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HIGHER CLASSIFICATION, HOST PLANT SELECTION AND FEEDING STRATEGY IN MOMPHINAE (LEPIDOPTERA: GELECHIOIDEA: COLEOPHORIDAE)

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HIGHER CLASSIFICATION, HOST PLANT SELECTION AND FEEDING STRATEGY IN THE MOMPHINAE (LEPIDOPTERA: GELECHIOIDEA: COLEOPHORIDAE)

By

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ABSTRACT

HIGHER CLASSIFICATION, HOST PLANT SELECTION AND FEEDING STRATEGY IN THE MOMPHINAE (LEPIDOPTERA: GELECHIOIDEA: COLEOPHORIDAE)

By

John H. Wilterding III

The higher classification and evolutionary biology for Nearctic and Palearctic Momphinae is completely revised by cladistic analysis of morphological characters of the adults. A total of 69 ingroup taxa were used along with four outgroup taxa. Approximately 61 morphological characters were coded as unordered binary or multistate characters. A total of 24 equally parsimonious trees of 181 steps (CI=0.6348) were found. Based on these results, the monophyly of Momphinae was strongly supported, as well as three monophyletic genera: *Anybia*, *Lophoptilus* and *Mompha*. Two large genera, *Lophoptilus* (27 species) and *Mompha* (40 species) were further divided into subgenera and informal species groups based on cladistic characters. The classification of *Lophoptilus* appears most in doubt, largely due to the exclusion of a number of key species that are poorly known; analysis of more species will likely lead to splitting of this genus in the future.

Feeding strategy and host plant utilization was also examined using the results of cladistic analysis. *Anybia*, containing two species, are leaf miners strictly associated with two tribes in the Onagraceae, Epilobiaeae and Circeaeeae. *Mompha* species are also exclusively associated with plants in the Onagraceae, feeding on a limited number of species in two tribes, the Epilobiaeae and Onagreae. Feeding strategy, however, has diversified in this genus. *Mompha* species are leaf miners, stem borers, seed capsule

borers, flower gall inducers, stem gall inducers, root crown borers and leaf tiers. Feeding strategy appears to have evolved independently nine times, with most evolutionary shifts in feeding guild resulting in the diversification of species into a species swarm. Although life history strategies are incomplete for most species, at least two species are polymorphic for feeding strategy.

Host plant selection within *Lophoptilus* differs from *Anybia* and *Mompha* in that basal species in the genus feed on Lythraceae and Onagraceae exclusively, with derived species shifting to monophyletic groups feeding on the Rubiaceae and Cistaceae. Feeding strategy is predominately leaf mining in *Lophoptilus* when compared to *Mompha*, with basal species boring in stems but not inducing galls and the most derived species boring in seed capsules.

The two largest genera, *Mompha* and *Lophoptilus* contrast sharply in evolutionary direction. Host plant utilization is much more conservative but tissue exploited is more diverse in *Mompha*. However, in *Lophoptilus* the pattern is reversed.

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Introduction

The Momphinae (Gelechioidea: Coleophoridae) is a small subfamily of perhaps 200 species of microlepidoptera which has been poorly covered in systematic and phylogenetic studies. Although representatives are known from every major biotic region, based on present information, momphine diversity is centered in the western Nearctic, with upwards of 50% of the species found there. Additional diversity occurs in the eastern Nearctic, and lesser diversity in the Palearctic. Species diversity rapidly decreases in the Neotropics, and three species are known from Eastern Australia and New Zealand, and one species in Madagascar and another from India.

One of the most striking features of the Momphinae is their predominate specialization on the Onagraceae (evening primroses) (Powell 1980). Species within the subfamily employ a great variety of feeding strategies in their radiation on the Onagraceae. All species are concealed feeders, with varied feeding strategies as leaf miners, stem, root, and fruit-borers, leaf tiers and gall inducers (Forbes 1923, Meyrick 1928, Koster and Biesenbaum 1994, Hodges 1998). In addition to feeding predominately on the Onagraceae, *Mompha* have been reported from scattered associations on Fabaceae, and Fagaceae (Powell 1980), Cistaceae (Meyrick 1928), Lythraceae (Hodges 1992), Melastomataceae, Rubiaceae (Forbes 1923, Becker 1999).

The strong association of Nearctic momphines prompted Powell (1980) to declare these moths to be the most highly host specialized of all Lepidoptera. However, the strength of this conclusion was hindered by the lack of a coherent classification of the Momphinae. Despite the striking biology of this group, very little was known about the species, or more importantly, the natural phylogenetic groups within momphines. For the later half of this century, it has been customary to place all taxa within the Momphinae in the "catch-all" genus *Mompha* (hereon referred to as *Mompha s. str.).* Because of this, it was uncertain whether the remarkable association with the Onagraceae fell along phyletic lines, or whether momphines in general were more broadly polyphagous. In the same way, while the diversity of feeding strategies used by momphines is quite remarkable, until this study it was not clear whether the evolution of feeding strategy falls along phyletic lines, or was the result of convergence.

None of these questions, of course, could adequately be addressed without a coherent higher classification, nor could they be sufficiently tested without a phylogenetic hypothesis to which such questions could be applied. Therefore, the objective of this study was to perform a cladistic analysis of the Momphinae and develop a coherent classification. In addition, two questions concerning the biology of the Momphinae were addressed: 1) How is host association related to the phylogeny of the Momphinae? 2) How are life history traits distributed in the Momphinae?

Historical systematics of Momphinae

Mompha is presently placed within the superfamily Gelechioidea, and their position within the superfamily does not appear to be in question (Scoble 1992, Hodges 1998). The Gelechioidea is the largest of the microlepidoptera superfamilies (Powell 1980) with an estimated 12,000 described species (Scoble 1992, Hodges 1998) and perhaps as many as 50,000 species worldwide (Sinev 1993). Within the superfamily, the diversity in form is apparent when one considers that there are 86 family names that have been proposed by various authors (Sinev 1993).

Historically, the higher classification of Momphinae has been subject to a variety of treatments by authors, usually as a restricted genus or group of genera (*s. str.)* or in a more inclusive family (*s. l.)* within the Gelechioidea. Five species were described in the late 18th century and placed in the all inclusive microlepidopteran genus *Tinea*. In 1816 Hübner described *Mompha conturbatella*, which would eventually become the earliest family group name available. Shortly thereafter, Curtis (1839) proposed the genus *Laverna* with his description of the Palearctic *L. ochraceella*. These two genera then became the two family group names available for the placement of momphine species considered here.

The common family group name for momphines in the 19th century was Lavernidae, and was first proposed by Walker (1871); it included momphines *s. str.* as well as other gelechioids, forming a very heterogeneous group. In a similar way, momphines were placed in Lavernidae by a wide variety of authors with varying definitions of the family group limits (Walsingham 1891, 1909; Forbes 1923).

Mompha s. str. have been placed by workers in more restricted but heterogeneous groups such as the Lavernidae (Forbes 1923), Momphidae (Hodges 1962, 1978), and Cosmopterygidae (Common 1970). All were larger assemblages of gelechioids in which *Mompha* was one of many genera. Sinev (1993) noted that many of the older classifications arose out of erroneous conclusions due to the convergence of morphological characteristics necessary for evolution of an internal feeding strategy from an external one. This meant that before the examination of morphological features other than superficial *facies*, authors created heterogeneous assemblages of moths that resembled each other due to convergence and not genealogy.

The classification of species included in this analysis never reached a level of maturity or coherence until the present time. This is in large part due to the lack of any comprehensive modern treatment of Nearctic momphines, where their diversity is highest. It is noteworthy that the Momphidae *s. str.* did not receive any detailed comprehensive treatment by systematists since the first species was described nearly 200 years ago. Despite their overwhelmingly North American distribution, study of the Nearctic Momphinae in the later half of this century was limited to scattered species descriptions (Clarke 1990, Hodges 1992, Sinev 1993, Sinev and Koster 1995, Harrison and Koster 1997,) and to isolated comments in systematic treatments of related gelechioid families (Hodges 1978; Adamski and Brown 1989, Landry 1991). In all these works, *Mompha* appears on occasion in the discussion, but is curiously absent from the cladistic analysis.

The vast majority of proposed generic names were proposed for Palearctic taxa, and while a number of European revisions supported the use of some of these, it was never clear how these proposed genera related to the more diverse Nearctic fauna. By contrast, *Mompha* is most well studied in the Palearctic (Riedl 1969) but this is far from the primary region of diversity for *Mompha*. No fewer than six generic names are available for Momphinae in the Palearctic alone. Riedl (1969) treated the European Momphidae *s.l.* (Momphinae and other gelechioids) and supported fully four genera for *Mompha s. str.* Therefore, in the latter half of the 20th century, it has been increasingly customary to simply place all momphines in the all-inclusive genus, *Mompha*.

Contemporary work by Hodges (1962, 1978, 1992) has slowly revealed the polyphyletic nature of the Momphidae *s. l.* (Cosmopterygidae of authors). His work gradually resulted in the removal of all but six genera from the *Mompha s. str. Mompha* was first placed in its own family (Hodges 1978, 1992) but Hodges' recently (1998) published higher classification of the Gelechioidea (Hodges 1998) resulted in its treatment as a subfamily of a more inclusive concept of the Coleophoridae, now containing four subfamilies (Coleophorinae, Blastobasinae, Momphinae, and Pterolonchinae). This is reflected well in previous treatments of *Mompha* as a distinct family or subfamily in the Gelechioidea by various authors who intuitively recognized the unique attributes of these moths (Mosher 1916 and Forbes 1923, Hodges 1978, Kuznetsov and Stekol'nikov 1984, Minet 1986, 1990, and Nielson and Common 1991).

In addition to the poorly developed systematics of the adults, little work has been done on the immature stages of *Mompha*, and the classifications discussed above appear to have largely ignored features of the immature stages. Stehr noted (1987) in his study of *Mompha* larvae the presence of only two L group setae on the first thoracic segment. This diverges from the typical Gelechioid state of three L group setae on T1 (but is found also in other widespread gelechioid taxa).

Materials and methods

Selection of taxa

Cladistic analysis of the Momphinae in this study was restricted to the Palearctic and Nearctic regions subsequent to a broader attempt at inclusion of taxa from South America and New Zealand (*Zapyrasta*). Inclusion of these taxa was abandoned due to the lack of sufficient material for study, the frequent lack of representatives of both sexes, and the high number of autapomorphies and restricted synapomorphies (i.e. only two taxa showing the character). With the exception of one species from Florida, which has greater affinity to the Neotropical taxa, all species found outside the Nearctic and Palearctic regions were excluded from this study. However, a number of extralimital species have been examined by me and Sjaak Koster, and will be discussed when relevant to the present analysis.

The present study included representatives of all the type species of nominate genera except for *Synallagma* Busck, 1907 from the Nearctic, two South American genera, *Anchimompha* Clarke, 1965 and *Moriloma* Meyrick, 1890 and *Zapyrasta* Meyrick, 1889 from New Zealand and Australia. Two genera, *Echinophrictis* Meyrick, 1922 and *Palaeomystella* Fletcher, 1940 were recently associated by Becker (1999) with the Momphinae, but excluded from this analysis. The possible relationship of all these genera to the classification proposed in this study is discussed in the results.

In all cases where sufficient material was at hand, sibling and closely related species were included to avoid instances where synapomorphies would be interpreted as autapomorphies (Muona 1995). Several species in North America were represented by a single specimen. In most cases, these could be unambiguously associated with closely related species following cladistic analysis (i.e., coded identically) and these additional species are indicated in the generic classification proposed below. These species were eliminated from the analysis to reduce computational time, since the absence of one sex results in a high number of "?" in the data matrix. This results in arbitrarily assigned character states, which in some cases generates numerous trees. Several taxa known from one specimen however, were not easily associated with related species (i.e., not coding identically with any other taxa). In cases where these were included in the analysis, the presence of pleisiomorphies made placement of the taxa problematic, resulting in overwhelmingly high numbers of equally parsimonious trees. For the present analysis two species were excluded for this reason, and another two were retained in the analysis. Normally, the removal of taxa is discouraged except in cases where computational efficiency is compromised (Kitching et al. 1998).

Selection of characters and terminology

Every attempt was made to minimize assumptions of the phylogenetic value of individual characters. Although species in the Momphinae are rich in taxonomic characters, the general morphological *bauplan* of most Momphinae restricts the number of potentially useful characters that can be coded unambiguously. This means that much of the useful variation in the group is meristic and/or continuously variable, making it difficult to partition character systems into discreet states without the influence of expectation and bias. Also, in some instances, such as the shape of the juxtal lobes (Figures 88-93), variation was so great that meaningful partitioning of the observed variation into discreet states exceeded the number of allowable states for parsimony analysis (ten).

Due to the rarity of a number of taxa, larval characters and those characters of the internal thoracic architecture such as the metafurcal sterna, were also not included in this study. The overwhelming amount of missing data ("?") would lead to the generation of thousands of equally parsimonious trees. This might potentially mask relationships that would be evident if these characters were excluded. With regard to thoracic characters, Landry (1991) pointed out the potential utility of using internal thoracic characters for uncovering phylogenetic relationships, but did not include them in his cladistic analysis of the Scythrididae, presumably for similar reasons. Recently, in a cladistic analysis of the Elachistidae, Kaila (1999), included a number of internal thoracic characters, but in this case, none were useful for the delimitation of broad phyletic lineages (i.e., highly homoplastic).

Perhaps the most unusual morphological feature in the momphinae is the transtilla. This feature is very diverse in form and structure in the Momphinae. Because of its complexity, I have divided it into two morphological categories, the lateral transtillae (arms) (Figure 79) and the mesotranstilla (Figure 78). The lateral transtilla are typically sclerotized apodemes arising from the junction of the valval base and the tegumen. While common in widespread taxa in the Gelechioidea (Hodges 1998), its structure in Momphinae is somewhat different in that the apodemes are dorsally projected to varying degrees (Figure 79). The transtillar arms usually are somewhat broad, usually with two or more distinct, heavily sclerotized apodemes within (Figure 68). The apex of the lateral transtilla is usually membranous, and connects with the mesotranstilla. The mesotranstilla is highly variable in form, but in general appears to be an extension of the diaphragma of the tegumen (Figure 53). The diaphragma descends to the base of the valve and is projected posteriorly, producing a pronounced, tongue-like feature. The diaphragma usually then folds ventrally and anteriorly, making this structure bilayered (Figure 53). The mesotranstilla is usually bilayered, sometimes membranous, but typically sclerotized with microtrichia (Figure 71) or flat, smooth rugosities (Figure 68) on its ventral surface. See character number 43 in the description of character states for more details (pg??).

Morphological terminology was adopted from a variety of sources, but in to encourage consistency of morphological terminology within the Gelechioidea, I followed primarily the contemporary work of Adamski and Brown (1989), Landry (1991), Hodges (1998) and Kaila (1999).

Selection of outgroups

Because one of the objectives of this study was to clarify the higher classification within the Momphinae, and not the relationships of Momphinae to other gelechioids, only four outgroup taxa were included. In the only comprehensive cladistic analysis of the Gelechioidea, Hodges (1998) redefined the Coleophoridae to include four subfamilies: Momphinae, Coleophorinae, Blastobasinae, and Pterolonchinae. While this move has been seen by some workers as controversial, it seems clear that the nearest related higher group taxa to the Momphinae are indeed Coleophoridae and Blastobasidae.

Although the Pterolonchinae were also associated by Hodges (1998) the Blastobasinae + Momphinae + Coleophorinae, it is clear from his analysis that the Pterolonchinae is more distantly related to these three subfamilies. The Pterolonchinae are represented by a single Palearctic genus, *Pterolonche*, with 12 described species (Vives Moreno 1986). This genus shows greater divergence in morphology than the other three subfamilies in the Coleophoridae and was treated as the remote sister group to them by Hodges (1998). Inclusion of *Pterolonche* as an outgroup would have necessitated re-casting of a number of morphological characters to accommodate its structural anomalies.

Since the use outgroups was applied to polarize characters in the present analysis, it was determined that inclusion of *Pterolonche* would do little to clarify relationships within the Momphinae. In addition, as was implied in Hodges (1998), it is not at all clear that the association of *Pterolonche* with the Coleophoridae is very strong. Therefore, the Pterolonchinae were not included in the analysis.

Composite outgroups from the Blastobasidae were established based on examination of two genera, *Mastema* and *Blastobasis* as well as consulting Adamski and Brown (1989). Outgroups representative of Coleophoridae were derived from a study of *Coleophora deauratella* Lienig and a hypothetical coleophorid based on a composite of features found in other Nearctic *Coleophora* (Landry and Wright 1993). The Coleophorinae are highly diverse, with over 1000 described species (Hodges 1998; Landry and Wright 1993) exhibiting a great deal of homoplasy despite the restricted morphological *bauplan* of *Coleophora.* Because of this great diversity, a hypothetical representative of *Coleophora* was generated which would contrast with *C. deauratella* in those cases where character states are known to be polymorphic in the genus.

Specimen preparation

Specimens for dissection were macerated in a cold 15% solution of KOH for 12-24 hours, followed by a 15-minute rinse in distilled water. Specimens were dissected in distilled water, and placed in a solution of mercurochrome (in 70% ethanol) for five to ten minutes and stained further for an equal period of time in chlorozol black (in distilled water). Specimens were cleaned and scales removed in 2-propanol. Most preparations were stored in glycerol for further examination, since mounting on permanent microscope slides can distort or mask features useful for higher classification. Some genitalia preparations were mounted permanently in Canada balsam following Clarke (1941) or in Euparol (Robinson 1976) to facilitate rapid study and coding of features.

Wing venation was studied by removing the wings and soaking in 2-propanol where the scales are more easily removed than when using ethanol. The wings were then stained in acid fuschin for 24 hours, briefly rinsed and cleaned in 70% ethanol and fixed in 2-propanol. Wings were then directly transferred from 2-propanol and mounted in Euparol. Observations were made using a Wild dissecting stereomicroscope and Wild compound microscope, each equipped with a drawing tube.

Parsimony Analysis

Parsimony analysis was performed using PAUP *ver.* 4.0b3a (Swofford 1998) on a 233 MHz G3 iMac computer. A total of 61 morphological binary and multistate characters were used. All characters were treated as unordered Wagner characters and were optimized using the ACCTRAN function. ACCTRAN character optimization will favor the earliest origin of character states at the lowest possible branches, and subsequent loss and gain of a character will then be interpreted as homoplasy (Farris 1970, Kitching et al. 1998).

Outgroups were rooted using both constrained analysis (Maddison et al. 1984, Kitching et al. 1998) and simultaneous unconstrained analysis (Nixon and Carpenter 1993, Kitching et al. 1998, Maddison 1984). In constrained analysis, outgroups are designated *a priori*, and held invariant as the outgroup. This method, however, does not test the monophyly of the hypothesized ingroup with respect to the outgroup, and when using parsimony, may actually lead to a less parsimonious cladogram than when outgroups were not designated *a priori*. The second, more widely preferred method of rooting, is to not designate the ingroup and outgroup before analysis (simultaneous, unconstrained analysis). This method provides for the testing of the monophyly of the ingroup (Nixon and Carpenter 1993, Kitching etal.1998).

Initial iterations using simultaneous unconstrained analysis demonstrated the monophyly of the outgroup taxa in relation to the ingroup. Curiously, however, outgroup placement was not restricted to the root. For example, while some of the cladograms placed the Coleophorinae and Blastobasinae at the root, supporting the monophyly of the ingroup, in other most parsimonious reconstructions the outgroup was placed as a derived group within one of the three major clades (*Lophoptilus*). This is unusual, but by no means improbable, simply because parsimony analysis is the search for the shortest number of character transformations that will explain the data set. In some cases, simultaneous unconstrained analysis might be susceptible to the amount of homoplasy within the hypothesized data set *and* the outgroup. In this case, placement of the outgroup at multiple positions on the tree was possible because doing so did not increase the total number of steps over other most parsimonious reconstructions (MPR's) that placed the outgroup at the root.

This result suggests one of two possible conclusions: First, that Momphinae, Coleophorinae and Blastobasinae are paraphyletic as presently characterized. Or second, that the interaction of the characters, and shared homoplasy between the hypothesized ingroup and outgroup taxa, result in multiple hypotheses which at this time can not establish definitively the relationship of the outgroup taxa to the ingroup. Nixon and

Carpenter (1993) suggest that synapomorphic and variable characters found exclusively within the outgroup could be used during simultaneous unconstrained analysis. But as has been pointed out (Kitching et al. 1998), this may give the appearance of performing a constrained analysis because transformations exclusively found in the outgroup might add a greater number of steps when the clade is swapped to positions within the ingroup. Ultimately, since simultaneous unconstrained analysis led to ambiguous placement of the outgroup, constrained analysis (Maddison etal.1984, Kitching et al. 1998) was the preferred approach.

Characters and character definitions

Below is a summary of characters and character state definitions used for the cladistic analysis of Momphinae. Discussion of these characters is given for some characters and references to figures for clarification are given where appropriate. Missing and non-applicable characters are coded as "?". The complete matrix can be seen in Appendix A.

Head:

1. *Eyes*: (0) eyes round, entire, only slightly emarginate around antennae (Figure 1): (1) eyes round, emarginate, with a prominent antennal notch (Figures 2-3).
2. *Scales on vertex*: (0) scales slender near base, rounder towards apex (Figure 4): (1) scales slender, slightly wider near apex, but not appreciably rounded at apex (Figure 5).

3. *Length of third labial palpal segment*: (0) long, greater than half the length of the second palpal segment (Figure 7): (1) short, less than half the length of the second palpal segment (Figure 6).
4. *Scales on second labial palpal segment*: (0) adpressed to palpi, or only slightly tufted (Figure 1, 3): (1) with tuft of scales that is greater than twice the width of third palpal segment (Figure 2).
5. *Basal process of first flagellomere with notch*: (0) present (Figure 9): (1) absent (Figure 8).

Thorax:

6. *Forewing scales*: (0) adpressed to wing: (1) raised, scales along antemedial and postmedial lines. This character is sometime difficult to code, particularly with worn specimens, or in those cases where the wing was held in place during specimen preparation. In these cases, however, the scales do not rest in a shingle-like fashion, indicating they were once raised.
7. *Forewing pterostigma*: (0) absent (Figure 10, 12): (1) present (Figure 14).
8. *Forewing vein R4 and R5*: (0) branched from radius (Figure 10): (1) branched from M1 (Figure 15).
9. *Forewing vein CuA2*: (0) origin before end of cell (Figure 10): (1) arising near the end of cell (Figure 14).

10 *CuP of forewing*: (0) anastomosing with 1A+2A (Figure 10): (1) separate from 1A + 2A (Figure 12).

11. *Rs of hindwing*: (0) terminating at wing margin before end of cell (Figure 11): (1) terminating at wing margin beyond the end of cell.

12. ***Hindwing M1 and M2***: (0) separate from cell (Figure 13): (1) strongly fused to Rs (Figure 11): (2) branched, but weakly fused to Rs (Figure 16). State two for this character appears to be stable, although coding for this trait might prove difficult in some circumstances, or subject to some polymorphism. However, in cases where enough material was present to make multiple observations, this state did not appear to be polymorphic. A separate analysis was run in which state two was synonymized with state one, and in this case, no significant alteration of the tree topology was observed.
13. *Hindwing M1 and M2:* (0) separate (Figure 13): (1) branched from Rs (Figure 11). This character system shares some characteristics with state 12, but here it is assumed that the branching character of M1 and M2 is under different genetic control from how strongly these are connected to Rs.
14. *Apex of forewing:* (0) without descending hook of scales: (1) with descending hook of scales.
15. ***Retinaculum***: (0) anteriorly directed scales between Sc and R: (1) anteriorly directed scales on CuA.
16. ***Frenulum*** (Figure 11*) in female*: (0) with one acanthus: (1) with two acanthi: (2) with three acanthi.

Abdomen:

17. ***Tergite two apodeme***: (0) absent (Figure 17): (1) present (Figure 19).
18. ***Tergite one apodeme***: (0) base tapered (Figure 17): (1) hooked at base, appearing to fuse with abdominal wall (19): (2) rounded, expanded, base fusing with abdominal

suture (Figure 18): (3) appearing tapered, with a degenerate hook appearing to fuse with abdominal wall (Figure 20).

19. *Spines on abdominal segment T2-8*: (0) in a continuous row (Figure 21): (1) paired rows with spines absent in medial section of abdominal tergite (Figure 22). Sinev (1993) suggested that these were modified lanceolate scales that evolved to prevent the adult from moving backward when emerging from the cocoon. These features are widespread in the Gelechioidea.
20. ***Male abdominal hair pencil on apex of eight segment***: (0) absent: (1) present (Figure 23). The degree of expression in this character is somewhat variable. In *Lophoptilus* there is a tendency for this to be greatly developed when compared to species in *Mompha*. However, the character appears continuously variable, and no reliable way to separate the degree of development was found.
21. *Female 7th abdominal segment*: (0) continuous, or only slightly invaginated (Figure 24): (1) invaginated, with slightly developed, lightly sclerotized lobes (Figure 25): (2) deeply invaginated, with strong, heavily sclerotized lateral lobes (Figure 27): (3) slightly invaginated, with a slight medial lip. State one and two may be homologous, however, structurally they appear different. A separate analysis was run where the two states were homologized, but doing so had no impact on the topology of the trees found.
22. *Lateral portion of female 7th abdominal segment*: (0) unmodified (Figure 25): (1) lightly sclerotized, lateral pockets with heavy spines (Figure 28): (2) slight, lateral, spineless pockets (Figure 24): (3) slight broad pockets very near pleuron (Figure 29).

23. ***Plueron of seventh abdominal segment in female***: (0) unmodified (Figure 25): (1) with gland-like pockets (Figure 29).

Female genitalia:

24. ***Anterior of ostial opening***: (0) unmodified (Figure 30): (1) slight membranous furrow descending from abdominal segment eight (Figure 31): (2) slight furrow forming a pit or cusp with microtrichia (Figure 32): (3) similar to state two, but sclerotized (Figure 33): (4) anterior margin produced into a small, posterior sclerotized post (Figure 36): (5) anterior margin expanded to near abdominal segment eight (Figure 35): (6) anterior margin with an anterior projecting, conical, sclerotized rod (Figure 34).

25. Ductus bursae near antrum (colliculum?): (0) simple, narrow (Figure 30): (1) square or nearly so, with internal, sclerotized fold (Figure 32): (2) similar to state one, but with transverse sclerotized band (Figure 37): (3) simple, square with no internal fold (Figure 35): (4) similar to state one, but longer than wide (Figure 38): (5) similar to state four but seven times as long as wide (Figure 36): (6) internal sclerotized fold vestigial (Figure 39).

26. ***Ductus bursae anterior of ductus seminalis***: (0) membranous, narrow tube not appreciably wider than colliculum (Figure 32, 40): (1) long sclerotized, narrow tube, not appreciably wider than the colliculum (Figure 41): (2) variously sclerotized, broader, at least twice as wide as colliculum (Figure 38): (3) long, narrow tube with small, narrow spines throughout (Figure 31)

27. ***Origin of ductus seminalis***: (0) arising approximate to ostium bursae (Figure 32): (1) arising distally away from ostial opening (Figure 38): arising from corpus bursae (Figure 39). Coding of *Mompha conturbatella* poses some difficulty in regard to this

character because the ductus seminalis appears to arise from the corpus bursae, a trait not commonly encountered in the Lepidoptera. In *Mompha (Laverna)* the ductus bursae is greatly expanded, with the ductus seminalis arising from the posterior edge of the expanded region (Figure 38). It seems far more likely that the position of the ductus seminalis is similar to that found in *Laverna*, and the appearance of its origin on the ductus bursae is due to the overall shortening of the ductus bursae. The degenerate colliculum (Figure 39) which arises distal from the ostial opening, is another line of evidence that supports the contention that in *Mompha conturbatella* the ductus bursae is simply reduced.

28. *Ductus bursae*: (0) not coiled (Figure 38): (1) one turn (Figure 32): (2) more than one turn.
29. *Heavy spines in ductus bursae*: (0) absent: (1) present (Figure 42).
30. *Ostial fold*: (0) absent (Figure 30): (1) present, infolded (Figure 33, 34, 44): (2) reduced, with no internal fold (Figure 43, 45).
31. *Ostial plate*: (0) setae present (Figure 33, 34): (1) setae absent (Figure 43).
32. *Ostial plate*: (0) microtrichia absent (Figure 31): (1) microtrichia present (Figure 33, 34).
33. *Signum*: (0) absent: (1) present paired and sickle shaped with serrated margin (Figure 46, 47): (2) a single sclerotized signum (Figure 48): (3) thorn-like signum (Figure 49).
34. *Ductus seminalis*: (0) membranous (Figures 32, 50): (1) with small, grain-like sclerotizations (Figure 38): (2) fine spines throughout (Figure 31).

35. *Lamella antevaginalis*: (0) membranous (Figure 45): (1) membranous with microtrichiate spines (Figure 43).

36. *Ovipositor*: (0) simple, paired setiferous lobes (Figure 51): (1) as in previous state but with sclerotized rugosities (Figure 52).

Male genitalia:

37. *Diaphragma of tegumen*: (0) without microtrichia: (1) with microtrichia (53).

38. *Gnathos* (Figure 54): (0) present: (1) absent. See page XX for discussion of the transtilla and associated structures in Mompha, and its possible homology with the gnathos.

39. *Uncus*: (0) absent: (1) present (Figure 53).

40. *Meso region of uncus dorsally*: (0) simple, without raised ridge or keel (Figure 56): (1) with broad high keel (Figure 57): (2) long, broad apical keel (Figure 58): (3) slight, long apical keel (Figure 59); (4) slight keel to apex (Figure 60).

41. *Apex of uncus*: (0) simple, tapered to a point (Figure 56): (1) lateral flanges (Figure 61): (2) developed into broad lobes (Figure 62, 63): (3) reduced, slight lateral flanges (Figure 60): (4) broadly rounded, with an apical knob (Figure 64): (5) recurved anteriorly (Figure 65). Further modifications are found in the uncus in species occurring in the neotropics, but these do not appear to be homologous to any of the above states.

42. *Ventral apex of uncus*: (0) simple (Figure 63): (1)with a slight, sclerotized keel (Figure 66, 67). This character is very subtly expressed in many taxa, particularly those in the *lophoptilus* group.

