; 122, dorsal view of abdominal segments 8–10; 123, labrum, dorsal view; 124, ventral view (0.05 mm); 125, mandible (0.05 mm). (Scale lengths in parentheses.)

eral spine slightly reduced; epipharyngeal sclerite not observed; numerous secondary spines covering inner, ventral perimeter of labrum (Figure 124). Mandible (Figure 125) with three large median cusps and one smaller lateral and one smaller mesal cusps; a single mandibular seta present. Hypopharynx with ventral rows of spines relatively short, strongly hooked; dorsal spines well developed, dense. Maxilla as in Fig-

ure 112. Spinneret (Figure 110) a relatively short, stout tube with a fleshy, strongly bifurcate lobe arising from ventral apex. Labial palpus with a relatively long basal segment bearing one short sensillum and a minute, globose apical segment bearing a longer sensillum apically.

Thorax: Pronotal plate unpigmented, indistinct, relatively smooth and reduced with SD1 and SD2 arising separately. XD2



FIGURES 126, 127.—*Phyllonorycter nipigon*, pupa: 126, ventral view (0.5 mm); 127, lateral view. (A=accessory cremaster; scale = 0.5 mm.)

absent. D1 arising dorsal to D2. L group bisetose on T1–T3. SV bisetose on T1, unisetose on T2 and T3. Legs (Figure 107) well developed, with coxae widely separated; pretarsal claw strongly curved, with a relatively large, blunt, axillary spine.

Abdomen: Dorsal plates of A3–A8 triangular, dark brown, rugose, with that of A3 usually lighter in color. A1, A2, A6, A8 with six pairs of primary setae; A3–A5 with eight pairs and A9 with five pairs of primary setae. Crochets of A3–A5 (Figure 113) with 1 or 2 anterior rows of 5–7 hooks and usually a single posterior row of 5 or 6 hooks. D1 absent on A9. Anal plate (A10) with four pairs of setae (Figure 114, 122); chaetotaxy of A10 as shown in Figures 115, 116; anal crochets with numerous (~30–34) hooks arranged in two irregular, circular rows (Figures 116, 117).

LARVAL MINE (Figure 19).—As illustrated.

PUPA (Figures 126–136).—Maximum length 5 mm; width 0.9 mm. Vertex with triangular cocoon cutter similar to *P. apparella*. Forewing and antenna extending to caudal margin of

A5. Hindleg extending to A7. Dorsum of A2–A8 almost completely covered with dense concentration of short scattered spines (Figures 127, 130); intersegmental surfaces as in Figure 131. Caudal half of sternum A7 with a raised triangular area (accessory cremaster) bearing 3 or 4 small stout spines laterally (Figures 132, 133). Cremaster consisting of two pairs of widely separated, short, broad-based spines (Figures 135, 136), the ventral pair the most widely separated. A9 with sternum sharply indented to A10 (Figure 134).

HOLOTYPE.—Canada: Fort William, Ontario, ♂; CNC.

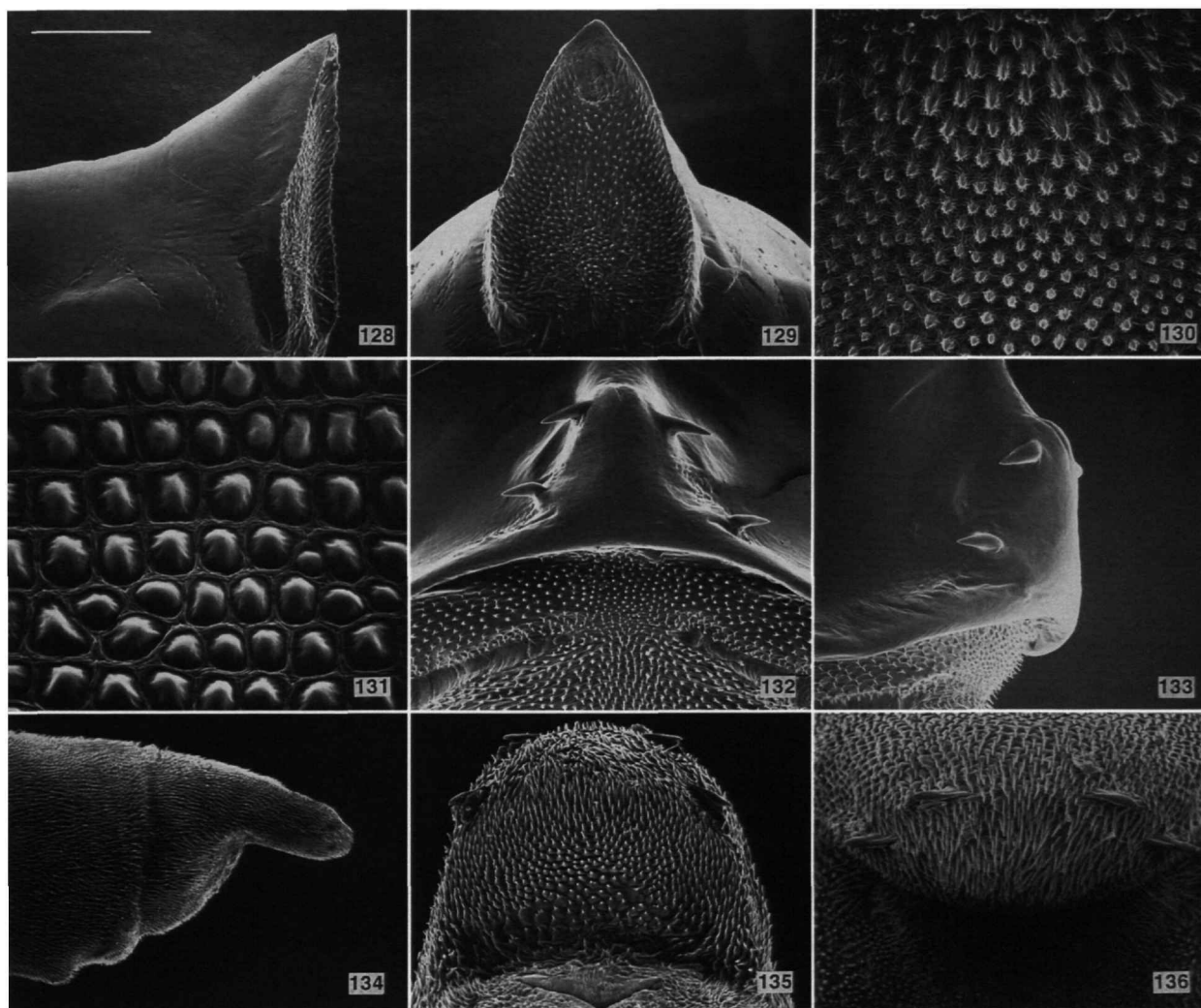
HOSTS (Table 1).—Primarily on *Populus balsamifera* L. (Freeman, 1970); less commonly on *P. balsamifera trichocarpa* (Torr. and Gray) ex Hook., *P. x acuminata* Rydb. (*P. angustifolia* x *deltoides*), *P. angustifolia* James, *P. fremontii* S. Wats., *P. nigra* L., *P. nigra* var. *italica* Muenchh., *P. tremuloides* Michx., *Salix* spp.

PARASITOIDS (Table 2).—Eulophidae: *Prnigalio* sp., *Sympiesis stigmata* Girault, *Zagrammosoma americanum* Girault, *Z. multilineatum* Ashmead.

FLIGHT PERIOD.—Early May (single record), late July to late October; apparently univoltine at any particular site with the adult overwintering.

DISTRIBUTION (Map 2).—Widespread across northern North America from Ontario, Canada, to Alaska (about 64°N) south to Colorado and the Sierra Nevada Mts (about 34°N) of California.

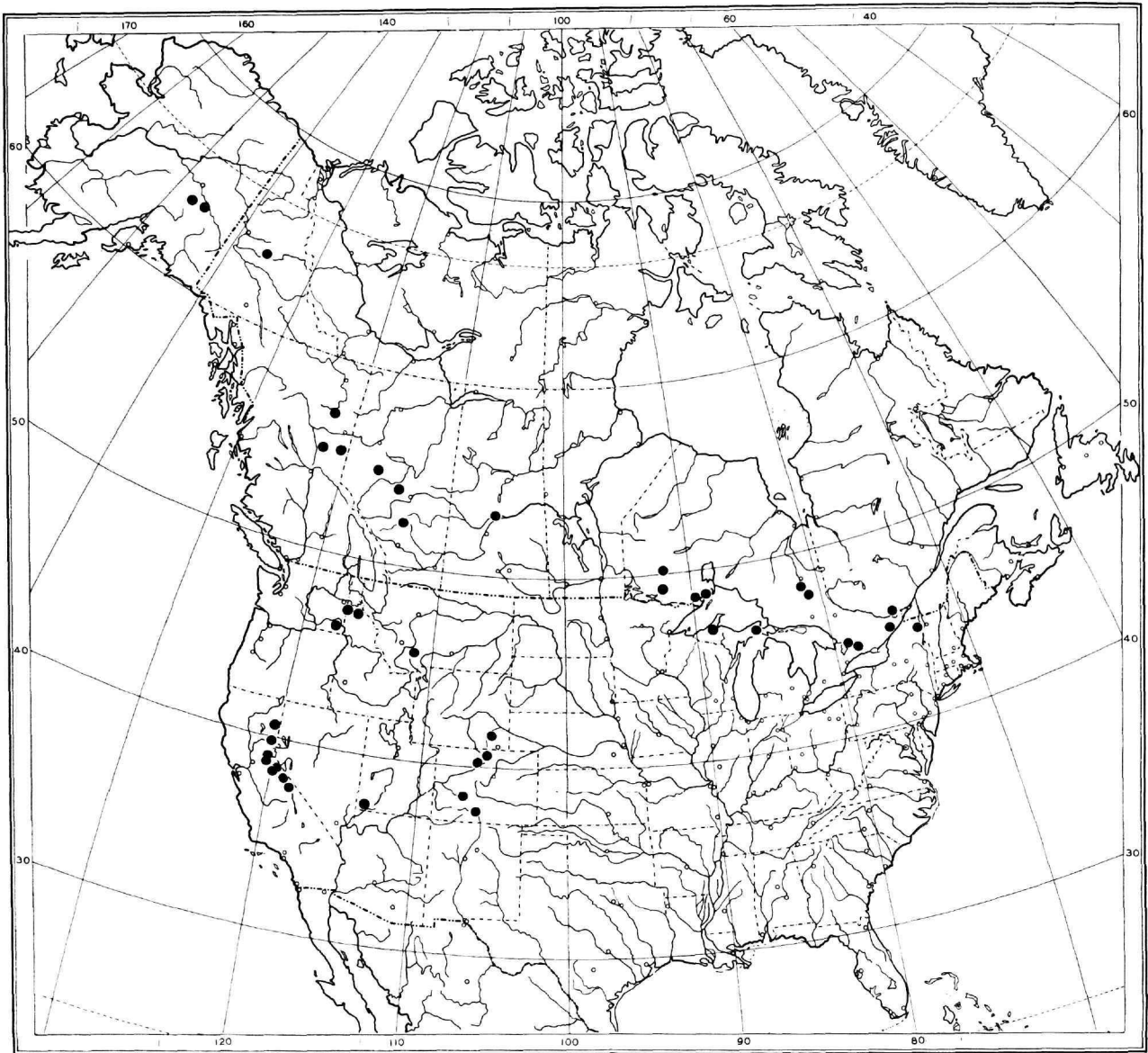
MATERIAL EXAMINED.—CANADA: ALBERTA: Fawcett, 2055 ft. [626.5 m]: 1♂, 2♀, mine: 13 Jul 1982, e. 23–27 Jul 1982, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1652, slide GD 1652 (GD). 25 km E. of Red Deer, 853 m: 5♂, 1♀, mine: 27 Aug 1982, e. 2–9 Sep 1982 [e.=emerged], G. Deschka, mine in *Populus balsamifera*, zucht nr. 1698, slide GD 1769 (GD). Sturgeon Lake 2300 [701.2 m]: 5♂, 7♀, mine: 16 Jul 1982, e. 26–31 Jul 1982, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1655, slide GD 1739 (GD). BRITISH COLUMBIA: 10 km SW of Dawson Creek, 650 m: 3♂, 5♀, mine: 17 Jul 1982, e. 25–31 Jul 1982, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1660, slide GD 1747 (GD). 73 km SE of Fort Nelson, 418 m: 1♂, 3♀, mine: 18 Jul 1982, e. 2–9 Aug 1982, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1662, slide GD 1749 (GD). Summit Lake, 1281 m: 4♂, 9♀, mine: 18 Jul 1982, e. 28 Jul–6 Aug 1982, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1665, slide GD 1751 (GD). ONTARIO: Bobcaygeon: 1♂, 1♀, 15–24 Jul 1932, J. McDunnough, *Populus balsamifera*, CNC slide MIC 2225 (CNC). Cochrane: 5♂, 6♀, 4–9 Aug 1967, T. Freeman, *Populus balsamifera*, 67–45, slides CNC 2876, 2877, MIC 2210, 2212 (CNC). Elk Lake: 2♂, 1♀, e. 24 Aug–3 Sep 1965, *Populus balsamifera* (CNC). Fort William: 4♂, 4♀, 8–22 Aug 1967, T. Freeman, *Populus balsamifera*, 67–42, 55, CNC slides MIC 2206–2209; 2♂, 4♀, e. 20 Aug 1962, T. Freeman, paratype, *Populus balsamifera*, slides DRD 3598, USNM 28406 (CNC, USNM). Kapuskasing: 5♂, 2♀, 25 Mar 1965, C. Miller, *Populus balsamifera*, CNC slides MIC 2213, 2214; 1♂, 3♀, 29 Aug 1965, *Populus balsamifera* (CNC). Kivikoski: 5♂, 6♀, 20–27 Aug 1962, paratype, *Populus balsamifera*,



FIGURES 128–136.—*Phyllonorycter nipigon*, pupa: 128, frontal process (cocoon-cutter), lateral view (86 μ m); 129, dorsal view of Figure 128 (86 μ m); 130, tergal spines of abdominal segment 4 (86 μ m); 131, intersegmental area between abdominal terga 4–5 (10 μ m); 132, accessory cremaster, abdominal sternum 7 (86 μ m); 133, lateral view of Figure 132 (75 μ m); 134, abdominal segments 8–10, lateral view (150 μ m); 135, abdominal segment 10, ventral view (75 μ m); 136, caudal view of Figure 135 (75 μ m). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 128.)

slides MIC 2195–2199, 2201, DRD 3597, USNM 28405 (CNC, USNM). Kakebeka Falls: 2 σ , 2 f , e. 19–26 Aug 1968, *Populus balsamifera* (CNC). Manotick: 1 f , 27 Jul 1955, 55–61; 1 σ , 1 f , 16–17 Sept 1968, T. Freeman, *Populus balsamifera*, 68–64, slide GD 1322 (GD). Ono Park: 1 f , e. 22 Aug 1962, paratype, T. Freeman, *Populus balsamifera* (CNC). Ontario: 1 σ , 17 Aug 1955, T. Freeman, *Populus balsamifera*, 55–100 (CNC). Sioux Lookout: 1 f , 23 Jul 1966, paratype, *Populus balsamifera*; 1 f , 2 Aug 1962, T. Freeman, paratype, *Populus balsamifera*, CNC slide MIC 2200; 1 σ , 1 f , 18 Aug–14 Sep 1967, T. Freeman, *Populus balsamifera*, 67–57, 64 (CNC). Thunder Bay, Stanley

Area: 7 σ , 8 f , e. 15–25 Aug 1982, J. Walas, *Populus* (CNC); 1 σ , e. 22 Aug 1982, slide USNM 31135 (USNM). QUEBEC: Kingsmere: 1 f , 26 Aug 1959, T. Freeman, *Populus balsamifera*, CNC slide MIC 2203 (CNC). SASKATCHEWAN: Prince Albert: 1 σ , 25 Aug 1986, *Populus balsamifera*, slide DRD 3829 (CNC). YUKON: Stewart Crossing, 2000 ft [610 m]: 22 σ , 25 f , mine: 30 Jul 1982, e. 17–24 Aug 1982, mine in *Populus balsamifera*, zucht nr. 1666, slide GD 1752 (GD, USNM). UNITED STATES: ALASKA: Delta Junction, 280 m: 5 σ , 2 f , e. 3–4 Aug 1979, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1446, slide GD 1526 (GD, USNM). 10 mi [16.1 km] SW of



MAP 2.—Distribution of *Phyllonorycter nipigon*.

Fairbanks: 2♂, mine: 3 Aug 1979, e. 12–15 Aug 1979, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1456, slide GD 1521 (GD). CALIFORNIA: Alameda Co., Berkeley: 1♀, “out” 6 Jun 1947, F. Rindge, ex Lombardy poplar [*Populus nigra* var. *italica* Muenchh.] (AMNH). Fresno Co., Kings Canyon, near Cedar Grove, 1400 m: 5♂, 2♀, mine: 26 Jul 1977, e. 27–30 Jul 1977, G. Deschka, mine in *Populus trichocarpa*, zucht nr. 1279, slide GD 1405 (GD). Inyo Co., Inyo National Forest, near Lake Sabrina: 1♂, 18 Aug 1981, e. 3 Sep 1981, J. Whitfield, ex *Populus tremuloides*, JW no. 81H6, slide DRD

3772 (DLW). Mariposa Co., Yosemite Village, 1350 m: 1♂, 2♀, mine: 28 Jul 1977, e. 2–8 Aug 1977, G. Deschka, mine in *Populus trichocarpa*, zucht nr. 1282, slide GD 1408 (GD). Mono Co., 4 air mi [6.4 km] ESE of June Lake, Glass Creek Campground: 7♂, 4♀, 26 Aug 1983, e. 2–9 Sept 1983, D. Wagner, ex *Populus trichocarpa*, JAP no. 83H103, slide USNM 30387 (DLW, USNM). Lee Vining, 2350 m: 9♂, 8♀, mine: 30 Jul 1977, e. 11–14 Aug 1977, G. Deschka, mine in *Populus trichocarpa*, zucht nr. 1285 (GD); 3♀, mine: 31 Jul 1977, e. 9–11 Aug 1977, G. Deschka, mine in *Populus nigra*, zucht nr. 1286

(GD). 4.5 mi [7.2 km] E of Sonora Pass Summit: 1♀, 28 Aug 1983, e. 8 Sep 1983, D. Wagner, ex *Populus tremuloides*, JAP no. 83H129 (DLW). Nevada Co., Donner Lake, 5950 ft [1814 m]: 6♀, 12 Sep 1988, e. 19/25 Sep 1988, Wagner & De Benedictis, DLW 88J25, *Populus tremuloides* (DLW); 1♀, slide 30806 (DLW, USNM). Sierra Co., 5 mi [8 km] SE Sierraville, Cold Springs Campground: 2♀, 9 Sep 1983, e. 16 Sep 1983, J. Whitfield, ex *Populus tremuloides*, JW no 83 J30 (DLW). Tuolumne Co., near Kennedy Meadows: 1♂, 12 Sep 1981, e. 17 Sep 1981, D. Wagner, ex *Populus tremuloides*, JAP no. 81J37 (DLW). 5 mi [8 km] E. of Kennedy Meadows: 1♀, 12 Sep 1981, e. 23–25 Sep 1981, D. Wagner, ex *Populus tremuloides*, JAP no. 81J37 (DLW). 4 mi [6.4 km] W of Sonora Pass: 2♀, 4? [abdomens missing], 13 Sep 1981, e. 14–18 Sep 1981, J. Whitfield, ex *Populus tremuloides*, JW no. 81I12 (DLW). COLORADO: Alamosa Co., Alamosa City, 2250 m: 9♂, 13♀, mine: 26 Jul 1978, e. 11–18 Aug 1978, G. Deschka, mine in *Populus x acuminata*, zucht nr. 1344, slide GD 1547 (GD, USNM). Grand Co., Grand Lake, 2450 m: 1♂, mine: 30 Jul 1978, e. 14–21 Aug 1978, G. Deschka, mine in *Populus tremuloides*, zucht nr. 1346, slide 1519 (GD). Hinsdale Co., Lake City, 2500 m: 1♂, 3♀, mine: 20 Aug 1987, e. 24 Aug–3 Sep 1987, G. Deschka, *Populus angustifolia*, zucht nr. 2027 (BMNH). Jefferson Co., Turkey Creek: 2♂, 3 Jun 1990, P. Opler (CSU). Larimer Co., Rist Cyn., 2.7 mi [4.3 km] NW Bellvue: 2♂ 1♀, 21 Apr–22 May 1989, P. Opler (CSU). Livermore, 2210 m: 1♂, 1♀, mine: 14 Aug 1978, e. 12–16 Aug 1978, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1352, slide 1554 (GD, USNM). Poudre Valley, 2800 m: 13♂, 5♀, mine: 5 Aug 1978, e. 14–19 Aug 1978, G. Deschka, mine in *Populus angustifolia*, zucht nr. 1353, slide 1555 (GD, USNM); 34♂, 38♀, mine: 5 Aug 1978, e. 12–22 Aug 1978, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1354, slide 1554 (GD, USNM). IDAHO: Kootenai Co., Coeur d'Alene: 6♂, 1♀, 5 Oct 1920, J. Everden, ex *Populus trichocarpa*, slide USNM 28430 (USNM). MICHIGAN: Alger Co., Munising: 1♀, 13 Sep 1967, G. Lewis, *Populus balsamifera* (CNC). MINNESOTA: Clearwater Co., Itasca State Park: 3♂, 3♀, e. Aug 1992, M. Auerbach, ex *Populus balsamifera*, slide 31182 (USNM). MONTANA: Gallatin Co., Bozeman: 2♂, 2♀, 28 Aug 1985, e. 29 Aug–2 Sep 1985, D. Wagner, ex *Populus ?deltoides* or *tremuloides*, JAP no. 85H 12/13 (DLW); 1♂, e. 29 Aug 1985 (USNM). NEW YORK: Essex Co., Giant Mtn., Roaring Brook Trail: 3♀, 28 Jul–4 Aug, 1988, e. 9/21 Aug 1988, D. Wagner, ex *Populus balsamifera*, DLW lot 88G110, slides DRD 3779, USNM 30807 (DLW, USNM). UTAH: Washington Co., Zion National Park: 2♀, 23 Oct 1968, B. Baker & L. Sandin, in flight around *Populus fremonti* (USNM). WASHINGTON: Spokane Co., Spokane: 1♀, 14 Sep 1920, E. Newcomer, ex *Populus* sp., slide USNM 18056 (USNM). Whitman Co., Pullman: 6♂, 14–21 Sep 1929, J. Clarke, slides USNM 17099, 17465 (USNM). WYOMING: Albany Co., Laramie: 4♂, 2♀, 7 pupae, 28 Aug 1986, E. Spackman, e. *Salix* sp., slide 28668 (USNM); 68 larvae, 14 pupae, 28 Jul 1988, 6♂, 2♀, 26 Aug 1987, E. Spackman, e. *Populus acuminata*, slides USNM 28432, 29510, 30391, 30470,

30799 (USNM); 3♂, 1♀, 3 Sep 1995, e. 5–6 Sep 1995, *Populus*, M. & S. Shaw, slide USNM 31826 (UWL, USNM); 7600 ft [2317 m]: 3♂, 2♀, mine: 20 Jul 1988, e. 30 Jul–8 Aug 1988, G. Deschka, mine in *Populus* sp., zucht nr. 2097, slide GD 2435 (GD). Teton Co., Grand Teton Nat. Park: 2♂, 4♀, e. 2–18 Aug 1934, A. Braun, B.1458 (ANSP); 1♂, e. 18 Aug 1934, A. Braun, *Populus balsamifera*, B.1458, slide USNM 31102 (USNM).

REMARKS.—This species is most frequently confused with the even more widespread *Populus* miner, *P. apparella*. The two are best distinguished by male genital characters, in particular the less sinuate apex of the valvae, more quadrate transtilla, and more slender eighth sternite of *P. nipigon*. Although both species have been reported mining several species of *Populus*, *P. nipigon* shows a distinct preference for *P. balsamifera* and *P. apparella* for *P. tremuloides* in North America.

Phyllonorycter deserticola, new species

FIGURES 20, 29, 137–160, 242–244, 429, 430; MAP 3

ADULT (Figure 29).—Length of forewing: 2.9–3.8 mm. Small moths, with slender, relatively pale reddish brown forewings mostly traversed by approximately 5 irregularly oblique white bands. Valvae of male genitalia symmetrical, slender, slightly curved ventrad and tapering to an acuminate, relatively sinuate apex.

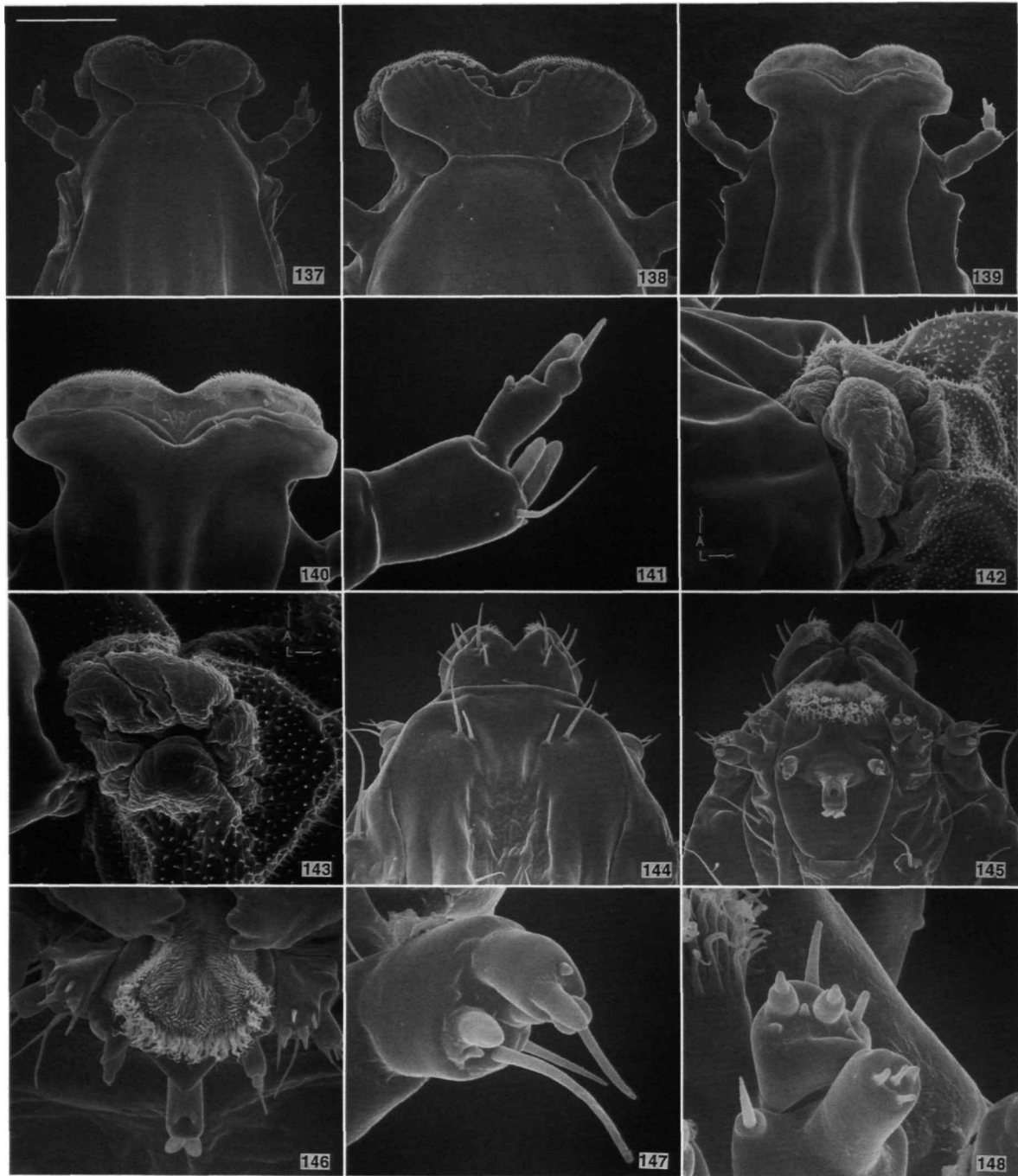
Head: Vertex rough, with white piliform scales occasionally with a few brownish scales intermixed; frons smooth, lustrous white. Antenna white; apex of each segment lightly ringed with brown. Labial palpus uniformly lustrous white.

Thorax: Dorsum mostly white with a reddish brown spot centered posteriorly; tegula mostly white, with light to heavy suffusion of brown. Venter lustrous white. Forewing variable, light reddish brown, usually with five costal white strigulae and four dorsal white strigulae; second dorsal strigula from base usually confluent with costal first and second strigulae; specimens from California and Utah often with white strigulae more heavily speckled with dark brown tipped scales; reddish bands margined distally with dark brown; elongate, subapical, dark brown spot usually distinct. Fringe pale gray. Hindwing and fringe uniformly pale gray. Legs mostly silvery white, with dark brown suffusion dorsally over tibia and tarsomeres, usually forming two dark dorsal bands on tibia and three on tarsus.

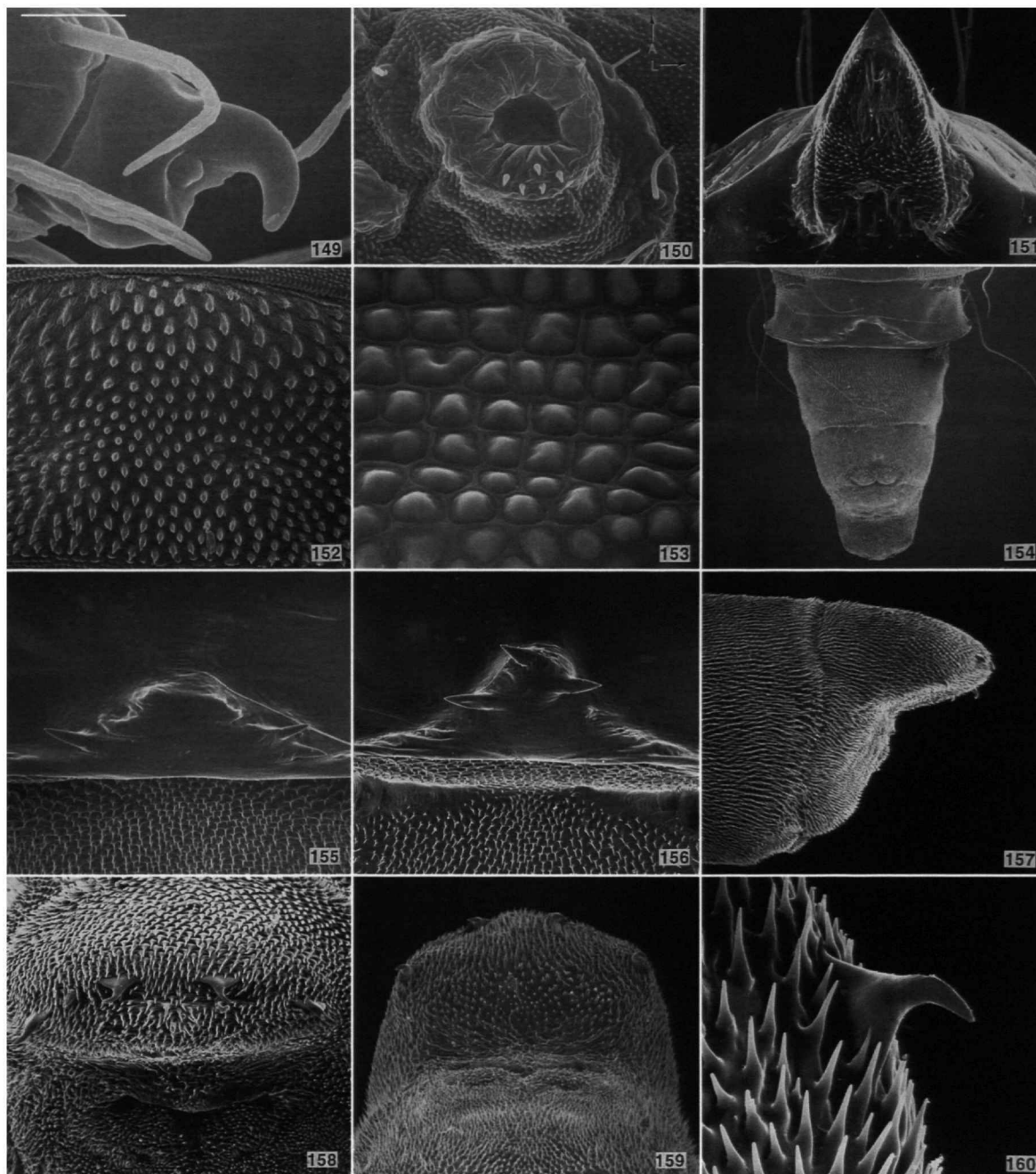
Abdomen: Light to dark reddish brown dorsally, silvery white ventrally; conspicuous sex-scaling absent. Eighth sternum of male moderately elongate and broad; apex broadly round to slightly emarginate (Figure 244).

Male Genitalia (Figures 242, 243): Vinculum broadly V-shaped. Transtilla thickened, quadrate. Valva symmetrical, elongate, moderately slender, tapering to a slightly sinuate, acuminate apex. Anellus completely membranous. Aedoeagus slender, approximately equal to length of eighth sternum, with a minute, subapical lobe.

Female Genitalia (Figures 429, 230): Duct of accessory bursa moderately long, about 0.6× the length of ductus bursae,



FIGURES 137–148.—*Phyllonorycter deserticola*, third instar (sap-feeding) larva: 137, head, dorsal view (67 μm); 138, labrum, dorsal view (43 μm); 139, head, ventral view (67 μm); 140, labium, ventral view (43 μm); 141, antenna, dorsal view (13.6 μm); 142, ventral ambulatory callosity, prothorax (38 μm); 143, ventral ambulatory callosity, abdominal segment 5 (27 μm). Fifth instar (tissue-feeding) larva: 144, head, dorsal view (60 μm); 145, head, ventral view (60 μm); 146, hypopharynx, maxillae, labial palpi, spinneret (38 μm); 147, antenna, distal view (12 μm); 148, maxilla (13.6 μm). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 137.)



FIGURES 149–160.—*Phyllonorycter deserticola*, larval and pupal morphology. Fifth instar (tissue-feeding) larva: 149, prothoracic pretarsus (10 μm); 150, proleg of abdominal segment 5 (43 μm); 151, pupa: frontal process (cocoon-cutter), dorsal view (86 μm); 152, tergal spines of abdominal segment 5 (86 μm); 153, dorsal intersegmental area between abdominal segments 4–5 (10 μm); 154, abdominal terga 7–10 (38 μm); 155, accessory cremaster, abdominal sternum 7 (75 μm); 156, accessory cremaster, abdominal sternum 7 (75 μm); 157, abdominal segments 8–10, lateral view (120 μm); 158, caudal view, abdominal segment 10 (60 μm); 159, ventral view of Figure 158 (75 μm); 160, lateral cremasteral hook (12 μm). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 149.)

and arising caudally immediately anterior to moderately broad antrum. Signum a single, round, sclerotized disk bearing a pair of minute spines.

LARVA (Figures 137–150).—Similar to *P. nipigon*. Length of largest third instar 3.5 mm; head width 0.4 mm. Fifth instar: Length of largest larva 6.2 mm; head width 0.43 mm. A1, A2, and P1 arising distant from adfrontal suture. Apical spines of hypopharynx (Figure 146) reduced. Prothorax with D1 anterior to D2. Pronotum with D1 anterior to D2. Crochets on A3–A5 with 3–5 hooks in caudal row and 5–7 hooks in two anterior rows.

LARVAL MINE (Figure 20).—As illustrated.

PUPA (Figures 151–160).—Maximum length 3.8 mm; width 0.7 mm. Vertex with triangular cocoon cutter similar to *P. apparella*. Forewing and antenna extending to middle of A6. Hindleg extending to caudal margin of A7. Dorsum of A2–A8 almost completely covered with dense concentration of moderately large to small, scattered spines, the largest situated cephalad; intersegmental surfaces as in Figure 153. Caudal half of sternum A7 with a slightly raised triangular area bearing 3 small stout spines laterally (Figure 156), 2 spines on left side and one on right in single ♂ and ♀ examined. Cremaster consisting of usually two pairs of widely spaced, short spines; the ventral, subterminal pair the most lateral and most widely separated (Figures 158, 159). A9 with sternum abruptly constricting to A10 (Figure 157).

HOLOTYPE.—California: Inyo Co. Wildrose Canyon, 5500 ft. [1677m], ♂; e. larva 11–19 Aug 1977 [e.=emerged], G. Deschka, mine in *Populus ?macdougalii* Rose [*P. x parryi* Sarg.], zucht nr. 1293, mine: 10 Aug 1977, USNM slide 30777 (GD 1410), USNM.

