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TAXONOMIC REVIEW OF APPLE-FEEDING SPECIES OF *PHYLLONORYCTER* HÜBNER (LEPIDOPTERA, GRACILLARIIDAE) IN NORTH AMERICA

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Abstract.—Four species of *Phyllonorycter* whose larvae mine apple leaves are recognized in North America: *P. blancardella* (F.), *P. crataegella* (Clemens), *P. elmaella* Doğanlar and Mutuura, and *P. mespilella* (Hübner). The former two species are widely distributed in the eastern United States and southeastern Canada. We confirm the presence of *P. blancardella* in the Pacific Northwest, earliest records being from Oregon in 1985, Washington in 1986, and British Columbia in 1987. *Phyllonorycter mespilella* occurs over much of western North America, from California north to British Columbia, and east to Utah and New Mexico. *Phyllonorycter elmaella* is known from Oregon, Washington, and British Columbia. *Lithocolletis malimalifoliella* Braun is synonymized under *P. crataegella.* Records of *Phyllonorycter sorbi* (Frey) in North America and of *P. scudderella* (Frey and Boll) on apple are regarded as erroneous. *Phyllonorycter deceptusella* (Chambers), also wrongly mentioned as feeding on apple is here regarded as a *nomen dubium.* We provide keys based on external features and on genitalia of adults, as well as diagnoses and notes on the geographical distribution and biology of each species.

Key Words: Lepidoptera, taxonomy, biology, distribution, apple, tentiform leaf miner, North America, Gracillariidae, *Phyllonorycter*

With nearly 80 described species (Davis 1983) and dozens of as yet undescribed entities, the genus *Phyllonorycter* is one of North America's most taxonomically diverse genera of leafmining Lepidoptera. The larvae feed on a variety of woody perennials, usually forming tentiform mines on the underside of leaves (Needham et al. 1928). Eight species have been reported to feed on apple leaves in North America: *P. blancardella* (F.), *P. crataegella* (Clemens), *P. malimalifoliella* (Braun), *P. sorbi* (Frey), *P. mespilella* (Hübner), *P. elmaella* Doğanlar and Mutuura, *P. deceptusella* (Chambers), and *P. scudderella* (Frey and Boll) (Stultz 1964, Pottinger and LeRoux 1971: 6–9, Doğanlar and Mutuura 1980, Weires et al. 1980). *Phyllonorycter blancardella, P. crataegella,* and *P. elmaella* have often been reported as orchard pests. A fourth species, of European origin, *P. mespilella,* occurs abundantly on apples and related rosaceous plants, yet its presence in western North America has been all but overlooked. Our studies indicate that *P. mespilella* has been established in the western United States for at least 50 years, and that recent literature treating *P. elmaella* (e.g. Weires and Forshey 1978, Orphart 1982, Hoyt 1983, Barrett and Jorgensen 1986, Barrett and Brunner 1990, Jones 1991) likely refers to *P. mespilella.*

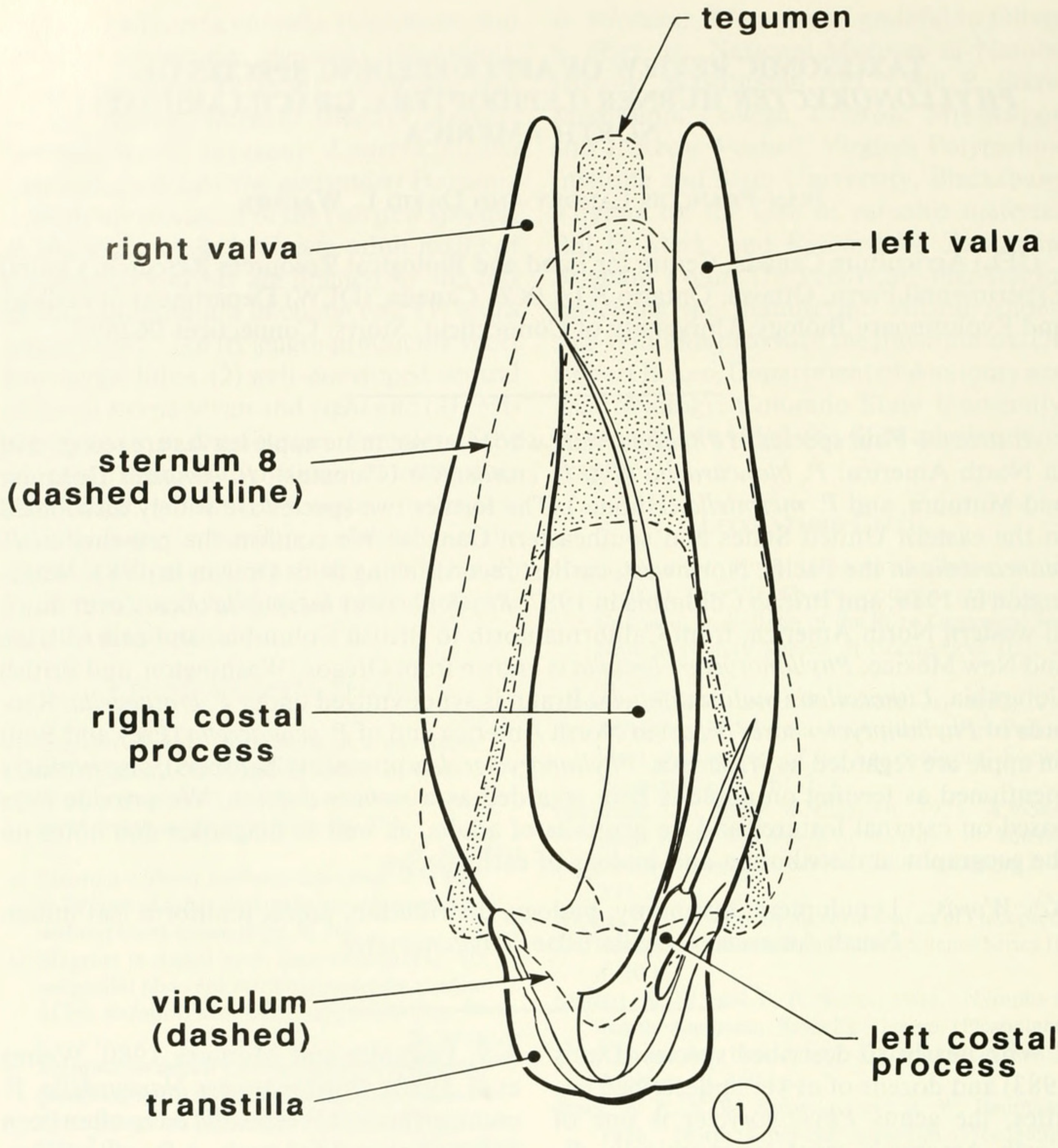


Fig. 1. Male genitalia of *Phyllonorycter* species, unspread, showing the position of tegumen (stippled) and sternum VIII (dashed); aedeagus omitted.

Pottinger and LeRoux (1971) comprehensively reviewed literature on the apple-feeding *Phyllonorycter* in North America up to 1964. They pointed out that there was much confusion, particularly among economic entomologists, as to what species they actually worked with, and that virtually all papers lacked reliable determinations. All the apple-feeding species are superficially very similar to one another. There are small differences in coloration and pattern among species, but these are often muddled by pronounced intraspecific, especially brood-related, variation. Stultz (1964) provided the first North American work in which male genital characteristics of *P. blancardella* and *P. crataegella* were compared and illustrated. Pottinger and LeRoux (1971) distinguished and illustrated the male genitalia of *P. blancardella, P. crataegella,* and *P. mespilella.* Neither work compared the female genitalia of these species. Doğanlar and Mutuura (1980) provided illustrations of both the male and female genitalia of *P. elmaella* but they did not compare them to other apple-feeding *Phyllonorycter.*

In order to clear the taxonomic confusion surrounding the apple-feeding species of *Phyllonorycter* in North America, we present diagnoses of adults, keys for separating them based on genital features and on adult coloration, and summaries of biological and distributional data for the species. We regard as valid four species for which we have examined specimens reared unequivocally from larvae mining apple (*Malus* spp.) leaves: *P. blancardella, P. crataegella, P. elmaella,* and *P. mespilella.* The first and the last are introduced from Europe; the other two are believed indigenous species, which transferred to apple from *Crataegus* and other native Rosaceae. Of the remaining species reported in the literature, one is a junior synonym [*P. malimalifoliella* (Braun, 1908a) = *P. crataegella* (Clemens, 1859), new synonymy], two are thought to have been reported in error [*P. sorbi* (Frey) and *P. scudderella* (Frey and Boll)], and the status of one remains uncertain [*P. deceptusella* (Chambers)]—it most resembles cherry feeding members of the genus.

