Journal of the Lepidopterists' Society
57(1), 2003, 36–42

A FIELD INVESTIGATION OF *DEPRESSARIA* (ELACHISTIDAE) HOST PLANTS AND ECOLOGY IN THE WESTERN UNITED STATES

DUANE D. MCKENNA

Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford St., Cambridge, Massachusetts 02138, USA,
E-mail: dmckenna@oeb.harvard.edu

AND

MAY R. BERENBAUM

Department of Entomology, University of Illinois, 320 Morrill Hall, 505 S. Goodwin, Urbana, Illinois 61801, USA

ABSTRACT. *Depressaria* Haworth is a relatively species-rich group of moths with a Holarctic distribution. In western North America there has been a striking radiation of Apiaceae-feeding members of the genus. To understand patterns of *Depressaria* distribution, host usage, and natural history in the western United States, we surveyed select potential host plants for larvae. Particular emphasis was placed on surveying plants in the genus *Lomatium* Raf. because most published *Depressaria* host plant records are from this genus. Surveys took place throughout the western United States from Utah and Wyoming to the Pacific Ocean, and from the Canadian border in Washington State to California and northern Arizona. Approximately 32,000 km of roadway were covered. When larvae were encountered they were collected and reared to adulthood. Ten species of *Depressaria* were reared. Two additional potentially undescribed species, represented only by female specimens, were also reared. Our data support previously published accounts of *Depressaria* biology, host usage, and distribution, consistent with the fact that known host plant genera were targeted in the surveys. Substantial changes in land use have occurred in some parts of the western United States since the work of J. F. G. Clarke, an early student of *Depressaria*. Several of his published collection localities, including the type locality for *D. whitmani* Clarke and most collection localities near the Pacific Coast and in dry grasslands, have been destroyed or seriously degraded by agriculture, grazing, roadway improvements, and other forms of development.

Additional key words: host-plants, *Lomatium.*

Depressaria Haworth (Elachistidae) is a relatively species-rich group of small moths with a Holarctic distribution (Hodges 1998). There are approximately 100 species of *Depressaria*, of which 24 (and 2 potentially undescribed species discussed herein) are found only in the Nearctic region (Hodges 1974). Three species (*D. artemisiae* Nickerl, *D. daucella* Denis & Schiffermüller, and *D. pastinacella* Duponchel) have been introduced from the Palearctic and have established Nearctic ranges. Twenty-five of the 27 described species that occur in North America have been reported from the western United States. Adult *Depressaria* are similar in appearance to adults of the genera *Agonopterix* Hübner, *Apachea* Clarke, *Exaeretia* Stainton, and *Nites* Hodges, and can be separated from *Apachea* by the absence of a strong anteriorly directed scale tuft on the second segment of the labial palpus, from *Nites* by the presence of ocelli, and from *Agonopterix* and *Exaeretia* by the presence of veins Cu_1 and Cu_2 separate basally in the forewing (Hodges 1974).

All *Depressaria* for which feeding habits are known feed on Apiaceae or Asteraceae (Berenbaum & Passoa 1999). In western North America there has been a striking radiation of Apiaceae-feeding *Depressaria*. Seventeen of the 24 endemic North American species are known to feed on plants in the family Apiaceae (Hodges 1974). Hannemann (1953) first noted that the North American Apiaceae-feeding *Depressaria* form two morphologically distinct groups: the *douglasella*-group and the *pastinacella*-group. Fourteen of the 24 described species of *Depressaria* reported from North America belong to the *douglasella*-group (sensu Hannemann 1953) and 5 species belong to the *pastinacella*-group. The remaining 5 described species belong to two groups: the *artemisiae*-group (2 species) and *thomaniella*-group (3 species) (Hannemann 1953, Hodges 1974). Larvae of all species in the *douglasella*-group feed on plants in the genus *Lomatium* and a few other closely related genera of Apiaceae. The *pastinacella*-group also feeds only on Apiaceae, but their host plants belong to several distantly related genera (Plunkett & Downie 1999). The *artemisiae*-group and the *thomaniella*-group feed only on Asteraceae (Clarke 1933, 1941, 1947, 1952, Hodges 1974).