PARATYPES.—MEXICO: DURANGO: 25 km S. of Durango, 1890 m: 2♂, mine: 17 Aug 1980, e. larva 18–30 Aug 1980, G. Deschka, mine in *Populus* sp. zucht nr. 1531, GD slide 1705. SONORA: 8 km S. of Nogales, 1080 m: 2♂, mine: 22 Aug 1980, e. larva 22 Aug–2 Sep 1980, G. Deschka, mine in *Populus* sp., zucht nr. 1536, GD slide 1703. UNITED STATES: CALIFORNIA: Inyo Co., Wildrose Canyon, 5500 ft. [1677]: 3♂, 5♀, mine: 10 Aug 1977, e. larva 11–19 Aug 1977, G. Deschka, mine in *Populus ?macdougalii* Rose [*P. x parryi* Sarg.], zucht nr. 1293, slides USNM 22910, 22911. Madera Co., 5 mi [8 km] E. Delhi, McConnell State Park: 1♀, 12 Jul 1969, e. 24 Jul 1969, P. Opler, JAP 69G26, *Populus fremontii*. Riverside Co., Joshua Tree Nat'l Monument, Yucca Valley, 1070 m: 8♂, 7♀, mine: 17 Jul 1977, e. larva 19–29 Jul 1977, G. Deschka, mine in *Populus macdougalii* Rose [*P. x parryi* Sarg.], zucht nr. 1270, GD slide 1401, 1402. San Bernardino Co., Death Valley, Scotty's Castle: 2♀, mine: 12 Aug 1977, e. larva 13–20 Aug 1977, G. Deschka, mine in *Populus* sp., zucht nr. 1295. San Diego Co., Scissors Crossing: 1♂, 2♀, 5 Oct 1967, e. 13–17 Oct 1967, P. Opler, JAP67K69, *Populus fremontii*, DRD slide 3733. Sutter Co., Feather River, nr. Nicolaus: 2♂, 2♀, 1 Sep 1981, e. 10–18 Sep 1981, D. Wagner, JAP 81J1, *Populus fremontii*. 1 mi [1.626 km] E. Nicolaus, Feather River: 4♂, 2♀, 31

Aug 1981, e. 18 Sep., D. Wagner, JAP81J1, *Populus fremontii*, USNM slide 30382. Tulare Co., Porterville: 11♂, 3♀, 13–20 Jun 1968, 1♂, 8♀, 21–24 Jun 1968, C. Eads, e. cottonwood, slides 17090, 17463, 18055. COLORADO: Jefferson Co., Denver: 2♂, 2♀, 11–16 Jul 1901, Dyar 1038 [=17183], cottonwood, USNM slides 17464, 30882, 30884. NEVADA: Churchill Co., Fallon: 3♂, 3♀, 25 Sep 1975, R. Alcorn, e. *Populus fremontii*, slide 30818. Swingle Bench: 7♂, 9♀, 1 Oct 1975, R. Bechtel, e. *Populus fremontii*, slide 28429. Douglas Co., Topaz Lake: 4♂, 1♀, 14 Dec 1978, J. Doyen, under *Populus* bark, DRD slide 3735. NEW MEXICO: Eddy Co., Atoka: 1♂, mine: 22 Jul 1978, e. larva 5 Aug 1978, G. Deschka, mine in *Populus fremontii* S. Wats., zucht nr. 1339, GD slide 1543. Otero Co., White Sands Nat. Monument, Great Dunes, 1250 m: 6♂, 4♀, mine: 22 Jul 1978, e. larva 1–9 Aug 1978, G. Deschka, mine in *Populus fremontii [deltoides] wislizenii* S. Wats., GS slide 1544. Sandoval Co., Rio Grande and Rt 44, about 40 km N. of Albuquerque: 1♂, 1♀, 5 larvae, 31 Jul 1989, e. 3/6 Aug 1989, D. Davis, DRD 668.1, e. *Populus fremontii*, slides 30459–30461. Socorro Co., San Acacia, 1555 m: 1♂, 4♀, mine: 23 Jul 1978, e. larva 4–9 Aug 1978, G. Deschka, mine in *Populus fremontii [deltoides] wislizenii* S. Wats., zucht nr. 1341, GD slides 1545, 1712. ~2 km E. of Escondido: 1♀, 25 Jul 1989, e. 8 Aug 1989, D. Davis, DRD 668, e. *Populus fremontii*. TEXAS: Brewster Co., Castolon, 661 m: 20♂, 17♀, mine: 24 Jul 1987, e. larva 29 Jul–5 Aug 1987, G. & L. Deschka, mine in *Populus fremontii* S. Wats., zucht nr. 1988, GD slides 2235. UTAH: Washington Co., Zion National Park: 7♂, 4♀, 17 Oct 1940, R. Furniss, e. cottonwood, slide 20428. Wayne Co., Capitol Gorge, Fremont River: 1♂, 2♀, mine: 10 Aug 1978, e. larva 16–21 Aug 1978, G. Deschka, mine in *Populus fremontii* S. Wats., zucht nr. 1359, GD slide 1558. Paratypes in BMNH, DLW, GD, UCB, and USNM.

HOST (Table 1).—*Populus fremontii* S. Wats., *P. deltoides wislizenii* S. Wats., *P. x parryi* (*P. fremontii* x *trichocarpa*), *Populus* sp.

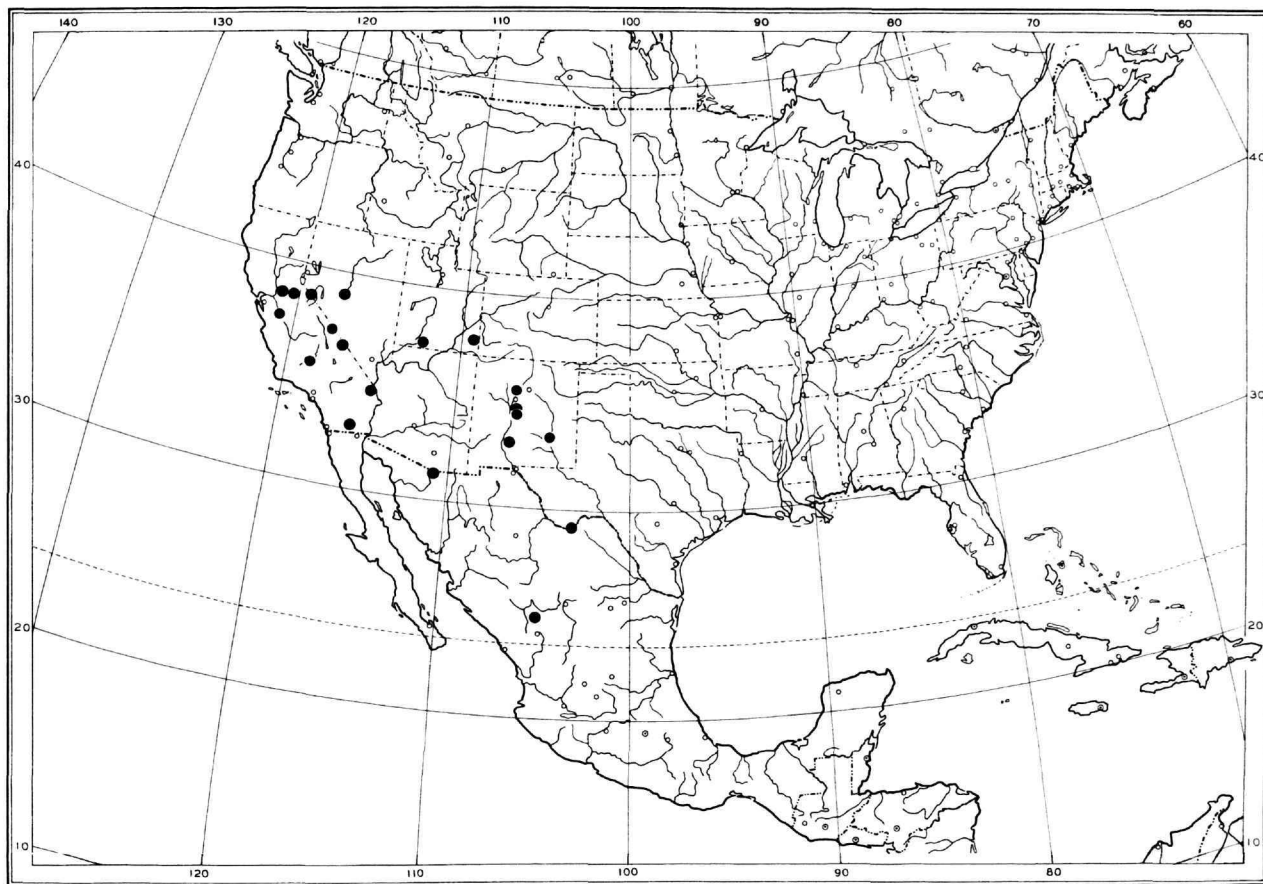
PARASITIDS (Table 2).—Eulophidae: *Pediobius* sp., *Pnigalio flavipes* Ashm., *Sympiesis marylandensis* Girault, *Sympiesis* sp.

FLIGHT PERIOD.—Late July to early October; bivoltine, with the second generation overwintering.

DISTRIBUTION (Map 3).—This species occurs in restricted, mostly arid habitats over a broad portion of the southwestern United States and northern Mexico from southern Utah to Durango and west to northern California.

ETYMOLOGY.—The specific name is derived from the Latin *desertum* (a waste place) and *cola* (dwelling in), in reference to the general habitat of this species.

REMARKS.—*Phyllonorycter deserticola* is the most distinctive member of the *Populus*-mining *apparella* group, both morphologically and biologically. It appears to be the most deserticolous member of the group, adapted to withstanding temperatures over 50°C in the shade (Death Valley, California). General wing color tends to be lighter in most specimens, par-

MAP 3.—Distribution of *Phyllonorycter deserticola*.

ticularly those from drier habitats and from the first (midsummer) generation. Populations from more boreal or montane habitats and from the second (overwintering) generation are generally darker and more irrorated with dark scales. Morphologically the species can be most easily distinguished by the relatively broad valvae (for this group) in the male and by the broad antrum in the female.

Phyllonorycter salicifoliella (Chambers)

FIGURES 13–17, 21–23, 32–34, 161–194, 245–250, 269–308, 343–350, 431, 432, 446, 447; MAP 4

Lithocolletis salicifoliella Clemens, 1861:81 [nomen nudum]; 1872:69.—Packard, 1869:353 [nomen nudum].—Chambers, 1871:163, 185; 1875:126, 302; 1877:139.—Walsingham, 1889:54.—Riley, 1891:109 [*Lithocolletes* (sic)].—Dyar, 1903a:556 [*Lithocolletes* (sic)]; 1903b:411.—Braun, 1908b:316 [in part]; 1914:115, 153 [in part]; 1923:192.—Meyrick, 1912a:9; 1912b:9.—Barnes and McDunnough, 1917:187.—McDunnough, 1939:96.—Martin, 1956:155.—Watson, 1956:168.—Freeman, 1970:272.

Lithocolletis atomariella Braun [not Zeller, 1876], 1908b:316 [synonym of *salicifoliella*].—Meyrick, 1912a:9 [synonym of *L. salicifoliella*]; 1912b:37 [synonym of *L. salicifoliella*].

Phyllonorycter atomariella (Braun).—Ely, 1917:64 [synonym of *L. salicifoliella*].

Phyllonorycter salicifoliella (Clemens).—Ely, 1918:64.

Lithocolletis kenora Freeman, 1970:280. [New synonymy.]

Phyllonorycter kenora (Freeman).—Davis, 1983:10.

Phyllonorycter salicifoliella (Chambers).—Davis, 1983:10.—Maier and Davis, 1989:16.

ADULT (Figures 32, 33).—Length of forewing: 3–4 mm. Small moths with slender, golden brown forewings with a large to greatly reduced basal-dorsal white spot, usually 5 costal and 4 dorsal white strigulae. Male genitalia with symmetrical and ridged apical processes. Antrum of female genitalia 0.3 mm or less in length. Larva usually on *Salix*, rarely on *Populus*.

Head: Vertex rough, with a variable mixture of white and brown, piliform scales, usually mostly white. Frons smooth, rarely with light brownish suffusion. Antenna with scape and pedicel usually entirely white, occasionally with slight brownish suffusion dorsally; flagellomeres variable, usually mostly white with brownish suffusion over dorsal apex, to mostly brown with whitish basal annulations. Labial palpus entirely white or with brownish suffusion ventrally.

Thorax: Dorsum variable, usually white and lightly irrorated with dark brown to fuscous, sometimes mostly reddish brown. Venter white. Forewing light golden to reddish brown, variably marked with white streaks and scattered dark brown to fuscous scales as follows: 5 white costal strigulae with basal two most oblique and sometimes indistinct; usually a large, white basal spot on dorsum that may be largely obliterated by reddish brown; 4 white strigulae usually present distad to basal spot with basal two strigulae the broadest and sometimes joined to costal strigulae; outer two strigulae narrow, costal and dorsal pairs often joined but with distal-most band usually separated by an elongate, subapical fuscous spot; termen with a fuscous margin; fringe pale gray. Hindwing uniformly gray. Legs generally light fuscous dorsally, white ventrally, becoming progressively paler on mid- and hindlegs; apices of tibial and tarsal segments white.

Abdomen: Pale to dark grayish brown dorsally, white ventrally; conspicuous sex-scaling absent. Seventh sternum of female usually rough (Figures 431, 446, 447). Eighth sternum of male (Figures 246, 249) elongate, triangular, tapering to a narrowly rounded apex.

Male Genitalia (Figures 245, 247, 248, 250, 269–308): Vinculum V-shaped, tapering to rounded apex. Transstilla moderately robust, quadrate. Valvae symmetrical, variable in form, relatively slender, usually broadest near middle to distal third then tapering to slightly curved apical process bearing 10–14 longitudinal ridges and an apical pore (Figures 272, 276, 280, 284, 288, 292, 296); subapical brush consisting of a tight bundle of ~15–50 long setae arising from a low tubercle immediately basad of apical process (Figures 248, 270, 274, 278, 283, 287, 291). Anellus membranous. Aedoeagus slender, elongate, 1.7–2.3× the length of eighth sternum, with a short, subapical lobe (Figures 247, 250, 342–350).

Female Genitalia (Figures 431, 432): Antrum tubular, sclerotized, moderately elongate, ~0.5–1.2× the length of posterior apophyses, ranging 0.13–0.3 mm in length. Accessory bursa slightly larger in diameter than corpus bursae; accessory duct ~0.5× the length of ductus bursae, both arising from anterior end of antrum. Signum a circular plate near caudal end of corpus with a pair of widely spaced minute spines and a slightly larger, less sclerotized, oval plate near opposite end.

EGG (Figures 13–17).—Approximately 0.34–0.37 mm long, 0.20–0.21 mm wide, and 0.14 mm deep. Upper half of chorion reticulate, underside smooth. Both surfaces separated by an irregular zone of rugose tissue; circumferential fringe poorly developed. Two micropyles present at anterior pole surrounded by low ridges (Figure 17).

LARVA (Figures 161–185).—Similar to *P. nipigon*. Length of largest third instar 3.3 mm; head width 0.37 mm. Fifth instar: Length of largest larva 6 mm; head width 0.4 mm. A1, A2, and P1 arising distant from adfrontal suture. S2, S3 present. Apical spines of hypopharynx (Figure 174) elongate, approximately 0.8× the length of spinneret. Prothorax with D1

below D2. Crochets on A3–A5 with 5 hooks in caudal row and 3 or 4 in anterior row.

LARVAL MINE (Figures 21–23).—As illustrated.

PUPA (Figures 186–194).—Maximum length 4.2 mm, width 0.9 mm. Vertex with relatively broad, triangular, dorsally flattened cocoon cutter with minutely serrated lateral ridges (Figure 186). Forewing extending to caudal margin of A6; hindleg to caudal margin of A8. Dorsum of A2–A8 densely covered with evenly scattered, short spines, with those of anterior third slightly enlarged (Figure 188); intersegmental surfaces reticulated as in Figure 189. Accessory cremaster of A7 with 1 or 2 pairs of lateral spines (Figure 190). Terminal cremaster consisting of 2 pairs of broad-based hooks, with one pair more laterad and slightly more ventrad (Figures 191, 193). A9 with sternum abruptly constricted to flattened A10 (Figure 194).

TYPES.—Syntypes (2), “Ky, near Cincinnati, O”; deposition unknown, currently believed not to exist (*salicifoliella* Cham.). Neotype (new designation), ♀, Fort Washington, Prince Georges Co, Maryland, 15 Sep 1974, e. 28 Sep 1974, D.R. Davis, *Salix babylonica* L., DRD 362, USNM (*salicifoliella* Cham.). Holotype, ♂, Ramsay, Ont., Canada, 3 Aug 1962, no. 10,889, CNC (*kenora* Freeman).

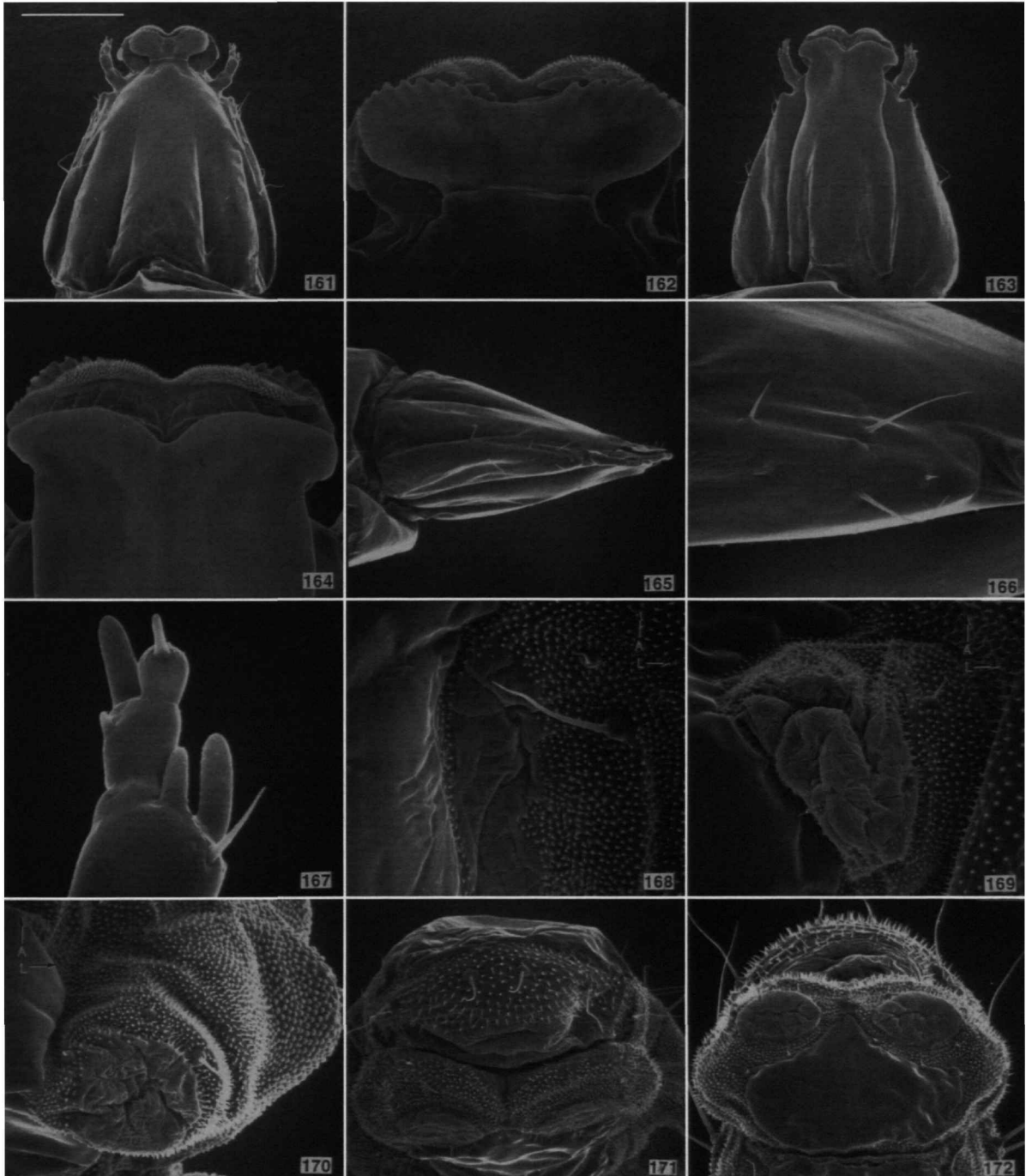
HOSTS (Table 1).—Several species of *Salix* are preferred hosts, with *S. alba* L., *S. amygdaloides* Anderss., *S. babylonica* L., *S. bebbiana* Sarg., *S. bonplandiana* Kunth (= *laevigata* Bebb), *S. caroliniana* L., *S. eriocephala* Michx., *S. lasiolepis* Benth., *S. “longifolia”* [? *S. interior* Rowlee (= *fluviatilis* (Anderss.) Ball)], *S. lutea* Nutt., *S. monticola* Bebb, *S. purpurea* L., *S. x rubens* Schrank (*S. alba* x *fragilis*), *S. scouleriana* J. Barratt ex Hook., and *S. sericea* Marshall being reported. Much less commonly, larvae also may mine *Populus*, particularly *P. balsamifera* L. and *P. tremuloides* Michx.

PARASITIDS (Table 2).—Braconidae: *Mirax minuta* Ashmead, *Parahormius pallidipes* Ashmead; Eulophidae: *Aprostocetus* sp., *Chrysocharis boriquensis* Hanssen, *Chrysocharis* sp., *Didlyphus* sp., *Horismenus* sp., *Sympiesis marylandensis* Girault, *Sympiesis* sp.

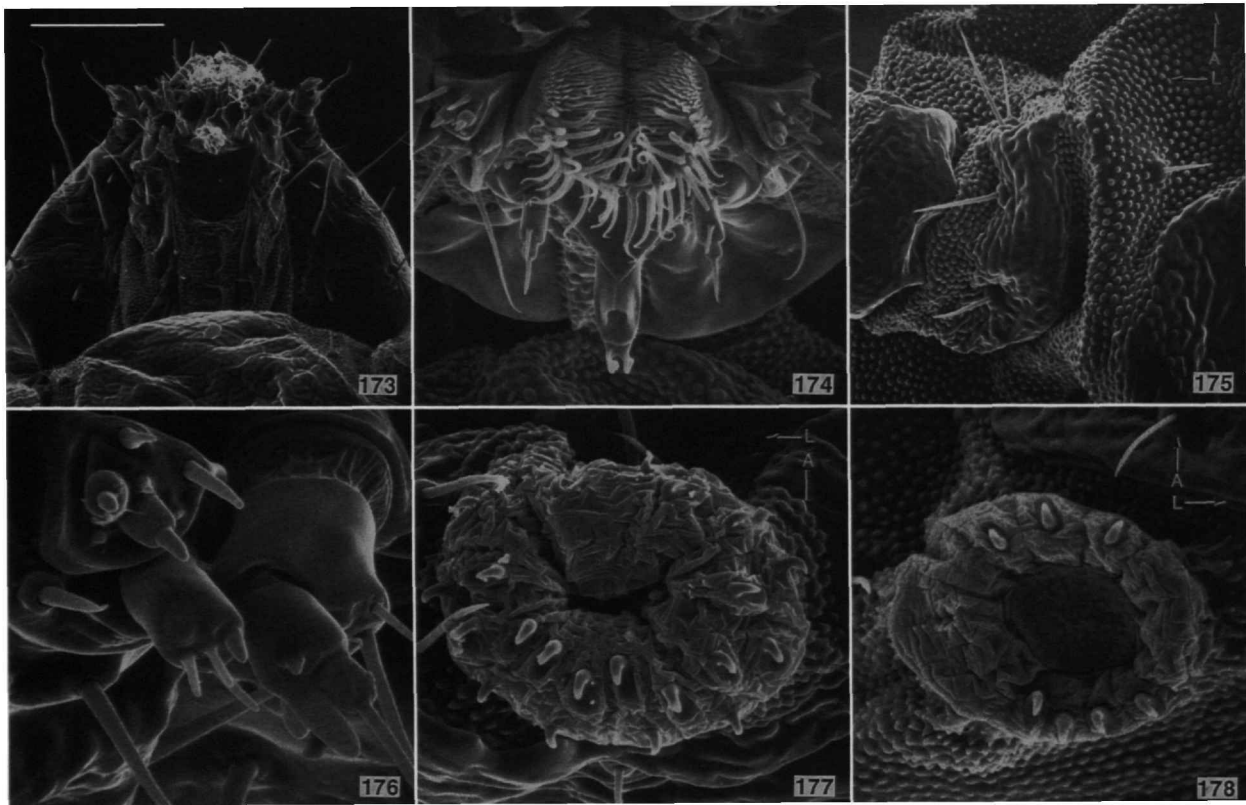
FLIGHT PERIOD.—Apparently bivoltine (July to mid-August and late August to November), at least at lower elevations or in southern part of range, with the adults overwintering and flying again in May to early June.

DISTRIBUTION (Map 4).—Widespread across North America between latitudes 30°N and 60°N, from Mississippi to Ontario in the East and from southern California to northern British Columbia in the West.

MATERIAL EXAMINED.—CANADA: ALBERTA: 6 km W Drumheller: 15♂, 13♀, mine: 22–23 Aug 1982, e. 23 Aug–5 Sep 1982 [e.=emerged], G. Deschka, mine in *Salix* [possibly *monticola*], zucht nr. 1691, slide GD 1765 (GD); same data: 1♂, 4♀, slides USNM 22905, 22906, 30875 (USNM). Edmonton, 600 m: 1♂, 1♀, mine: 9 Jul 1979, e. 27–28 Jul 1979, G. Deschka, mine in *Salix*, zucht nr. 1430, slides GD 1526, 1537 (GD); same data: 1♂ (USNM). Mitsue Lake North, 544 m: 5♂,



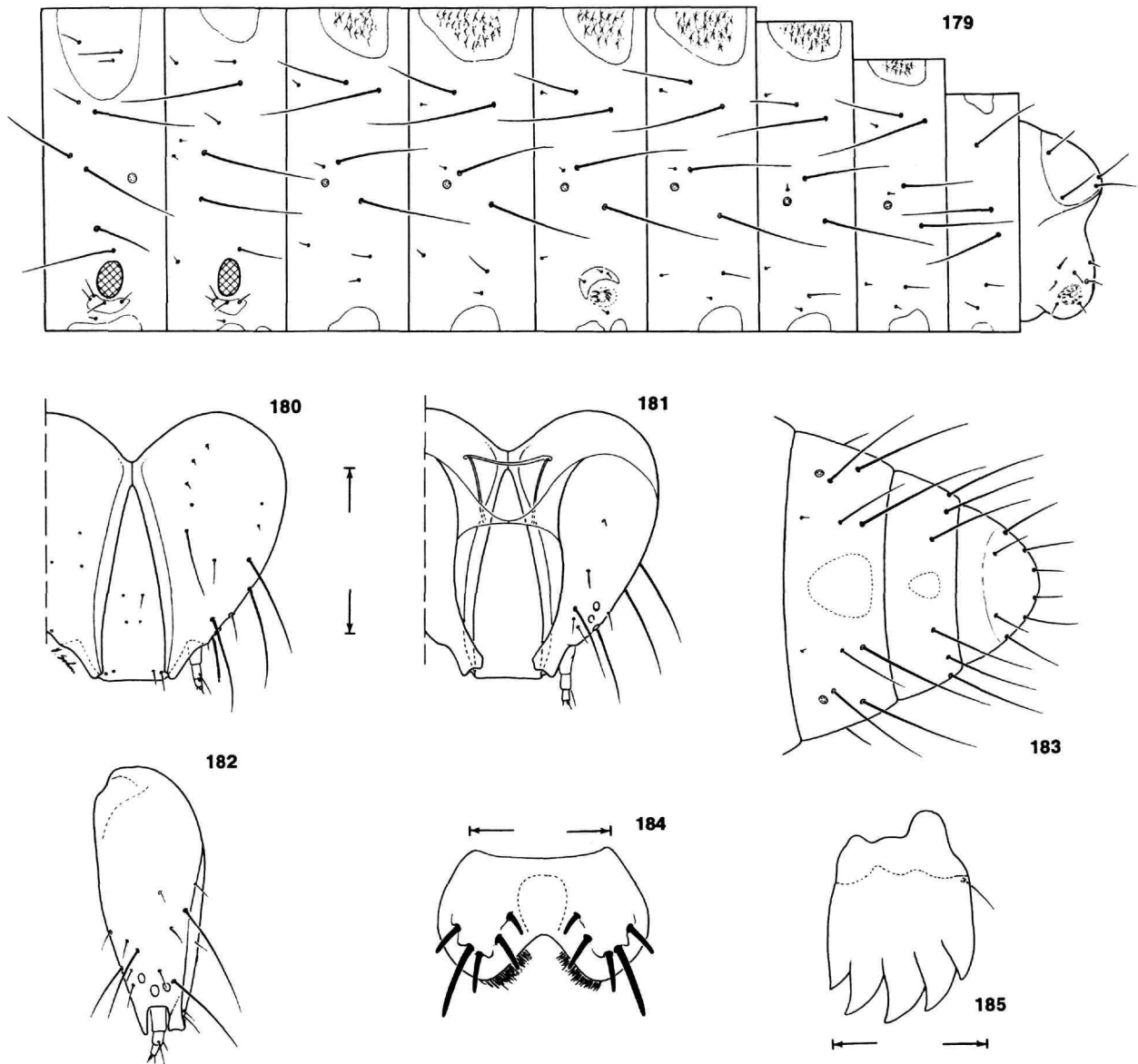
FIGURES 161–172.—*Phyllonorycter salicifoliella*, third instar (sap-feeding) larva: 161, head, dorsal view (107 μm); 162, labrum (27 μm); 163, head, ventral view (107 μm); 164, labium, hypopharynx (30 μm); 165, head, lateral view (107 μm); 166, stemmatal area (25 μm); 167, antenna, dorsal view (8.6 μm); 168, dorsal ambulatory callosity of prothorax (27 μm); 169, ventral ambulatory callosity of prothorax (30 μm); 170, ventral ambulatory callosity, abdominal segment 5 (30 μm); 171, abdominal segment 10, caudal view (60 μm); 172, ventral view of Figure 171 (60 μm). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 161.)



FIGURES 173–178.—*Phyllonorycter salicifoliella*, fifth instar (tissue-feeding) larva: 173, head, ventral view (91 μm); 174, hypopharynx, spinneret, dorsal view (33 μm); 175, four coxal setae, prosternum (43 μm); 176, antenna, maxilla, anterodorsal view (12 μm); 177, proleg of abdominal segment 10 (23.1 μm); 178, proleg of abdominal segment 3 (25 μm). (A=anterior; L=lateral; scale lengths in parentheses; bar scale for all photographs shown in Figure 173.)

3♀, mine: 14 Jul 1982, e. 21–27 Jul 1982, G. Deschka, mine in *Salix*, zucht nr. 1654, slides GD 1736, 1737 (GD); same data: 2♂ (USNM). 11 km W Red Deer, 853 m: 4♂, 6♀, mine: 28 Aug 1982, e. 31 Aug–8 Sep 1982, G. Deschka, mine in *Salix*, zucht nr. 1697 (GD); same data: 2♂, 1♀ (USNM). Sturgeon Lake, 2300 ft [854 m]: 5♂, 2♀, mine: 16 Jul 1982, e. 25–30 Jul 1982, G. Deschka, mine in *Salix*, zucht nr. 1656, slide GD 1741 (GD); same data: 1♂, 1♀, slide USNM 30786 (USNM). BRITISH COLUMBIA: Clinton, 887 m: 1♂, mine: 12 Aug 1982, e. 22–25 Aug 1982, G. Deschka, mine in *Salix*, zucht nr. 1680, slide GD 1762 (GD); same data: 1♂, 2♀, slides USNM 30787, 30872 (USNM). 10 km SW Dawson Creek, 650 m: 16♂, 12♀, mine: 17 Jul 1982, e. 28 Jul–3 Aug 1982, G. Deschka, mine in *Salix* [*bebbiana*], zucht nr. 1658 (tomentose), slide GD 1745 (GD); same data: 2♂, 3♀, slide USNM 30877 (USNM); same data: 2♂, 5♀, mine in *Salix* (glabrous) [*scouleriana*], zucht nr. 1659 (GD); same data: 1♂, 2♀ (USNM). Fort Nelson: 1♂, 28 Jul 1967, Freeman and Lewis, *Salix*, 67–41, CNC slide MIC 309 (CNC). 73 km SE Fort Nelson, 418 m: 1♂, mine: 18 Jul

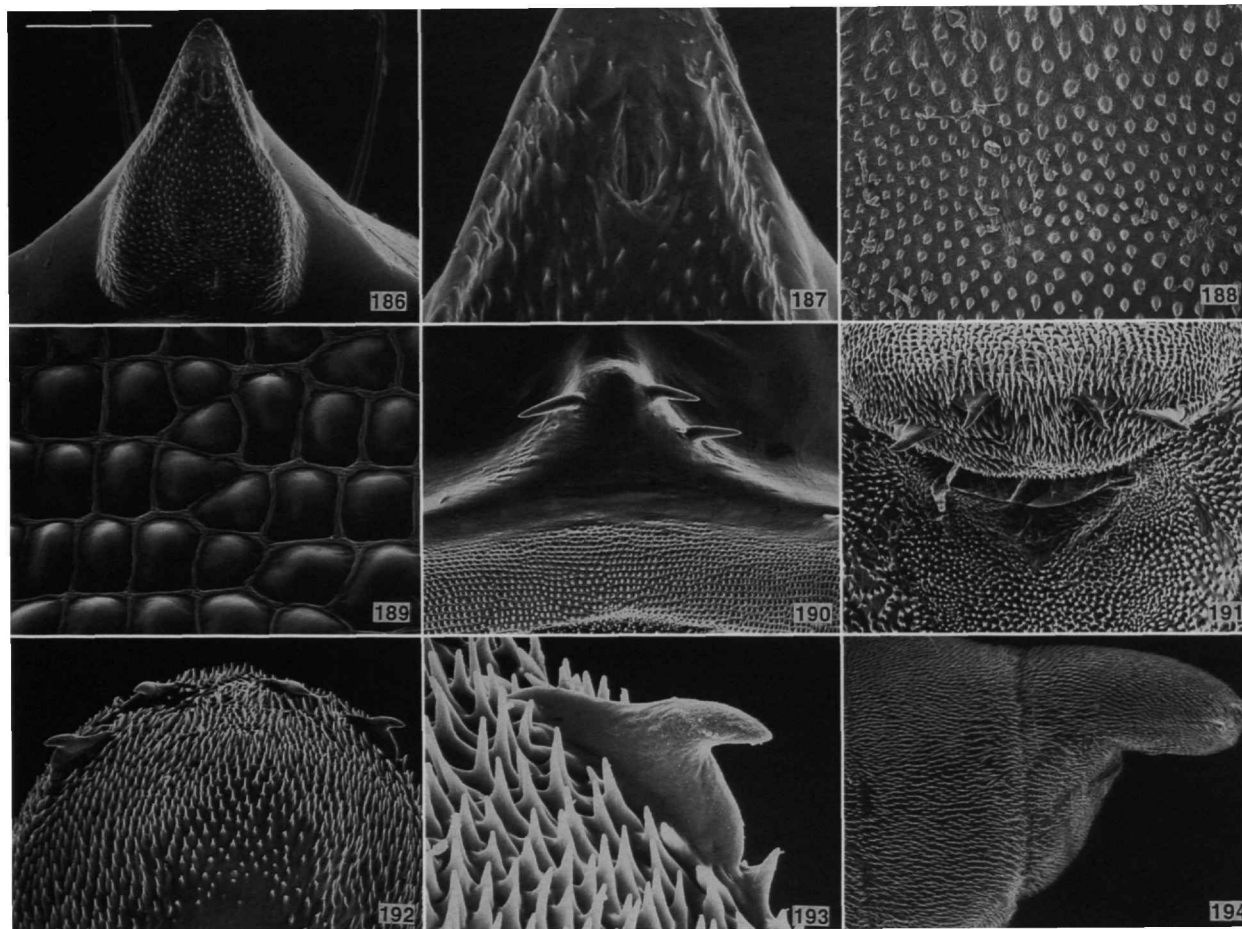
1982, e. 3 Aug 1982, G. Deschka, mine in *Salix*, zucht nr. 1663 (GD); same data: 1♀ (USNM). Hazelton, 330 m: 9♂, 11♀, mine: 16 Jul 1982, e. 21–29 Jul 1982, G. Deschka, mine in *Salix* [*bebbiana*], zucht nr. 1439, slides GD 1518, 1535 (GD); same data: 2♀, slides 22908, 22909 (USNM). Hikon: 1♀, 27 Jul 1967, Freeman and Lewis, *Salix*, 67–10 (CNC). Keremeos: Shingle Creek Road: 1♂, 3♀, 20–31 Aug 1934, *Salix* (CNC). Manson Creek: 2♂, 2♀, 8–9 Aug 1967, Freeman and Lewis, *Salix*, 67–51, CNC slides MIC 2307, 2308 (CNC). Penticton: Shingle Creek: 1♂, 1♀, 7–8 Sep 1934, A. Gartrell, *Salix*, CNC slide MIC 2310 (CNC). Summerland: 2♂, 2♀, 13–17 Aug 1934, A. Gartrell, *Salix* (CNC). Thornhill, 250 m: 12♂, 9♀, mine: 17 Jul 1979, e. 24 Jul–3 Aug 1979, G. Deschka, mine in *Salix* ?*bebbiana*, zucht nr. 1442, slides GD 1520, 1530, 1536 (GD); same data: 1♂, 1♀, slide USNM 30876. Vernon: 1♂, 3♀, 22 Aug 1927, L. Ward, CNC slide MIC 2246 (CNC). ONTARIO: Ignace: 1♂, 1♀ (paratypes *L. kenora*), e. 29 Aug 1962, S62-5480-01, *Salix*, slides CNC 2033, 2481 (CNC). Porcupine: 1♀, 4 Aug 1967, *Salix* (CNC); 2♂, 13 Sep 1967, *Salix*, slides



FIGURES 179-185.—*Phyllonorycter salicifoliella*, chaetotaxy of fifth instar larva: 179, lateral schematic of prothorax, mesothorax, and abdominal segments 1, 2, 5-10; 180, dorsal view of head (0.2 mm); 181, lateral view of head; 182, dorsal view of head; 183, dorsal view of abdominal segments 8-10; 184, labrum, dorsal view (0.05 mm); 185, mandible (0.05 mm). (Scale lengths in parentheses.)

CNC 2856, 2857 (CNC). Red Lake: 1♂, 1♀ (paratypes *L. kenora*), e. 15 Aug 1962, S62-5446-01, *Salix*, slides 2107 (CNC). Shebandowan: 1♂ (paratype *L. kenora*), e. 9 Aug 1963, A63-3782-01, *Salix*, slide CNC 2034 (CNC). UNITED STATES: CALIFORNIA: Alameda Co., Berkeley: 2♂, 18 Oct 1981, e. 24-26 Oct 1981, D. Wagner, *Salix laevigata*, JAP 81 K11, slide GD 1983 (DLW). Tilden Park: 1♂, 13 Oct 1981, e.