43. *Mesotranstilla*: (0) absent (Figure 55): (1) a round, sclerotized lip-like structure with small round rugosities on dorsal surface (Figure 68): (2) as in state one, but with dorsal process (sometimes this process is slightly expressed) (Figure 69, 70): (3) rounded, not appreciably sclerotized with microtrichia (Figure 71): (4) membranous (Figure 72 (5) a simple membranous band, not produced outwardly (Figure 73): sclerotized with rugosities, and broader sclerotized lobes (Figure 78). The morphology of the medial portion of the transtilla (=mesotranstilla) is very complex and variable in the Momphinae. In many ways, this structure is prominent and produced to the upper portion of the tegumen where the gnathos resides in related groups (Coleophoridae and Blastobasidae). It is possible that the mesotranstilla serves a similar function to the gnathos in copulation.
44. *Vinculum*: (0) roughly triangular, slightly curved in lateral profile (Figure 53, 74): (1) similar to "0", but broader and more rounded ventrally (Figure 75): (2) similar to state one but longer and more narrow (Figure 76).
45. *Lateral transtilla*: (0) absent (Figure 75): (1) present, extending laterally, nearly parallel with base of tegumen (Figure 55): (2) present, extending dorso-ventrally (Figure 68, 77): (3) as in state two, but greatly extending toward hood of tegumen (Figure 79). Structural features of the lateral transtilla are also very complex in Momphinae. As a generalization, the arms are usually dorsally produced, and composed of one or more heavily sclerotized regions. These regions may be apodemes fused in various ways in order to facilitate movement of the mesotranstilla.
46. *Junction of saccular and distal lobe of valva*: (0) simple (Figure 79): (1) with a triangular, ventrally projected notch (Figure 80). Examination of *Mompha (Laverna)*

circumscriptella and *definitella* revealed a smaller, but structurally similar feature that may be homologous with *Mompha* (*Mompha*) *conturbatella*.

47. *Distal lobe of valva*: (0) simple (Figure 70): (1) base of costal lobe with one to several, raised, peg-like, setose structures (Figure 81): (2) a raised, setiferous plateau (Figure 83).

48. *Basal lobe of valva (sacculus)*: (0) simple (Figure 83); (1) produced into a perpendicular thumb (Figure 81).

49. *Basal sacculus*: (0) simple, fold restricted to near ventral margin (Figure 79, 80): (1) expanded into a broad lobe, nearly meeting junction of valval division (Figure 86); (2) saccular process (Figure 82).

50. *Apex of saccular lobe*: (0) broadly tapering (Figure 80, 84): (1) produced dorsally into a dorsal hook (Figure 82): (2) tapering, slightly upwardly curved (Figure 87) (3) broadly rounded (Figure 85): (4) broad hook arising from ventral margin (Figure 86): (5) shorter than apical valval lobe (Figure 55): (6) apex of sacculus developed into a strong, curved hook (Figure 79).

51. *Apical third of basal saccular lobe*: (0) setiferous: (1) setiferous with numerous, slightly elevated teeth (Figure 85): (2) small triangular teeth with setae arising from the base of each (Figure 84).

52. *Apex of basal saccular lobe*: (0) simple: (1) two to five stout spinose processes (Figure 84): (2) similar to state one, but longer, narrower, and restricted to a single slightly more elongate, stout spine.

53. *Apex of juxta* (Figure 88): (0) continuous, with no processes (Figure 89): (1) apical margin with triangular, weakly asymmetrically triangular processes (Figure 90): (2)

with slight, smooth, rounded processes (Figure 88): (3) triangular symmetrical teeth on margin (Figure 91): (4) raised processes with setae at base, not reaching apex (Figure 92).

54. *Juxta*: (0) a simple sclerotized shield: (1) paired, sclerotized processes (Figure 88).

55. *Juxta*: (0) fused to diaphragma: (1) fused to aedeagus. This character is difficult to assess, but was coded "0" if, during dissection, the juxta remains in association with the valves, and "1" when the juxtal remains attached to the aedeagus.

56. *Base of juxta*: (0) short, base resting close to aedeagus (Figure 88): (1) elongate, broad, base not resting at base of aedeagus (Figure 93,94): (2) anteriorly recurved from aedeagus (Figure 95): (3) absent.

57. *Aedeagus*: (0) a long, sclerotized tube, at least twice as long as wide: (1) reduced, endophallus enlarged (see Landry and Wright 1993). The typical condition of the Lepidoptera aedeagus is a sclerotized tube or sheath, with an eversible membrane, or vesica imbedded within. In *Coleophora*, the outer tube of the aedeagus is greatly reduced, and the vesica is not contained within it, but arises from the reduced aedeagus.

58. *Aedeagus*: (0) free: (1) strongly ankylosed (fused) to diaphragma (see Landry and Wright 1993).

59. *Dorsal apex of tegumen*: (0) gradually tapered in profile (Figure 53): (1) with a prominent, flat shelf (Figure 96).

60. *Articulation of uncus*: (0) absent: (1) basal apodeme present (Figure 97): (2) basal apodeme reduced (Figure 98).

61. *Apex of uncus*: (0) degree of sclerotization similar to that found on the rest of the uncus (Figure 56): (1) heavily sclerotized, nearly lacking any translucence (Figure 62, 63, 99)

Results and classification

Cladistic analysis of 61 unweighted Wagner characters lead to the generation of 24 equally parsimonious cladograms of 181 steps (CI= 0.6348, HI= 0.3591, RI= 0.9020). All trees showed remarkable stability of three major clades, with only slight variation within them, the preferred cladogram is shown in Figure 100. The variation in the overall topology of the tree was not significant enough to require the exclusive use of the concensus tree. The variation in the trees generated was the result of uncertain placement of *Lophoptilus (Lophoptilus)* nsp6 basal (Figure 100), or included in a clade with *Lophoptilus* (*Lophoptilus*) *cephalonthiella* and *L. (L.)* nsp3. Reconstructions that place *Lophoptilus (L.)* nsp6 basal to these taxa were preferred, in order to exemplify the uncertain placement of these species on the tree.

A second source of variation in the 24 trees was the placement of *Mompha* (*Laverna*) nsp8 and *Mompha (Laverna.)* nsp9 (Figure 100). As in the previous example, placement of these taxa was variable due the lack of decisive synapomorphies that would place these two taxa in strong association with another clade. Variation however, was restricted to basal placement in other clades with the exception of the clade containing the *stellella*, *murtfeldtella* and *claudiella* groups. Again, cladograms that treated *Mompha (Laverna.)* nsp8 and *Mompha (Laverna)* nsp9 within a separate clade were preferred to highlight the problematic position of these taxa.

Lastly, some variation in the association of *Lophoptilus* (*Cyphophora*) *cleidorotrypa* and *Lophoptilus (Cyphophora)* nsp5 was found, but this was restricted to the placement of these two taxa in a basal polytomy or separately, and did not significantly impact the overall systematics of the subgenus *Cyphophora.*

Cladistics of Momphinae

The monophyly of *Momphinae* was supported by 12 synapomorphies (numbers refer to characters and character state transformations, see character description for more detail): 2: 1 ⇒ 0 (scales slender near base, expanding towards apex, unique), 5: 0 ⇒ 1 (basal process of first flagellomere with notch absent, unique), 6: 0 ⇒ 1 (forewing with raised scales along antemedial and postmedial lines, unique), 15: 0 ⇒ 1 (retinaculum with anteriorly directed scales on CuA in female, unique), 18: 2 ⇒ 1 (apodeme of tergite one hooked at base, appearing to fuse with abdominal wall), 24: 0 ⇒ 2 (medial portion of ostial plate in female with slight furrow forming a pit with microtrichia), 27: 1 ⇒ 0 (origin of ductus bursae approximate to ostium bursae), 30: 0 ⇒ 1 (ostial fold present), 38: 0 ⇒ 1 (gnathos absent, unique), 43: 0 ⇒ 1 (mesotranstilla round, sclerotized, with round to rectangular smooth rugosities), 45: 0 ⇒ 2 (arms of transtilla long, dorsally and mesially projected), 60: 0 ⇒ 1 (articulation of uncus with tegumen with paired, horizontal apodemes).

Based on these characters, the support for the monophyly is strong. It should be pointed out that these character states are quite widespread in the Gelechioidea, with many of these characters appearing in other families and subfamilies (i.e., the loss of the gnathos, features of the retinaculum (Hodges 1998). However, the presence of some of these characters within other gelechioids does not establish homoplasy, simply because the hypothesized homologies of these features are not firmly established.

Generic summaries of Momphinae

While the assignment of genera is arguably somewhat arbitrary, as a general working principle, generic limits were established here using the following guiding principles: First, only sound cladistic characters that support monophyly were used. This means that broadly homoplastic characters, or poorly characterized features (i.e., meristic or continuously variable characters) were avoided for delimiting taxa (and ideally uniquely synapomorphic) as they are potentially unstable upon the addition of new characters or species.

Second, unwarranted establishment of many genera jeopardizes the proposed classification when new taxa are found and new character systems are resolved (Kaila 1998). This is particularly true for momphines, which are still poorly known, with many new species likely to be discovered. In addition, since many speciose groups have a preponderance of generic names available, adding to the pool of names can inhibit or confuse subsequent work in the group.

Lastly, genera should reflect a morphological gap, and not appear as an artificial division between continuously intergrading taxa. In some ways, this last point is addressed when giving special attention to clade support by synapomorphy. However, particularly in some species-rich groups, we might expect that what appears to be a strong morphological character supporting the monophyly of a group, may be interpreted as synapomorphy simply due to the species included in the analysis. In these instances, addition of more species to the analysis (and more homoplasy potentially), or addition of a new character, may lead to the once presumed informative character, interpreted as homoplastic and uninformative. It is important to remember that parsimony analysis will attempt to "make" characters phylogenetically informative, even in their complete absence.

A number of undescribed species were examined during the course of study, and associated with the new classification as a serial number system (i.e. *Mompha* (*Laverna*) nsp1. Images (some) in this dissertation are presented in color.

The genus *Anybia* Stainton 1854

Anybia Stainton, 1854. Insecta Britannica. Lepidoptera:Tineina, 244.

Type: *Tinea langiella* Hübner, 1801. By monotypy.

Cladistics: The monophyly of *Anybia* was supported by four synapomorphies: 8: 0 ⇒ 1 (forewing R4 + 5 branched from M1, unique), 26: 0 ⇒ 1 (ductus bursae, long sclerotized tube, infolded, not wider than colliculum, parallelism), 35: 0 ⇒ 1 (lamella antevaginalis with microtrichia, parallelism), 56: 0 ⇒ 1 (base of juxta with medial extended process, unique). Support for this clade is strong, especially for *Anybia langiella*.

In all trees, *Anybia* is placed at the basal node of Momphinae (Figure 100). This is in part due to the shared characteristics of *Anybia* to the other two major clades (*Mompha* and *Lophoptilus*). For example, in *Anybia nigrella* the mesotranstilla is sclerotized with rugosities (Figure 68) and appears very similar to *Mompha (Mompha) conturbatella*, while in *A. langiella* it is only lightly sclerotized, almost appearing membranous without rugosities (i.e., more similar to *Lophoptilus).* In the females of these two species, the ductus bursae are more similar to those found in *Mompha (Laverna)* (wider, heavily sclerotized Figure 41), while the colliculum and characters surrounding the ostial opening are more similar to species in *Lophoptilus.* The basal placement of *Anybia* based on the present data seems a reasonable hypothesis, especially considering the shared features of these species to other Momphinae.

Species: Anybia langiella (Hübner, 1796) and *Anybia nigrella* Sinev, 1986.

Biology (Table 1)*: Anybia langiella* is a leaf miner on onagraceous species of *Epilobium hirsutum*, *Epilobium montanum*, *Epilobium palustre, E. angustifolium* and *Circea lutetiana* (Riedl 1969). The dominant plant association appears to be with *Circaea* (Koster personal communication 1999). *Anybia nigrella* is a leaf miner of *Circea alpina* L. (Sinev 1986).

Distribution: Anybia species are strictly Palearctic. *Anybia langiella* is distributed in the Baltic regions, central and south Caucasus, and central Europe (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Anybia nigrella* replaces *Anybia langiella* in central and western Asia (Sinev 1986).

Table 1. Life history data for *Anybia* and *Lophoptilus* (*Cyphophora*) species examined. Additional data obtained from museum records or personal observation.

Species	Host*	Family	Feeding Guild	Distribution
Anybia langiella	*Epilobium* spp *Circaea* spp.	Onagraceae	Leaf miner	Eastern Nearctic
Anybia nigrella	*Circea alpina*	Onagraceae	Leaf miner	Palearctic
Lophoptilus (C.) eloisella	*Epilobium* spp *Oenothera* spp *Lythrum salicarum*	Onagraceae Lythraceae	Stem miner	Nearctic
Lophoptilus (C.) ideai	*Epilobium* spp	Onagraceae	Stem miner	Holarctic
Lophoptilus (C.) locupletella	*Epilobium* spp	Onagraceae	Leaf miner	Palearctic
Lophoptilus (C.) nsp5	*Epilobium sp*	Onagraceae	Leaf miner	Western Nearctic
Lophoptilus (C.) nsp1	*Epilobium ciliatum*	Onagraceae	Leaf miner	Western Nearctic

* References to plant species for oligophagous species of Momphinae are indicated in the classification summary.

The genus *Lophoptilus* Sircom 1848

Lophoptilus Sircom, 1848. Zoologist, 6: 2037

Type: *Lophoptilus staintoni* Sircom, 1848 [= *miscella* D. & S. 1775]. By monotypy.

Cyphophora Herrich-Schaeffer, [1853]. Systematische Bearbeitung der Schmertterlinge von Europa, 5:45; 6: plate 13 figures 7-9. Type *Elachista ideai* Zeller, 1839. By monotypy.

Psacaphora Herrich-Schaeffer, [1853]. Systematische Bearbeitung der Schmertterlinge, 5:48; 6: plate 13, figure 22-24. Type: *Tinea schrankella* Hübner, [1800-1805]. By subsequent designation, Walsingham and Durrant, 1909, 45:155.

Leucophryne Chambers, 1875. Canadian Entomologist, 7:210.

Type: *Leucophryne tricristatella*, Chambers 1875. By monotypy.

Synallagma Busck, 1907. Entomological News, 18: 277.

Type: *Synallagma busckiella* Engel, 1907. By monotypy.

Cladistics: The monophyly of *Lophoptilus* was weakly supported by three synapomorphies: 13: 0 ⇒ 1 (hindwing with M1 + M2 branched, parallelism), 28: 0 ⇒ 1 (ductus bursae with one turn, one reversal), 55: 1 ⇒ 0 (juxta ankylosed to diaphragma, two reversals).

The genus *Lophoptilus* (in the broad sense, *s. l.)* as presently defined is a broad, certainly monophyletic group of species that likely will be split into several smaller monophyletic genera in subsequent analyses. At this time, however, there exists is an insufficient sample of some of the rarer "black and white" species to allow for meaningful interpretation of the homoplasy that occurs among these taxa. At the present time, there appears to be no convenient way split this clade into smaller genera without leaving some species in the clade without synapomorphies supporting their monophyly. Splitting out some of the derived species would leave some portion of the remaining species paraphyletic. Until types for a number of species can be located, the preferred approach is to cast *Lophoptilus* as a more inclusive genus. To clarify discussion of species in *Lophoptilus*, two subgenera are defined, *Cyphophora* and *Lophoptilus*. Within each subgenus are several distinct monophyletic groups that at this time are treated as informal species groups. Placement of the species groups and subgenera are plotted on the cladogram of *Lophoptilus* in Figure 101.

Lophoptilus* subgenus *Cyphophora

Cladistics: The monophyly of *Cyphophora* was supported by two synapomorphies: 12: 0 ⇒ 2 (hindwing M1 and M2 branched, weakly anastomosing with R1, unique) and 43: 1 ⇒ 3 (mesotranstilla round with microtrichia, unique). Character support for clades within the subgenus *Cyphophora* is weak, with the exception of *Lophoptilus* (*C.*) sp1, *L.* (*C.*) *locupletella* and *L.* (*C.*) *maculata*. This clade (hereon the *locupletella* group) of three species is very unique, and further analysis will likely allow these species be placed in their own genus (*Psacaphora*), perhaps with other associated species. Doing so at this time, however, would result in the remaining taxa in the subgenus *Cyphophora* to be paraphyletic with respect to the *locupletella* group.

Synallagma is tentatively treated as a synonym of the subgenus *Cyphophora* based solely on its superficial similarity to *eloisella*, particularly in maculation and the hooked apex of the forewing, but this is also common to some Neotropical material. Until the type specimens of *buskiella* can be located to evaluate its association with *eloisella*, the present synonymy should be retained. Location of the female type is still not likely to resolve this issue, primarily because structurally, the female genitalia in all species of *Cyphophora* are remarkably close. What makes *eloisella* intriguing is the morphology of the mesotranstilla (Figure 78). While structurally retaining some similarity to *Anybia* and *Mompha* (sclerotized with smooth rugosities), the presence of two, large, lateral, and lightly sclerotized lobes is quite unique in *Lophoptilus* (*Cyphophora*) *eloisella* (Figure 78). Should the male of *Synallagma* be found to be similar to *L.* (*C.*) *eloisella*, there may be sufficient evidence to erect this generic name

The *locupletella* group of *Lophoptilus* (*Cyphophora*) (Figure 101)

Cladistics. The monophyly of the *locupletella* group is supported by three unique synapomorphies: 18: 0 ⇒ 3 (tergite one apodeme weakly curved and fusing to tergite wall), 24: 2 ⇒ 5 (medial portion of ostial plate greatly expanded), and 36: 0 ⇒ 1 (ovipositor tip with small, stout, sclerotized rugosities). In addition following synapomorphies support this clade: 3: 0 ⇒ 1 (third palpal segment less that 1/2 the length of segment two, parallelism), 17: 1 ⇒ 0 (tergite two apodeme lost, parallelism), 21: 0 ⇒ 1 (seventh abdominal segment deeply invaginated, parallelism), 25: 1 ⇒ 3 (colliculum absent, parallelism), and 47: 2 ⇒ 1 (base of costal lobe of valve with setiferous pegs, reversal). Not surprisingly, due to the striking number of unique characters in this clade, the position of the *locupletella* group position within *Cyphophora* is difficult to determine.

Species: *Lophoptilus (Cyphophora) locupletella* (D. & S. 1775), *Lophoptilus (Cyphophora) maculata* (Sinev in prep), and *Lophoptilus (Cyphophora)* nsp1. The later species may be conspecific with *Lophoptilus (C.) maculata.*

*Biology (*Table 1): Moths in the *locupletella* group are exclusively leaf miners of *Epilobium* spp. *Lophoptilus* (*C.*) *locupletella* is oligophagous on *Epilobium angustifolium, E. palustre*, *E. alpinum, E. montanum*, *E. alpestre* (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Lophoptilus* (*C.*) sp1 is known from associations with *Epilobium ciliatum* (personal observation). The life history of *Lophoptilus* (*C.*) *maculata* is not known, but is hypothesized to be similar to the other species in the group.

Distribution: *Lophoptilus* (*C.) locupletella* is known from alpine and boreal habitats in the north, northwest, west and central parts of Europe (Zagulaev and Sinev 1981, Riedl 1969) and Kuril Islands (eastern Russia) and south central Russia (border of Mongolia) (Sinev and Koster 1995). *Lophoptilus* (*C.*) nsp1 is known from a single specimen in the Cascades of Washington, and a small series from a remnant coastal old-growth forest tract in the Puget Sound of Pacific Northwest (personal observation).

The *ideai* group of *Lophoptilus* (*Cyphophora*) (Figure 101)

Species: *Lophoptilus* (*Cyphophora*) *edithella* (Barnes and Busck, 1920), *Lophoptilus* (*Cyphophora*) *idaei* (Zeller, 1839), *Lophoptilus* (*Cyphophora*) *minorella* (Sinev, 1993), *Lophoptilus* (*Cyphophora*) *luciferella* (Clemens, 1860), *Lophoptilus* (*Cyphophora*) *eloisella* (Clemens, 1860), *Lophoptilus* (*Cyphophora*) *cleidorotrypa* (Koster and Harrison, 1997), *Lophoptilus* (*Cyphophora*) nsp1, *Lophoptilus* (*Cyphophora*) nsp4 and *Lophoptilus* (*Cyphophora*) nsp5. *Lophoptilus* (*Cyphophora*) nsp4 is not included in the analysis but is clearly related to *L.* (*C.*) *edithella*.

Biology (Table 1): Of the nine species in the *ideai* group, host and life history data are known for two species, all which are longitudinal stem borers on plants in the Onagraceae, with one of these species feeding on *Lythrum* (Lythraceae).

Lophoptilus (*C.*) *eloisella* is a polyphagous stem-borer on larger species (stem diameter) of *Oenothera* spp, *Epilobium angustifolium* (personal observation) and recently, from purple loosestrife, *Lythrum salicaria* L. (Lythraceae) (T. Harrison personal communication). Records of *Epilobium* boring *L.* (*C.*) *eloisella* are known only from California and Washington. Hodges (personal communication) was under the impression that *L.* (*C.*) *eloisella* formed a species complex, although examination of a large series from numerous localities in North America failed to find useful characteristics to split the species. It is possible that feeding diversity is representative of host races or species, particularly since some examples are half as large as typical *L.* (*C.*) *eloisella* in the East, and may represent radiation of these insects on smaller species of Onagraceae. However, size polymorphism is also seen in *Mompha* (*Laverna*) *circumscriptella*, and appears only to be a result of the size of fruit capsule in which the larvae feed.

Lophoptilus (*C.*) *ideai* is known to feed on *Epilobium angustifolium* and *E. spicatum*, (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). The life history of *L.* (*C.*) *minorella* is not known, but hypothesized to be similar. The remaining species are quite similar to the preceding, and are also hypothesized to be stem borers based on their cladistic position. In particular, the size of *L.* (*C.*) *edithella* and *L.* (*C.*) sp4 is quite large which would make the leaf mining strategy quite unlikely in these species. Lastly, *L.* (*C.*) nsp5 is a leaf miner on an unspecified species of *Epilobium*.

Distribution: The general distribution of the *ideai* group is Palearctic and Nearctic, with some species exhibiting a Holarctic distribution. *Lophoptilus* (*C.*) *ideai* is distributed in the mountains of central Europe and south and western Europe, England, and the Caucasus and Transcaucasus Mountains (Zagulaev and Sinev 1981, Riedl 1969). In the Nearctic it ranges from the St. Lawrence Seaway to the Rocky Mountains and west to British Columbia (Sinev and Koster 1995). *Lophoptilus* (*C.) minorella* is rare, known only from a few examples from Siberia (Sinev 1993). *Lophoptilus* (*C.) eloisella* is a common species, generally distributed in all of North America, north to the southern boreal regions of Canada. *Lophoptilus* (*C.) edithella*, *L.* (*C.) cleidorotrypa*, *L.* (*C.)* sp3, and *Lophoptilus* (*C.*) sp4 are known from only from Northern Arizona, and *L.* (*C.*) sp5 from California.

Lophoptilus* subgenus *Lophoptilus

Cladistics. The subgenus *Lophoptilus* was supported by the following synapomorphies: 12: 2 ⇒ 1 (hindwing M1 + M2 branched from Rs, reversal) and 43: 3 ⇒ 4 (mesotranstilla membranous, unique). Support for this clade is strong, particularly so based on the hindwing venation. The mesotranstilla is extremely complex in form (page 9). Presently, a membranous transtilla is seen as homologous in all species expressing this character. However, in species that have shifted from the Onagraceae, there is some reduction in size and shape of this structure (character 43 state 5). This might represent a new character state distinct from the Onagraceae feeding clades that arise below them, but requires further analysis. In addition, most of the Neotropical taxa examined by myself and S. Koster (personal communication) also have an entirely membranous mesotranstilla, and often appear to have greater affinities to the Cistaceae and Rubiaceae feeding clades. In the interest in maintaining stability in the nomenclature, a broader conception of the subgenus *Lophoptilus* is favored.

There are a number of clades within the subgenus *Lophoptilus* that are highly supported monophyletic lineages. Furthermore, a number of these clades, and a few unique taxa, will likely be elevated to distinct genera in future analyses. The subgenus is divided into five species groups of variable character support.

Species of *Lophoptilus* are phytophagous on plants in the Onagraceae, Lythraceae, Cistaceae, and Rubiaceae. Of the 22 species in the genus, rearing records show four are associated with the Rubiaceae, five are associated with the Cistaceae, five with the Onagraceae, and one with the Lythraceae.

The *raschkiella* group of *Lophoptilus* (*Lophoptilus*) (Figure 101)

Cladistics. The monophyly of the *raschkiella* is supported by the following synapomorphies: 21: 0 ⇒ 2 (female 7th abdominal sternite deeply invaginated, parallelism), 25: 1 ⇒ 3 (colliculum reduced, parallelism), 28: 1 ⇒ 0 (ductus bursae without turn, reversal). In addition, *Lophoptilus* (*Lophoptilus*) *raschkiella* and *Lophoptilus* (*Lophoptilus*) *sexstrigell*a are characterized by an expanded saccular lobe (Figure 86). However, it should be pointed out that a number of other taxa show a similar expansion of the saccular lobe, particularly some members of the black and white species group (*metallifera* group). This character likely intergrades with species outside of the *raschkiella* group.

Species: Lophoptilus (*Lophoptilus*) *raschkiella* (Zeller, 1839), *Lophoptilus* (*Lophoptilus*) *complexa* (Svensson, 1982), *Lophoptilus* (*Lophoptilus*) *achlyognoma* (Koster and Harrison, 1997), *Lophoptilus* (*Lophoptilus*) *sexstrigella* (Braun, 1920).

Biology (Table 2)*: Lophoptilus (L.) raschkiella* is a leaf miner on *Epilobium angustifolium*, *E. hirsutum* and *E. spicatum* (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Lophoptilus (L.) achlyognoma* is a leaf miner of *Epilobium brachycarpum* (Harrison and Koster 1997) and *L. (L.) complexa* is a leaf miner on *Epilobium angustifolium* (Svensson 1982).

Distribution: Lophoptilus (L.) raschkiella is known from Europe (except southern Europe, southern and eastern Siberia (Riedl 1969, Zagulaev and Sinev 1981, Sinev and

Koster 1995). *Lophoptilus (L.) complexa* is known from northern Norway, Sweden, Finland, temperate regions of south and eastern Russia (Sinev and Koster 1995), Alaska, Washington and Oregon. *Lophoptilus* (*L.*) *achlyognoma* is known from a site in Northern California, while the distribution of the related *L.* (*L.*) *sexstrigella* is more generally distributed in the western mountains of North America as far north as Alaska.

The *cephalonthiella* group of *Lophoptilus* (*Lophoptilus*) (Figure 101)

Cladistics: The *cephalonthiella* group is supported by four unique synapomorphies: 23: 0 ⇒ 1 (abdominal pleura with folded, glandular pockets), 24: 2 ⇒ 6 (ostial fold with projected, sclerotized knob), 40: 0 ⇒ 1 (dorsal uncus with high, narrow keel), and 59: 0 ⇒ 1 (dorsal apex of tegumen, flat, shelf-like). The dorsal keel of the uncus (Figure 57) is also found in the three species of *Zapyrasta* known from New Zealand and Australia (excluded from this analysis). *Zapyrasta* is an unusual genus of leaf miners which specializes on *Muelenbeckia* (Polygonaceae) (Dugdale 1971). The keel of the uncus in *Zapyrasta* is very similar to that found in the *cephalonthiella* group. In addition, I am aware of several more species of Momphinae from Argentina which also express this character. This biogeographic association between South America and Australia, in particular, is suggestive of a genealogical link between *Zapyrasta*, and the Rubiaceae feeding clade in the New World tropics.

Table 2 Life history data for *Lophoptilus* (*Lophoptilus*).

Species	Host*	Family	Life History	Distr.
Lophoptilus (*L.*) *terminella*	*Circea* spp	Onagraceae	Leaf miner	Western Nearctic
Lophoptilus. (*L.*) *raschkiella*	*Epilobium spp*	Onagraceae	Leaf miner	Palearctic
Lophoptilus. (*L.*) *achlyognoma*	*Epilobium brachycarpum*	Onagraceae	Leaf miner	Western Nearctic
Lophoptilus. (*L.*) *cephlonthiella*	*Cephalanthus occidetalis*	Rubiaceae	Leaf miner	Nearctic
Lophoptilus. (*L.*) nsp3	*Cephalanthus occidentalis*	Rubiaceae	Leaf miner	Nearctic
Lophoptilus. (*L.*) *miscella*	*Helianthemum* spp	Cistaceae	Leaf miner	Palearctic
Lophoptilus. (*L.*) *passerella*	*Helianthemum* spp	Cistaceae	Leaf miner	Eastern Nearctic
Lophoptilus. (*L.*) nsp5	*Helianthemum* spp	Cistaceae	Leaf miner	Eastern Nearctic
Lophoptilus. (*L.*) *bottimeri*	*Helianthemum* spp.	Cistaceae	Seed Capsules	Eastern Nearctic
Lophoptilus (*L.*) *capella*	*Helianthemum* spp	Cistaceae	Seed Capsules	Eastern Nearctic
Lophoptilus (*L.*) nsp6	*Hamelia patens*	Rubiaceae	Leaf miner	Eastern Nearctic
Lophoptilus (*L.*) *powelli*	*Epilobium californica*	Onagraceae	Leaf miner	Western Nearctic
Lophoptilus (*L.*) *nsp*	*Galium*	Rubiaceae	Leaf miner	Western Nearctic
Lophoptilus (*L.*) *metallifera* complex	*Cuphea vicosissima*	Lythraceae	Leaf miner	Eastern Nearctic

Species: *Lophoptilus* (*Lophoptilus*) *cephalonthiella* (Chambers, 1871), *Lophoptilus* (*Lophoptilus*) nsp3, *Lophoptilus* (*Lophoptilus*) nsp9.

Biology (Table 2): *Lophoptilus (L.) cephalonthiella* and *L. (L.)* nsp3 are leaf miners on *Cephalanthus occidentalis* (Rubiaceae) (T. Harrison personal communication and personal observation 1998).

Distribution: The species of the *cephalonthiella* group are not completely resolved. There are at least two species, and perhaps three or more species in this group. At least two species are generally distributed East of the Mississippi from southern Canada to Florida; I have also studied representatives of this group from California.

The *miscella* group of *Lophoptilus* (*Lophoptilus*) (Figure 101)

Cladistics. The monophyly of the *miscella* species group is supported by three synapomorphies: 22: 0 ⇒ 1 (lateral abdomen on female with lateral, sclerotized, spinose pockets, unique), 25: 1 ⇒ 2 (colliculum with a lateral sclerotized band, unique), 37: 0 ⇒ 1 (diaphragma of tegumen with microtrichia, parallelism). The last character offers only weak support, but the other two synapomorphies offer strong support. These characters, and the restricted association to a single genus, *Helianthemum,* suggest that this group should be given generic status, however, as stated before, this would leave the remaining taxa in the subgenus paraphyletic with respect to the *miscella* group, because the synapomorphies supporting the more inclusive genus would be lost.

