

Larval Case Architecture and Implications of Host-Plant Associations for North American *Coleophora* (Lepidoptera; Coleophoridae)¹

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The case-bearing moths of North America are represented by a single genus, *Coleophora*, which contains approximately 144 described species. All are external seed or leaf miners that inhabit portable silk cases during most of the larval stage. Architectural and ecological characters from larval cases were used in cladistic analysis to investigate existing case groups for 32 North American species of *Coleophora*. Cladistic analysis confirmed monophyly of certain case groups, but not of others. Host-plant preferences were also examined. The pattern of host plant use reflects more closely preference for certain plant tissues (seeds versus leaves) and growth forms (herbaceous versus woody) with exploitation of different plant taxa, rather than preference for certain plant taxa with exploitation of different plant tissues. © 2002 The Willi Hennig Society

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INTRODUCTION

Plant–insect herbivore relationships are difficult to quantify because each lineage is under many selective pressures, including the pressures supplied by each

other. Cladistic methods provide a means to examine coevolutionary situations empirically.

Mitter and Brooks (1983) set the standard for phylogenetic analysis of coevolutionary events by constructing phylogenies of the insects and their host plants and comparing the two cladograms to ascertain the level of coevolution. Two expectations must be met to argue that a host plant and its herbivore have undergone reciprocal evolution: (1) There must be a nonrandom fit overall to association by descent (the overall branching patterns of the cladograms must be congruent) and (2) derivations from this fit should be predictable and occur within groups of plants with similar herbivore defenses. One widely accepted example of insect–plant cospeciation has been shown between *Phyllobrotica* leaf beetles (Chrysomelidae) and Lamiales (Farrell and Mitter, 1990).

Insect–plant coevolution and cospeciation have been investigated in many systems since Ehrlich and Raven's 1964 publication, and several alternative hypotheses have been suggested to describe patterns of host choice by insects. Among these theories are colonization (Futuyma, 1983; Janzen, 1980; Jermy, 1976, 1984; Menken *et al.*, 1992; Miller, 1987; Powell, 1980; Powell *et al.*, 1999), competition (Bernays and Graham, 1988;

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Denno *et al.*, 1995), and habitat specialization (Courtney, 1984; Janz and Nylin, 1998).

Mechanisms of Host-Plant Selection

Colonization. Host-plant selection by phytophagous insects may be the result of colonization events rather than reciprocal evolution or cospeciation. Random colonization events of novel host plants would result in completely random cladogram patterns when the plant and herbivore phylogenies are compared. Oftentimes, though, a degree of congruence is seen between host and herbivore cladograms (Jermy, 1976; Mitter and Brooks, 1983; Miller and Wenzel, 1995). In this situation, insects and their host plants may not be evolving reciprocally; but rather, insects may be tracking a particular plant chemical, a process termed sequential evolution by Jermy (1976). Insects that are able to digest noxious secondary chemicals of a particular plant may be preadapted to digest the same or very similar chemicals of novel unrelated plants. Colonization of host plants based on plant chemical cues, or resource tracking, may produce very similar cladograms (Jermy, 1976; Mitter and Brooks, 1983; Miller and Wenzel, 1995). In resource tracking, host-plant cladogenesis takes place prior to and independent of insect cladogenesis. Insects subsequently colonize plants that produce particular chemicals. The plants colonized may have similar chemicals either because of phylogenetic relatedness or through convergent evolution. Sequential evolution may be much more common than nearly simultaneous coevolution in the sense of Ehrlich and Raven (Jermy, 1976; Miller and Wenzel, 1995).

Janz and Nylin (1998) reconsidered the relationship between angiosperms and butterflies in light of the Chase *et al.* (1993) comprehensive angiosperm phylogeny. By comparing major butterfly lineages to a modified version of the tree, they support Ehrlich and Raven's original hypothesis, and Mitter *et al.*'s (1988) later concurrence that groups of closely related butterflies feed on groups of closely related plants, but the preponderance of butterfly host-plant groups may be the product of convergent evolution. Butterflies colonize groups of phylogenetically or chemically related plant groups. Reversals by the butterflies to the ancestral food source may be more likely than unique colonization events, assuming there is a plesiomorphic ability

to locate ancestral plants (Futuyma, 1983, 1991; Janz and Nylin, 1998).

Within Lepidoptera, there is a trend for externally feeding species to be generalists and internally feeding species to be specialists (Gaston *et al.*, 1992). Internal feeders, such as gall formers and leaf and seed miners, are dependent on their host plants for not only food, but also shelter. The more intimate the relationship with the host plant, the more complex the interaction between plant and herbivore, resulting in a higher degree of host specificity. Concealed-feeding British microlepidoptera show a close association with their host plants, especially in early instars (Gaston *et al.*, 1992).

Habitat specialization. Janz and Nylin (1982) illustrate that colonization of plants by butterflies is greatly influenced by the habitat in which the butterflies live. Insects may specialize on plants occurring in specific habitats, such as open fields or forests, as opposed to specializing on groups of phylogenetically related plants. Habitat specialization may be based on three factors: female search time for a suitable oviposition site, plant growth form, or chemical convergence (Bernays and Graham, 1988; Janz and Nylin, 1998; Feeny, 1975). Courtney (1984), based on a study by Rausher (1978), argued that specializing in a certain habitat might reduce time spent searching for a suitable host. Searching only in an open field, rather than in open field and forest, would optimize the time spent foraging for a host plant if plants growing in that habitat were suitable hosts. When a group of 48 temperate butterflies consisting of three guilds was categorized according to food plant preference and also habitat type, only habitat type showed a phylogenetic pattern (Courtney, 1984). Often, only a few plants grow in a particular habitat. Insects that seem to be specialists may accept many other hosts that they do not normally encounter if given the opportunity (Courtney, 1984).

Janz and Nylin (1998) suggest that specialization within certain habitats may restrict colonization events seen among butterflies. Plants that are adapted to certain habitat conditions such as amount of light available, average growing season temperature, or amount of water available tend to be similar. Therefore, certain growth forms tend to dominate certain habitats. Recognition of a plant by females as a proper oviposition site may depend on many external signals, such as search images and tactile appropriateness (size, shape, texture, etc.) of the host plant, as well as secondary

plant chemicals (Feeny, 1975). Plants inhabiting specific localities may be very similar in oviposition appropriateness through convergent evolution. Herbaceous plants tend to be more diverse in tactile cues and chemical composition (termed qualitative chemicals by Feeny, 1975) than woody plants because of a small growth form and relatively short growing seasons. Woody plants tend to be more homogeneous in tactile cues and chemical composition but have other defense mechanisms (termed quantitative chemicals by Feeny, 1976), which make them less nutritious to insect herbivores. Insects that rely on specific tactile cues or chemical cues for oviposition may not be able to discriminate between different trees as well as those that oviposit on herbs. Lepidoptera larvae that are specialized to feed on toxic plants tend to show a higher degree of diet specialization (Feeny, 1975).

Comparison of butterfly and host phylogenies showed a significant association between tree feeding and the number of host switches (Janz and Nylin, 1998). More host shifts occurred within butterfly clades containing tree-feeding species than butterfly clades containing herb-feeding species. There was also a low degree of host switching between tree feeding and herb feeding. Janz and Nylin conclude that plant growth form appears to play a role in the evolution of host-plant choice, perhaps as much as the identity of the hosts themselves.

Competition. Analyzing 193 pairwise comparisons of phytophagous insect interactions, Denno *et al.* (1995) found that 76% were under interspecific competitive influences, while the remaining 24% were facilitative or neutral. Among mandibulate phytophages, they found the greatest degree of competition between internal feeders (stem borers, wood borers, and seed feeders), followed by competition between concealed feeders (leaf miners), with the least degree of competition occurring between free-living feeders.

A Synthetic Model

Synthesis of the theories presented by Gaston (1992), Denno *et al.* (1995), Feeny (1975), and Janz and Nylin (1998) results in a model useful for predicting patterns of host-plant use and degree of host fidelity among phytophagous insects (Fig. 1, Table 1). We predict the following pattern of evolution: (1) internal feeders (such as seed mining and stem boring) of herbaceous

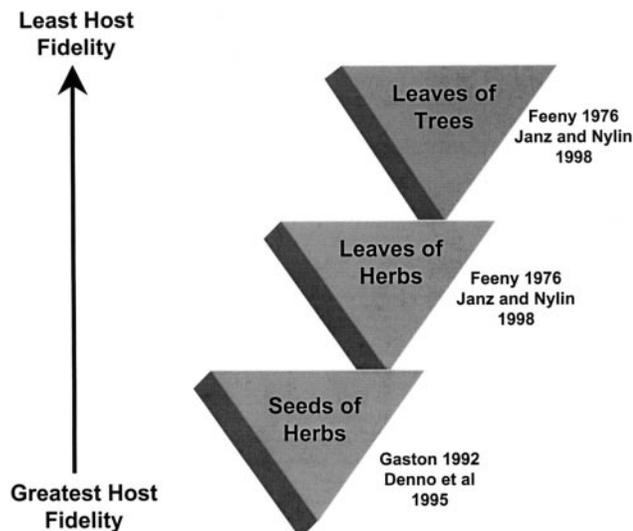


FIG. 1. A synthetic model derived from combining the theories of Gaston (1992), Denno *et al.* (1995), Feeny (1975), and Janz and Nylin (1999) useful for predicting evolution of host-plant choice and degree of specialization.

plant families should be the most faithful to their host plants, or have the fewest host-switching events (Gaston, 1992; Denno *et al.*, 1995), (2) host-switching events would be more common in clades of leaf-feeding larvae than in clades of internal-feeding larvae and would occur often among host plants similar in physical and chemical attributes in the same microhabitat (Gaston, 1992; Denno *et al.*, 1995; Feeny, 1975; Janz and Nylin, 1998), (3) leaf feeders of woody plants should be the least faithful to their hosts, or have the most numerous host-switching events, due to the homogeneity of woody plant defenses (Feeny, 1975; Janz and Nylin, 1998). The pattern of host plant use, therefore, would reflect more closely preference for certain plant tissues (seeds versus leaves) and growth forms (herbaceous versus woody) with exploitation of different plant taxa, rather than preference for certain plant taxa with exploitation of different plant tissues. Because this model is presented as an unrooted network, the ancestral conditions may be specialized seed feeding or generalized leaf feeding. This perspective produces a scale that relates host fidelity to feeding syndrome. As an evolutionary proposal, there is no a priori reason to root the diagram in any particular location, but we will show that for *Coleophora*, the plesiomorphic or apomorphic status of characters of interest is as shown in Fig. 1.