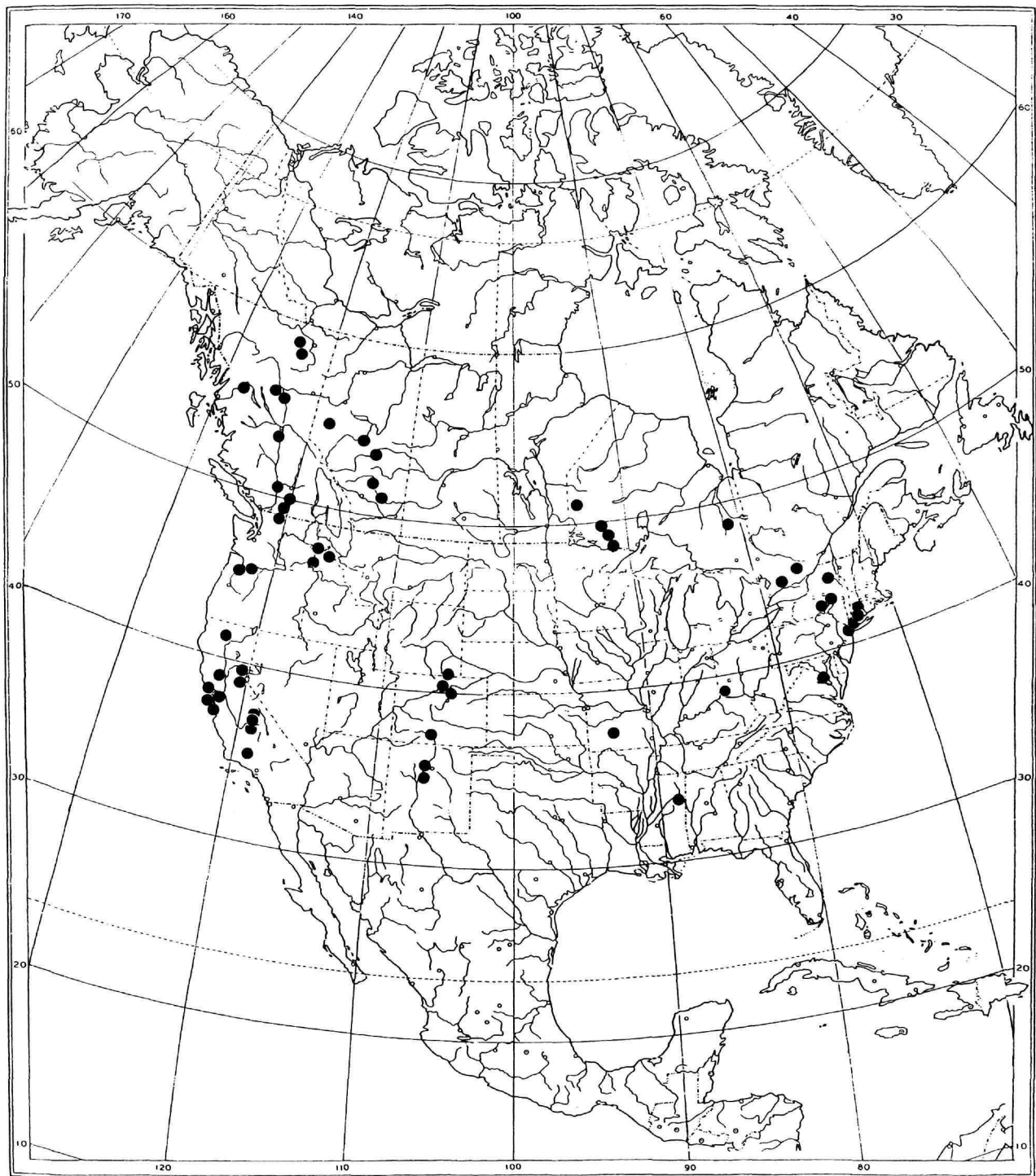
18 Oct 1981, D. Wagner, *Salix lasiolepis*, JAP 81 J46.5 (DLW); 1♀, 18 Oct 1981, e. 1 Nov 1981, D. Wagner, *Salix lasiolepis*, JAP 81 K13 (DLW); 1♂, 21 Nov 1981, e. DOA 13 Dec, JAP 81 J50 (DLW). Contra Costa Co., Briones Park: 4♂, 1♀, 21 Oct 1981, e. 21-27 Oct 1981, D. Wagner, *Salix lasiolepis*, JAP 81 K16 and 17, slide USNM 30403 (DLW, USNM). Tilden Regional Park: 1♂, 20 Aug 1983, e. 28 Aug 1983, D. Wagner,



FIGURES 186–194.—*Phyllonorycter salicifoliella*, pupa: 186, frontal process (cocoon cutter), dorsal view (100 μ m); 187, detail of subapical pore in Figure 186 (29 μ m); 188, tergal spines of abdominal segment 4 (86 μ m); 189, intersubapical area between abdominal terga 4–5 (9.2 μ m); 190, accessory cremaster, abdominal sternum 7 (86 μ m); 191, abdominal segment 10, caudal view (60 μ m); 192, ventral view of Figure 192 (50 μ m); 193, lateral cremasteral hook in Figure 192 (12 μ m); 194, abdominal segments 8–10, lateral view (139 μ m). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 186.)

Salix laevigata, JAP 83 H52, slide GD 1982 (DLW); 1 σ , 15 Sep 1981, e. 1 Oct 1981, D. Wagner, *Salix laevigata*, JAP 80 I 35 (DLW); 2 σ , 3 ϕ , 6 Nov 1982, e. 19 Oct–20 Nov 1982, J. Whitfield, *Salix ?laevigata*, JAP 82 L52, slides USNM 30823, 31074 (DLW, USNM). El Dorado Co., Fallen Leaf Lake: 1 σ , 2 ϕ , 22 Aug 1982, e. 2–9 Sep 1982, D. Wagner, *Salix lutea*, JAP 82 H38, slides GD 1976, USNM 30402 (DLW, USNM). Fresno Co., Cedar Grove, 1414 m: 1 σ , mine: 26 Jul 1977, e. 31 Jul–2 Aug 1977, G. Deschka, mine in *Salix*, zucht nr. 1276, slide GD 1403 (GD). Kern Co., 6 mi [9.6 km] S. Monolith: 1 σ , 2 ϕ , 15 Sep 1968, e. 26 Sep 1968, P. Opler, *Salix*, JAP 68 J60, slides DRD 3814, USNM 30386, 30822 (DLW, USNM). 5 mi [8 km] S. Monolith: 2 σ , 3 ϕ , 2 Oct 1967, e. 12–18 Oct 1967, J. Powell, *Salix*, JAP 67 K25, slides USNM 30821, 31021 (DLW, USNM). Mono Co., Glass Creek Campground, 4 air mi [6.4 km] ESE June Lake: 2 σ , 26 Aug 1983, e. 12–15 Sep 1983, D.

Wagner, *Salix ?lutea*, JAP 83 H104 (DLW). Rock Creek, 1.4 mi [2.2 km] W Tom's Place: 2 σ , 26 Aug 1983, e. 10–12 Sep 1983, D. Wagner, *Salix ?lutea*, JAP 83 M119 (DLW). Monterey Co., Monterey: 4 σ , 5 ϕ , mine: 9 Oct 1992, e. 20–26 Oct 1992, L.B. Turner, *Salix laevigata*, DRD 1207, slide 31145 (USNM). Nevada Co., Old Donner Pass, 7000 ft [2134 m]: 5 σ , 9 ϕ , 12 Sep 1988, e. 14–25 Sep 1988, Wagner and DeBenedictis, *Salix lutea*, DLM 88 J32, slides USNM 30802, 30809, 31075 (DLW, USNM). Placer Co., Sugar Bowl Ski Area: 1 σ , 25 Sep 1982, e. 3 Oct 1982, D. Wagner, *Salix lutea*, JAP 82 J136 (DLW). 3 mi [4.8 km] S Tahoe City along Ward Creek: 1 σ , 2 ϕ , 15 Aug 1981, e. 7 Sep 1981, D. Wagner, *Populus tremuloides*, JAP 81 H19, slides USNM 30388, 30883 (DLW, USNM). San Mateo Co., near Pacifica: 1 σ , 30 Sep 1981, e. 13 Oct 1981, D. Wagner, *Salix*, JAP 81 J57, slide GD 1981 (DLW). Santa Clara Co., Mt. Hamilton: 1 ϕ , 10 Sep 1983, e. 20 Oct 1983, D. Green,



MAP 4.—Distribution of *Phyllonorycter salicifoliella*.

Salix laevigata, JAP 83 K2 (DLW). Siskiyou Co., Mt. Shasta: 2♂, 3♀, 2 Aug–1 Sep 1871, Walsingham, BMNH slide 3967 (BMNH); 6♂, 3♀, Aug 1871 (BMNH); 1♂, 1♀, Aug 1871,

Walsingham, *Salix*, slides USNM 28414, 30881 (USNM). Sutter Co., Feather River, near Nicolaus: 1♀, 11 Oct 1982, e. 28 Oct 1982, D. Wagner, *Salix*, JAP 82 K16.5 (DLW); same data:

1♀, e. 16 Oct 1982, *Salix* sp. near *goodingii*, JAP 82 K45 (DLW); same data: 2♀, JAP 82 K16 (DLW). COLORADO: Alamosa Co., Alamosa City, 2250 m: 24♂, 29♀, mine: 26 Jul 1978, e. 9–17 Aug 1978, G. Deschka, mine in *Salix* ?*amygdaloides* [probably *x rubens* Schrank (*S. alba* *x fragilis*)], zucht nr. 1345, slides GD 1548, USNM 30874 (GD, USNM). Boulder Co., Boulder: 2♀, e. 11–16 Aug 1916, A. Braun, *Salix bebbiana*, B.1021, slide DRD 3825 (ANSP). Grand Co., Grand Lake, 2450 m: 54♂, 57♀, 30 Jul 1978, e. 10–21 Aug 1978, G. Deschka, mine in *Salix* [*monticola* Bebb], zucht nr. 1347, 1348, slides GD 1550, 1551, USNM 30785, 30873 (GD, USNM). Larimer Co., Livermore, 2210 m: 11♂, 12♀, 4 Aug 1978, e. 16–22 Aug 1978, G. Deschka, mine in *Salix amygdaloides*, zucht nr. 1351, slides GD 1553, USNM 30879 (GD, USNM). CONNECTICUT: Litchfield Co., Goshen: 1♂, 1♀, 26 Aug 1981, *Salix* (CTM); 1♂, larva, 26 Aug 1981, C. Maier, *Salix*, slide 22080 (USNM). New Haven Co., 1 mi [1.6 km] N Cheshire: 1♀, 15 Sep 1979, *Salix* (CTM); 1♂, pupa 15 Sep 1979, C. Maier, *Salix*, slide 21271 (USNM). Norwalk: 86J61, 2♂ (DLW). DISTRICT OF COLUMBIA [WASHINGTON]: 1♀, 1 May 1971 (BMNH); 3♂, e. 2 Aug 1898, *Salix* (USNM); 1♀, 25 Sep 1920, A. Busck, slide USNM 31087 (USNM); National Arboretum: 1♂, 17 Jul 1985, H. Larew, *Salix purpurea*, slide USNM 23684 (USNM). IDAHO: Kootenai Co., Coeur d'Alene: 1♂, 2♀, 21 Aug 1936, H. Rust, *Salix*, Hopk. no. 21905, slide 31086 (USNM). Latah Co., Moscow: 1♂, 25 Oct 1982, M. Furniss, *Salix alba*, slide 23623 (USNM). MARYLAND: Prince Georges Co., Beltsville: 1♂, Sep 1974, R. Webb, *Salix*, slide 17926 (USNM). Henson Creek, Fort Washington: 1♂ (neotype), 15 Sep 1974, e. 28 Sep 1974, D. Davis, *Salix babylonica* L., DRD 362 (USNM); same data as neotype except: 15♂, 11♀, 15 Sep 1974, e. 28 Sep–3 Oct 1974, slides USNM 17901, 17926, 17937, 22735, 22931, 28409, 30784, 31069 (USNM); 1♂, 26 Sep 1992, e. 22 Oct 1992, D. Davis, *Salix* sp., DRD 1240 (USNM). MASSACHUSETTS: Cambridge: 1♀ (syntype, *L. atomariella*), slide BMNH 26071 (BMNH); 1♂, 3♀, slide BMNH 26072 (BMNH). MICHIGAN: Clinton Co., Bath: 1♀, 9 May 1957, R. Hodges (USNM). MISSISSIPPI: Clay Co., 1 mi [1.6 km] east of West Point: 2♂, 1♀, 1 Sep 1984, R. Brown, *Populus* sp., USNM slide 31427 (MEM, USNM). MISSOURI: Crawford Co., Meramac River, near Steelville: 1♀, 15 Aug 1985, e. 17 Aug 1985, J. Whitfield, *Salix caroliniana*, JBW 18-14-88, slide DRD 3776 (DLW). MONTANA: Mineral Co., Cabin City: 5♂, 3♀, e. 11–18 Aug 1936, A. Braun, *Salix*, B.1509, slide USNM 31101 (ANSP, USNM). NEW JERSEY: Essex Co., Essex County Park: 1♂, 10 May (USNM). NEW MEXICO: Bernalillo Co., Juniper Canyon, Sandia Mts: 4♂, 1♀, 27–28 Jul 1989, e. 3–7 Aug 1989, D. Wagner, *Salix*, DLW 89 G90, slides DRD 3812, USNM 30496 (DLW, USNM). Sandoval Co., Pakitza Campground, 7000–7500 ft [2134–2287 m], 4 mi [6.4 km] east of Ponderosa: 4 larvae, 31 Jul 1989, D.R. Davis, *Salix*, DRD 678, slides USNM 30462, 30463 (USNM). NEW YORK: Essex Co., Giant Mtn., Roaring Brook Trail: 1♂, 28 Jul–4 Aug 1988, e. 9 Aug 1988, D. Wagner, *Salix*, DLM 88 M13, slide DRD 3775 (DLW); same data: 1♂, e. 9–21 Aug 1988, *Populus balsamifera*, DLM 88 G110, slide DRD 3778 (DLW). Oswego

Co., Hannibal: 1♀, 30 Aug 1972, *Salix*, E. Jäckh (USNM). Otsego Co., Milford: 3♂, 2♀, larvae, eggs, R. Fritz, *Salix eriocephala*, *S. sericea*, slides USNM 30440, 30678, 30804, 30805, 31070 (USNM). Tompkins Co., Six Mile Creek, Ithaca: 1♂, 1♀, 10, 17 May 1959, R. Hodges (USNM). Slaterville Springs: 3♂, 3♀, e. 12–15 Sep 1960, R. Hodges, *Salix*, slide USNM 28426 (USNM). OHIO: Hamilton Co., Cincinnati: 1♀ (ANSP). OREGON: Clackamas Co.: 1 mi [1.6 km]: 2♂, 13 Sep 1988, e. 29 Sep 1988, D. Wagner, *Salix*, DLW 88 J54, slide USNM 30803 (DLW, USNM). Clatsop Co., Warrington: 7♂, 1♀, 9 Sep 1944, *Salix*, lot 44-25293, slide USNM 18318 (USNM). Hood River Co., Cooper's Spur Inn, 4000 ft [1219.5 m]: 1♂, 5♀, 14 Sep 1988, e. 15–28 Sep 1988, D. Wagner, *Salix* ?*lutea*, DLW 88 J39, slide USNM 30824 (DLW, USNM). Jackson Co., to Rogue River: 1♀, 4–6 May 1872, Walsingham (BMNH). VIRGINIA: Alexandria Co., Veitch: 6♂, 4♀, 10 Oct 1913, C. Heinrich, *Populus*, Hopk. no. 11195, slides USNM 28415, 31071, 31072 (USNM). Fairfax Co., Falls Church: 6♂, 3♀, 15–16 Oct 1915, J. DeGryse, *Populus*, slides USNM 30880, 31136 (USNM).

REMARKS.—Most authors previous to Martin (1956) and Watson (1956) considered Clemens as the author of *salicifoliella*. Clemens (1861) proposed the name without describing the insect or its mine—merely mentioning the host (yellow willow, *Salix vitellinae* var. *alba*, [= *Salix alba* var. *vitellina* (L.) J. Stokes]) and where the mine was located. Packard (1869) repeated Clemens' brief remarks without further comment. The species was not formerly described until Chambers (1871:163) provided a rather detailed description of an adult reared from weeping willow. Earlier in the same series of papers, Chambers (1871:54) stated that his material was collected in Kentucky [probably around Covington] near Cincinnati. Neither the adult he reared from *Salix babylonica* nor a second specimen from *S. "longifolia"* are known to exist. Consequently, a neotype, reared from *Salix babylonica* in Prince Georges County, Maryland, is proposed in order to stabilize this troublesome name.

This species is the most common, widespread *Phyllonorycter* mining the leaves of North American *Salix*. It also exhibits the greatest amount of morphological variation, which has long caused confusion to workers in this group. As one example, adults mostly reared and previously identified as *P. salicifoliella* by Annette Braun, who was probably the most knowledgeable worker on Gracillariidae for much of the past century, were found by the senior author to contain representatives of five species of *Phyllonorycter* (including *P. apparella*, *P. deserticola*, *P. mildredae*, and *P. nipigon*) and only a single specimen of *P. salicifoliella*. Most of the variation is expressed in the forewing pattern and male genitalia, especially the valva (Figures 269–308). The latter is particularly confusing because of normal within-population uniformity and often conspicuous between-population differences, even in some adjacent populations (Figures 277–288). Most of the between-population variation is manifested in the relative elongation of the apical region (cucullus) of the valva, particularly that area between the dorsal spine patch (DS, Figure 248) and the apical process (AP, Figure 248) and its closely associated subapical brush of spines

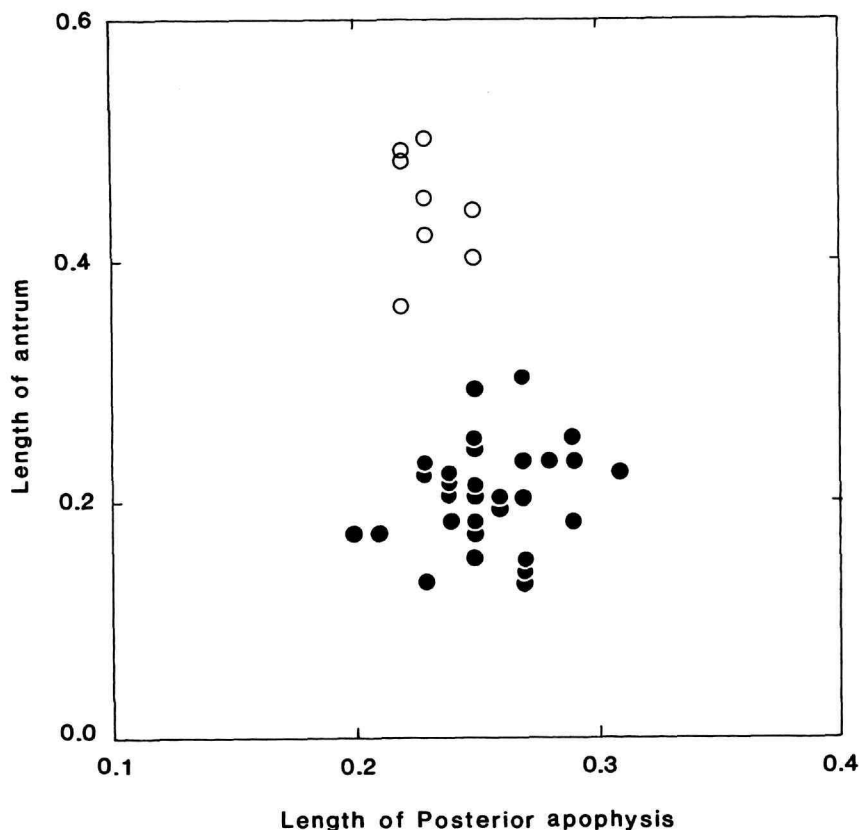
TABLE 4.—Length of antrum and posterior apophyses of female *Phyllonorycter salicifoliella* and *P. erugatus*.

Slide no.	Locality	Host	Length (mm)	
			Antrum	Apophyses
<i>P. salicifoliella</i>				
17902	Fort Washington, Maryland	<i>Salix</i>	0.13	0.23
31069	Fort Washington, Maryland	"	0.13	0.27
28409	Fort Washington, Maryland	"	0.14	0.21
31070	Milford, New York	"	0.15	0.27
30880	Falls Church, Virginia	<i>Populus</i>	0.15	0.25
31072	Veitch, Virginia	"	0.17	0.21
30877	Dawson Creek, British Columbia	<i>Salix</i>	0.17	0.20
3778	Giant Mountain, New York	"	0.17	0.25
30873	Grand Lake, Colorado	"	0.18	0.24
30876	Thornhill, British Columbia	"	0.18	0.25
30872	Clinton, British Columbia	"	0.18	0.29
30824	Cooper's Spur Inn, Oregon	"	0.19	0.26
30809	Old Donner Pass, California	"	0.19	0.26
30874	Alamosa City, Colorado	"	0.20	0.24
1737	Mitsue Lake, Alberta	"	0.20	0.24
31075	Old Donner Pass, California	"	0.20	0.25
1535	Hazleton, British Columbia	"	0.20	0.26
1537	Edmonton, British Columbia	"	0.20	0.27
3750	Cambridge, Massachusetts	"	0.21	0.24
28412	Pullman, Washington	"	0.21	0.25
30879	Livermore, California	"	0.22	0.23
30402	Fallen Leaf Lake, California	"	0.22	0.24
30883	Tahoe City, California	<i>Populus</i>	0.22	0.24
3812	Sandia Mountains, New Mexico	<i>Salix</i>	0.22	0.24
30875	Drumheller, Alberta	"	0.22	0.31
3811	Feather River, California	"	0.23	0.23
31074	Tilden Park, California	"	0.23	0.27
30823	Tilden Park, California	"	0.23	0.28
1536	Thornhill, British Columbia	"	0.23	0.29
30881	Mount Shasta, California	"	0.24	0.25
30443	Briones Park, California	"	0.25	0.25
1530	Thornhill, British Columbia	"	0.25	0.29
3014	Monolith, California	"	0.29	0.25
30822	Monolith, California	"	0.30	0.27
<i>P. erugatus</i>				
30450	Wilsonville, Oregon	<i>Populus</i>	0.36	0.22
30871	Rocky Mountain National Park, Colorado	"	0.40	0.24
31068	Haynes, Alberta	"	0.42	0.23
30384	Wilsonville, Oregon	"	0.44	0.25
30819	Haynes, Alberta	"	0.45	0.23
31088	Yoho National Park, British Columbia	"	0.48	0.22
30870	Yoho National Park, British Columbia	"	0.49	0.22
31067	Alameda, California	"	0.50	0.23

(SB, Figures 248, 269, 273, 277, 281, 285, 289, 293, 297, 301, 305). Because *P. kenora* merely represents one extreme of that range, it has been synonymized.

A similar range of variation involving the cucullus was found to occur in the closely allied and newly proposed species, *P. erugatus*. A clear understanding of *P. erugatus* and *P. salicifoliella* was not possible until a detailed examination was conducted on the male and female genital morphology from several, sometimes overlapping, populations within this difficult complex. Two features of the apical lobe of the valva—best observed with SEM photographs—help to separate the males of all populations of *P. salicifoliella* from *P. erugatus*. In

P. salicifoliella the apical process is longitudinally ribbed and usually is well separated from the more basal setal cluster (Figures 283, 287, 291, 295, 299, 303, 307). Both characters are correlated with the shorter antrum length in female *P. salicifoliella* (Table 4; Figure 431). To test possible correlation of antrum length of both *P. salicifoliella* and *P. erugatus* to overall body size (expressed by relative length of the posterior apophyses), a scatterplot was prepared using the computer program SYSTAT. Results showed that no correlation existed. Instead, the small sample ($n=8$) of *P. erugatus* (with significantly longer female antra) was clustered slightly toward shorter posterior apophyses (Graph 1).



GRAPH 1.—Scatterplot diagram showing disjunct length of female antrum between *Phyllonorycter salicifoliella* (dark circles) and *P. erugatus* (open circles) plotted against length of posterior apophysis. (Scatterplot is based on data listed in Table 4.)

Morphological variation of the valvae within some populations of *P. salicifoliella* also can resemble that of a few Palearctic members of this complex. For example, valvae of the European *P. pastorella* (Figure 332) superficially resemble that possessed in some western populations of *P. salicifoliella* (Figures 293, 297). The apical process of *P. pastorella*, however, is smooth and more elongate, with the subapical pore extending as an elongate groove along the inner side of the process (Figures 333, 334G).

***Phyllonorycter acanthus*, new species**

FIGURES 25, 37, 195–203, 251–253, 309–312, 351, 352, 433, 434, 450, 451; MAP 5

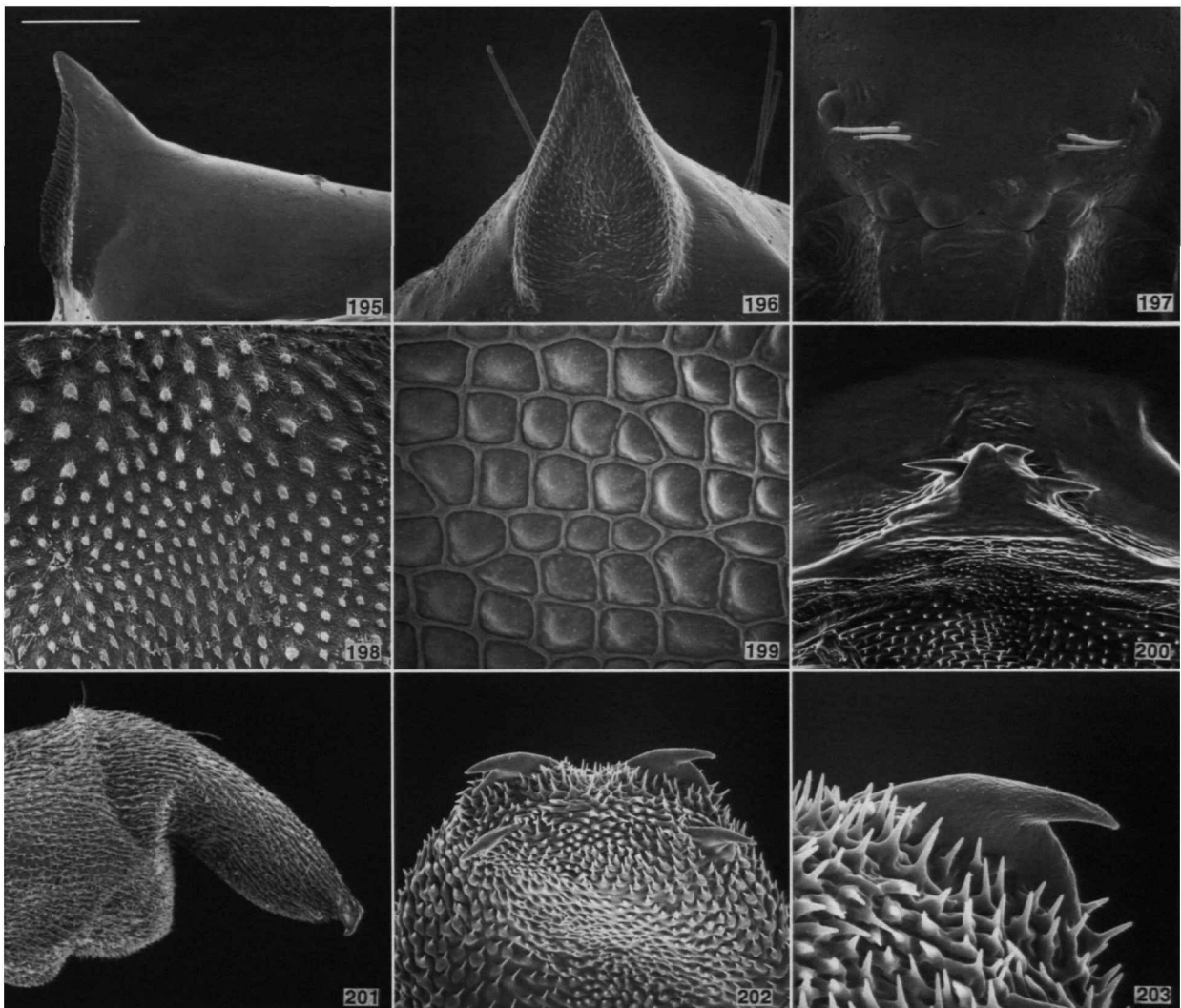
ADULT (Figure 37).—Length of forewing: 2.7–3.6 mm. Small moths with slender golden brown forewings with a large basal-dorsal white spot, five white costal strigulae, and three white dorsal strigulae. Male genitalia with symmetrical valvae. Larva on *Salix*.

Head: Vertex rough, with largely white, sometimes heavily

mixed with brown, piliform scales; frons smooth, lustrous white. Antenna ringed with light brown dorsally, entirely white ventrally. Labial palpus white dorsally, mostly brown ventrally.

Thorax: Dorsum mostly white, often with suffusion of pale brown near center of mesonotum and over tegula. Venter lustrous white. Forewing light golden brown heavily marked with white as follows: a large, basal-dorsal spot usually with faint brown suffusion near center; five costal strigulae with basal two slanted obliquely toward apex; three dorsal strigulae with basal two the broadest and most oblique, third dorsal strigula usually connecting fourth costal strigula to form a thin band across outer fifth of wing; most strigulae margined basad with dark brown; a more or less distinct, dark brown subapical spot present; fringe gray. Hindwing uniformly gray. Legs dark grayish brown dorsally, becoming progressively paler on mid- and hindlegs, with white banding dorsally on tibia and at apices of tarsal segments; entirely white ventrally.

Abdomen: Grayish brown dorsally, white ventrally; conspicuous sex-scaling absent. Seventh sternite of female moderately rough; anterior margin without follicles, smooth, except



FIGURES 195–203.—*Phyllonorycter acanthus*, pupa: 195, frontal process (cocoon cutter), lateral view (100 μ m); 196, dorsal view of Figure 196 (86 μ m); 197, labrum (99.8 μ m); 198, tergal spines of abdominal segment 5 (75 μ m); 199, intersegmental area between abdominal terga 5–6 (10 μ m); 200, accessory cremaster, abdominal sternum 7 (75 μ m); 201, abdominal segments 8–10, lateral view (120 μ m); 202, cremasteral spines of abdominal segment 10, ventral view (38 μ m); 203, dorsal-mesal cremasteral spine of Figure 202. (Scale lengths in parentheses; bar scale for all photographs shown in Figure 195.)

for rugose lateral angles (Figures 450, 451). Eighth sternite of male elongate, triangular, tapering to narrowly rounded caudal apex (Figure 252).

Male Genitalia (Figures 254, 256): Vinculum U-shaped. Transtilla moderately robust, quadrate. Valvae symmetrical, moderately long, broadest near middle, terminating in a minute, apical process bearing longitudinal ridges and an apical pore (Figure 312); a dense, rugose cluster of short, nonarticulated spines located immediately basad to subapical cluster of

more elongate spinose setae (Figures 310, 311). Anellus completely membranous. Aedoeagus slender, elongate, approximately twice the length of eighth sternite, with a short subapical lobe.

Female Genitalia (Figures 433, 434): Accessory bursa well developed, ductus approximately two-thirds the length of ductus bursae, both uniting at anterior end of elongate, tubular antrum that extends about one-third the length of ductus bursae, or ~ 0.5 mm in length. Signum circular, with a pair of

minute spines; a secondary, faintly sclerotized oval plate also present at anterior end.

LARVA.—Not examined.

LARVAL MINE (Figure 25).—As illustrated.

PUPA (Figures 195–203).—Maximum length 3.7 mm, width 0.8 mm. Vertex with triangular cocoon cutter similar to *P. apparella*. Forewing and antenna extending to A6; hindleg to A8. Dorsum of A2–A8 almost completely covered with dense concentration of small to minute, scattered spines, the largest situated cephalad; intersegmental surfaces reticulate as in Figure 199. Caudal half of sternum A7 with a slightly raised area (accessory cremaster) bearing 3 or 4 laterally projecting spines, usually 1 or 2 on each side (Figure 200). Cremaster consisting of two pairs of bilateral hooks with broad bases; ventral pair more separated than dorsal pair (Figure 202). A9 with sternum abruptly constricting to flattened A10 (Figure 201).

HOLOTYPE.—Mexico: Durango, El Salto, 2100 m, ♂; e. 26–31 Jul 1980 [e.=emerged], G. Deschka, mine in *Salix* sp. [*bonplandiana*], zucht nr. 1516, 25 Jul 1980, slide USNM 30779 (GD 1704) (USNM).

PARATYPES.—MEXICO: DURANGO: Same data as holotype: 3♀. JALISCO: Ajijic, 1700 m: 2♀, 1 Aug 1980, e. 2–3 Aug 1980, G. Deschka, mine in *Salix* sp. [*bonplandiana*], zucht nr. 1521; El Salto, 1590 m: 3♂, 3♀, 30 Jul 1980, e. 2–5 Aug 1980, G. Deschka, mine in *Salix* sp. [*bonplandiana*], zucht nr. 1520, slide GD 1687. MICHOACAN: Paricutin, 2000 m: 1♂, 2♀, 11 Aug 1980, e. 12–29 Aug 1980, G. Deschka, mine in *Salix* sp. [*bonplandiana*], zucht nr. 1526, slide USNM 22740 (USNM). Paratypes deposited in GD and USNM.

HOST (Table 1).—*Salix bonplandiana* Kunth.

FLIGHT PERIOD.—August; univoltine.

DISTRIBUTION (Map 5).—This species ranges in scattered riparian habitats in otherwise generally arid, montane regions of the Trans-Mexican Volcanic Belt of Jalisco and Michoacan.

ETYMOLOGY.—The specific name is derived from the Greek *acanthus* (thorny) in reference to the short, apomorphic spine cluster on the male valva.

REMARKS.—In addition to its more southern distribution, two apomorphies distinguish *Phyllonorycter acanthus* from all members of the *salicifoliella* group: the short, subapical spine cluster on the male valva and the paired, rugose, lateral tubercles on the seventh sternum of the female. With *P. salicifoliella* it shares the ribbed apical process of the male valva, and with *P. erugatus* it shares an elongate antrum (0.5 mm or more in length) in the female.

Phyllonorycter erugatus, new species

FIGURES 24, 35, 36, 204–214, 254–256, 313–328, 353–356, 435, 436, 448, 449; MAP 5

ADULT (Figures 35, 36).—Length of forewing: 3.7–4.8 mm. Small moths with slender, golden brown forewings usually

with a large basal-dorsal white spot, 4 or 5 slender white costal strigulae, and 3 or 4 relatively broad, white dorsal strigulae. Male genitalia with symmetrical valvae and smooth apical processes. Antrum of female genitalia 0.36–0.5 mm in length. Larva on *Populus*.

Head: Vertex rough, with an almost equal mixture of brown and white piliform scales but mostly brown between antennal bases; frons smooth, lustrous white. Antenna with segments darker at their apex dorsally and usually entirely white ventrally. Labial palpus varying from entirely white to brownish ventrally.

Thorax: Dorsum whitish, heavily irrorated with brown. Venter white. Forewing light golden brown, almost equally marked with white as follow: a large basal white spot on dorsal margin, sometimes heavily suffused with brown; 4 or 5 narrow, white costal strigulae with basal-most slanted toward apex; 3 or 4 broader, white dorsal strigulae; strigulae usually margined basally with dark brown, sometimes with obscure or irregular margins; a usually distinct dark spot present at apex of cell and at subapex of wing; fringe pale gray. Hindwing uniformly gray. Legs uniformly white ventrally, mostly dark grayish brown dorsally, becoming progressively paler on mid- and hindlegs, with white banding dorsally on tibia and at apices of tarsal segments.

Abdomen: Grayish brown dorsally, white to cream ventrally; conspicuous sex-scaling absent. Seventh sternum of female relatively smooth (Figures 448, 449). Eighth sternum of male (Figure 255) elongate, triangular, tapering to a broadly rounded to slightly bilobed apex.