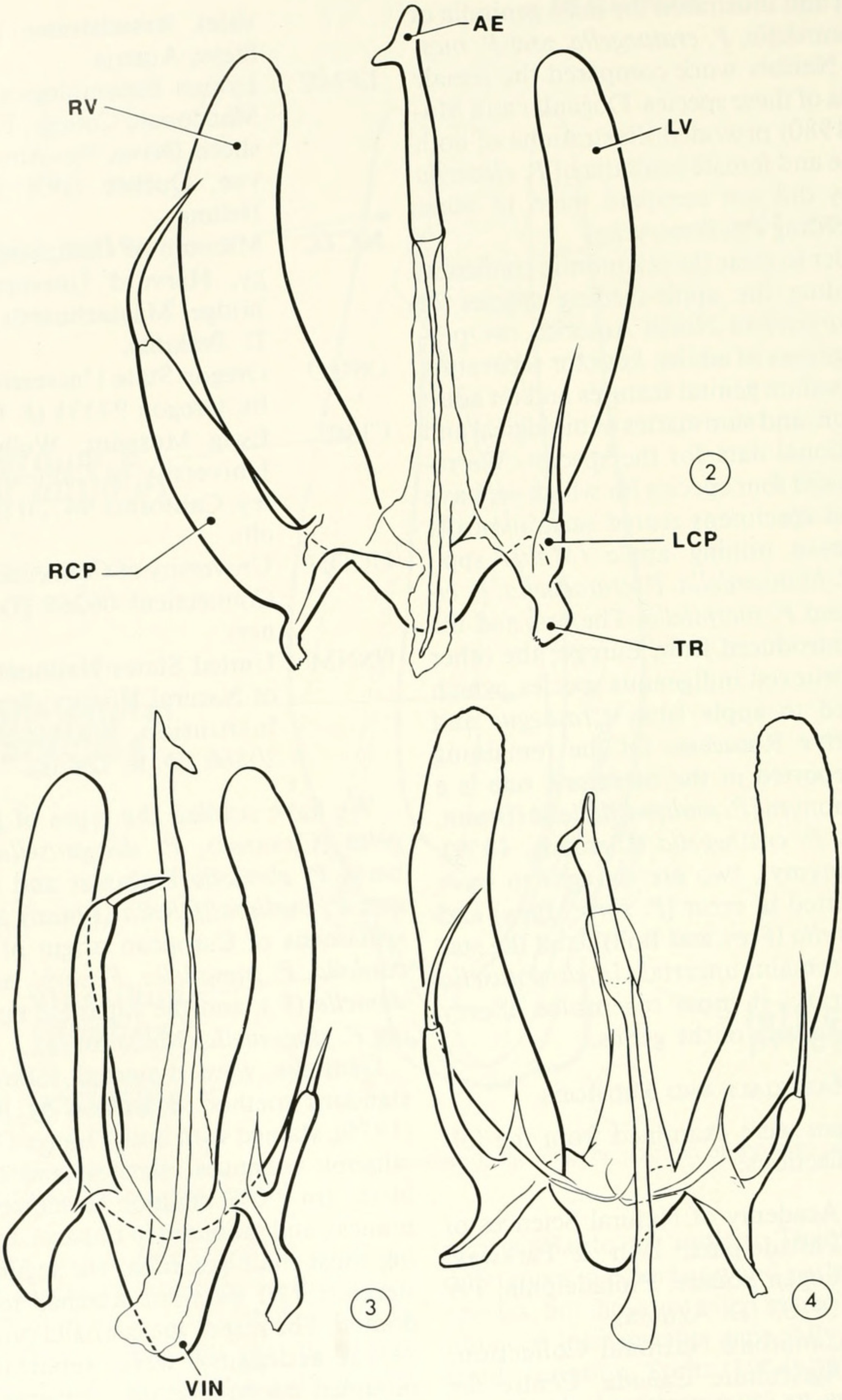
Materials and Methods

Specimens were examined from the following collections:

ANSP	Academy of Natural Sciences of Philadelphia, 19th & Parkway, Logan Square, Philadelphia, PA 19103 (D. Azuma).
CNCI	Canadian National Collection, Agriculture Canada, Centre for Land and Biological Resources Research, C.E.F., Ottawa, Ontario K1A 0C6 (J.-F. Landry).
DESC	Gerfried Deschka Collection (private), Resselstrasse 18, A-4400 Steyr, Austria.
LEMC	Lyman Entomological Museum, Macdonald College, 21111 Lakeshore Drive, Ste-Anne-de-Bellevue, Québec H9X 1C0 (C.-C. Hsiung).
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 (P. D. Perkins).
OSUO	Oregon State University, Corvallis, Oregon 97331 (J. D. Lattin).
CISC	Essig Museum, Wellman Hall, University of California, Berkeley, California 94720 (J. A. Powell).
UCON	University of Connecticut, Storrs, Connecticut 06269 (D. L. Wagner).
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (D. R. Davis).

We have studied the types of *P. crataegella* (Clemens), *P. deceptusella* (Chambers), *P. elmaella* Doğanlar and Mutuura, and *P. malimalifoliella* (Braun) as well as specimens of European origin of *P. blancardella, P. mespilella, P. sorbi,* and *P. cydoniella* (F.), and the Japanese apple-feeding *P. ringoniella* (Matsumura).

Genitalia were dissected following the standard method described by Robinson (1976), stained with both Orange G (in 30% ethanol; enhances sclerites) and chlorazol black (in 70% ethanol; enhances membranes), and mounted in Euparal. In mounting most male genitalia, the tegumen and sternum VIII were left attached to the abdomen. The rest of the genitalia (vinculum-valvae-aedeagus) were separated and mounted dorsal side up after severing the transtilla medially and prying the valvae apart, in order to expose dorsally the costal processes, thereby providing a diagnostic view of the genitalia (e.g. Figs. 2–4). Female



Figs. 2–4. Male genitalia of *Phyllonorycter* species, dorsal aspect, with tegumen, sternum VIII, and setae of valvae omitted; transtilla cut medially with valvae and their processes spread flat; posterior end oriented towards top of page. Abbreviations are as follows: AE, aedeagus; LCP, left costal process; LV, left valva; RCP, right costal process; RV, right valva; TR, transtilla; VIN, vinculum. 2, *mespilella* (slide MIC 2071); 3, *crataegella* (slide JFL 785); 4, *elmaella* (slide JFL 860).

genitalia were left within the abdomen and mounted ventral side up (removing the genitalia can cause much distortion or damage).

Records that we mention below have been confirmed by genital dissections and are deposited in the collections indicated in parentheses.

Drawings were prepared with a drawing tube mounted on a Nikon Optiphot compound microscope, at magnifications of 100× or 200×. Drawings were prepared from single specimens whenever possible, but parts have been re-arranged slightly on some drawings to compensate for distortions present in slide preparations. In the illustrations, the posterior end is directed upward on the page. Male genitalia are shown in dorsal aspect, females in ventral aspect; hence in male illustrations, the actual right side appears on the left. Positions of the costal processes are affected by preparation and therefore are not indicative of specific differences.

Photographs of the adults were taken with a Nikon F3 camera fitted with a Leitz 63 mm objective, using Kodak Technical Pan film (set at 12 ASA) and processed in Kodak Technidol.

General Aspects of Life History

The species in this group have closely similar life histories. The eggs, about 0.3 mm in length, are flat and oval, and laid on the lower leaf surface. All species have three sap-feeding and two tissue-feeding larval instars. The legless sap-feeding instars expand the mine to its full extent, separating the lower leaf surface from the overlying parenchymic tissues. From below the mine appears waxy white to greenish; the early instar mine is not visible from above.

The fourth and fifth tissue-feeding instars are legged with a fully developed spinneret that they use to lay down silk within the mine, that pulls the edges of the mine inwards, drawing the mine into an elongate tentiform bubble. The lower leaf surface is drawn into a set of four to numerous closely set creases. The larvae remove small patches of tissue up to the upper leaf surface, giving the upper side of the leaf a shot-hole or skeletonized appearance, and hence the common name for the group, the "spotted tentiform leafminers." The size of the mines may vary depending on the host, e.g. on apple cultivars with thick leaves the mine may average considerably smaller. The fifth instar spins a sparse cocoon against the upper side of the mine and pupates within a few days. The pupa is extruded through the lower leaf surface prior to eclosion of the adult.

The species in this group are multivoltine with pupae overwintering within the mines. At least two broods and as many as five broods, are inferred. For example, in California, *P. mespilella* has up to five generations in the Central Valley, three to four broods in coastal areas, and as few as two generations in higher elevation apple and pear orchards in the Sierra Nevada (L. Varela, in litt. 1993). Three broods are reported for both *P. crataegella* and *P. blancardella* in the northeastern United States (Maier 1985, Maier and Davis 1989). The presence of summer-diapausing sap-feeding instars is reported for second-generation individuals of *P. blancardella* (Laing et al. 1986) and probably occurs in other members of the group as well (Maier and Davis 1989). For more information on biology, consult Pottinger and LeRoux's (1971) monographic treatment of *P. blancardella*; much contained therein is likely applicable to the other apple-feeding species.

Some populations of *Phyllonorycter crataegella* and *P. blancardella* have developed insecticide resistance in sprayed orchards in eastern North America (Maier 1983, Pree et al. 1986, Barrett and Brunner 1990). In California *P. mespilella* has developed resistance to both guthion and vygate (L. Varela, in litt.). Thus, accurate species identification may be necessary if effective control is intended.

We have acquired numerous collections of active mines throughout our study from apple trees growing in Arkansas, British Columbia, California, Connecticut, New York, Ontario, Oregon, Utah, Vermont, and Washington, and in only one case has a collection yielded more than a single species. This is surprising in that both *P. blancardella* and *P. crataegella* are broadly sympatric over much of eastern North America and *P. blancardella, P. elmaella,* and *P. mespilella* over the Pacific Northwest. Weires et al. (1980) reported several sites in New York where both *P. crataegella* and *P. blancardella* co-occurred although the latter species predominated in most orchards.

Early collections from Nova Scotia (pre-1950) were all *P. crataegella,* but beginning in 1957, *P. blancardella* began outbreaking in Nova Scotia (Stultz 1964). All recent collections from eastern Canada in the CNCI have been of *P. blancardella.* Stultz (1964), in his studies of apple-feeding *Phyllonorycter* in Nova Scotia, was unable to locate a single population of *P. crataegella* on apple during the several years of his survey efforts. In Europe, *P. blancardella* tends to replace other species of *Phyllonorycter* once established in an area (G. Deschka, in litt. 1993). If competitive displacement is a common outcome among these apple-feeding species, the situation in the Pacific Northwest should prove especially interesting in that both *P. blancardella* and *P. mespilella* are introduced-the former presumably has been present little more than a decade. Indeed, *P. elmaella* may have been common on apple prior to the arrival of these two moths, but presently we do not know of a single orchard where *P. elmaella* can be reliably obtained.

Related to the above may be the fact that the apple-feeding species may respond to a common, or at least to common components of the female sex pheromone. A female-produced sex attractant of *P. blancardella,* identified by Roelofs et al. (1977) as (E10)-Dodecenyl acetate, has also been used to survey for adults of *P. mespilella* (Cossentine and Jensen 1992, Gries et al. 1993). However, it is scarcely, if at all, attractive to males of *P. crataegella* (Weires et al. 1980). In Europe Deschka (in litt. 1993) noted that related Rosaceae-feeding species of *Phyllonorycter* (but not all of them) have one and the same pheromone, and the males of two or more species may be attracted to a single female.