TABLE 1
Overview of Coevolutionary Theories Discussed in the Text

Author	Taxa	Pattern	Cladogenesis?	Comments
Ehrlich and Raven (1964)	Papilionid butterflies and <i>Passiflora</i> plants	Coevolution	No	Escape and radiation of butterflies and host plants may drive evolution
Feeny (1975)	Butterflies and their host plants	Biochemical coevolution	No	Biochemical identity of host plants leads to diet specialization
Rausher (1978)	Butterflies and their host plants	Diet specialization	No	Leaf search image will lead to diet specialization
Mitter and Brooks (1983)		Cospeciation	Yes	Mirror image cladograms to test for coevolution
Berenbaum (1983)	Caterpillars and host plants	Coevolution	No	Secondary chemicals drive insect evolution
Courtney (1984)	Butterflies and host plants	Habitat specialization	No	Classification by habitat type shows a phylogenetic pattern
Miller (1987)	Papilionid butterflies and <i>Passiflora</i> plants	Resource tracking or sequential evolution	No	Insects colonize plants, but do not drive plant evolution
Bernays and Graham (1988)	Phytophagous insects and their predators	Diet specialization	No	Predation may drive diet specialization
Farrell and Mitter (1990)	<i>Phyllobrotica</i> beetles and host plants	Cospeciation	Yes	Cladogenesis of host drives cladogenesis of parasites
Bell (1990)	Search behavior in insects	Diet and habitat specialization	No	
Menken <i>et al.</i> (1992)	Ermine moths and their host plants	Colonization	No	6 to 9 host-switch events are due to colonization
Denno <i>et al.</i> (1995)	Phytophagous insects	Competition	No	Interspecific competition leads to host specialization
Gaston <i>et al.</i> (1992)	Concealed Lepidoptera larvae and host plants	Diet specialization	No	A concealed feeding habit may lead to diet specialization
Powell (1980) and Powell <i>et al.</i> (1999)	Evolution of host plant use in microlepidoptera	Colonization	No	Majority of microlepidopteran host-plant groups are the result of colonization
Janz and Nylin (1998)	Papilionid butterflies and <i>Passiflora</i> plants	Habitat specialization	No	Habitat specialization may lead to diet specialization
Berenbaum and Passoa (1999)	Depressariine moths and host plants	Resource tracking or sequential evolution	No	Moths are tracking plant chemicals within certain plant clades

Phylogenetic testing of the model in Fig. 1 requires a single clade of closely related insects that feed on seeds and leaves of herbaceous and woody plant families. Microlepidopteran moths of the genus *Coleophora* present an interesting group to study processes governing host-plant selection. Although considered internal seed or leaf miners primarily of herbaceous and woody angiosperm plant families, larvae of *Coleophora* construct a portable, protective case that enables a greater degree of mobility than seen in other families of internal feeders. The purpose of this study is to examine the synthetic model presented above. We illustrate the evolution of use of plant tissue and growth form in *Coleophora* and determine the root and polarity of the

model. We rely on behavioral and ecological characters to group species of *Coleophora* and provide the first cladogram of *Coleophora* using exemplars representing the bulk of known North American diversity. In addition, we comment on the concept of homoplasy as applied to ecological characters and the distinction between intrinsic characters that represent descent with modification and extrinsic features that are best not included in definitions of homology and homoplasy.

The Biology of Coleophora

Coleophora is a cosmopolitan genus of leaf and seed miners on primarily temperate woody and herbaceous

plant families (Emmet *et al.*, 1996; Heinrich, 1923; Hering, 1951). Members of *Coleophora* receive their common name of the “sheath” or “case” bearers because the larvae construct portable cases in which they spend nearly all of their immature lives. Early instars (usually only the first) are internal miners, but later instars feed from the case, rarely leaving it. The case is composed mostly of silk and often contains plant tissue or frass. Cases may also be decorated, or perhaps camouflaged, with bits of plant material such as entire florets, bracts, leaf edges, seeds, or even sand. Cases are built with a valved anal end for frass ejection and adult emergence and an oral end for feeding, locomotion, and attachment (Fig. 2). As the larvae grow, the cases are enlarged to accommodate the increase in body size (Emmet *et al.*, 1996; Heinrich, 1923; Hering, 1951). Species may be recognized by case architecture and host-plant record, although genital dissection should be made for a positive identification.

Species of *Coleophora* historically have been categorized for ease of reference and identification based on the case morphology. Heinrich (1923) was the first to place species into distinct groups based on features of the case. Later, McDunnough (1933) divided Heinrich's two groups into four. Emmet *et al.* (1996) credits Hering (1951) as describing the principal European case types. He categorized these species into seven case types. Toll (1952, 1962) accepted Hering's case descriptions and key with minor modifications, but organized adult and larval groups into a numerical system based on adult external characters, genitalia, and case type. Emmet *et al.* (1996) later rearranged the European species based on Toll and then Patzak's descriptions. Landry (1998) divided McDunnough's North American groups into eight types based on Emmet's treatment (Emmet *et al.*, 1996), as follows: seed-case group (Fig. 3A), silk-case group (Fig. 3B), composite leaf-case group (Fig. 3C), lobe-case group (Fig. 3D), pistol-case group (Fig. 3E), annulate-case group (Fig. 3F), spatulate leaf-case group (Fig. 3G), and tubular leaf-case group (Fig. 3H).

Case-based groups discussed above commonly conflict with one another and also with genitalia-based groups. For example, Emmet's (Emmet *et al.*, 1996) *lutipennella* group (based on Toll's group 2) contains species that belong to the composite leaf-, tubular leaf-, and spatulate leaf-case groups, but not all of the species within these groups.

Despite this traditional use of case-type groups and

genitalia groups to classify members of *Coleophora*, the monophyly of these groups has never been established through cladistic methods. Without a phylogenetic tree, it is impossible to tell which grouping schemes may be natural, as well as to investigate patterns of host-plant choice.

PHYLOGENETIC ANALYSIS AND HOST-PLANT CHOICE INVESTIGATION

Selection of Taxa

This study is based on the examination of larval cases of 32 species of North American *Coleophora* on loan from the Canadian National Collection (Ottawa). A few of the species used in this study are not endemic to North America, but are used because the morphology of the case is typical of the group. Exemplars were chosen from each of the eight North American case types as described by Landry (1998), based on either overall similarity to other cases in the group or uniqueness of the case compared to other cases in the group, so that a range of case architecture was coded for each group. At least two, usually three or more, cases from each group were investigated. Species omitted from this analysis are either unknown for these characters or redundant with species coded here. An asterisk next to the name in Appendix 2 indicates species used in the analysis.

Selection of Outgroups

No phylogeny for genera within Coleophoridae exists, and there is no sister group hypothesis for the genus *Coleophora*. Other genera within Coleophorinae are seed miners and form galls or pupate within a seed capsule or floret, but do not form a case such as those of *Coleophora* (Emmet *et al.*, 1996). Life histories for *Augasma aeratella* (Zeller), *Metriotes lutarea* (Haworth), and *Goniodoma limoniella* (Stainton) were taken from the literature, and larval shelters on loan from the National Museum of Natural History (Washington, DC) were examined.

Selection of Characters

The character set is based on ecological data, building behavior, and end-product architecture of the cases.

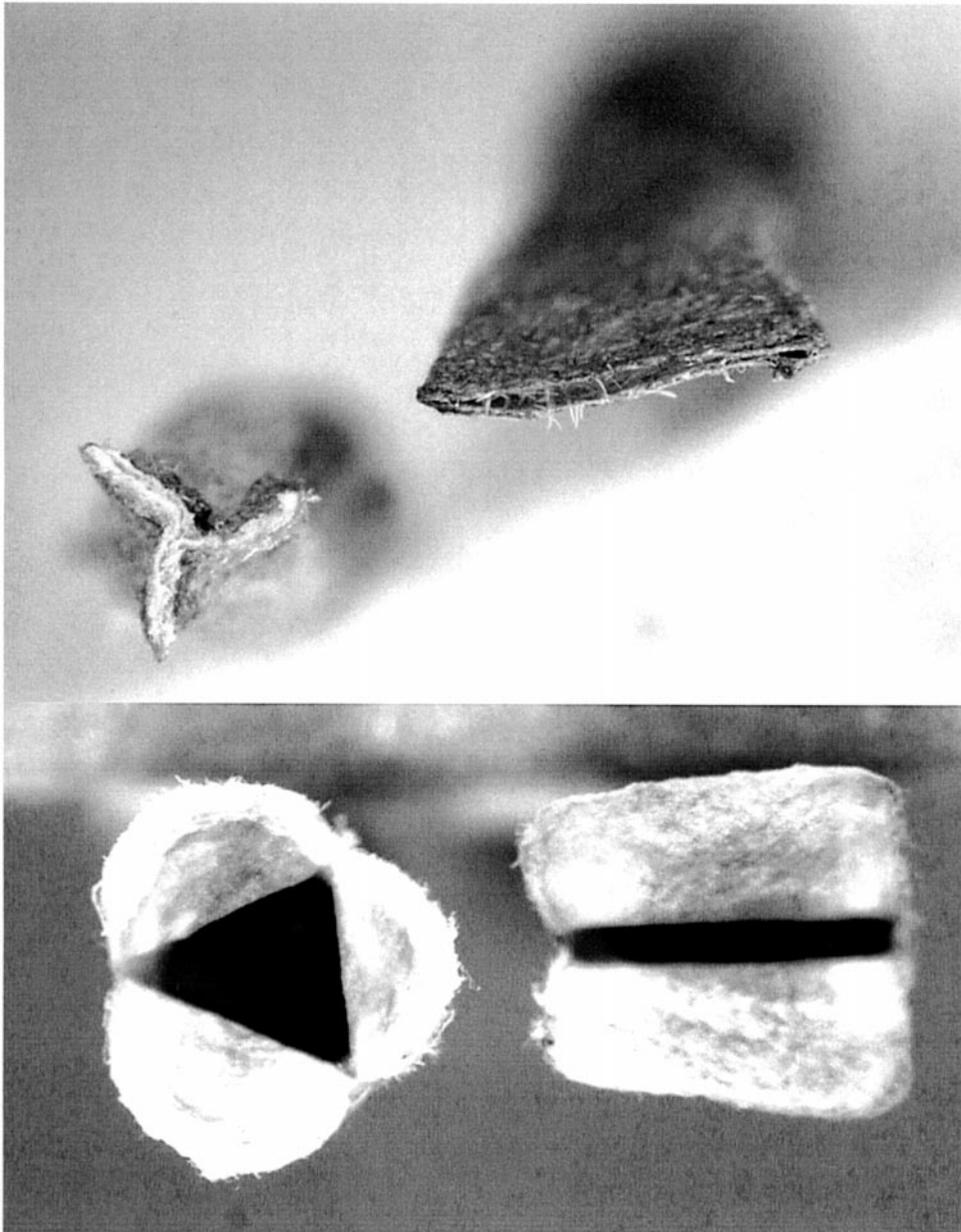


FIG. 2. Anal end of *Coleophora* larval case viewed on end, showing valve arrangement; left, trivalved; right, bivalved. (Top) Closed (natural position); (bottom) pulled back to show geometry.