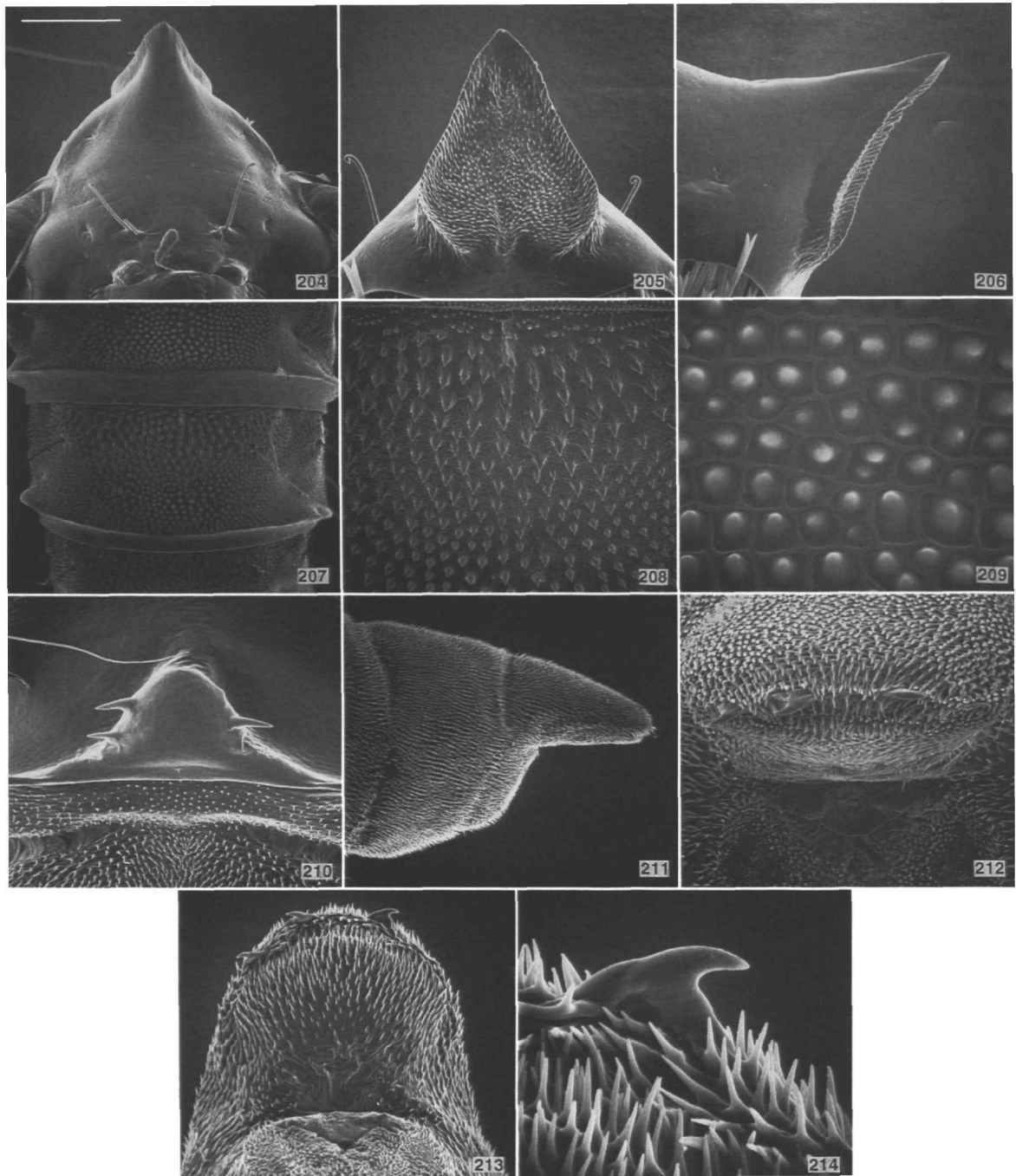
Male Genitalia (Figures 254, 256, 313–328): Vinculum approximately V-shaped, tapering to rounded apex. Transtilla moderately robust, quadrate. Valvae symmetrical, variable in form, usually moderately long, broadest near apex then abruptly tapering to slender, smooth apical process (Figures 316, 320, 324, 328); subapical brush consisting of a tight bundle of ~12–55 setae arising halfway up lobe bearing apical process. Anellus membranous. Aedoeagus slender, elongate, 2.1–2.7× the length of eighth sternum, with a short, subapical lobe (Figures 256, 353–356).

Female Genitalia (Figures 435, 436): Antrum tubular, sclerotized, greatly elongated, ~1.5–2× the length of posterior apophyses, ranging 0.36–0.5 mm in length. Accessory bursa ~1.5× the diameter of corpus bursae; ductus 0.5× the length of ductus bursae, both arising from anterior end of antrum. Signum a circular plate near caudal end of corpus with a pair of widely spaced minute spines and a slightly larger, less sclerotized, oval plate near opposite end.

LARVA.—Not examined.

LARVAL MINE (Figure 24).—As illustrated.

PUPA (Figures 204–214).—Maximum length 4.3 mm, width 0.9 mm. Vertex with relatively broad, triangular, dorsally flat-



FIGURES 204–214.—*Phyllonorycter erugatus*, pupa: 204, frontal area, ventral view (200 μm); 205, frontal process (cocoon cutter), dorsal view (100 μm); 206, lateral view of Figure 204 (100 μm); 207, abdominal terga 3–6 (231 μm); 208, tergal spines of abdominal segment 4 (85.8 μm); 209, intersegmental area between abdominal terga 3–4 (100 μm); 210, accessory cremaster, abdominal sternum 7 (86 μm); 211, abdominal segments 8–10, lateral view (120 μm); 212, abdominal segment 10, caudal view (50 μm); 213, ventral view of Figure 212 (67 μm); 214, lateral cremasteral hook in Figure 213 (12 μm). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 204.)

tened cocoon cutter with minutely serrated lateral ridges (Figures 204–206). Forewing extending to caudal margin of A6. Hindleg to middle of A8. Dorsum of A2–A8 densely covered with evenly scattered, short spines, with those of anterior fourth slightly enlarged (Figure 208); intersegmental surfaces reticulated as in Figure 209. Accessory cremaster of A7 with 1–3 pairs of lateral spines (Figure 210). Terminal cremaster consisting of 2 pairs of broad-based hooks, with one pair more laterad (Figures 212–214). A9 with sternum abruptly constricted to flattened A10 (Figure 211).

HOLOTYPE.—Canada: British Columbia, Golden, 784 m, ♂; e. 27 Aug–1 Sep 1982 [e.=emerged], G. Deschka, mine in *Populus balsamifera*, zucht nr. 1685, 17 Jul 1982 (USNM).

PARATYPES.—CANADA: BRITISH COLUMBIA: Same data as holotype: 3♂, 2♀, slide GD 1771. Hoodoos, 1500 m, Yoho National Park: 28♂, 30♀, 18 Aug 1982, e. 29 Aug–2 Sep 1982, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1687, slides GD 1764, USNM 30870. Thornhill, 250 m: 14♂, 12♀, 17 Jul 1979, e. 25 Jul–2 Aug 1979, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1441, slide GD 1519. UNITED STATES: ALASKA: Glacier Highway, 300 m, 20 km N of Haynes [Haines]: 18♂, 14♀, 23 Jul 1979, e. 2–11 Aug 1979, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1443, slides GD 1522, USNM 30786, 30819, 31068. CALIFORNIA: Alameda Co., Alameda: 3♂, 5♀, no. 26 [larva probably on *Populus dilatata*], USNM slides 17953, 28413, 30811, 31067. Santa Clara Co., specific locality unknown: 2♂, Aug, larva on *Populus dilatata*, no. 26. COLORADO: Holzwarth Homestead, 2800 m, Rocky Mountain National Park: 11♂, 13♀, 3 Aug 1978, e. 5–14 Aug 1978, G. Deschka, mine in *Populus balsamifera*, zucht nr. 1350, slides GD 1552, USNM 30871, 31073. OREGON: Clackamas Co., 1 Mi [1.6 km] S of Wilsonville: 7♂, 11♀, 20 Sep 1980, e. 25 Sep–7 Oct 1980, D. Wagner, ex *Populus* sp., JAP 80 I 51, slides GD 1975, USNM 30383, 30384, 30450, 31085. Paratypes deposited in BMNH, DLW, GD, and USNM.

HOSTS (Table 1).—*Populus balsamifera* L., *Populus* sp.

PARASITIDS (Table 2).—Eulophidae: *Sympiesis conica* (Provancher) and *S. marylandensis* Girault.

FLIGHT PERIOD.—Late July to early October; possibly bivoltine in southern part of the range.

DISTRIBUTION (Map 5).—Known from widely scattered localities from Santa Clara County near sea level in midcoastal California north to southern Alaska and west to the Rocky Mountains of Colorado to elevations of 2800 m.

ETYMOLOGY.—The specific name is derived from the Greek *erugo* (smooth, clear of wrinkles), in reference to the smooth, apical process of the male valvae.

REMARKS.—*Phyllonorycter erugatus* shows nearest affinities to *P. salicifoliella* and shares with that species such features as similar male genitalia, especially in regard to the porous apical process and dense cluster of subapical setae on the male valvae, the sclerotized antrum of the female, and similar maculation. The male valvae also exhibits considerable varia-

tion within *P. erugatus* (Figures 313–328), which parallels that shown in *P. salicifoliella* in ranging from genitalia with a relatively broad, truncate cucullus to those in which the valva is more slender and attenuated. It differs from *P. salicifoliella* in the male genitalia possessing a smooth apical process with the subapical setal cluster arising more terminally on the apical lobe (Figures 315, 319, 323, 327). The females of *P. erugatus* can be distinguished by their longer antrum (0.36–0.5 mm; Table 4; Graph 1), which always exceeds the length of the posterior apophyses, and smoother seventh sternum. The larva of *P. erugatus* has been reared only from *Populus*, whereas that of *P. salicifoliella* prefers *Salix* as a host and only rarely switches to *Populus*. Although differing from *P. mildredae* in several features of the male valva, the male genitalia of *P. erugatus* agrees with that *Salix*-feeding species in possessing a smooth apical process.

Phyllonorycter mildredae, new species

FIGURES 26, 38, 257–259, 329–331, 357, 358, 437, 438; MAP 5

ADULT (Figure 38).—Length of forewing: 2.4–3.0 mm. Small moths with slender, golden brown forewings with basal median and dorsal streaks of white, four costal white strigulae, and three to four dorsal white strigulae. Valva of male symmetrical, broadest at apex.

Head: Vertex rough, entirely white or with a few brownish, piliform scales intermixed; frons smooth, lustrous white. Antenna entirely white to annulated with light brown dorsally. Labial palpus white.

Thorax: Dorsum usually white, sometimes with slight suffusion of pale brown over tegula. Forewing light golden brown marked with white as follow: a basal median streak; four costal strigulae with the basal-most pair strongly slanted toward apex; three to four dorsal strigulae of variable width with basal-most strigula often joining apex of basal median streak; white strigulae usually bordered basally with dark brown and sometime lightly speckled with dark brown scales; a small dark brown to black subapical spot. Hindwing and fringe uniformly gray. Foreleg dark grayish brown dorsally, white ventrally. Mid- and hindlegs light brown dorsally, white ventrally; tarsal banding barely evident.

Abdomen: Dark brown dorsally, white ventrally; conspicuous sex-scaling absent. Eighth sternite of male relatively broad; apex broadly rounded (Figure 258).

Male Genitalia (Figures 257, 259, 329–331, 357, 358): Vinculum V-shaped. Transtilla moderately thickened and quadrate. Valvae symmetrical, moderately long, gradually increasing in width to rounded apex; apical process smooth; subapical setal brush reduced to 3–6 spinose setae arising from a small tubercular lobe (Figure 330). Anellus completely membranous, elongate, about as long as valva. Aedoeagus slender, elongate, approximately twice the length of eighth sternite, with a short subapical process (Figures 357, 358).

PLATE 1

- a. Discocyathus eudesii* from Croisille, Calvados (near Bayeux), France, Middle Jurassic (Bojajian), MNHN M00086, calicular and basal views of same specimen, $\times 2.7$ (courtesy J. Stolarski).
- b-d. Areopsammia mastrichtensis*, holotype, Netherlands, Late Cretaceous (Maastrichtian), Museum für Naturkunde, Berlin, MBK 1303: *b*, oblique view of two reconstructed fragments, $\times 2.7$; *d*, stereo view of calice, $\times 2.4$. *c. Porosmilia alacca* as figured by Umbgrove (1925), National Museum of Natural History (Naturalis), Leiden, 76599, cast of lower corallum, $\times 2.7$.
- e,g,h. Balanophyllia (B.) calyculus*: *e,h*, neotype, Red Crag, Suffolk, England, late Pliocene, USNM 94469, calicular and side views, $\times 3.2$, $\times 1.8$, respectively; *g*, Red Crag, England, late Pliocene, USNM M156433, polycyclic base, $\times 5$.
- f,j. Balanophyllia (E.) caribbeana* from Oregon station 5696, $12^{\circ}05'N$, $72^{\circ}13'W$, 33 m, USNM 62612: *f*, detail of axial edges of several septa showing both minute serration of septal edge resulting from closely spaced, small-diameter trabeculae and fenestration on face of septum, $\times 28$; *j*, hispid costae covered with diaphanous epitheca, $\times 18$.
- i,k. Balanophyllia (B.) floridana*: *i*, Dry Tortugas, Florida, 71 m, USNM 81003, side view of largest known specimen, $\times 2.5$; *k*, Fish Hawk station 7516, off Fowey Rocks, Florida, 82 m, USNM 22037, detail of hispid costae, $\times 95$.



MAP 6.—Distribution of *Phyllonorycter apicinigrella*, *P. populiella*, and *P. scudderella*.

FLIGHT PERIOD.—April to early May, July and September; probably univoltine, with the adults overwintering.

DISTRIBUTION (Map 6).—Probably widespread through the eastern United States but currently reported from only Washington, D.C., Kentucky, and Ohio.

MATERIAL EXAMINED.—UNITED STATES: DISTRICT OF COLUMBIA [Washington]: 3♂, 3–10 May 1885, slide USNM 18435 (USNM). KENTUCKY: Grayson Co., Summit: 1♂, e. 16 Sep 1940, *Populus*, B.1837 (ANSP). OHIO: Hamilton Co., Cincinnati: 3♂, e. 26 Apr–6 May 1911, A. Braun, on *Salix*

(ANSP); 5♂, 4♀, e. 25–28 Apr 1917, A. Braun, *Populus alba*, B.76 (ANSP); same data, 3♂, 1♀, slides CNC 2096, MIC 2254 (CNC); 1♀, e. 12 Jul 1908, *Populus alba*, B.378 (ANSP); 1♂, e. 16 Aug 1917, A. Braun, on *Populus canescens*, slide CNC 2 (CNC); 1♂, e. 22 Jul 1910, A. Braun, *Salix* sp., B.596 (ANSP); 4♂, 3♀, e. 22 Apr–15 May 1917, A.F. Braun, slides USNM 17012, 18026, 30446; 1♂, 25 Aug 1907; 1♀, 8 Sep 1907, A.F. Braun (USNM); 2♀, e. 3 Sep 1907, A. Braun, *Populus alba*, B.76 (ANSP). Scioto Co., Roosevelt Lake: 1♂, e. 18 Apr 1957, A. Braun, on *Populus grandidentatum* (ANSP).

REMARKS.—As pointed out by Freeman (1970), the type of this species consists of only two forewings glued to a pin. The wing pattern generally agrees with specimens reared by Braun from *Populus*.

Records of this species on *Populus tremuloides* from western North America (Busck, 1904; Dyar, 1904) represent misidentifications of *P. apparella* as suspected by Braun (1908b) and later confirmed by genitalic examination by the senior author (DRD).

Braun described the larval mine as a relatively small, 9–10 mm long and 4–5 mm broad, lower side, tentiform blotch. It is rather inconspicuous ventrally because of the tomentosity of the primary host (*Populus alba*). The male genitalia of this species closely resembles that of the European *P. connexella* and *P. quinqueguttella*. Both differ from *P. populiella* in the right valva possessing a more rounded apex to the cucullus and a variably developed apical spine. All are members of the *hilarella* group (Table 1) as suggested by their asymmetrical valvae; however, pupae are needed for further confirmation.

Phyllonorycter scudderella (Frey and Boll)

FIGURES 40, 215–223, 263–265, 338–340, 443–445; MAP 6

Lithocolletis scudderella Frey and Boll, 1873:212.—Chambers, 1875a:126; 1875b:230; 1877a:156; 1879:72.—Riley in Smith, 1891:109 [*Lithocolletes* (sic)].—Dyar, 1903:552 [*Lithocolletes* (sic)].—Braun, 1908:276; 1914:116, 154.—Meyrick, 1912a:32; 1912b:7.—Barnes and McDunnough, 1917:187.—Braun in Forbes, 1923:191.—McDunnough, 1939:95.—Brower, 1984:40.

Phyllonorycter scudderella (Frey and Boll).—Ely, 1918:59.—Davis, 1983:10.—Maier and Davis, 1989:17.—Landry and Wagner, 1995:621.

Lithocolletis salicivorella Braun, 1908a:101; 1908b:276; 1914:116, fig. 29.—Meyrick, 1912a:32; 1912b:7.—Barnes and McDunnough, 1917:187.—Braun in Forbes, 1923:192.—McDunnough, 1939:95.—Brower, 1984:40. [New synonymy.]

Phyllonorycter salicivorella (Braun).—Ely, 1918:60.—Davis, 1983:10.

ADULT (Figure 40).—Length of forewing: 3.0–4.3 mm. Small moths with slender, olive to golden brown forewings with a median basal white streak and four costal and three dorsal white strigulae. Male genitalia with asymmetrical valvae.

Head: Vertex rough, with a thin band of reddish brown, piliform scales between antennae overlaid by a band of white, piliform scales more posteriorly; frons smooth, with broad, lustrous white scales. Antenna sometimes entirely white, usually light brown dorsally except for white scape and basal flagellomeres. Labial palpus white.

Thorax: Dorsum variable, usually white with a pair of large reddish brown spots on either side of midline and heavy brownish suffusion anteriorly on tegula. Venter lustrous white. Forewing reddish to olive brown marked with white as follows: a slender median line at basal one-third, basal one-fourth of dorsal margin edged with white, four costal strigulae with the most basal one near middle of wing strongly oblique toward apex; dorsal margin with three strigulae, the most basal one strongly oblique toward costa; basal first and second white

strigulae on dorsal margin with heavy dark brown suffusion toward base; a minute white, subapical streak mostly enclosed dorsally by dark brown; fringe gray. Hindwing uniformly gray. Legs dark to light brown dorsally, darkest on foreleg progressing to light on hindleg, white ventrally with 2 or 3 broad white bands on tarsus, becoming indistinct on hind tarsus.

Abdomen: Dark brownish gray dorsally, white ventrally; conspicuous sex-scaling absent. Eighth sternum of male elongate, nearly equalling length of valva, tapering rather abruptly to a narrowly rounded apex (Figure 264).

Male Genitalia (Figures 263, 265, 338–340): Vinculum slender and Y-shaped, abruptly constricted to form a short saccus. Valvae asymmetrical; left valva broad, variable in width, at least twice the width of right valva, much broader near middle, and with a stout, sinuate spine arising near apex; length of spine slightly greater than maximum width of valva; a minute, oval pore located subapically on spine (Figure 340); right valva slender, only slightly broader near base, with a smaller, usually curved spine arising further from apex. Aedoeagus slender, with a small subapical spine; approximately equal to eighth sternite in length.

Female Genitalia (Figures 443–445): Lamella antevaginalis well developed, projecting caudally free from abdominal wall as a thin, quadrate plate about as broad as long; caudal margin truncate to broadly rounded. Antrum terminating abruptly, with a relatively long accessory duct arising medially and the equally slender but more elongate ductus bursae arising laterally. Signum a small elliptical disk bearing a single, slightly furcate spine (Figure 445).

LARVA.—Not examined.

PUPA (Figures 215–223).—Similar to *P. apicinigrella*, except as follows: Dorsal spines of A2–A8 less developed, cuticle smoother between enlarged anterior and caudal spines (Figure 218). Sternum of abdominal segment 7 smooth, without accessory cremaster (Figure 219). A9 less truncate (viewed laterally) and more tapered to A10 (Figure 220). Caudal margin of A10 truncate (Figure 222); cremaster consisting of a bilateral pair of stout hooks (Figures 222, 223).

TYPES.—Lectotype, ♂, Cambridge, Massachusetts, designated by Freeman (1970) as “type,” BMNH (*P. scudderella* Frey and Boll). Holotype, ♂, Essex County Park, N.J., USNM (*P. salicivorella* Braun).

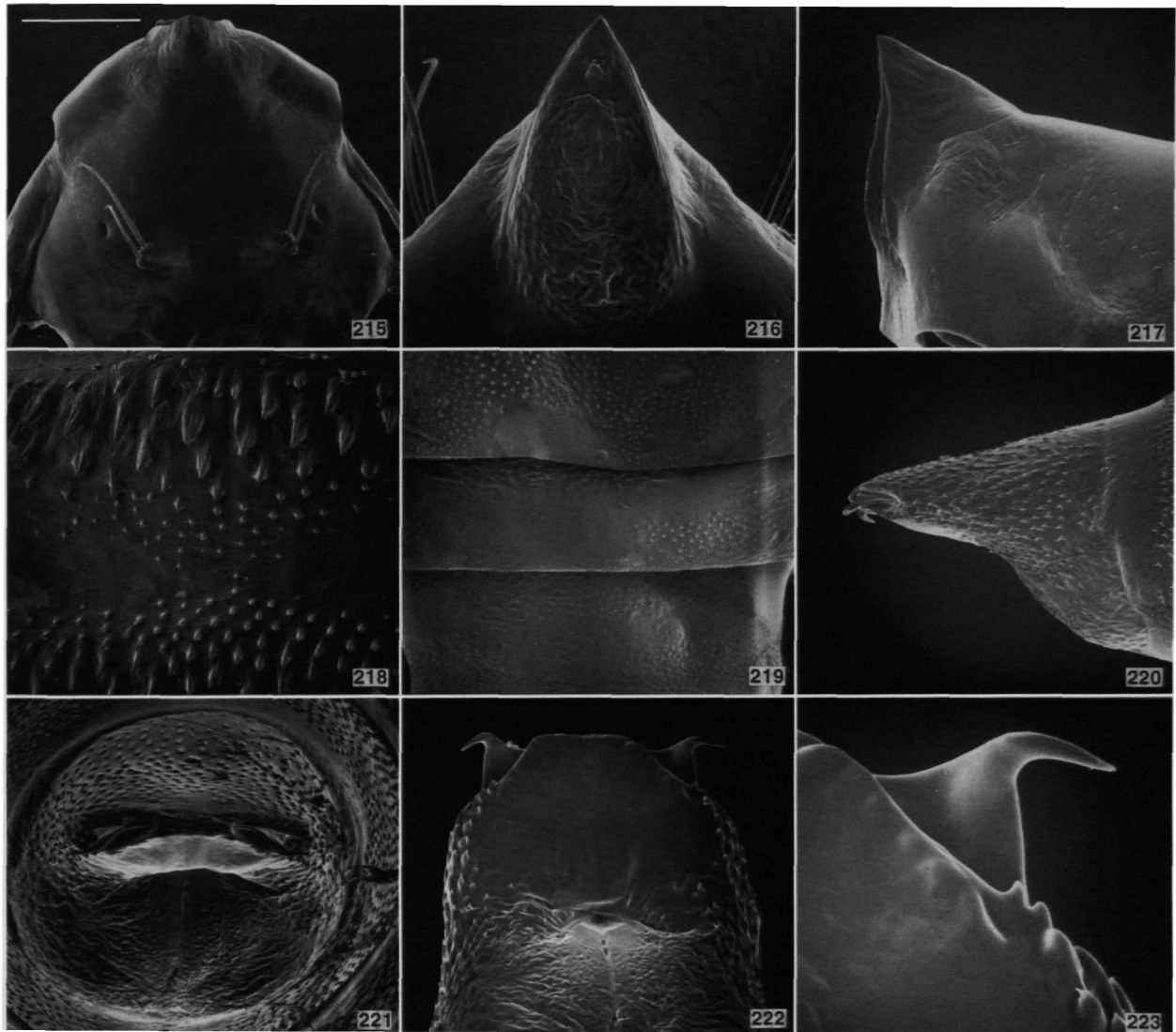
HOSTS (Table 1).—*Salix babylonica* L., *Salix bebbiana* Sargent, *Salix discolor* Muhl. (Maier and Davis, 1989), *Salix* species (Frey and Boll, 1873), *Salix candida* Flugge.

PARASITOID (Table 2).—Eulophidae: *Sympiesis* sp.

FLIGHT PERIOD.—Mid-March to early May, late June to early October; probably bivoltine, with the adults overwintering, but not trivoltine (Maier and Davis, 1989).

DISTRIBUTION (Map 6).—Relatively widespread in eastern North America from Ontario, Canada, to Ohio and in western North America from southeastern Alaska to Oregon.

MATERIAL EXAMINED.—CANADA: BRITISH COLUMBIA: Fraser Mills: 2♂, 1♀, 25 May 1922, L.E. Marmont, slide DRD



FIGURES 215–223.—*Phyllonorycter scudderella*, pupa: 215, head, ventral view (136 μ m); 216, frontal process (cocoon cutter) dorsal view (60 μ m); 217, lateral view of Figure 216 (75 μ m); 218, tergal spines of abdominal segment 5 (75 μ m); 219, abdominal sterna 6–8, without accessory cremaster (120 μ m); 220, abdominal segments 8–10, lateral view (86 μ m); 221, caudal view of Figure 220 (67 μ m); 222, ventral view of Figure 221 (75 μ m); 223, lateral cremasteral hook of Figure 222 (17.6 μ m). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 215.)

3985 (CNC). Vancouver: 1 σ , 20 Jan 1939, J. Jacob (CNC); 1 ϕ , 10 May 1924, E. Blackmore (CNC). NOVA SCOTIA: Digby Co., Saunierville: 1 ϕ , 24 Jul 1987, e. 30 Jul 1987 [e.=emerged], D. Wagner, ex *Salix*, DLW no. 87G58 (DLW). Lunenburg Co., Big Mushamush Lake, Aulenbach Point: 4 σ , 3 ϕ , 22 Jul 1987, e. 28 Jul–8 Aug 1987, D. Wagner, ex *Salix*, DLW 87G40 (DLW); 1 σ (USNM). ONTARIO: Ottawa: 9 σ , 6 ϕ , 29 Jan–8 Feb

1971, G. Lewis, *Salix*, 70-153, 154 (CNC); 1 σ , 1 ϕ , 3–5 Feb 1969, G. Lewis, *Salix*, 68-118 (CNC); 3 σ , 5 ϕ , 19–24 Apr 1967, Freeman and Lewis, *Salix*, 66-166, slides CNC 2808, 2811 (CNC); 1 ϕ , 17–18 May 1933, C. Young, slide DRD 3831 (ANSP); 2 σ , 3 ϕ , 1 Aug 1984, 6–9 Aug 1984, D. Wagner, JAP 84H28, *Salix*, slide GD 1980 (DLW). Ottawa East: 2 σ , 3 ϕ , 29 Apr–8 May 1919, J. McDounough, *Salix*, slides CNC 477,

2813 (CNC). Overbrook: 2♂, 2♀, 25 Feb–8 Mar 1958, Freeman and Lewis, *Salix*, 57-198, slides CNC 2090, 2125 (CNC); 1♂, 2♀, 30 Jan 1969, G. Lewis, *Salix*, 68-117 (CNC). Simcoe: 2♂, 1♀, 29 Aug–5 Sep 1957, Freeman and Lewis, *Salix*, 57-167, 57-168, slides CNC 2089, 2809 (CNC). QUEBEC: St. L. de Blandford: 1♂, 3♀, 15–18 Mar 1968, T. Freeman, *Salix*, 67-135 (CNC). UNITED STATES: ALASKA: Delta Junction: 1♂, mine: 26 Jul 1979, e. larva 29 Jul 1979, G. Deschka, mine in *Salix* species, zucht nr. 1447, slide GD 1531 (GD). CONNECTICUT: Chittenden Co., Essex Jct: 1♀, 23 Jul 1988, e. 30 Jul 1988, D. Wagner, ex *Salix*, DLW 88G102 (DLW). Fairchild Co., Norwalk: 2♀, 28/29 Sep 1986, DOA 20 Mar 1987, Wagner and Glazer, ex *Salix*, DLW 87KG1 (DLW). Litchfield Co., Goshen: 1♂, 26 Aug 1981, e. 26 Aug 1981, C. Maier, *Salix* (USNM). Salisbury, near Beeslick Pond: 1♀, mine: 25 Jul 1990, C. Maier, *Salix candida*, lab reared (CTM); 2♂, 2♀, mine: 11 Oct 1988, C. Maier, *Salix candida*, lab reared (CTM, USNM). New Haven Co., Guilford: 2♀, 25 Jun 1985, C. Maier, *Salix discolor* (CTM). Oakland Co., Waterford, fen near Townsend Lake: 1♂, mine: 15 Jul 1990, C. Maier, *Salix candida*, lab reared (CTM). Tolland Co., Union: 1♂, 5 Oct 1983, C. Maier, *Salix*, slide 3566 (CTM). KENTUCKY: Kenton Co., Doe Run Lake County Park: 2♀, 15 Oct 1997, e. (in unheated garage) 5 Apr 1998, J.A. Merkle, *Salix sericea*, DRD slide 4098 (JAM, USNM). MASSACHUSETTS: Middlesex Co., Cambridge: 1♂ (lectotype, *P. scudderella*), slide 12101, 2♀ (BMNH); 4♂, 2♀ (paralectotypes, *P. scudderella*), type 1340, slides DRD 3638, 3639 (MCZ). MICHIGAN: Marquette Co., near Humboldt: 1♀, e. 31 Jul 1943, A. Braun, *Salix*, B.2060 (ANSP). NEW JERSEY: Essex Co., Essex County Park: 1♂ (holotype, *P. salicivorella*), 6 Jul 1902, e. 19 Jul 1902, W. Kearfolt, willow, slide USNM 30447 (CNC 2594) (USNM). NEW YORK: St. Lawrence Co., Oak Point: 2♂, 2♀, 12/17 Aug 1988, e. 12/18 Aug 1988, D. Wagner, on *Salix*, DLW 88H36 (DLW); 1♂, 1♀, slide USNM 30800 (USNM). OHIO: Butler Co., Oxford: 1♀, e. 12 Aug 1909, A. Braun, *Salix* sp. (pubescent), B.526 (ANSP); 1♂, e. 10 Aug 1911, A. Braun, *Salix* sp. (pubescent), B.526, slide USNM 17016 (USNM). Hamilton Co., Cincinnati: 4♂, 6♀, e. 17 Mar–12 Apr 1916, A. Braun, *Salix*, B.901 (ANSP); 1♀, e. 12 Apr 1916, A. Braun, B.901 (CNC); 1♂, 29 Apr 1906, A. Braun (ANSP); 4♀, 21–25 Jul 1910, A. Braun, *Salix* sp., B.596 (ANSP); 1♀, e. 28 Jul 1913, A. Braun, *Salix* (ANSP); 1♂, Jun 1914, A. Braun, *Salix* (ANSP); 2♂, e. 21–22 Jul 1910, A. Braun, slides USNM 18035, 30449 (USNM); 1♂, e. 31 Aug 1911, A. Braun, slide USNM 30448 (USNM). OREGON: Clackamas Co., Wilsonville: 1♂, 16–14 Jun 1983, e. 3 Jul 1983, D. Wagner, JAP 83f106, *Salix* sp.; 1 m [1.6 km] south of Wilsonville: 3♂, 16 Jun 1983, e. 16–28 Jun 1983, D. Wagner, JAP 83f106, *Salix* sp. (DLW).

REMARKS.—Although differing greatly in wing pattern, *Phyllonorycter scudderella* and *P. apicinigrella* are closely related on the basis of similar genital morphology and pupal characters. The male genitalia of *P. scudderella* differs by the more elongated saccus. The female genitalia of the two species

differ in the form of the lamella antevaginalis, with that of *P. scudderella* being more quadrate and less broad; the short spine of the signum also is slightly furcate in *P. scudderella* and simple in *P. apicinigrella*. Their pupae agree in the absence of an accessory cremaster on A7, in possessing smooth, abdominal, intersegmental membranes, and in having only one pair of cremasteral hooks. Two males originally included in the type series of *P. apicinigrella* are believed to be *P. scudderella* (see "Remarks" under *P. apicinigrella*).

On the basis of their very similar male genital morphology, *P. hilarella* (Figure 408) of Europe appears to be the species most allied to *P. scudderella* (Figure 263). The forewing pattern of these two species differ, with *P. hilarella* possessing a complete basal fascia.

No morphological distinction supports the separation of *P. scudderella* and *P. salicivorella*; consequently, the latter name has been synonymized. Freeman (1970, fig. 15) showed the left valva of *P. scudderella* to be more slender, but this feature is variable. The forewing pattern also varies, with a faint trace of a fourth dorsal strigula sometimes evident.

Phyllonorycter apicinigrella (Braun)

FIGURES 41, 224–232, 266–268, 441, 442; MAP 6

Lithocolletis apicinigrella Braun, 1908:307; 1914:114, 156.—Meyrick, 1912a: 32; 1912b:7.—Barnes and McDunnough, 1917:187.—McDunnough, 1939: 96.

Phyllonorycter apicinigrella (Braun).—Ely, 1918:62.—Davis, 1983:10.

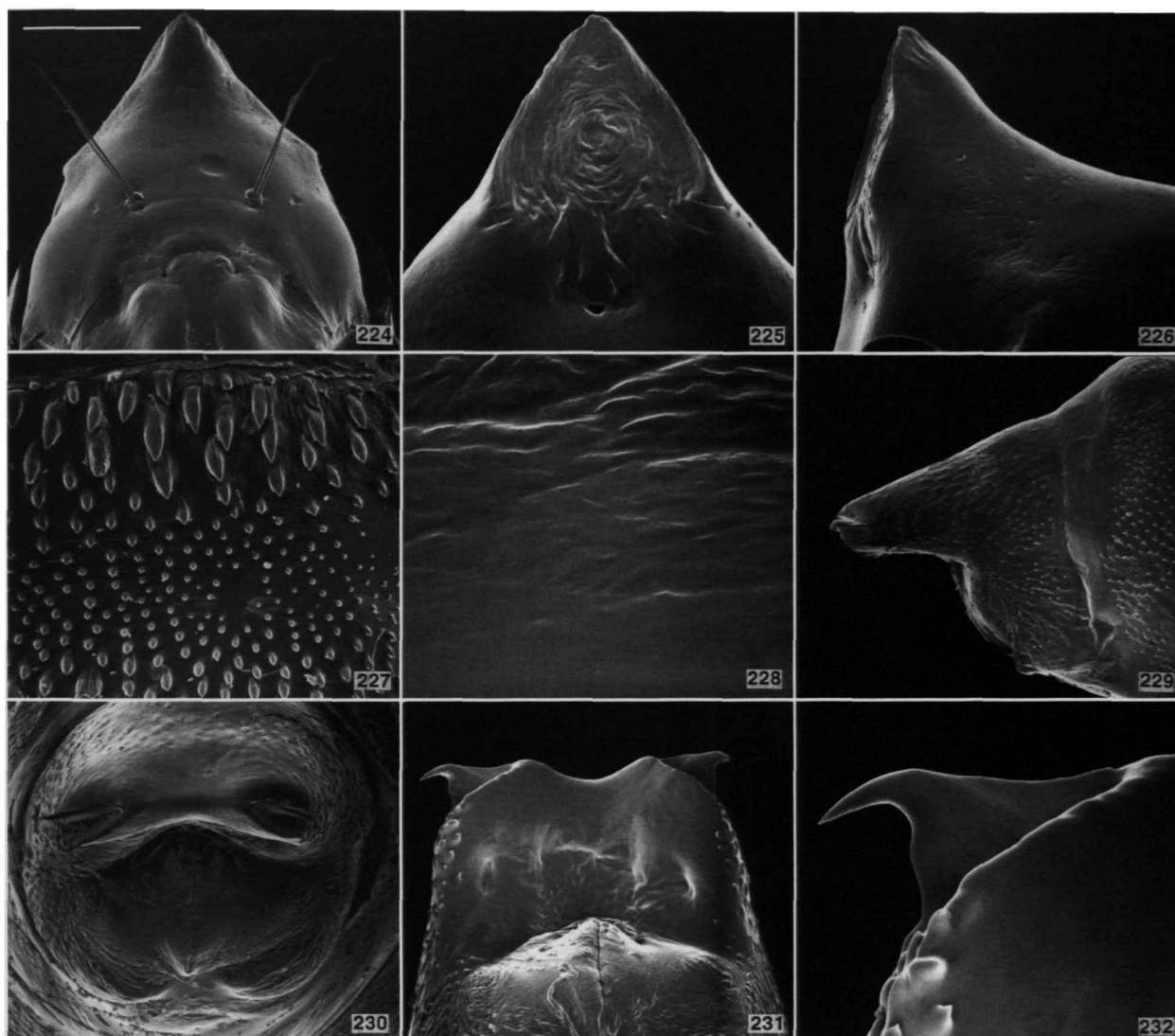
ADULT (Figure 41).—Length of forewing: 2.7–3.8 mm. Small moths with slender, mostly pale ochreous forewings with a darker brown, basal costal half and nearly black terminal band. Male genitalia with asymmetrical valvae.

Head: Vertex rough, with a mixture of dark brown to cream, piliform scales; frons smooth, with broad, lustrous white to cream white scales. Antenna with dorsal scales smooth, mostly light fuscous except white at base and apical one-fifth; venter entirely white; length about 0.8× that of forewing. Labial palpus white.

Thorax: Pronotum cream to brownish ochreous. Venter lustrous white. Forewing unusually marked, without striae; predominantly pale ochreous with a large dark brown costal spot at basal one-third and nearly black terminal band; apex of discal cell sometimes suffused with light brown; fringe mostly pale gray except for apical suffusion of black extending from terminal band. Hindwing pale gray. Legs mostly shiny gray dorsally and white ventrally; tibial and tarsal banding very faint; hindleg mostly unicolorous, white to cream white.

Abdomen: Light brown with slight golden luster dorsally, mostly white to cream ventrally; without conspicuous sex-scaling. Eighth sternum of male moderately long and broad, length 1.6× width; apex rounded (Figure 267).

Male Genitalia (Figures 266, 268): Vinculum short broadly V-shaped. Valvae asymmetrical; left valva broadest at middle, tapering to apex with an elongate, curved, subapical spine;



FIGURES 224–232.—*Phyllonorycter apicinigrella*, pupa: 224, head, ventral view (150 μ m); 225, frontal process (cocoon cutter), dorsal view (60 μ m); 226, lateral view of Figure 225 (75 μ m); 227, tergal spines of abdominal segment 5 (75 μ m); 228, intersegmental area between abdominal terga 4–5 (10 μ m); 229, abdominal segments 8–10, lateral view (86 μ m); 230, caudal view of Figure 229 (67 μ m); 231, ventral view of Figure 230 (60 μ m); 232, lateral cremasteral hook of Figure 231 (17.6 μ m). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 224.)

right valva slender throughout, less than 0.25 \times the width of left valva at middle, without prominent spine. Aedoeagus slender, approximately 0.9 \times the length of valva and 0.8 \times the length of eighth sternum, with a subapical spinose process.

Female Genitalia (Figures 441, 442): Lamella antevaginalis broader than long. Accessory bursa with moderately long duct, approximately 0.5 \times the length of ductus bursae, and arising near caudal end of latter where they empty into a broad an-

trum. Signum a single round disk bearing a single spinose papilla.

LARVA.—Not examined.