All North American *Depressaria* are univoltine. After overwintering as adults they emerge from prereproductive diapause, mate, and oviposit on the emerging umbels (Apiaceae-feeders) and meristematic tissue of their host plants. Except for some perennial *Artemisia* L. species, all *Depressaria* host plants in North America are herbaceous perennials. Generally, newly hatched first instars build small silk webs in the developing umbels and leaves of their host plants. Larvae tie together a small amount of umbel or leaf material, forming a tube from which they reach to feed on nearby plant parts (Clarke 1952, Hodges 1974). Species-specific variations on this general feeding pat-

tern observed during this study are discussed in the results section.

Depressaria pastinacella, an introduced species in North America, has played an important role as a model system for the study of plant-insect coevolution. This is due in part to its host specificity on a few genera of Apiaceae with copious secondary defenses (Thompson & Price 1977, Berenbaum 1981, 1983, 1990, Hendrix 1984, Zangerl & Berenbaum 1993). In contrast, there have been relatively few studies of the native North American *Depressaria*, or of introduced species other than *D. pastinacella* (Thompson 1983a, b, 1998, Thompson & Moody 1985).

This study further elucidates the distribution, host usage, and natural history of *Depressaria* in the western United States by surveying potential host plants for *Depressaria* larvae and rearing them to adulthood. Special emphasis was placed on the *douglasella*-group and its known host plant genera *Lomatium, Pteryxia,* and *Angelica* (all Apiaceae).

MATERIALS AND METHODS

To elucidate patterns of *Depressaria* distribution, host usage, and natural history in the western United States, we surveyed potential host plants of *Depressaria* in the region for larvae. Potential hosts included all plant genera from which *Depressaria* species had been reported in the literature as well as additional genera reported to be closely allied to the primary host genus, *Lomatium* Raf. (Plunkett & Downie 1999). The most frequent and widespread of these allied genera included *Aletes* J. M. Coult. & Rose, *Angelica* L., *Cymopterus* Raf., *Pteryxia* (Nuttall ex Torrey et A. Gray) J. M. Coult. & Rose, and *Tauschia* Schltdl. Particular emphasis was placed on the genus *Lomatium* in the surveys because most reared specimens of *Depressaria* from the western United States have been obtained from larvae found feeding on *Lomatium*.

Survey sites were identified by consulting annotations on herbarium specimens from the University of Illinois at Urbana-Champaign, University of Michigan at Ann Arbor, Michigan State University at East Lansing, the Rocky Mountain Herbarium at Laramie, and from published type locality and other data for *Depressaria* species collected in Arizona, California, Idaho, Montana, Oregon, Washington, and Wyoming (Clarke 1933, 1941, 1947, 1952, Hodges 1974). Additional populations of *Depressaria* were located by searching for potential larval host plants in suitable habitat along roadsides. Clarke (1933, 1941, 1947, 1952) effectively employed the same general method of collecting *Depressaria* in the western United States.

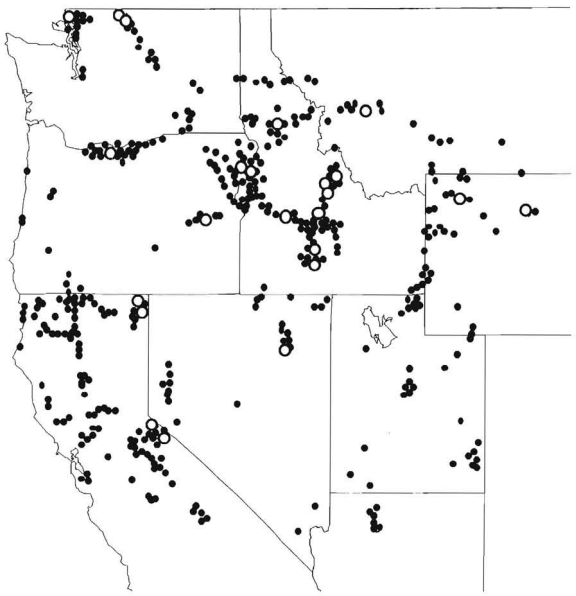

FIG. 1. Approximate location of survey sites in the western United States. Filled black circles represent sites where potential host plants were encountered and searched for larval *Depressaria*. Open circles indicate location of survey sites from which *Depressaria* were reared.