Behavioral processes are preserved in the architectural end-products of the case that can be interpreted as behavioral characters. Accounts of building behavior were taken from the literature (Baldizzone and Landry, 1993; Braun, 1914, 1919, 1940; Emmet *et al.*, 1996; Fal-kovitch, 1989; Heinrich, 1915, 1920, 1923; McDun-nough, 1933, 1940, 1944a,b, 1945, 1946a,b,c, 1954, 1955,

1956, 1957, 1958, 1962) as well as from original data (Landry, 1991, 1998; Landry and Wright, 1993, Landry, unpublished) and our examination of exemplar cases. A list of the characters and states used in the analysis is shown in Appendix 1.

Shelter and case type (characters 0–6). The larva of *Augasma* forms a floret gall on herbaceous plants

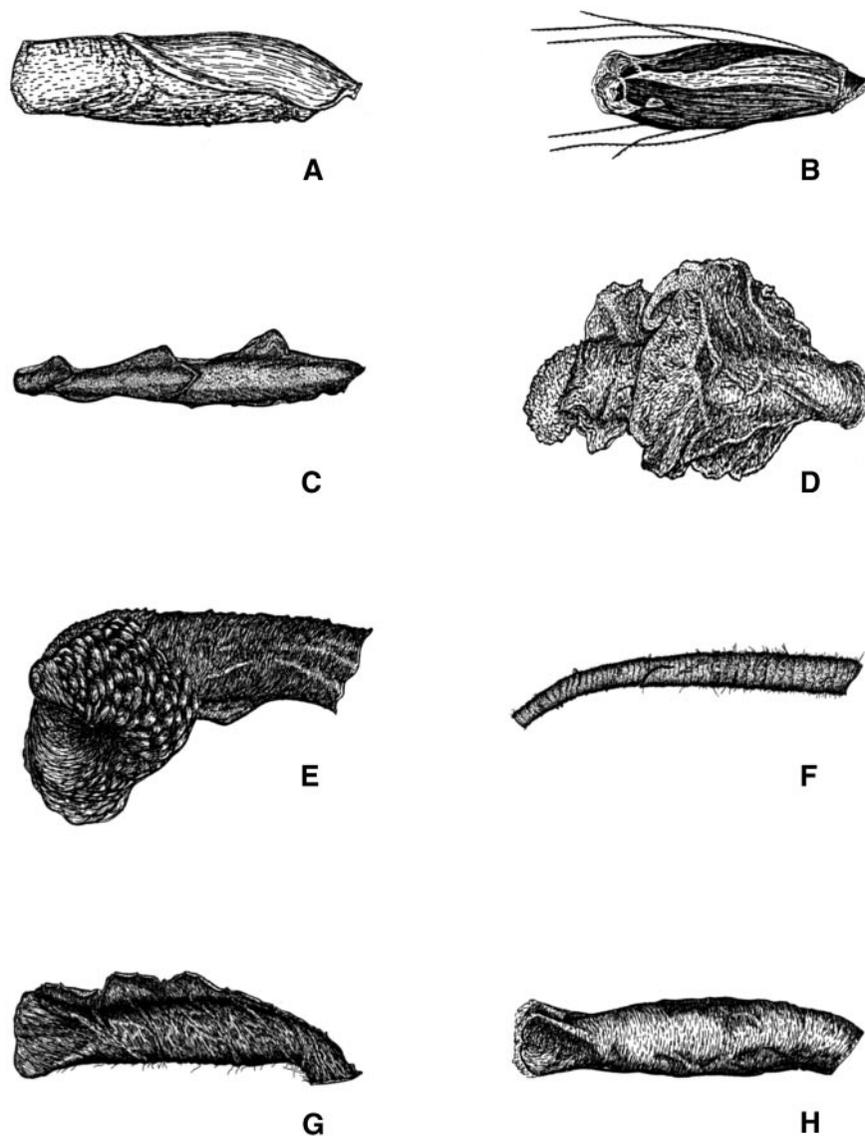


FIG. 3. Examples of case types used in the analysis. See text for a detailed description of each type. (A) Seed case (*C. quadrilineella*); (B) tubular silk case (*C. dextrella*); (C) composite leaf case (*C. canadensisella*); (D) lobe case (*C. accordella*); (E) pistol case (*C. sacramenta*); (F) annulate case (*C. monardella*); (G) spatulate leaf case (*C. limosipennella*); (H) tubular leaf case (*C. rosacella*). Illustrations drawn by Barry Wright.

where it feeds and pupates. The larva of *Goniodoma* hollows out a seed capsule to form a temporary shelter before leaving it to bore into the stem of its host plant for pupation. The larva of *Metriotes* makes a temporary shelter in a floret at the end of its larval life and uses it to move away from its host plant to a pupation site, where the shelter is abandoned outside the entrance hole of the pupal cavity.

First-instar larvae of *Coleophora* are internal miners

of ovules and later seeds or leaves. Second and later instar larvae construct a portable case (Fig. 3). Some seed-feeding species adopt the floret or seed capsule of the host plant as their initial case that is later enlarged (Fig. 3A). Others construct a case immediately that is composed of silk (which may or may not be decorated with seed pappus, sand, etc.) (Fig. 3B). Others construct a case of leaf cut-outs that are reinforced with silk. The leaf cut-outs are the remaining epidermal

layers of mined leaves (Figs. 3C–3G). Larvae of *Colopophora* pupate inside their case.

Case enlargement (characters 7–15). Some larvae enlarge the initial case as they grow, while others abandon it and build a new one. Enlargement may be by stretching the case or adding on new case materials. Additions may be in the form of silk or leaves. These additions may be oral or anal. Other larvae enlarge the existing case by cutting it and then adding silk. The case may be slit longitudinally at several points around its girdle (silk added laterally, called gussets) or cut along a single ventral line (silk added ventrally).

Leaf cases are enlarged with leaf sheets or leaf rings. Leaf sheets either are neatly wrapped around and glued down with silk (Fig. 3C) or project from the case irregularly (Fig. 3D). Cases may have a prominent dorsal keel formed from the leaf edges (Fig. 3G or 3H). Leaf rings are formed by cutting a circle around the entrance and later exit holes of the mine. Cases formed by rings are gradually increased each time the larva leaves a mine. The earlier rings are the smallest; successive ring diameter increases as the larvae grow (Fig. 3F).

Larvae that add silk orally may change their position during early case enlargement, which ultimately produces a snail-shell-shaped case. Some larvae remain straight, some bend themselves slightly and build a case that is slightly curved, and others add new silk at a 90° angle to the old case (Fig. 3E).

Valve construction (characters 17–19). Cases are built with a valved anal end. The valve may be built during initial case construction or cut into the case once it is built. Cases may be bivalved or trivalved (Fig. 2). Bivalved cases may have a rounded shape (Figs. 3C, 3D, and 3E) or a broad, spatulate shape (Fig. 3G). Larvae that construct new cases instead of enlarging the old one build either a replica of the original case with the same valve shape and number as the original case (bivalved) (Fig. 3G) or a novel case with a valve shape and number different from those of the original case (older case valve is bivalved, later case is trivalved) (Fig. 3H).

Host-plant data (characters 20–23). Host-plant data were organized into tissue preference of the larvae (seeds versus leaves) and host-plant growth form (herbaceous versus woody) and also generic and family level associations. These generic and family taxonomic

groupings of host plants (e.g., *Juncus* versus *Asteraceae*) were not used in phylogenetic reconstruction, but were mapped onto the final consensus phylogeny.

Phylogenetic Analysis

A character set of 24 characters in 58 derived states (character 7 is nonadditive) was constructed from case morphology, building behavior data, and ecological data, and a character matrix was compiled in DADA (Nixon, 1998) (Table 2). Missing data and nonapplicable character states to some taxa are indicated in the data matrix as “?” and “-”, respectively. These data were analyzed according to the parsimony method using NONA (Goloboff, 1994) with the host characters (22 and 23) turned off. The command “mult*100” followed by “max” was used to search for trees, and all trees were saved using the “ksv*” function. The successive approximations weighting function was used to weight the characters. The command sequence used was “swt.run mult*20” and trees were saved using the “ksv*” function. The “best” function was used to eliminate all nodes that were optimization sensitive and keep only those that had unambiguous support. Final trees and a strict consensus tree of both analyses were viewed using ClaDos (Nixon, 1993).

Host-Plant Analysis

Family level host-plant associations (characters 22 and 23) were mapped on the final tree and analyzed in ClaDos. Host-plant data were coded separately for herbaceous feeders and woody feeders, with each of the prior categories as a character. Families of host plants mined by the larvae are represented as character states for each character. For polymorphic data, or larvae that have more than one host, the host-plant character state was coded as “*”.

Some species were not included in the cladistic analysis because they had the same character vectors as species that were included. However, these species were considered in the host-plant analysis. For example, all species within the pistol-group construct and enlarge the case identically and feed on leaves of trees. Species that were included after the cladistic analysis were considered part of the pistol case-type polytomy.