PUPA (Figures 224–232).—Maximum length 3.5 mm; width 0.7 mm. Vertex with triangular cocoon cutter similar to *P. apparella*, but with pore located more posteriorly (Figures 224–226). Forewing extending to A8, antenna to middle of A8, and hindleg to middle of A9. Dorsum of A2–A8 almost completely covered with dense concentration of small to minute,

scattered spines, the largest situated cephalad (Figure 227); intersegmental surfaces smooth, without reticulate pattern (Figure 228). Caudal half of sternum A7 smooth, without spines or raised triangular area. Caudal margin of A10 slightly concave and smooth (Figure 231); cremaster consisting of a single bilateral pair of moderately large hooks (Figure 232). A9 with sternum abruptly constricting to A10 (Figure 229).

TYPE.—Lectotype, ♀; Alameda Co. California, iss VII.20, G.R. Pilate; B.311; ♀ genitalia on slide DRD 3640; designated by D. Davis; (ANSP).

HOSTS (Table 1).—*Salix lasiandra* Bentham, *Salix sitchensis* Bongard, *Salix* sp.

FLIGHT PERIOD.—May, mid-June to mid-September; apparently either bi- or trivoltine.

DISTRIBUTION (Map 6).—Along the western coast of the United States from San Luis Obispo County, California, north to Whatcom County in extreme northwestern Washington.

MATERIAL EXAMINED.—UNITED STATES: CALIFORNIA: Alameda Co.: 1 ♀ (paralectotype), e. 16 Jun 1908 [e. = emerged], 1 ♀ (lectotype), 1 ♀ (paralectotype), 20 Jun 1908, 1 ♀ (paralectotype), 21 Jun 1908, G.R. Pilate, B.311, willow (ANSP); 1 ♀ (paralectotype), e. 24 Jun 1908, G.R. Pilate, USNM slide 17966 (USNM). Mills College: 1 ♂ (paralectotype), e. 18 May 1908; 1 ♀ (paralectotype), e. 21 Jun 1908, G.R. Pilate, B.311, willow (USNM). San Luis Obispo Co., Dune Lakes, 3 mi [4.8 km] S. Oceano: 1 ♂, 1 ♀, 24 Aug 1973, e. 7–11 Sep 1973, J. Powell 73H23, ex *Salix* (DLW). San Mateo Co., near Pacifica: 2 ♀, 1 Sep 1980, e. 14 Sep 1980, D.L. Wag-

ner, JAP 8012, ex *Salix*, slide DRD 3747 (DLW). Sonoma Co., Bodega Marine Lab: 1 ♂, 30 Jun 1982, e. 12 Jul 1982, D.L. Wagner, JAP 82F131, ex *Salix* (DLW). WASHINGTON: Skamania Co., Mt. St. Helens, Bear Meadow, 1800 m: 2 ♂, 2 ♀, mine: 21 Jul 1986, e. larva 23 Jul–6 Aug 1986, G. Deschka, mine in *Salix sitchensis*, zucht nr. 1929B (GD). Whatcom Co., Lyman, 30 m: 4 ♂, 2 ♀, mine: 14 Jul 1986, e. larva 17–26 Jul 1986, G. Deschka, mine in *Salix lasiandra*, zucht nr. 1917; slide GD 2150 (GD).

REMARKS.—This strikingly marked species differs in wing pattern from all other *Phyllonorycter*. The forewing pattern is unusual in lacking any indication of the white streaks and striae, basally margined with black scales, so characteristic of most species of *Phyllonorycter*. Male genital features, particularly the asymmetrical valvae, indicate nearest affinity is to *P. scudderella*. Differences of the genitalia between the two species are discussed under *P. scudderella*. The pupae of *P. apicinigrella* and *P. scudderella* are distinct among the *Phyllonorycter*-mining Salicaceae by the absence of an accessory cremaster on the sternum of A7.

Although not stated by Braun, the type series was found to consist of one male and six females from Alameda County, California, and two males from Seattle, Washington. The latter two specimens possess a typical *Phyllonorycter* wing pattern and are not believed to be conspecific with the series from Alameda County. Unfortunately, because both males are lacking abdomens, specific identification is not possible at present.

Catalog of the Palearctic *Phyllonorycter* Leafminers on Salicaceae

Phyllonorycter Hübner, 1822

Lithocolletis Hübner, 1825

Eucestis Hübner, 1825

1. *apparella* (Herrich-Schäffer, 1855:5:33) (*Lithocolletis*).
Figures 359–361.
Type locality: GERMANY: Frankfurt am Main.
=*atomariella* (Zeller, 1875:350) (*Lithocolletis*), new synonymy.
Type locality: UNITED STATES: Cambridge, Massachusetts.
=*ontario* (Freeman, 1970:273) (*Lithocolletis*), new synonymy.
Type locality: CANADA: Simcoe, Ontario.
=*tremuloidiella* (Braun, 1908b:317) (*Lithocolletis*), new synonymy.
Type locality: CANADA: Kaslo, British Columbia.
Distribution: AUSTRIA (Hauder, 1912:256, misidentification; Hoffmann and Klos, 1929:296, misidentification; Klimesch, 1961:743, misidentification; Hartig, 1964:193; Buszko, 1996:51, misidentification). BELGIUM (Staudinger and Rebel, 1901:216; Spuler, 1910:418; Lhomme, 1963:1032; Leraut, 1980:62; Buszko, 1996:51). CENTRAL ASIA (Puplesis et al., 1996:197). CZECH REPUBLIC: Bohemia (Sterneck and Zimmermann, 1933:134, ?misidentification; Buszko, 1996:51, ?misidentification). DENMARK (Schnack, 1985:51; Buszko, 1996:51). ESTONIA (Buszko, 1996:51). EUROPE (north and central) (E.M. Hering, 1957:807). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:51). FRANCE (Le Marchand, 1936:31; Lhomme, 1963:1032; Leraut, 1980:62; Buszko, 1996:51). GERMANY (Herrich-Schäffer, 1855:334; Heinemann and Wocke, 1877:694; Reutti, 1898:277; Staudinger and Rebel, 1901:216; Spuler, 1910:418; Petry, Beer, and Hockemeyer, 1936:195; Buszko, 1996:51). HUNGARY (Buszko, 1996:51, misidentification). ITALY (Buszko, 1996:51, ?misidentification). LATVIA (Buszko, 1996:51). LITHUANIA (Buszko, 1996:51). NORWAY (Buszko, 1996:51). POLAND (Buszko, 1987:640, 1990:414, 1996:51). SLOVAKIA (Hruby, 1964:209, ?misidentification; Buszko, 1996:51, ?misidentification). SWEDEN (Svensson et al., 1987:355; Buszko, 1996:51). SWITZERLAND (Buszko, 1996:51, misidentification).
Hosts: *Populus alba* Linnaeus, (Reutti, 1898:277, ?misidentification; Le Marchand, 1936:31; Lhomme, 1963:1032, ?misidentification); *P. nigra* Linnaeus, (Hauder, 1912:256, misidentification; Le Marchand, 1936:31; Petry, Beer, and Hockemeyer, 1936:195; Klimesch, 1961:743, misidentification; Lhomme, 1963:1032; Hartig, 1964:193, misidentification; Buszko, 1990:415; Kuznetsov and Baryshnikova, 1998:30); *P. pyramidalis* Salisbury, (Kuznetsov and Baryshnikova, 1998:30); *P. tremula* Linnaeus, (E.M. Hering, 1957:807; Lhomme, 1963:1032; Kuznetsov and Baryshnikova, 1998:30). *Salix alba* Linnaeus (Kuznetsov and Baryshnikova, 1998:30); *Salix* sp. (Staudinger and Rebel, 1901:216; Klimesch, 1961:743, misidentification; Hruby, 1964:209, ?misidentification).
2. *armeniella* (Kuznetsov, 1958:53) (*Lithocolletis*).
Figures 362–364.
Type locality: ARMENIA.
Distribution: ARMENIA (Kuznetsov, 1958:53). TURKEY (Gümüşhane) (Deschka, new record).
Host: *Salix* sp. (narrow-leaved) (Kuznetsov, 1958:53; Deschka, new record).
asiatica (Gerasimov, 1931). Synonym of *connexella*.
atomariella (Zeller, 1875). Synonym of *apparella*.
brevilineatella (Benander, 1944). Synonym of *salicicolella*.
capreella (Nicelli, 1851). Synonym of *salicicolella*.
cerrutiella (Hartig, 1952). Synonym of *comparella*.
3. *chiclanella* (Staudinger, 1859:256) (*Lithocolletis*).
Figures 371–373.
Type locality: SPAIN (southern): Chiclana.
Distribution: IBERIAN PENINSULA (Vives Moreno, 1994:54). SPAIN (Staudinger and Rebel, 1901:216; Spuler, 1910:418; E.M. Hering, 1957:806; Buszko, 1996:5); Chiclana (Stainton, 1869:142); Malaga (Deschka).
Host: *Populus alba* Linnaeus, (Stainton, 1869:142; Staudinger and Rebel, 1901:216; Spuler, 1910:418; E.M. Hering, 1957:806; Deschka).
4. *comparella* (Duponchel, 1843:318) (*Elachista*).
Figures 365–370.
Type locality: FRANCE.

=*cerrutiella* (Hartig, 1952:1) (*Lithocolletis*). Synonym of *comparella*.

Type locality: ITALY: Riofreddo, Lazio.

Distribution: AUSTRIA (Zeller, 1846:257; Frey, 1856:367; Hauder, 1912:256; Hoffmann and Klos, 1929:296; Klimesch, 1961:743, 1990:151; Hartig, 1964:194; Issekutz, 1972:88; Buszko, 1996:52; Deschka). BELGIUM (Lhomme, 1963:1033; Leraut, 1980:62; Buszko, 1996:52). BULGARIA (Buszko, 1996:52). CENTRAL ASIA (Puplesis et al., 1996:195). CZECH REPUBLIC: Bohemia (Nickerl, 1908:107; Sterneck and Zimmermann, 1933:134; Buszko, 1996:52), Moravia (Skala, 1912:221). EUROPE (central and south) (Spuler, 1910:418; Meyrick, 1927:781; E.M. Hering, 1957:806). FRANCE (Le Marchand, 1936:31; Lhomme, 1963:1033; Leraut, 1980:62; Buszko, 1996:52; Deschka); Corsica (Buszko, 1996:52), GERMANY (Zeller, 1846:257; Frey, 1856:367; Sorhagen, 1886:288; Reutti, 1898:277; Petry, Beer, and Hockemeyer, 1936:195; Buszko, 1996:52). HUNGARY (Buszko, 1996:52). IBERIAN PENINSULA (Vives Moreno, 1994:54). ITALY (Frey, 1856:367; Stainton, 1869:352; Staudinger and Rebel, 1901:216; Gianelli, 1910:112; Spuler, 1910:418; Hartig, 1964:194; Triberti, 1979:270; Buszko, 1996:52); Sardinia (Buszko, 1996:52); Sicily (Buszko, 1996:52). LATVIA (Buszko, 1996:52). LITHUANIA (Buszko, 1996:52). NETHERLANDS (Kuchlein, 1987:17; Buszko, 1996:52). POLAND (Buszko, 1990:412, 1996:52; Deschka). ROMANIA (Buszko, 1996:52). SLOVAKIA (Hruby, 1964:209; Buszko, 1996:52). SPAIN (Buszko, 1996:52). SWITZERLAND (Frey, 1856:367; Reutti, 1898:277; Vorbrod and Müller-Rutz, 1914:534; Buszko, 1996:52). TURKISTAN (Spuler, 1910:418; Meyrick, 1927:781; Watkinson, 1985:359). UNITED KINGDOM (Stainton, 1854:282, 1859:423; Frey, 1856:367; Meyrick, 1927:781; Ford, 1949:161; Kloet and Hincks, 1972:10; Watkinson, 1985:359; Buszko, 1996:52). UZBEKISTAN: (Samarkand, Bukhara) (Staudinger and Rebel, 1901:216).

Hosts: *Populus alba* Linnaeus, (Stainton, 1854:282; Heinemann and Wocke, 1877:695; Sorhagen, 1886:288; Reutti, 1898:277; Nickerl, 1908:107; Gianelli, 1910:112; Spuler, 1910:418; Hauder, 1912:256; Skala, 1912:221; Vorbrod and Müller-Rutz, 1914:534; Meyrick, 1927:781; M. Hering, 1932:76; Le Marchand, 1936:31; Petry, Beer, and Hockemeyer, 1936:195; Ford, 1949:161; Klimesch, 1951:51, 1961:743, 1990:151; E.M. Hering, 1957:806; Lhomme, 1963:1033; Hartig, 1964:194; Hruby, 1964:209; Triberti, 1979:270; Watkinson, 1985:359; Buszko, 1990:415; Deschka); *P. x canescens* (Aiton) J.E. Smith, (Watkinson, 1985:359; Buszko, 1990:415; Kuznetsov and Baryshnikova, 1998:31); *P. nigra* Linnaeus, (Sorhagen, 1886:288; Hauder, 1912:256; Skala, 1912:221; Meyrick, 1927:781; M. Hering, 1932:76; Ford, 1949:161; Lhomme, 1963:1033; Klimesch,

1990:151; Kuznetsov and Baryshnikova, 1998:31); *P. pyramidalis* Salisbury (Kuznetsov and Baryshnikova, 1998:31); *P. tremula* Linnaeus, (Deschka). ?*Pyrus malus* Linnaeus, (= *Malus domestica* Borkhausen) (Sorhagen, 1886:288).

5. *connexella* (Zeller, 1846:226) (*Lithocolletis*).

Figures 400–403.

Type locality: POLAND: Glogau (=Glogow).

=*asiatica* (Gerasimov, 1931:130) (*Lithocolletis*). Synonym of *connexella*. (Puplesis et al., 1996:196).

Type locality: UZBEKISTAN: Staraja Buchara (Bukhara, Baga-Absal).

Distribution: AUSTRIA (Zeller, 1846:226; Herrich-Schäffer, 1855:330; Staudinger and Rebel, 1901:214; Spuler, 1910:416–417; Hauder, 1912:252; Klimesch, 1961:741, 1990:147–148; Hartig, 1964:189; Kasy, 1965:200; Buszko, 1996:52). BELGIUM (Leraut, 1980:62). CROATIA: Dalmatia (Staudinger and Rebel, 1901:214; Spuler, 1910:416). CZECH REPUBLIC: Bohemia (Zeller, 1846; Nickerl, 1908:105; Sterneck and Zimmermann, 1933:134; Buszko, 1996:52). DENMARK (Karlsholt and Nielsen, 1976:24; Schnack, 1985:51; Buszko, 1996:52). ESTONIA (Buszko, 1996:52). EUROPE (central and southeast) (E.M. Hering, 1957:806). EUROPE (eastern) (E.M. Hering, 1957:921; Buszko, 1996:52). FINLAND (Varis, Jälava, and Kyrki, 1987:55; Buszko, 1996:52). FRANCE (Le Marchand, 1936:29; Lhomme, 1963:1029; Leraut, 1980:62; Buszko, 1996:52). GERMANY (Nicelli, 1851:41–42; Sorhagen, 1886:279; Reutti, 1898:274; Stange, 1899:59; Staudinger and Rebel, 1901:214; Spuler, 1910:416; M. Hering, 1932:73; Buszko, 1996:52). HUNGARY (Buszko, 1996:52). ITALY (Klimesch, 1951:50; Hartig, 1964:189; Buszko, 1996:52). LATVIA (Buszko, 1996:52). LITHUANIA (Buszko, 1996:52). NETHERLANDS (Staudinger and Rebel, 1901:214; Spuler, 1910:416; Kuchlein, 1987:17; Buszko, 1996:52). NORWAY (Buszko, 1996:52). POLAND (Herrich-Schäffer, 1855:330; Buszko, 1990:413, 1996:52). RUSSIA (Minusinsk, Jenisej Gouv. (Gerasimov, 1931:130; E.M. Hering, 1957:806). SLOVAKIA (Hruby, 1964:206; Buszko, 1996:52). SWEDEN (Svensson et al., 1987:no 352, leg. Svensson, in coll. Deschka). SWITZERLAND (Staudinger and Rebel, 1901:214; Vorbrod and Müller-Rutz, 1914:532; Buszko, 1996:52). TAJIKISTAN (Noreika and Puplesis, 1992a:39, 1992b:136). TURKMENISTAN (Noreika, 1991:438; Puplesis and Noreika, 1993:56 (as *P. asiatica*)). UZBEKISTAN: Bukhara (Bukhara, Baga-Absal) (Gerasimov, 1931:130, 1932:234; E.M. Hering, 1957:806; Noreika and Puplesis, 1992a:39).

Hosts: *Populus alba* Linnaeus, (Sorhagen, 1886:279; Reutti, 1898:274); *P. x berolinensis* L. Dippel, (Buszko, 1990:413); *P. canadensis* Moench, (Buszko, 1990:413; Klimesch, 1990:147–148; Deschka); *P. nigra* Linnaeus,

(Sorhagen, 1886:279; Reutti, 1898:274; Stange, 1899:59; Staudinger and Rebel, 1901:214; Gerasimov, 1932:235; Le Marchand, 1936:29; Lhomme, 1963:1029; Hruby, 1964:206; Buszko, 1990:413; Klimesch, 1990:147–148; Kuznetsov and Baryshnikova, 1998:31); *Populus* sp. (Nickerl, 1908:105; Spuler, 1910:416–417; M. Hering, 1932:73; E.M. Hering, 1957:921). *Salix alba* Linnaeus, (Heinemann and Wocke, 1877:677; Sorhagen, 1886:279; Reutti, 1898:274; Staudinger and Rebel, 1901:214; Hauder, 1912:252; Gerasimov, 1932:235; Le Marchand, 1936:29; Klimesch, 1961:741, 1990:147–148; Lhomme, 1963:1029; Hartig, 1964:189; Hruby, 1964:206; Buszko, 1990:413; Kuznetsov and Baryshnikova, 1998:31); *S. appendiculata* D. Villars, (Deschka); *S. babylonica* Linnaeus, (Reutti, 1898:274); *S. blakii* R. Goerz, (Noreika and Puplesis, 1992a:39); *S. fragilis* Linnaeus, (Heinemann and Wocke, 1877:677–678; Sorhagen, 1886:279; Reutti, 1898:274; Staudinger and Rebel 1901:214; Gerasimov, 1932:235; Le Marchand, 1936:29; Lhomme, 1963:1029; Hruby, 1964:202; Buszko, 1990:413; Kuznetsov and Baryshnikova, 1998:31); *S. pentandra* Linnaeus, (Stange, 1899:58); *S. purpurea* Linnaeus, (Klimesch, 1951:50; 1990:147–148; Deschka); *S. viminalis* Linnaeus, (Buszko, 1990:413); *Salix* sp. (narrow-leaved), rare on broad-leaved *Salix* (many authors).

6. *crocinella* (Sorhagen, 1900:212) (*Lithocolletis*). Nomem dubium.

Type locality: GERMANY: Eppendorfer Moor, SW of Dresden.

Distribution: GERMANY (Sorhagen, 1900:212).

Host: *Salix alba* Linnaeus, (Sorhagen, 1900:212; E.M. Hering, 1957:921).

Remarks: The identity of this species remains questionable. No type material of *crocinella* is known to exist, and no further collections have been authenticated since it was described (Buszko, 1992). Although it was originally reported as a leafminer on *Salix*, Spuler (1910) considered it only as a form of *P. kleemannella* (Fabricius), which mines the leaves of *Alnus*.

7. *dentifera* (Noreika in Noreika and Duplesis, 1992a:39) (*Lithocolletis*).

Figures 394–396.

Type locality: TAJIKISTAN (southern): 20 km S of Dzhi-likul.

Distribution: CENTRAL ASIA (Puplesis et al., 1996:196). TAJIKISTAN (southern), TURKMENISTAN (Noreika and Puplesis, 1992a:39).

Host: *Populus pruinosa* Schrenk, (Noreika and Puplesis, 1992a:39; Kuznetsov and Baryshnikova, 1998:33).

8. *dubitella* (Herrick-Schäffer, 1855:325) (*Lithocolletis*). Figures 417–419.

Type locality: GERMANY: Regensburg.

=*spinicolella* (Herrick-Schäffer 1855:782) (*Lithocolletis*).
Synonym of *dubitella*.

Type locality: GERMANY: Regensburg.

Distribution: AUSTRIA (Frey, 1856:346; Staudinger and Rebel, 1901:212; Mitterberger, 1909:293; Spuler, 1910:414; Hauder, 1912:252; Hoffmann and Klos, 1929:294; Klimesch, 1961:737, 1990:136; Hartig, 1964:182; Buszko, 1996:52). BELGIUM (Leraut, 1980:62; Buszko, 1996:52). BULGARIA (Buszko, 1996:52). CROATIA: Dalmatia (Staudinger and Rebel, 1901:212; Spuler, 1910:414; Klimesch, 1961:737). CZECH REPUBLIC: Bohemia (Nickerl, 1908:102; Sterneck and Zimmermann, 1933:132), Bohemia and Moravia (Buszko, 1996:52). DENMARK (Karlsholt and Nielsen, 1976:23; Schnack, 1985:50; Buszko, 1996:52). EUROPE (central and north) (E.M. Hering, 1957:921; Watkinson, 1985:332). EUROPE (eastern) (Buszko, 1996:52). FINLAND (Varis, Jalava, and Kyri, 1987:55; Buszko, 1996:52). FRANCE (Staudinger and Rebel, 1901:212; Le Marchand, 1936:18–19; Lhomme, 1963:1014; Leraut, 1980:62; Buszko, 1996:52). GERMANY (Herrick-Schäffer, 1855:325; Frey, 1856:346–348; Sorhagen, 1886:277–278; Reutti, 1898:273; Stange, 1899:58; Staudinger and Rebel, 1901:212; Spuler, 1910:414; M. Hering, 1932:75; Petry, Beer, and Hockemeyer, 1936:190; Buszko, 1996:52). HUNGARY (Buszko, 1996:52). ITALY (Buszko, 1996:52; Deschka). LATVIA (Buszko, 1996:52). LITHUANIA (Buszko, 1996:52). NETHERLANDS (Kuchlein, 1987:17; Buszko, 1996:52). NORWAY (Buszko, 1996:52). POLAND (Buszko, 1990:407, 1996:52). SLOVAKIA (Hruby, 1964:202; Buszko, 1996:52). SWEDEN (Svensson et al., 1987: no322; Buszko, 1996:52). SWITZERLAND (Frey, 1856:346; Staudinger and Rebel, 1901:212; Spuler, 1910:414; Vorbrodt and Müller-Rutz, 1914:529; Buszko, 1996:52). UNITED KINGDOM (Le Marchand, 1936:18–19; Kloet and Hincks, 1972:10; Watkinson, 1985:332; Buszko, 1996:52).

Hosts: *Salix alba* Linnaeus, (Klimesch, 1990:136); *S. aurita* Linnaeus, (Hartig, 1964:182; Deschka); *S. caprea* Linnaeus, (Herrick-Schäffer, 1855:325; Frey, 1856:346; Heinemann and Wocke, 1877:672; Reutti, 1898:273; Stange, 1899:58; Staudinger and Rebel, 1901:212; Nickerl, 1908:102; Mitterberger, 1909:293; Spuler, 1910:414; Hauder, 1912:252; Le Marchand, 1936:18; Petry, Beer, and Hockemeyer, 1936:190; Klimesch, 1961:737, 1990:136; Lhomme, 1963:1014; Hartig, 1964:182; Hruby, 1964:202; Watkinson, 1985:331; Buszko, 1990:407; Kuznetsov and Baryshnikova, 1998:33); *S. cinerea* Linnaeus, (Petry, Beer, and Hockemeyer, 1936:190; Klimesch, 1990:136); *S. fragilis* Linnaeus, (Petry, Beer, and Hockemeyer, 1936:190).

eophanes (Meyrick, 1931). New synonym of *iteina fainae* (Gerasimov, 1931). Synonym of *pastorella*.

9. *graeseriella* (Sorhagen, 1900:212) (*Lithocolletis*). Nomen dubium.

Type locality: GERMANY: Eppendorfer Moor, W of Dresden.

Distribution: GERMANY: Hamburg (Staudinger and Rebel, 1901:212; Spuler, 1910:414; E.M. Hering, 1957:920).

Host: *Salix repens* Linnaeus, (Sorhagen, 1900:213; Staudinger and Rebel, 1901:212; Spuler, 1910:414; M. Hering, 1932:72; E.M. Hering, 1957:920).

Remarks: The identity of this species remains questionable. No type material of *graeseriella* is known to exist, and no further collections have been authenticated since it was described.

groenlieni (M. Hering, 1926). Synonym of *hilarella*.
heringiella (Grønlien, 1932). Synonym of *salictella*.

10. *hilarella* (Zetterstedt, 1839:1010) (*Elachista*).

Figures 408–410.

Type locality: SWEDEN: Umea, Lappmark.

=*spinolella* (Duponchel, 1840:535) (*Elachista*). Synonym of *hilarella*.

Type locality: FRANCE.

=*groenlieni* (M. Hering, 1926:468) (*Lithocolletis*). Synonym of *hilarella*.

Type locality: NORWAY: Odda.

Distribution: AUSTRIA (Mitterberger, 1909:293; Hauder, 1912:251; Hoffmann and Klos, 1929:294; Klimesch, 1961:736, 1990:137; Buszko, 1996:52). BELGIUM (Lhomme, 1963:1016; Leraut, 1980:62; Buszko, 1996:52). CZECH REPUBLIC: Bohemia (Nickerl, 1908:101; Sterneck and Zimmermann, 1933:132), Bohemia and Moravia (Buszko, 1996:52), Moravia (Skala, 1912:219). DENMARK (Karlsholt and Nielsen, 1976:23; Schnack, 1985:50; Buszko, 1996:52). ESTONIA (Buszko, 1996:52). EUROPE (central and north) (Meyrick, 1927:777; E.M. Hering, 1957:920). EUROPE (central and south) (Staudinger and Rebel, 1901:212). EUROPE (eastern) (Buszko, 1996:52). FINLAND (Buszko, 1996:52). FRANCE (Frey, 1856:348; Le Marchand, 1936:21; Lhomme, 1963:1016; Leraut, 1980:62; Buszko, 1996:52). GERMANY (Nicelli, 1851:42; Herrich-Schäffer, 1855:330; Frey, 1856:348; Sorhagen, 1886:280; Reutti, 1898:275; Stange, 1899:58; M. Hering, 1932:72; Petry, Beer, and Hockemeyer, 1936:189; Buszko, 1996:52). HUNGARY (Buszko, 1996:52). IBERIAN PENINSULA (Vives Moreno, 1994:54). IRELAND (Buszko, 1996:52). ITALY (Klimesch, 1951:48; Hartig, 1964:131; Buszko, 1996:52). LATVIA (Buszko, 1996:52). LITHUANIA (Buszko, 1996:52). NETHERLANDS (Kuchlein, 1987:17; Buszko, 1996:52). NORWAY (M. Hering, 1926:468; Buszko, 1996:52). POLAND (Nicelli, 1851:42–44; Buszko, 1996:52). PORTUGAL (Buszko, 1996:52). ROMANIA (Buszko, 1996:52). SCANDINAVIA (E.M. Hering, 1957:921, as *grönlieni*). SLOVAKIA (Hruby, 1964:201; Buszko,

1996:52). SPAIN (Buszko, 1996:52). SWEDEN (Svensson et al., 1987:no 323 (as *hilarella*); Buszko, 1996:52). SWITZERLAND (Frey, 1856:348; Reutti, 1898:275; Vorbrodt and Müller-Rutz, 1914:528; Buszko, 1996:52). UNITED KINGDOM (Stainton, 1854:273, 1859:417; Frey, 1856:348; Meyrick, 1927:777; Ford, 1949:161; Kloet and Hincks, 1972:10; Watkinson, 1985:332; Buszko, 1996:52).

Hosts: *Alnus* sp. (M. Hering, 1926:468–470 (as *grönlieni*, rare)). *Populus tremula* Linnaeus, (Svensson, 1966:191, rare). *Salix appendiculata* D. Villars, (Klimesch, 1961:736); *S. arbuscula* complex, (Klimesch, 1961:736, 1990:137); *S. aurita* Linnaeus, (Sorhagen, 1886:280; Le Marchand, 1936:21; E.M. Hering, 1957:921; Lhomme, 1963:1016; Hartig, 1964:181; Svensson, 1966:191; Klimesch, 1990:137; Kuznetsov and Baryshnikova, 1998:35); *S. caprea* Linnaeus, (Frey, 1856:348; Heineemann and Wocke, 1877:680; Sorhagen, 1886:280; Reutti, 1898:275; Stange, 1899:58; Staudinger and Rebel, 1901:212; Nickerl, 1908:101; Mitterberger, 1909:293; Spuler, 1910:414; Hauder, 1912:251; Skala, 1912:219; Vorbrodt and Müller-Rutz, 1914:528; Meyrick, 1927:777; Le Marchand, 1936:21; Petry, Beer, and Hockemeyer, 1936:189; Ford, 1949:161; Klimesch, 1951:48, 1961:736; E.M. Hering, 1957:921; Lhomme, 1963:1016; Hartig, 1964:181; Hruby, 1964:201; Svensson, 1966:191; Watkinson, 1985:332; Klimesch, 1990:137; Kuznetsov and Baryshnikova, 1998:35); *S. cinerea* Linnaeus, (Sorhagen, 1886:280; Le Marchand, 1936:21; E.M. Hering, 1957:921; Lhomme, 1963:1016; Svensson, 1966:191; Kuznetsov and Baryshnikova, 1998:35); *S. fragilis* Linnaeus, (Svensson, 1966:191 (as *S. grönlieni*)); *S. hastata* Linnaeus, (Petry, Beer, and Hockemeyer, 1936:189); *S. pentandra* Linnaeus, (Deschka, new record); *S. silesiaca* Willdenow, (Heineemann and Wocke, 1877:680).

11. *iteina* (Meyrick, 1918:173) (*Lithocolletis*).

Figures 386–389.

Type locality: INDIA: Pusa, Bengal.

=*eophanes* (Meyrick, 1931:46) (*Lithocolletis*). New synonymy.

Type locality: INDIA: Mahableswar, Bombay.

Distribution: INDIA: Bengal, Bombay.

Host: *Salix* sp. (Meyrick, 1918:173); *S. tetrasperma* Roxburgh, (Meyrick, 1931:46).

jaeckhi (M. Hering, 1934:70) (*Lithocolletis*). Synonym of *salictella*.

12. *pastorella* (Zeller, 1846:250) (*Lithocolletis*).

Figures 332–334, 383–385.

Type locality: GERMANY: Frankfurt.

=*fainae* (Gerasimov, 1932:240) (*Lithocolletis*). Synonym of *pastorella*.

Type locality: UZBEKISTAN: Novyi (Novyy) Urgench.

Distribution: AUSTRIA (Hauder, 1912:256; Hoffmann and Klos, 1929:296; Klimesch, 1961:742, 1990:148; Issekutz, 1972:88; Buszko, 1996:53). BELGIUM (Staudinger and Rebel, 1901:216; Spuler, 1910:418; Lhomme, 1963:1031; Leraut, 1980:62; Buszko, 1996:53). BULGARIA (Buszko, 1996:53). CENTRAL ASIA (Puplesis et al., 1996:196). CHINA: Beijing (Deschka). CZECH REPUBLIC: Bohemia (Zeller, 1846:250; Nickerl, 1908:107; Sterneck and Zimmermann, 1933:134), Bohemia and Moravia (Buszko, 1996:53). EUROPE (central and north) (E.M. Hering, 1957:922). EUROPE (eastern) (Buszko, 1996:53). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). FRANCE (Le Marchand, 1936:30; Lhomme, 1963:1031; Leraut, 1980:62; Buszko, 1996:53). GERMANY (Zeller, 1846:250; Nicelli, 1851:50; Heinemann and Wocke, 1877:693; Sorhagen, 1886:287; Reutti, 1898:277; Staudinger and Rebel, 1901:216; Spuler, 1910:418; Petry, Beer, and Hockemeyer, 1936:195; Buszko, 1996:53). HUNGARY (Buszko, 1996:53). IBERIAN PENINSULA (Vives Moreno, 1994:54). ITALY (Gianelli, 1910:111; Buszko, 1996:53). JAPAN (Kumata, 1963:54; Noreika and Puplesis, 1992a:37). KAZAKHSTAN (Puplesis et al., 1992:60). KIRGIZIYA (Noreika and Puplesis, 1992a:37). KOREA (Kumata, Kuroko, and Park, 1983:217; Noreika and Puplesis, 1992a:37). LATVIA (Buszko, 1996:53). LITHUANIA (Buszko, 1996:53). NETHERLANDS (Staudinger and Rebel, 1901:216; Spuler, 1910:418; Kuchlein, 1987:17; Buszko, 1996:53). NORWAY (Staudinger and Rebel, 1901:216; Spuler, 1910:418). POLAND (Herrich-Schäffer, 1855:334; Buszko, 1990:414, 1996:53). ROMANIA (Draghia, 1966: 119; Buszko, 1996:53). SLOVAKIA (Hruby, 1964:208; Buszko, 1996:53). SPAIN (Buszko, 1996:53). SWEDEN (Svensson et al., 1987:no 353). SWITZERLAND (Buszko, 1996:53). TAJIKISTAN (Noreika and Puplesis, 1992a:37). TURKMENISTAN (Kuznetsov, 1960:27; Noreika, 1991:436; Noreika and Puplesis, 1992a:37). YUGOSLAVIA (Buszko, 1996:53).
 Hosts: *Chosenia arbutifolia* A. Skvortz, (Kumata, Kuroko, and Park, 1983:217; Kuznetsov and Baryshnikova, 1998:42). *Populus koreana* Rehder, (Kuznetsov and Baryshnikova, 1998:42); *P. laurifolia* von Ledebour, (Kuznetsov and Baryshnikova, 1998:42); *P. nigra* Linnaeus, (Kumata, 1963:54; Kuznetsov and Baryshnikova, 1998:42); *P. sieboldi* Miquel, (Kumata, 1963:54; Kuznetsov and Baryshnikova, 1998:42); *P. tremula* Linnaeus, (Kuznetsov and Baryshnikova, 1998:42). *Salix alba* Linnaeus, (Sorhagen, 1886:287; Nickerl, 1908:107; Hauder, 1912:256; Petry, Beer, and Hockemeyer, 1936:195; Klimesch, 1961:742, 1990:148; Lhomme, 1963:1031; Hruby, 1964:208; Buszko, 1990:414; Deschka); *S. babylonica* Linnaeus, (Kumata, 1963:54; Noreika and Puplesis, 1992a:37; Kuznetsov and Baryshnikova, 1998:42); *S. ca-*

prea Linnaeus, (Kuznetsov and Baryshnikova, 1998:42); *S. fragilis* Linnaeus, (Sorhagen, 1886:287; Spuler, 1910:418; Hauder, 1912:256; Klimesch, 1961:742; Lhomme, 1963:1031; Hruby, 1964:208; Buszko, 1990:414; Deschka); *S. purpurea* Linnaeus, (Sorhagen, 1886:287; Klimesch, 1961:742; Lhomme, 1963:1031); *S. raddeana* Laksch. ex Nasarov, (Kuznetsov and Baryshnikova, 1998:42); *S. triandra* Linnaeus, (Noreika and Puplesis, 1992a:37); *S. viminalis* Linnaeus, (Staudinger and Rebel, 1901:216; Nickerl, 1908:107; Gianelli, 1910:111; Spuler, 1910:418; Hauder, 1912:256; Klimesch, 1961:742; Hruby, 1964:208); *Salix* sp. (narrow-leaved) (Nicelli, 1851:50; Le Marchand, 1936:30; Kumata, 1963:54).

petrazzaniella (Costantini, 1923). Synonym of *populifoliella*.

13. *populi* (Filipjev, 1931:73) (*Lithocolletis*). Replacement name for *populiella* (Filipjev, 1926).

Figures 374–376.

Type locality: UZBEKISTAN: Staraja Buchara (= Bukhara).

=*populiella* (Filipjev, 1926:289). Homonym of *populiella* (Chambers, 1878:101).

Distribution: KAZAKHSTAN (south), TAJIKISTAN (Noreika and Puplesis, 1992a:35, 1992b:134). TURKMENISTAN (Noreika and Puplesis, 1992a:35). UZBEKISTAN (Noreika and Puplesis, 1992a:35).

Hosts: *Populus alba* Linnaeus, *P. nigra* Linnaeus, (Filipjev, 1926:289; Noreika and Puplesis, 1992a:35; Kuznetsov and Baryshnikova, 1998:42).

14. *populialbae* (Kuznetsov, 1961:229) (*Lithocolletis*).

Figures 391–393.

Type locality: AZERBAIJAN.

Distribution: RUSSIA: Caucasus (Kuznetsov, 1961:229).

Host: *Populus alba* Linnaeus, (Kuznetsov, 1961:229; Kuznetsov and Baryshnikova, 1998:42).

15. *populicola* (Kuznetsov, 1975:128) (*Lithocolletis*).

Figure 390.

Type locality: TAJIKISTAN.

Distribution: TAJIKISTAN (Kuznetsov, 1975:128; Noreika and Puplesis, 1992a:35, 1992b:136).

Hosts: *Populus afghanica* (Aitchison and Hemsley) C.K. Schneider, (Noreika and Puplesis, 1992a:35, 1992b:137); *P. tadshikistanica* Komarov, (Kuznetsov and Baryshnikova, 1998:43); *Populus* sp., (Kuznetsov, 1975:128–31).

16. *populifoliella* (Treitschke, 1833:188) (*Elachista*).

Figures 377–379.

Type locality: GERMANY: Dresden.

=*petrazzaniella* (Costantini, 1923:70) (*Lithocolletis*). Synonym of *populifoliella*.

Type locality: ITALY: Emilia, Bologna.