Species: *Lophoptilus* (*Lophoptilus*) *bottimeri* (Busck, 1940), *Lophoptilus* (*Lophoptilus*) *passerella* (Busck, 1909), *Lophoptilus* (*Lophoptilus*) *miscella* (D. & S.

1775), *Lophoptilus* (*Lophoptilus*) *capella* (Busck, 1940) and *Lophoptilus* (*Lophoptilus*) nsp5.

Biology (Table 2): *Lophoptilus (L.) miscella* and *L. (L.) passerella* are oligophagous leaf miners of *Helianthemum* species (personal observation, Riedl 1969, Zagulaev and Sinev 1981). *Lophoptilus (L.) capella* and *L. (L.)* nsp5 are seed capsule feeders on species of *Helianthemum* (personal observation and T. Harrison personal communication).

Distribution: The *miscella* group includes taxa from both the Palearctic (one species) and Nearctic regions. *Lophoptilus* (*L.*) *miscella* is known from all of Europe including the Mediterranean region and Asia Minor (Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Lophoptilus (L.) bottimeri* appears to be largely restricted to the Atlantic and Gulf coasts from NC to Florida an isolated population in Arkansas. *Lophoptilus (L.) capella* and *L. (L.)* nsp5 have a similar Atlantic Coastal distribution from Connecticut to Florida, and an additional Atlantic coastal disjunct of *Lophoptilus* (*L.*) *capella* from Michigan (personal observation and G. Balogh rearing). In the *miscella* group, species are associated with xeric, sandy habitats where Cistaceae are common.

The *terminella* group of *Lophoptilus (Lophoptilus)* (Figure 101)

Cladistics: The *terminella* group is synapomorphic for the slight lateral pockets on the seventh abdominal sternite of the female (22: 0 ⇒ 2).

Species: *Lophoptilus* (*Lophoptilus*) *terminella* (Westwood, 1851) and *Lophoptilus* (*Lophoptilus*) *nancyae* (Clarke, 1990).

Biology (Table 2): *Lophoptilus (L.)* feeding on the Onagraceae include *L. (L.) terminella* as a leaf miner on *Circea* species (Forbes 1923, Riedl 1969, Zagulaev and Sinev 1981).

Distribution: *Lophoptilus* (*L.) terminella* is a widespread Holarctic species. In Europe and Asia it is known from the Baltic region, and Central Europe (Riedl 1969, Zagulaev and Sinev 1981) and the eastern coast of Russia (Sinev 1981). In North America it appears restricted in humid forest habitats of Eastern North America. Riedl (1969) suggested that this species is introduced into North America, but Sinev (1995) points out that its presence in the Russian far east casts doubt to Riedl's supposition. The related *L.* (*L.*) *nancyae* is so far known only from a small series from Queen Victoria Island, British Columbia.

The *metallifera* group of *Lophoptilus* (*Lophoptilus*) (Figure 101)

Cladistics: The remaining species do not clearly fall into distinct monophyletic groups supported by cladistic characters. The *metallifera* group at present is not clearly defined, and includes *Lophoptilus* (*Lophoptilus*) *powelli* (Hodges, 1992), *Lophoptilus* (*Lophoptilus*) *franclemonti* (Hodges, 1992), *Lophoptilus* (*Lophoptilus*) *annulata* (Braun 1923) and perhaps 10 or more undescribed species. Hodges (1992 and personal communication) identified at least eight new species from this group, most known from only a single specimen or a small series of specimens. Some of these may represent previously published names proposed by Clemens and Chambers. The present analysis failed to resolve a single synapomorphy that would unite these species, although it is possible that a broader sample from this group might lead to the uncovering of characters that are informative or forcing homoplastic characters into informative characters.

Provisionally, *Lophoptilus* (*L.*) nsp2 is associated with the *metallifera* group based on wing maculation and the structure of the mesotranstilla. This species, known from two males and one female from California, is an autapomorphic species whose relationship to other *Lophoptilus* (*Lophoptilus*) is unresolved. It is distinct in a single, highly unusual autapomorphy, namely the development of a recurved, spatulate process arising from the apex of the uncus (Figure 65). This unusual feature intuitively suggests this is a significant divergence, and worthy of the establishment of a new genus. However, it should be kept in mind, that changes in the morphology of the uncus are quite common in *Momphinae*, and in particular among species from South America belonging to the genus *Moriloma*, and several new species examined by myself and S. Koster. In the case of *Moriloma* the uncus is completely divided into two halves, giving the uncus a bifid appearance. Other taxa show varying degrees of development of medial lateral lobes and various keels (see *L. cephalonthiella)* and apical lateral processes. Until a broader analysis of these taxa can be undertaken, it would be premature to establish a genus based on this single autapomorphy.

Lophoptilus (*Lophoptilus*) nsp6 has recently been discovered in South Florida by D. L. Wagner. In many respects it is a highly unusual species, possessing a number of autapomorphic characters. Since autapomorphies can not establish relationship with other taxa, its placement within *Lophoptilus* is problematic. This highly derived species is supported by the following autapomorphies: 22: 0 ⇒ 3 (unique), 24: 2 ⇒ 4 (unique), 25: 1 ⇒ 5 (unique), 27: 0 ⇒ 1 (parallelism), 30: 1 ⇒ 0 (reversal), 31: 0 ⇒ 1 (parallelism), 32: 1 ⇒ 0 (reversal), 44: 0 ⇒ 3 (unique), 56: 0 ⇒ 2 (unique). In the preferred cladogram (Figures 101, 106), this species is placed basal to the Rubiaceae feeding clade, which appears to be a sound cladistic hypothesis.

Species: Lophoptilus (*Lophoptilus*) *annulata* (Braun, 1923), *Lophoptilus* (*Lophoptilus*) *franclemonti* (Hodges, 1992), *Lophoptilus* (*Lophoptilus*) *powelli* (Hodges, 1992), *Lophoptilus* (*Lophoptilus*) nsp1, *Lophoptilus* (*Lophoptilus*) nsp7, *Lophoptilus* (*L.*) nsp10, *Lophoptilus* (*Lophoptilus*) nsp2, and *Lophoptilus* (*Lophoptilus*) nsp11. Unplaced: *Lophoptilus* (*Lophoptilus*) nsp6.

Biology (Table 2): *Lophoptilus (L.) powelli* is a leaf miner on *Epilobium (sect. Zauschneria) canum latifolia* (Hook.) (Onagraceae). An undescribed species from the *metallifera* group is also known from rearing on *Cuphea* (Lythraceae) (Hodges 1992). *Lophoptilus (L.)* nsp6 is a leaf miner on *Hamelia patens* Jacq.(Rubiaceae). An additional species from California, not included in the analysis, has been reared on *Galium* (Rubiaceae), and probably is associated with other rubiaceous feeders.

Distribution: Species in the *L.* (*L.*) *metallifera* group are exclusively Nearctic in distribution. Species of *L.* (*L.*) *franclemonti*, *L.* (*L.*) *powelli*, *L.* (*L.*) nsp1, *L.* (*L.*) nsp7, *L.* (*L.*) nsp2 are all known from restricted localities in Northern California. *Lophoptilus* (*L.*) nsp10 is known from a single specimen taken in Illinois.

The genus *Mompha* Hübner, 1816[1826]

Mompha Hübner, 1816[1826]:414. Verzeichniss Bekannter Schmetterlinge.

Type: *Tinea conturbatella* Hubner [(1818-1819)]. By subsequent designation, Walsingham and Durrant, 1909, 45:173.

Laverna Curtis, 1839. British Entomology, 16: 735.

Type: *Laverna ochraceella,* Curtis, 1839. By monotypy.

Wilsonia Clemens, 1864. Proceedings of the Entomological Society of Philadelphia, 2:428. Type: *Wilsonia brevivitella* Clemens, 1864. By monotypy.

Cladistics: The genus *Mompha* was supported by the following three synapomorphies: 4: 0 ⇒ 2 (second palpal segment with well developed, expanded tuft of scales, unique), 25: 1 ⇒ 4 (colliculum with internal sclerotized fold, at least three times as long as wide), and 27: 0 ⇒ 1 (ductus seminalis arising distally from antrum, parallelism). *Mompha* forms a large clade of species feeding exclusively on the plants in the Onagraceae and is divided into two formal subgenera, *Mompha* and *Laverna*. Placement of the species groups, clades and subgenera are plotted on the cladogram of *Mompha* in Figure 102.

Mompha Subgenus *Mompha* (Figure 102)

Cladistics: The monobasic subgenus *Mompha* (*Mompha*) is supported by the following synapomorphies: 25: 4 ⇒ 6 (colliculum reduced, reversal), 27: 1 ⇒ 2 (ductus seminalis appearing to arise from corpus bursae, unique), and 46: 0 ⇒ 1 (mesocucullus with ventrally produced, triangular process, unique). The clade is composed of the single, autapomorphic species *Mompha conturbatella* (Hübner 1819). The treatment of this taxon poses a slight dilemma, since it represents the type species of *Mompha.* Given the autapomorphic nature of this species, it is troubling that the species has priority to delimit higher group names in this group (i.e., Momphinae). However, its association with the subgenus *Laverna* is not in doubt.

Species: *Mompha (Mompha) conturbatella* (Hübner, 1819).

Biology (Table 3)*:* In addition to being morphologically distinct, *conturbatella* also possesses an unusual feeding strategy, found in only one other species of *Mompha*. *Mompha conturbatella* has two distinct life histories, both as an internal stem borer not inducing galls and as a leaf tier (Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). The species is oligophagous on *Epilobium angustifolium*, *Epilobium montanum* and *Epilobium spicatum* (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994).

Distribution: Holarctic. *Mompha conturbatella* is distributed in the north and central mountains of Europe, southern Siberia and the mountains of central Asia (Riedl 1969, Zagulaev and Sinev 1981, Sinev 1995). It is also known from western North America in the northern tier of states and southern Canada, east to Minnesota.

Mompha Subgenus *Laverna* (Figure 102)

Cladistics: Monophyly of the subgenus *Laverna* is supported by a single synapomorphy: 24: 2 ⇒ 3 (medial region posterior of antrum with an infolded, sclerotized cup, with two reversals). The subgenus is very speciose, with 38 species included in the analysis, and doubtless more species (perhaps 20 or more) to be found in the Nearctic and Neotropics. Stability of nodes within the subgenus is high, but their interrelationships poorly resolved. The subgenus *Laverna* is divided into six seven groups (Figure 102).

The *murtfeldtella* group of *Mompha* (*Laverna*) (Figure 102)

Cladistics: The *murtfeldtella* species group is supported by the following two synapomorphies: 44: 2 ⇒ 3 (lateral arms of transtilla greatly developed, nearing hood of

Table 3. Life history data for *Mompha* (*Mompha*) and *Mompha (Laverna)* part.

Species	Host*	Family	Life History	Distr.
Mompha (*M.*) *conturbatella*	*Epilobium spp*	Onagraceae	Leaf tier, stem borer	Holarctic
Mompha (L.) murtfeldtella	*Oenothera* spp.	Onagraceae	Flower bud gall	Nearctic
Mompha (*L.*) *claudiella*	*Oenthera biennis*	Onagraceae	Root crown borer	Nearctic
Mompha (*L.*) *stellella*	*Oenothera* spp.	Onagraceae	Flower bud gall	Eastern Nearctic
Mompha (*L.*) *rufocristatella*	*Guara* spp.	Onagraceae	Stem gall	Nearctic
Mompha (*L.*) nsp8 (species complex?)	*Epilobium* spp. *Cammissonia claviformis*	Onagraceae	Leaf miner	Western Nearctic
Mompha (*L.*) *lacteella*	*Epilobium hirsutum*	Onagraceae	Leaf miner	Palearctic
Mompha (*L.*) *propinquella*	*Epilobium hirsutum*	Onagraceae	Leaf miner	Palearctic
Mompha (*L.*) *ochraceella*	*Epilobium hirsutum*	Onagraceae	Leaf miner	Palearctic
Mompha (*L.*) nsp12	*Epilobium canum &* *E. canum latifolium*	Onagraceae	Leaf miner	Western Nearctic
Mompha (*L.*) nsp13	*Camissonia cheiranthifolia*	Onagraceae	Leaf miner	Western Nearctic
Mompha (L.) nsp22	*Clarkia quadrivulnera*	Onagraceae	Leaf miner	Western Nearctic
Mompha (*L.*) *bradleyi*	*Epilobium hirsutum*	Onagraceae	Stem gall	Palearctic
Mompha (*L.*) *subdivisella*	*Epilobium hirsutum*	Onagraceae	Stem miner	Palearctic
Mompha (*L.*) *confusella*	*Epilobium* spp.	Onagraceae	Stem gall	Palearctic
Mompha (*L.*) *divisella*	*Epilobium* spp	Onagraceae	Stem gall	Palearctic
Mompha (*L.*) *unifasciella*	*Epilobium ciliatum*	Onagraceae	Stem gall	Nearactic

Table 3 continued. Life history data for *Mompha* (*Mompha*) continued. See Table XX for the remaining data.

Species	Host*	Family	Life History	Distr.
Mompha (*L.*) *nodicollella*	*Epilobium angustifolium*	Onagraceae	Stem galls	Palearctic
Mompha (*L.*) *subbistrigella*	*Epilobium* spp.	Onagraceae	Seed pod miner	Palearctic
Mompha (*L.*) *fulvescens*	*Epilobium* spp.	Onagraceae	Seed pod miner, spun shoots	Palearctic
Mompha (*L.*) *circumscriptella*	*Oenothera* spp.	Onagraceae	Seed pod miner	Nearctic
Mompha (*L.*) *brevivitella*	*Oenothera* spp.	Onagraceae	Seed pod miner	Eastern Nearctic
Mompha (*L.*) *definitella*	*Oenothera caespitosa*	Onagraceae	Seed pod miner	Nearctic
Mompha (*L.*) nsp18	*Clarkia* sp.	Onagraceae	Leaf miner	Western Nearctic
Mompha (*L.*) nsp11	*Clarkia concinna*	Onagraceae	Leaf miner	Western Nearctic
Mompha (L.) nsp9	*Epilobium canum*	Onagraceae	Leaf miner	Western Nearctic
Mompha (L.) nsp5	*Oenothera* spp	Onagraceae	Flower galls	Eastern Nearctic
Mompha (*L.*) nsp4	*Oenothera sp*	Onagraceae	Flower galls	Western Nearctic

tegumen, unique), 50: 1 ⇒ 6 (apex of saccular lobe developed into a strong, curved process, unique). This last character may also be interpreted as homologous with a similar, but less strongly developed process in the *stellella* group. The female is somewhat unusual in the strongly reduced features of the ostial plate, however, the male is very similar to that of *Mompha (L.) murtfeldtella.*

Species: Mompha (Laverna) murtfeldtella (Chambers, 1875) and *Mompha (Laverna)* nsp1.

Biology (Table 3)*: Mompha* (*L.*) *murtfeldtella* is an oligophagous feeder on *Oenothera* spp, with specific host records for *Oenothera hookeri*, *Oenothera deltoides* and the *Oenothera biennis* complex. Larvae are floral bud gall formers and feeders, with unconfirmed reports of some populations feeding within seed capsules (Forbes 1923). Host and life history data for *M. (L)* nsp1 are not known.

Distribution: *Mompha* (*L.*) *murtfeldtella* is generally distributed in the temperate Nearctic east of the Mississippi River, with scattered populations in Iowa, Wyoming, Colorado, Arizona, California, and Washington. *Mompha* (*L.*) nsp1 is known from Texas, Oklahoma, Nebraska, and Colorado.

The *claudiella* group of *Mompha* (*Laverna*) (Figure 102)

Cladistics: The *claudiella* group circumscribes two unusual taxa whose monophyly is supported by the following synapomorphies: 24: 3 ⇒ 2 (medial region posterior of antrum with an infolded, membranous cup, reversal), and 50: 1 ⇒ 3 (apex of sacculus produced into a round, broad lobe, unique). The relationship of these species to other *Mompha* is not clear in the present analysis. Species in the *claudiella* group appear to lack concrete characters shared with other *Mompha* that would allow for a more certain association with other species. It is placed basal to the *stellella* group (see below) which is one of several possible hypotheses. Alternatively, it is conceivable that these species arose from within the *stellella* group.

Species: *Mompha (Laverna) claudiella* (Kearfott, 1907) and *Mompha (Laverna)* nsp2.

Biology (Table 3): *Mompha (L.) claudiella* feeds on the root crown of *Oenothera* sp. (G. Balogh personal communication). The life history of *Mompha (L.)* nsp2 is not known.

Distribution: Mompha (*L.*) *claudiella* is an infrequently encountered species known from Nova Scotia, Michigan, Minnesota, Utah, Arizona, Colorado, and Oregon. The related *Laverna* nsp2 is known from several male specimens from the San Bernardino Mountains in southern California.

The *stellella* group of *Mompha* (*Laverna*) (Figure 102)

The *stellella* group includes at least nine species, but the limits of these species are now well understood. The monophyly of the group is supported by the following three unique synapomorphies: 41: 0 ⇒ 2 (apex of uncus heavily sclerotized, with small to round broad lobes, slightly divided medially, unique), 43: 1 ⇒ 2 (mesotranstilla developed into a sclerotized triangular lip, with recurved basal process variously produced to the hood of the tegumen), and 49: 0 ⇒ 2 (medial saccular with a triangular tooth-like lobe, unique).

Species: *Mompha* (*Laverna*) *stellella* (Busck, 1906), *Mompha* (*Laverna*) *rufocristatella* (Chambers 1875), *Mompha* (*Laverna*) *pecosella* Busck, 1907, *Mompha* (*Laverna*) *farinacea* Walsingham 1909 and at least five new *Mompha* (*Laverna*) species: nsp3-7.

Biology (Table 3): Species of *Mompha* (*L.*) *stellella* feed in closed floral buds of *Oenothera* species (Onagraceae). The bud expands slightly, reminiscent of a gall, but does not open. The larva feeds within the bud, on the developing ovaries, style, stigma, and anthers. Apparently the larva does not pupate within the bud. It is unknown, but suspected that the larva pupates in the soil or associated detritus. This assumption is based on rearing of *Mompha Laverna* nsp4 which was reared from *Oenothera* sp. in eastern Montana (personal observation), which pupated in vermiculite following exit from the flower bud. Another species, *M.* (*L.*) *rufocristatella* forms galls within the stem and the apical branch tips of species of *Guara* (Onagraceae). The life histories of the remaining species are not known, but hypothesized to be mainly flower gall inducing species of *Oenothera*.

Distribution: The stellella group is generally distributed in the Nearctic region from the Atlantic to the Pacific Coasts, with the greatest concentration of species in Texas and Oklahoma. Species of the *stellella* group are not known from the Palearctic or other biogeographic regions with the exception of one species from Baja California (not included in this analysis).

The *paniculatum* group of *Mompha* (*Laverna*) (Figure 102)

Cladistics: The *paniculatum* group is a poorly defined group of two undescribed taxa that account for much of the variation seen in the 24 equally parsimonious cladograms. Given the uncertain placement of these species within the *Laverna* species group, it is best at this time to leave them in a separate group, however, additional characters may eventually resolve the association of these species. In the favored cladogram (Figure 100), the *paniculatum* group is supported by a single synapomorphy: 26: 2 ⇒ 1 (ductus bursae a sclerotized tube not significantly wider than antrum, reversal).

Species: *Mompha* (*Laverna*) nsp8 and *Mompha* (*Laverna*) nsp9.

Biology (Table 3)*: Mompha* (*L.*) nsp8 is a polyphagous leaf miner on *Epilobium paniculatum* and *Camissonia claviformis* (Onagraceae); it should be pointed out that this species might represent a species complex. *Mompha* (*L.*) nsp9 is a leaf miner on *Epilobium canum* (Onagraceae).

Distribution: The two species in the *paniculatum* group are generally distributed in the western Nearctic (Pacific Northwest). *Mompha* (*L.*) nsp8 is known from Northern California, Washington, Idaho, and Utah. *Mompha* (*L.*) nsp9 is known from Central California and Northern Arizona.

The *lacteella* group *of Mompha* (*Laverna*)(Figure 102)

The *lacteella* group is a large species group whose monophyly is supported by the following synapomorphies: 50: 0 ⇒ 2 (apex of saccular lobe of valve elongate and tapering, unique) and 53: 4 ⇒ 2 apex of juxta with small round processes along the margin, reversal). The preferred reconstruction has two stable, invariant clades within the *lacteella* group (Figure 102). One clade, referred to hereon as the *divisella* clade, is well supported by the following synapomorphy: 34: 0 ⇒ 1 (ductus seminalis with slight, sclerotized denticles, unique). The other clade, hereon known as the *lacteella* clade is however, not supported by a single synapomorphy. Species in the *lacteella* clade are extremely similar in overall morphology, so the placement of species within it can be in little doubt.

Species: Within the *lacteella* clade species included are *Mompha (Laverna) lacteella* (Stephens, 1834), *Mompha (Laverna) propinquella* (Stainton, 1851), *Mompha (Laverna) ochraceella* (Curtis, 1939), and four new *Mompha (Laverna)* species: nssp10-14. Within the *divisella* clade species included are *Mompha (Laverna) unifasciella* (Chambers, 1876), *Mompha (Laverna) bradleyi* Riedl, 1965, *Mompha (Laverna) confusella* Koster and Sinev, 1996, *Mompha (Laverna) subdivisella* Bradley, 1951, *Mompha (Laverna) divisella* H.-S., 1854, and *Mompha (Laverna)* nsp15.

Biology (Table 3): Known species within the *lacteella* clade are all leaf miners in the later instars, some species initially boring in the stems and roots during early instars (Koster and Biesenbaum 1994). Species in the *divisella* clade all feed in the stem, all but one species forming a gall. Both clades feed exclusively on members in the Onagraceae.

Within the *lacteella* clade, the species *M. (L.) ochraceella*, *M. (L.) propinquella*, and *M. (L.) lacteella* are monophagous on *Epilobium hirsutum* (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Mompha (L.)* nsp12 is a leaf miner of *Epilobium canum latifolium* while *Mompha* (*L*). nsp11 is leaf miner on *Clarkia concinna*. Lastly, *Mompha (L.)* nsp13 is a leaf miner on *Camissonia cheiranthifolia* and *Mompha (L.)* nsp22 on *Clarkia quadrivulnera* (personal observation, sometimes considered a subspecies of *Clarkia purpurea*).

Species in the *divisella* clade all induce galls in stems of the Onagraceae with the exception of *M.* (*L.*) *subdivisella* which is a longitudinal stem borer. *Mompha (L.) bradleyi* and *M. (L.) subdivisella* feed exclusively on *Epilobium hirsutum* (Riedl 1969, Koster and Sinev 1996), while the similar species *M. (L.) confusella* is oligophagous on *Epilobium hirsutum* and *E. angustifolium* (Koster and Sinev 1996). *Laverna divisella* is oligophagous, with reported host data from a wide range of *Epilobium* species: *angustifolium* (Zagulaev and Sinev 1981), *E. montanum, E. palustre* L., *E. ceolatum* (Riedl 1969), *E. lanceolatum*, *E. parviflorum* and *E. adenoscaulon*, a species originally from North America (Koster and Sinev 1996). Some of these records may be confused with other species in the *divisella* clade, and in particular, the record for *Mompha* (*L.*)

divisella on *E. angustifolium* and *E. alpinum* needs to be confirmed (Koster and Sinev 1996). Lastly, *M. (L.) unifasciella* is known to feed on *Epilobium ciliatum* (personal observation).

Distribution: Species in the *divisella* clade are found both in the western Nearctic and Palearctic regions. *Mompha (L.) unifasciella* is known only from the Pacific Northwest (Washington and Oregon), British Columbia and Alberta. *Mompha (L.)* nsp15 is known from scattered material from New York and Washington. The remaining species are found in the Palearctic region. *Mompha (L.) bradleyi* is somewhat restricted in distribution, known from Austria, England, Germany, the Netherlands and Poland (Koster and Sinev 1996). *Mompha (L.) confusella* is found in Austria, Hungary, Ukraine and Azerbaijan (Koster and Sinev 1996). *Mompha (L.) subdivisella* is restricted to the British Isles (Koster and Sinev 1996). *Mompha (L.) divisella* has a broad distribution, known from the Caucasus, Trans Caucasus, Turkestan, Kazakhstan, mountains of central Asia, central and southwestern Europe (Riedl 1969, Zagulaev and Sinev 1981, Koster and Sinev 1996). None of the species in the *divisella* clade have a Holarctic distribution.

Species in the *lacteella* clade are known from the western Nearctic and Palearctic regions. *Mompha (L.) lacteella* is known from northwest and west central Asia (border of Mongolia), all of Europe (Zagulaev and Sinev 1981), and the southeastern coast of Russia (Zagulaev and Sinev 1981, Sinev 1995). *Mompha* (*L.*) *propinquella* is known from the North and central portions of western Europe, northwest part of central Asia (Riedl 1969, Zagulaev and Sinev 1981), while *M. (L.) ochraceella* is known from west central part of western Europe (Riedl 1969, Zagulaev and Sinev 1981). None of the species in the *lacteella* clade have a Holarctic distribution.

The *subbistrigella* group of *Mompha* (*Laverna*) (Figure 102)

The monophyly of the *subbistrigella* group is supported by one unique synapomorphy: 41: 0 ⇒ 1 (apex of uncus with lateral flanges arising below apex). The group is undoubtedly monophyletic, especially in its derived members. Relationships within the clade are still obscure, however, and additional data is needed to resolve them. *Mompha* (*L.*) nsp16 superficially appears nearly identical to species in the *divisella* clade (above), but it shares no key characteristics with them.

Species: Mompha (*Laverna*) *fulvescens* (Haworth, 1828), *Mompha (Laverna) circumscriptella* (Zeller, 1873), *Mompha (Laverna) nodicollella* Fuchs, 1902, *Mompha (Laverna) brevivitella* (Clemens, 1864), *Mompha (Laverna) definitella* (Zeller, 1873) four new *Mompha (Laverna)* species: nspp. 16-19. In addition the extralimital *Mompha* (*Laverna*) *melaleuca* Clarke, 1965 from South America is provisionally associated with *Mompha.*

Biology (Table 3): All species in the *subbistrigella* group whose biology is known are borers in the seed capsules of onagraceous plants, with the exception of *M. (L.) nodicollella,* which induces stem galls. *Mompha (L.) subbistrigella* is oligophagous on *Epilobium angustifolium, Epilobium montanum, Epilobium palustre*, and *Epilobium parviflorum* (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Mompha* (*L.*) *fulvescens* is also oligophagous on the same species of *Epilobium* as *Mompha* (*L.*) *subbistrigella*, and also feeds on *Epilobium hirsutum* (Riedl 1969). *Mompha* (*L.*) *nodicollella* feeds on *Epilobium angustifolium* (Riedl 1969, Zagulaev and Sinev 1981, Koster and Biesenbaum 1994). *Mompha* (*L.*) *circumscriptella* and *M. (L.)*

brevivitella feed on *Oenothera* (Forbes 1923 and personal observation) and is likely oligophagous on a wide range of species within the genus. *Mompha (L.) definitella* feeds on *Oenothera ceaspitosa M. (L.)* nsp19 is a leaf miner on *Clarkia* sp.

Distribution: With the exception of a few Neotropical species, namely *M. (L.) melaleuca*, the distribution is restricted to all of the sub-boreal Nearctic and Palearctic regions. *Mompha (L) definitella* is widespread in the mountains of the West (Utah, Arizona, Colorado, California, and Wyoming), with literature records from Texas and New Jersey (Forbes 1923). *Mompha (L.) circumscriptella,* a close relative of *M. (L.) definitella,* has a similar distribution, but unlike the previous species, is more common in the East. West of the Mississippi it is known from California, Oregon, Idaho, Washington, Oklahoma, and Texas. *Mompha (L.) brevivitella* appears to be a more restricted species, found in scattered populations from Missouri north to Michigan and New Jersey (Forbes 1923). *Mompha (L.)* nsp17 is a western species known from California, Alberta, Arizona, and Colorado and *Mompha (L.)* nsp16 is known only from California and South Dakota. *Mompha (L.)* nsp19 is known from only a few specimens reared in California.

The Holarctic *Mompha (L.) fulvescens* is known from Western Europe, mountains of central Asia (Zagulaev and Sinev 1981, Sinev 1995) and New York (personal observation) Wyoming and Alaska (Sinev 1995). *Mompha (L.) subbistrigella* Western Europe, Asia minor, Caucasus, and all of Russia (Riedl 1969, Zagulaev and Sinev 1981). Lastly, *M. (L.) nodicollella* is found in northern parts of western Europe (except Spain and Scandinavian countries), southern Siberia and southeastern coastal Russia, eastern

Russia near the Kamchatka peninsula and Alaska (Yukon River) (Zagulaev and Sinev 1981, Sinev 1995).

The Evolution of Feeding Strategy and Host Preference in Momphinae

The Momphinae are best known for their high degree of specialization on the evening primroses (Onagraceae). This association has led workers in the past to state that the Momphinae are the most host-specific of all the lineages of Lepidoptera (Powell 1980). Yet despite this strong association, widespread host records from other plant families (Lythraceae, Rubiaceae, Melastomataceae, Cistaceae, Polygonaceae) made the biological and evolutionary context of this association difficult to understand, especially in the absence of a modern classification. In addition to their intriguing host associations, and plant tissues utilized by momphines are very diverse, with nearly all known lepidopteran feeding stragies represented (leaf mining, leaf tying, stem boring, gall inducing, seed feeding, and root boring). Despite the intriguing biology of the Momphinae, the absence of a comprehensive classification and a phylogenetic hypothesis have prevented the question of the evolution of host association and life history in Momphinae from being adequately addressed.

Completion of the first phylogenetic hypothesis for the momphinae allows for the examination of host preference and feeding strategy of Momphinae within an evolutionary context, with emphasis on their relationship to the Onagraceae. In the following discussion, the preferred cladogram will also be considered as a possible phylogenetic hypothesis (Figure 100). It should be pointed out however, that a cladogram represents the distribution of characters on a branching network, and a single cladogram can often generate multiple phylogenetic hypothesis that are consistent with it (Kitching et al. 1998). This section examines host utilization and feeding strategy in an evolutionary context.