TABLE 2
Data Matrix for the Cladistic Analysis Used to Produce the
Cladograms in Figs. 4–7

Taxon	Character state		
	0123456789	1111111111 0123456789	2222 0123
<i>Augasma</i>	0--0-----	-----	00--
<i>Goniodoma</i>	1000-----	-----	00--
<i>Metroites</i>	1000-----	-----	00--
<i>C. quadrilineella</i>	111010-12-	----00-001	001-
<i>C. sexdentatella</i>	111010-12-	----00-001	001-
<i>C. fagicorticella</i>	111010-12-	----00-001	001-
<i>C. bispinatella</i>	11111100--	----001001	000-
<i>C. latronella</i>	11111100--	----001001	000-
<i>C. glaucicolella</i>	111111011-	1---001001	000-
<i>C. lineapulvella</i>	111111011-	1---001001	002-
<i>C. acuminatoides</i>	111111011-	0---001001	000-
n. sp. 1	111111011-	0---001001	?0-
<i>C. heinrichella</i>	111111011-	0---001001	000-
<i>C. astericola</i>	1111110??-	?---001010	100-
<i>C. canadensisella</i>	1111111101	-00-01-010	11-3
<i>C. cretaticostella</i>	1111111101	-00-01-010	11-4
<i>C. leucochrysell</i>	1111111101	-00-01-010	11-2
<i>C. kearfottella</i>	1111111101	-01-01-010	11-7
<i>C. ledi</i>	1111111101	-01-01-010	11-5
<i>C. accordella</i>	1111111101	-01-01-010	11-6
<i>C. elaeagnisella</i>	1111110100	----110010	11-1
<i>C. malivorella</i>	1111110100	----110010	11-?
<i>C. tiliaefoliella</i>	1111110100	----110010	11-0
<i>C. asterophagella</i>	1111111101	-1--01-1--	100-
<i>C. monardella</i>	1111111101	-1--01-1--	100-
n. sp. 2	1111111101	-1--01-1--	100-
<i>C. glaucella</i>	11111112--	-0-001-0-0	11-5
<i>C. cornella</i>	11111112--	-0-001-0-0	11-3
n. sp. 3	11111112--	-0-001-0-0	11-?
<i>C. juglandella</i>	11111112--	-0-001-0-0	11-8
<i>C. limospennella</i>	11111112--	-0-001-0-0	11-9
<i>C. comptoniella</i>	11111112--	-0-001-0-0	11-?
<i>C. rosacella</i>	11111112--	-0-101-0-1	11-4
<i>C. serratella</i>	11111112--	-0-101-0-1	11-?
<i>C. spinella</i>	11111112--	-0-101-0-1	11-?

Note. Characters 22 and 23 were turned off for the analysis. Missing data and nonapplicable character states to some taxa are indicated in the data matrix as "?" and "-", respectively. Polymorphic data for character 23 are indicated by "?" in the matrix.

Only species that had host records including tissue type were used in the host-plant analyses. (See Appendix 2 for a complete list of host records.) Host-plant data were compiled as number of species of *Coleophora* of certain groups (herbaceous versus woody feeders and seed versus leaf miners) found on number of host plants (generic versus family level).

RESULTS

Results of Parsimony Analysis

The original tree search in NONA was repeated several times and found approximately 152 trees each time. Eight most parsimonious trees remained after the "best" command. A strict consensus tree was calculated from these trees. The successive approximations weighting procedure using the trees from the original search stabilized after one iteration, yielding 128 trees. Eight most parsimonious trees remained after the "best" command ($L = 26$; $CI = 0.92$; $RI = 0.98$) (Figs. 4 and 5). A strict consensus tree was taken from these

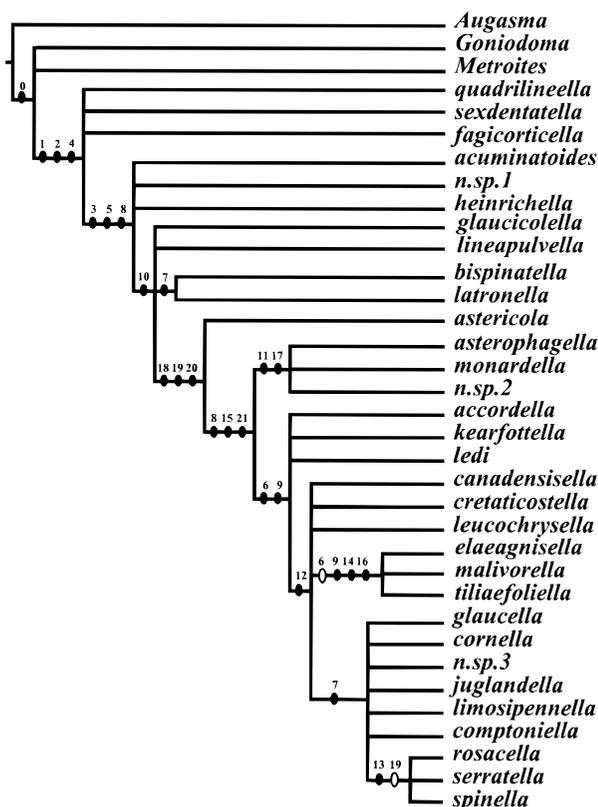


FIG. 4. One alternative phylogeny (length 26; $CI = 0.92$; $RI = 0.98$) produced by parsimony analysis of the data matrix in Table 2. Characters and states mapped on the tree are described in the text. *C. acuminatoides*, n. sp. 1, and *C. heinrichella* basal to *C. lineapulvella* and *C. glaucicolella*, alternative to Fig. 5. The annulate-case group is basal to the remaining leaf-case groups, alternative to Fig. 5. The composite leaf-case group polytomy is basal to the lobe-case group polytomy, alternative to Fig. 5. Solid circles represent synapomorphies, open circles represent parallelisms and reversals.

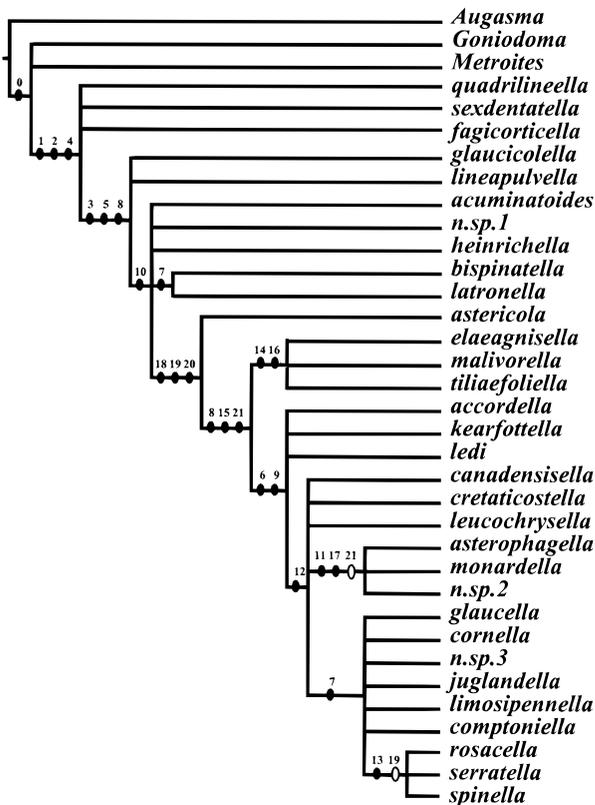


FIG. 5. One alternative phylogeny (length 26; CI = 0.92; RI = 0.98) produced by parsimony analysis of the data matrix in Table 2. Characters and states mapped on the tree are described in the text. *C. lineapulvella* and *C. glaucicolella* basal to *C. acuminatoides*, *n. sp. 1*, and *C. heinrichella*, alternative to Fig. 4. The pistol-case group is basal to the remaining leaf-case groups, alternative to Fig. 4. The lobe-case group polytomy is basal to the composite leaf-case group polytomy, alternative to Fig. 4. Solid circles represent synapomorphies, open circles represent parallelisms and reversals.

trees ($L = 29$, CI = 0.82; RI = 0.95) (Fig. 6). The eight alternative trees obtained from the two analyses (with and without successive approximations weighting) were identical. The trees were viewed in ClaDos, and character polarities were determined directly from the consensus tree.

The eight phylogenies are the result of all permutations of three pairs of alternative topologies ($2 \times 2 \times 2$). The annulate-case group and the pistol-case group alternate in position. The lobe-case polytomy and the composite leaf-case polytomy alternate in position. The species *C. acuminatoides*, *n. sp. 1*, and *C. heinrichella* alternate in position with the species *C. lineapulvella* and *C. glaucicolella*. We have chosen to illustrate only

two versions of these eight phylogenies, the two versions that are opposite in topology (Figs. 4 and 5). These phylogenies represent alternative explanations for the evolution of the case types and architectural processes; however, in all of the alternative phylogenies, the hypotheses of ecological associations (such as tissue preference and habitat use by particular clades) remain the same.

Monophyly of Case Types

Gall forming (0-0) is the plesiomorphic condition for the subfamily. There is a single derivation of building

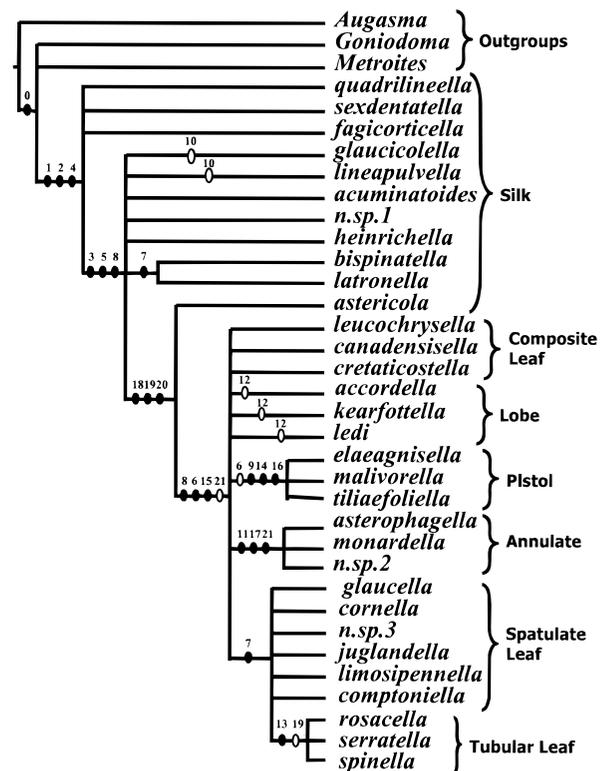


FIG. 6. Strict consensus phylogeny of the phylogenies in Figs. 4 and 5 (length 29; CI = 0.82; RI = 0.95) produced by parsimony analysis of the data matrix in Table 2. Characters and states mapped on the tree are described in the text. *C. lineapulvella*, *C. glaucicolella*, *C. acuminatoides*, *n. sp. 1*, and *C. heinrichella* are included in the silk-case groups polytomy. The annulate-case group and the pistol-case group are included in the leaf-case groups. The composite leaf-case group polytomy and the lobe-case group polytomy are included in the leaf-case groups. Case types are shown in brackets. Solid circles represent synapomorphies, open circles represent parallelisms and reversals.

a shelter (0-1) in the ancestor of *Goniodoma* + *Metriotes* + *Coleophora*. Monophyly of *Coleophora* is supported by building a feeding case (2-1) that is reinforced with silk spinning (1-1) when pupation occurs (4-1). The seed-case group, *C. quadrilineella*, *C. fagicorticella*, and *C. sexdentatella*, is part of a quadritomy, the fourth component being a clade of all remaining taxa. The remaining taxa, silk cases + *C. astericola* + leaf cases, form a monophyletic group whose members construct cases, which may or may not be reinforced with plant tissues (5-1), as early instar larvae (3-1). The cases are enlarged by cutting and adding silk laterally or ventrally (8-1) (Fig. 6).