Remarks on Identification

External characters.—Considerable phenotypic differences occur both within and between broods such that it is virtually impossible to identify reliably all adults using only scaling characters. But because color characters have been used extensively in the past, we provide a discussion of features that have diagnostic value. Series rather than individuals should be examined whenever possible. Antennal and hindleg coloration applies to the scaling of the dorsal surfaces. The white scales of the mesoscutellum are easily abraded during the process of pinning.

Individuals of the overwintering or spring brood tend to be larger and more darkly marked. In some specimens of *P. blancardella* the orange forewing scales may be mostly replaced or overlaid with dark scales. The legs and antennae also tend to be more fuscous in the spring generation. Summer generation moths vary greatly in size, but average smaller (for each species, our measurements are based on the examination of more than 20 specimens, except where noted), black scaling is much reduced, and the orange ground color appears paler. Moths emerging in the fall display both spring (few) and summer (most) phenotypes.

Genital characters.—Reliable identification of *Phyllonorycter* species feeding on pomoid and prunoid Rosaceae should be based on examination of the genitalia. Vouchers with their dissected abdomen and genitalia should always be preserved. Whenever possible adult moths should be pinned, preferably on minutens and staged (double-mounted). They should *never* be glued on points, as this often renders removal of the abdomen for genital examination difficult or impossible. A simple and rapid method for mounting microlepidoptera is described in Landry and Landry (1994). Dry specimens from light traps or sticky specimens from pheromone traps should be relaxed and pinned, preserved in ethanol, or placed into small microvials mounted on pins. In the latter case a tiny plug of cotton within the microvial will reduce excessive movement.

To dissect and examine the genitalia, the whole abdomen (on dry specimens, easily removed by applying from beneath gentle upward pressure with fine forceps) is soaked in 20% KOH (aqueous solution) for 2–3 hours at room temperature, or for 3–5 minutes in a warm (but not boiling) water bath. The abdomen is then descaled in 30% ethanol using very fine camel hair brushes to expose the genitalia; the digested abdominal content should be extruded through the anterior (proximal) opening by gentle pushes with the brush. A less satisfactory result can be obtained by gently rolling away the abdominal contents and scales with the head of an insect pin. It is usually not necessary to separate the genitalia from the abdomen to view diagnostic characters. The genitalia may be then examined in alcohol, glycerine, or lactic acid, and stored in glycerine in a microvial kept with the specimen. Permanent slide mounts, such as in Euparal or Canada balsam, are desirable but not essential for routine identifications. For the preparator inexperienced with permanent slide mounts, glycerine preservation of dissected vouchers is preferable to poor permanent slides. Before storage into glycerine the abdomen-genitalia should be briefly soaked in lactic acid or in 30% ethanol acidified to pH 4 with a few drops of acetic acid, to ensure that all KOH is neutralized, then rinsed in water.

Terms.—Terms for genitalia are shown in Figs. 1–3 and 9, those for forewing maculation in Fig. 13. We refer to the sterigma as any sclerotized area that surrounds the female copulatory opening or ostium bursae. In *Phyllonorycter* species treated here, the sterigma derives from modification of the posterior margin of sternum VIII and the attached anterior apophyses.

Externally males can be separated from females by examining either the frenulum or the apex of the abdomen. Males have a single frenular bristle, females have two. In males the valvae, tegumen, and sternum VIII, though covered by scales, are usually discernable; ventrally a longitudinal slit is visible where the valvae come together. In females the apex of the ovipositor usually protrudes from the abdomen, appearing as a setose lobe.

Key to Adults Based on Genital Characters

1a. Males 2
1b. Females 5
2a. Right costal process dilated, thicker than left process. Valvae asymmetrical, right valva broader than left valva (Fig. 2) ... *P. mespilella*
2b. Right costal process slender, comparatively as thin as left process. Valvae symmetrical or nearly so, right valva as wide as left valva (Figs. 3–5) 3
3a. Right costal process (excluding apical spine) subequal to or slightly longer than left costal process (Fig. 4) .... *P. elmaella*
3b. Right costal process (excluding apical spine) at least twice as long as left costal process (Figs. 3, 5–7) 4
4a. Spines of costal processes long and slender, setiform. Left costal process very short and stubby (Fig. 5), exceptionally in few specimens left process about one-third length of right process (Figs. 6–7) .... *P. blancardella*
4b. Spines of costal processes short and stout, spiniform. Left costal process about half length of right process (Fig. 3) .... *P. crataegella*
5a. Posterior margin of sternum VIII markedly projected into truncate cone (Figs. 9–10) .... *P. blancardella*
5b. Posterior margin of sternum VIII not projected or only slightly protruded (Figs. 8, 11–12) 6

6a. Ostium bursae surrounded by ringlike thickening (Fig. 12) .... *P. mespilella*
6b. Ostium bursae without sclerotized ring 7
7a. Posterior margin of sternum VIII concave (Fig. 11). Base of ovipositor distad of ostium bursae membranous, flat. Anterior apophyses situated closer to middle of sternum VIII than to its lateral margins .... *P. elmaella*
7b. Posterior margin of sternum VIII straight or slightly convex. Base of ovipositor distad of ostium bursae sclerotized, medially elevated, laterally steeply sloped, with transverse cuticular creases just caudad of ostium bursae (Fig. 8). Anterior apophyses situated closer to lateral margins of sternum VIII than to its middle .... *P. crataegella*

Key to Adults Based on External Characters

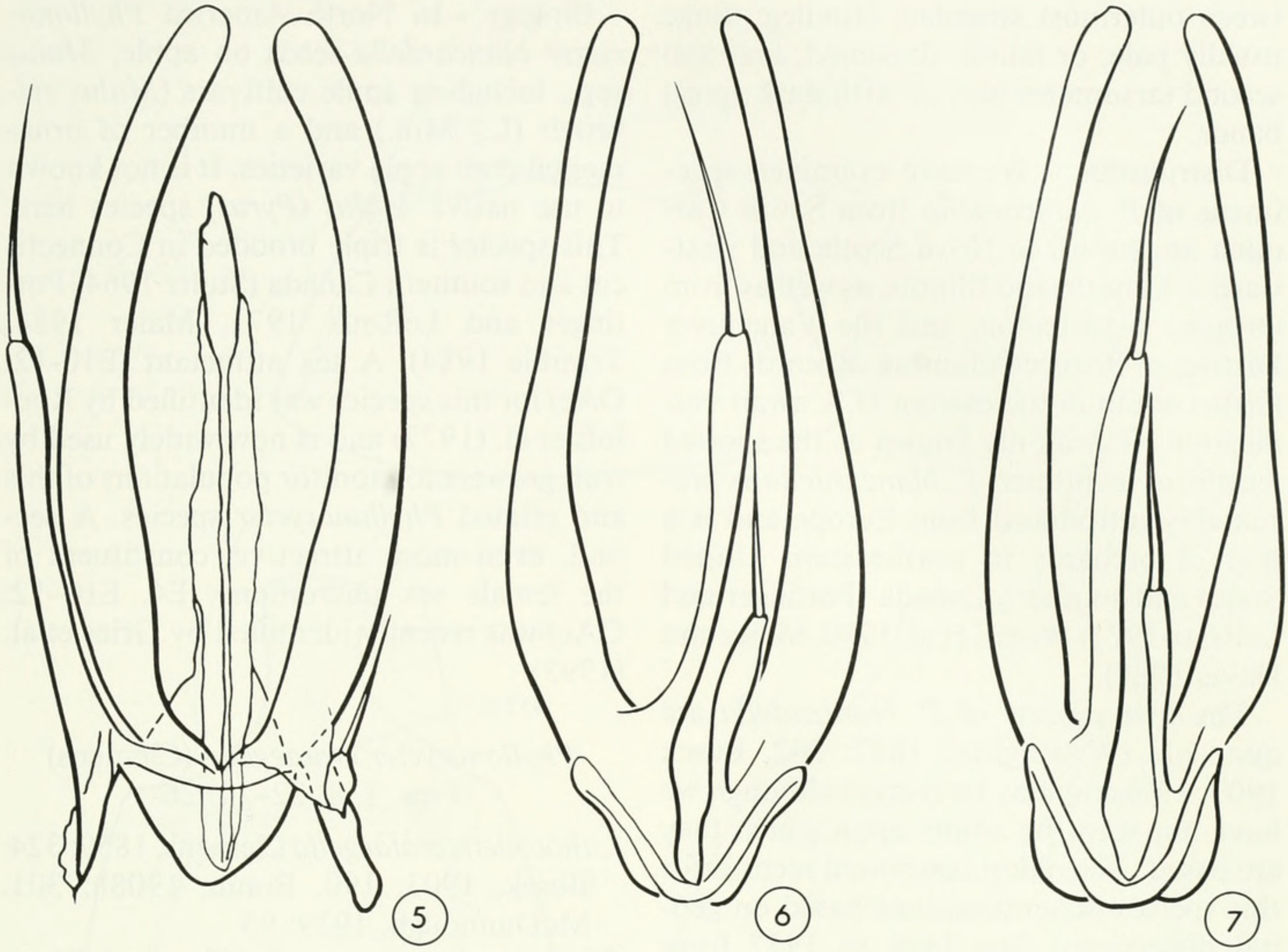
This key is provided for convenience, but results should *always* be checked by examining genitalia. Some variant individuals will not key out. Diagnostic features may not be well rendered in our black and white photographs. Lastly, scale colors lighten appreciably as specimens age in collections.