Systematics of the Onagraceae

The Onagraceae, as presently defined, is comprised of seven tribes, 16 genera, over 650 valid species worldwide (Table 4) (Raven 1979, 1988). The tribes and genera are well characterized, monophyletic lineages (Hoch et al. 1993) whose interrelationships are not well known (Raven 1988). While found in all major biogeographic regions, the center of diversity is clearly in the western Nearctic, particularly California, a biogeographic pattern which parallels that seen in *Mompha*. The Onagraceae is the most well known plant family of moderate size, with numerous taxonomic revisions, phylogenetic studies involving morphology and molecules, palynology, biogeography, paleobotany and pollination biology (Raven 1988).

The Onagraceae are subdivided into seven, clearly differentiated and monophyletic tribes of varying size and diversity (Table 4). Of these seven tribes, Momphinae are not known to be associated with three, the Neotropical bird pollinated Fuchsieae, and two smaller Neotropical tribes, Hauyeae (2 spp) and Lopezieae (22 species). Furthermore, only one (unconfirmed) rearing of a momphine has been reported from *Ludwegia* placed in the monobasic Jussiaeeae. The Jussiaeeae is the presumed sister group to the remaining tribes in the Onagraceae (Hoch etal.1993, Bult and Zimmer 1993).

The Circaeeae, is a small monobasic tribe containing seven species of low-growing, small-flowering, fly-pollinated herbaceous annuals concentrated in temperate and boreal habitats in the Northern Hemisphere (Raven 1988, Conti etal.1993). *Circaea* is utilized by three momphine species, but several other species, particularly in *Lophoptilus (Cyphophora)* are expected. For example, the largest known series of *Lophoptilus* (*Cyphophora*) *luciferella* was found in a woodland setting with *Circea* being the only onagraceous plant observed in the area. In addition, there was no sign of leaf mining

Table 4. Summary of classification, diversity, and biogeography of Onagraceae (Modified from Hoch et al., 1993; Raven 1988).

Genus	Tribe	Number of species in genus	Distribution
Ludwigia	Jussiaeeae	82	Pantropical; temperate N. America
Fuchsia	Fuchsieae	105	Mostly Neotropical, 4 Indo-Australian
Circaea	Circaeeae	7	Holarctic; forests and alpine regions
Lopezia	Lopezieae	22	Neotropical; central american
Hauyeae	Hauyeae	2	Neotropical; central american
Gongylocarpus	Onagreae	2	Neotropical; Baja (endemic); Mexico and Guatamala
Gayophytum	Onagreae	9	Western North American; two South America
Xylonagra	Onagreae	1	Baja California
Camissonia	Onagreae	61	West Nearctic; one South America
Calylophus	Onagreae	6	Central and western Nearctic to Mexico
Gaura	Onagreae	21	Nearctic to Mexico
Oenothera	Onagreae	123	Highest diversity in Western Nearctic; 49 South American sp; one Palearctic
Stenosiphon	Onagreae	1	Central Nearctic
Clarkia	Onagreae	44	Western North America; one South American
Epilobium	Epilobieae (in seven sections)	168	Cosmopolitan; high altitudes

damage, and based on the position of this species in the phylogeny, one possible hypothesis is that this species is a stem borer of *Circea* (T. Harrison, personal communication).

By far the greatest radiation of Momphinae is confined to the Onagreae and Epilobieae. The Onagreae are divided into nine, well characterized, monophyletic genera (Table 4) of at least 268 species confined to the Nearctic and Neotropical region with an apparent origin and center of diversity in the western Nearctic (Raven 1998). In contrast, the Epilobieae contains the single, large genus *Epilobium* with over 160 species (Raven 1988). *Epilobium* is hypothesized to have originated in the Western Hemisphere (Hoch et al. 1993), but is widespread and circumboreal in the Northern Hemisphere, with a smaller radiation in the montane neotropics, and a significant radiation in Indo-Australia (more than 40 species) and southern Africa (Raven 1988). *Epilobium* is further subdivided into eight, well characterized, monophyletic sections (Table 5) (Raven 1988, Hoch et al.1993).

Pollen samples of the Onagraceae are known from 73-65 MYA (Drugg 1967) from West Gondwanaland, which corresponds well with the contemporary biogeographic pattern of Onagraceae (Conti et al. 1993). The phylogenetic isolation of the genera in the Onagraceae, prompted Raven (1988) to suggest that individual lineages within the Onagraceae have been phylogenetically isolated for a long period of time.

Table 5. Summary of the present sectional divisions in *Epilobium* (Raven and Raven 1976, Hoch et al 1994).

Epilobium	Growth form and habitat	Number of species in genus	Distribution
Sect. *Epilobium*	Low herbs, mesic montane, small flowered, many with reduced leaf surface area.	150+	Concentrated in northern hemisphere, major Australasia radiation, lesser S. America and S. Africa
Sect. *Chamaenerion*	Tall to moderately tall herbs, large flowered perennials	7	Circumboreal, with five species restricted to Asia
Sect. *Boisduvalia*	Low herbs, reduced leaves, flowers, mesic habitats	4	North and South America
Sect. *Zauschernia*	Tubular flowers, low herbs, mesic habitats	2	Western North America
Sect. *Xerolobium*	Xeric habitats, tall to moderate herbs, reduced leaves and flowers, xeric habitats	1	Western North America
Sect. *Cordylophorum*	Xeric habitats	3	Western North America
Sect. *Crossostigma*	Xeric habitats	2	Western North American

Host Utilization in Mompha

Summary of host plant family associations

Of the 75 (68 in the analysis) (Table 6) Nearctic and Palearctic species of Momphinae examined in this study, the host associations and life histories (partial) are known for 48 species (64%) from four plant families (Table 6). At least 37 species of Momphinae are exclusively associated with the Onagraceae, or 49% of the species examined. A further five species (or six, T. Harrison personal communication) (7%) feed on Cistaceae, four species on Rubiaceae (6%) and a two host records from the Lythraceae (3%). Host associations for the remaining 35% are not known, but the cladogram might be used to predict associations of these species. A complete summary of known host associations can be found in Tables 6 and 7.

In addition to the above host association, life histories of several species of Momphinae from outside the Nearctic and Palearctic are known from Melastomataceae and Polygonaceae. Placement of these species within the present classification is provisional, with a number of these undescribed species probably representing new genera. *Lophoptilus* (*L.*) *millotella* (Viette 1954) is known from flower galls of *Dichaetantera hirsuta* (Melastomataceae) in Madagascar. *Lophoptilus* (*L.*) *trithalma* (Meyrick 1922) is a known leaf miner of *Clidemia hirta* (Melastomataceae). In addition, several undescribed species of *Lophoptilus* are either leaf miners or induce galls on various Melastomataceae in Brazil (Becker 1999). In New Zealand, at least three species of *Zapyrasta* are leaf miners of *Muelenbeckia* spp. (Polygonaceae), and inclusion of these species in the cladistic analysis demonstrated them to be derived members of *Lophoptilus* (*L.*) species in the non-onagraceous feeding group. This genus will likely be placed as a distinct monophyletic group, part of a larger monophyletic group that includes Momphinae associated with Cistaceae or Rubiaceae.

Generic patterns of host association in Momphinae

Two genera, *Anybia,* and *Mompha* are strictly associated with the Onagraceae. *Anybia* feeds on two tribes in the Onagraceae, Circaeeae and Epilobieae. Both species of *Anybia* are associated with *Circea*, while one (*langiella*) is also associated with species of *Epilobium*, although *Circea* appears to be the most common host association (S. Koster personal communication).

Table 6. Number of species records in Momphinae by plant genera and family.

Family	Genera	Total number of spp records	% Total of known host records (53)
Onagraceae	*Epilobium, Circea, Oenothera, Gaura, Clarkia, Ludwigia, Camissonia*	39	73%
Melastomataceae	*Clidemia, Dichaetantera*	2	4%
Lythraceae	*Cuphea, Lythrum*	2	4%
Polygonaceae	*Muelenbeckia*	3	6%
Rubiaceae	*Cephalanthus, Galium, Hamelia*	4	7%
Cistaceae	*Helianthemum*	5	9%

Within *Mompha*, all species feed on the Onagraceae, and are specialized on two monophyletic tribes within the family, the Onagreae and the Epilobieae (Figure 103). The monobasic *Mompha* (*Mompha) conturbatella* is oligophagous on species of *Epilobium* (Figure 104-105). The diverse subgenus *Laverna* has species feeding on both the Onagreae and the Epilobieae. Thirteen species are specialists on the Onagreae, 14 are specialists on the Epilobieae, and one species is oligophagous on both tribes (Figure 103). This last case (*Mompha (L.)* nsp8) may actually represent a host race or cryptic species complex, but additional data is needed to establish this. Two clades in the subgenus *Laverna* are strictly associated with one tribe (Figure 103). The clade containing the *stellella*, *murtfeldtella*, and *claudiella* groups (Figure 102) is strictly associated with the Onagreae (Figure 103). The *divisella* clade is restricted to the Epilobieae (Figure 103). The remaining species groups (*lacteella*, *paniculatum* and *subbistrigella*) have mixed associations on the Onagreae and Epilobieae (Figure 103). Overall, thirteen species in

Mompha are monophagous, the remaining 15 are known to be oligophagous (Figure 105). However, it seems likely that more of these monophagous species will prove to be oligophagous within a genus of plants.

Species in *Mompha* (*Laverna*) 13 species are associated with *Epilobium* spp., two species on *Camissonia*, one species on *Guara*, two species on *Clarkia* and nine species on *Oenothera* (Figure 104).

Host relationships within the final genus, *Lophoptilus,* are considerably more complex than those observed in *Anybia* and *Mompha*. This however, is probably more artificial than real, since in the present cladistic analysis the relationships within *Lophoptilus* are not well established. As presently characterized, *Lophoptilus s.l.* is most certainly monophyletic, although additional species will likely change some of the relationships within, and result in the formation of at least three, possibly more genera, when extralimital taxa are considered (see cladistic discussion of *Lophoptilus*). Host records are known from Onagraceae, Lythraceae, Rubiaceae, and Cistaceae (Figure 106). Also, excluded from this analysis, but falling near the derived members of *Lophoptilus s. l.* are extralimital species feeding on Melastomataceae, and Polygonaceae.

The subgenus *Cyphophora* feeds mainly on Onagraceae, with one record from the Lythraceae (Figure 106). The single *Lythrum* record is known for *Lophoptilus* (*Cyphophora*) *eloisella*, and likely represents a recent host shift since the modern advent and spread of purple loosestrife in North America (although the possibility of this species feeding on native *Lythrum* can not be ruled out). The remainder of the subgenus *Cyphophora* feeds exclusively on *Epilobium* (Onagraceae) (Figure 107).

In *Lophoptilus* (*Lophoptilus*) the situation is more complex (Figures 106-107), with four families utilized (Cistaceae, Rubiaceae, Onagraceae and Lythraceae). Basal to the Cistaceae/Rubiaceae species are species primarily associated with the Onagraceae, and another species associated with Lythraceae (*Cuphea*). One species in the subgenus feeds on *Circea*, while the remaining three species are associated with the Onagraceae, all on *Epilobium*. Derived members in this clade have shifted from the Onagraceae/Lythraceae to the Cistaceae and Rubiaceae, with taxa feeding on the Cistaceae forming a monophyletic group (*miscella* group) (Figure 106). Only one species could be considered to be broadly polyphagous (Table, *Lophoptilus eloisella*. The remainder of oligophagous species are narrowly so, feeding on only a few species within the same genus, while a nearly equal number are strictly monophagous. Monophagy in *Lophoptilus*, however, may be a result of sampling bias (Figure 108).

To summarize, *Anybia* and *Mompha* are highly restricted to a limited group of species in the Onagraceae. Basal species in *Lophoptilus* are also strongly tied to the Onagraceae, with two shifts to the Lythraceae, whereas derived species in *Lophoptilus* shift to the Cistaceae and Rubiaceae. In addition, the phylogeny demonstrates that related clades and species groups from all genera in the Momphinae are very closely tied to particular plant families or monophyletic tribes within the Onagraceae, and not randomly distributed on the cladogram.

Evolutionary patterns of host utilization in Momphinae

Considering the strong phylogenetic association of these moths to plants in the Onagraceae, coevolution (cospeciation) or host shifting may be operating in this case.

However, considering that the phylogenetics of Momphinae is in its infancy, and that no single comprehensive species phylogeny exists for any of the host taxa, it is too soon to answer this question in any definitive way. But, since there is a phylogeny on hand for Momphinae, an examination of the issue is appropriate. Also, I acknowledge that the literature is rich in claims of coevolution, and agree with Janzen's (1979) criticism that the use of the term has been greatly misused and over-generalized. Below I evaluate two possible models of evolutionary host association, and evaluate how well they apply to the Momphinae.

Parallel cladogenesis

Since the publication of Ehrlich and Raven's (1964) paper on butterfly and plant evolution, a number of studies (some modifications to their central thesis) have been published which attempt to demonstrate some form of coevolution between hosts and parasites. The most restrictive interpretation (not initially proposed by Ehrlich and Raven) is known as parallel cladogenesis (cospeciation). In this model, plants evolve defenses against herbivory, later resulting in speciation of the ancestral herbivore to overcome the new plant's defense mechanism. In this case, direct comparison of species phylogenies of both plants and herbivores are expected to be congruent (Thompson 1999, Farrell and Mitter 1998) when parallel cladogenesis has occurred (i.e., the most primitive herbivore would be feeding on the most primitive plant and so forth through the phylogeny).

In order to fulfill this model (parallel cladogenesis), herbivores should be monophagous and the adult and larvae strongly tied to the host (Miller and Wenzel

1995). In addition there should be host and herbivore phylogenies available. Not surprisingly, very few studies convincingly demonstrate this phenomenon. Perhaps the best heralded study (Farrell and Mitter 1998) concerns the evolutionary relationships of *Tetraopes* beetles on *Asclepias*. Their study demonstrated a nearly one to one correspondence of the plant and herbivore phylogenies

In the Momphinae, it seems readily apparent that the data do not support the hypothesis of parallel cladogenesis. Both primary assumptions needed to support parallel cladogenesis are violated in the Momphinae. Many of the species are narrowly polyphagous (oligophagous), feeding on one or more species in a genus (Tables 105, 108) rather than strictly monophagous. Narrowly oligophagous species are common in the Momphinae, and it seems unlikely that strict monophagy would be operational in a plant family that is composed of pioneer species. In general, populations of Onagraceae and certainly the Momphinae are subject to local population extinctions and recolonizations (personal observation and J. Powell personal communication). Under these circumstances, it seems more reasonable to expect a certain degree of host generalization favored by selection to accommodate for localized extinction of host species. The second major assumption for parallel cladogenesis, that of the adults and larvae being strongly tied to the host plant, is also likely violated. There is no evidence that the adults are strongly tied to the biology of the host in the Momphinae, although future clarification of the biology may suggest otherwise.

Finally, similar host species are utilized in two or more monophyletic lineages within Momphinae, which seriously compromises any attempt to argue that the evolutionary histories of the host and herbivore are similar. For example, *Lophoptilus* (*Cyphophora*) *eloisella* attacks *Oenothera biennis*, as do several species within *Mompha* (*Laverna*): two distinctly different monophyletic lineages. Similarly, *Epilobium angustifolium* is utilized by numerous momphines from all three monophyletic genera: one species of *Anybia*, five species of *Lophoptilus*, and six species of *Mompha*. These two examples, among others, demonstrate that across phyletic lines, there is little support that host and plant phylogenies are congruent.

Colonization by host chemistry

Examination of the phylogeny, however, demonstrates the narrow host specialization of momphine species along phyletic lines. Given that the evidence at hand does not suggest parallel cladogenesis, what might account for these broad patterns in host utilization in the Momphinae? Based on the present data, the most defensible response is that host plant selection in momphinae may occur around one or more chemical characteristics of the Onagraceae. In the model, a phytophagous lineage evolves and diversifies around a previously evolved plant diversity (Jermy 1984, Miller and Wenzel 1987). In this case diversification and exploitation does not occur in one-to-one evolutionary correspondence, but is more randomly distributed. A number of recently published papers suggest that this is a mechanism functioning in some phytophagous insects (Becerra 1997, Bush and Smith 1997).

This question can not be addressed in any detail based on the present data. At a minimum, a phylogeny of plant chemistry would be needed to address this question, and at this point it is only speculative what these insects might be using as a host cue.

However, possible evidence as to host plant defense can be found by examining host phytochemistry in the plants exploited by momphines. In examination of the literature, at least one phytochemical aspect was found to be common to all of the plant family hosts examined in this study. Namely, all five families utilized by Momphinae in this study are characterized by high concentrations of calcium oxalate in parenchymous plant tissues (Cronquist 1981) (although, this is also a widespread feature of many, unrelated plant lineages) (Table 7). High concentrations of oxalic acid and raphides, specialized plant tissues which concentrate calcium oxalate, are one very notable phytochemical characteristics of the Onagraceae and Rubiaceae (Cronquist 1983, Bernays and Chapman 1994), and may limit radiation of phytophagous insects not specialized to these phytochemicals. It is possible that the presence of high concentrations of calcium oxalate may have an influence on the evolutionary biology of Momphinae. However, this would not entirely explain their lack of radiation on the Rubiaceae (which also contain raphides), unless, other phytochemistry prevents such an event (although this may be an artifact of undersampling in the Neotropics). Certainly other chemical characteristics are likely used as cues. Perhaps momphines are characterized by a dietary tolerance to high concentrations of oxalic acid, and use other cues for host plant selection. This might explain why, for example, in the Nearctic, the vast majority (well over 200 species) of *Oenothera*, *Camissonia*, *Clarkia* (and five other genera) in the Onagreae are not exploited by Momphinae.

Table 7. Classification, biogeography, and occurrence of calcium oxalate in host plant families of Momphidae (Cronquist 1983).

Family	Order	Calcium Oxalate	Diversity & distribution
Onagraceae	Myrtales	Present	600 spp; Western U.S.
Melastomaceae	Myrtales	Present	4000 spp; Tropical
Lythraceae	Myrtales	Present	500 spp; Tropical
Rubiaceae	Rubiales	Present	6500 spp; tropical
Cistaceae	Violales	Present	200 spp; Temperate

Momphinae have also shifted to the Lythraceae at least two times in the genus *Lophoptilus*. Botanists are in agreement that the nearest sister group to the Onagraceae is the Lythraceae (Raven 1988; Crisci etal.1993), which, if chemically similar, offer at least anecdotal evidence that these insects are tracking chemical features of the host.

The evolution of feeding strategy in Momphinae

Feeding strategies in the Momphinae are diverse, and contrast sharply with the conservatism in feeding strategy observed in many monophyletic lineages in the Lepidoptera (Scoble 1992). At first glance, feeding guilds in Momphinae appear to be highly diverse and malleable (Tables 1-3). But careful examination of these mapped on the preferred cladogram (Figure 100) demonstrates significant phylogenetic patterns in the evolution of tissue attacked in the Momphinae.

Both *Anybia* and the majority of *Lophoptilus s. l.* species are leaf miners (14 species). Within *Lophoptilus,* three feeding guilds evolve at various positions within the clade. First, the basal species in the subgenus *Cyphophora* are longitudinal stem borers (Figure

109) that do not induce galls in infected stems (two known species). Leaf mining emerges near the base of the clade in the *Locupletella* group (Figure 109) and continues through the phylogeny to the derived clades shifting to Cistaceae and Rubiaceae (Figure 106). While all known species associated with the Rubiaceae retain the leaf mining condition, within the Cistaceae-feeding clade, two of five species have shifted to feeding within seed capsules. Overall, however, feeding strategy appears concentrated on leaf mining, and is more conservative when compared to *Mompha.*

Mompha demonstrate the greatest plasticity in the evolution of feeding strategy, but do so conservatively, almost along phyletic lines (Figure 110), with very little observed homoplasy. The monobasic *Mompha* (*Mompha)* is nearly unique (one other occurrence) in possessing a leaf tying feeding strategy. Flower gall inducing is derived in the *stellella* + *murtfeldtella* group and appears in no other species in the Momphinae (Figure 110). Flower galls are formed in all species within the *stellella* group, with the exception of *Mompha* (*L.*) *rufocristatella.* This species has shifted from flowers to stem galls (also shifting from *Oenothera* to *Guara*). Within the flower-gall inducing clade is the *claudiella* group which shifted to the unusual strategy of boring into the root crown.

The *paniculatum* group and the *lacteella* clade are all leaf miners. Within the later group, three species that are specialists on one species of *Epilobium* are leaf miners in the later instars, while the earlier instars are stem borers (Koster and Biesenbaum 1994). It is not known precisely how these species partition themselves in the later instars.

Species in the *divisella* clade are typically stem gall inducers on the upper third of the plant (Figure 106). One species, however, is a longitudinal stem borer that does not induce galls. The final clade, the *subbistrigella* group is predominately borers of seed capsules, with a single species inducing stem-galls not unlike those found in the *divisella* group, and another species being polymorphic for leaf tying and seed pod boring.

Evolutionary trends in feeding strategy

Most of the life history traits evolved in the Momphinae appear in monophyletic groups, with some shifting (homoplasy) of feeding guilds within clades. When feeding strategy is optimized on the cladogram, it is possible to generate hypotheses for the ancestral states of internal nodes. The ancestral life history condition in Momphinae appears to be leaf mining, evolving at least once above the root, and continuing through *Anybia* and *Mompha* (*Laverna*). The branch leading to *Lophoptilus* is equivocal for either the leaf mining condition, or stem boring, but given the large size of the moths at the base of *Lophoptilus*, the ancestral condition will likely prove to be stem boring.

In Momphinae, gall forming can occur in the stem or in the flower, and is restricted to *Mompha* (*Laverna*) and it is not known if the two types of gall forming are related or independently derived. Based on the present phylogeny, flower gall induction occurred once in the phylogeny (Figure 110). Within this clade, there is a reversal to stem gall inducing in *Mompha* (*Laverna*) *rufocristatella* occurring with a shift from *Oenothera* to *Gaura*. Since the flower is reduced in size in *Guara* compared to *Oenothera*, it is possible that a shift occurred when the ancestor to *M. (L.) rufocristatella* oviposited on the stem, rather than the bud of *Oenothera*. It is also interesting to note that the galls of this species occur high on the stem, very near the leaf and bud terminals of *Guara*. This contrasts sharply with galls formed in the *divisella* and *subbistrigella* groups which occur lower on the stem.

Stem gall induction also occurs in the *divisella* clade and once for a single species in the *subbistrigella* clade of *Mompha* (*Laverna*) *nodicollella* (Figure 110). Based on the present phylogeny, it appears that this condition evolved independently three times. However, since the relationships among the various clades within *Mompha* (*Laverna*) are not very clear, the possibility that both forms of gall induction (flower and stem) are related to two evolutionary events cannot be ruled out. But this is far from the most parsimonious solution, requiring movement of the *divisella* group in relationship to the *stellella* group.

Internal feeding within the seed capsule evolved independently twice in Momphinae. Once in the *subbistrigella* group in *Mompha (Laverna)* (Figure 110), and again in two species in the *miscella* group of *Lophoptilus* which shifted to Cistaceae (Figure 109).

Stem boring also evolved twice in the Momphinae. Once in the *divisella* group in *Mompha* (*Laverna*) *subdivisella* as a shift from gall inducing, and in the basal species of *Lophoptilus*, probably from the ancestral leaf mining condition.

Two feeding strategies, root crown boring and leaf tying are uncommon in the Momphinae. Root crown boring evolved once in the *claudiella* group and leaf tying in *Mompha (Mompha) conturbatella* and again in *Mompha* (*Laverna*) *fulvescens*, which is polymorphic for seed capsule boring and leaf tying (Figure 110).

The evolutionary biology of Momphinae

As has been shown, host association and feeding strategy are very complex in the Momphinae. Based on the present analysis, several hypotheses can be formulated which may account for the evolutionary patterns observed in their biology.

The placement of *Anybia* basal to the two other large clades, *Lophoptilus* and *Mompha*, suggests that the earliest ancestor of Momphinae was a polyphagous leaf miner on onagraceous species. It is interesting to note in this case, that while the species of *Anybia* feed on two tribes, Circaeeae and Epilobieae, the predominate association for the two extant species is with *Circea.* Interesting, because there are multiple lines of evidence, both morphological and molecular (Bult et al. 1993, Crisci et al. 1990 Hoch et al.1993) that the Circaeeae are basal to the two derived tribes, Epilobieae and Onagreae.

The phylogeny also suggests the following hypotheses concerning the evolution and diversification of the two major lineages, *Lophoptilus* and *Mompha*, each which appear to have taken slightly different evolutionary courses. Of the two genera, *Mompha* is more constrained than *Lophoptilus* in host use and is restricted to Epilobieae and Onagreae. This suggests the hypothesis that host selection in *Mompha* is highly constrained, perhaps to a narrow chemical component, preventing host shifts outside of two tribes in the Onagraceae. It also may be that there is a chemical component that is essential for development or synthesis of some reproductive compound (Bush, personal communication). Their host utilization is also limited to a small number of species within these two tribes. This strong host association may have in part fueled niche diversification within *Mompha*. *Mompha* evolved seven feeding strategies that attack various portions of their host plants. When homoplastic strategies are taken into account, feeding guilds evolved nine separate times. It appears that diversification may have occurred by varying the tissue-type exploited by Momphines, leading to the evolution of a variety of feeding strategies. This contrasts with the evolution of three feeding guilds in *Lophoptilus* with leaf mining predominating.

The phylogeny of *Mompha* demonstrates that frequently, when an ancestor evolves a new strategy, there is a resulting diversification of species. This is particularly true for leaf mining that resulted in the diversification of seven confirmed species, flower gall inducing (at least five species), gall inducing (at least five species) and seed capsule feeding (at least four species). Root crown feeding and leaf tying are more conservative, not showing the degree of diversification found in other clades.

The evolutionary history of *Lophoptilus,* contrasts somewhat with *Mompha.* In *Lophoptilus* host utilization appears to be broader and less constrained when compared to *Mompha*. While basal species in the clade appear to be predominately associated with the Epilobieae, species in the genus have shifted to at least three other plant families (Lythraceae, Cistaceae, and Rubiaceae) and one other tribe in the Onagraceae, the Circaeeae. Although not included in this analysis, Neotropical forms feeding on the Melastomataceae and Polygonaceae are probably most closely related to the derived forms shifting to Rubiaceae and Cistaceae. Taken together, *Lophoptilus* appears less constrained in host utilization, and perhaps this has fueled diversification in this genus. Furthermore, while seed capsule feeding is known from two species in the *miscella* group, and stem boring in at least two species (and probably more) in the subgenus *Cyphophora*, in general, the evolution of feeding strategy appears to be much less diversified in *Lophoptilus* than that of *Mompha.*

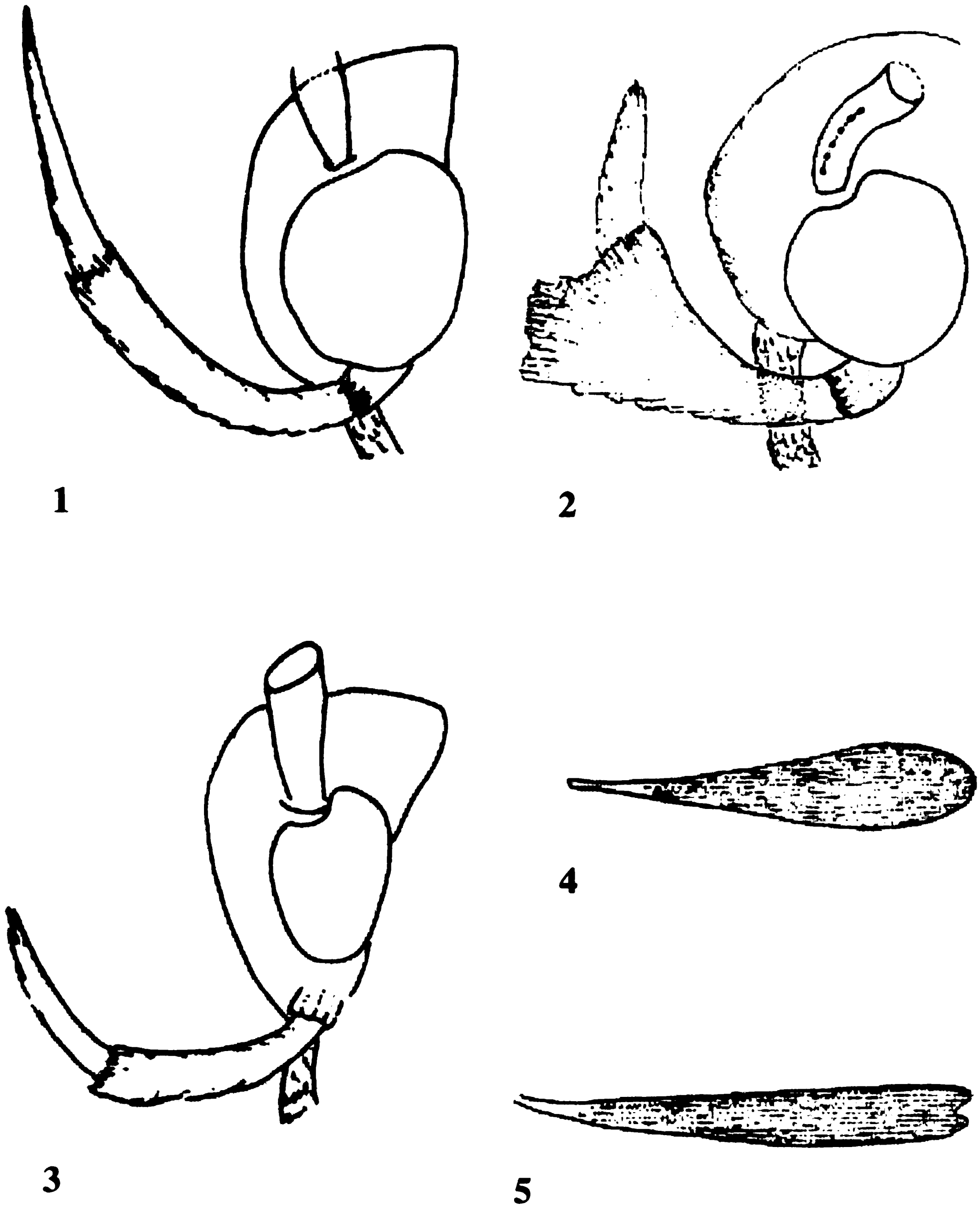
The results of this study demonstrate that the Momphinae are fertile ground for further study and may offer insight into the processes and patterns of evolution in phytophagous insects, but a number of questions remain to be answered. For example, the age of the Momphinae is not known. The placement of the Momphinae near the basal

10% of all Lepidoptera, suggests that this lineage is old, and perhaps has a long association with the Onagraceae, however, in the absence of fossil data, molecular data will be needed before a reliable estimate can be made.