The silk cases are a paraphyletic group basal to the leaf-case groups (Fig. 6). In some of the topologies, *C. acuminatoides*, n. sp. 1, and *C. heinrichella* are part of a quadritomy, the fourth component being a clade of all remaining species, defined by cutting the case anally and adding silk ventrally (10-1) (Fig. 4). In alternative topologies, *C. linaepulvella* and *C. glaucicolella* are basal to the clade containing all remaining species defined by cutting the case laterally and adding silk in strips (10-0) (Fig. 5). Within the silk cases, *C. bispinatella* + *C. latronella* form a monophyletic group that enlarge the case by stretching it (7-0) (Fig. 6). The clade containing *C. astericola* + leaf-case groups forms a monophyletic group present in all alternative topologies. It is supported by the characters of constructing a case with a rounded (18-1), bivalved end (19-0), and feeding on leaves (20-1) (Fig. 6).

The leaf-case groups form a monophyletic clade present in all of the alternative topologies (Fig. 6). It is supported by characters of constructing a leaf case reinforced by silk (6-1), which is enlarged orally (8-0) with a marginally constructed lip (15-1), and a woody feeding habit (21-1). This includes the pistol-, annulate, lobe-, composite leaf-, spatulate leaf-, and tubular leaf-case groups.

This pistol-case group always forms a monophyletic clade within the leaf-case group and contains *C. elaeagnisella*, *C. malivorella*, and *C. tiliaefoliella* (Fig. 6). It is supported by the character of adding on silk at the oral region of the case (9-0) at an angle to the existing case (14-1) and a reversal from a leaf case (6-1) to a silk case (6-0). The case is not decorated or camouflaged (16-0). Its position is variable. In some topologies, this clade is the sister group to the remaining leaf-case

groups (Fig. 5), and in alternative topologies it is a clade within the leaf-case group (Fig. 4).

The annulate-case group always forms a monophyletic clade within the leaf-case group and contains n. sp. 2, *C. asterophagella*, and *C. monardella* (Fig. 6). It is supported by characters of having a case that is constructed of leaf rings derived from the entrance to the mine (11-1), and a valve that is constructed after the original case has already been built (17-1), and a reversal from feeding on woody plants (21-1) to feeding on herbaceous plants (21-0). The position of this group is variable. In some topologies, this clade is the sister group to the remaining leaf-case groups (Fig. 4), and in alternative topologies it is a clade within the leaf-case group (Fig. 5).

Neither the lobe-case group nor the composite leaf-case group formed a monophyletic group in the consensus phylogeny or any of most parsimonious trees. In some topologies, *C. accordella*, *C. kearfottella*, and *C. ledi* are part of a quadritomy, the fourth component being a clade of all remaining species defined by constructing a leaf case with the leaf sheets tied down (12-0) (Fig. 5). In alternative topologies, *C. canadensisella*, *C. cretaticostella*, and *C. leucochrysella* are part of a quadritomy, the fourth component being a clade of all remaining species defined by constructing a leaf case with the leaf sheets projecting at irregular angles (12-1) (Fig. 4).

The spatulate leaf-case plus the tubular leaf-case groups form a monophyletic group supported by the character of abandoning the old case and constructing a new one (7-2) in all of the eight alternative topologies (Fig. 6). The tubular leaf-case group forms a monophyletic group and is supported by constructing a case that is different from the original case (13-1) and a reversal from having a bivalved to having a trivalved anal end (19-0 to 19-1).

Host-Plant Use

A total of 129 ingroup species were analyzed for host-plant use. They were divided into herbaceous feeders versus woody feeders. A total of 66 herbaceous feeders were recorded. Of these, 40 are seed miners and 25 are leaf miners. Seed miners were recorded using a total of 16 plant genera belonging to 10 families. Leaf miners were recorded using 18 plant genera on the same 10 families. A total of 53 woody feeders were recorded

on 40 plant genera belonging to 13 families. See Appendix 2 for details of host-plant use.

DISCUSSION

Behavioral characters have been used in cladistic analysis to determine phylogenetic relationships for a range of taxa. Wenzel (1993) and de Queiroz and Wimberger (1993) have demonstrated that behavioral characters are no more homoplasious than morphological characters and should be treated as such. Nest architecture and building behavior have been used to investigate the phylogeny of several groups of animals, including spiders (Coddington, 1986; Eberhard, 1982),

wasps (Wenzel, 1993), birds (Patterson *et al.*, 1995; Kennedy *et al.*, 1996), fish (McLennan *et al.*, 1988; McLennan, 1993), and black flies (Stuart and Hunter, 1998). In most analyses, the phylogeny as determined by nest architecture and building behavior agrees with those determined by morphology and molecular data. The main reason systematists do not include behavioral characters in the analysis is not out of concern that they are too homoplasious, but because these characters are not available for the taxa they study (Proctor, 1996). The main reasons Proctor found for mapping behavioral characters onto the final tree are: (1) the majority of scientists that have mapped on behavioral characters are not systematists and may lack the skills required for phylogenetic analysis and (2) there is not a complete behavioral account for the taxa.

The use of ecological characters in a cladistic study is a relatively new practice and still has not gained widespread acceptance. Basic in cladistic theory is the principle that heritable attributes can be used as cladistic characters (Miller and Wenzel, 1995). Because certain ecological attributes are heritable, such as diet requirements, it logically follows that those ecological attributes can be used as statements of homology. Luckow and Bruneau (1997) state that ecological characters, such as host data, are erroneously kept from the analysis and mapped on the final tree to avoid creating circularity in the analysis. Of course, it is character coding that introduces circularity in the matrix, not the characters themselves (Deleporte, 1993), and the issue is not actually circularity, but type II error, failure to reject a null hypothesis (Wenzel, 1997). Sometimes ecological characters are kept separate from the analysis in the belief that they are more labile than morphological or molecular characters and will not reflect phylogeny as accurately (Luckow and Bruneau, 1997). By including ecological characters in the analysis, then, one might bias the final outcome of the analysis toward convergent adaptations. Adaptive characters that are under stabilizing pressure are *less* likely to change, ultimately providing useful statements of homology. Phylogenies constructed with ecological characters have shown that ecological characters do not contain any more homoplasy than morphological or molecular characters (Luckow and Bruneau, 1997). It is now accepted that homoplasy can be informative and that there is no necessary relationship between level of homoplasy in a cladogram and decisiveness

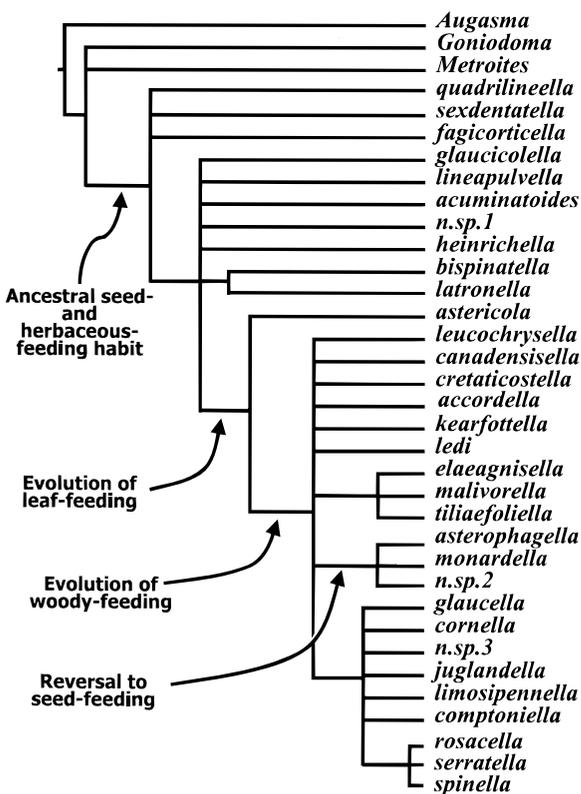


FIG. 7. Strict consensus phylogeny of the eight possible phylogenies represented in Figs. 4 and 5 (length 29; CI = 0.82; RI = 0.95) produced by parsimony analysis of the data matrix in Table 2. Evolution of leaf-feeding from a seed-feeding ancestor is shown. Evolution of woody-feeding from an herbaceous-feeding ancestor is shown. Family of plant mined is shown in Appendix 2.

of a data matrix (Goloboff, 1991). Character congruence is the final test of homology, so if nonhomologous characters are congruent to some degree with homologous ones, they contain phylogenetic information (de Pinna, 1991). Ecological homoplasy is no different from morphological or molecular homoplasy and contains no less information about evolutionary processes. By excluding ecological characters from the analysis and later mapping them onto a finished tree as attributes, one sacrifices the information contained in those characters (Luckow and Bruneau, 1997; Wenzel, 1997; Grandcolas *et al.*, 2001).

We used the ecological features of host-plant tissue and growth form as characters based on the argument that they may hold informative phylogenetic relevance. The ability to digest seeds as opposed to leaves, or the ability of the female to search for trees instead of herbs, may be encapsulated by the character “eats seeds/eats leaves” or “eats herbaceous plants/eats woody plants” (but see Grandcolas *et al.*, 2001). The host families are not used as phylogenetic characters but rather are mapped onto the final tree because the hierarchy of plant taxonomy and the naming of groups do not represent heritable qualities of the moths.

Ecological and Architectural Synapomorphies of Case Groups

This is the first study using primarily architectural characters to construct a phylogeny for a lepidopteran group. Despite the low resolution of the consensus phylogeny, the architectural and ecological characters used in the analysis have provided sufficient data to examine the relationships of North American *Coleophora* and their host plants.

Outgroup analysis of other genera in Coleophoridae would indicate that the ancestral coleophoran case was a mined seed capsule (or floret) strengthened by silk and later enlarged by anal additions of silk, and the ancestral feeding condition was seed mining of herbaceous plant families (Figs. 6 and 7).