1a. Forewing with basal patch that tends to bulge toward basal streak (e.g. Figs. 17, 20); mesoscutellum with prominent patch of white scales; basal streak broad, of 4–6 scale rows, often subequal or exceeding width of orange-scaled area between basal streak and costa (Figs. 16–18, 20) .... *P. blancardella*
1b. Forewing with basal patch narrow, parallel to wing margin (few individuals in series with bulge); mesoscutellum with few or no white scales; basal streak narrow, of 3–4 scale rows, often subequal or much narrower than width of orange-scaled area between basal streak and costa (Figs. 22–24, 26–37) 2
2a. Axis of first costal strigula running to dorsal (posterior) margin, less than twice as long as broad, often touching or confluent with first dorsal strigula (Figs. 27–29); fourth costal strigula often expanded toward wing apex and broader than third; ground color orange; first metatarsomere pale white or gray scaled (rarely with subapical dark band) ...... *P. elmaella*
2b. Axis of first costal strigula running to tornus or outer margin, usually more than twice as long as broad, infrequently touching or confluent with first dorsal strigula (Figs. 22–24, 26, 30–37); fourth costal strigula reduced or absent; ground color coppery, fiery or red orange; first metatarsomere with conspicuous black subapical dark band or black scaling dorsad 3
3a. Antenna mostly pale to fuscous, terminal articles occasionally darkened; first metatarsomere mostly pale, often with apical band of dark scales; forewing with apical row of lamelliform scales (before ciliary fringe) dark only in distal half, forming narrow iridescent blue-black band between outermost fasciae (Figs. 30–37); forewing ground color fiery orange or red orange .... *P. mespilella*
3b. Antenna mostly dark (especially dorsal surface); first metatarsomere dorsally entirely dark (some specimens with light scales apically); forewing with apical row of lamelliform scales dark for at least two-thirds of their length, forming broad iridescent blue-black band between outermost fasciae (Figs. 22–24); ground color with decided metallic or coppery luster .... *P. crataegella*

Phyllonorycter blancardella (F.)
Figs. 5–7, 9–10, 14–21

Tinea blancardella Fabricius, 1781: 305.
Lithocolletis blancardella (F.): Pottinger and LeRoux, 1971.
Phyllonorycter blancardella (F.): Bradley, 1972: 10. Davis, 1983: 10. Emmet et al., 1985: 319.
Lithocelletis concomitella Bankes, 1899: 246.

Diagnosis.—In male genitalia (Fig. 5), *P. blancardella* is recognized by the markedly different costal processes, the right process being slender, with a slender apical spine that is about one-third the length of the process and extends nearly to the apex of the valva. The valvae are the narrowest of the species here treated. The left process is very short and stubby in most specimens (Fig. 5), but some variation occurs in its length, and exceptionally it can be up to nearly half the length of the right process (Figs. 6–7). Specimens with an unusually long left process resemble in that respect specimens of *P. elmaella,* but in the latter the right process is much shorter and the valvae are broader than in *P. blancardella.* The apical hooklike lobe of the aedeagus is barely sug-



Figs. 5–7. Male genitalia of *P. blancardella* in dorsal aspect with tegumen, sternum VIII and setae of valvae omitted; posterior end oriented towards top of page; 5, transtilla cut medially with valvae and their processes spread flat (slide MIC 2077); 6, redrawn from Pottinger and LeRoux (1971, p. 217, fig. 18-B), showing variation in length of left costal process; 7, *id.* (p. 220, fig. 21-F).

gested in *P. blancardella* (Fig. 5), whereas it is distinct in *P. elmaella* (Fig. 4).

In female genitalia (Figs. 9–10) *P. blancardella* is the most distinctive of the species. It is recognized by the markedly projected sterigma which forms a truncate cone extended far beyond the posterior margin of sternum VIII. The length and width of the conical projection vary somewhat, but the overall aspect is unlike that of any of the other species.

Forewing length: spring generation, 3.1–4.5 mm (n = 20); summer generation, 3.0–4.3 mm (n = 20). Antenna often fuscous in winter generation and pale with conspicuously darkened terminal articles in summer broods. Mesothoracic scutellum with distinct patch of white scales, 3–6 rows wide. Forewing (Figs. 14–21) with white and black scales more or less equal in number to orange scales; black scaling especially prominent in spring brood (Figs. 18–20); white basal patch (anal macula) 2–5 scale rows wide, often bulging toward basal streak; first costal strigula usually at least twice as long as broad, axis usually intersecting tornus or outer margin, rarely confluent with first dorsal strigula (Fig. 16); fourth costal strigula often subequal to third; basal streak broad, of 4–6 scale rows, often subequal or exceeding width of orange-scaled area between basal streak and costa, in some specimens, basal streak connected to first dorsal strigula (Fig. 20); outer row of lamelliform fringe scales with distal ½ darkened, forming narrow iridescent blue-black band between outermost strigulae. Hindleg: tibiae usually pale, or faintly darkened; first and second tarsomeres pale or with dark apical bands.

Distribution.—We have examined specimens of *P. blancardella* from South Carolina northward to Nova Scotia and westward to Ontario and Illinois, as well as from Oregon, Washington, and the Vancouver District of British Columbia. Records from farther south in the eastern U.S. await verification. Commonly known as the spotted tentiform leafminer, *P. blancardella* is presumably introduced from Europe and is a pest of orchards in northeastern United States and southern Canada (Pottinger and LeRoux 1971, Weires et al. 1980, Maier and Davis 1989).

The first reports of *P. blancardella* are quite old (Walsingham 1882: 202, Busck 1903: 190) and may be correct although we have not seen the adults upon which they are based. The oldest confirmed records for this species (determinations based on genital dissections) date back to 1957 from Nova Scotia (Stultz 1964), but presumably the insect was established here well before this time. The oldest specimens of *P. blancardella* that we have examined were collected in 1959 in Québec and Nova Scotia (CNCI).

The occurrence of *P. blancardella* on the West Coast is probably recent. The first confirmed West Coast specimens were collected from cultivated apple in November 1985 from Wilsonville, Clackamas Co., Oregon (UCON), August 1986 from Concrete, Skagit Co., Washington (DESC), and October 1987 from a nursery orchard in Chilliwack, Vancouver District, British Columbia (CNCI). R. Duncan (pers. comm.) of Agriculture Canada in Victoria noted that a species of *Phyllonorycter* first appeared as a pest in Victoria in 1987; specimens from infested orchards, which turned out to be *P. blancardella,* were sent to DLW in the summer of 1988. Thus the western distribution of *P. blancardella* already may be more extensive than our records indicate.

Biology.—In North America *Phyllonorycter blancardella* feeds on apple, *Malus* spp., including apple cultivars (*Malus sylvestris* (L.) Mill.) and a number of ornamental crab apple varieties. It is not known to use native *Malus* (*Pyrus*) species here. This species is triple brooded in Connecticut and southern Canada (Stultz 1964, Pottinger and LeRoux 1971, Maier 1984, Trimble 1984). A sex attractant (E10-12: OAc) for this species was identified by Roelofs et al. (1977) and is now widely used by fruit growers to monitor populations of this and related *Phyllonorycter* species. A second, even more attractive, constituent of the female sex pheromone (E4, E10–12: OAc) was recently identified by Gries et al. (1993).

Phyllonorycter crataegella (Clemens)
Figs. 3, 8, 22–24, 26

Lithocolletis crataegella Clemens, 1859: 324. Busck, 1903: 190. Braun, 1908b: 301. McDunnough, 1939: 95.

Phyllonorycter crataegella (Clemens): Davis 1983: 10.

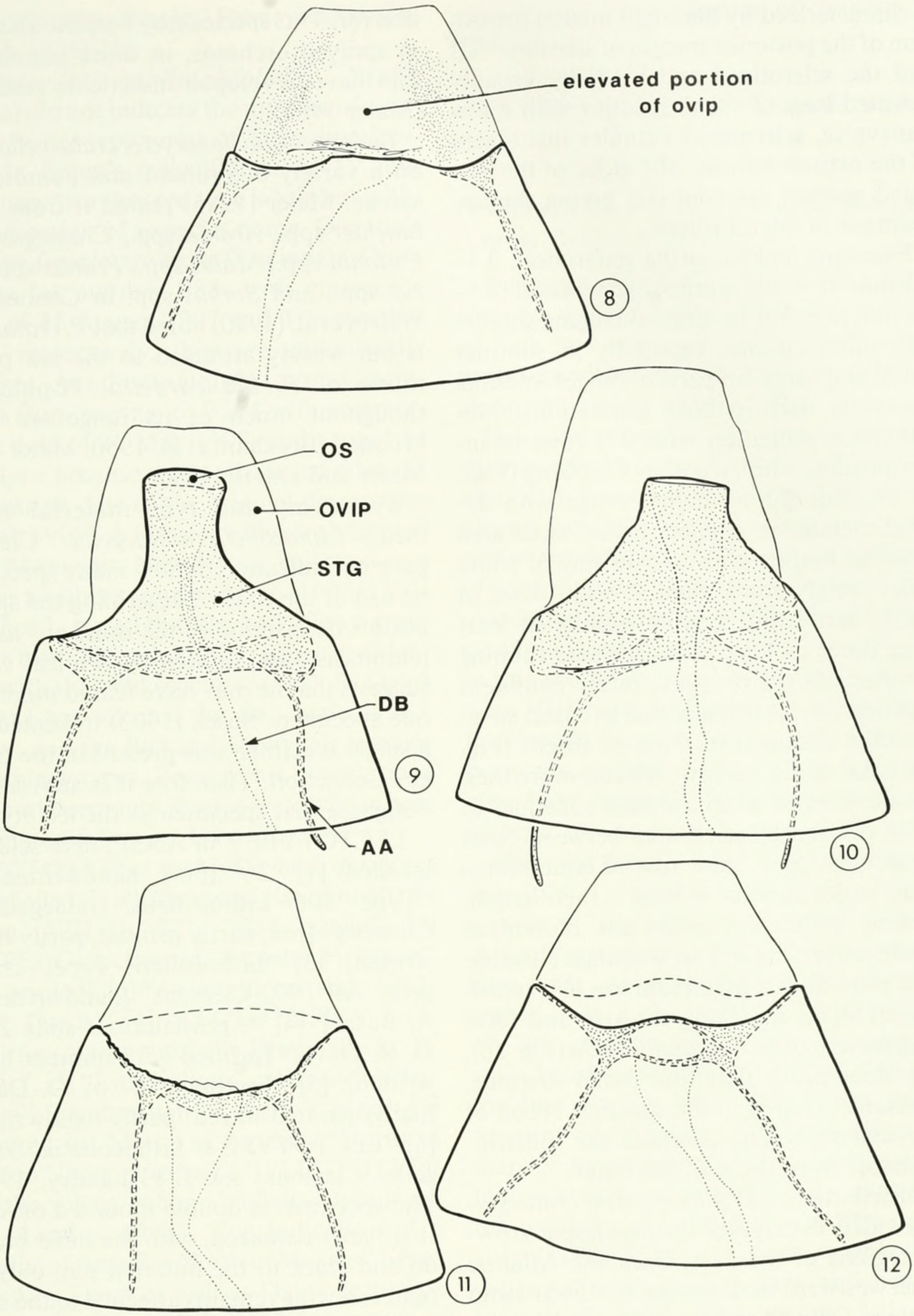
Lithocolletis malimalifoliella Braun, 1908a: 101 (New synonymy). Braun, 1908b: 300. McDunnough, 1939: 95.