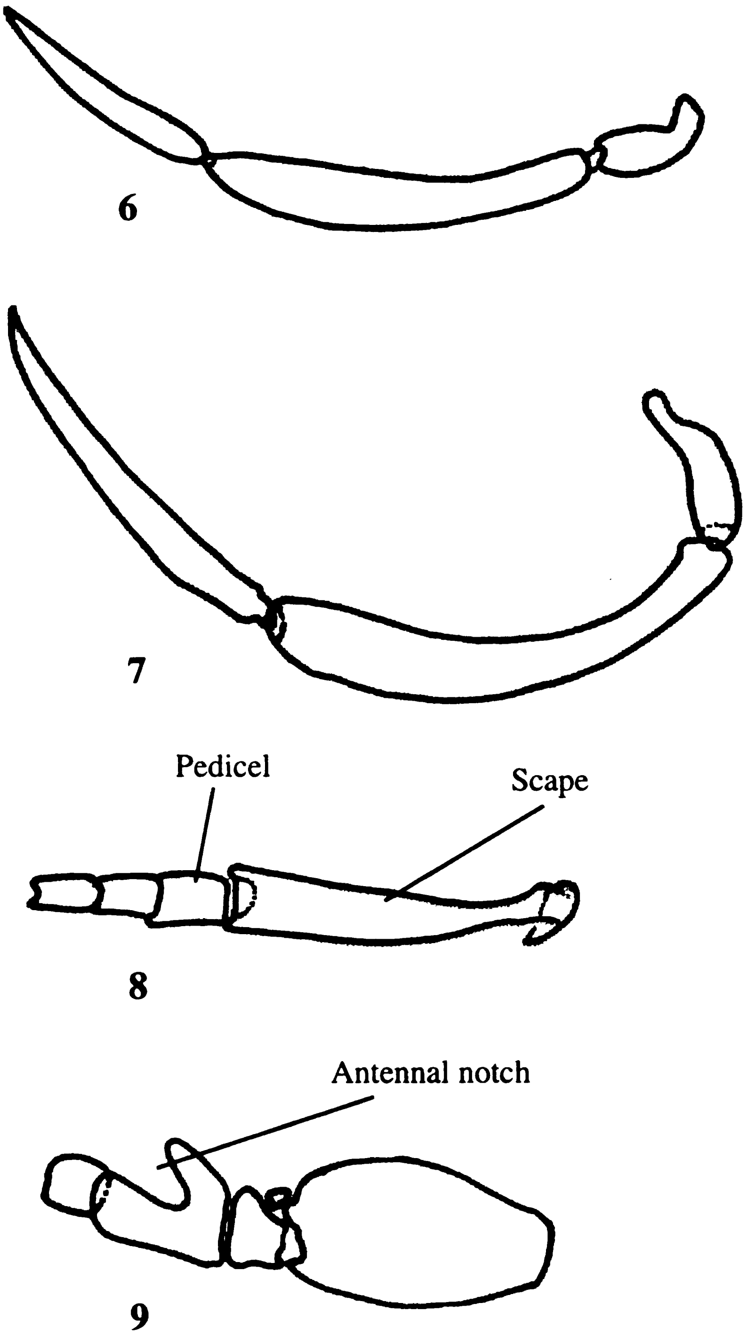
The plasticity of feeding strategy in the Momphinae suggests the possibility that niche partitioning may be occurring in some instances on the same plant. However, at this time, field-work seems to show that several species may be found in the same general area exploiting the same species of plant, but I have been unable to confirm a single instance where this has been documented nor have I observed this first hand.

The relationship of species in the present phylogeny to those found outside of the Nearctic and Palearctic is not known. In particular, it seems certain that these taxa are more closely related to *Lophoptilus*, but their inclusion in a phylogenetic study may change the cladistics of this clade as presently characterized, potentially resulting in the description of new genera. But even if this were the case, preliminary inclusion of extralimital species in the present analysis consistently demonstrates their evolutionary association with *Lophoptilus*.

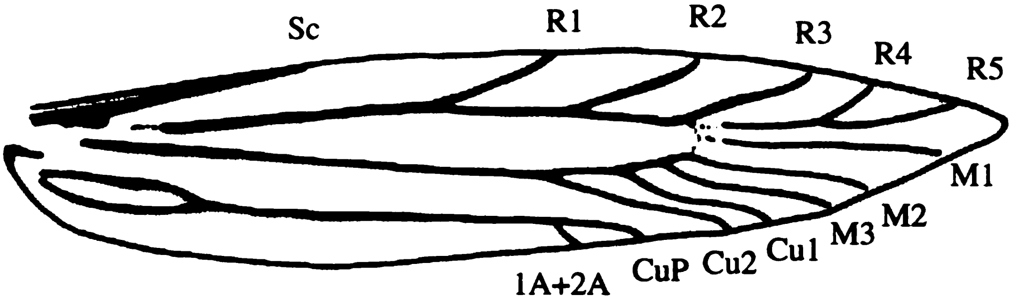
Molecular data may be useful in uncovering the relationships of unresolved polytomies, particularly in *Mompha*, and also uncover relationships, and test the validity of the five monophyletic groups in this genus. These data may also further test the validity of the present phylogeny, particularly in clarifying the relationships of all three genera proposed in this study.



Figures 1-5. Head features of Gelechioidea. 1) Lateral aspect of *Blastobasis* sp. 2) Lateral aspect of *Mompha* (*Laverna*) *claudiella*. 3) Lateral aspect of *Lophoptilus* (*Lophoptilus*) *locupletella*. 4) Scale from vertex of *Mompha* sp. 5) Scale from vertex of head of *Blastobasis* sp.



Figures 6-9. Palpi and antennal features of Gelechioidea. 6) Lateral aspect of *Lophoptilus* labial palpus. 7) Lateral aspect of *Mompha* palpus. 8) Scape and pedicel of *Mompha*. 9) Scape and pedicel of *Holcocera* (Blastobasinae)(modified from Adamski and Brown 1989).



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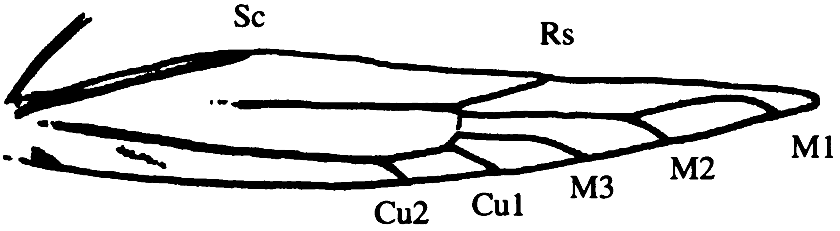

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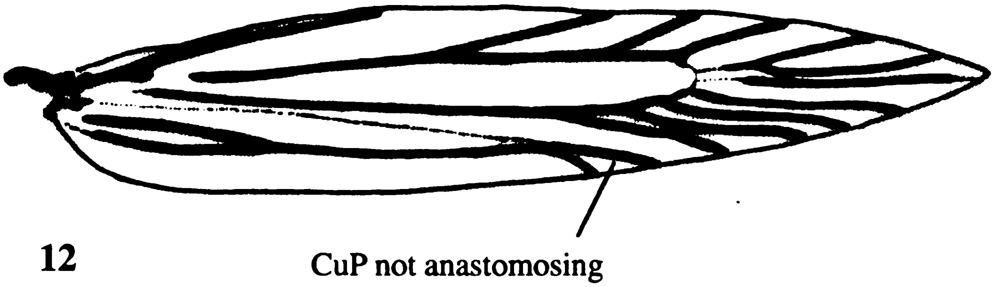

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Figures 10-13. Wing venation of Momphinae. 10) Forewing of *Lophoptilus*. 11) Hindwing of *Lophoptilus*. 12) Forewing of *Mompha*. 13) Hindwing of *Mompha*.

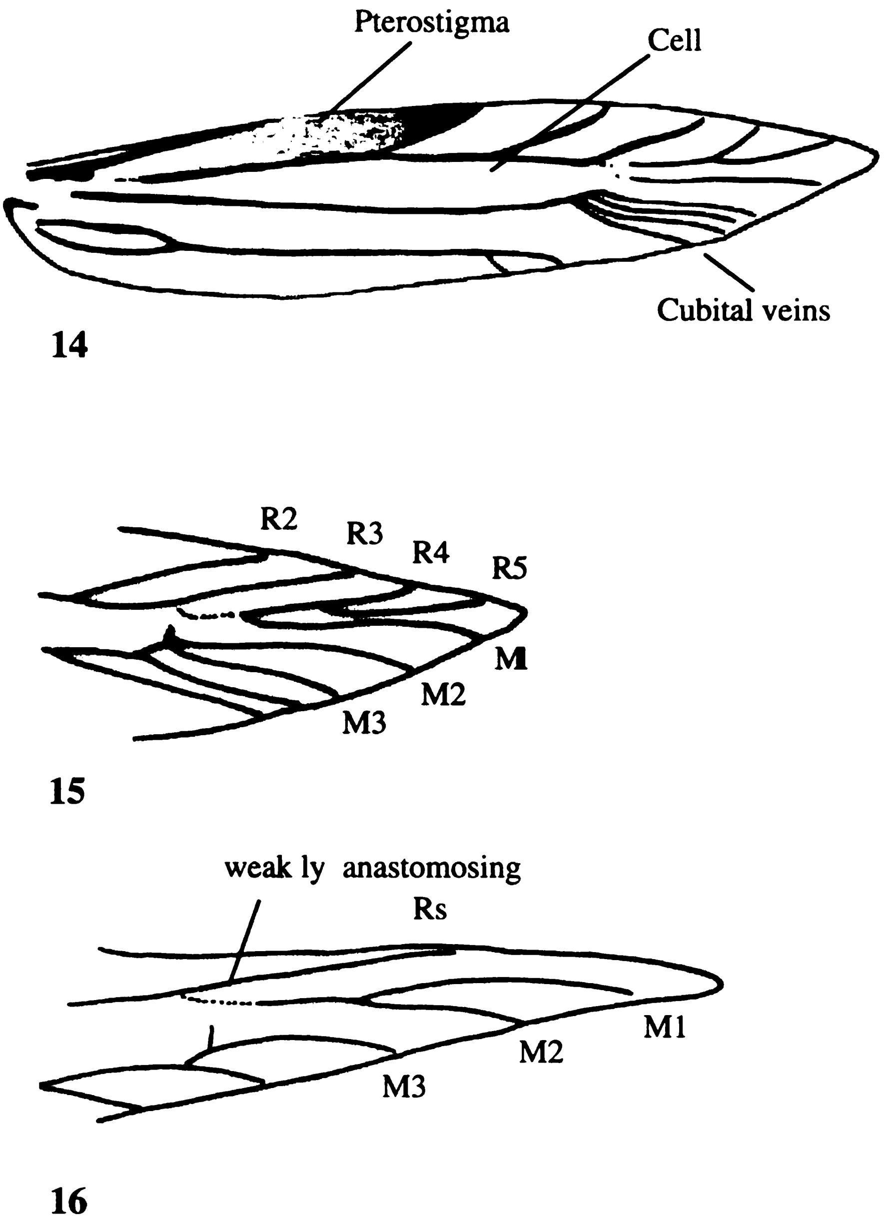
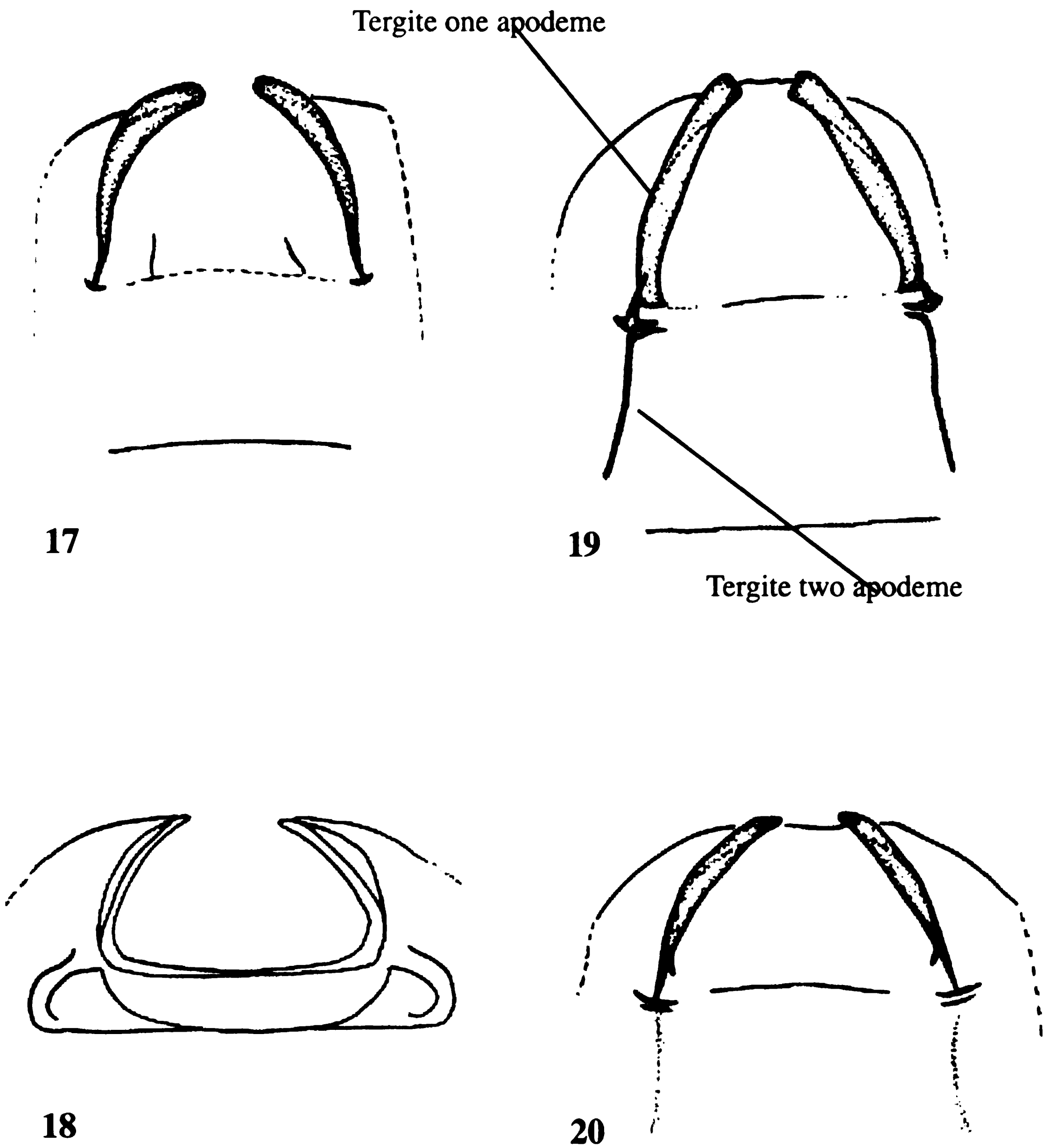
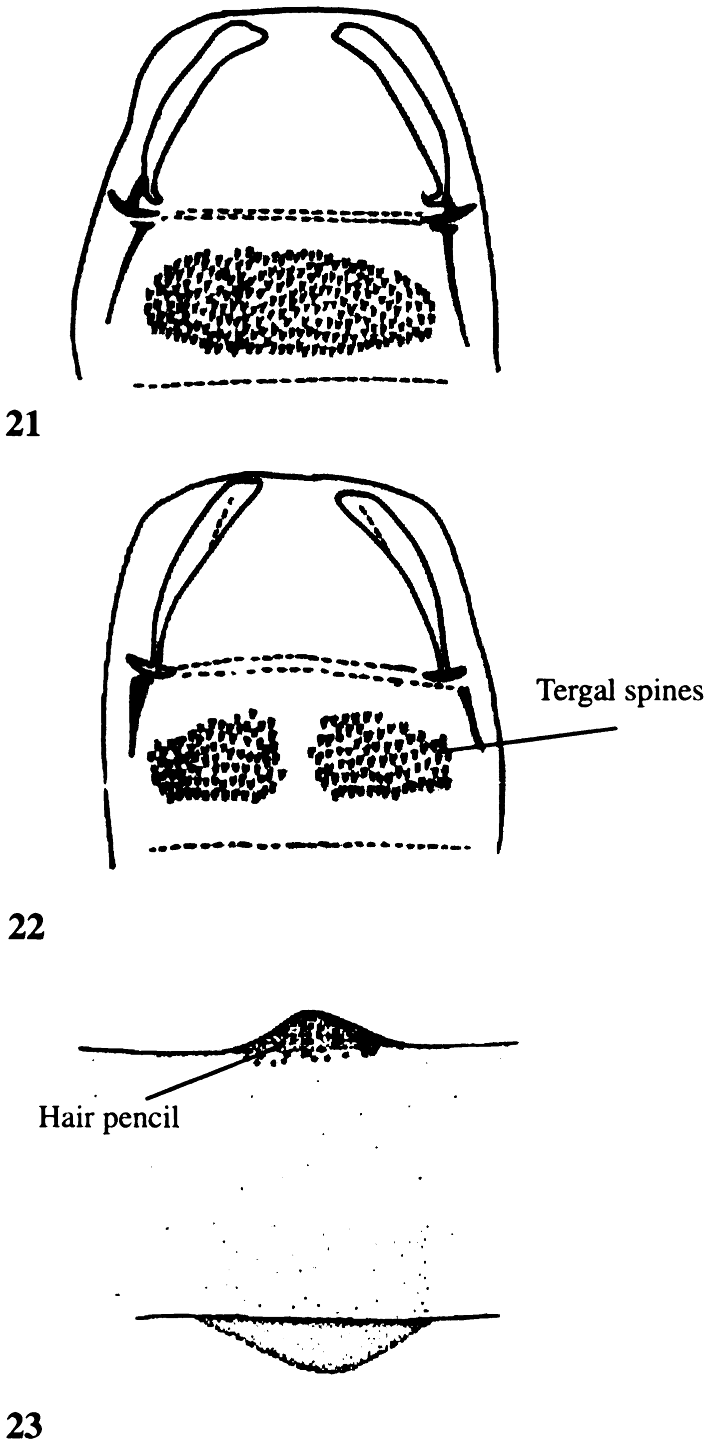


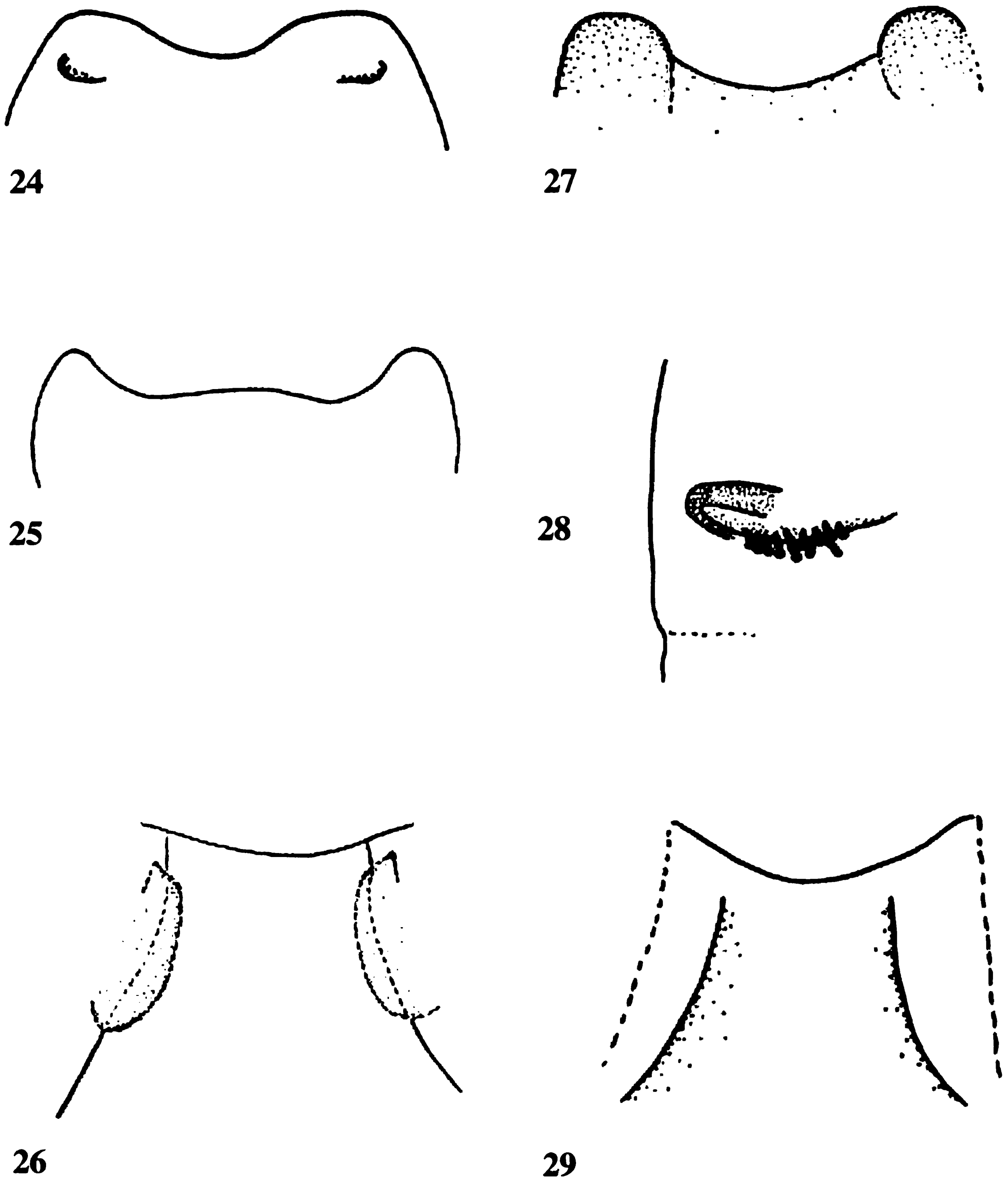
Figure 14-16. Wing venation of Coleophoridae. 14) Generalized forewing of Blastobasinae. 15) Apical forewing venation of *Anybia* showing R4+R5 branched from M1. 16) Apical hindwing of *Lophoptilus* (*Cyphophora*).



Figures 17-20. Tergal apodemes of Gelechioidea. 17) Tergal apodemes of *Lophoptilus terminella*. 18) Tergal apodemes of *Mompha*. 19) Tergal apodemes of Blastobasinae (modified from Adamski and Brown 1980). 20) Tergal apodeme of *Lophoptilus locupletella*.



Figures 21-23. Abdominal features of Momphinae. 21) Tergal spines of *Mompha ochraceella* positioned in a continuous row. 22) Tergal spines of *Mompha* arranged in two patches. 23) Male abdominal segment eight of *Lophoptilus.*



Figures 24-29. Features of the female 7th abdominal sternites of Momphinae. 24) *Lophoptilus terminella* showing slightly invaginated pits. 25) Slightly invaginated lobes of *Lophoptilus*. 26)*Laverna ochraceella* showing slight medial lip. 27) Deeply invaginated pits with anterior spines. 28) Pleural pockets of the *miscella* group. 29) Broadly invaginated fold of *Lophoptilus*.

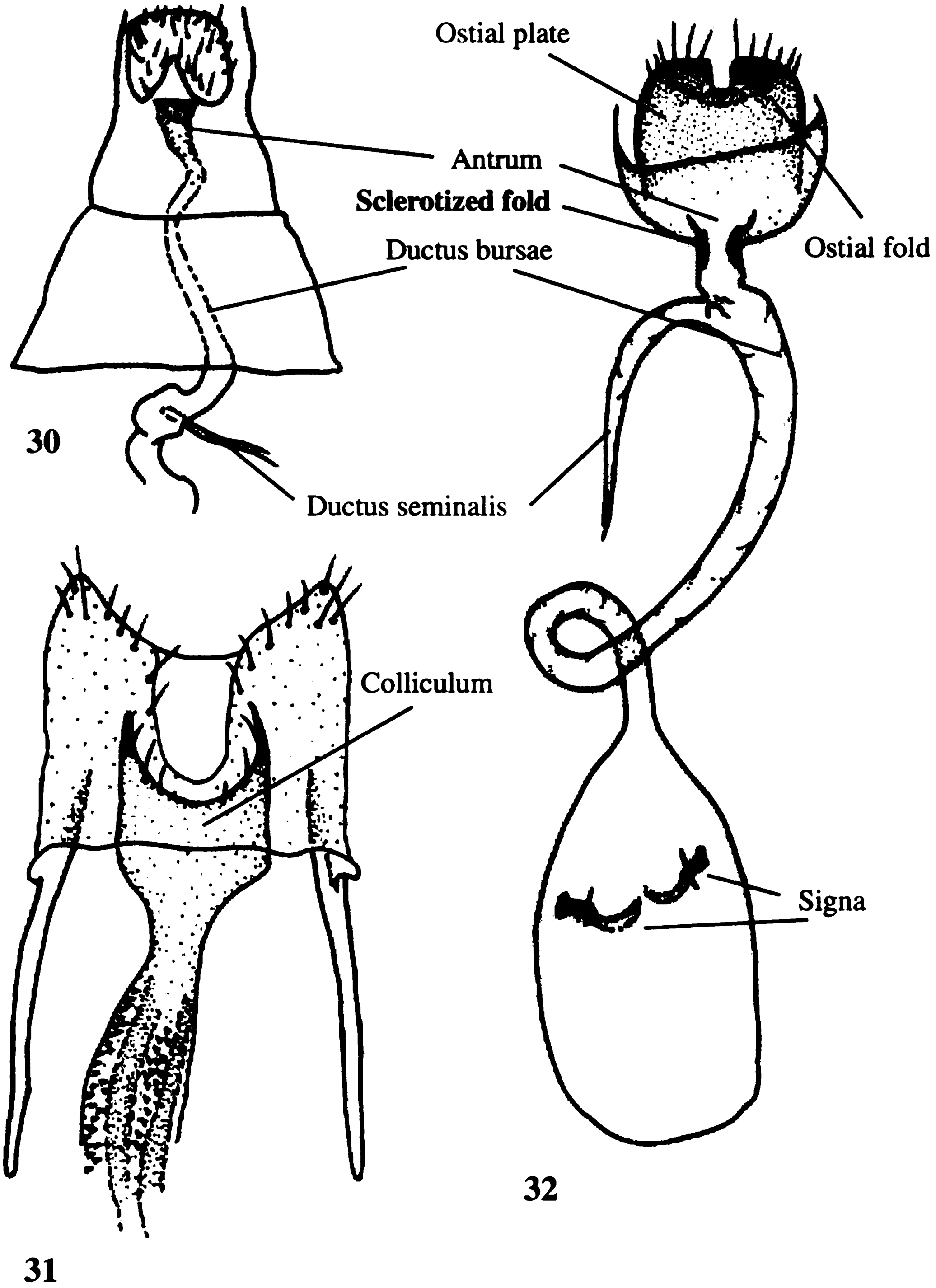


Figure 30-32. Female genital morphology of Coleophoridae. 30) Blastobasinae (modified from Adamski and Brown 1989). 31) Coleophorinae (Modified from Landry and Wright 1996). 32) Momphinae (*Lophoptilus*).

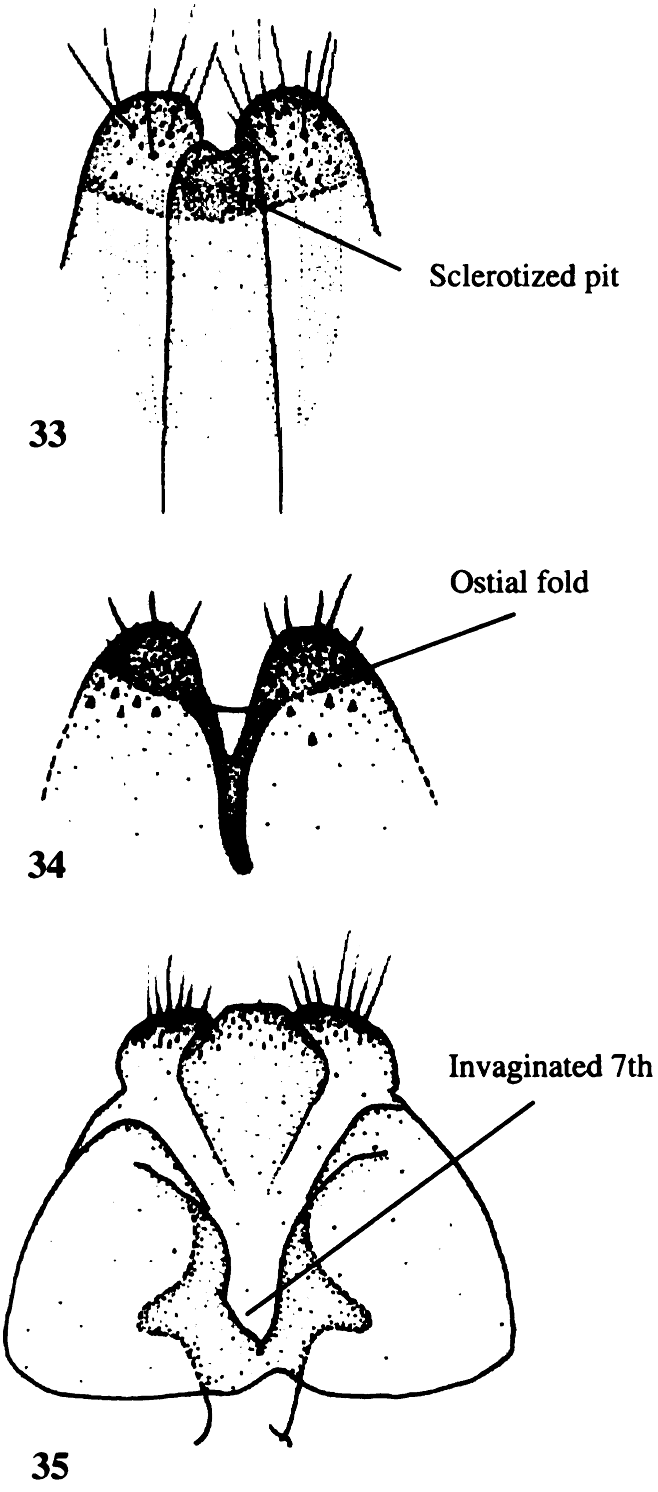


Figure 33-35. Details of posterior female genitalia of Momphinae. 33) *Mompha* (*Laverna*) *definitella*. 34) *Lophoptilus* (*Lophoptilus*). 35) *Lophoptilus* (*Cyphophora*) *maculata* (modified Koster and Biesenbaum 1994).