The silk-case taxa may comprise a paraphyletic group. There may be several derivations of a type of silk case within *Coleophora*. Silk cases are not all constructed or enlarged in the same fashion, and it is equivocal as to which character states are derived. The appearances of the cases are rather different as well, and they segregate more or less into two groups: in

one group, cases are short and generally darker in color and harder in composition. This group is composed of seed-mining species. In the other group cases are slender, lighter in color, and flimsier. Some members of this group mine leaves of herbaceous plants.

There is a single derivation of the leaf-feeding habit at the ancestor of *C. astericola* and the leaf-case groups. More importantly, however, there are no reversals back to the ancestral condition of seed feeding within this clade (Fig. 7).

C. astericola may represent an intermediate stage between the decorated silk case and the fully covered leaf case. This species and larvae similar to it mine the leaves of herbaceous plant families. They construct a bivalved tubular silk case, which they cover completely with sand. It is not known how the case is enlarged. In all of the topologies, this species comes out as the sister taxon to the leaf-case groups (Fig. 7).

The leaf-case groups form a monophyletic clade. In the consensus phylogeny, there is a single derivation of woody feeding and the use of leaf cut-outs in case construction in the ancestor of the leaf-case groups. The positions of the annulate-case group and the pistol-case group relative to the remaining leaf-case groups have an interesting implication on the evolution of case architecture and host-plant choice. In the consensus phylogeny, there is a single reversal back to the ancestral condition of herbaceous feeding in the annulate-case group (21-0) and a single reversal back to building a case composed of silk in the pistol-case group (6-0) (Fig. 7).

In one hypothesis, the annulate-case group evolved as the sister group to the remaining leaf-case groups from an ancestor that mined leaves of herbaceous plants (21-0) (Fig. 4). One lineage continued to feed on herbaceous plants while the other lineage colonized woody plants (21-1). In this hypothesis, the annulate-case group evolved from an ancestor that added leaf cut-outs orally (9-1). These cut-outs were the margins of mined leaves (11-0). The ancestor of the annulate-case group switched from using leaf margins to using the entrance/exit holes of mines (11-1). In this scenario, the ancestor of the pistol-case group evolved from a leaf-adding ancestor that reversed back to the plesiomorphic condition of using mostly silk (6-0), but retained the behavior of enlarging the case through oral additions.

In the alternative hypothesis, the pistol-case group

evolved as a sister group to the leaf-case group from an ancestor that mined the leaves of woody plants (21-1) and enlarged the case by oral additions (7-0) (Fig. 5). One lineage retained the ancestral condition of using only silk (9-0), and the other incorporated leaf cut-outs into the case (8-1). In this hypothesis, the annulate-case group evolved from a woody-feeding ancestor that built a composite leaf-case. The annulate-case group switched from feeding on woody plants to feeding on herbaceous plants and from adding leaf margins to adding the entrance/exit holes of the mine.

Members of the pistol-case group incorporate pieces of chewed leaves into the case. Some of these larvae emerge as young larvae and feed on leaf buds in early spring until the leaves form. The bud is mined from the inside and the bud scale is often left. This is similar to the way in which seed miners eat away the embryonic tissue, leaving only the seed capsule behind. After the buds break, pistol-case larvae generally do not mine leaves, but rather will “graze” on the leaf upper surface, similar in manner to leaf-skeletonizing larvae of other families (Emmet *et al.*, 1996).

Colonization and Habitat Specialization

Ehrlich and Raven's (1964) proposition that host plants and their insect herbivores coevolve by an escape and radiation mechanism has received considerable attention. Several authors believe this mechanism to be the underlying theme governing most insect-plant interactions while others believe it to be the exception. While Berenbaum (1983), Farrell and Mitter (1990), Powell (1992), and Menken *et al.* (1992) are credited with illustrating the few examples of insect-plant cospeciation thus far, other authors have shown that many diverse aspects may be driving other insect-plant interactions (Bernays and Graham, 1988; Courtney, 1984; Denno *et al.*, 1995; Jermy, 1976, 1984; Miller, 1987; Mitter *et al.*, 1988; Thompson, 1998; Berenbaum and Passoa, 1999). These factors include resource tracking, colonization, competition, and habitat specialization. The best solution to date may be to accept the coevolutionary hypothesis as one of the many diverse influences affecting insect-plant interactions (Berenbaum and Passoa, 1999).

Whether host choice in *Coleophora* shows much or little evolution depends on the way in which we examine our primary data. Focusing on such things as plant

tissue type and host growth form, all of which seem likely to be part of an inherited search image, we find little evolution and little homoplasy. The transition from mining seeds to mining leaves is a good synapomorphy for a major clade, and although the character is not unique to that clade, there is no evidence of any reversal to seed feeding (Fig. 7). Similarly, a transition from herbs to woody plants is possibly a unique synapomorphy (or possibly shows one reversal, see Fig. 6). By contrast, examining the genus or family of plants used demonstrates that *Coleophora* are not faithful to groups recognized in our Linnaean classification. Of course, there is no reason to assume that the characters of plant taxonomy can be considered heritable for moths. A good classification may serve to summarize a great quantity of biological data, some of which may relate to heritable features of the insect, such as preference for a given chemical profile (see Berenbaum and Passoa, 1999), but in that case the character of interest is actually the chemical, not the host (Berenbaum, 1983). Thus, high “homoplasy” is found only when misapplied to extrinsic features that are not expected to relate to descent with modification regarding the moths of interest, and when a concept of homoplasy is properly applied to heritable aspects of the moths' search behavior, we find little homoplasy of ecological characters. This is consistent with recently published positions of various cladists (Deleporte, 1993; Luckow and Brueneau, 1997; Wenzel, 1997; Grandcolas *et al.*, 2001).

The findings of this study suggest that members of the microlepidopteran genus *Coleophora* are able to specialize on certain plant tissue types within certain habitats. This investigation illustrates that patterns of host-plant choice may more closely reflect preference for certain plant growth forms (herbaceous versus woody) and tissues (leaves versus seeds) with exploitation of different plant taxa, rather than preference for certain plant taxa with exploitation of different plant tissues. Host-plant fidelity appears to be conserved more among herbaceous feeders than it is among woody feeders. Within the herbaceous feeders, those that feed on seeds may have a higher degree of host fidelity than those that feed on leaves, especially at a generic level. There is a trend in *Coleophora* for evolution of host-plant selection to have occurred from a specialist herbaceous-feeding ancestor to a generalist tree-feeding habit. This pattern of evolution agrees with the predictions of the host-plant fidelity model presented in the Introduction

and suggests that for *Coleophora*, the model can be rooted at a specialist ancestor (Figs. 1 and 7).

Coleophora are initially constrained to the site of oviposition because first-instar larvae are obligatory internal miners. The location of oviposition is a function of female host recognition. Patterns of host-plant use may therefore depend greatly on the females' ability to locate appropriate host plants for their larvae. Host-plant recognition within *Coleophora* may depend first on recognition of a proper oviposition habitat, then recognition of proper host plants within those habitats. Diet specialization by coleophoran larvae may be dependent on such aspects as secondary plant chemicals, a close physical association with their host plants, and, to a lesser degree, interspecific competition.

Janz and Nylin (1998) suggest that habitat specialization may be the result of chemical convergence, in addition to habitat and host-plant physical stimuli. As explained previously, herbaceous plants tend to be more diverse in chemical composition (qualitative chemicals) than woody plants. Woody plants, because they are larger and longer lived, tend to be more homogeneous in chemical composition but have quantitative defenses, such as low nitrogen content and tannins, which make them less nutritious to insect herbivores. Insects that rely on chemical cues for oviposition may not discriminate between different trees as much as those that oviposit on herbs (Feeny, 1975). Females may find it easier to oviposit on phylogenetically unrelated plants that are similar in physical oviposition cues rather than oviposit on phylogenetically related plants that are very different in oviposition cues. For example, some species of *Senecio* (ragworts) grow in temperate open fields and resemble common daisies while other species (string of pearls) are adapted to live under desert conditions. They have short, round succulent leaves and a low, trailing habit. Although phylogenetically related, they have very dissimilar growth forms. If search image is an important factor of insect host-plant selection, insects ovipositing on temperate *Senecio* may be more likely to colonize a novel phylogenetically unrelated plant more similar in growth form than to colonize the phylogenetically related desert *Senecio*, especially if these plants are very similar in their secondary chemical composition.

The homogeneous chemical background of forest plants may promote host switching, while the diversity of secondary chemicals in herbaceous plants would

inhibit host switching. Larval feeding strategies may also inhibit host switching because the same physiological arguments apply to herbivory itself. This pattern is evident among members of *Coleophora*. The herbaceous-feeding seed-case groups use fewer plant hosts than the woody-feeding leaf-case groups. Woody-feeding species tend to use a higher number of host-plant genera per individual than herbaceous-feeding species. Woody-feeding species also tend to use host plants from different families, whereas if herbaceous-feeding species have multiple host-plant records, they tend to use genera within the same families. Even at a more inclusive taxonomic level, herbaceous-feeding clades tend to exploit the same plant clades sensu Chase *et al.* (1993). For example, *C. malivorella*, a leaf miner of the pistol-case group, mines the leaves of *Salix* (Salicaceae; Rosid 1A), *Prunus* (Rosaceae; Rosid 1B), *Populus* (Salicaceae; Rosid 1A), and *Tilia* (Tiliaceae; Rosid 2). *Coleophora lynosyridella*, a leaf miner of the silk-case group, mines the leaves of *Chrysothamnus* and *Baccharis*, both of the same family, Asteraceae (Asterid 2A).

There is at least one, perhaps more, derivation of the leaf-feeding habit within the silk-case groups, but there is only one derivation of the woody-feeding habit. In the consensus phylogeny, there is only one reversal to the ancestral herbaceous-feeding habit in the common ancestor of the annulate-case group (Fig. 7). In an alternative phylogeny, the annulate-case group may represent a sister taxon of the remaining woody-feeding clades, thereby suggesting no reversals back to the ancestral herbaceous-feeding habit (Fig. 4).