Phyllonorycter malimalifoliella (Braun): Davis, 1983: 10.

Lithocolletes [sic] *blancardella* (F.): *sensu* Dyar, 1902: 551.

Diagnosis.—In male genitalia (Fig. 3), *P. crataegella* is characterized by the regularly tubular costal processes with short and stout apical spines. The left costal process is about one-third the length of the right one. The apical portion of the right costal process is slightly bent. Some specimens of *P. blancardella* with an unusually long left costal process are the only other members of the group with costal processes of approximately similar relative length as those of *P. crataegella,* but they are easily distinguished by their slender, setalike spines and narrow valvae.

In female genitalia (Fig. 8), *P. crataegella*



Figs. 8–12. Female genitalia of *Phyllonorycter* species, ventral aspect; posterior end oriented toward top of page. Abbreviations are as follows: AA, anterior apophysis; DB, ductus bursae; OS, ostium bursae; OVIP, base of ovipositor; STG, sterigma. 8, *crataegella* (slide MIC 2099); 9, blandardella (slide JFL 833); 10, *blancardella* (slide JFL 817); 11, *elmaella* (slide JFL 830); 12 *mespilella* (slide JFL 834).

is characterized by the slight medial protrusion of the posterior margin of sternum VIII and the sclerotized and medially broadly elevated base of the ovipositor with a few transverse, sclerotized wrinkles just distad of the ostium bursae. The sides of the elevated portion are concave, giving the appearance of lateral ridges.

Forewing length: spring generation, 3.1–4.3 mm (n = 30); summer generation, 2.5–3.6 mm (n = 30), in series averaging smaller than other species, especially in summer brood and southern parts of range. Antenna uniformly dark in both generations. Mesothoracic scutellum with 2–3 rows of inconspicuous whitish scales. Forewing (Figs. 22–24, 26): ground color orange with decided metallic or coppery luster; basal area of dorsal margin with narrow line of white scales, rarely more than 2 scale rows in width; first costal strigula usually at least three times as long as broad, axis running to outer margin or apex, rarely confluent with first dorsal strigula; fourth costal strigula often subequal to third or absent (Fig. 26); basal streak narrow, seldom more than 4 scale rows in width, always subequal to width of orange-scaled area between basal streak and costa; outer row of lamelliform fringe scales dark for at least ⅔ their length, forming prominent iridescent blue-black band between outermost strigulae. Hindleg: tibia black above; all tarsomeres blackened.

Individuals matching the size and forewing pattern of *P. malimalifoliella* (Fig. 26), with three rather than four costal strigulae, represent variants of the summer brood of *P. crataegella*. The genitalia are indistinguishable from those of the latter.

Distribution.—*Phyllonorycter crataegella* is widely distributed through apple-growing regions of the East, from the Atlantic Coast westward to Arkansas, northward into southern Ontario and Nova Scotia. Western North American records (Wilson 1915, Braun 1939, Pottinger and LeRoux 1971: 16) remain unconfirmed and are probably in error. This species may be quite abundant in sprayed orchards, in those populations that have developed insecticide resistance (Maier 1983).

Biology.—*Phyllonorycter crataegella* feeds on a variety of prunoid and pomoid Rosaceae. Maier (1985) reared it from *Amelanchier* spp., *Aronia* spp., *Crataegus* spp., *Cydonia* spp., *Malus* spp., *Prunus* spp., *Pyrus* spp., and *Sorbus* spp. in Connecticut. Weires et al. (1980) noted that *P. crataegella* is but weakly attracted to the sex pheromone of *P. blancardella*. Populations thoughout much of its range are triple brooded (Beckham et al. 1950, Maier 1981, Maier and Davis 1989).

Synonymy and type material examined.—*Lithocolletis crataegella:* Clemens gave no indication of how many specimens he had at the time of describing the species but his description of the mine as "*usually* [emphasis ours] limited by two leaf veins" suggests that he may have reared more than one specimen. Busck (1903) indicated that a single specimen was present in the Clemens Collection. Therefore it is advisable to designate that specimen as the lectotype.

LECTOTYPE ♂ in ANSP, here selected, labelled: [1] "26" [pink, handwritten]; [2] "Type 7506/ Lithocolletis/ crataegella/ B. Clemens" [red, partly printed, partly handwritten]; [3] "Lithocolletis Type!/ crataegella/ AB 1902 Clemens" [handwritten by A. Busck]; [4] "♂ genitalia on/ slide 2938/ D. R. Davis" [printed with number handwritten]; [5] "Lectotype ♂ / by D. Davis" [partly printed in red, partly handwritten]; [6] "LECTOTYPE ♂/ Lithocolletis/ crataegella/ Clemens/ sel. J.-F. Landry, 1993". The specimen is double mounted on cork. It is badly damaged, with the head broken off and stuck to the minuten pin; only the right forewing remains attached to the specimen; the metathorax, hindwings, and hindlegs are broken off and in a gelatin capsule pinned with the specimen. The lectotype selection by Davis is unpublished. Type locality: probably Easton, Pennsylvania (see Hodges 1986: 36).

Lithocolletis malimalifoliella: Braun (1908a) did not indicate the number of specimens in her type series of *L. malimalifoliella.* In Braun's collection at ANSP four specimens bear her red type labels but without indication of a species name. One male and one female are from Cincinnati, Ohio, rearing lot number B88, with emergence dates of 31 August 1907 and 1 September 1907, respectively; they are undoubtedly syntypes. Another male, also from Cincinnati is from rearing lot B264 with an emergence date of 26 May 1908, and cannot be a syntype because the moth issued after the publication date of the original description (March 1908). A female (without abdomen) from Montclair, New Jersey, collected in a trap, is another syntype; Braun (1908a: 101) specifically stated that she had "flown specimens from Montclair, N.J., which are identical with the bred specimens." D. R. Davis (in litt.) has selected the B88 male as lectotype, and the B88 and Montclair females as paralectotypes. Because his designations have not been published, a lectotype is here designated following Davis' intent.

LECTOTYPE ♂ in ANSP, here designated, labelled: [1] "Cincinnati, O./ Annette F. Braun/ VIII-31. 07"; "B88/ apple"; [2] "TYPE/ Collection of/ Annette F. Braun" [red, printed]; [3] "♂ genitalia on/ slide 3283/ D. R. Davis"; [4] "LECTOTYPE ♂/ Lithocolletis/ malimalifoliella Braun/ By D. R. Davis"; [5] "Lithocolletis/ malimalifoliella/ Braun" [handwritten in Braun's hand]; [6] "Figured in/ Moths of America/ North of Mexico" [blue, printed]; [7] "LECTOTYPE ♂/ Lithocolletis/ malimalifoliella/ Braun/ sel. J.-F. Landry, 1993". The indication of a "Moths of America North of Mexico" figure added by Davis as well as Davis' lectotype selection are unpublished. The specimen is spread and double-mounted on cork. Type locality: Cincinnati, Ohio.

All three specimens bear a red label marked: "TYPE/ Collection of/ Annette F. Braun."

Phyllonorycter elmaella Doğanlar and Mutuura
Figs. 4, 11, 27–29

Phyllonorycter elmaella Doğanlar and Mutuura, 1980: 311.

Diagnosis.—In male genitalia (Fig. 4), *P. elmaella* differs from all other species treated here in having slender subequal costal processes with slender spines that extend to about the middle of the valvae.

In female genitalia (Fig. 11), the concave, slightly crenulate posterior margin of sternum VIII, reduction of the sterigma to very narrow rim, lack of thickening of the basal part of the ductus bursae (antrum), and lack of sclerotization in the proximal part of the ovipositor are diagnostic. Reduction of the sterigma is also found in *P. crataegella,* but in this species the posterior margin of sternum VIII is slightly protruded (Fig. 8). In *P. elmaella* the proximal portion of the ovipositor is membranous, whereas it is sclerotized and has cuticular wrinkles in *P. crataegella.*

Forewing length: spring generation, 4.0 mm (n = 1); summer generation, 3.1–4.0 mm (n = 20). Antenna uniformly fuscous in both generations. Mesothoracic scutellum with inconspicuous patch of white scales, 2 or 3 rows wide. Forewing (Figs. 27–29): ground color coppery to pale orange; basal area of dorsal margin with narrow line of white scales, rarely more than 3 rows in width; first costal strigula often less than twice as long as broad, axis usually intersecting dorsal margin before tornus, often touching or confluent with first dorsal strigula (Fig. 27); fourth costal strigula often expanded toward wing apex and broader than third; basal streak narrow, 3–4 scale rows, always subequal to width of orange-scaled area between basal streak and costa; outer row of lamelliform fringe scales dark