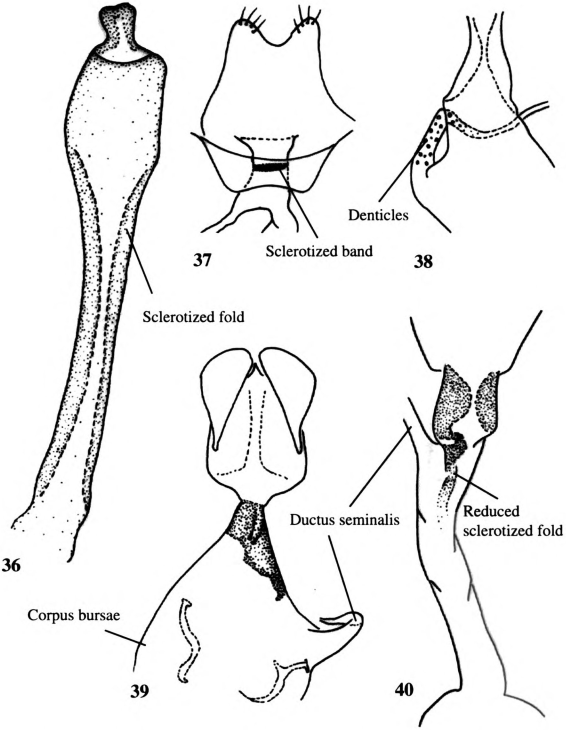
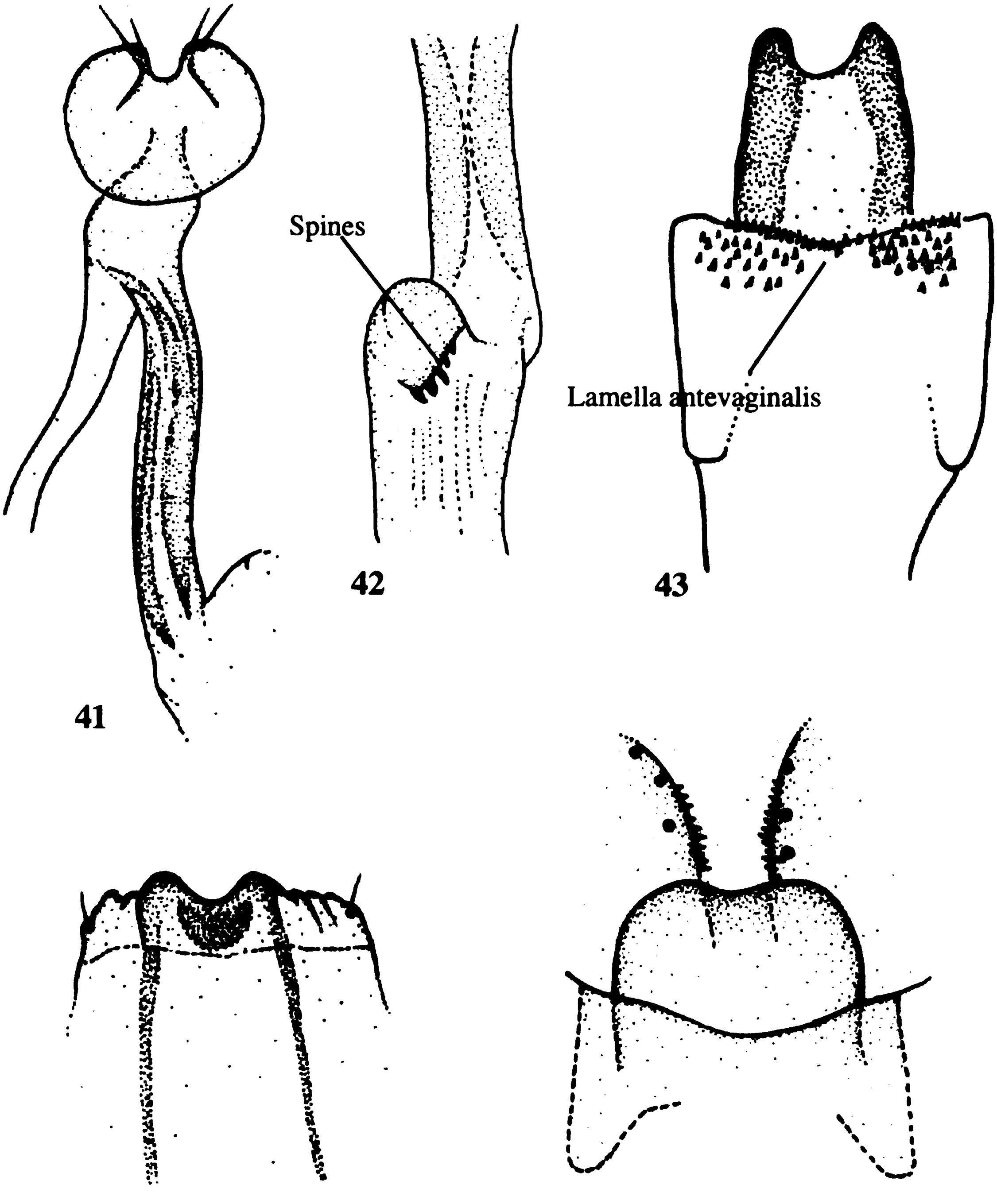
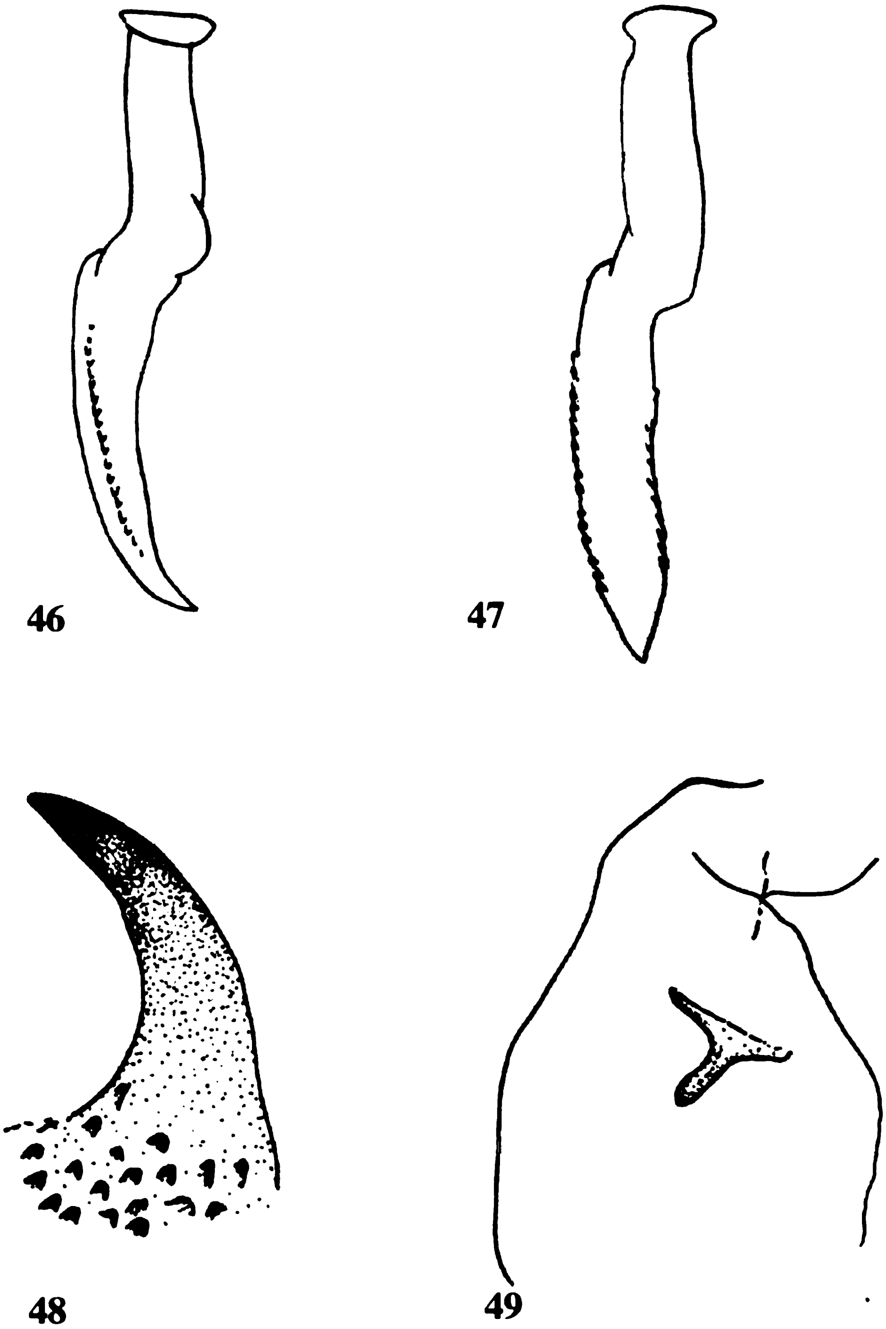


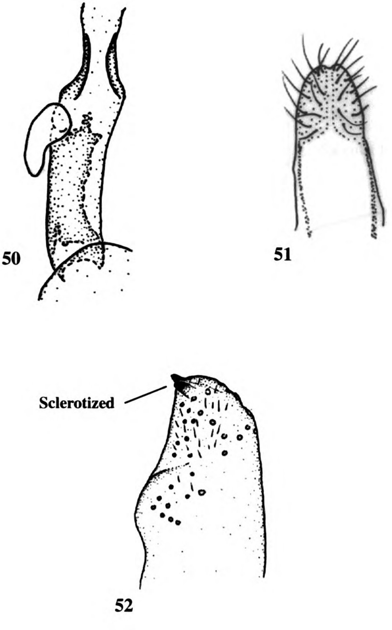
Figure 36-40. Genitalic features of female Momphinae. 36) Ductus bursae of *Lophoptilus* nsp6. 37) Sclerotized band across antrum of *Lophoptilus (Lophoptilus) miscella*. 38) Ductus seminalis of the *divisella* group.. 39) Reduced ductus bursae of *Mompha (Mompha) conturbatella*, and ductus seminalis apparently arising form the corpus bursae. 40) Ductus bursae of the *paniculatum* group showing reduced internal sclerotized fold.



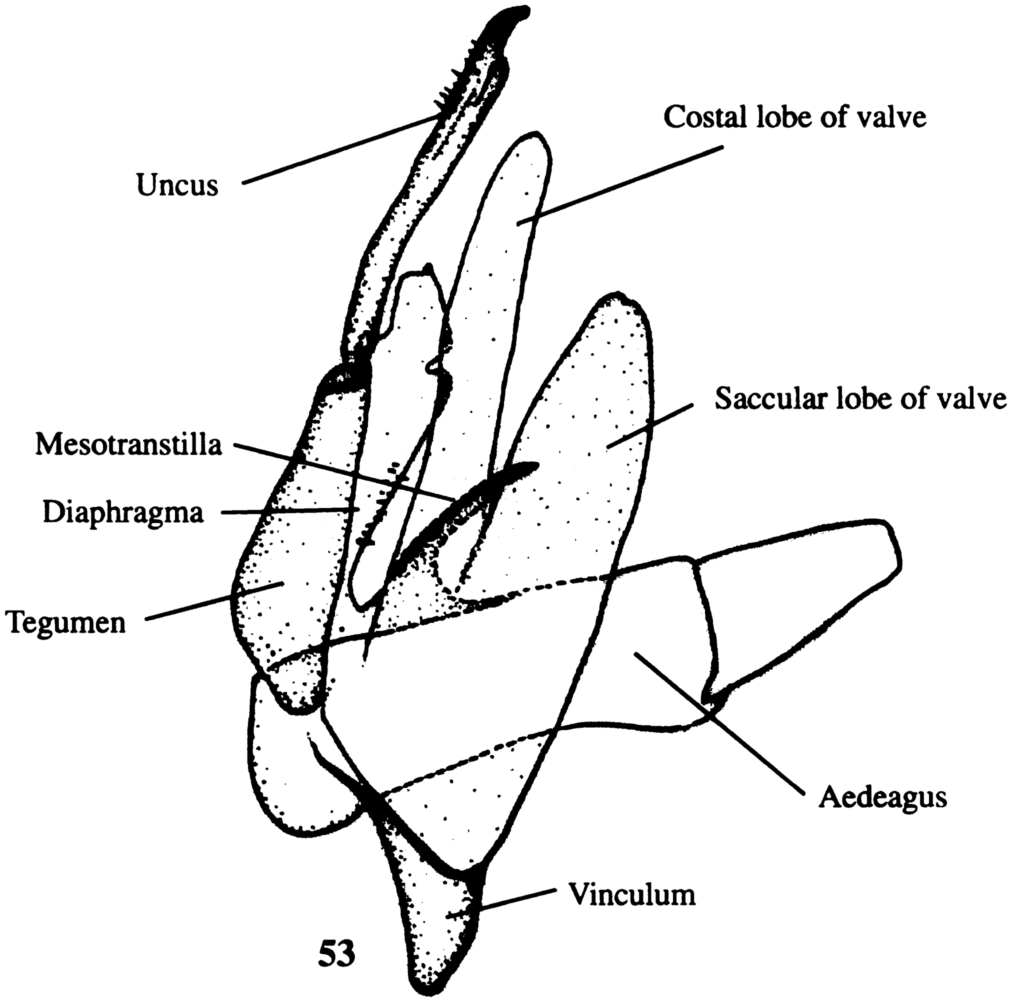
Figures 41-45. Female genital morphology of Momphinae. 41) Genitalia of *Anybia* showing infolded sclerotized ductus bursae (modified from Koster and Biesenbaum 1994). 42) Ductus bursae of *Mompha* (*Laverna*) sp (semi-schematic). 43) Ostial plate of *stellella* group (semi-schematic). 44) Ostial plate of *Mompha* (*Laverna*) *farinacea*. 45) Ostial plate of *Mompha* (*Laverna*) *rufocristatella*.



Figures 46-49. Signa of Coleophoridae. 46-47) Signum of Momphinae, showing serrated teeth. 48) Signum of Blastobasidae (modified from Adamski and Brown 1989). 49) Signum of Coleophoridae (modified from Landry and Wright 1996).



Figures 50-52. Female genitalic features of Momphinae. 50) Female ductus bursae of *Mompha (Laverna) lacteella* (modified from Koster 1994). 51) Typical ovipositor morphology of Momphinae (semi-schematic). 52) Lateral aspect of ovipositor lobes of *Lophoptilus (Cyphophora) locupletella.*



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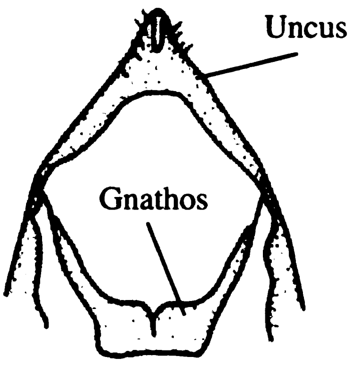

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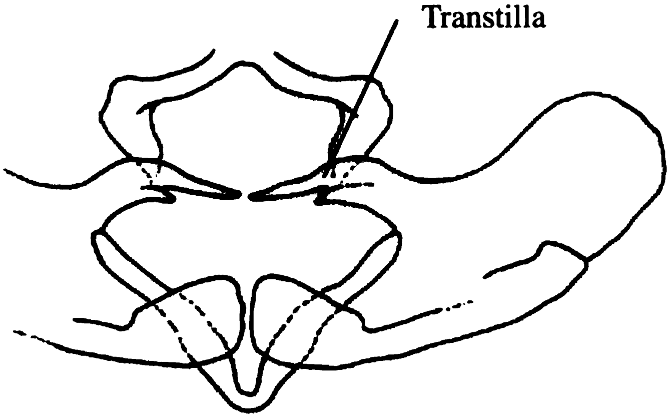

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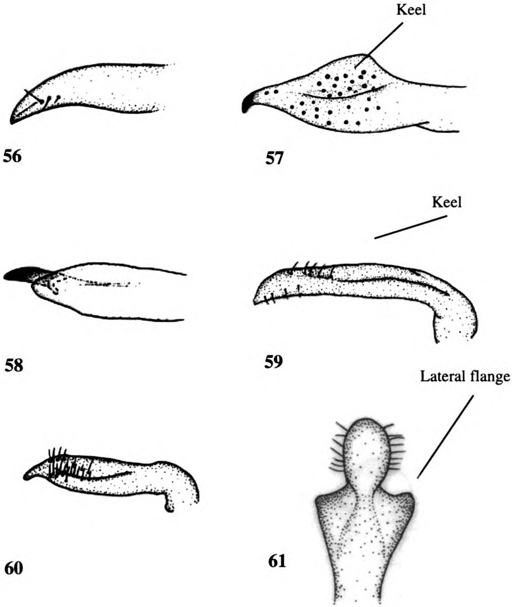
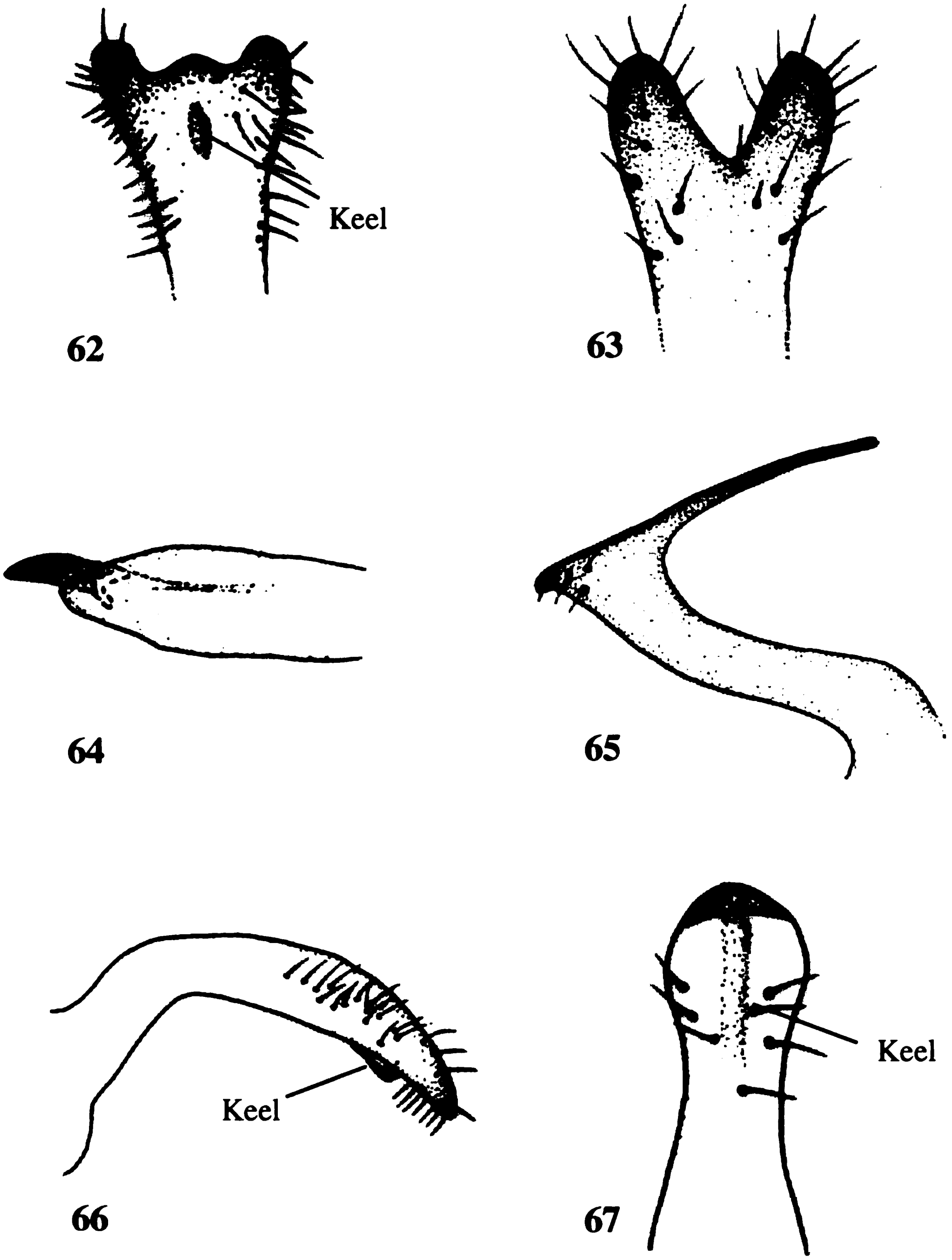
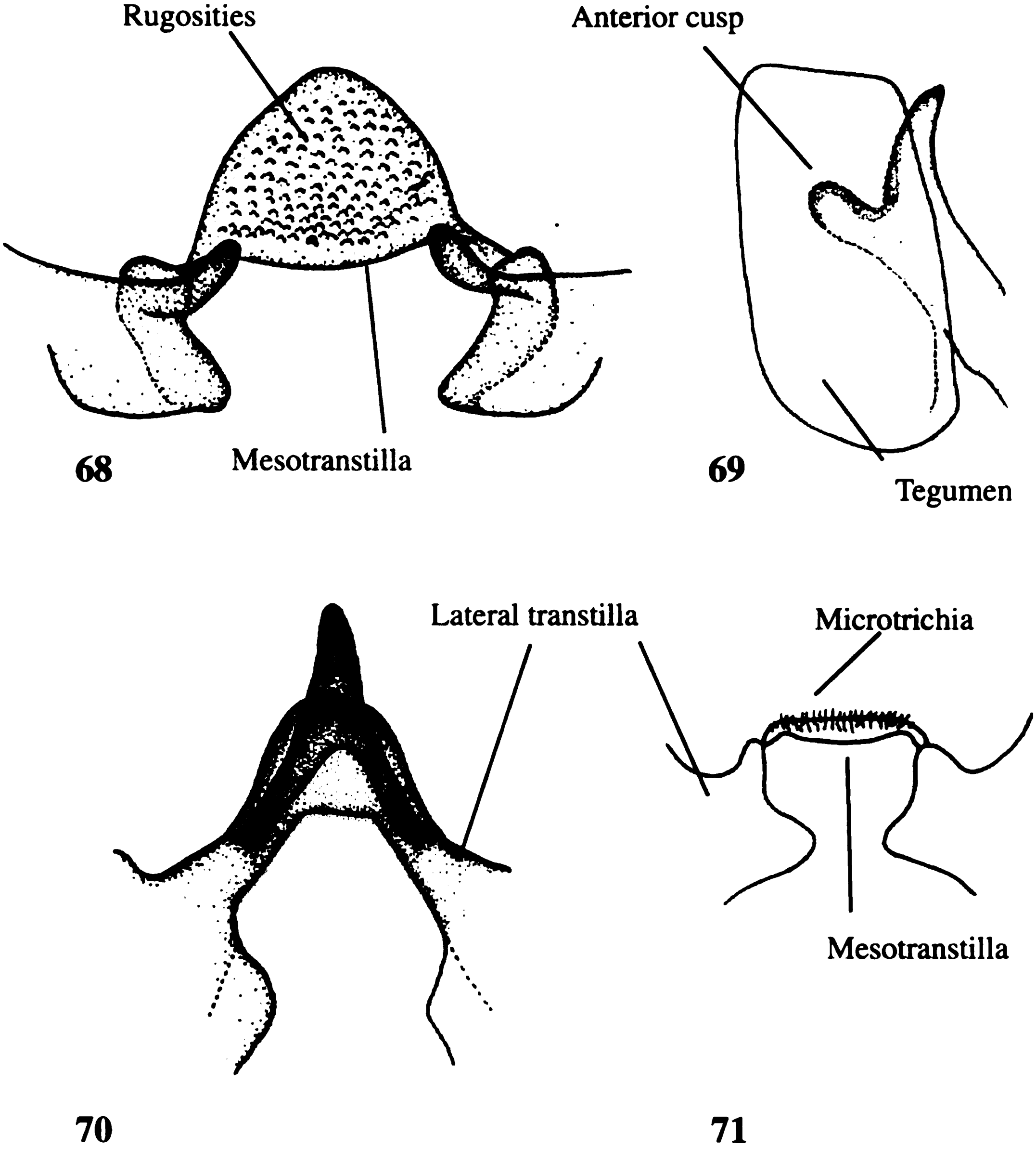
Figures 53-55. 53) Lateral aspect of *Mompha* (*Laverna*). 54) Tegumen, gnathos and uncus of Blastobasinae (modified from Adamski and Brown 1989). 55) Valve of *Coleophora* showing detail of transtilla (modified from Landry and Wright 1996).



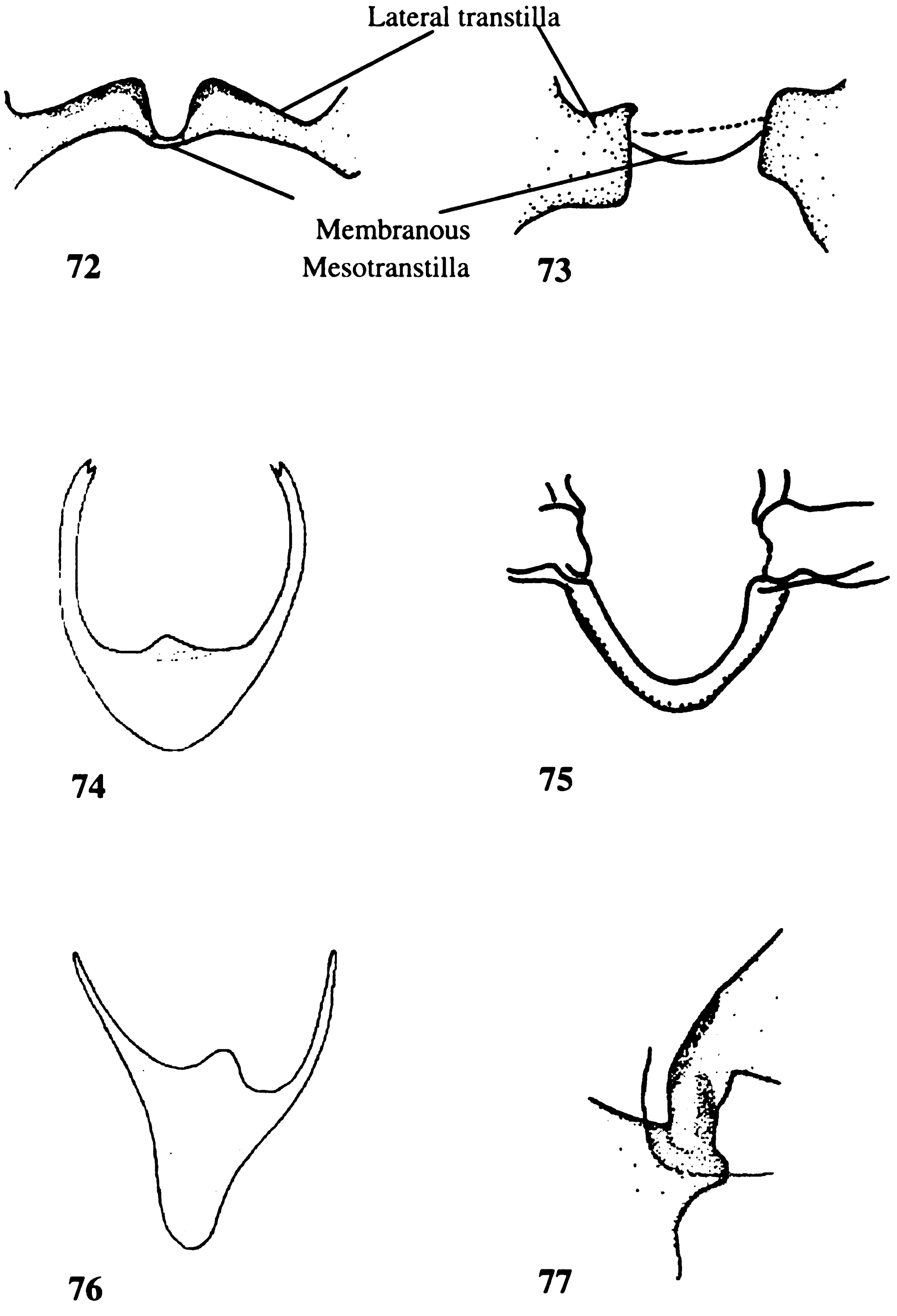
Figures 56-61. Details of apex of uncus in Momphinae (all perspectives are lateral with exception of Figure 61). 56) *Lophoptilus (Lophoptilus) terminella.* 57) *Lophoptilus (Lophoptilus) cephalonthiella.* 58)Generalized feature of the *Mompha (Laverna) divisella* group. 59) Generalized feature of *Mompha (Laverna).* 60) Generalized features of *Mompha (Laverna) propinquella* group. 61) Ventral aspect of uncus *Mompha (Laverna) definitella.*



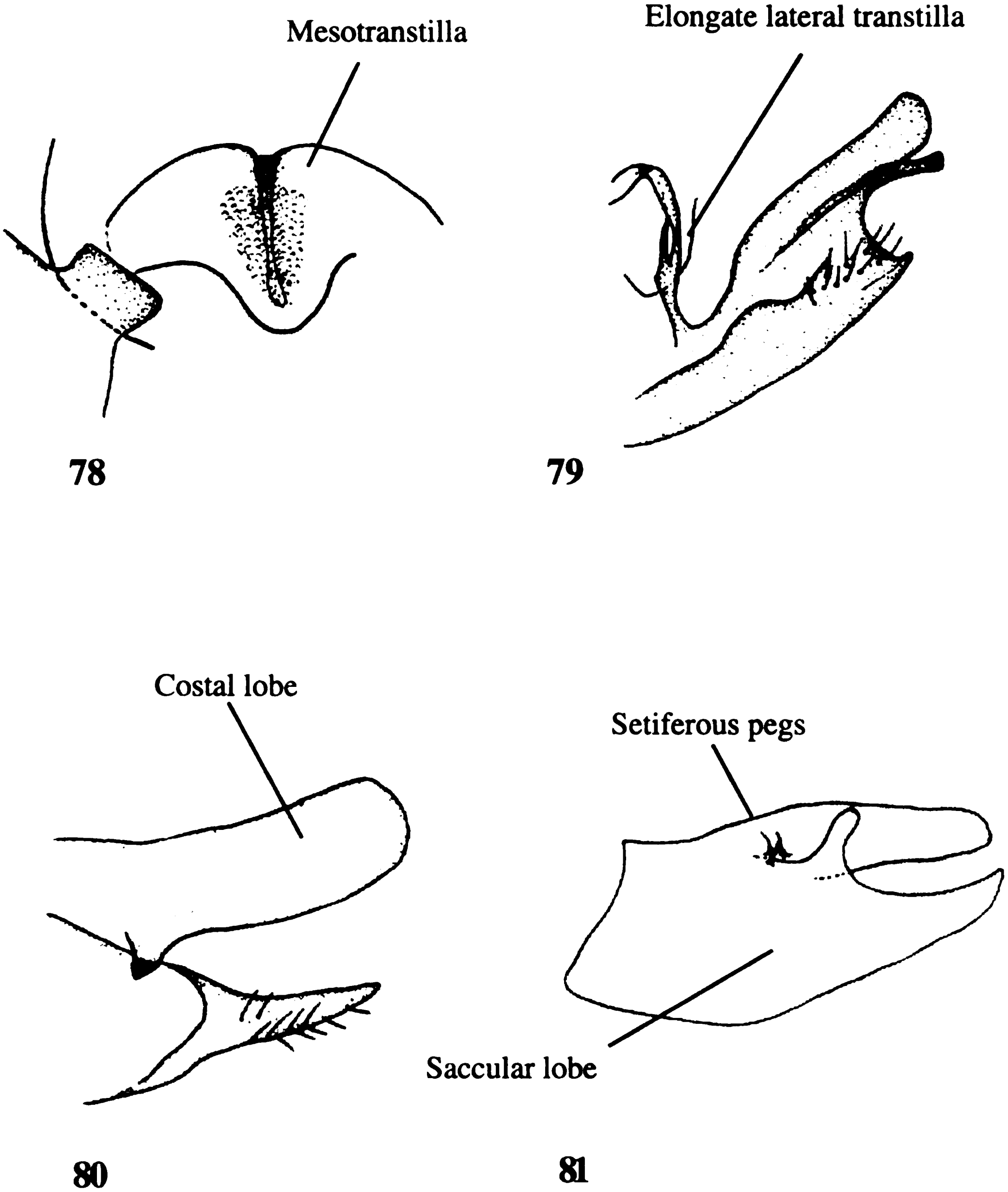
Figures 62-67. Uncus features of Momphinae. 62-63) Generalized uncus of the *stellella* group of *Mompha* (*Laverna*). 64) Generalized uncus of *Mompha* (*Laverna*) *divisella* group. 65) Uncus of *Lophoptilus* (*Lophoptilus*) nsp2. 66) Lateral aspect of uncus of *stellella* group of *Mompha* (*Laverna*). 67) Uncus of *Lophoptilus* (*Lophoptilus*) *terminella*.