In four trips to the western United States, more than 300 sites were surveyed for *Depressaria* species over the course of two spring-fall cycles (Fig. 1). "Sites" were discrete locations of variable size where potential host plants were found to grow and were searched for *Depressaria*. At least 54 species of Apiaceae, including 43 species of *Lomatium,* were surveyed for larval *Depressaria* (Table 1). We identified *Lomatium* species and other host plants using keys in Cronquist et al. (1997). We photographed plants of uncertain identity and made notes on morphology to facilitate later identification using keys and herbarium specimens (herbarium specimens were identified by Professor R. Hartman, University of Wyoming, Laramie, a specialist on *Lomatium* and allied genera).

All insect specimens were identified by the first author using keys and published descriptions (Clarke 1933, 1941, 1947, 1952, Hodges 1974). Surveys took place primarily in Arizona, California, Idaho, Montana, Nevada, Oregon, Utah, Washington, and Wyoming. More than 32,000 km of roadway were covered.

Umbels, leaves, stems, and other above-ground structures of potential host plants encountered were searched for larval *Depressaria*. If the larval population at a site was greater than approximately 10 individuals, one or more larvae were collected and placed with adequate plant material to support their development into a self-sealing plastic bag lined on the bottom with damp, long-fiber sphagnum moss. The larvae in plastic

TABLE 1. Apiaceae surveyed for *Depressaria*. Abbreviations for states: AZ, Arizona; CA, California; ID, Idaho; MT, Montana; NV, Nevada; OR, Oregon; UT, Utah; WA, Washington; and WY, Wyoming.

Apiaceae	States
Angelica arguta Nutt.	CA, ID, MT, OR, NV, UT, WA, WY
Angelica lucida L.	WA
Cicuta douglasii (DC.) Coult. & Rose	CA, OR, WA
Cicuta maculata L.	ID, MT, OR, WA, WY
Cymopterus acaulis (Pursh) Raf.	ID
Cymopterus corrugatus M. E. Jones	UT
Cymopterus duchesnensis M. E. Jones	UT
Cymopterus ibapensis M. E. Jones	UT
Daucus carota L.	CA, ID, MT, OR, UT, WA, WY
L. ambiguum (Nutt.) J. M. Coult. & Rose	ID, OR, WA, WY
L. bicolor (S. Wats.) J. M. Coult. & Rose	CA, ID, OR, WA
L. brandegei (J. M. Coult. & Rose) J. F. Macbr.	WA
L. californicum (Nutt.) Mathias & Constance	CA, OR
L. canbyi (J. M. Coult. & Rose) J. M. Coult. & Rose	CA
L. caruifolium (Hook. & Arn.) J. M. Coult. & Rose	CA
L. ciliolatum Jepson	CA
L. circumdatum (S. Wats.) J. M. Coult. & Rose	ID
L. columbianum Mathias & Constance	OR, WA
L. cous (S. Wats.) J. M. Coult. & Rose	ID, WA
L. dasycarpum (Torr. & Gray) J. M. Coult. & Rose	CA
L. dissectum (Nutt.) Mathias & Constance	AZ, CA, ID, MT, NV, OR, UT, WA, WY
L. engelmannii Mathias	ID
L. farinosum (Hook.) J. M. Coult. & Rose	OR
L. foeniculaceum (Nutt.) J. M. Coult. & Rose	AZ, CA, ID, MT, NV, OR, WY
L. geyeri (S. Wats.) J. M. Coult. & Rose	ID
L. gormanii (T. J. Howell) J. M. Coult. & Rose	ID, OR
L. graveolens (S. Wats.) Dorn & Hartman	ID
L. grayi (J. M. Coult. & Rose) J. M. Coult. & Rose	ID, NV, OR, WA
L. hallii (S. Wats.) J. M. Coult. & Rose	WA
L. hooveri (Mathias & Constance) Constance & Ertter	CA
L. idahoense Mathias & Constance	ID
L. laevigatum (Nutt.) J. M. Coult. & Rose	OR
L. latilobum (Rydb.) Mathias	CO, UT
L. macrocarpum (Nutt. ex Torr. & Gray) J. M. Coult. & Rose	CA, ID, MT, NV
L. marginatum (Benth.) J. M. Coult. & Rose	CA
L. martindalei (J. M. Coult. & Rose) J. M. Coult. & Rose	WA
L. nevadense (S. Wats.) J. M. Coult. & Rose	CA
L. nudicaule (Pursh) J. M. Coult. & Rose	CA, ID, NV, OR, WA
L. orientale J. M. Coult. & Rose	ID
L. parryi (S. Wats.) J. F. Macbr.	UT
L. peckianum Mathias & Constance	CA
L. piperi J. M. Coult. & Rose	CA
L. rollinsii Mathias & Constance	ID
L. salmoniflorum (J. M. Coult. & Rose) Mathias & Constance	ID
L. sandbergii (J. M. Coult. & Rose) J. M. Coult. & Rose	ID
L. scabrum (J. M. Coult. & Rose) Mathias	NV
L. serpentinum (M.E. Jones) Mathias	ID
L. simplex (Nutt.) J. F. Macbr.	AZ, ID, UT
L. stebbinsii Schlessman & Constance	CA
L. suksdorfii (S. Wats.) J. M. Coult. & Rose	WA
L. torreyi (J. M. Coult. & Rose) J. M. Coult. & Rose	CA
L. tracyi Mathias & Constance	CA
L. triternatum (Pursh) J. M. Coult. & Rose	CA, ID, MT, WA, WY
L. utriculatum (Nutt. ex Torr. & Gray) J. M. Coult. & Rose	CA, OR
L. vaginatum J. M. Coult. & Rose	CA, NV
L. vaseyi (J. M. Coult. & Rose) J. M. Coult. & Rose	CA
L. watsonii (J. M. Coult. & Rose) J. M. Coult. & Rose	MT
Oreoxis alpina (Gray) Coult. & Rose	UT
Perideridia bolanderi (Gray) A. Nels. & J. F. Macbr.	CA, ID, NV, OR, UT, WA
Perideridia gairdneri (Hook. & Arn.) Mathias	AZ, CA, ID, NV, OR, UT, WA, WY
Pseudocymopterus montanus (Gray) Coult. & Rose	WY
Pteryxia petraea (M. E. Jones) Coult. & Rose	CA
Pteryxia terebinthina (Hook.) Coult. & Rose	CA, ID, MT, OR, NV, UT, WA, WY
Tauschia glauca (Coult. & Rose) Mathias and Constance	CA