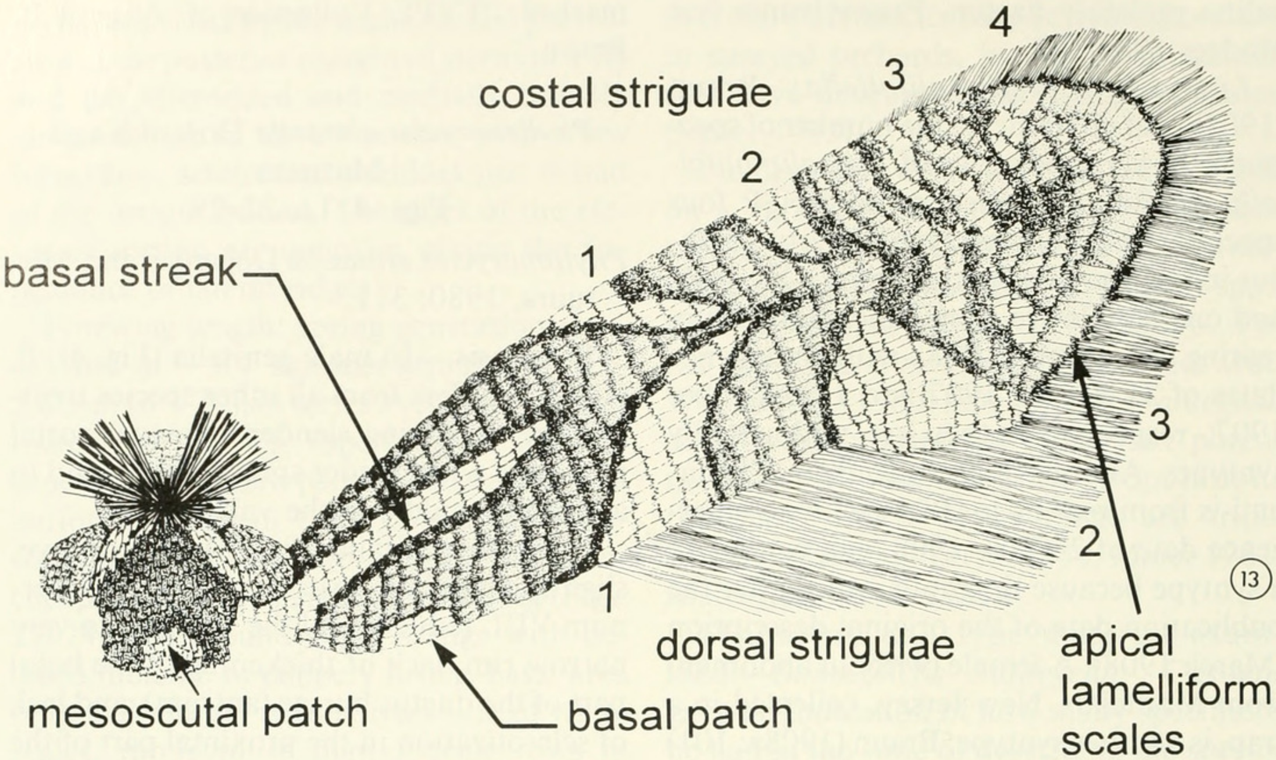
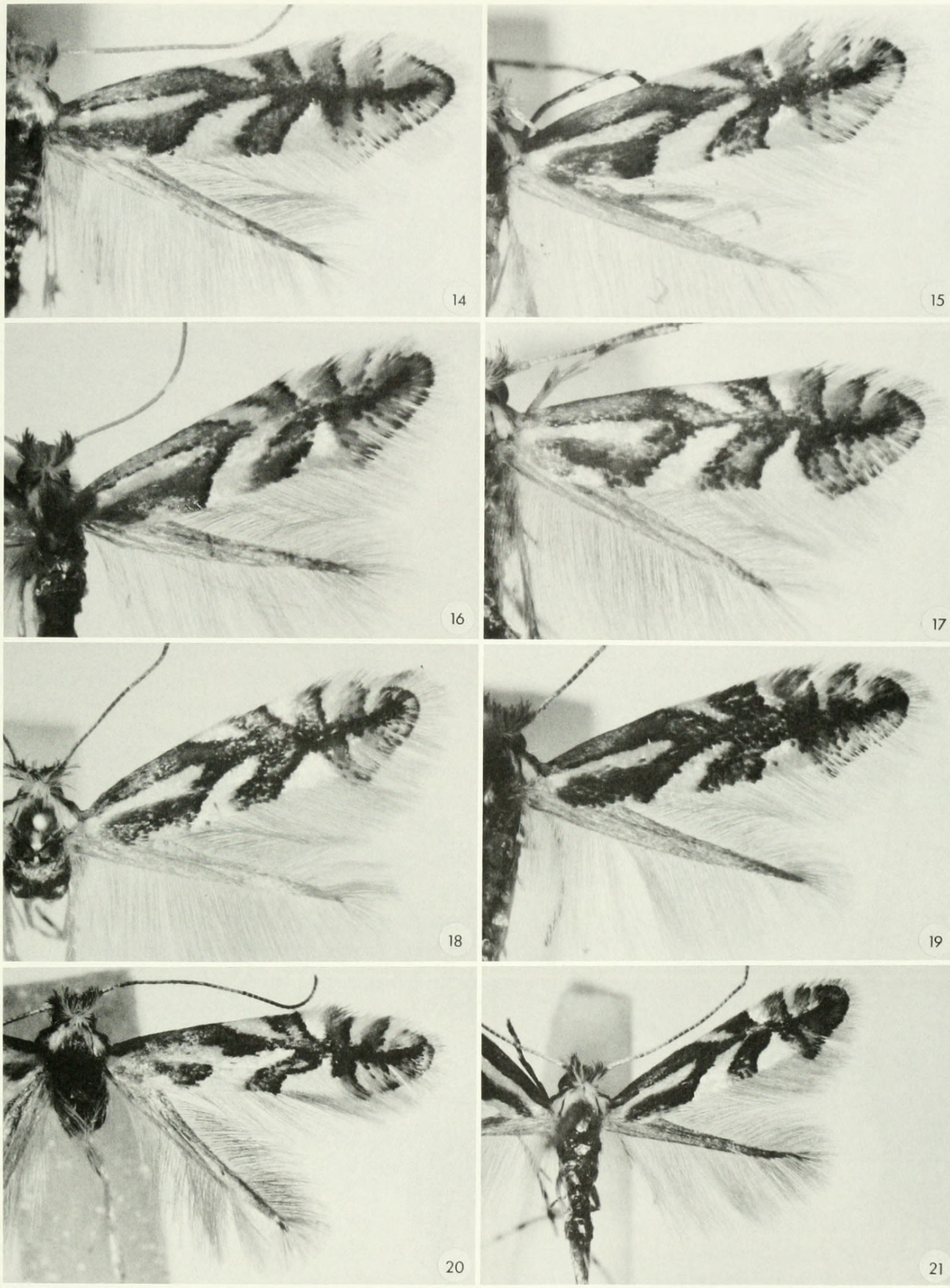


Fig. 13. Dorsal aspect of *Phyllonorycter* species illustrating forewing pattern, with terms used to designate markings.

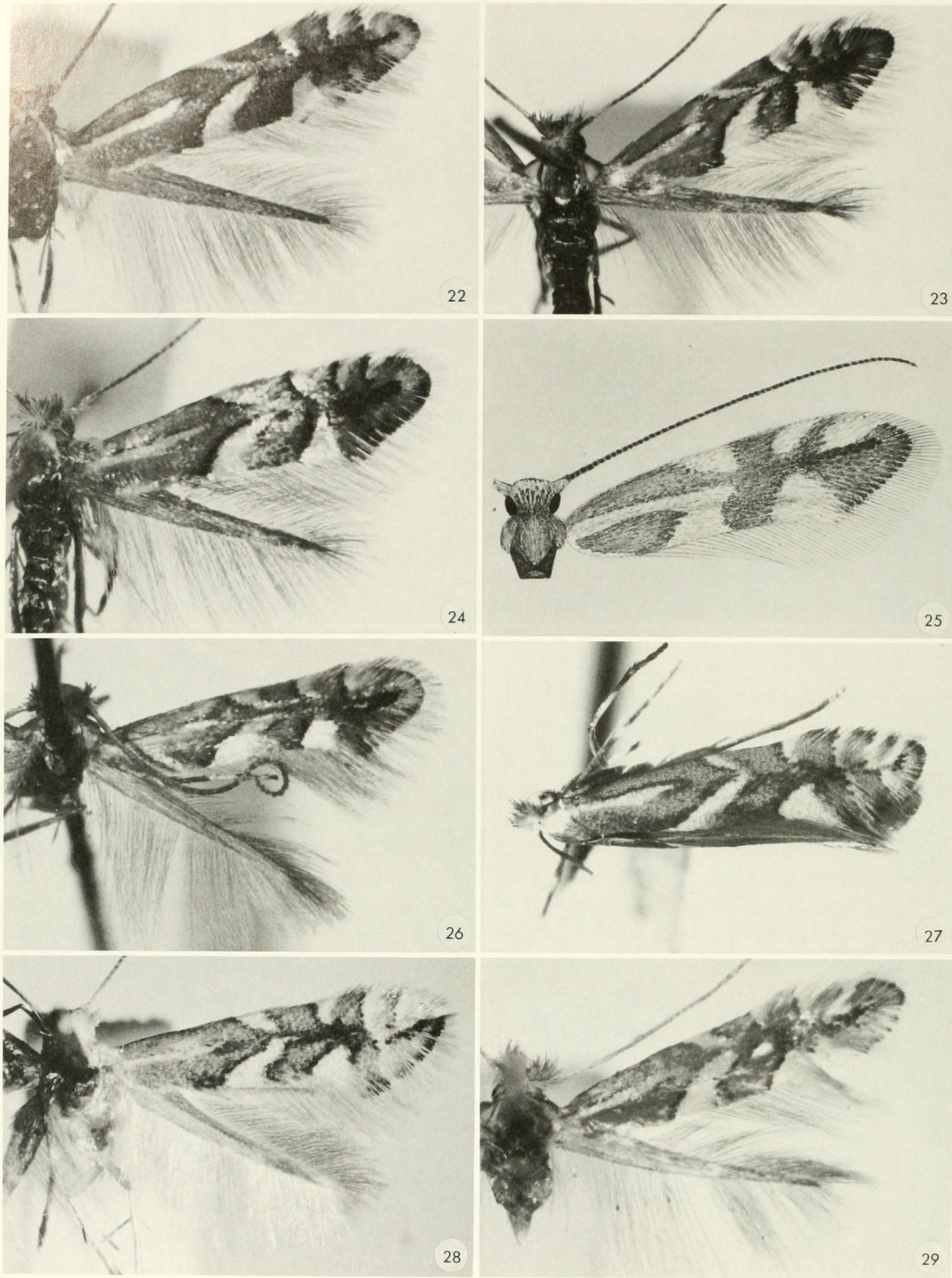
for about ½ their length, forming narrow black band without iridescent blue-black reflections. Hindleg: coloration varying from straw colored to pale fuscous, if present, fuscous scales cover entire dorsal surface of tibia and at least first two tarsomeres.