Distribution: AUSTRIA (Zeller, 1846:255; Staudinger and Rebel, 1901:216; Mitterberger, 1909:299; Spuler, 1910:418; Hauder, 1912:256; Hoffmann and Klos, 1929:296; Klimesch, 1961:742, 1990:151; Hartig, 1964:193; Kasy, 1965:200; Buszko, 1996:53). BELGIUM (Staudinger and Rebel, 1901:216; Spuler, 1910:418; Lhomme, 1963:1032; Buszko, 1996:53). BULGARIA (Buszko, 1996:53). CENTRAL ASIA (Noreika and Puplesis, 1992b:134). CROATIA: Dalmatia (Stainton, 1869:352). CZECH REPUBLIC: Bohemia (Nickerl, 1908:107; Sterneck and Zimmermann, 1933:134), Bohemia and Moravia (Buszko, 1996:53), Moravia (Skala, 1912:221). DENMARK (Staudinger and Rebel, 1901:216; Spuler, 1910:418; Karsholt and Nielsen, 1976:24; Schnack, 1985:51; Buszko, 1996:53). ESTONIA (Buszko, 1996:53). EUROPE (E.M. Hering, 1957:807). EUROPE (eastern) (Buszko, 1996:53). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). FRANCE (Le Marchand, 1936:30; Lhomme, 1963:1032; Leraut, 1980:62; Buszko, 1996:53), Corsica (Buszko, 1996:53). GERMANY (Zeller, 1846:255; Nicelli, 1851:51; Herrich-Schäffer, 1855:334; Frey, 1856:366; Heinemann and Wocke, 1877:694; Sorhagen, 1886:287; Reutti, 1898:277; Staudinger and Rebel, 1901:216; Spuler, 1910:418; Petry, Beer, and Hockemeyer, 1936:195; Buszko, 1996:53). HUNGARY (Buszko, 1996:53). IBERIAN PENINSULA (Staudinger and Rebel, 1901:216; Vives Moreno, 1994:54). ITALY (Gianelli, 1910:112; Hartig, 1964:193; Triberti, 1979:271; Buszko, 1996:53). KAZAKHSTAN (Gerasimov, 1932:242; Noreika and Puplesis, 1992a:33). LATVIA (Frey, 1856:366; Staudinger and Rebel, 1901:216; Spuler, 1910:418; Buszko, 1996:53). LITHUANIA (Buszko, 1996:53). NETHERLANDS (Staudinger and Rebel, 1901:216). NORWAY (Buszko, 1996:53). POLAND (Zeller, 1846:255; Buszko, 1990:415, 1996:53). ROMANIA (Buszko, 1996:53). RUSSIA (Caucasus, Ural), Western Siberia, northern part of Central Asia (Noreika and Puplesis, 1992b:134; Puplesis et al., 1996:196); Siberia (Deschka). SLOVAKIA (Hruby, 1964:208; Buszko, 1996:53). SPAIN (Buszko, 1996:53), Catalonia (Staudinger and Rebel, 1901:216; Spuler, 1910:418). SWEDEN (Staudinger and Rebel, 1901:216; Spuler, 1910:418; Svensson et al., 1987:no 356). SWITZERLAND (Frey, 1856:366; Heinemann and Wocke, 1877:694; Staudinger and Rebel, 1901:216; Spuler, 1910:418; Vorbrodt and Müller-Rutz, 1914:533; Buszko, 1996:53). TAJIKISTAN (Noreika and Puplesis, 1992a:33). TURKEY (Anatolia) (Deschka, new record). TURKMENISTAN (Noreika, 1991:438). UNITED KINGDOM (Stainton, 1854:273, 1859:417; Frey, 1856:348; Meyrick, 1927:777; Ford, 1949:161; Kloet and Hincks, 1972:10; Watkinson, 1985:332; Buszko, 1996:52). YUGOSLAVIA (Buszko, 1996:53).
 Hosts: *Populus alba* Linnaeus, (Kuznetsov and Baryshnikova, 1998:43); *P. balsamifera* Linnaeus, (Noreika and Puplesis, 1992a:33); *P. x berlinensis* Dippel, (Buszko,

1990:415); *P. x canadensis* auct. mult., (Zeller, 1846:255; Frey, 1856:366; Sorhagen, 1886:287; Staudinger and Rebel, 1901:216; Gianelli, 1910:112; Spuler, 1910:418; Hoffmann and Klos, 1929:296; Klimesch, 1961:742; Lhomme, 1963:1032; Buszko, 1990:415; Deschka); *P. deltooides* Marshall, (Hruby, 1964:208); *P. laurifolia* von Ledebour, (Noreika and Puplesis, 1992a:33; Kuznetsov and Baryshnikova, 1998:43); *P. monilifera* Aiton, (Le Marchand, 1936:30); *P. nigra* Linnaeus, (Nicelli, 1851:51; Herrich-Schäffer, 1855:334; Frey, 1856:366; Sorhagen, 1886:287; Staudinger and Rebel, 1901:216; Nickerl, 1908:107; Gianelli, 1910:112; Spuler, 1910:418; Skala, 1912:221; Hoffmann and Klos, 1929:296; M. Hering, 1932:76; Le Marchand, 1936:30; Petry, Beer, and Hockemeyer, 1936:195; Klimesch, 1961:742, 1990:151; Lhomme, 1963:1032; Hartig, 1964:193; Hruby, 1964:208; Kasy, 1965:200; Triberti, 1979:271; Buszko, 1990:415; Noreika and Puplesis, 1992a:33; Kuznetsov and Baryshnikova, 1998:43); *P. tremula* Linnaeus, (Sorhagen, 1886:287; Nickerl, 1908:107; Le Marchand 1936:30; Lhomme, 1963:1032; Hruby, 1964:208; Noreika and Puplesis, 1992a:33; Kuznetsov and Baryshnikova, 1998:43); *Populus* sp., (Zeller, 1846:255; Frey, 1856:366; Heinemann and Wocke, 1877:694; Reutti, 1898:277; Hauder, 1912:256; E.M. Hering, 1957:807). *Salix* sp. (narrow-leaved), (E.M. Hering, 1957:807; Deschka).

17. *pruinosa* (Gerasimov, 1931:130) (*Lithocolletis*).

Figure 404.

Type locality: UZBEKISTAN: Buchara (Bukhara).

Distribution: CENTRAL ASIA (Puplesis et al., 1996:196). KAZAKHSTAN (Noreika, 1991:429; Noreika and Puplesis, 1992a:37). TAJIKISTAN (Noreika and Puplesis, 1992a:37, 1992b:136). TURKMENISTAN (Kuznetsov, 1960:27; Noreika, 1991:438; Noreika and Puplesis, 1992a:37). UZBEKISTAN (Bukhara, Chiva, and Novyi Urengich) (Gerasimov, 1931:130, 1932:227; E.M. Hering, 1957:919).

Hosts: *Populus diversifolia* Schrenk, (Kuznetsov and Baryshnikova, 1998:43); *P. euphratica* Oliver, (Kuznetsov and Baryshnikova, 1998:43); *P. pruinosa* Schrenk, (Gerasimov, 1931:130, 1932:227; Noreika and Puplesis, 1992a:37); *Populus* sp., (E.M. Hering, 1957:919). *Salix* sp., (Gerasimov, 1931:130; E.M. Hering, 1957:919; Kuznetsov and Baryshnikova, 1998:43; Noreika and Puplesis, 1992a:37).

18. *quinqueguttella* (Stainton, 1851:12) (*Lithocolletis*).

Figures 397–399.

Type locality: ENGLAND: Cumbria (=Cumberland).

=*repentella* (Sorhagen, 1900:232) (*Lithocolletis*). New synonymy.

Type locality: GERMANY: Eppendorfer Moor, SW of Dresden.

Distribution: AUSTRIA (Klimesch, 1961:739; Buszko, 1996:53; Deschka). BELGIUM (Lhomme, 1963:1013; Leraut, 1980:62; Buszko, 1996:53; Deschka). CZECH REPUBLIC: Bohemia and Moravia (Buszko, 1996:53). DENMARK (Lhomme, 1963:1013; Karsholt and Nielsen, 1976:24; Schnack, 1985:50; Buszko, 1996:53). EUROPE (eastern) (Buszko, 1996:53). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). FRANCE (Meyrick, 1927:776; Buszko, 1996:53). GERMANY (Sorghagen, 1886:282; Heinemann and Wocke, 1877:684; Reutti, 1898:275; Stange, 1899:59; Staudinger and Rebel, 1901:214; Spuler, 1910:416; M. Hering, 1932:74; Buszko, 1996:53). HUNGARY (Buszko, 1996:53; Deschka). IRELAND (Buszko, 1996:53). LATVIA (Buszko, 1996:53). LITHUANIA (Buszko, 1996:53). NETHERLANDS (Staudinger and Rebel, 1901:214; Spuler, 1910:416; Meyrick, 1927:776; Buszko, 1996:53). NORWAY (Buszko, 1996:53). POLAND (Buszko, 1990:409, 1996:53; Deschka). RUSSIA: Siberia (eastern) (Meyrick, 1927:776). SLOVAKIA (Buszko, 1996:53). SWEDEN (Svensson et al., 1987:no 334; Buszko, 1996:53). SWITZERLAND (Staudinger and Rebel, 1901:214; Spuler, 1910:416; Vorbrodt and Müller-Rutz, 1914:531; Meyrick, 1927:776; Buszko, 1996:53). UNITED KINGDOM (Stainton, 1854:268, 1859:419; Staudinger and Rebel, 1901:214; Spuler, 1910:416; Meyrick, 1927:776; Ford, 1949:160; Kloet and Hincks, 1972:10; Watkinson, 1985:342; Buszko, 1996:53).

Hosts: *Salix arenaria* Linnaeus, (Watkinson, 1985:343; Buszko, 1990:409); *S. repens* Linnaeus, (Stainton, 1859:419; Heinemann and Wocke, 1877:684; Sorhagen, 1886:282, 1900:212; Reutti, 1898:277; Staudinger and Rebel, 1901:214; Spuler, 1910:416; Vorbrodt and Müller-Rutz, 1914:531; Meyrick, 1927:776; M. Hering, 1932:74; Le Marchand, 1936:10; Ford, 1949:160; E.M. Hering, 1957:919; Klimesch, 1961:739; Lhomme, 1963:1013; Watkinson, 1985:343; Kuznetsov and Baryshnikova, 1998:44); *S. rosmarinifolia* Linnaeus, (Buszko, 1990:409; Deschka).

repentella (Sorghagen, 1900). Synonym of *quinqueguttella*.

19. *rolandi* (Svensson, 1966:191) (*Lithocolletis*).

Figures 411–413.

Type locality: SWEDEN: Kummavuopio.

Distribution: FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). NORWAY (Buszko, 1996:53). SWEDEN (Svensson, 1966:191; Svensson et al., 1987:no 324; Buszko, 1996:53).

Host: *Salix lapponum* Linnaeus, (Svensson, 1966:192; Kuznetsov and Baryshnikova, 1998:43).

20. *sagitella* (Bjerkander, 1790:132) (*Phalaena*).

Figures 380–382.

Type locality: Not stated.

=*tremulae* (Zeller, 1846:251) (*Lithocolletis*). Synonym of *sagitella*.

Type locality: GERMANY: Reichsstadt and Frankfurt am Main.

=*tremulella* (Herrich-Schäffer, 1855:334) (*Lithocolletis*). Synonym of *sagitella*.

Type locality: Not stated.

Distribution: AUSTRIA (Hauder, 1912:256; Hoffmann and Klos, 1929:296; Klimesch, 1961:743, 1990:150; Hartig, 1964:194; Issekutz, 1972:88; Buszko, 1996:53). BELGIUM (Lhomme, 1963:1032; Buszko, 1996:53). CZECH REPUBLIC: Bohemia (Frey, 1856:366; Nickerl 1908:107; Sterneck and Zimmermann, 1933:134), Bohemia and Moravia (Buszko, 1996:53), Moravia (Skala, 1912:221). DENMARK (Karsholt and Nielsen, 1985:24; Schnack, 1985:51; Buszko, 1996:53). ESTONIA (Buszko, 1996:53). EUROPE (central and north) (E.M. Hering, 1957:807). EUROPE (eastern) (Buszko, 1996:53). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). FRANCE (Le Marchand, 1936:30; Lhomme 1963:1032; Leraut, 1980:62; Buszko, 1996:53). GERMANY (Zeller, 1846:251; Nicelli, 1851:50; Frey, 1856:366; Heinemann and Wocke, 1877:695; Sorhagen, 1886:288; Reutti, 1898:277; Stange, 1899:60; Petry, Beer, and Hockemeyer, 1936:195; Buszko, 1996:53). HUNGARY (Buszko, 1996:53). ITALY (Klimesch, 1951:51; Hartig, 1964:194; Buszko, 1996:53; Deschka). LATVIA (Buszko, 1996:53). LITHUANIA (Buszko, 1996:53). NETHERLANDS (Kuchlein, 1987:17; Buszko, 1996:53). NORWAY (Buszko, 1996:53). POLAND (Zeller, 1846:251; Frey, 1856:366; Buszko, 1990:414, 1996:53). RUSSIA (Staudinger and Rebel, 1901:216; Spuler, 1910:418). SLOVAKIA (Hruby 1964:209; Buszko, 1996:53). SWEDEN (Svensson et al., 1987:354; Buszko, 1996:53). SWITZERLAND (Frey, 1856:366; Heinemann and Wocke, 1877:695; Spuler, 1910:418; Vorbrodt and Müller-Rutz, 1914:533; Buszko, 1996:53). UNITED KINGDOM (Buszko, 1996:53), England (south) (Watkinson, 1985:359).

Hosts: *Populus davidiana* Dode, (Kuznetsov and Baryshnikova, 1998:45); *P. nigra* Linnaeus, (Hruby, 1964:209 [?error]); *P. suaveolens* Fish. ex Loud., (Kuznetsov and Baryshnikova, 1998:45); *P. tremula* Linnaeus, (Zeller, 1846:251; Nicelli, 1851:50; Frey, 1856:366; Heinemann and Wocke, 1877:695; Sorhagen, 1886:288; Reutti, 1898:277; Staudinger and Rebel, 1901:216; Nickerl, 1908:107; Spuler, 1910:418; Vorbrodt and Müller-Rutz, 1911–1913:533; Hauder, 1912:256; Skala, 1912:221; Hoffmann and Klos, 1929:296; M. Hering, 1932:78; Le Marchand, 1936:30; Petry, Beer, and Hockemeyer, 1936:195; Klimesch, 1951:51, 1961:743, 1990:150; E.M. Hering, 1957:807; Lhomme, 1963:1032; Hartig, 1964:194;

Hruby, 1964:209; Issekutz, 1972:88; Watkinson, 1985:360; Kuznetsov and Baryshnikova, 1998:45; Buszko, 1990:414). "an Eschen" (= *Fraxinus* sp.) [error]. Recte "an Eспен" (= *Populus tremula* Linnaeus), (Stange, 1899:60). *Salix viminalis* Linnaeus, (Hruby, 1964:209).

21. *salicicolella* (Sircom, 1848:271) (*Argyromiges*).

Figures 414–416.

Type locality: ENGLAND: Brislington, Somerset.

= *brevilineatella* (Benander, 1944:108) (*Lithocolletis*).

Synonym of *salicicolella*.

Type locality: SWEDEN.

= *capreella* (Nicelli, 1851:42) (*Lithocolletis*). Synonym of *salicicolella*.

Type locality: GERMANY: Eckerberg.

= *fusca* (Waters, 1929:169). Synonym of *salicicolella*.

Type locality: ENGLAND: Caernarvonshire, Oxfordshire.

Distribution: AUSTRIA (Hauder, 1912:252; Hoffmann and Klos, 1929:294; Klimesch, 1961:737, 1990:135, 136; Hartig, 1964:182; Kasy, 1965:200; Buszko, 1996:53). BELGIUM (Lhomme, 1963:1015; Leraut, 1980:56; Buszko, 1996:53). CZECH REPUBLIC: Bohemia (Nickerl, 1908:102; Sterneck and Zimmermann, 1933:132), Bohemia and Moravia (Buszko, 1996:53), Moravia (Skala, 1912:219). DENMARK (Karsholt and Nielsen, 1976:23; Schnack, 1985:50; Buszko, 1996:53). ESTONIA (Buszko, 1996:53). EUROPE (central) (Staudinger and Rebel, 1901:212). EUROPE (eastern) (Buszko, 1996:53). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). FRANCE (Le Marchand, 1936:22; Lhomme, 1963:1015; Leraut, 1980:62; Buszko, 1996:53), Corsica (Buszko, 1996:53). GERMANY (Frey, 1856:348 (as *P. capreella* Wocke); Heinemann and Wocke, 1877:679; Sorhagen, 1886:280; Reutti, 1898:275; Stange, 1899:58, misidentification; M. Hering, 1932:72; Petry, Beer, and Hockemeyer, 1936:190; Buszko, 1996:53). HUNGARY (Buszko, 1996:53). IRELAND (Meyrick, 1927:777; Buszko, 1996:53). ITALY (Buszko, 1996:53). JAPAN (Kumata, 1963:55). LATVIA (Staudinger and Rebel, 1901:212; Spuler, 1910:414; Buszko, 1996:53). LITHUANIA (Buszko, 1996:53). NETHERLANDS (Kuchlein, 1987:17; Buszko, 1996:53). NORWAY (Buszko, 1996:53). POLAND (Nicelli, 1851:42 (as *P. capreella* Wocke); Buszko, 1990:407, 1996:53). ROMANIA (Drăghia, 1970:229). SLOVAKIA (Buszko, 1996:53). SWEDEN (Staudinger and Rebel, 1901:212; Spuler, 1910:414; Meyrick, 1927:777; E.M. Hering, 1957:920 (as *P. brevilineatella*), 1957:921 (as *P. salicicolella*); Svensson et al., 1987:no 320 (as *P. salicicolella* and *P. brevilineatella*); Buszko, 1996:53). SWITZERLAND (Frey, 1856:348 (as *P. capreella* Wocke); Heinemann and Wocke, 1877:679; Vorbrodt and Müller-Rutz, 1914:529; Buszko, 1996:53). UNITED KINGDOM (Stainton, 1854:271, 1859:418; Frey, 1856:348 (as *P. capreella* Wocke); Meyrick, 1927:777; Ford, 1949:161; E.M. Hering, 1957:

921; Kloet and Hincks, 1972:10; Watkinson, 1985:330; Buszko, 1996:53).

Hosts: *Salix aurita* Linnaeus, (Sorhagen, 1886:280; Klimesch, 1961:737, 1990:135; Lhomme, 1963:1015; Buszko, 1990:407; Kuznetsov and Baryshnikova, 1998:45); *S. babylonica* Linnaeus, (Stange, 1899:58, misidentification of *salicicolella*); *S. caprea* Linnaeus, (Nicelli, 1851:42; Sorhagen, 1886:280; Staudinger and Rebel, 1901:212; Nickerl, 1908:102; Spuler, 1910:414; Hauder, 1912:252; Skala, 1912:219; Meyrick, 1927:777; Le Marchand, 1936:22; Ford, 1949:161; Klimesch, 1961:737; Lhomme, 1963:1015; Kasy, 1965:200; Kuznetsov and Baryshnikova, 1998:45); *S. cinerea* Linnaeus, (Sorhagen, 1886:280; Staudinger and Rebel, 1901:212; Spuler, 1910:414; Skala, 1912:219; Lhomme, 1963:1015; Le Marchand, 1936:22; Petry, Beer, and Hockemeyer, 1936:190; Klimesch, 1961:737; Drăghia, 1970:229; Buszko, 1990:407; Kuznetsov and Baryshnikova, 1998:45); *S. pentandra* Linnaeus, (Kuznetsov and Baryshnikova, 1998:45); *S. viminalis* Linnaeus, (Kuznetsov and Baryshnikova, 1998:45).

22. *salictella* (Zeller, 1846:207) (*Lithocolletis*).

Figures 420–422.

Type locality: AUSTRIA: Vienna.

= *heringiella* (Grønlien, 1932:115) (*Lithocolletis*). Synonym of *salictella*.

Type locality: NORWAY.

= *jaeckhi* (M. Hering, 1934:70) (*Lithocolletis*). Synonym of *salictella*.

Type locality: GERMANY: Bavaria: Ammermoos.

= *viminiella* (Sircom, 1848:271) (*Argyromiges*). Synonym of *salictella*.

Type locality: ENGLAND: Brislington, Somerset.

Distribution: AUSTRIA (Zeller, 1846:207; Herrich-Schäffer, 1855:759; Frey, 1856:345; Mitterberger, 1909:293; Hauder, 1912:252; Hoffmann and Klos, 1929:294 (as *P. viminiella* Stainton); Klimesch, 1961:737 (as *P. salictella*) and 740 (as *P. viminiella* Stainton), 1990:136; Hartig, 1964:182; Issekutz, 1972:87; Buszko, 1996:53). BELGIUM (Lhomme, 1963:1014 (as *P. salictella*) and 1029 (as *P. viminiella* Stainton); Leraut, 1980:62; Buszko, 1996:53). BULGARIA (Buszko, 1996:53). CZECH REPUBLIC: Bohemia (Nickerl, 1908:102; Sterneck and Zimmermann, 1933:132), Bohemia and Moravia (Buszko, 1996:53). DENMARK (Karsholt and Nielsen, 1976:23; Schnack, 1985:50; Buszko, 1996:53). ESTONIA (Buszko, 1996:53). EUROPE (eastern) (Buszko, 1996:53). EUROPE (north) (Meyrick, 1927:781; E.M. Hering, 1957:921 (as *P. viminiella*)). FINLAND (Varis, Jalava, and Kyrki, 1987:55; Buszko, 1996:53). FRANCE (Le Marchand, 1936:18–19 (as *P. salictella* and *P. viminiella* Stainton); Lhomme, 1963:1014 (as *P. salictella*) and 1020 (as *P. viminiella* Stainton); Leraut, 1980:62; Buszko, 1996:53).

GERMANY (Herrich-Schäffer, 1855:759; Heinemann and Wocke, 1877:674 (as *P. viminiella* Stainton); Sorhagen, 1886:278, 1900:212–213 (as *P. crocinella* Sorhagen); Reutti, 1898:274 (as *P. salictella* and *P. viminiella* Stainton); Stange, 1899:58 (misidentification); Staudinger and Rebel, 1901:214 (as *P. viminiella* Stainton); Meyrick, 1927:781 (as *P. viminiella* Stainton); M. Hering, 1932:72, 73; Petry, Beer, and Hockemeyer, 1936:190; Buszko 1996:53). HUNGARY (Buszko, 1996:53). IBERIAN PENINSULA (Vives Moreno, 1994:54). IRELAND (Buszko, 1996:53). ITALY (Frey, 1856:345; Stainton, 1869:352; Staudinger and Rebel, 1901:212; Spuler, 1910:414 and 417 (as *P. viminiella* Stainton); Klimesch, 1951:48; E.M. Hering, 1957:922; Hartig, 1964:182). JAPAN (Kumata, 1963:54). LATVIA (Buszko, 1996:53). LITHUANIA (Buszko, 1996:53). NETHERLANDS (Staudinger and Rebel, 1901:214 (as *P. viminiella* Stainton); Spuler, 1910:417 (as *P. viminiella* Stainton); Meyrick, 1927:781 (as *P. viminiella* Stainton); Kuchlein, 1987:17; Buszko, 1996:53). NORWAY (E.M. Hering, 1957:922 (as *P. heringiella*); Buszko, 1996:53). POLAND (Buszko, 1990:407, 1996:53; Deschka). PORTUGAL (Buszko, 1996:53). RUSSIA (north) (Staudinger and Rebel, 1901:212; E.M. Hering, 1957:922). RUSSIA (northwest) (Staudinger and Rebel, 1901:212, 214 (as *P. viminiella* Stainton); Spuler, 1910:414, 417 (as *P. viminiella* Stainton). RUSSIA (southeast, Primorskyi Krai (Ermolaev, 1977:112). SLOVAKIA (Hruby, 1964:201; Buszko, 1996:53). SPAIN (Buszko, 1996:53). SWEDEN (Staudinger and Rebel, 1901:214 (as *P. viminiella* Stainton); Svensson et al., 1987:no 319; Buszko, 1996:53). SWITZERLAND (Herrich-Schäffer, 1855:759; Frey, 1856:345; Heinemann and Wocke, 1877:674; Rebel, 1901:212, 214 (as *P. viminiella* Stainton); Spuler, 1910:414, 417 (as *P. viminiella* Stainton); Vorbrodt and Müller-Rutz, 1911–1914:529; Buszko, 1996:53). UNITED KINGDOM (Stainton, 1854:275, 1859:420 (as *P. viminiella* Stainton); Staudinger and Rebel, 1901:214 (as *P. viminiella* Stainton); Spuler, 1910:414; Meyrick, 1927:781 (as *P. viminiella* Stainton); Ford, 1949:161 (as *P. viminiella* Stainton); E.M. Hering, 1957:921 (as *P. viminiella* Stainton); Kloet and Hincks, 1972:10; Watkinson, 1985:328, 330; Buszko, 1996:53).
 Hosts: *Salix acutifolia* Willdenow, (Buszko, 1990:407); *S. alba* Linnaeus, (Heinemann and Wocke, 1877:675; Sorhagen, 1886:278; Nickerl, 1908:102; Mitterberger, 1909:293; Hauder, 1912:252; Le Marchand, 1936:19 (as *P. viminiella* Stainton); Petry, Beer, and Hockemeyer, 1936:190; Klimesch, 1951:48, 1961:737, 1990:136; Lhomme, 1963:1014; Hruby, 1964:201; Ermolaev, 1977:112; Buszko, 1990:407; Kuznetsov and Baryshnikova, 1998:46); *S. amygdalina* Linnaeus, (Buszko, 1990:407); *S. appendiculata* Villars, (Deschka, new record); *S. aurita* Linnaeus, (E.M. Hering, 1957:921 (as *heringiella*), 921 (as *P. viminiella* Stainton); Kuznetsov and Baryshnikova, 1998:46); *S. ?aurita* Linnaeus, (Svensson, 1966:191–194 (as *P. heringiella*)); *S. babylonica* Linnaeus, (Klimesch, 1951:48; Hartig, 1964:182; Hruby, 1964:201; Ermolaev, 1977:112); *S. caprea* Linnaeus, (Staudinger and Rebel, 1901:214 (as *P. viminiella* Stainton); Spuler, 1910:417 (as *P. viminiella* Stainton); Meyrick, 1927:781 (as *P. viminiella* Stainton); Le Marchand, 1936:19 (as *P. viminiella* Stainton); Ford, 1949:161 (as *P. viminiella* Stainton); E.M. Hering, 1957:921 (as *P. viminiella* Stainton), 922; Klimesch, 1961:737 (as *P. salictella*) and 740 (as *P. viminiella* Stainton); Lhomme, 1963:1029 (as *P. viminiella* Stainton); Hartig, 1964:182); *S. cinerea* Linnaeus, (Petry, Beer, and Hockemeyer, 1936:190; Ermolaev, 1977:112); *S. daphnoides* Villars, (Kuznetsov and Baryshnikova, 1998:46); *S. dasyclados* Wimmer, (Deschka, new record); *S. eleagnos* Scopoli, (Klimesch, 1951:48 (as *P. incana* Schrank), 1990:136; Hartig, 1964:182 (as *P. incana* Schrank); Deschka); *S. fragilis* Linnaeus, (Petry, Beer, and Hockemeyer, 1936:190; Ford, 1946:161 (as *P. viminiella* Stainton); Watkinson, 1985:328 (as *P. viminiella*); Buszko, 1990:407); *S. nigricans* Smith, (Svensson, 1966:191 (as *P. heringiella*)); *S. pentandra* Linnaeus, (Heinemann and Wocke, 1877:675; Ermolaev, 1977:112); *S. purpurea* Linnaeus, (Frey, 1856:345; Klimesch, 1951:48, 1990:136; Lhomme, 1963:1014; Hartig, 1964:182; Ermolaev, 1977:112; Buszko, 1990:407; Deschka); *S. repens* Linnaeus, (Petry, Beer, and Hockemeyer, 1936:190; Lhomme, 1963:1014; Kuznetsov and Baryshnikova, 1998:46); *S. rossica* A. Skvortz, (Kuznetsov and Baryshnikova, 1998:46); *S. rosmarinifolia* Linnaeus, (Buszko, 1990:407); *S. sibirica* (=caesia Villars), (Frey, 1856:345); *S. siuzevii* Seeman, (Kuznetsov and Baryshnikova, 1998:46); *Salix* sp., (Watkinson, 1985:328 (as *P. viminiella*)); *S. triandra* Linnaeus, (Klimesch, 1951:48; Lhomme, 1963:1014; Hartig, 1964:182); *S. viminalis* Linnaeus, (Frey, 1856:345; Stainton, 1859:420 (as *P. viminiella* Stainton); Heinemann and Wocke, 1877:675, and 674 (as *P. viminiella* Stainton); Reutti, 1898:274 (as *P. viminiella* Stainton); Staudinger and Rebel, 1901:212; Nickerl, 1908:102; Mitterberger, 1909:293; Spuler, 1910:414; Le Marchand, 1936:19 (as *P. viminiella* Stainton); Petry, Beer, and Hockemeyer, 1936:190; Ford, 1949:161 (as *P. viminiella* Stainton); E.M. Hering, 1957:922; Lhomme, 1963:1014 (as *P. salictella*) and 1029 (as *P. viminiella* Stainton); Hruby, 1964:201; Svensson, 1966:191; Ermolaev, 1977:112; Kuznetsov and Baryshnikova, 1998:50 (as *P. viminiella* Stainton); Buszko, 1990:407).

23. *salincolella* (Sorhagen: 1900:249). Nomem dubium.
 Type locality: GERMANY.

Distribution: GERMANY (north) (E.M. Hering, 1957:920).
 Host: *Salix caprea* Linnaeus, (Sorhagen, 1900:249; E.M. Hering, 1957:920).

Remarks: The current identity of this species remains questionable. No type material of *salincolella* is known to exist, and no further collections have been authenticated since it was described. Without explanation, Kuznetsov (1981) treated *salincolella* as a form of *rajella* L., which feeds on *Alnus*.

spinolella (Duponchel, 1840). Synonym of *hilarella*.

tremulae (Zeller, 1846). Synonym of *sagitella*.

tremuloidiella (Braun, 1908). Synonym of *apparella*.

viminetella (Herrich-Schäffer, 1855). Unjustified emendation of *viminetorum*.

24. *viminetorum* (Stainton, 1854:272) (*Lithocolletis*).

Figures 405–407.

Type locality: ENGLAND: Lewisham, Kent.

=*viminetella* (Herrich-Schäffer, 1855:326). Unjustified emendation of *viminetorum*.

Distribution: AUSTRIA (Klimesch, 1961:737, 1990:135; Hartig, 1964:181; Buszko, 1996:54; Deschka). BELGIUM (Lhomme, 1963:1015). CHINA (Sichuan) (Deschka, new record). CZECH REPUBLIC: Bohemia and Moravia (Buszko, 1996:54). EUROPE (central) (Spuler, 1910:414; Meyrick, 1927:777; E.M. Hering, 1957:920). FRANCE (Staudinger and Rebel, 1901:212; Spuler, 1910:414; Le Marchand, 1936:22; Lhomme, 1963:1015; Leraut, 1980:62). GERMANY (Sorghagen, 1886:280; Reutti 1898:274; Stange, 1899:58; M. Hering, 1932:72; Petry, Beer, and

Hockemeyer, 1936:189; Buszko, 1996:53). IRELAND (Buszko, 1996:54). ITALY (Hartig, 1964:181; Buszko, 1996:54). LATVIA (Buszko, 1996:54). LITHUANIA (Buszko, 1996:54). NETHERLANDS (Kuchlein, 1987:17; Buszko, 1996:54). POLAND (Buszko, 1990:406, 1996:54, Deschka). UNITED KINGDOM (Stainton, 1854:272, 1859:417; Herrich-Schäffer, 1855:326 (as *P. viminetella*); Meyrick, 1927:777; Ford, 1949:161; E.M. Hering, 1957:920; Kloet and Hincks, 1972:10; Watkinson, 1985:329; Buszko, 1996:54).

Hosts: *Salix ?aurita* Linnaeus, (Svensson, 1966:191); *S. caprea* Linnaeus, (Heinemann and Wocke, 1877:678; Sorhagen, 1886:280; Le Marchand, 1936:22; E.M. Hering, 1957:920; Lhomme, 1963:1015; Hartig, 1964:181; Kuznetsov and Baryshnikova, 1998:50); *Salix* sp. (broad, hairy leaves, in Sichuan), (Deschka); *S. viminalis* Linnaeus, (Stainton, 1859:417; Heinemann and Wocke, 1877:678; Sorhagen, 1886:280; Reutti, 1898:274; Stange, 1899:59; Staudinger and Rebel, 1902:212; Spuler, 1910:414; Meyrick, 1927:777; Le Marchand, 1936:22; Petry, Beer, and Hockemeyer, 1936:189; Ford, 1949:161; E.M. Hering, 1957:920; Klimesch, 1961:737, 1990:135; Lhomme, 1963:1015; Hartig, 1964:181; Svensson, 1966:191; Watkinson, 1985:329; Kuznetsov and Baryshnikova, 1998:50; Buszko, 1990:406).

viminiella (Sircom, 1848:271) (*Argyromiges*). Synonym of *salictella*.