Figures 68-71. Features of the transtilla in Momphinae. 68) Transtilla of *Mompha* (*Laverna*) *circumscriptella*. 69) Generalized features of *Mompha* (*Laverna*) *stellella* group showing anterior cusp of mesotranstilla, lateral aspect. 70) Generalized features of *Mompha* (*Laverna*) *stellella* group. 71) Mesotranstilla of *Lophoptilus* (*Cyphophora*).



Figures 72-77. Transtillar complex and vincula of Gelechioidea. 72) Transtillar complex of *Lophoptilus* (*Lophoptilus*). 73) Membranous transtillar complex of *Lophoptilus* (*Lophoptilus*). 74) Vinculum of *Mompha* (*Laverna*). 75) Vinculum of Blastobasinae, modified from Adamski and Brown (1989). 76) Vinculum of *Lophoptilus* (*Lophoptilus*) nsp2). 77) Lateral transtillar arms of *Mompha* (*Laverna*).



Figures 78-81. Male genitalia of Momphinae. 78) Transtillar complex of *Lophoptilus* (*Cyphophora*) *eloisella*. 79) Valve and transtilla of *Mompha* (*Laverna*)*murtfeldtella*. 80) Valve of *Mompha* (*Mompha*) complex. 81) Valve of *Lophoptilus* (*Lophoptilus*) *achylognoma*.

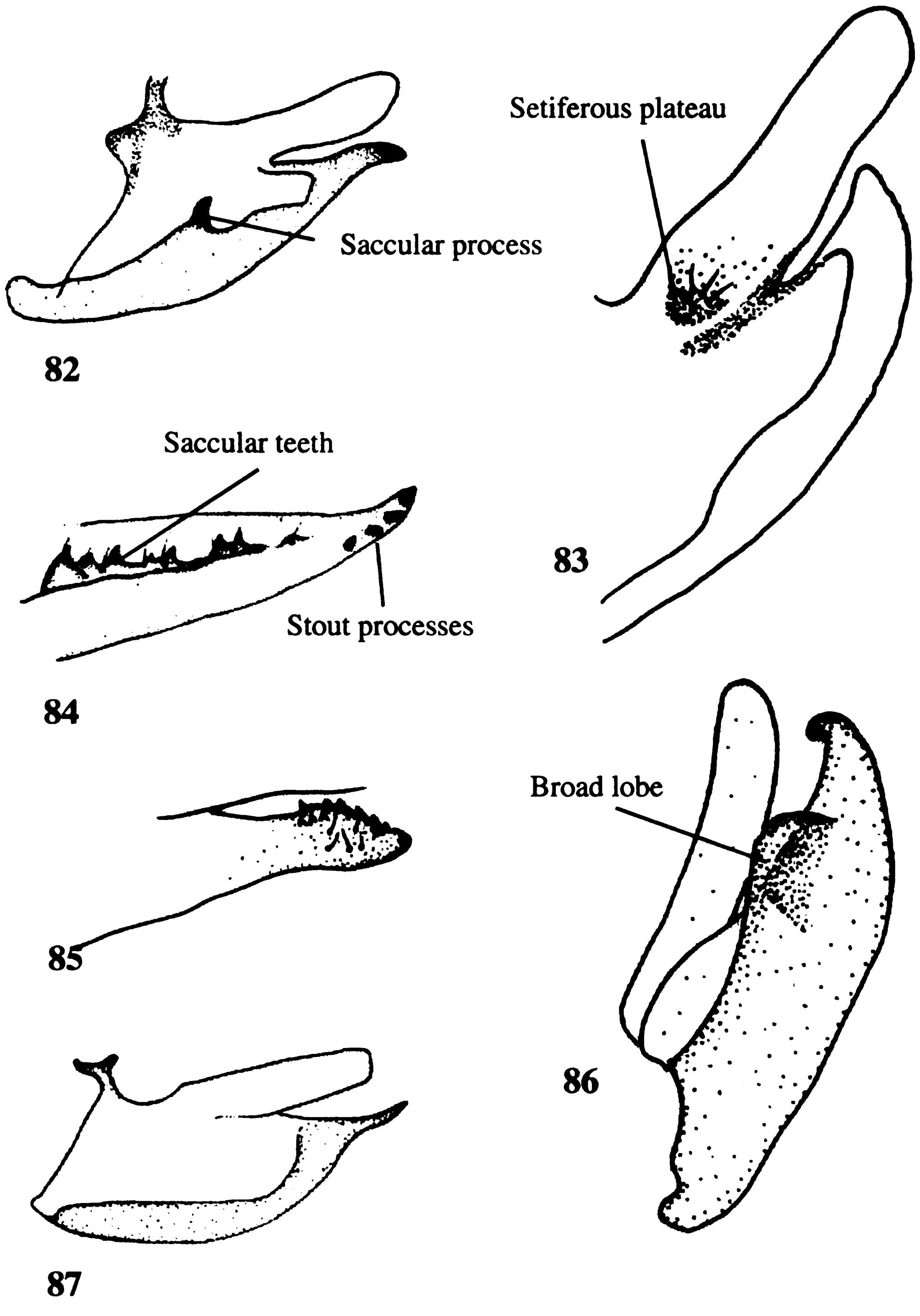
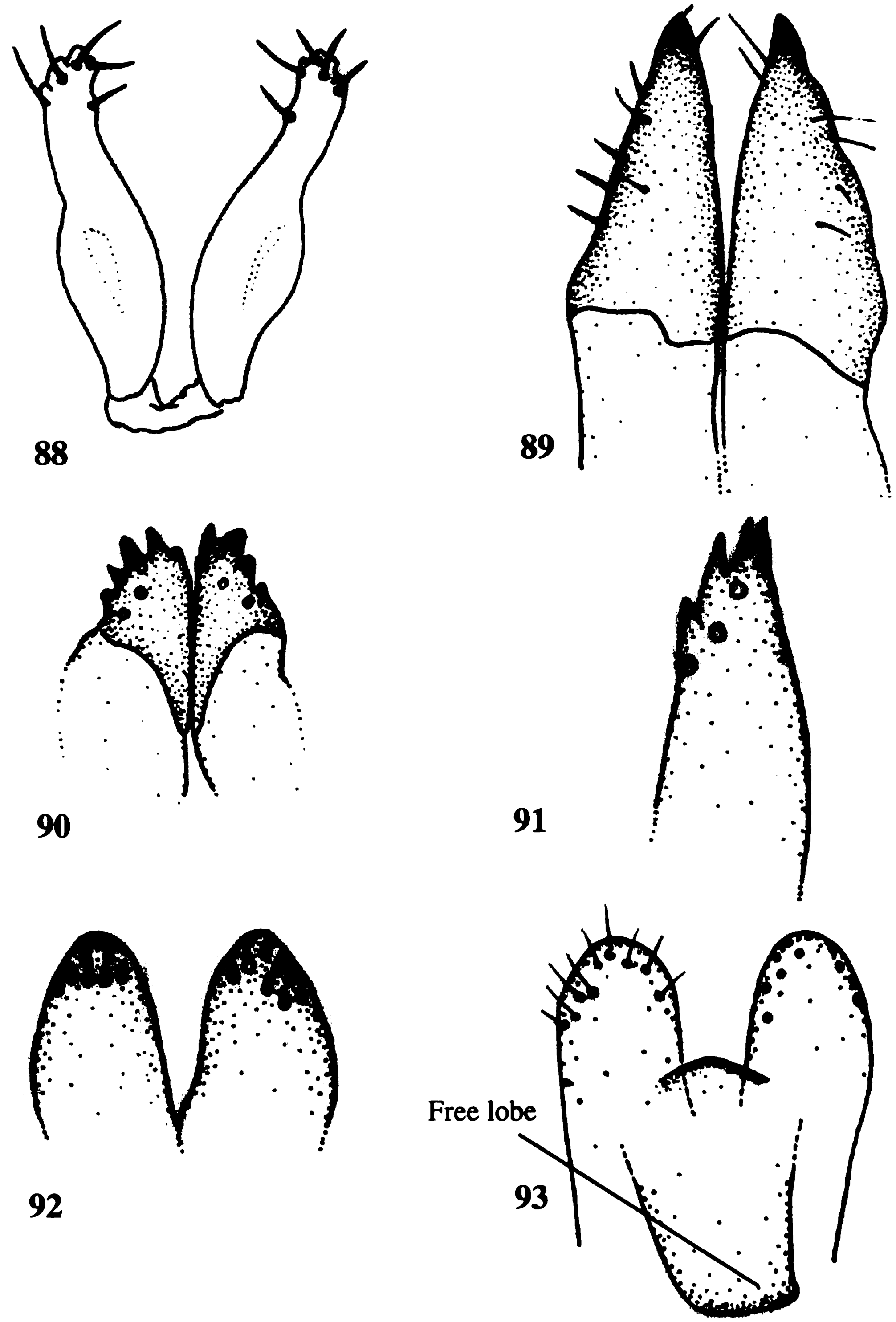
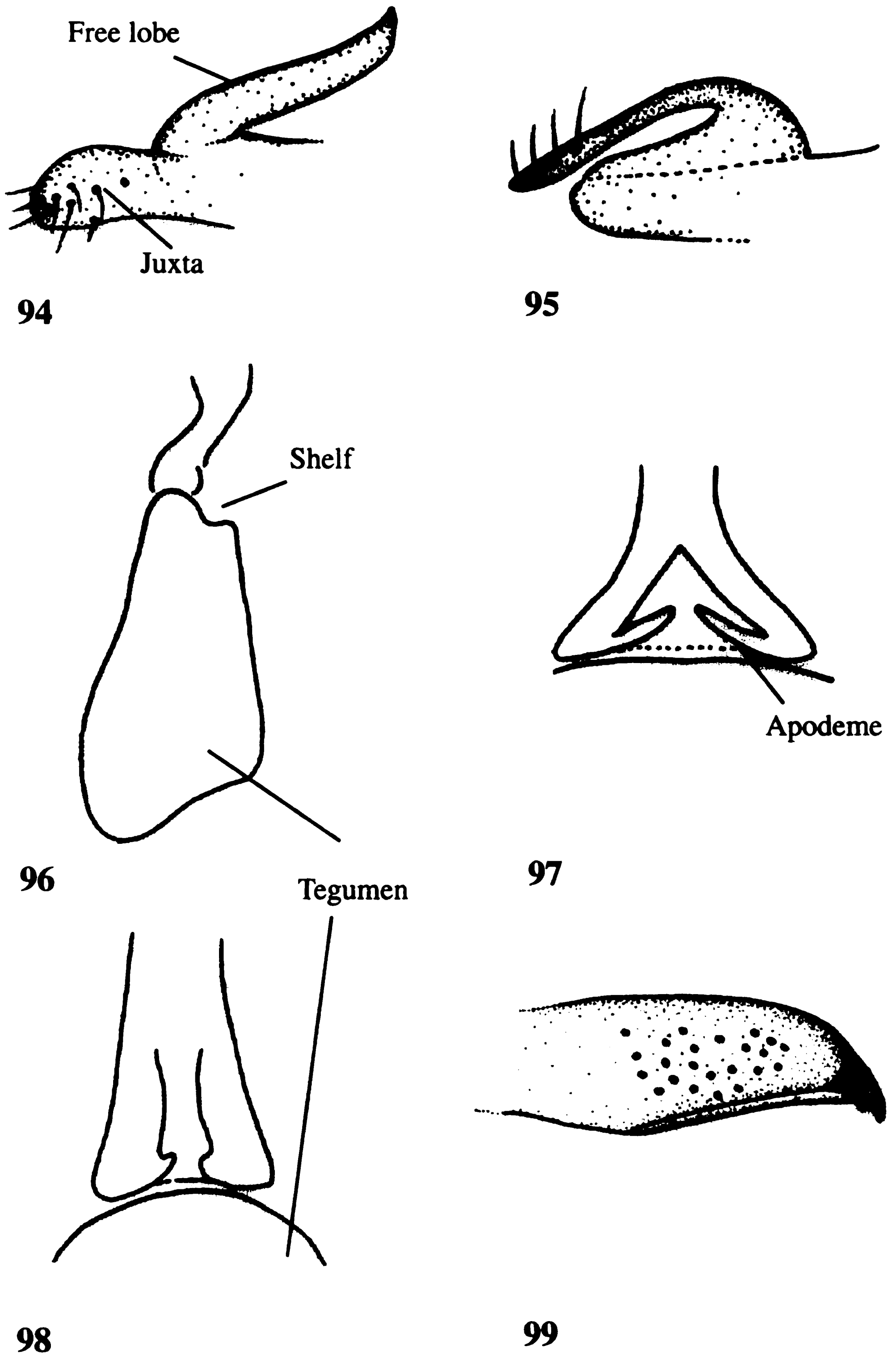


Figure 82-87. Male genitalia of Momphinae. 82) Valve of *Mompha* (*Laverna*) *stellella.* 83) Valve of *Lophoptilus* (*Cyphophora*). 84) Saccular lobe of valva of *Mompha* (*Laverna*) *circumscriptella.* 85) Sacculus of *Mompha* (*Laverna*) *claudiella.* 86) Valve of *Lophoptilus* (*Lophoptilus*) *raschkiella.* 87) Valve of *Mompha* (*Laverna*) *propinquella.*



Figures 88-93. Juxta of Momphinae. 88) Juxta of *Mompha* (*Laverna*) *ochraceella*. 89) Juxta of *Mompha* (*Laverna*) *claudiella*. 90) Juxta of *Mompha* (*Laverna*) *circumscriptella*. 91) Juxta of *Lophoptilus* (*Lophoptilus*). 92) Juxta of *Mompha* (*Laverna*) *fulvescens*. 93) Juxta of *Anybia langiella*.



Figures 94-99. Male genitalia of Momphinae. 94) Lateral aspect of *Anybia langiella*. 95) Lateral aspect of *Lophoptilus* (*Lophoptilus*) nsp6. 96) Lateral aspect of *Lophoptilus* (*Lophoptilus*) *cephalonthiella* showing dorsal flatregions of tegumen. 97) Generalized articulation of basal uncus (Momphinae). 98) Uncus articulation of *Lophoptilus* (*Lophoptilus*) *cephalonthiella*. 99) Apex of uncus of *Mompha* (*Laverna*) *farinacea*.

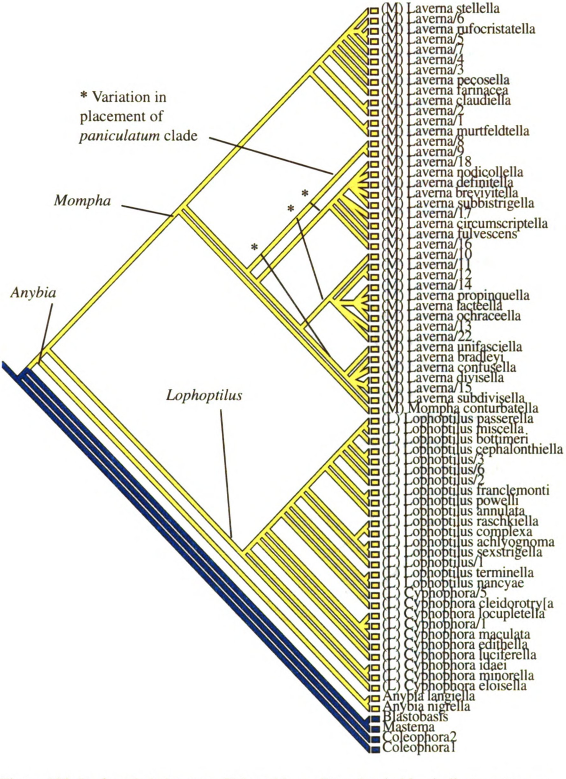


Figure 100. Preferred cladogram of Momphinae. Branches in blue indicate outgroup, branches in yellow indicate the subfamily Momphinae. Major differences among the 24 most parsimonious reconstructions were the result of uncertain placement of the *paniculatum* group.

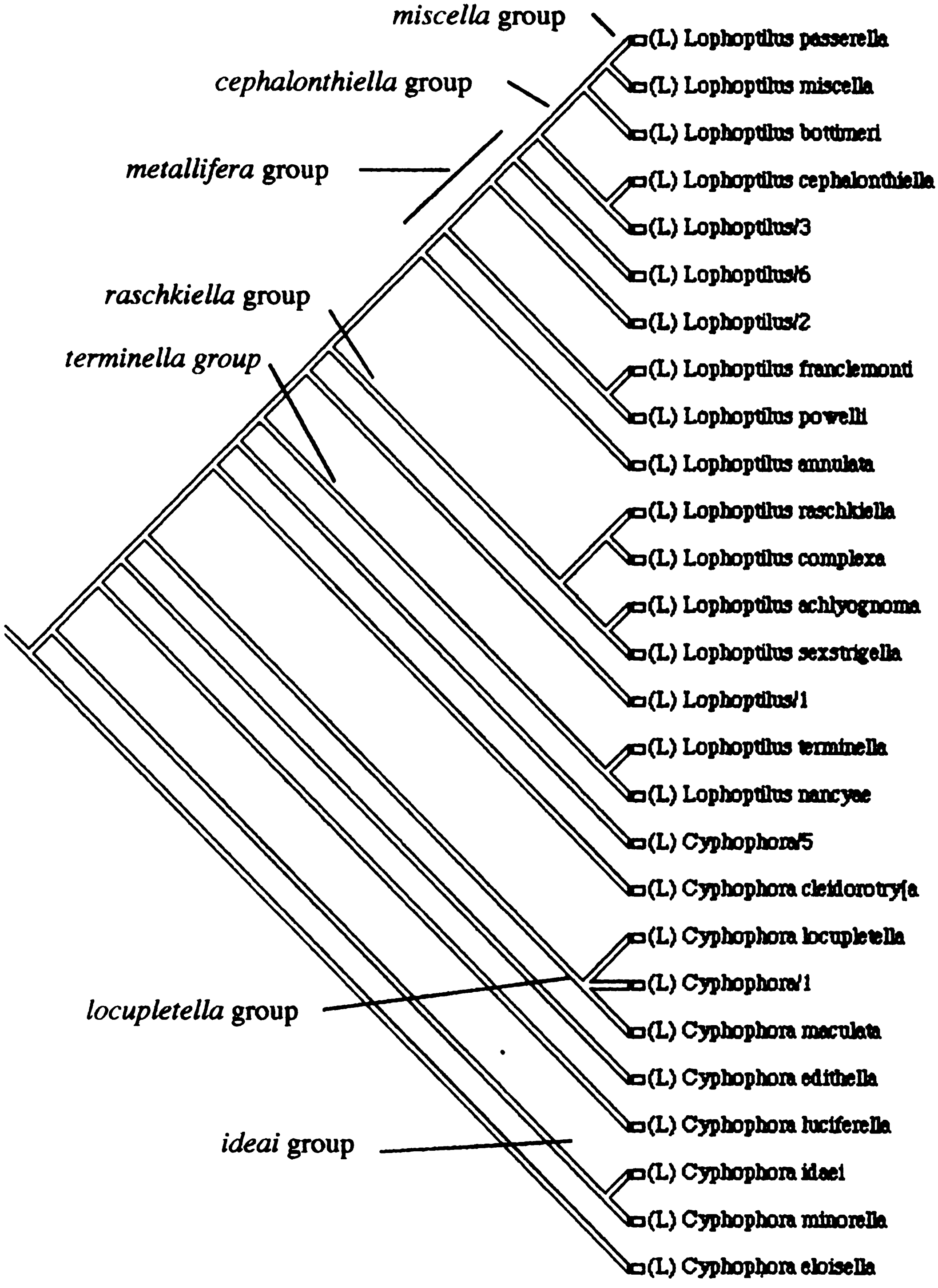


Figure 101. Preferred cladogram of *Lophoptilus*. Branches are labelled as to the group or clade as identified in the cladistic treatment of *Lophoptilus*.

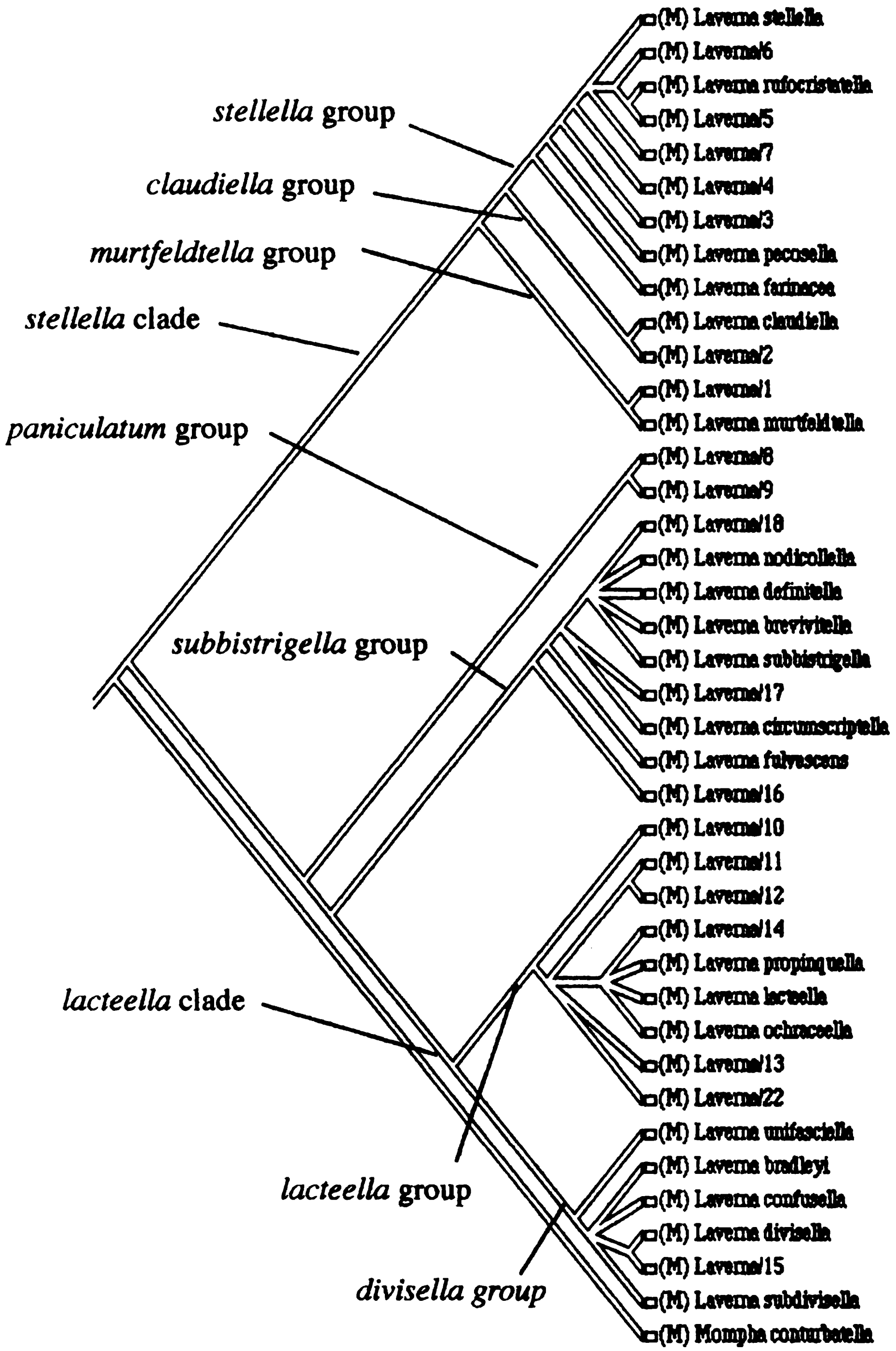


Figure 102. Preferred cladogram of *Mompha*. Branches are labelled as to the group or clade as identified in the cladistic treatment of *Mompha*.

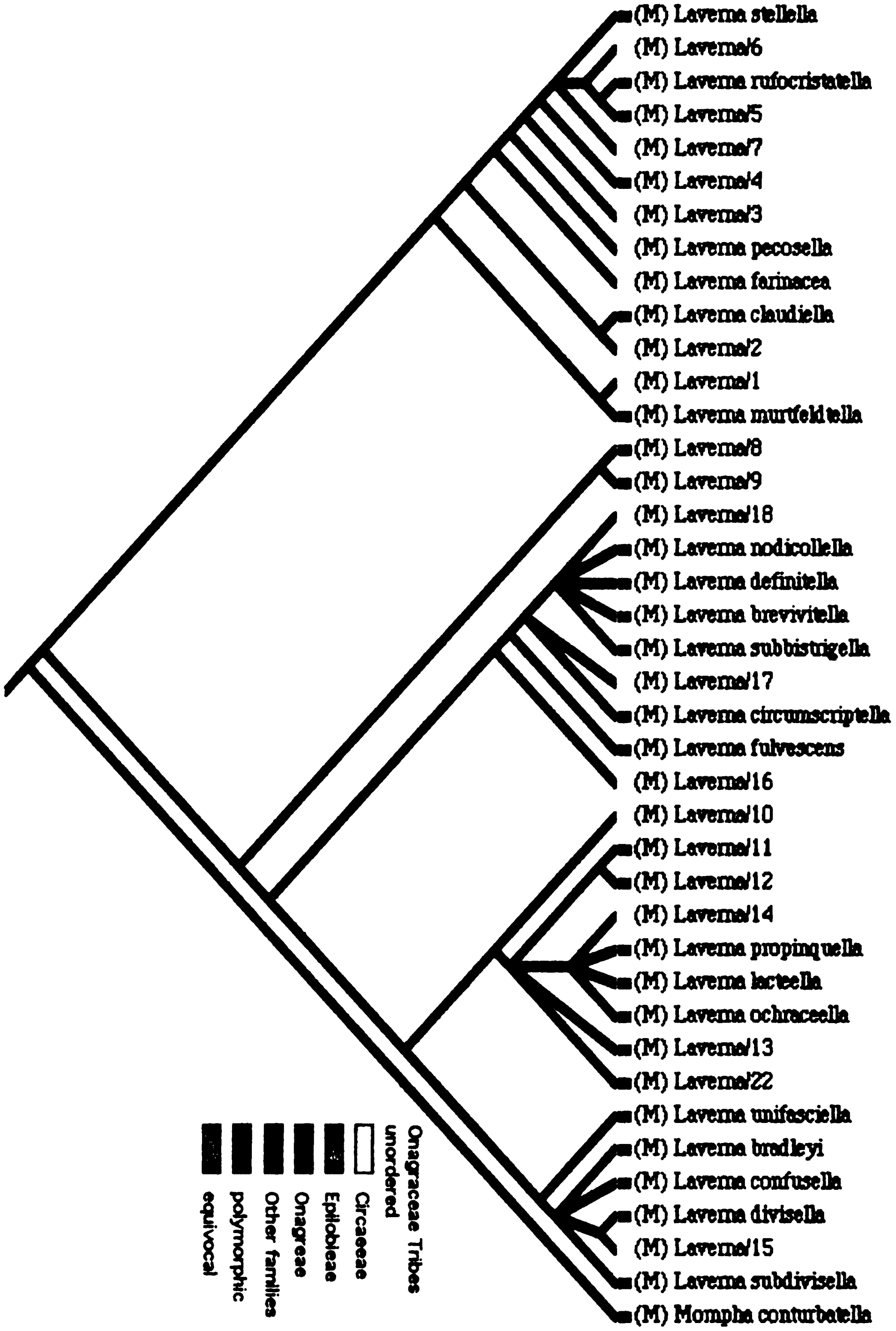


Figure 103. Patterns of tribal host associations in the *Mompha* clade on Onagraceae. Boxes next to species names indicate known host associations. Numbers in taxon names refer to undescribed species. Branch shading indicates predicted ancestral condition.