Remarks.—The forewing pattern of *P. elmaella* illustrated by Doğanlar and Mutuura (1980) is not diagnostic. Considerable variation is present in the type series, which includes individuals from two generations. The wing pattern shown by Doğanlar and Mutuura is that of the dark spring form, in addition to being a variant in which the first dorsal and first costal strigulae are broadly confluent medially.

The narrow slender valvae of the male genitalia described and illustrated by Doğanlar and Mutuura (1980) is the result of a preparation artifact and is misleading the valvae are not flattened in their preparations (in CNCI, examined), but merely shown on edge. The valvae do not afford a diagnostic difference from those of the European *P. sorbi,* as may be interpreted from their figure of the latter, which shows the valvae mounted flat. The valvae of *P. elmaella* are subspatulate and very similar to those of *P. sorbi* when both are compared in flat view. Differences between *P. sorbi* and *P. elmaella* are as follows. In the male of *P. elmaella,* the costal processes extend to one-third the valva length and the apical spines are nearly as long as the processes; in the male of *P. sorbi,* the costal processes are relatively longer and extend to about the middle of the valvae and the apical spines are proportionally shorter, at most one-third the length of the costal processes. In the female of *P. elmaella,* the posterior margin of sternum VIII is concave, finely serrate, and the sclerotization reduced to a very narrow margin; in the female of *P. sorbi,* the posterior margin of sternum VIII has a broader sclerotization and is medially produced into a short, blunt cone. There are no significant differences in the signum between these two species, contrary to Doğanlar and Mutuura's (1980) statement. Furthermore Doğanlar and Mutuura erro-



Figs. 14–21. Forewings of apple-feeding *Phyllonorycter blancardella.* 14, Vancouver, B. C., ex crab apple 4.viii.1992 (CNCI); 15, Mecklenburg, Germany, ex *Malus sylvestris,* 6.vii.1948 (CNCI); 16, Ottawa, Ontario, ex *Malus* sp., 9.viii.1984 (UCON); 17, Shenandoah Nat. Pk., Virginia, ex cultivated apple, 12–22.viii.1976 (DESC); 18, Wilsonville, Oregon, ex *Malus sylvestris,* 23.ii.1986 (UCON); 19, Hamden, Connecticut, ex apple, iv.1989 (UCON); 20, Ste. Anne de Bellevue, Québec, ex cultivated apple, 19.v.1963 (CNCI); 21, Ellington, Connecticut, ex ornamental apple, 12.vii.1993 (UCON).



Figs. 22–29. Forewings of apple-feeding *Phyllonorycter crataegella* and *P. elmaella*. 22, *crataegella*, Southington, Connecticut, ex apple, 10–17.iii.1988 (UCON); 23, *crataegella*, Wallingford, Connecticut, ex ornamental apple, 14–15.vii.1993 (UCON); 24, *crataegella*, Wallingford, Connecticut, ex ornamental apple, 14–15.vii.1993 (UCON); 25, *deceptusella*, Kentucky, holotype (MCZC); 26, *crataegella*, Cincinnati, Ohio, ex *Malus*, 31.viii.1907, lectotype of *Lithocolletis malimalifoliella* Braun (ANSP); 27, *elmaella*, Burnaby, British Columbia, ex *Malus*,

neously referred to Fig. 5 of Kumata (1963) as showing the female genitalia of *P. sorbi*, but the latter species is not even mentioned in Kumata's paper. As noted in the Introduction, *P. sorbi* is not known to occur in North America.

Distribution.—*Phyllonorycter elmaella* is presently known only from the Pacific Coast region from central Oregon to southern British Columbia. Doğanlar and Beirne (1980) reported that *P. elmaella* occurred commonly on unsprayed apple in 1976 and 1977 in the Vancouver District. Except for 13 specimens from the type series (in CNCI), of which six examples were collected in 1978, no other specimens seem to exist to support their contention that *P. elmaella* was in fact the infesting species throughout the Vancouver District. No voucher material is deposited at Simon Fraser University in Burnaby (where Doğanlar did his work), and no additional specimens could be found in the CNCI.

DLW reared four specimens from *Crataegus* sp. near Wilsonville, Clackamas Co., Oregon, in June 1982 (UCON). In addition, we have examined photographs of genitalia of a male from Concrete, Skagit Co., Washington, reared from cultivated apple in July 1986 (DESC).

We examined the eight specimens from Monroe, Oregon, reared from apple foliage in July and August 1954 by Jones and Goeden (OSUO), referred to as *P. sorbi* by Pottinger and LeRoux (1971: 35). We examined a further 18 specimens from near Dallas, Polk Co., Oregon, reared from apple foliage in August 1970 and July 1971 by S.C. Jones (OSUO). Reports of *P. elmaella* from western apple orchards (e.g. Weires and Forshey 1978, Orphart 1982, Hoyt 1983, Barrett and Jorgensen 1986, Barrett and Brunner 1990, Jones 1991) likely refer to misidentifications of *P. mespilella*.

Biology.—Specimens have been reared from domestic apple cultivars, *Malus* spp. (CNCI, DESC, OSUO), and hawthorn, *Crataegus* sp. (UCON). The relative scarcity of this species from recent apple collections in Oregon and Washington may indicate that it is being displaced by *P. blandcardella* and *P. mespilella*. Doğanlar and Mutuura (1980) noted that the species was triple brooded in the Vancouver District. The type material (CNCI) bears dates of March, late June, and September.

Type material examined.—HOLOTYPE ♂ in CNCI, labelled: [1] "Burnaby BC/ 3.I.1978/ Doğanlar" [handwritten]; [2] "Malus/ communis" [handwritten]; [3] "HOLOTYPE/ Phyllonorycter/ elmaella Do. and Mut./ CNC No." [red, part printed, part handwritten]; [4] "genitalia on slide MIC 2094 ♂". The specimen is glued on a point, unspread. Type locality: Burnaby, Vancouver District, British Columbia.

PARATYPES: 3 ♂, 8 ♀ in CNCI. ALLOTYPE ♀, data as holotype except dated 19.VI.1978; genitalia on slide JFL 1091).

Phyllonorycter mespilella (Hübner)
Figs. 2, 12, 30–37

Tinea mespilella Hübner, [1805]: series 8, pl. 39, fig. 272.

Lithocolletis mespilella (Hübner): Rebel, 1901: 213. Povolný, 1949. Pottinger and LeRoux, 1971: 35.

Lithocolletes [*sic*] *blancardella* (Hübner): *sensu* Dyar, 1902: 551.

Phyllonorycter mespilella (Hübner): Bradley, 1972: 10. Emmet et al., 1985: 317.

Lithocolletis pomifoliella Zeller, 1839: 218.

Lithocolletis pyrivorella Bankes, 1899: 252.

Diagnosis.—In male genitalia (Fig. 2) *P. mespilella* can be recognized by the large, dilated right costal process with a curved apical spine that is shorter than the process

←
3.i.1978, holotype male (CNCI); 28, *elmaella*, Burnaby, British Columbia, ex *Malus*, 3.i.1978, holotype male (CNCI); 28, *elmaella*, Burnaby, British Columbia, ex *Malus*, 19.vi.1978, allotype female (CNCI); 29, *elmaella*, Wilsonville, Oregon, ex *Crataegus*, 29.vi.1982 (UCON).

itself and the asymmetrical valvae with the right one being broader than the left one. The left costal process is short and stubby, similar to that of *P. blancardella.*

In female genitalia (Fig. 12), *P. mespilella* is easily distinguished from all other species of the group by the presence of an oval, ringlike sclerotization around the ostium bursae. The sclerotization of the sterigma is wider than in other species (except *P. blancardella*) and, with the apodemes, resembles an X.

Forewing length: spring generation, 3.3–4.5 mm (n = 30); summer generation, 2.7–3.8 mm (n = 30). Antenna uniformly fuscous, occasionally with darkened terminal articles. Mesothoracic scutellum with only small patch of white scales, 1 or 2 rows wide. Forewing (Figs. 30–37): ground fiery to reddish coppery orange, summer brood individuals often paler orange; basal area of dorsal margin with narrow line of white scales, rarely more than 3 scale rows in width; first costal strigula usually twice as long as broad, axis usually intersecting tornus or outer margin, rarely confluent with first dorsal strigula (Fig. 37); fourth costal strigula often subequal to third, rarely confluent with third costal strigula (Fig. 32), or absent (Fig. 35); white basal streak subequal to width of orange-scaled area between basal streak and costa, sometimes confluent with first dorsal strigula (Figs. 32, 35–36); outer row of lamelliform fringe scales with distal ¼ to ½ darkened, forming narrow iridescent blue-black band between outermost strigulae. Hindleg: tibia often smoky distad; first and second tarsomeres with dark apical bands.