Coleophora that mine seeds show the greatest degree of host fidelity. The seed-mining clades use the fewest number of hosts per species and also have the lowest diversity of host plants. Members of the seed-case group mine the seeds of *Juncus* (Juncaceae) or *Trifolium* or *Melilotus* (Fabaceae). Members of the silk-case groups mine the seeds or leaves of Asteraceae, Juncaceae, Chenopodiaceae, Polemoniaceae, Caryophyllaceae, and Amaranthaceae. Because it is equivocal as to the number of derivations of a leaf-feeding habit within the silk-case group, it is difficult to determine the number of host switches within this group. Conservatism in seed feeders may be the effect of an intense interspecific competition. Mandibulate phytophages exhibit the greatest degree of competition, especially between internal feeders such as seed miners (Denno *et al.*, 1995). Although Berenbaum and Passoa (1999) did not find

results consistent with proposals of Denno *et al.* (1995) and Janz and Nylin (1998), the present study not only corroborates these proposals, but supports a more comprehensive synthetic model of host-plant colonization.

CONCLUSIONS

Based on the phylogenetic analysis here, the case groups of *Coleophora* (of Landry, 1998) are generally uniquely derived, although sometimes successively so as to produce basally paraphyletic assemblages. Within the leaf-case groups, the placement of the annulate-case group and the pistol-case group is ambiguous. Each of these case types may be the sister taxon of the remaining leaf-case groups. The evolutionary history of the basal lineages of the leaf-case groups is also ambiguous. Within the composite-leaf group and the lobe-case group, it is equivocal as to which method of leaf sheet arrangement is the ancestral state. Despite the low resolution of the case-type phylogeny, the architectural and ecological characters used in the analysis have provided sufficient data to make statements regarding the relationships of North American *Coleophora* and their host plants. Case architecture and ecological associations are linked to one another.

The ancestor of the North American *Coleophora* probably was a seed miner of herbaceous plant families. The ancestral case type was most likely a seed case, which is a seed capsule that is reinforced with silk once the plant embryo has been eaten away. This case was trivalved. The ancestral method of enlargement was to anally add silk to the seed capsule. There is at least one derivation of a silk case in which the case is constructed immediately after the first larval instar. This case is often camouflaged with plant materials or frass. With the evolution of the silk case, the method of enlargement changed from anal additions to cutting the case laterally or ventrally and adding silk. Larvae that construct a silk case feed on the seeds or leaves of herbaceous plants. The leaf-feeding condition is most likely the derived one. *C. astericola* may represent an interesting transition stage from the ancestral state of a case composed primarily of silk to the derived condition in which the case is covered with leaves. *C. astericola* constructs a bivalved silk case that is completely covered in sand and feeds on the leaves of

herbaceous plants. The case enlargement method remains unknown.

In the most parsimonious trees, there is a choice as to whether there is a monophyletic woody-feeding clade (with the annulate-case group as sister to the remaining leaf-case groups) and a reversal to a silk case (in the pistol-case group) (Figs. 6 and 7), or there is a monophyletic leaf-case group (with the pistol-case group as sister to the remaining leaf-case groups) and a reversal to herbaceous feeding in the annulate-case group (Figs. 6 and 7).

Cospeciation between *Coleophora* and their host plants is not the best explanation for patterns of host choice. Rather, *Coleophora* appear to specialize in habitats. This investigation suggests that *Coleophora* may be more faithful to plant growth forms of particular habitats and tissue types rather than to host-plant clades. Host fidelity seems to be conserved more in the herbaceous feeders than in the woody feeders. Within the herbaceous feeders, host fidelity seems to be conserved more in seed miners than in leaf miners. These findings support a synthetic model that combines the findings of Janz and Nylin (1998) that the use of butterfly host-plant groups may be limited by habitat specialization and also support the suggestion by Gaston (1992) and Denno *et al.* (1995) that a close physical association between internal and concealed feeders, such as seed and leaf miners, and their host plants may lead to diet specialization.

APPENDIX 1

Character 0. Type of pupation shelter: (0) gall; (1) portable shelter.

Character 1. Silk used in constructing shelter: (0) no silk used; (1) silk used.

Character 2. Shelter is: (0) temporary—not used for feeding; (1) permanent—larvae feed from case.

Character 3. Stage when shelter is constructed: (0) late instar; (1) early instar.

Character 4. Site of pupation: (0) in host plant; (1) in shelter or case.

Character 5. Case type (from character 1, state 1): (0) seed capsule or floret is mined and then reinforced with silk; (1) silk case is constructed (may have leaf reinforcements).

Character 6. Silk case composition (from character 5, state 1): (0) case is composed entirely of silk; (1) case is leaf cut-outs reinforced with silk.

Character 7. Case enlargement (nonadditive): (0) stretched and silk is added; (1) additions after cutting in the oral or anal region of the case; (2) case is abandoned and a new one is constructed.

Character 8. Additions (from character 7, state 1) (nonadditive): (0) silk or leaves added in the oral region of the case; (1) case is cut laterally or ventrally and silk is added; (2) silk added in the anal region of the case.

Character 9. If additions are oral (from character 8, state 0): (0) silk; (1) leaves.

Character 10. If cut (from character 8, state 1): (0) laterally; (1) ventrally.

Character 11. Leaf cut-outs used in case construction (from character 9, state 1): (0) leaf margins; (1) mine entrance.

Character 12. Leaf sheet arrangement (from character 11, state 0): (0) leaf sheets are neatly tied down; (1) leaf sheets are not neatly glued down.

Character 13. Case made when abandoned (from character 7, state 2): (0) new case is similar to old case (spatulate and bivalved); (1) new case is different from old case (trivalved).

Character 14. Larval position during enlargement: (0) larva remains straight during enlargement; case

is straight; (1) larva reorients itself somewhat during enlargement; case is bent or curved.

Character 15. Case lip: (0) definitive structure; (1) marginally constructed.

Character 16. Decoration of silk case: (0) absent; (2) present.

Character 17. Valve construction: (0) valve is built during initial case construction; (1) valve is built after case is constructed.

Character 18. Valve shape when case is not abandoned (from character 13, state 1) (nonadditive): (0) angular; (1) rounded.

Character 19. Valve number of mature case: (0) two; (1) three.

Character 20. Food preference of larvae: (0) seeds; (1) leaves.

Character 21. Larval host woodiness: (0) herbaceous; (1) woody.

Character 22 (not used in reconstruction). Families used by herbaceous feeders (nonadditive): (0) Asteraceae; (1) Juncaceae; (2) Amaranthaceae.

Character 23 (not used in reconstruction). Families used by woody feeders (nonadditive): (0) Tiliaceae; (1) Elaeagnaceae; (2) Fagaceae; (3) Cornaceae; (4) Rosaceae; (5) Ericaceae; (6) Betulaceae; (7) Salicaceae; (8) Ulmaceae; (9) Juglandaceae; (*) more than one host plant record.

APPENDIX 2

Host Plant Records for Known (and Some Undescribed) Species of North American *Coleophora*

Missing data indicated by “-”. Unverified host records indicated by “?”. Species used in the analysis are denoted by “*” after the name.

Case type	Species	Host data				
		Genus	Family	Tissue	Type	
Pistol	<i>albovanescentis</i>	<i>Betula, Fagus, Fraxinus, Ostrya</i>	Fagaceae, Oleaceae, Betulaceae	Leaves	Woody	
	<i>atromarginata</i>	<i>Betula, Quercus, Carpinus, Ostrya, Carya</i>	Fagaceae, Juglandaceae, Betulaceae	Leaves	Woody	
	<i>discostrata</i>	<i>Ceanothus</i>	Rhamnaceae	Leaves	Woody	
	<i>elaeagnisella</i> *	<i>Elaeagnus, Shepherdia</i>	Elaeagnaceae	Leaves	Woody	
	<i>malivorella</i> *	<i>Salix, Malus</i>	Salicaceae, Rosaceae	Leaves	Woody	
	<i>querciella</i>	<i>Quercus, Prunus, Tilia, Castanea</i>	Tiliaceae, Fagaceae, Rosaceae			
	<i>sacramenta</i>	<i>Malus, Prunus, Populus, Tilia, Chaenomeles</i>	Rosaceae, Salicaceae, Tiliaceae	Leaves	Woody	
	<i>tiliaefoliella</i> *	<i>Tilia</i>	Tiliaceae	Leaves	Woody	
	n. sp. 4	<i>Vicia</i>	Fabaceae	Leaves	Herb	
	Annulate	<i>annulicola</i>	<i>Aster, Solidago</i>	Asteraceae	Leaves	Herb
		<i>asterophagella</i> *	<i>Aster</i>	Asteraceae	Leaves	Herb
		<i>laurentella</i>	<i>Aster</i>	Asteraceae	Leaves	Herb
<i>monardella</i> *		<i>Monarda</i>	Lamiaceae	Leaves	Herb	
<i>vancouverensis</i>		<i>Grindelia</i>	Asteraceae	Leaves	Herb	
<i>vernoniaeella</i>		<i>Vernonia, Helianthus</i>	Asteraceae	Leaves	Herb	
<i>wyethiae</i>		<i>Wyethia, Balsamorhiza</i>	Asteraceae	Leaves	Herb	
n. sp. 2*		<i>Artemisia</i>	Asteraceae	Leaves	Herb	
n. sp. 5		<i>Encelia</i>	Asteraceae	Leaves	Herb	
n. sp. 6		<i>Ambrosia</i>	Asteraceae	Leaves	Herb	
n. sp. 7		<i>Ambrosia</i>	Asteraceae	Leaves	Herb	
n. sp. 8		<i>Hymenoclea</i>	Asteraceae	Leaves	Herb	
n. sp. 9		<i>Ambrosia</i>	Asteraceae	Leaves	Herb	
n. sp. 10	<i>Ambrosia</i>	Asteraceae	Leaves	Herb		
n. sp. 11	<i>Phacelia</i>	Hydrophyllaceae	Leaves	Herb		
n. sp. 12	<i>Monardella</i>	Lamiaceae	Leaves	Herb		
Composite leaf	<i>canadensisella</i> *	<i>Cornus canadensis</i>	Cornaceae	Leaves	Herb	
	<i>cornivorella</i>	<i>Cornus</i>	Cornaceae	Leaves	Woody	
	<i>cretaticostella</i> *	<i>Rubus</i>	Rosaceae	Buds	Woody	
	<i>gaylussaciella</i>	<i>Gaylussacia</i>	Ericaceae	Leaves	Woody	
	<i>kalmiella</i>	<i>Kalmia</i>	Ericaceae	Leaves	Woody	
	<i>leucochrysell</i> *	<i>Castanea</i>	Fagaceae	Leaves	Woody	
	<i>multicristatella</i>	<i>Rhododendron, Gaylussacia</i>	Ericaceae	Leaves	Woody	
	<i>murinella</i>	<i>Vaccinium</i>	Ericaceae	Leaves	Woody	
	<i>pruniella</i>	<i>Prunus, Betula, Populus, Malus, Crataegus, Salix, Alnus</i>	Betulaceae, Rosaceae, Salicaceae	Leaves	Woody	
	<i>rupestrella</i>	<i>Fragaria, Potentilla</i>	Rosaceae	Leaves	Both	
	<i>salicivorella</i>	<i>Salix</i>	Salicaceae	Leaves	Woody	
	<i>spinella</i> *	<i>Crataegus, Malus, Pyrus, Prunus, Sorbus</i>	Rosaceae	Leaves	Woody	
	<i>vacciniivorella</i>	<i>Vaccinium</i>	Ericaceae	Leaves	Woody	
<i>viburniella</i>	<i>Viburnum</i>	Caprifoliaceae	Leaves	Woody		