TABLE 2. *Depressaria* reared during this study. State records are marked with a "*" preceding the name. County records are marked with a "#" preceding the name. Abbreviations for states as in Table 1.

Species	Collection site	Host plant	
**D. angelicivora*	Custer Co., ID; Hwy 26, 8 km west of Stanley	*Angelica arguta*	2♀
#D. betina	Modoc Co., CA; Hwy 395, 1 km N of Davis Creek (town)	*L. triternatum*	1♂
D. daucella	Whatcom Co., WA; S of Bellingham	*Oenanthe sarmentosa*	2♀
#D. juliella	Whatcom Co., WA; 13 km S of Hart's Pass	*Cicuta maculata*	2♀
**D. leptotaeniae*	Elko Co., NV; Hwy 227, 16 km SE of Elko	*L. dissectum*	2♂ 1♀
#D. leptotaeniae	Custer Co., ID; Hwy 75, 20 km S of Challis	*L. dissectum*	1♂
#D. leptotaeniae	Lemhi Co., ID; Hwy 93, S of Salmon	*L. dissectum*	1♂
#D. leptotaeniae	Jerome Co., ID; Hwy 93, 5 km N of Twin Falls	*L. dissectum*	1♂
#D. leptotaeniae	Lincoln Co., ID; Hwy 93, South of Shoshone	*L. dissectum*	1♂
D. leptotaeniae	Powell Co., MT; Hwy 90, 18 km NW of Deer Lodge	*L. dissectum*	1♀
D. multifidae	Idaho Co., ID; Hwy 13, 3 km S of intersection with Hwy 12	*L. grayi*	8♀
**D. multifidae*	Alpine Co., CA; Hwy 88, near intersection with Hwy 89	*P. terebinthina* var. *californica*	2♀
#D. multifidae	Wasco Co., OR; Rowena Plateau, near Tom McCall Nature Preserve	*L. grayi*	4♂
#D. multifidae	Harney Co., OR; Hwy 20 at Drinkwater Pass	*L. grayi*	1♂
#D. multifidae	Idaho Co., ID; Hwy 12 at intersection with Hwy 13	*L. grayi*	1♂ 1♀
**D. multifidae*	Alpine Co., CA; Hwy 89, W of intersection with Hwy 395	*P. terebinthina* var. *californica*	9♀
#D. multifidae	Adams Co, ID; Kleinschmidt Grade, 800 m from Snake R.	*L. grayi*	1♀
#D. multifidae	Lemhi Co., ID; Hwy 93, S of Salmon	*P. terebinthina* var. *foeniculacea*	1♀
#D. multifidae	Wallowa Co., OR; Opposite Idaho Powers' Snake River Campground	*L. grayi*	1♀
D. pastinacella	Specific locality data not recorded (see "Methods")	*Heracleum lanatum, Pastinaca sativa*	N/A
D. pteryxiphaga	Washakie Co., WY; Hwy 16, W of Ten Sleep	*P. terebinthina* var. *calcarea*	1♀
**D.* sp. A	Park Co., WY; Hwy 20/14/16, 16 km E of Yellowstone National Park	*P. terebinthina* var. *foeniculacea*	1♀
**D.* sp. A	Lemhi Co., ID; Hwy 93, S of Salmon	*P. terebinthina* var. *foeniculacea*	1♀
**D.* sp. A	Alpine Co., CA; Hwy 4, W of intersection with Hwy 89	*P. terebinthina* var. *californica*	2♀
**D.* sp. A	Alpine Co., CA; Hwy 4, W of intersection with Hwy 89	*P. terebinthina* var. *californica*	2♀
**D.* sp. B	Modoc Co., CA; Hwy 395, S of Davis Creek (town)	*L. bicolor*	1♀
D. togata	Whatcom Co., WA; Hart's Pass	*L. ambiguum*	1♂
D. togata	Whatcom Co., WA; Slate Peak	*L. brandegei*	1♀