Distribution.—*Phyllonorycter mespilella* is currently known only in the West from California north to British Columbia and eastward into Utah and New Mexico. It is presumably introduced from Europe and was first reported in North America by Pottinger and LeRoux (1971: 35) from California. Our verification of vouchers has confirmed that Pottinger and LeRoux's (1971) identification of *P. mespilella* was correct. The species was omitted from the most recent checklist of North American Lepidoptera (Davis 1983). A series of eight specimens in the CNCI collected at Petaluma, Sonoma Co., California by E.C. Johnston in 1936, 1937, and 1938 also belongs to *P. mespilella.* Hence the species has been present in western North America for at least 50 years. Material collected from apple leaves from several locations in California, Oregon, Washington, Utah (CISC, UCON), New Mexico (DESC), and British Columbia (CNCI, UCON) reveal that *P. mespilella* is widespread in western North America. The species referred to as undescribed *P.* near *elmaella* by Varela and Welter (1992) is *P. mespilella* (vouchers examined, UCON). With the exception of the original description, all reports of *P. elmaella* from western North America (e.g. Weires and Forshey 1978, Orphart 1982, Hoyt 1983, Barrett and Jorgensen 1986, Barrett and Brunner 1990, Jones 1991) likely represent *P. mespilella* and not *P. elmaella.*

Biology.—*Phyllonorycter mespilella* has the broadest host range of any of the North American apple-feeding *Phyllonorycter.* In the West, it commonly mines *Malus* (various cultivars as well as crab apples), *Prunus, Pyrus, Cydonia, Crataegus,* and *Cotoneaster* (Borden et al. 1953, DLW unpublished data). Povolný (1949) listed these same host genera for European populations of *P. mespilella,* as well as *Amelanchier* and *Mespilus.* In Great Britain, *Prunus* and *Sorbus* species are the primary hosts, although a variety of other Rosaceae are occasionally used (Emmet et al. 1985). Under outbreak densities females will oviposit on apricot but few larvae reach maturity (L. Varela, in litt. 1993). Up to five generations are produced in orchards of the Central Valley of California; three to four in coastal areas of California; three in the Okanagan Valley of southern British Columbia (Cossentine and Jensen 1992, Varela and Welter 1992). Varela and Welter (1992) used (E10)-Dodecenyl acetate to monitor the phenology of *P.*

mespilella in California. We examined specimens reared from domestic *Prunus* (cherry) cultivars from orchards in California and Oregon, which are true *P. mespilella.* However, there appears to be one or more undescribed species of *Phyllonorycter* on native *Prunus* species in the West (Deschka, in litt., DLW, unpublished data).

Nomen Dubium

Phyllonorycter deceptusella (Chambers)
Fig. 25

Lithocolletis deceptusella Chambers, 1879: 73.

Phyllonorycter deceptusella (Chambers): Davis, 1983: 10.

This species was described from a single specimen, recorded as follows (Chambers 1879: 73): "Among my captured specimens of *L. crataegella* Clem. I find a specimen of this species which at the time of its capture I regarded only as a variety, but which a more attentive examination convinces me is a distinct though allied species. The abdomen and two hinder pair of legs are wanting, though otherwise the insect is in good condition, and though there is but a single specimen, I described it for the purpose of discriminating it from *crataegella.*"

Lithocolletis deceptusella Chambers and *L. crataegella* Clemens were both synonymized by Walsingham (1891: 328) with the European *pomifoliella* Zeller, now a junior synonym of *mespilella* (Hübner), which at that time was confused with *blancardella* (F.). Busck (1903: 190), upon examining the type of *crataegella,* agreed with Walsingham. Of course at that time none of these authors examined genitalia, the study of which had not yet begun. *Phyllonorycter deceptusella* is listed as a valid species by Davis (1983: 10). Hagen (1884: 152) indicated that the type of this taxon was not recognizable. Braun (1908b: 298) indicated that based on color pattern, *P. deceptusella* was distinct and "not closely related to *crataegella* or the other apple feeding species." There is no indication in Chambers' (1879) description that the species feeds on apple, rather Chambers remarked that he suspected "that it feeds on Oak" (Chambers 1879: 74). Thus the statement in Pottinger and LeRoux (1971: 5) to the effect that Braun (1908b) listed *deceptusella* as feeding on apple is in error.

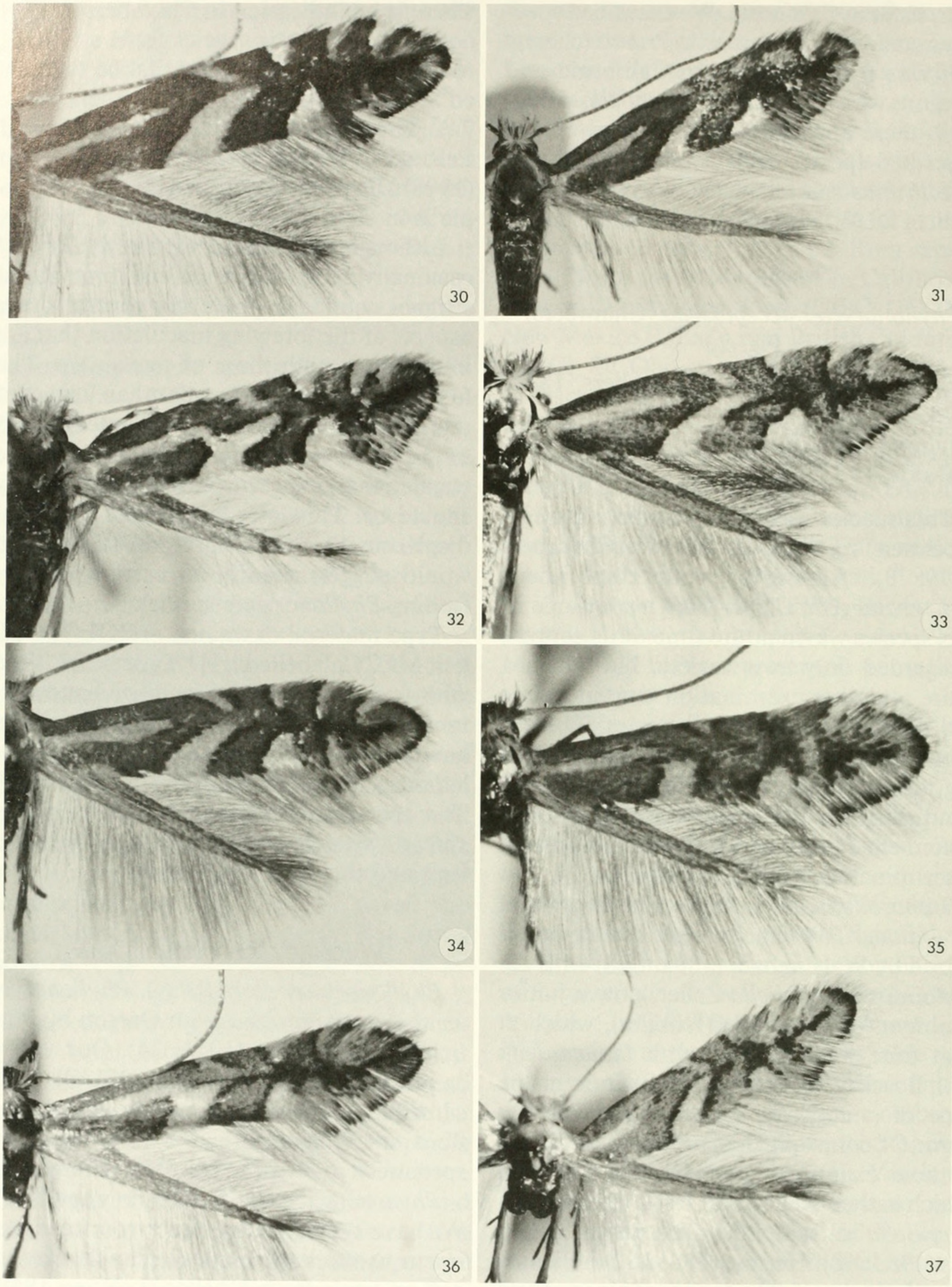
Although variants of *P. crataegella* occasionally have the basal and first dorsal strigula confluent, there are several other aspects of the forewing maculation that are inconsistent with those of *crataegella.* The first costal strigula is broader than long, and it is not obliquely angled to the outer margin as in typical *crataegella..* Nor are the white stigulae margined with black scales as they should be. This later feature and the basal displacement of the first dorsal strigula would suggest affinity to eastern cherry-feeding *Phyllonorycter* species.

Type material examined.—HOLOTYPE ♀ in MCZC, labelled: [1] "Type/1323" [red with top portion white, number handwritten]; [2] "Chambers/Kentucky" [partly handwritten, partly printed]; [3] "Lithocolletis/deceptusella Chamb" [handwritten]. The specimen is double mounted, partly spread, with the right antenna, all but two legs, and the abdomen missing.

Wrongly Recorded Taxa

Phyllonorycter sorbi (Frey). *Phyllonorycter sorbi* was reported from Oregon by Pottinger and LeRoux (1971: 35). Our verification of original vouchers (OSUO) indicates that their records were misidentifications of *P. elmaella.* We have seen no specimens of *P. sorbi* from North America.

Phyllonorycter scudderella (Frey and Boll). We have been unable to trace voucher specimens to check the single *P. scudderella* record on apple from Québec (LeRoux 1960: 107). We presume that it is based on a misidentification or a labelling error as the species is a willow feeder (Braun 1908b: 296, Ely 1917, Needham et al. 1928).



Figs. 30–37. Forewings of apple-feeding *Phyllonorycter mespilella.* 30, San Francisco, California, ex *Cotoneaster,* 20.i.1986 (UCON); 31, Hood River, Oregon, ex apple, 27.ii–14.iv.1990 (UCON); 32, Summerland, British Columbia, ex cultivated apple, 18–19.iii.1992 (CNCI); 33, Naramata, British Columbia, ex cultivated apple, 21–22.iii.1992 (CNCI); 34, Naramata, British Columbia, ex cultivated apple, 12.vi.1992 (CNCI); 35, Naramata, British Columbia, ex cultivated apple, 20–22.vi.1992 (CNCI); 36, Naramata, British Columbia, ex cultivated apple, 23.vi.1992 (CNCI); 37, Summerland, British Columbia, 5–21.viii.1992 (UCON).

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