Case type	Host data				
	Species	Genus	Family	Tissue	Type
Lobe	<i>accordella</i> *	<i>Hedysarum, Lotus</i>	Fabaceae	Leaves	Both
	<i>kearfottella</i> *	<i>Salix, Ribes</i>	Salicaceae	Leaves	Woody
	<i>ledi</i> *	<i>Ledum, Chamaedaphne</i>	Ericaceae	Leaves	Woody
	<i>persimplexella</i>	<i>Comptonia, Betula</i>	Myricaceae, Betulaceae	Leaves	Woody
	n. sp. 13	<i>Artemisia</i>	Asteraceae	Leaves	Herb
Tubular leaf	<i>irroratella</i>	<i>Crataegus</i>	Rosaceae	Leaves	Woody
	<i>laricella</i>	<i>Larix</i>	Pinaceae	Leaves	Woody
	<i>rosacella</i> *	<i>Rosa</i>	Rosaceae	Buds	Woody
	<i>rosaevorella</i>	<i>Rosa</i>	Rosaceae	Buds	Woody
	<i>serratella</i> *	<i>Betula, Alnus, Comptonia, Myrica, Salix</i>	Myricaceae, Salicaceae, Betulaceae	Leaves	Woody
Spatulate leaf	<i>affiliatella</i>	<i>Ledum, Rhododendron</i>	Ericaceae	Leaves	Woody
	<i>alniella</i>	<i>Alnus</i>	Betulaceae	Leaves	Woody
	<i>alnifoliae</i>	<i>Alnus</i>	Betulaceae	Leaves	Woody
	<i>badiipennella</i>	<i>Ulmus</i>	Ulmaceae	Leaves	Woody
	<i>comptoniella</i> *	<i>Betula, Comptonia, Alnus, Myrica</i>	Myricaceae, Betulaceae	Leaves	Woody
	<i>cornella</i> *	<i>Cornus</i>	Cornaceae	Leaves	Woody
	<i>corylifoliella</i>	<i>Corylus</i>	Betulaceae	Leaves	Woody
	<i>glaucella</i> *	<i>Arctostaphylos</i>	Ericaceae	Leaves	Woody
	<i>juglandella</i> *	<i>Juglans</i>	Juglandaceae	Leaves	Woody
	<i>laticornella</i>	<i>Carya</i>	Juglandaceae	Leaves	Woody
	<i>leneillalentella</i>	<i>Betula</i>	Betulaceae	Leaves	Woody
	<i>limosipennella</i> *	<i>Ulmus</i>	Ulmaceae	Leaves	Woody
	<i>ostryae</i>	<i>Ostrya</i>	Betulaceae	Leaves	Woody
	<i>paludoides</i>	<i>Myrica, Comptonia</i>	Myricaceae, Betulaceae	Leaves	Woody
	<i>umbratica</i>	<i>Prunus</i>	Rosaceae	Leaves	Woody
n. sp. 3*	<i>Carya</i>	Juglandaceae	Leaves	Woody	
Tubular silk, bivalved	<i>astericola</i>	<i>Aster</i>	Asteraceae	Leaves	Herb
	<i>granifera</i>	<i>Aster</i>	Asteraceae	Leaves	Herb
	<i>polemoniella</i>	<i>Polemonium</i>	Polemoniaceae	Leaves	Herb
	n. sp. 14	<i>Heterotheca</i>	Asteraceae	Leaves	Herb
	n. sp. 15	<i>Artemisia</i>	Asteraceae	Leaves	Herb
	n. sp. 16	<i>Chrysopsis</i>	Asteraceae	Leaves	Herb
	n. sp. 17	<i>Psoralea</i>	Fabaceae	Leaves	Herb
Tubular silk, seed	<i>deauratella</i>	<i>Trifolium</i>	Fabaceae	Seeds	Herb
	<i>dentiferoides</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>fagcorticella</i> *	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>mayrella</i>	<i>Trifolium</i>	Fabaceae	Seeds	Herb
	<i>quadrilineella</i> *	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>sexdentatella</i> *	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>trifolii</i>	<i>Melilotus</i>	Fabaceae	Seeds	Herb
Tubular silk, trivalved	<i>acamtopappi</i>	<i>Acamtopappus</i>	Asteraceae	—	Herb
	<i>acuminatoides</i> *	<i>Aster</i>	Asteraceae	Seeds	Herb
	<i>alticolella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>apicalbella</i>	<i>Silene virginica</i>	Caryophyllaceae	Leaves	Herb
	<i>atriplicivora</i>	<i>Atriplex, Suaeda</i>	Chenopodiaceae	—	Herb
	<i>bidens</i>	<i>Aster</i>	Asteraceae	Seeds	Herb
	<i>biforis</i>	<i>Echinata</i>	Juncaceae	Seeds	Herb
	<i>bispinatella</i> *	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>bistrigella</i>	<i>Hymenoxys</i>	Asteraceae	Leaves	Herb

Host data					
Case type	Species	Genus	Family	Tissue	Type
Tubular silk, trivalved— <i>Continued</i>					
	<i>borea</i>	<i>Polygonum</i>	Polygonaceae	Seeds	Herb
	<i>caespitiella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>coenosipennalla</i>	<i>Stellaria</i>	Caryophyllaceae	Seeds	Herb
	<i>concolorella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>cratipennella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>crinita</i>	—	—	—	—
	<i>detractella</i>	<i>Chenopodium</i>	Chenopodiaceae	Seeds	Herb
	<i>dextrella</i>	<i>Aster</i>	Asteraceae	Seeds	Herb
	<i>duplicis</i>	<i>Aster</i>	Asteraceae	Seeds	Herb
	<i>entoloma</i>	—	—	—	—
	<i>ericoides</i>	<i>Aster</i>	Asteraceae	Seeds	Herb
	<i>glaucolella*</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>glissandella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>heinrichella*</i>	<i>Rudbeckia, Helianthus, Aster</i>	Asteraceae	Leaves	Herb
	<i>infuscatella</i>	<i>Phlox</i>	Polemoniaceae	Leaves	Herb
	<i>intermediella</i>	<i>Solidago</i>	Asteraceae	Seeds	Herb
	<i>latronella*</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>lineapulvella*</i>	<i>Amaranthus</i>	Amaranthaceae	Seeds	Herb
	<i>littorella</i>	<i>Salicornia</i>	Chenopodiaceae	Seeds	Herb
	<i>lynosyridella</i>	<i>Chrysothamnus, Baccharis</i>	Asteraceae	Leaves	Herb
	<i>maritella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>mcdunnoughiella</i>	<i>Cerastium, Stellaria?</i>	Caryophyllaceae	Leaves	Herb
	<i>monardae</i>	<i>Monarda</i>	Asteraceae, Lamiaceae	Leaves	Herb
	<i>nemorella</i>	<i>Aster?</i>	Asteraceae	Seeds	Herb
	<i>portulacae</i>	<i>Portulaca</i>	Portulacaceae	Leaves	Herb
	<i>puberuloides</i>	<i>Solidago</i>	Asteraceae	Seeds	Herb
	<i>quadristrigella</i>	—	—	—	—
	<i>quadruplex</i>	<i>Achillea</i>	Asteraceae	Seeds	Herb
	<i>rugosae</i>	<i>Solidago</i>	Asteraceae	Seeds	Herb
	<i>salinoidella</i>	<i>Atriplex</i>	Chenopodiaceae	Seeds	Herb
	<i>seminella</i>	<i>Aster</i>	Asteraceae	Leaves	Herb
	<i>simulans</i>	<i>Antennaria</i>	Asteraceae	Seeds	Herb
	<i>sparsipuncta</i>	<i>Aster</i>	Asteraceae	Leaves	Herb
	<i>suaedicola</i>	<i>Suaeda</i>	Chenopodiaceae	Leaves	Herb
	<i>subapicis</i>	<i>Aster</i>	Asteraceae	Seeds	Herb
	<i>texanella</i>	<i>Portulaca</i>	Portulacaceae	—	Herb
	<i>therinella</i>	<i>Rumex</i>	Polygonaceae	Seeds	Herb
	<i>triplicis</i>	<i>Solidago</i>	Asteraceae	Seeds	Herb
	<i>vagans</i>	—	—	—	—
	<i>versurella</i>	<i>Chenopodium, Atriplex</i>	Chenopodiaceae	Seeds	Herb
	<i>viridicuprella</i>	<i>Juncus</i>	Juncaceae	Seeds	Herb
	<i>viscidiflorella</i>	<i>Chrysothamnus</i>	Asteraceae	Leaves	Herb
	n. sp. 18	<i>Chrysothamnus, Baccharis</i>	Asteraceae	Leaves	Herb
	n. sp. 19	<i>Baccharis</i>	Asteraceae	Leaves	Herb
	n. sp. 20	<i>Erigeron</i>	Asteraceae	Leaves	Herb
	n. sp. 1*	<i>Chrysopsis, Aster</i>	Asteraceae	Leaves	Herb
	n. sp. 21	<i>Aster</i>	Asteraceae	Seeds	Herb
	n. sp. 22	<i>Artemisia</i>	Asteraceae	Leaves	Herb
	n. sp. 23	<i>Psoralea</i>	Fabaceae	Leaves	Herb
	n. sp. 24	<i>Juncus</i>	Juncaceae	Seeds	Herb
	n. sp. 25	<i>Juncus</i>	Juncaceae	Seeds	Herb
	n. sp. 26	<i>Polygonum</i>	Polygonaceae	Leaves	Herb
	n. sp. 27	<i>Polygonella articulata</i>	Polygonaceae	Leaves	Herb
	n. sp. 28	<i>Xyris</i>	Xyridaceae	Seeds	Herb

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