bags were reared on plant material from the same species and same site from which they were collected. Larvae were not collected if fewer than 10 were found at a site, or if they were found within the boundaries of a national or state park. *Depressaria pastinacella* was encountered frequently but, because its life-history and ecology are so well documented, it was not collected in the surveys.

After emerging, the moth and a gelatin capsule containing the pupal exuviae were mounted on a pin. The abdomen was removed and frozen at –80°C for future DNA extraction and analysis, and the genitalia were cleared in KOH and mounted on a microscope slide (without staining) to facilitate identification. County and state records were determined by consulting the most recent published distribution data for the Oecophoridae (sensu Hodges 1983) of western North America (Powell & Opler 1996) and are listed in Table 2.

Vouchers have been deposited at the University of Illinois at Urbana-Champaign. Vouchers of the two potentially undescribed species and county records will be retained at Harvard University in Cambridge, Massachusetts until the completion of ongoing studies, at which time they will be deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

RESULTS

Fifty-four *Depressaria* larvae were collected and successfully reared (Table 1). These specimens represent eleven of the 22 described species of *Depressaria* known from western North America, and 2 potentially undescribed species. Additional species may have been encountered, but they were not collected due to small population sizes or their residence in national parks. Most reared specimens belong to the *douglasella*-group. Despite extensive surveys of their reported host plants (when known), no members of the *artemisiae*-group or the *thomaniella*-group were found.

Douglasella-group

An unusual *Depressaria* that is probably an undescribed species was reared from *Pteryxia terebinthina* (Hook.) Coult. & Rose var. *foeniculacea* (Nutt.) Mathias. *Pteryxia terebinthina* var. *foeniculacea* in Idaho and Wyoming, and *P. terebinthina* var. *californica* (Coult. and Rose) Mathias in California (Fig. 2a–c). A visit to the Wyoming locality adjacent to Yellowstone National Park on 24-VI-2000 found it destroyed by road construction. Hereafter this species will be referred to as *Depressaria* sp. "A." Females are closest in appearance to *D. multifidae* Clarke. We have

reared only female specimens, and it is for this reason that we do not formally describe this species here. This putative species can be differentiated from *D. leptotaeniae* Clarke, *D. multifidae,* and *D. pteryxiphaga* Clarke by the absence of a sclerotized, folded structure on the anterior margin of the female eighth abdominal sternum, and by the absence of heavy sclerotization of the ductus bursae. Maculation also differs somewhat from other members of the *douglasella*-group. Scales on the vertex of *Depressaria* sp. A are buff to rust-colored, and lighter-colored on the head, thorax, costal portion of the base of the forewings, and tegulae, than on the abdomen. The remainder of the forewing is covered with grey-brown, brown, and buff-tipped-brown scales. A white spot formed by 1–3 white scales surrounded by grey-brown and brown scales is located at 1/2 the length of the wing in the fold. This spot is absent in some specimens. A second white spot composed of 3–5 white scales surrounded by grey-brown and brown scales is located immediately distal to first near the end of the cell.