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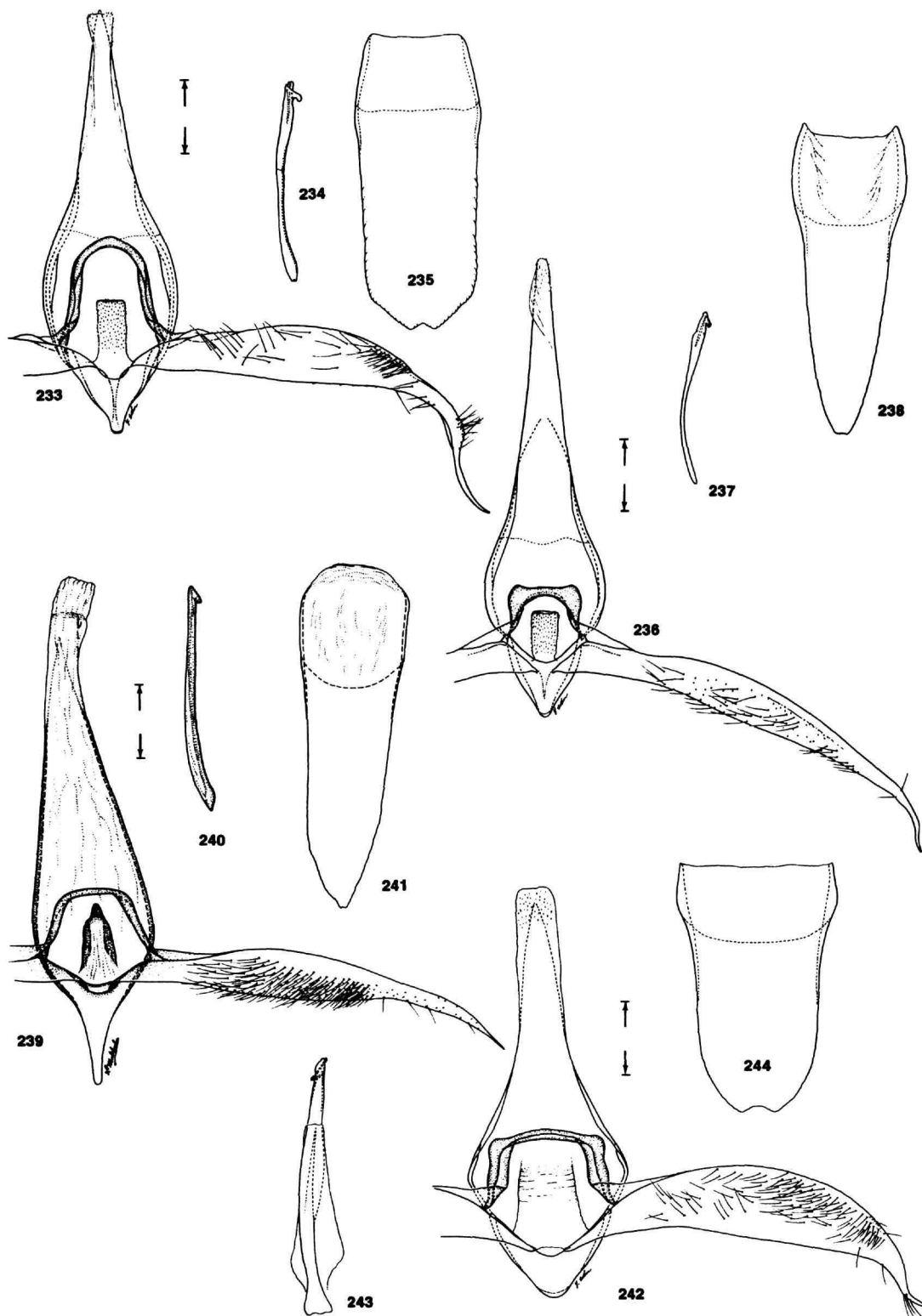
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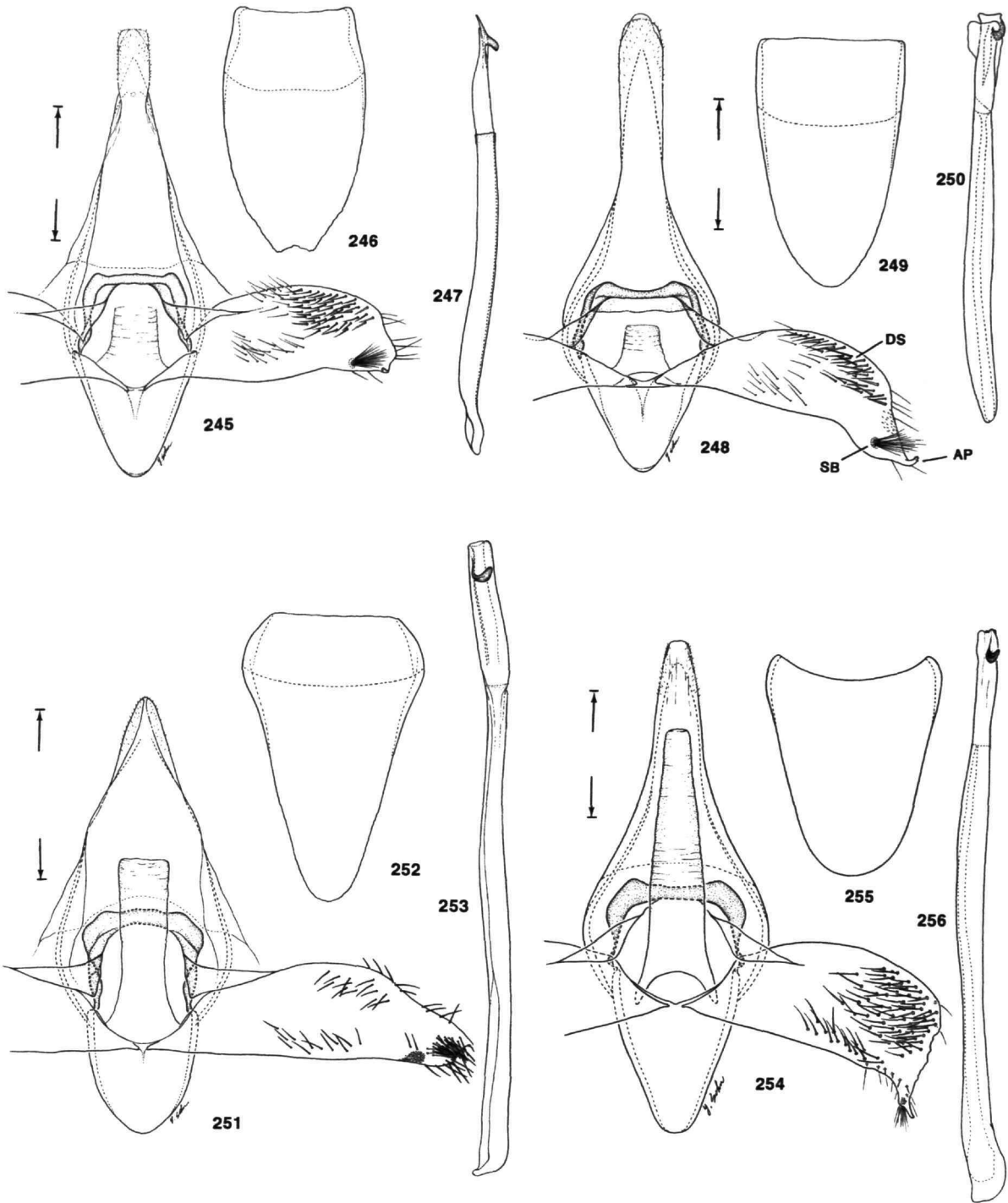
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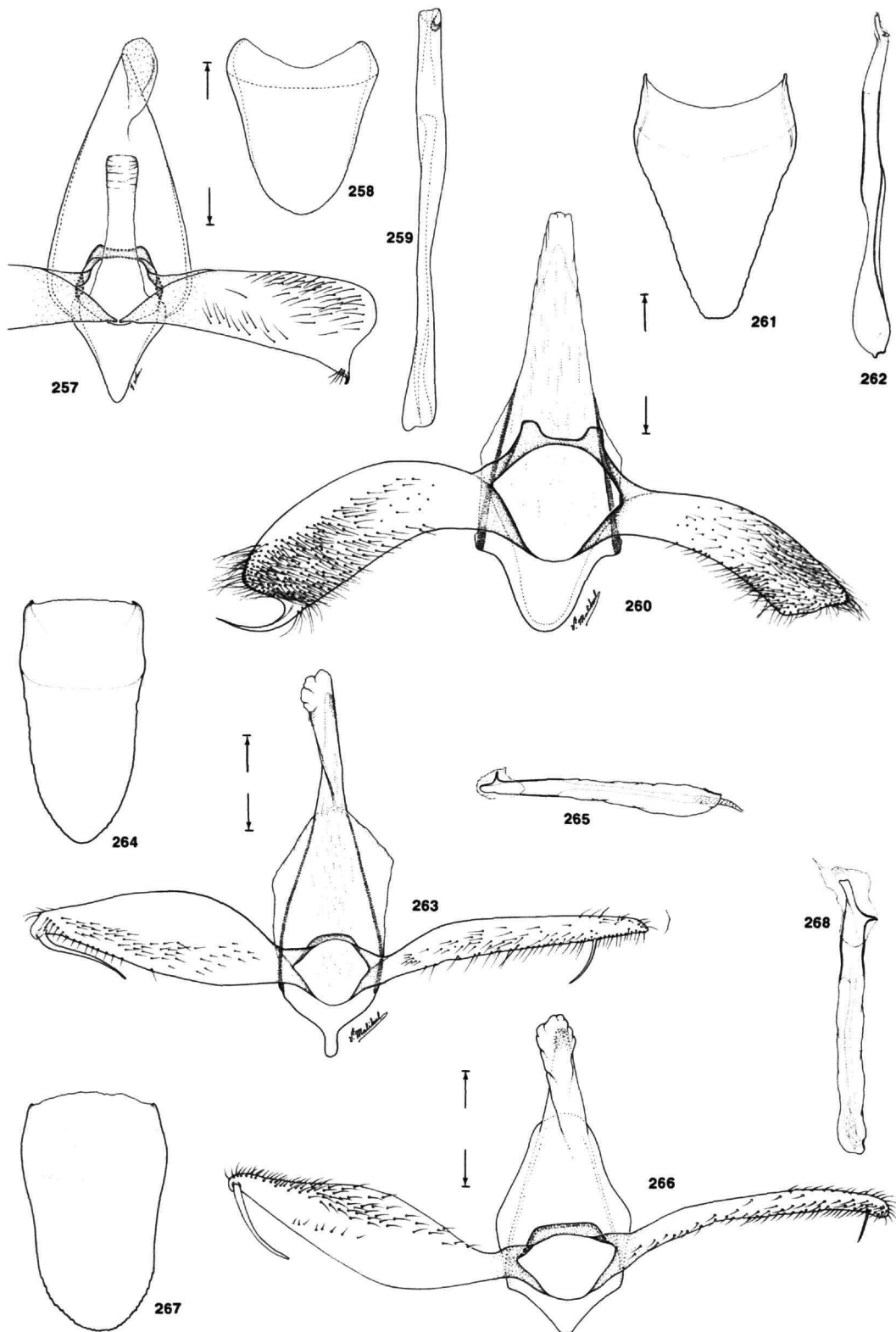
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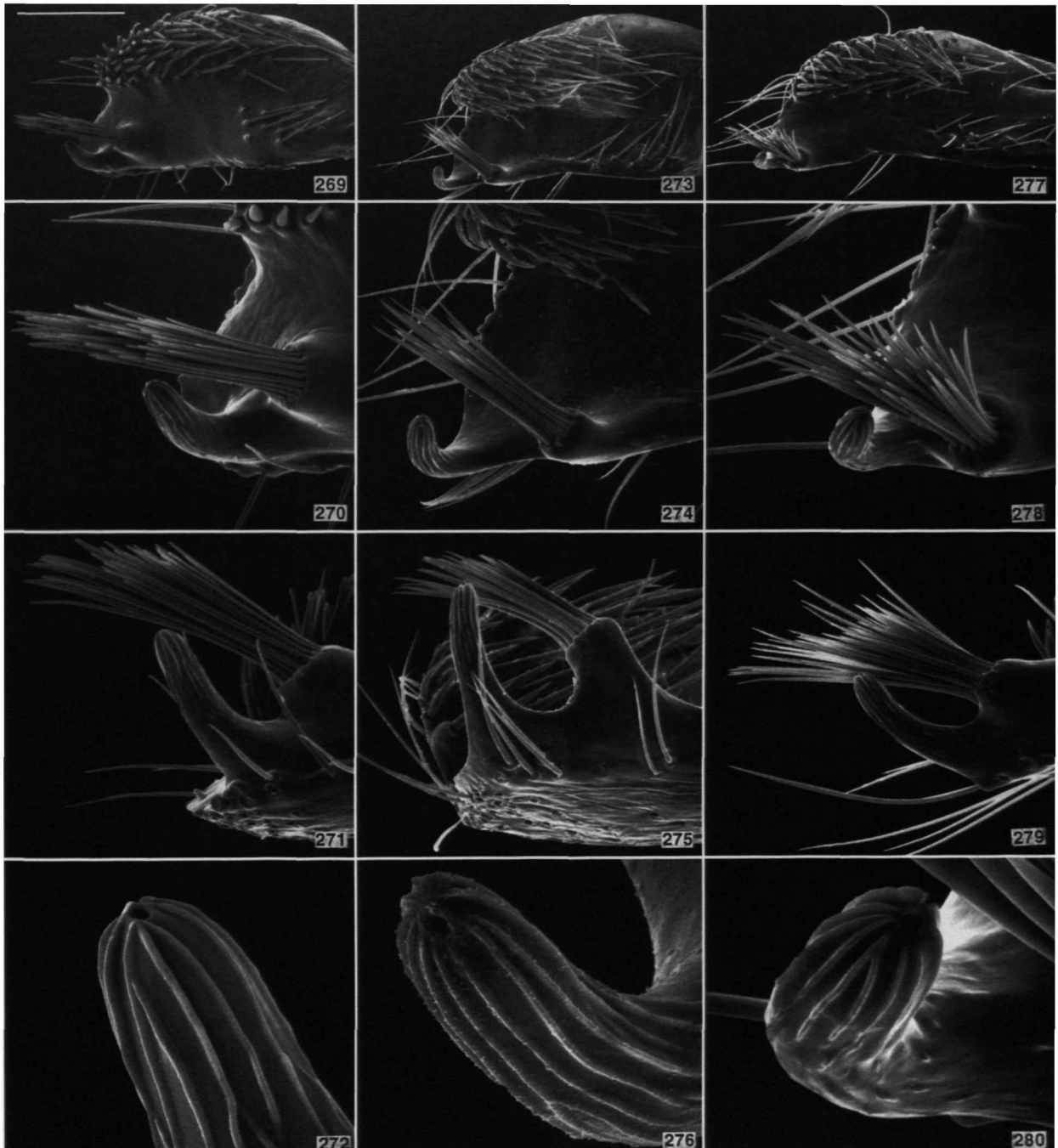
FIGURES 233–244.—North American *Phyllonorycter*, male genitalia and eighth abdominal sternite. *P. apparella*: 233, full view; 234, aedeagus; 235, sternite. *P. latus*: 236, full view; 237, aedeagus; 238, sternite. *P. nipigon*: 239, full view; 240, aedeagus; 241, sternite. *P. deserticola*: 242, full view; 243, aedeagus; 244, sternite. (All scales = 0.25 mm.)



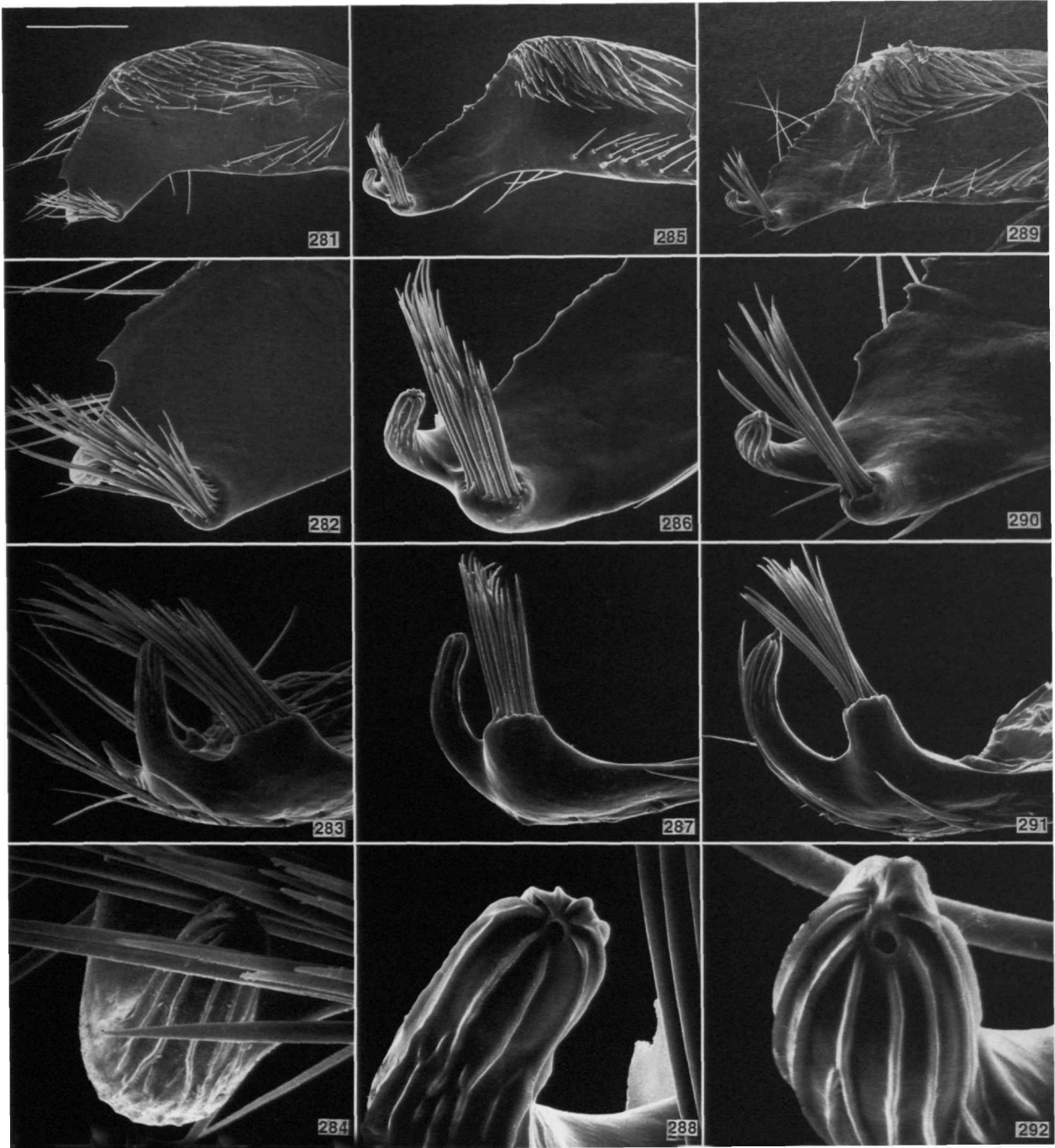
FIGURES 245–256.—North American *Phyllonorycter*, male genitalia and eighth abdominal sternite. *P. salicifoliella* (paratype of *P. kenora*): 245, full view; 246, sternite; 247, aedeagus. *P. salicifoliella*: 248, full view; 249, sternite; 250, aedeagus. *P. acanthus*: 251, full view; 252, sternite; 253, aedeagus. *P. erugatus*: 254, full view; 255, sternite; 256, aedeagus. (AP = apical process; SB=subapical brush; all scales=0.25 mm.)



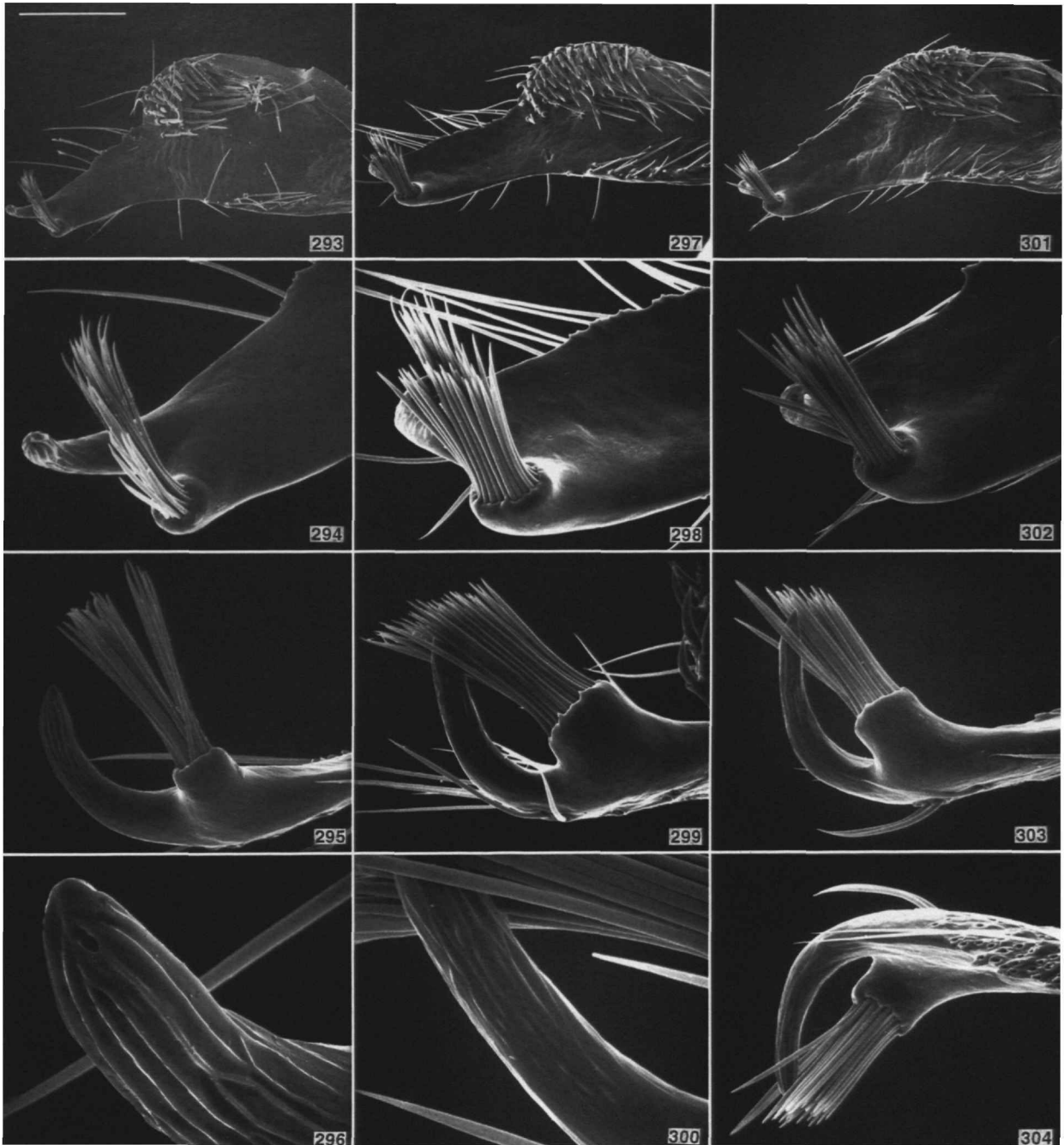
FIGURES 257–268.—North American *Phyllonorycter*, male genitalia and eighth abdominal sternite. *P. mildredae*: 257, full view; 258, sternite; 259, aedeagus. *P. populiella*: 260, full view; 261, sternite; 262, aedeagus. *P. scudderella*: 263, full view; 264, sternite; 265, aedeagus. *P. apicinigrella*: 266, full view; 267, sternite; 268, aedeagus. (All scales=0.25 mm.)



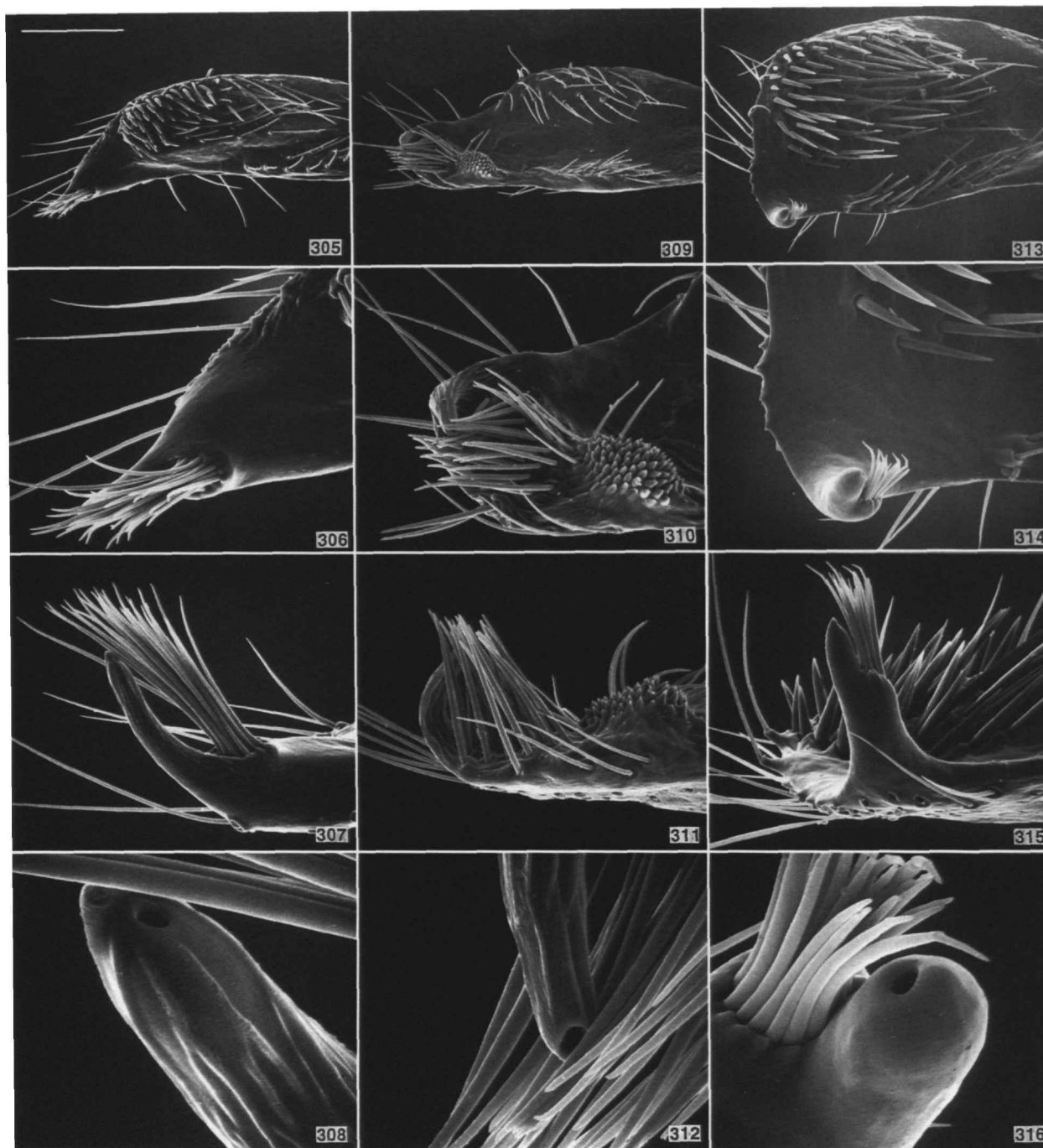
FIGURES 269–280.—*Phyllonorycter salicifoliella*, morphological variation of male valvae. Specimen from Red Lake, Ontario (= *P. kenora*): 269, lateral view, (100 μ m); 270, apex of valva (38 μ m); 271, ventral view of Figure 270 (38 μ m); 272, apical process (8.6 μ m). Specimen from Sturgeon Lake, Alberta: 273, lateral view (91 μ m); 274, apex of valva (38 μ m); 275, ventral view of Figure 274 (38 μ m); 276 apical process (7.5 μ m). Specimen from Fort Washington, Maryland: 277, lateral view (100 μ m); 278, apex of valva (38 μ m); 279, ventral view of Figure 278 (38 μ m); 280, apical process (7.5 μ m). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 269.)



FIGURES 281–292.—*Phyllonorycter salicifoliella*, morphological variation of male valvae. Specimen from Falls Church Virginia: 281, lateral view (120 μm); 282, apex of valva (43 μm); 283, ventral view of Figure 282 (40 μm); 284, apical process (8.6 μm). Specimen from Veitch, Virginia: 285, lateral view (120 μm); 286, apex of valva (43 μm); 287, ventral view of Figure 286 (43 μm); 288, apical process (6 μm). Specimen from Clinton, British Columbia: 289, lateral view (107 μm); 290, apex of valva (38 μm); 291, ventral view of Figure 290 (40 μm); 292, apical process (6 μm). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 281.)



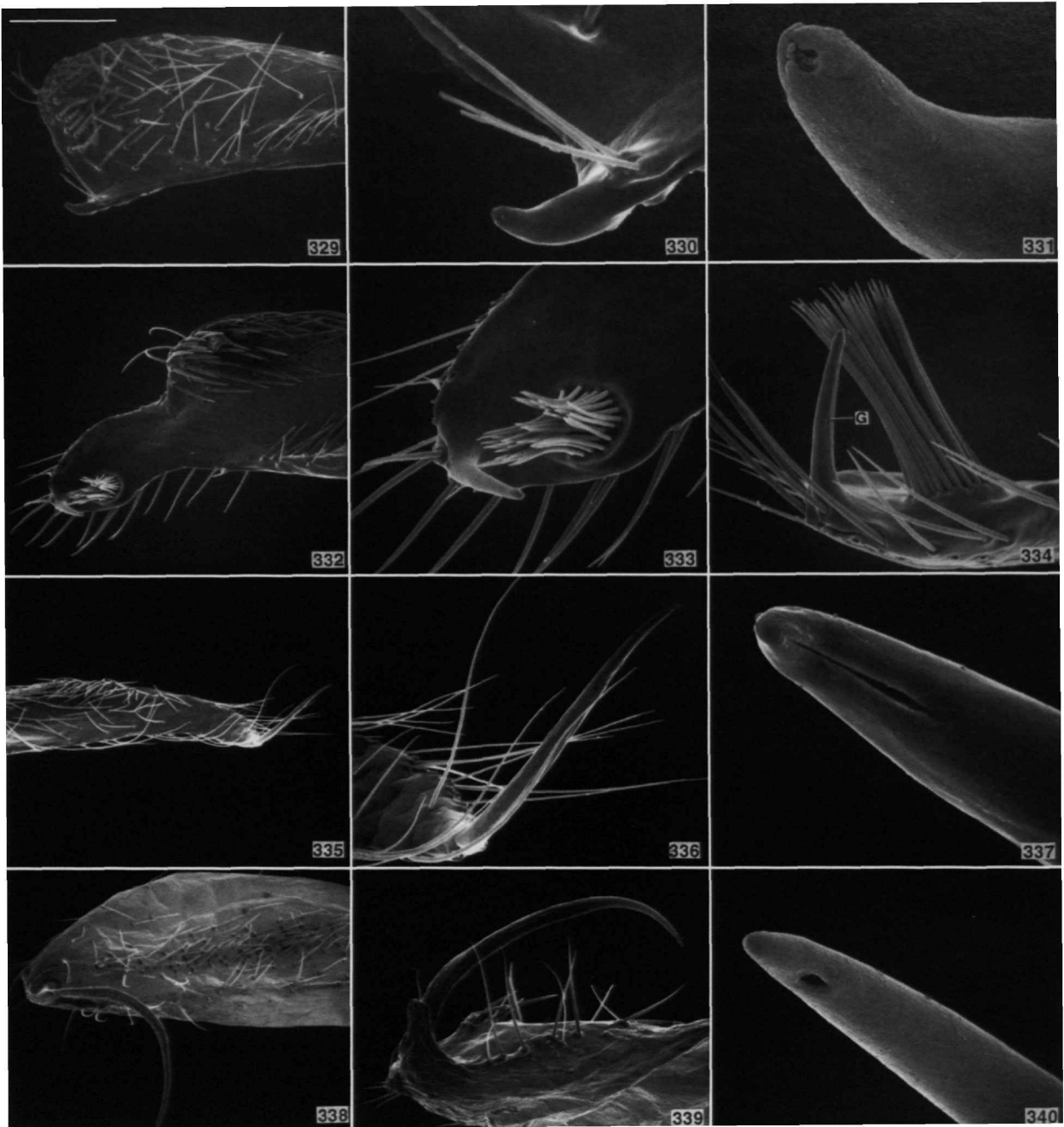
FIGURES 293–304.—*Phyllonorycter salicifoliella*, morphological variation of male valvae. Specimen from Old Donner Pass, California: 293, lateral view (120 μ m); 294, apex of valva (38 μ m); 295, ventral view of Figure 294 (38 μ m); 296, apical process (8.6 μ m). Specimen from Grand Lake, Colorado: 297, lateral view (120 μ m); 298, apex of valva (40 μ m); 299, ventral view of Figure 298 (40 μ m); 300, apical process (14.5 μ m). Specimen from Grand Lake, Colorado: 301, lateral view (120 μ m); 302, apex of valva (38 μ m); 303, ventral view of Figure 302 (38 μ m); 304, dorsal view of Figure 302 (38 μ m). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 293.)



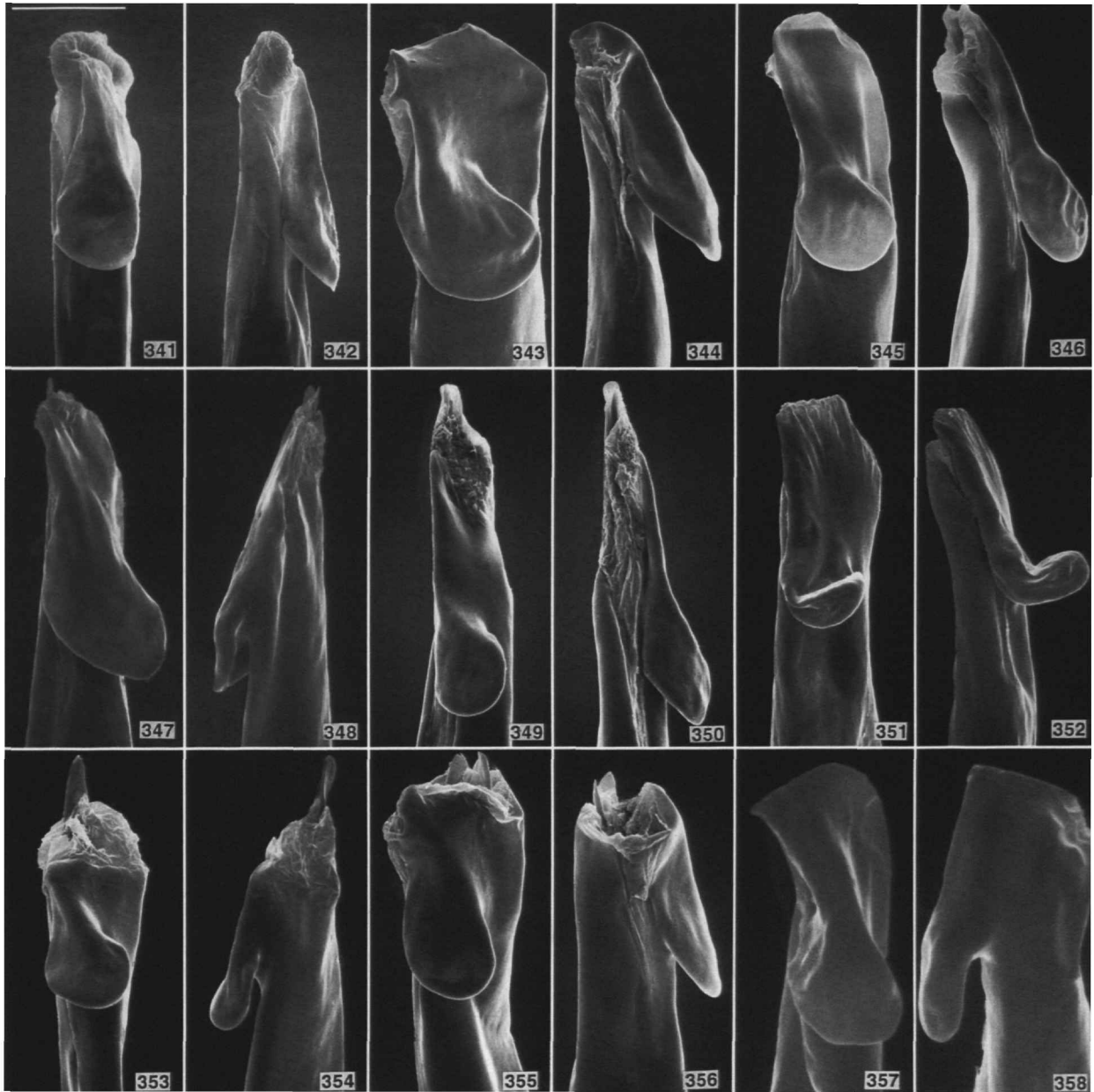
FIGURES 305–316.—Morphological variation of male valvae. *Phyllonorycter salicifoliella* (Monolith, California): 305, lateral view (120 μm); 306, apex of valva (38 μm); 307, ventral view of Figure 306 (38 μm); 308, apical process (6 μm). *Phyllonorycter acanthus* (Ajijic, Jalisco, Mexico): 309, lateral view (100 μm); 310, apex of valva (38 μm); 311, ventral view of Figure 310 (38 μm); 312, apical process (10 μm). *Phyllonorycter erugatus* (Rocky Mountain National Park, Colorado): 313, lateral view (100 μm); 314, apex of valva (38 μm); 315, ventral view of Figure 314 (38 μm); 316, apical process (10 μm). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 305.)



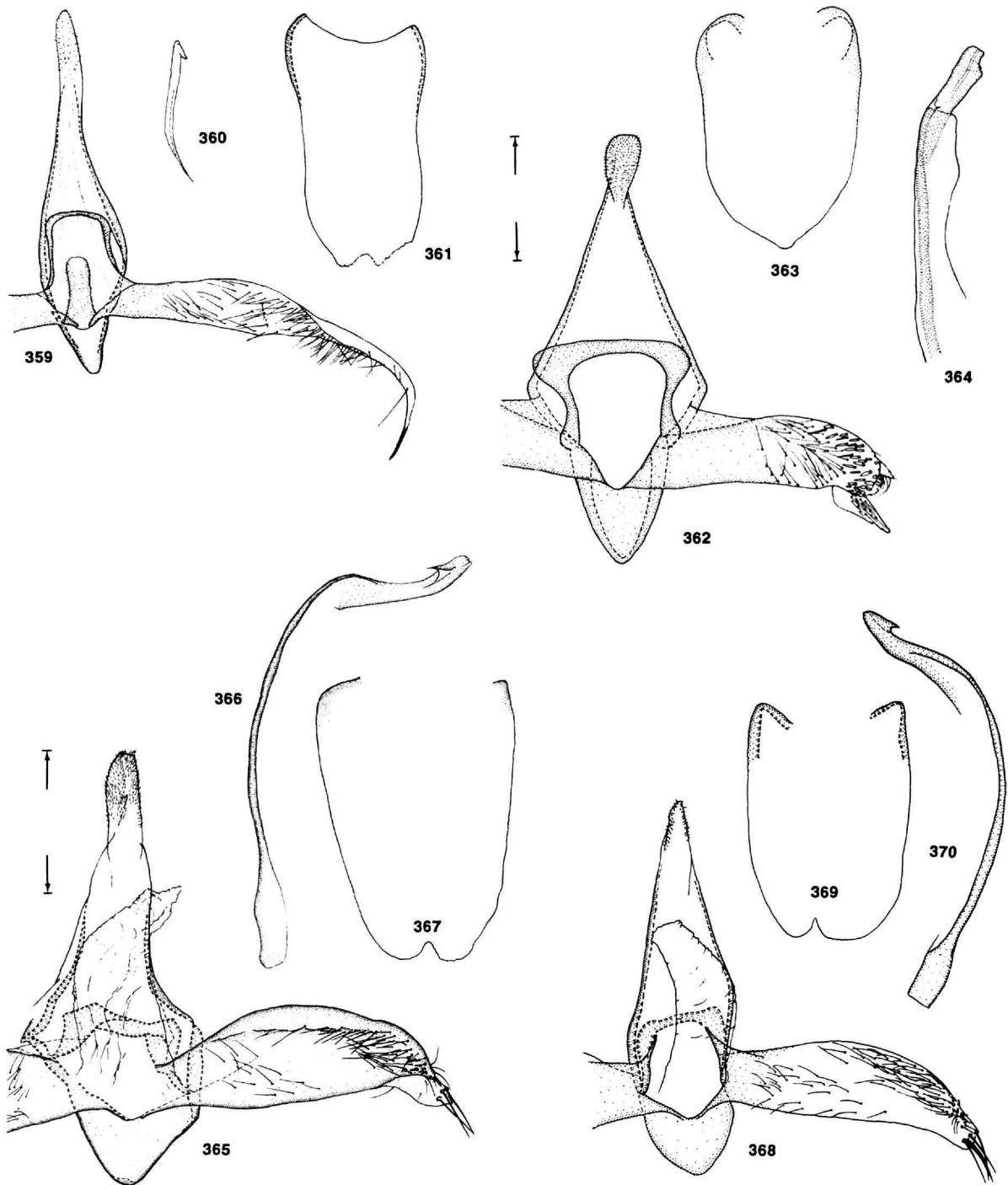
FIGURES 317–328.—*Phyllonorycter erugatus*, morphological variation of male valvae. Specimen from Haynes, Alaska: 317, lateral view (100 μm); 318, apex of valva (38 μm); 319, ventral view of Figure 318 (38 μm); 320, apical process (13.6 μm). Specimen from Alameda, California: 321, lateral view (100 μm); 322, apex of valva (38 μm); 323, ventral view of Figure 322 (38 μm); 324, apical process (25 μm). Specimen from Wilsonville, Oregon: 325, lateral view (120 μm); 326, apex of valva (43 μm); 327, ventral view of Figure 326 (43 μm); 328, apical process (10 μm). (Scale lengths in parentheses; bar scale for all photographs shown in Figure 317.)