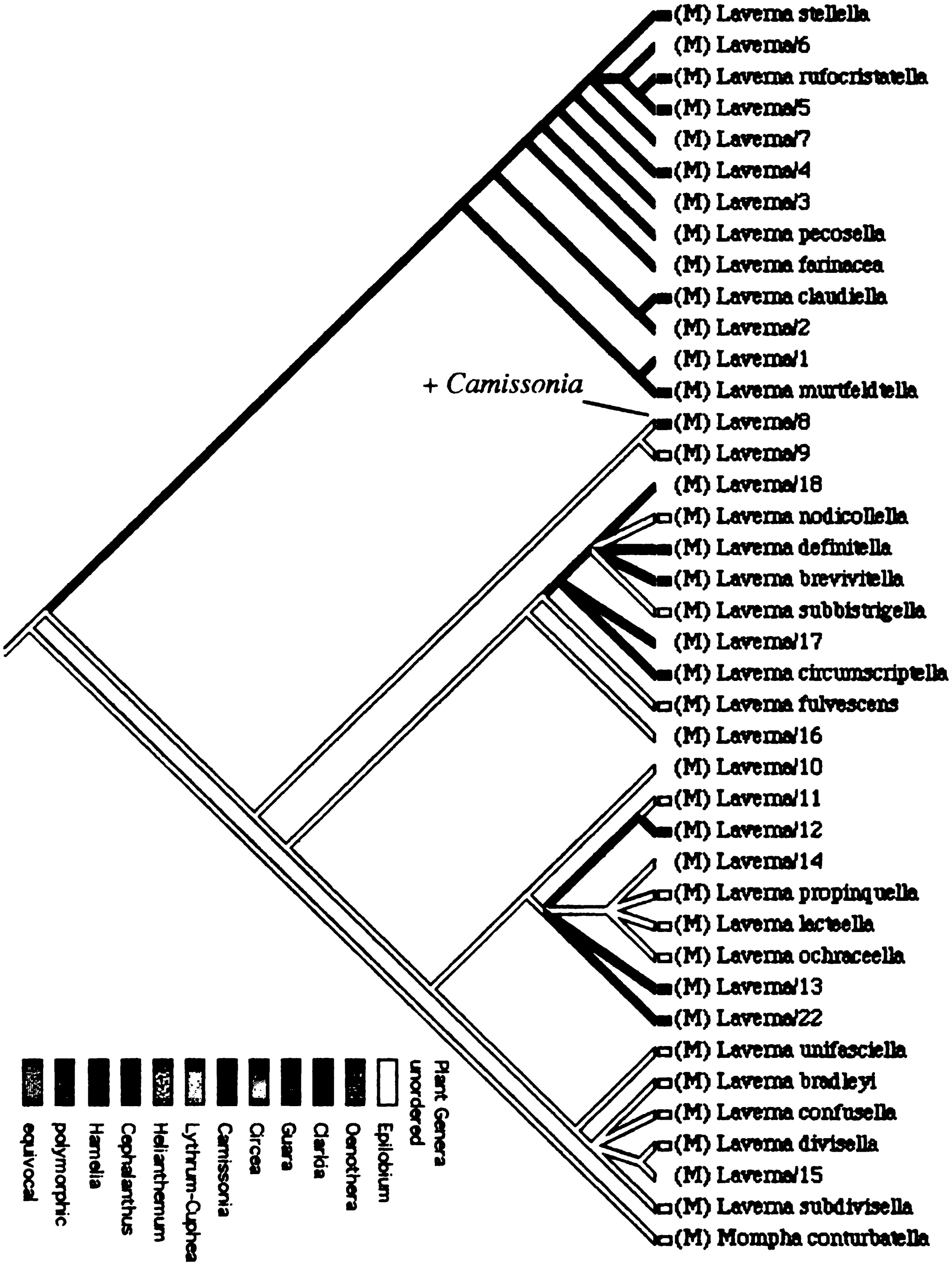


Figure 104. Pattern of generic host association in the *Mompha* clade. Boxes next to species names indicate known host associations. Numbers in taxon names refer to undescribed species. Branch shading indicates predicted ancestral condition. *Mompha* (*Laverna*) nsp8 is polymorphic for *Camissonia* and *Epilobium*, but may represent a species complex.

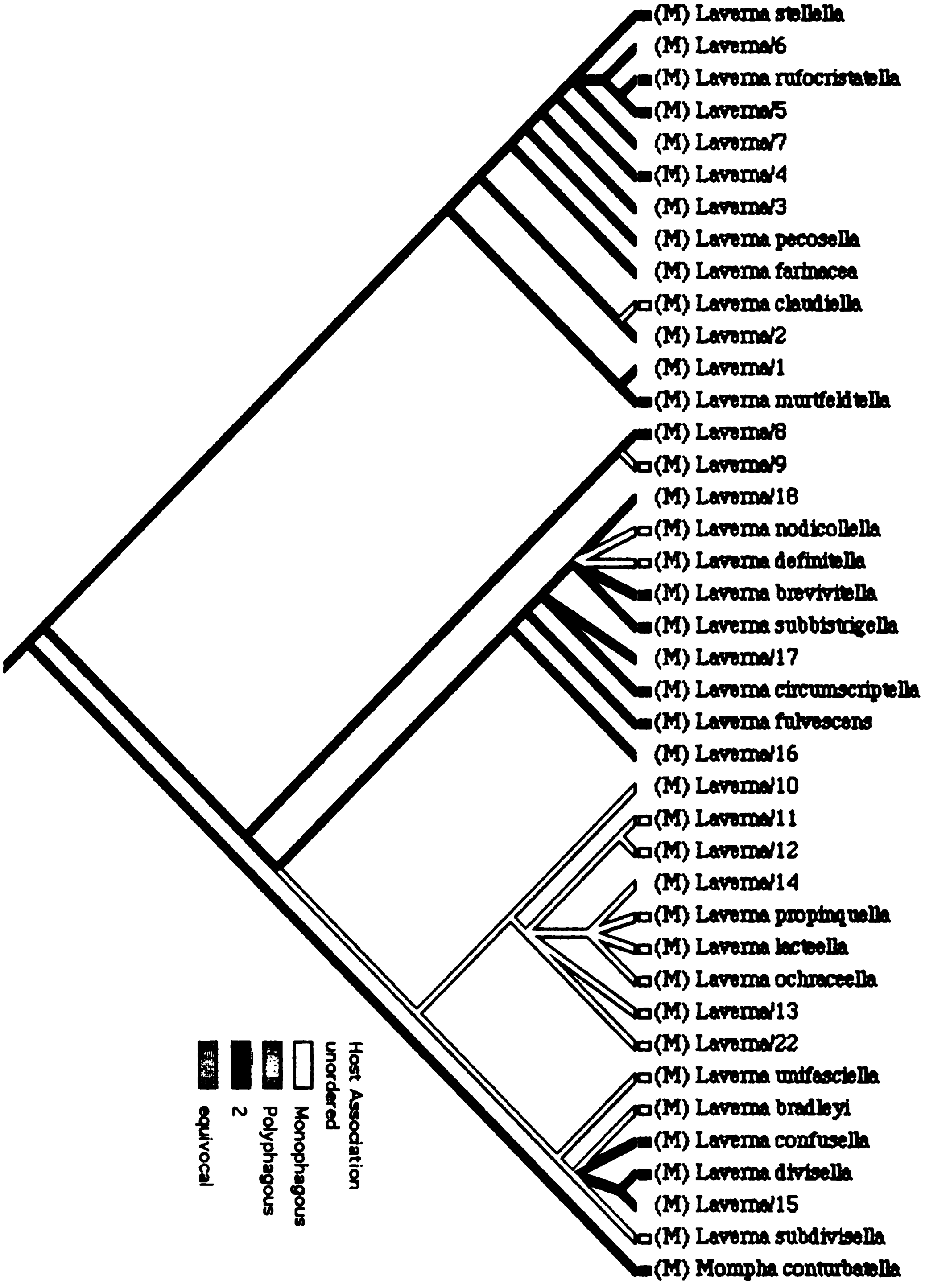


Figure 105. Pattern of phytophagy in the *Mompha* clade. Boxes next to species names indicate known host associations. Number in species names refer to undescribed taxa. Branch shading indicates predicted ancestral condition. Polyphagous = oligophagous.

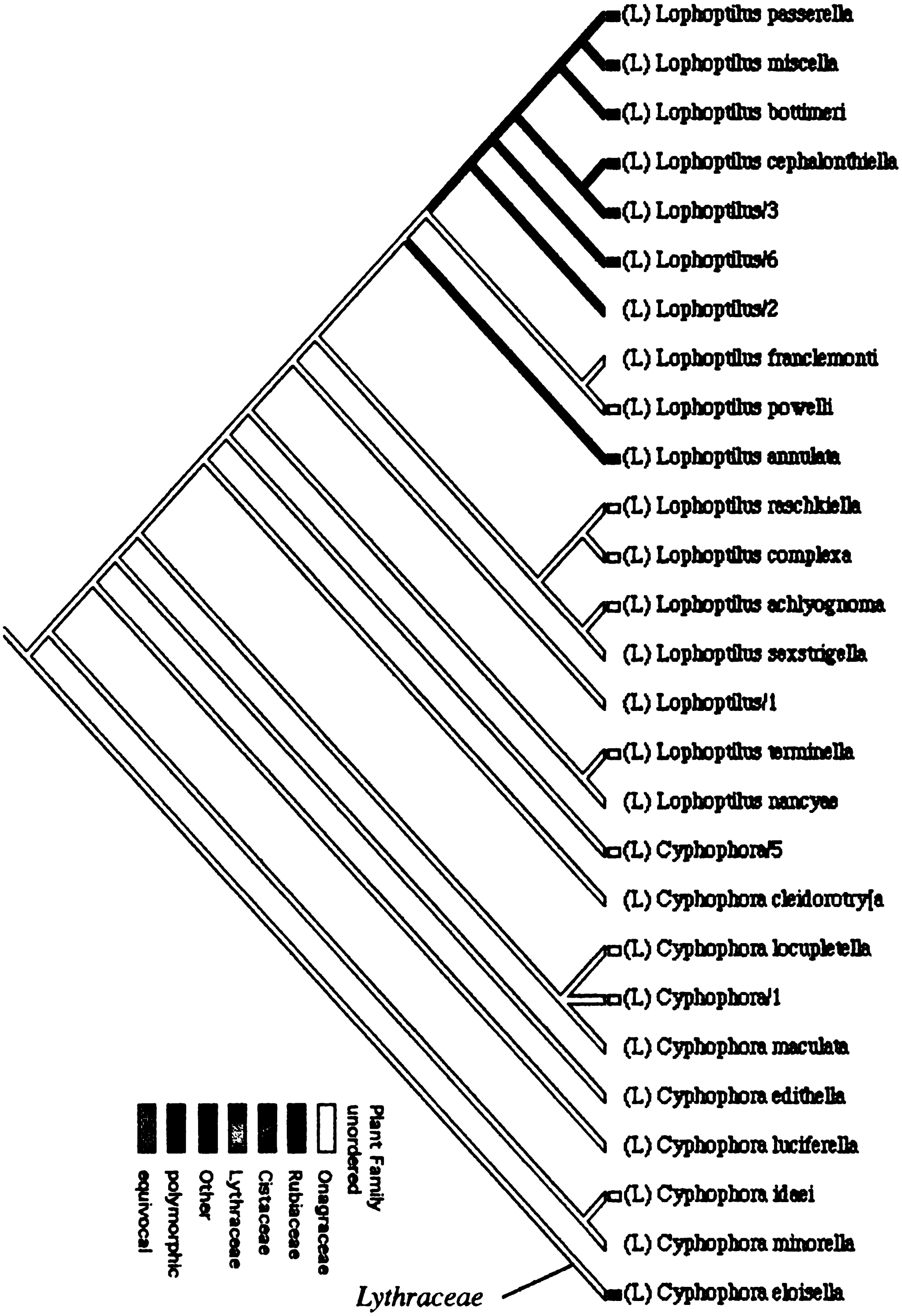


Figure 106. Plant family associations for species in the *Lophoptilus* clade. Boxes next to species names indicate known host associations. Numbers in taxa names refer to undescribed species. Branch shading indicates predicted ancestral condition.

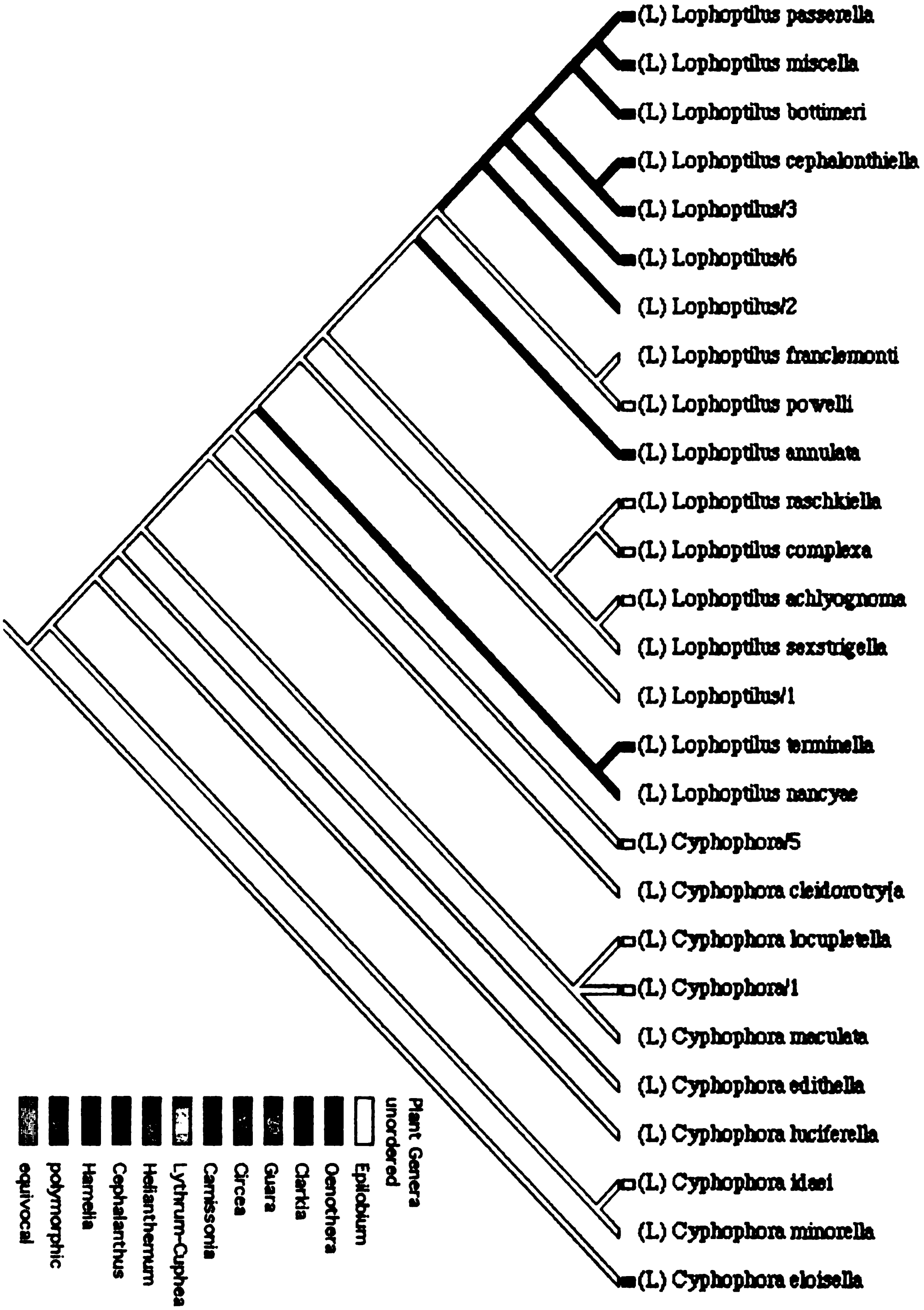


Figure 107. Patterns of generic host association in the *Lophoptilus* clade. Boxes next to species names indicate known host associations. Numbers in taxa names refer to undescribed species. Branch shading indicates predicted ancestral condition.

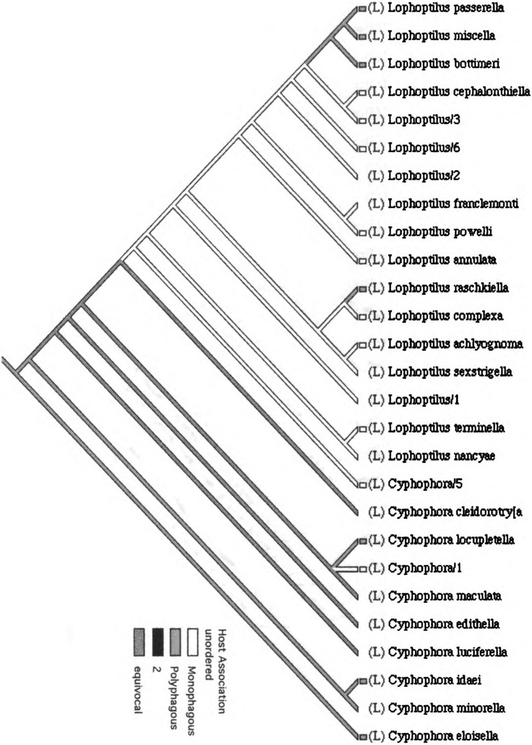


Figure 108. Patterns of phytophagy in the *Lophoptilus* clade. Boxes next to species names indicate known host associations. Numbers in taxa names refer to undescribed species. Branch shading indicates predicted ancestral condition. Polyphagous= oligophagous.

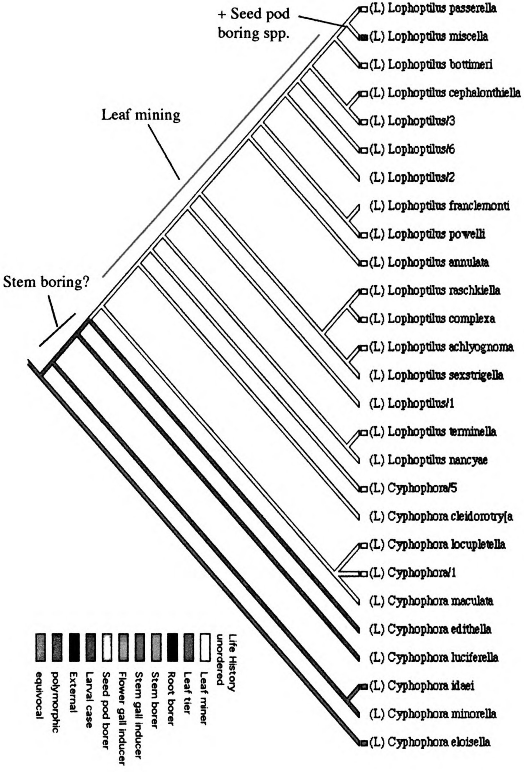


Figure 109. Patterns of life history strategy in the *Lophoptilus* clade. Boxes next to species names indicate known host associations. Numbers in taxa names refer to undescribed species. Branch shading indicates predicted ancestral condition.

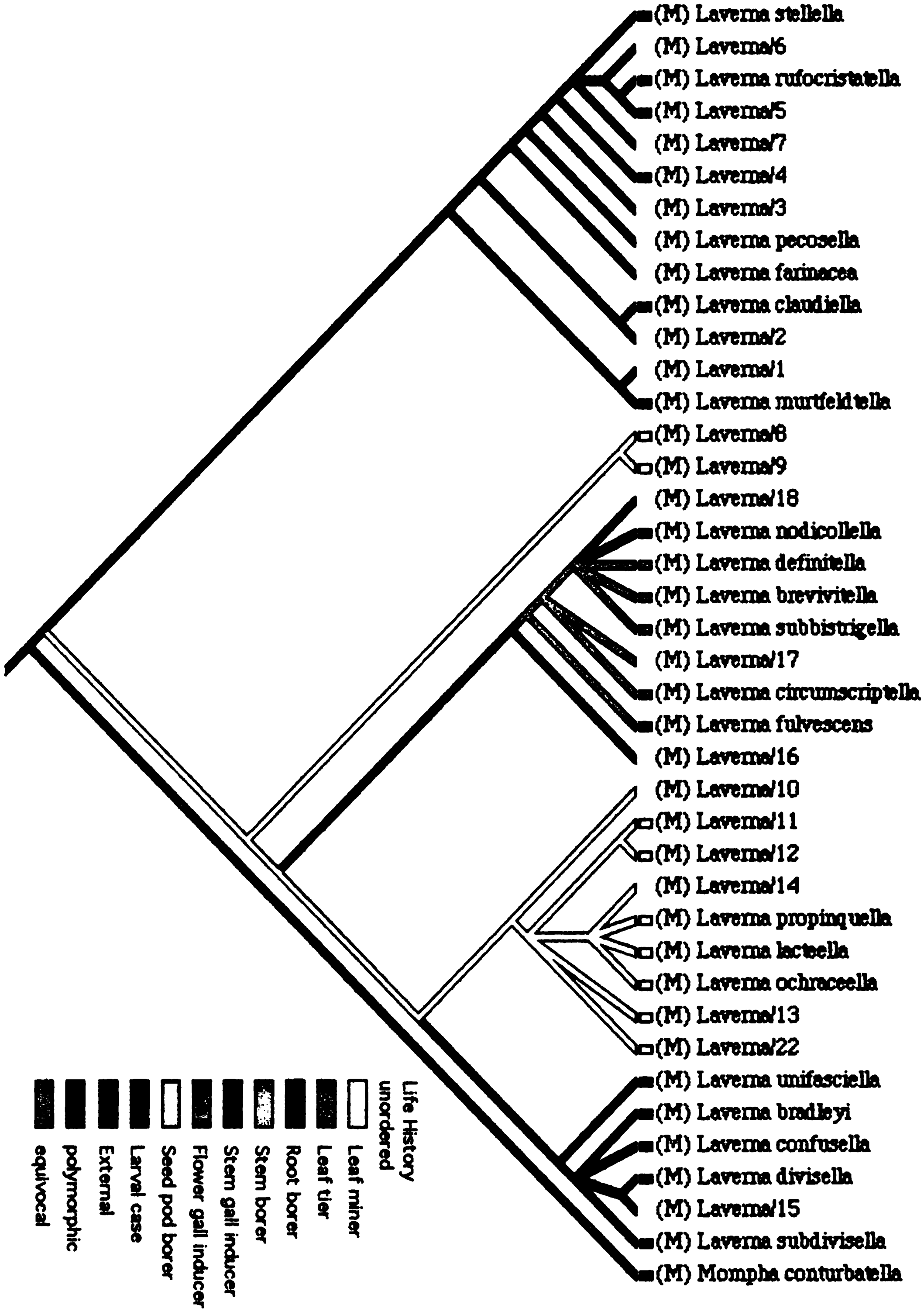


Figure 110. Life history strategy for species in the *Mompha* clade. Boxes next to species names indicate known host associations. Numbers in species names refer to undescribed species.

APPENDIX

APPENDIX

Character Codes for Cladistic Analysis of Momphinae

Mompha stellella	1002111001 0000111121 0003411002 0010001110 2120200021 0001100001 1
Mompha (*L.*) nsp6	1002111001 0000111121 0003411002 1010001110 2120200021 0001100001 1
Mompha (*L.*) nsp3	1002111001 0000111121 0003411002 0010101110 2020200021 0001100001 1
Mompha (*L.*) nsp4	1002111001 0000111121 0003411002 0010001110 2020200021 0001100001 1
Mompha rufocristatella	1002111001 0000111121 0003411002 1010101110 2120200021 0001100001 1
Mompha (L.) nsp5	1002111001 0000111121 0003411002 1010101110 2120200021 0001100001 1
Mompha (*L.*) nsp7	1002111001 0000111121 0003411002 0010001110 2120200021 0001100001 1
Mompha pecosella	1002111001 0000111121 0003411001 0110101110 2120200021 0001100001 1
Mompha farinacea	1002111001 0000111121 0003421001 0110101110 2020200021 2001100001 1
Mompha (*L.*) nsp18	1002111001 0000111121 0003421011 0110001110 1010200000 1111100001 0
Mompha nodicolella	1002111001 0000111121 0003421011 0110001110 1010200000 1111100001 0
Mompha definitella	1002111001 0000111121 0003421011 0110001110 1010200000 1111100001 0
Mompha brevivetella	1002111001 0000111121 0003421011 0110001110 1010200000 1111100001 0

Mompha fulvescens	1002111001 0000111121 0003421001 0110001110 1010200000 1141100001 0
Mompha subbistrigella	1002111001 0000111121 0003421011 0110001110 1010200000 1111100001 0
Mompha (*L.*) nsp10	1002111001 0000111121 0003421001 0110000114 0010200002 1221100001 0
Mompha (*L.*) nsp17	1002111001 0000111121 0003421001 0110001110 1010200000 1111100001 0
Mompha circumscriptella	1002111001 0000111121 0003421001 0110001110 1010200000 1111100001 0
Mompha (*L.*) nsp8	1002111001 0000111121 0003411001 0110001110 0010200000 1041100001 0
Mompha (*L.*) nsp9	1002111001 0000111121 0003411001 0110001110 0010200000 1041100001 0
Mompha (*L.*) nsp11	1002111001 0000111121 0003411001 0110001114 3010200002 1221100001 0
Mompha (*L.*) nsp12	1002111001 0000111121 0003411001 0110001114 3010200002 1221100001 0
Mompha (*L.*) nsp14	1002111000 0000111121 3003411001 0110001114 3010200002 1021100001 0
Mompha (*L.*) nsp13	1002111001 0000111121 0003411001 0110001114 3010200002 1021100001 0
Mompha propinquella	1002111001 0000111121 3003411001 0110001114 3010200002 1021100001 0
Mompha lacteella	1002111001 0000111121 3003411001 0110001114 3010200002 1021100001 0
Mompha ochraceella	1002111001 0000111111 3003411001 0110001114 3010200002 1021100001 0
Mompha (*L.*) nsp20	1002111001 0000111121 0006421001 1010001110 0010300006 0001100001 1

Mompha murtfeldtella	1002111001 0000111121 0003421011 0110001110 0010300006 0001100001 1
Mompha claudiella	1002111?01 0000111121 0002421001 0110101110 0010200003 2001100001 1
Mompha (L.) nsp2	1002111?01 0000111121 0002421001 0110101110 0010200003 2001100001 1
Mompha unifasciella	1002111001 0000111121 0003421001 0111001110 0010200002 1021100001 0
Mompha bradleyi	1002111001 0000111121 0003421001 0111001110 4010200002 1021100001 0
Mompha confusella	1002111001 0000111121 0003421001 0111001110 4010200002 1021100001 0
Mompha divisella	1002111001 0000111121 0003421001 0111001110 4010200002 0021100001 0
Mompha subdivisella	1002111001 0000111121 0003421001 0111001110 4010200002 1021100001 0
Mompha (L.) nsp15	1002111001 0000111121 0003421001 0111001112 4010200002 0021100001 0
Mompha (L.) nsp16	1002111001 0000111121 0002621001 0110001110 1010200000 1041100001 0
Lophoptilus idaei	1000111001 0210111121 0002100101 0110001110 0130202000 0031000001 0
Lophoptilus minorella	1000111001 0210111121 0002100101 0110001110 1130202000 0031000001 0
Lophoptilus eloisella	1000111001 0211111121 0002100101 0110001110 0060200000 0001000001 0
Lophoptilus conturbatella	1002111001 0000111121 0002622001 0110001110 0010210000 0001100001 0
Lophoptilus passerella	1010111000 0110111021 0102200101 0110001110 0050200000 0001100002 0

Lophoptilus miscella	1010111000 0110111021 0102200101 0110001110 0050200000 0001100002 0
Lophoptilus bottimeri	1010111000 0110111021 0102200101 0110001110 0050200000 0001000002 0
Lophoptilus cephalonthiella	1010111000 0110111021 0016100101 0110000111 0050200000 0001000012 0
Lophoptilus (L.) nsp3	1010111000 0110111021 0016100101 0110000111 0050200000 0001000012 0
Lophoptilus (L.) nsp7	1000111000 0210111021 0002100101 0110001110 0130202000 0031100001 0
Lophoptilus (C.) nsp4	1000111001 0210111021 ?????????? ??????1110 0130202000 1031000001 0
Lophoptilus raschkiella	1010111000 0110110021 2002300001 0110001110 0140201014 0001100001 0
Lophoptilus complexa	1010111000 0110110021 2002300001 0110001110 0140201014 0001100001 0
Lophoptilus (L.) nsp1	1000111000 0110111021 ?????????? ??????1110 0140201000 0001100001 0
Lophoptilus achlyognoma	1010111000 0110110021 2002300001 0110001110 0140201100 0001100001 0
Lophoptilus sexstrigella	1010111000 0110110021 2002300001 0110001110 0140201100 0001100001 0
Lophoptilus annulata	1010111000 0110110021 0002100101 0110001110 0140201000 0001000001 0
Lophoptilus locupletella	1010111001 0210110321 2005300101 0110011110 0130200000 1031100001 0
Lophoptilus nsp1	1010111001 0210110321 2005300101 0110011110 0130200000 1031100001 0
Lophoptilus maculata	1010111001 0210110321 2005300101 0110011110 0130200000 1031100001 0

Lophoptilus terminella	1000111000 0110111021 0202100101 0110001110 0140202000 1031100001 0
Lophoptilus nancyae	1000111000 0110110021 0202100101 0110001110 0140202000 1031100001 0
Lophoptilus cleidorotrypa	1000111000 0210111021 1002100101 0110001113 0130202000 1031100001 0
Lophoptilus edithella	1000111001 0210111021 0002100101 0110001110 0130202000 1031100001 0
*Lophoptilu*s *langiella*	1000111101 0000111120 0002110001 0010101110 1040200000 0001110001 0
*Lophoptilu*s *nigrella*	100011???? ???0??112? 0003110001 0010100110 0010200000 0001110001 0
*Lophoptilu*s *franclemonti*	1000111000 0110110021 0002100101 0010001110 0040200000 0001000001 0
*Lophoptilu*s *powelli*	1000111000 0110110021 0002100101 0010001110 0040200000 0031000001 0
*Lophoptilu*s (*L.)* nsp6	1010111000 0110111021 0304501100 1010000110 0053200000 0001?20001 0
*Lophoptilu*s (*L.)* nsp2	1010111000 0110110021 0002100101 0110001110 5050200000 0001000001 0
Coleophorinae sp1	0100001000 0110001210 0001131200 0032000000 0000100005 0001101100 ?
Coleophorinae sp2	0100001000 0110001220 0001131200 0032001000 0000100005 0001101100 ?
Blastobasis	1100000011 100?010210 0000001000 1020000010 0002000000 2000030000 0
Mastema	1110000011 100?020210 0000001000 1020001010 0002000000 2000130100 0

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