Larvae of *D. togata* Walsingham were observed to feed and lightly web in the developing umbels of *L. brandegei* (Coult. & Rose) Macbr. We have never observed *D. togata* feeding on the leaves of this host plant.

Larval *D. multifidae* were most frequently observed feeding in and webbing the developing umbels of *L. grayi* Coult. & Rose. Rarely, other host plants were used, such as *P. terebinthina* (Hook.) Coult. & Rose and *L. columbianum* Math. & Const. Larvae collected from *L. columbianum* stopped feeding and died before or shortly after pupation. After feeding in the umbels of *L. grayi* and *P. terebinthina*, *D. multifidae* larvae usually moved to the leaves where they tied together the ultimate divisions of the leaflets to form a small tube from which they fed on adjacent leaflet material. Most individuals pupated in litter at the bottom of the rearing containers, but some pupated in hollow peduncles of *L. grayi* placed in the containers.

We observed *D. pteryxiphaga* larvae feeding in the leaflets and umbels of *P. terebinthina*. The larvae appeared to move to the leaves from umbels as later instars. Like *D. multifidae*, the larvae form tubes of webbing from which they feed, and into which they retreat when disturbed. These tubes sometimes form extensive networks of light webbing involving several leaves and occasionally an umbel.

We observed abundant early instar *D. leptotaeniae* feeding gregariously in the developing umbels of *L. dissectum* (Nutt.) Math. & Const. As larvae mature, they disperse to feed on the leaves where they form small tubes of webbing that incorporate the ultimate segments of the leaflets. They do not form extensive tubes of webbing as *D. multifidae* and *D. pteryxiphaga* do. Occasionally, larvae continue to feed in the umbels, tying together several rays and feeding on the developing flowers or young, green fruits. Typically, nearly mature larvae move to the leaf axils where they feed lightly, deposit some frass, and pupate. The pupa is always oriented with the ventral surface downward and is covered with a small amount of silk that serves to anchor it in place. Reared larvae rarely pupated in broken *L. dissectum* peduncles or in litter at the base of the plant in the rearing container. We made many observations of pupal exuviae in leaf axils in the field. Near Twin Falls, Idaho, *D. leptotaeniae* is exceptionally abundant on *L. dissectum* in basaltic lava flows. Here, we observed thousands of *D. leptotaeniae* pupae and pupal exuviae in leaf axils in late May 1998.

Larvae of *D. angelicivora* Clarke begin life feeding in the developing umbels and leaves, of *Angelica arguta* Nutt. Their feeding often results in distortion of the emerging umbels and leaves making them easy to spot. Most larvae complete feeding by the time the umbels are fully expanded. Occasionally, larvae can be found feeding on the developing (still green) seeds or leaves, but apparently only when flowers are not available. In such situations we have observed the larvae to tie several developing fruits together with webbing to form a small tube from which they reach to feed in a manner similar to *D. pteryxiphaga*. Nearly mature larvae were observed to wander from the developing meristem of the host plant to debris in the bottom of the rearing container where they pupated.

Betina-group

Larval *D. betina* Clarke have been observed feeding in the umbels of *L. triternatum* (Pursh.) Coult. & Rose. At the one site where they were observed, late instars were inconspicuous, usually involving only three or fewer rays of the host umbel in their webbing. Tubes of webbing were not formed. The only adult we reared pupated in litter at the bottom of the rearing container.

Pastinacella-group

A single adult specimen of a strikingly-colored, apparently undescribed *Depressaria* was reared from a larva collected on *L. bicolor* var. *leptocarpum Lomatium bicolor* (S. Watson) J. Coulter & Rose var. *leptocarpum* (Torrey & A. Gray) M. Schlessman south of the town of Davis Creek, Modoc County, California. The larva was feeding in a webbed mass of leaf and umbel material and was the only larva of its kind observed. Because we have only a single specimen we do not formally describe it here. This female specimen is

dramatically distinct from other members of the *pastinacella*-group. For convenience, we will refer to this specimen hereafter as *Depressaria* sp. "B". *Depressaria* sp. B most resembles *D. juliella* Busck, *D. daucella* Denis and Schiffermüller, and *D. eleanorae* Clarke. It can be differentiated from them by the coloration of forewing and tarsomere maculation, the absence of a folded structure on the anterior margin of the eighth abdominal sternum, and the wide ostium bursae. Dorsum of head with rust to salmon scales. A tuft of red-rust scales protrude from posterior edge of each eye. Tegulae are salmon-colored, and nearly the same color as the thorax. The forewing is covered with off-white, rust, and salmon scales. Longitudinal streaks of dark rust scales are scattered across the surface of the forewing, mostly parallel to the wing margin. All scales appear pearlescent in reflected light. The forewing fringe is a uniform rusty salmon. The legs have off-white scales at the distal end of each tarsomere, and appear banded. The eighth abdominal sternum is weakly pigmented throughout. The ostium bursae is wider than in other *Depressaria* species.