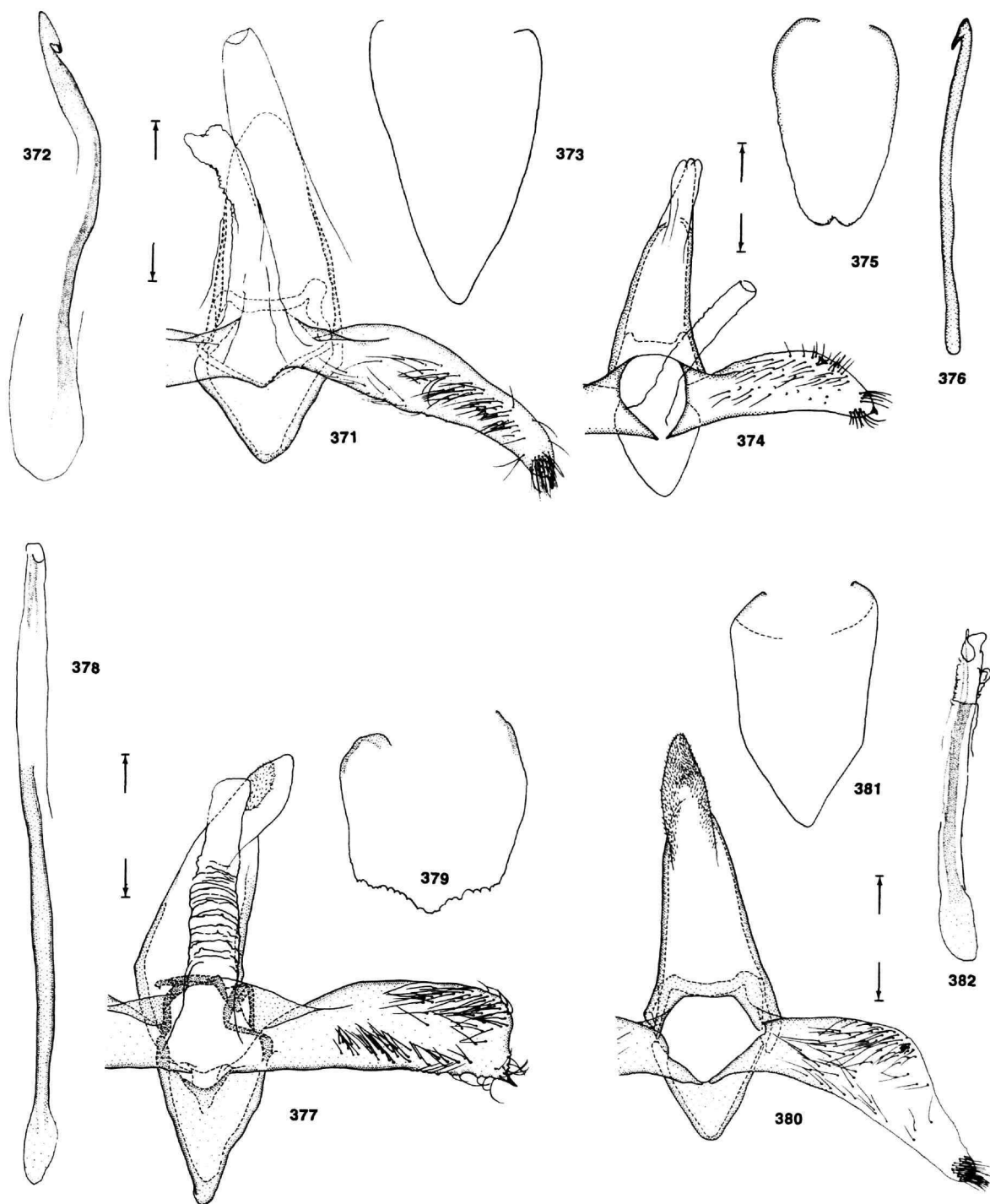
FIGURES 329–340.—Male valvae of North American *Phyllonorycter*. *P. mildredae*: 329, lateral view (75 μ m); 330, apex of valva (17.6 μ m); 331, apical process (5 μ m). *P. pastorella*: 332, lateral view (150 μ m); 333, apex of valva (50 μ m); 334, ventral view of Figure 333, apical process with lateral groove (G; 43 μ m). *P. apparella*: 335, lateral view (176 μ m); 336, apex of valva (50 μ m); 337, pore of apical process (3 μ m). *P. scudderella*: 338, lateral view (120 μ m); 339, apical process (75 μ m); 340, pore of apical process (6 μ m). (G=groove of subapical pore; scale lengths in parentheses; bar scale for all photographs shown in Figure 329.)



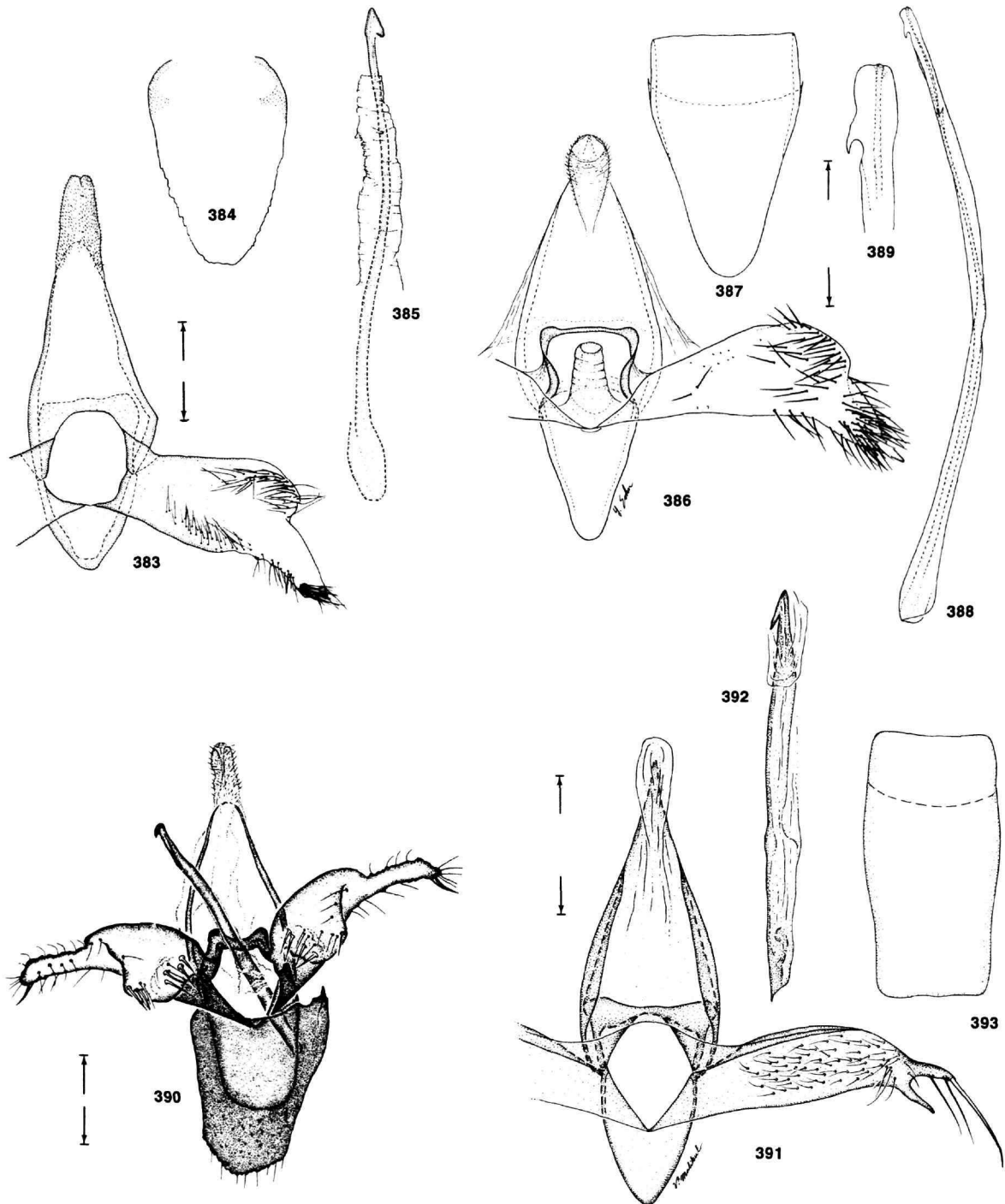
FIGURES 341–358.—North American *Phyllonorycter*, morphological variation of apex of aedeagus: *P. apparella* (Poudre Valley, Colorado): 341, ventral view (27 μ m); 342, lateral view. *P. salicifoliella* (= *kenora*; Red Lake, Ontario): 343, ventral view (27 μ m); 344, lateral view. *P. salicifoliella* (Veitch, Virginia): 345, ventral view (30 μ m); 346, lateral view. *P. salicifoliella* (Old Donner Pass, California): 347, ventral view (27 μ m); 348, lateral view. *P. salicifoliella* (Milford, New York): 349, ventral view (30 μ m); 350, lateral view. *P. acanthus* (El Salto, Jalisco, Mexico): 351, ventral view (27 μ m); 352, lateral view. *P. erugatus* (Alameda, California): 353, ventral view (27 μ m); 354, lateral view. *P. erugatus* (Rocky Mountain National Park, Colorado): 355, ventral view (27 μ m); 356, lateral view. *P. mildredae* (Cincinnati, Ohio): 357, ventral view (13.6 μ m); 358, lateral view. (Scale lengths in parentheses; bar scale for all photographs shown in Figure 341.)



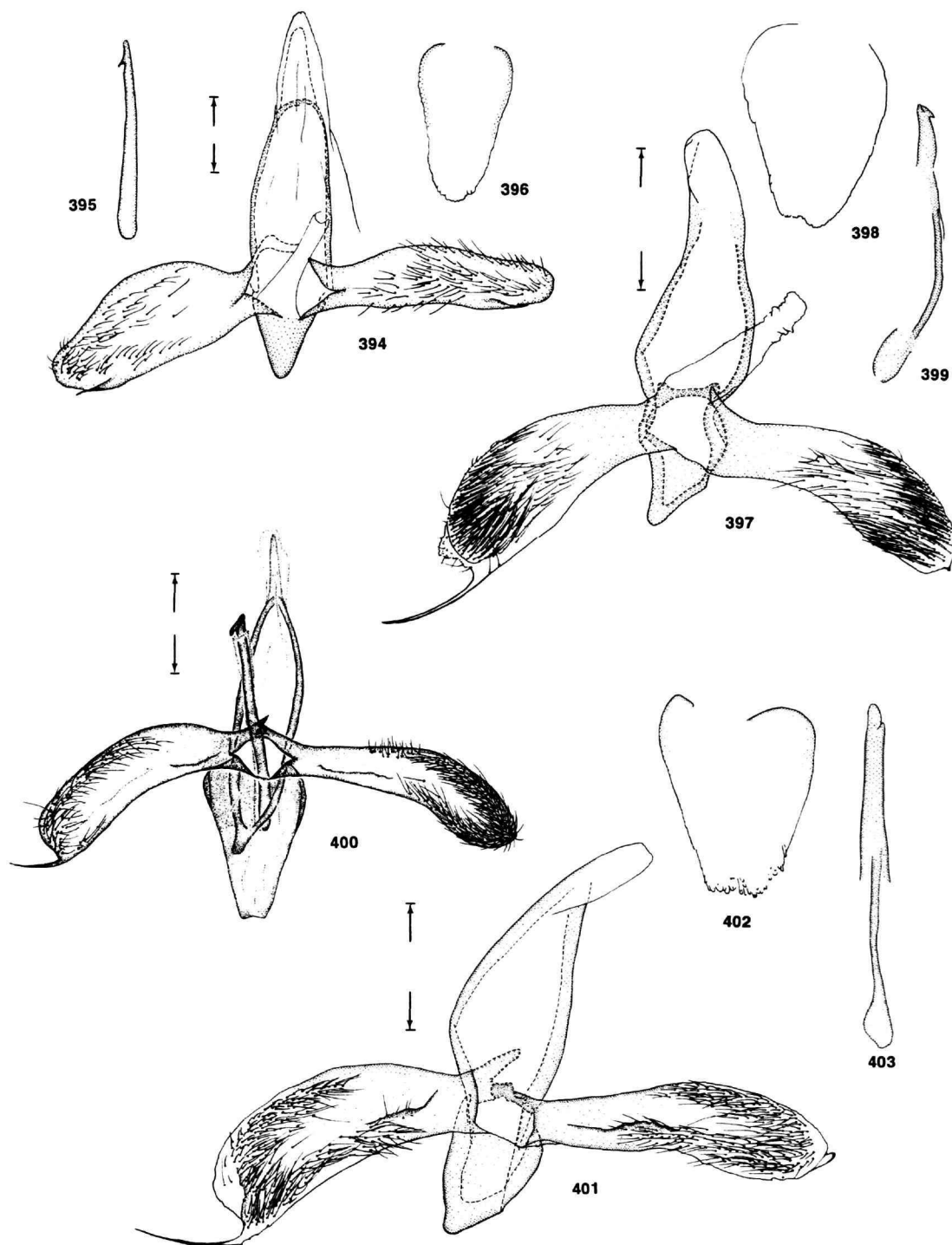
FIGURES 359–370.—Palearctic *Phyllonorycter*, male genitalia, eighth abdominal sternite. *P. apparella* (Poland): 359, full view; 360, aedeagus; 361, sternite. *P. armeniella* (Turkey): 362, full view; 363, sternite; 364, aedeagus. *P. comparella* (Yugoslavia): 365, full view; 366, aedeagus; 367, sternite. *P. comparella* (Italy): 368, full view; 369, sternite; 370, aedeagus. (All scales=0.25 mm.)



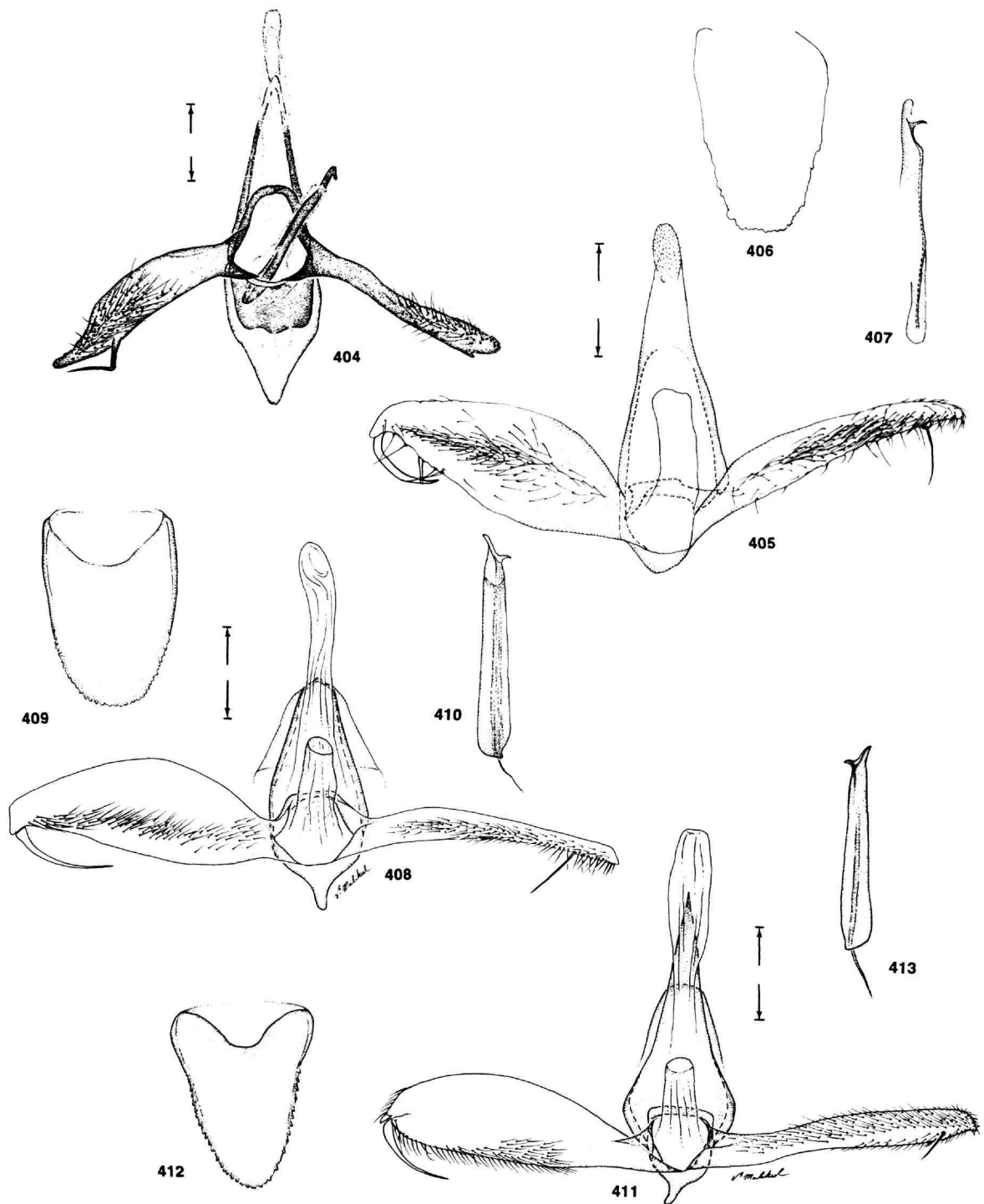
FIGURES 371-382.—Palearctic *Phyllonorycter*, male genitalia. *P. chicanella* (Spain): 371, full view; 372, aedeagus; 373, sternite. *P. populi* (central Asia): 374, full view; 375, sternite; 376, aedeagus. *P. populioliella* (Russia): 377, full view; 378, aedeagus; 379, sternite. *P. sagitella* (Germany): 380, full view; 381, sternite; 382, aedeagus. (All scales=0.25 mm.)



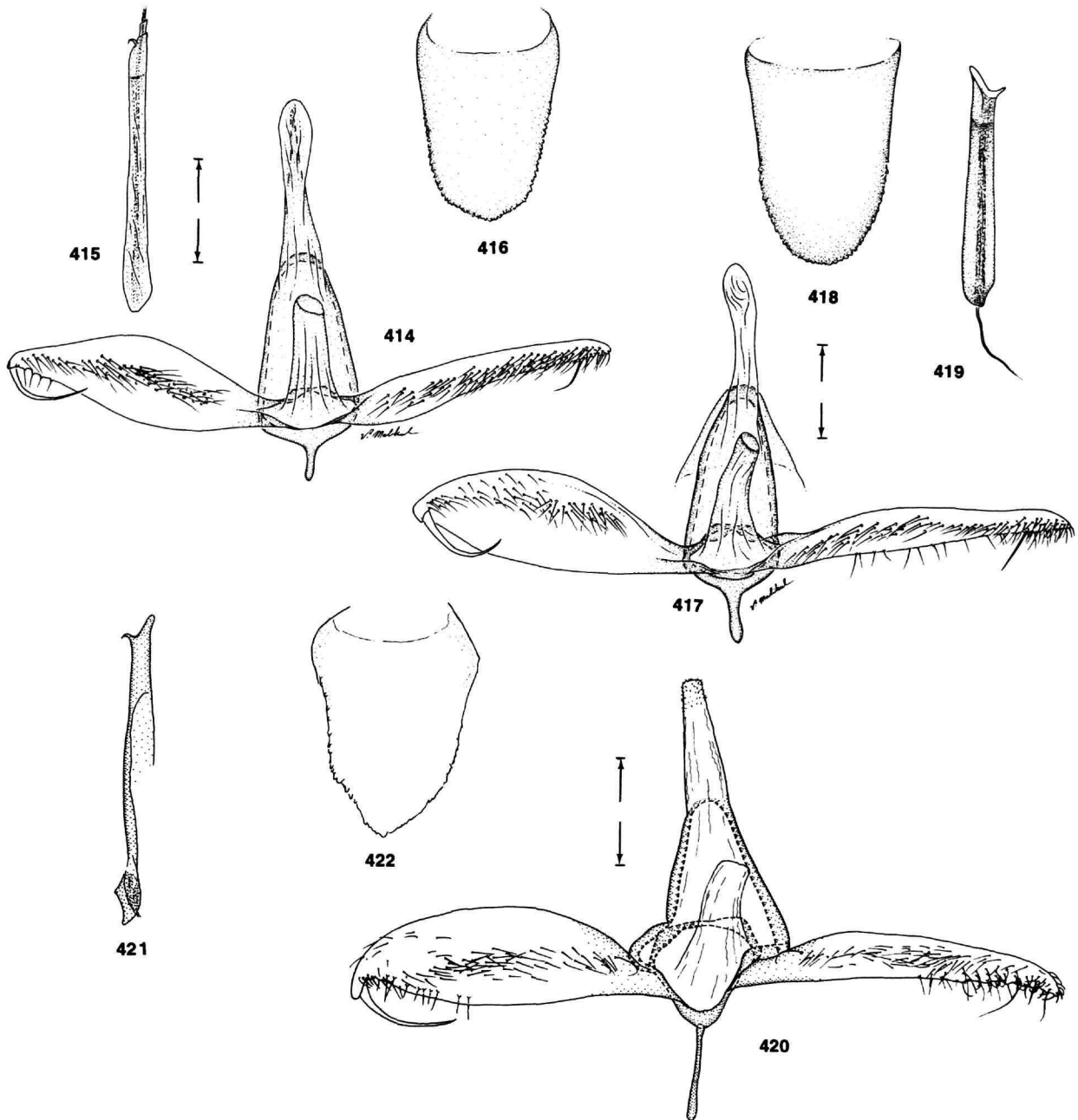
FIGURES 383–393.—Palearctic *Phyllonorycter*, male genitalia, eighth abdominal sternite. *P. pastorella* (Austria): 383, full view; 384, sternite; 385, aedeagus. *P. iteina* (India): 386, full view; 387, sternite; 388, aedeagus; 389, apical enlargement of Figure 388. *P. popualbae* (Tajikistan, after Noreika and Puplesis, 1992a): 390, full view. *P. popualbae* (central Asia): 391, full view; 392, aedeagus; 393, sternite. (All scales=0.25 mm.)



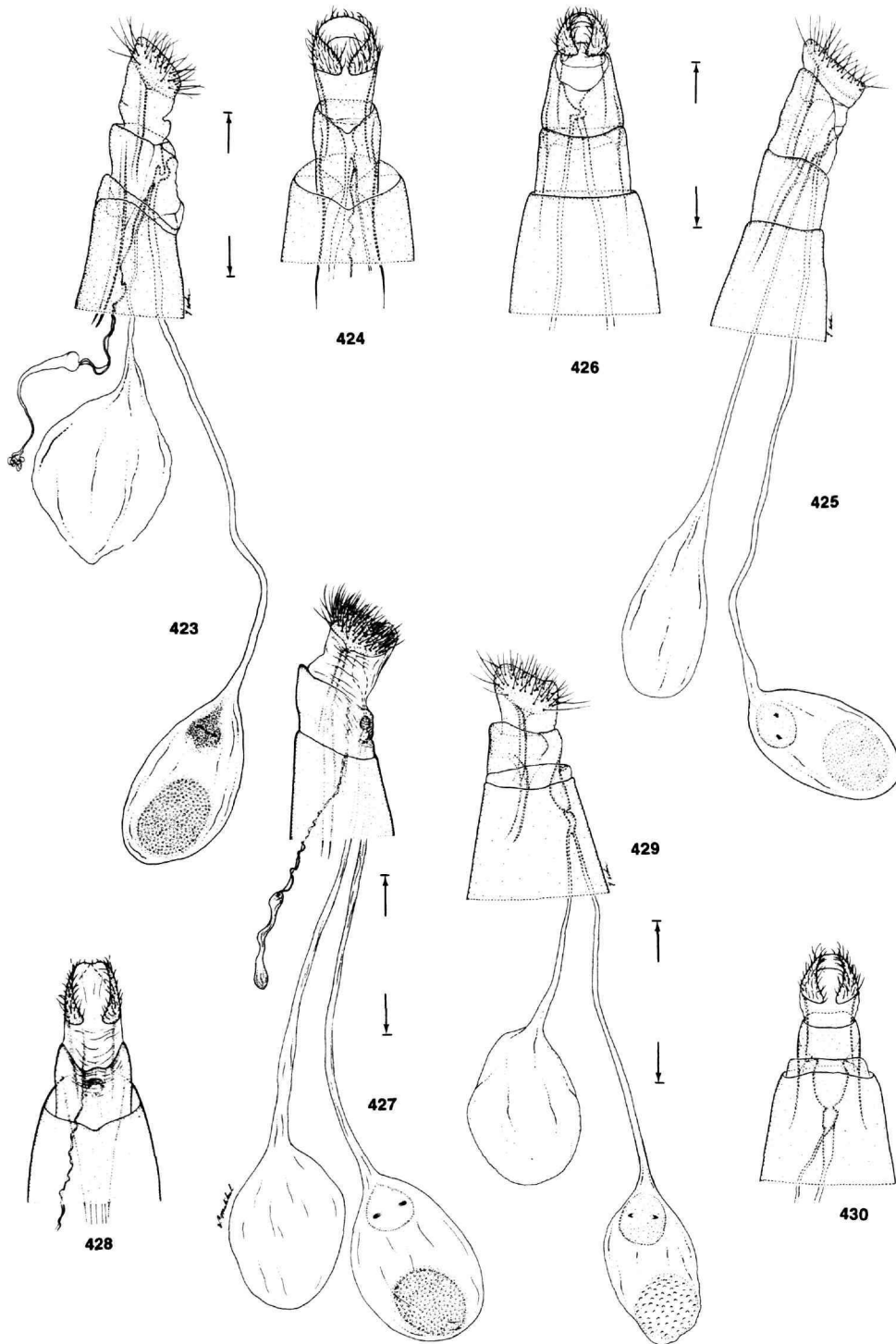
FIGURES 394–403.—Palearctic *Phyllonorycter*, male genitalia, eighth abdominal sternite. *P. dentifera* (central Asia; after Noreika and Puplesis, 1992a): 394, full view; 395, aedeagus; 396, sternite. *P. quinqueguttella* (Agasegyháza): 397, full view; 398, sternite; 399, aedeagus. *P. connexella* (=asiatica; central Asia; after Noreika and Puplesis, 1992a): 400, full view. *P. connexella* (Austria): 401, full view; 402, sternite; 403, aedeagus. (All scales=0.25 mm.)



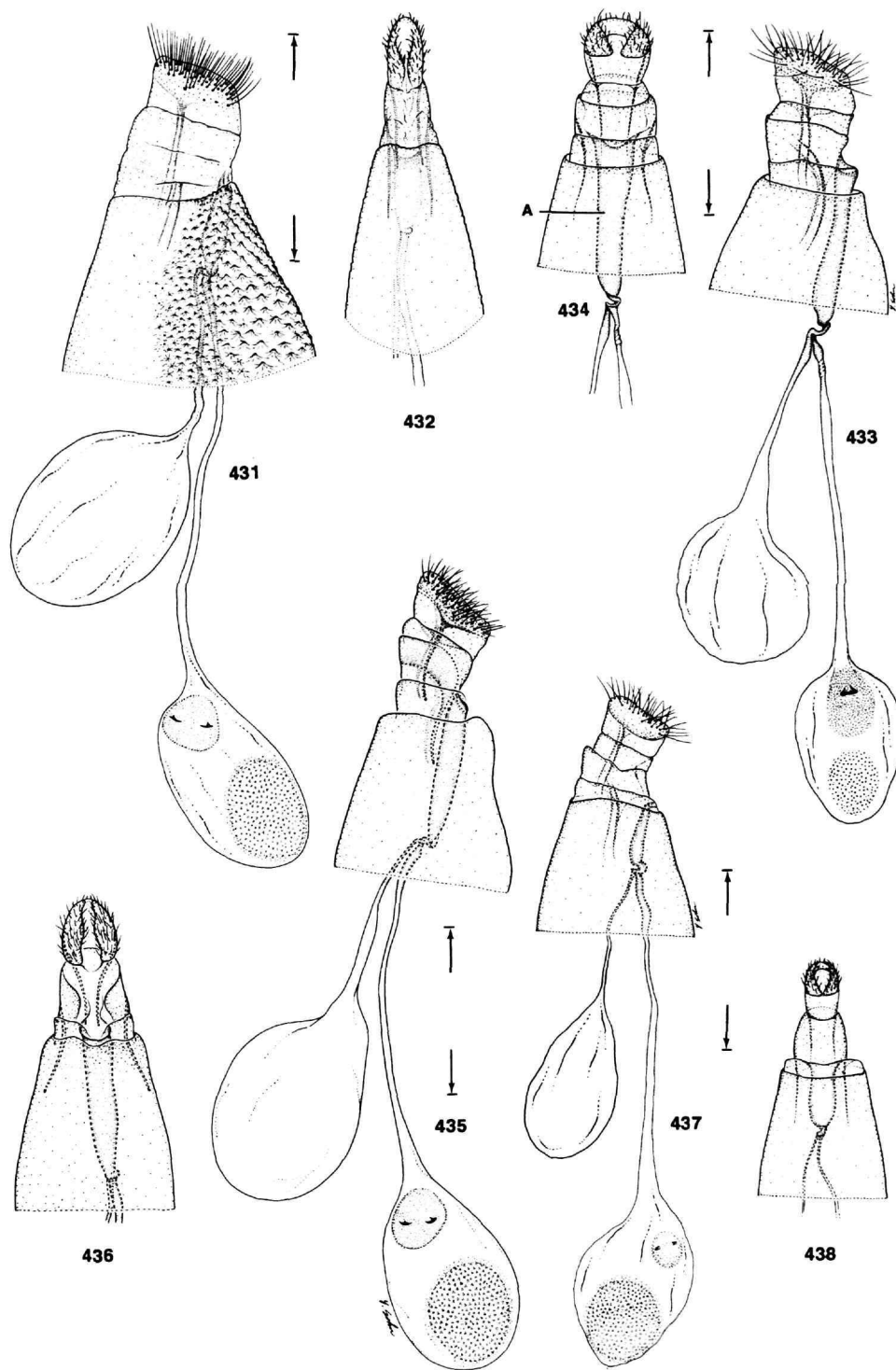
FIGURES 404–413.—Palearctic *Phyllonorycter*, male genitalia, eighth abdominal sternite. *P. pruinosella* (central Asia; after Noreika and Puplesis, 1992a): 404, full view. *P. viminetorum* (China): 405, full view; 406, sternite; 407, aedeagus. *P. hilarella* (Sweden): 408, full view; 409, sternite; 410, aedeagus. *P. rolandi* (Sweden): 411, full view; 412, sternite; 413, aedeagus. (All scales=0.25 mm.)



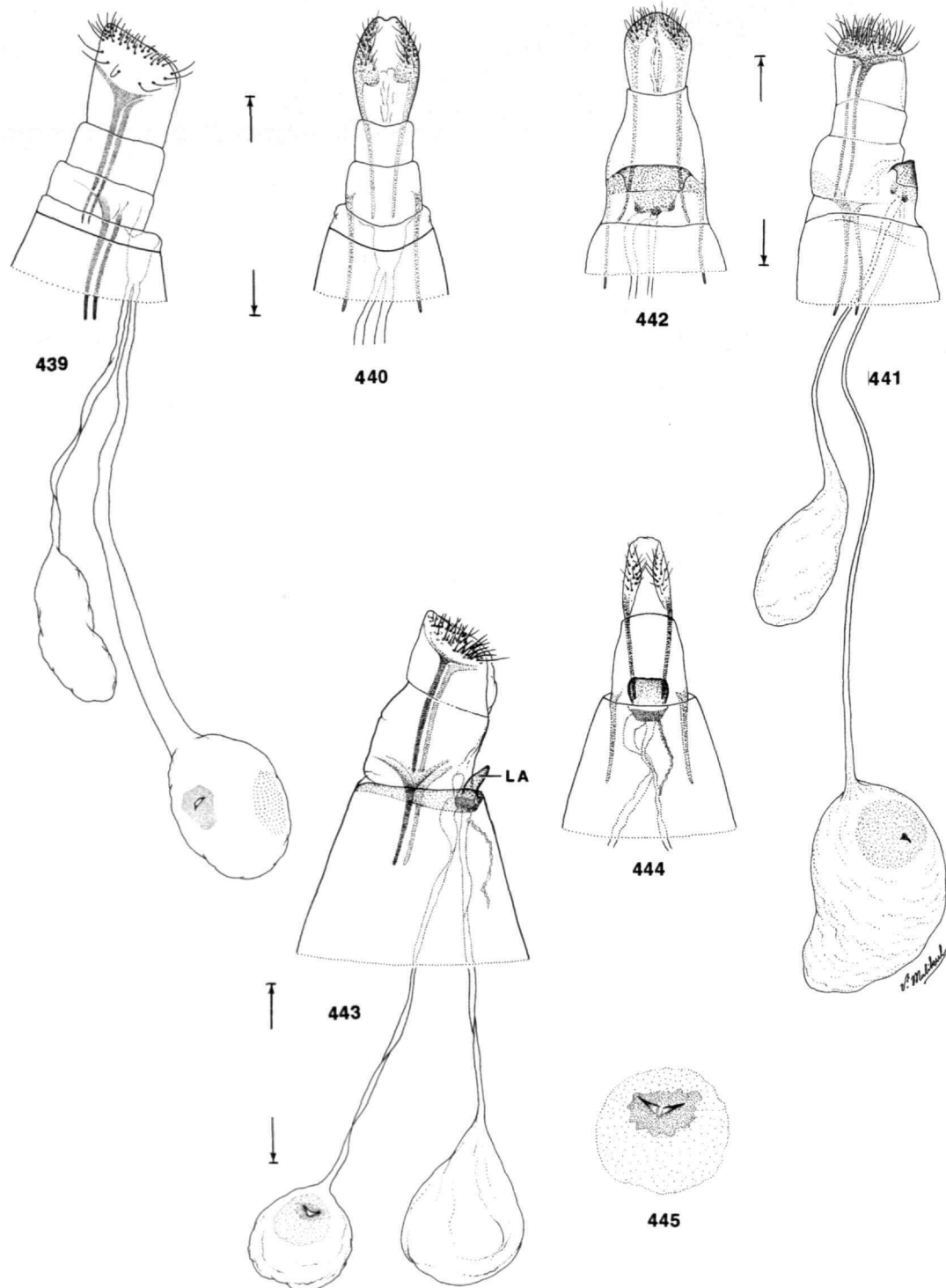
FIGURES 414–422.—Palearctic *Phyllonorycter*, male genitalia, eighth abdominal sternite. *P. salicicolella* (England): 414, full view; 415, aedeagus; 416, sternite. *P. dubitella* (Sweden): 417, full view; 418, sternite; 419, aedeagus. *P. salictella* (Italy): 420, full view; 421, aedeagus; 422, sternite. (All scales=0.25 mm.)



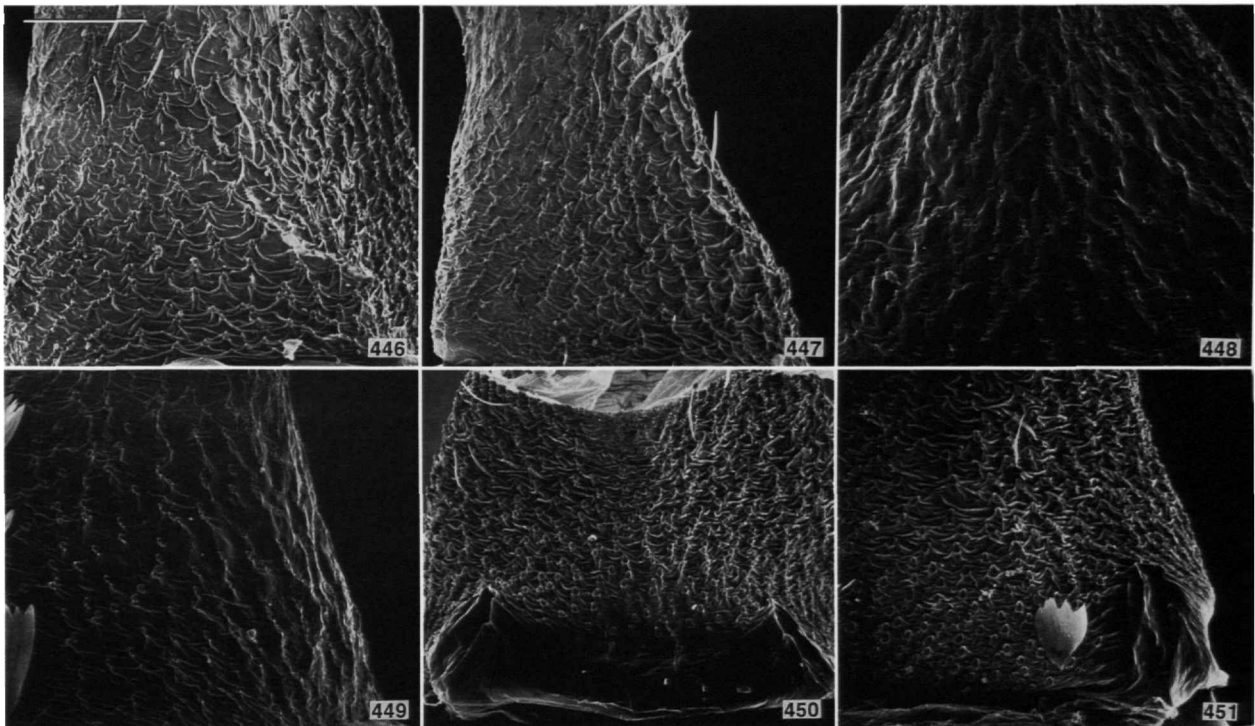
FIGURES 423–430.—North American *Phyllonorycter*; female genitalia. *P. apparella*: 423, lateral view; 424, ventral view. *P. latus*: 425, ventral view; 426, lateral view. *P. nipigon*: 427, ventral view; 428, lateral view. *P. deserticola*: 429, lateral view; 430, ventral view. (All scales=0.5 mm.)



FIGURES 431–438.—North American *Phyllonorycter*, female genitalia: *P. salicifoliella*: 431, lateral view; 432, ventral view. *P. acanthus*: 433, ventral view; 434, lateral view. *P. erugatus*: 435, ventral view; 436, lateral view. *P. mildredae*: 437, lateral view; 438, ventral view. (A=antrum; all scales=0.5 mm.)



FIGURES 439–445.—North American *Phyllonorycter*, female genitalia. *P. populiella*: 439, lateral view; 440, ventral view. *P. apicinigrella*: 441, ventral view; 442, lateral view. *P. scudderella*: 443, lateral view; 444, ventral view; 445, enlarged view of signum. (LA=lamella antevaginellus; all scales=0.5 mm.)



FIGURES 446–451.—North American *Phyllonorycter*; eighth abdominal sternum of female. *P. salicifoliella*: 446, ventral view (100 μm); 447, lateral view. *P. erugatus*: 448, ventral view (100 μm); 449, lateral view. *P. acanthus*: 450, ventral view (91 μm); 451, lateral view. (Scale lengths in parentheses; bar scale for all photographs shown in Figure 446.)

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