

Connecting the dots: Spots and bands on the wings of *Lichenaula* Meyrick, 1890 (Lepidoptera: Gelechioidea: Xyloryctidae) share a uniform relationship with wing venation

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Abstract

Recent studies have shown that wing pattern in various lineages of microlepidoptera follows one of two predictive models. In the first, called the “alternating wing-margin” model, dark and light pattern elements straddle alternating veins along the costal margin of the wing. In the second, called the “uniform wing-margin” model, pattern elements of a single color straddle all veins along the costa. However, of the dozens of families and superfamilies of moths, a small minority have been studied in this context. In the present contribution, the relationship between wing pattern and wing venation is examined in *Lichenaula* Meyrick, 1890 (Gelechioidea: Xyloryctidae). Species of *Lichenaula* have wing pattern elements ranging from spots to bands to mottled textures, and they all conform to the uniform wing-margin model. No plausible support was found for the alternating wing-margin model. In previous studies, the relationship between pattern and venation along the dorsal wing margin has remained unclear due to loss of wing veins and confluence of pattern elements, but certain species of *Lichenaula*, especially *L. maculosa* (Turner, 1898), provide evidence that the uniform wing-margin model holds for the dorsum as well as the costa. Previous studies have found that ancestral wing veins continue to influence the development of wing patterns that follow the alternating wing-margin model, even if not expressed in the adult wing, but the wing patterns of *Lichenaula* suggest that this is not the case for the uniform wing-margin model. Instead, it appears that the only veins that determine the development of wing pattern in *Lichenaula* are those that are expressed in the adult wing. Considered in preliminary phylogenetic context, it appears that multiple transitions have occurred between the ancestral alternating wing-margin model and the more derived uniform wing-margin model.

Key words

Color pattern, development, evolution, homology, microlepidoptera, morphology, scales.

1. Introduction

The paraphyletic grade microlepidoptera contains tens of thousands of species of moths (VAN NIEUKERKEN et al. 2011), often small and brown; the typically diminutive size and drab coloration of these moths belies the tremendous diversity of their wing patterns. Many decades ago, various researchers studied the evolution of wing pattern

in microlepidoptera and, more specifically, the relationship between wing pattern and wing venation (BRAUN 1914; VAN BEMMEL 1916; LEMCHE 1935). This area of study is now experiencing a revival that began with the proposal of a predictive model based on moths in the family Tortricidae (BROWN & POWELL 1991; BAIXERAS 2002).