Larvae of *Depressaria juliella* Busck were found feeding on the flowers of *Cicuta maculata* L. tying the rays of the inflorescence together, but not noticeably distorting the umbel. The two specimens reared pupated in debris at the bottom of the rearing container.

We collected larvae of *Depressaria daucella* while they were feeding on an umbel on *Oenanthe sarmentosa* J. S. Presl. We have not observed leaf-feeding. Larvae do not noticeably distort the umbels and produce relatively little webbing.

Depressaria pastinacella was abundant throughout the western United States wherever either of its common host plants, *Heracleum lanatum* and *Pastinaca sativa* L., (local and introduced, respectively) were found. Larvae were not found on any other plant species, (but no extensive effort was made to look for them on other known host genera such as *Angelica*). *Depressaria pastinacella* was by far the most frequently encountered *Depressaria* species.

Other Observations

Larvae whose behavior and ecology resembled those of known *Depressaria* and *Agonopterix* were observed, but not collected because of small population sizes or occurrence in national parks.

Surprisingly, no parasitoids were reared from any *Depressaria* species; however, during the course of this study several Ichneumonidae were reared from *Sparganothis* Hübner species (Tortricidae) that co-occurred with *D. multifidae* on *P. terebinthina*. In fact, *Sparganothis* co-occurred with *Depressaria* spp. on *L. dissectum* and *Pteryxia terebinthina* at several study sites. *Papilio indra* (Papilionidae), and *Agonopterix* spp. (Elachistidae: Depressariinae) were less frequently encountered than *Depressaria* or *Sparganothis*, but larvae occurred on nearly an identical suite of host plants as the *douglasella*-group of *Depressaria*. *Epermenia* Hübner spp. (Epermeniidae) were occasionally encountered as larvae feeding in the seeds of *L. dissectum* and *L. triternatum*. Adults were occasionally seen on the flowers of *Achillea millefolium* L. (Asteraceae). Relatively few other lepidopteran larvae were observed. Crab spiders (Thomisidae) were often abundant on flowering *Lomatium* but were not observed to take *Depressaria* larvae or adults as prey. On several occasions predacious Hemiptera were observed feeding on *Depressaria* larvae that were still in their webbed tubes.

Substantial changes in land use have occurred in some parts of the western United States since the works of Clarke (1933, 1941, 1947, 1952). Several sites, including the type locality for *D. whitmani* and most former collection locals near the Pacific Coast and in former dry grasslands, have been destroyed or seriously degraded by agriculture, grazing, and other forms of development.

Discussion and Conclusions

The host plant usage patterns documented for *Depressaria* in the literature accurately reflect contemporary patterns of host usage by North American *Depressaria* to the extent that they were encountered in this study. The relatively narrow search image we formed for potential *Depressaria* host plants (which included only select Asteraceae and Apiaceae) contributed to this view of patterns of host plant utilization. Our survey data are also complementary to the ecological work of Thompson and Moody (1985) and Thompson (1983a, b). Future surveys should include other potential host plant genera and families. Our observations and our survey results suggest that most *Depressaria* species are more widespread than existing published records indicate (Hodges 1974). Potential host plant species are widely distributed, and relatively abundant throughout much of the western United States, and considerable additional rearing is necessary from throughout the region to document the species richness of *Depressaria* and the systematic relationship of their hosts.

Acknowledgments

We would like to thank Katherine McKenna for her assistance in the field. Arthur Zangerl, Terry Harrison, and Stephen Downie provided helpful comments and guidance. Conversations with Walter Fertig, Ron Hartman, and John Thompson proved immensely help-

ful in locating extant potential host-plant populations to be surveyed, and provided other useful suggestions. David Adamski provided helpful editorial assistance with early drafts of this paper. National Science Foundation grant DEB 9903867, the University of Illinois *Program in Ecology and Evolutionary Biology*, and the Herbert H. Ross Memorial Fund partially funded this work.

LITERATURE CITED

BERENBAUM, M. R. 1981. Patterns of furanocoumarin distribution and insect herbivory in the Umbelliferae: plant chemistry and community structure. Ecology 62:1254–1266.

———. 1983. Coumarins and caterpillars: a case for coevolution. Evolution 37:163–179.

———. 1990. Evolution of specialization in insect-umbellifer associations. Annu. Rev. Entomol. 35:319–343.

BERENBAUM, M. R. & S. PASSOA. 1999. Generic phylogeny of North American Depressariinae (Lepidoptera: Elachistidae) and hypotheses about coevolution. Ann. Entomol. Soc. Am. 92 (6):971–986.

CLARKE, J. F. G. 1933. Notes and new species of microlepidoptera from Washington State. Can. Entomol. 65:85–91.

———. 1941. Revision of the North American moths of the family Oecophoridae, with descriptions of new genera and species. Proc. U.S. Nat. Mus. 90(3107):33–286.

———. 1947. Notes on Oecophoridae. J. Wash. Acad. Sci. 37(1):1–16.

———. 1952. Host relationships of moths of the genera *Depressaria* and *Agonopterix*, with descriptions of new species. Smithson Misc. Collec. 117:1–20.

CRONQUIST, A., N. H. HOLMGREN & P. K. HOLMGREN. 1997. Intermountain flora. Vol. 3, Part A. Rosidae other than Fabales. NYBG Press, New York. 446 pp.

HANNEMANN, J. H. 1953. Naturliche Gruppierung der europaischen Arten der Gattung *Depressaria* s. l. (Lepidoptera: Oecophoridae). Mitt. Zool. Mus. Berl., 29:270–372.

HENDRIX, S. D. 1984. Reactions of *Heracleum lanatum* to floral herbivory by *Depressaria pastinacella*. Ecology 65:191–197.

HODGES, R. W. 1974. Gelechioidea Oecophoridae. *In* Dominick, R. B., D. C. Ferguson, J. G. Franclemont, R. W. Hodges & E. G. Munroe [eds.], The moths of America north of Mexico. Fascicle 6:2. E. W. Classey, London. fasc. 6.2:i–x + 142 pp.

HODGES, R. W. [ED.]. 1983. Check list of the Lepidoptera of America north of Mexico; xxiv + 1–284. E. W. Classey Limited and Wedge Entomological Foundation, University Press, Cambridge, Great Britain.

PLUNKETT, R. & S. R. DOWNIE. 1999. Major lineages within Apiaceae subfamily Apioideae: a comparison of chloroplast restriction site and DNA sequence data. Am. J. Bot. 86(7):1014–1026.

POWELL, J. A. & P. A. OPLER. 1996. Moths of western North America. 4. Distribution of "Oecophoridae" (sense of Hodges 1983) of western North America. Contributions of the C.P. Gillette Museum of Arthropod Diversity. Colorado State University, Fort Collins, Colorado. 63 pp.

THOMPSON, J. N. 1983a. Selection of plant parts by *Depressaria multifidae* (Lepidoptera: Oecophoridae) on its seasonally-restricted hostplant, *Lomatium grayi* (Umbelliferae). Ecol. Entomol. 8:203–211.

———. 1983b. The use of ephemeral plant parts on small host plants: How *Depressaria leptotaeniae* (Lepidoptera: Oecophoridae) feeds on *Lomatium dissectum* (Umbelliferae). J. Anim. Ecol. 52:281–291.

———. 1998. Coping with multiple enemies: 10 years of attack on *Lomatium dissectum* plants. Ecology 79:7 255–2554.

THOMPSON, J. N. & M. E. MOODY. 1985. Assessing probability of interaction in size-structured populations: *Depressaria* attack on *Lomatium*. Ecology 66:1597–1607.

THOMPSON, J. N. & P. W. PRICE. 1977. Plant plasticity, phenology, and herbivore dispersion: wild parsnip and the parsnip webworm. Ecology 58:1112–1119.

ZANGERL, A. R. & M. R. BEREMBAUM. 1993. Plant chemistry and insect adaptations to plant chemistry as determinants of host plant utilization patterns. Ecology 74:478–504.

Received for publication 19 November 2001; revised and accepted 3 September 2002.