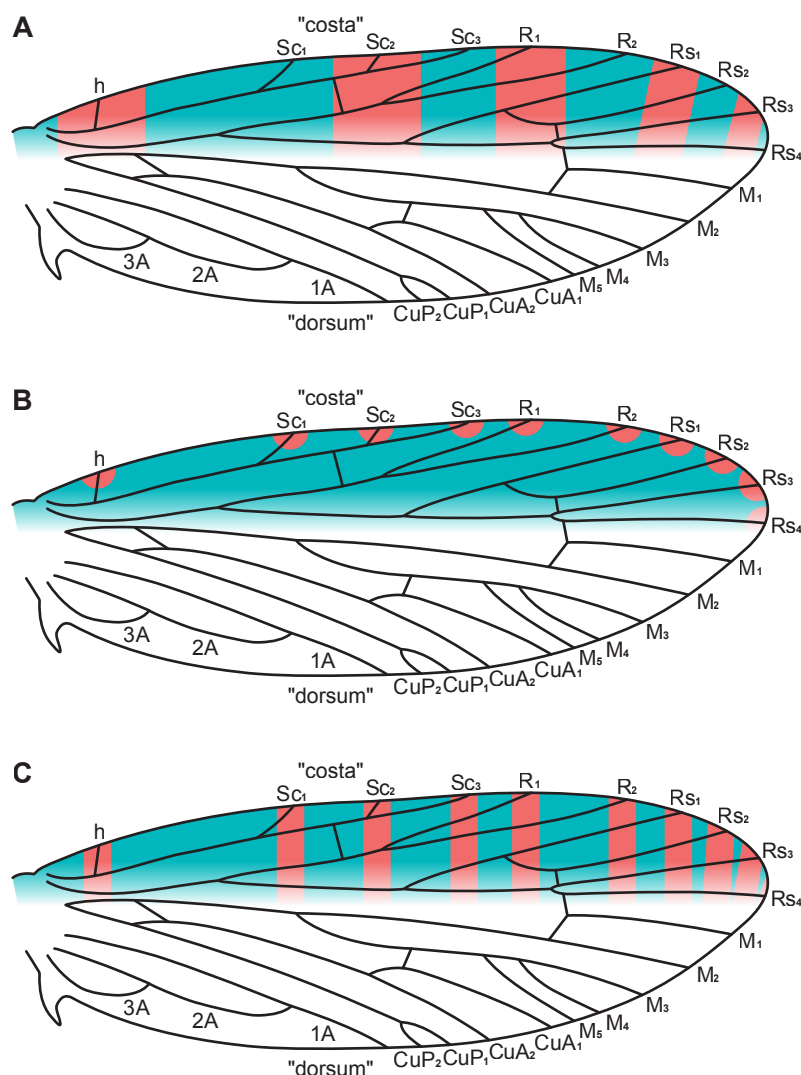


Fig. 1. The two variants of the “wing-margin” model. Either series of pattern elements – those illustrated in blue, or those illustrated in red – could develop a dark color. **A:** The original version of the model, called the “alternating wing-margin” model here. **B:** A hypothesized intermediate stage based on *Sabatinca demissa*. **C:** The “uniform wing-margin” model. The wing venation illustrated here is based on a recent update of the plesiomorphic groundplan for Lepidoptera (SCHACHAT & GIBBS 2016). — **Abbreviations:** h: humeral vein; Sc: subcosta; R: radius; Rs: radial sector; M: media; CuA: anterior cubitus; CuP: posterior cubitus; A: anals.

This model, now called the “alternating wing-margin” model, posits that microlepidopteran wing patterns are based on two alternating series of bands – one light, one dark – with each band straddling one vein along the costal margin of the wing (Fig. 1A). Support for this model has been found in various genera of Micropterigidae, a family that occurs within the most early-diverging lineage of Lepidoptera (SCHACHAT & BROWN 2015, 2016). The predictive power of this model was further bolstered by empirical confirmation of one of the model’s key assumptions, a primitive 3-branched Sc vein for Lepidoptera (SCHACHAT & GIBBS 2016).

However, the lepidopteran tree of life includes many dozens of microlepidopteran families other than Micropterigidae and Tortricidae (VAN NIEUKERKEN et al. 2011), and support for the alternating wing-margin model in these families has been equivocal thus far. At present, only a few representatives of a few families have been studied in this context. The wing patterns of tineoid moths most closely follow the “uniform wing-margin” model, in which every single vein along the wing costa – as opposed to every other vein – is surrounded by a pattern element of the same color (Fig. 1C). This variant of the “wing-margin” model was originally proposed

following observations of a handful of species belonging to the micropterigid genus *Sabatinca* Walker, 1863 (Fig. 1B); these species are derived within the genus and distantly related to each other, so wing patterns following the uniform wing-margin model were interpreted as representing a derived, convergent state (SCHACHAT & BROWN 2016). In Psychidae, very few wing patterns match the alternating wing-margin model, and such an interpretation relies on assumptions about the fusion of wing veins that are very difficult to test; however, many psychid wing patterns follow the uniform wing-margin model precisely (SCHACHAT & BROWN 2017). And in the tineid genus *Moerarchis* Durrant, 1914, color pattern in some specimens follows the alternating wing-margin model near the apex of the wing, but the uniform wing-margin model holds more broadly (SCHACHAT 2017).

Because the alternating wing-margin model holds for the most basal *Sabatinca* species and for most other micropterigid genera with patterned wings, this variant of the wing-margin model very likely represents the ancestral state for lepidopteran wing pattern. And because the alternating wing-margin model holds for Tortricidae as well, it could plausibly be used to predict wing pattern in any lineage of microlepidoptera. Because the uniform

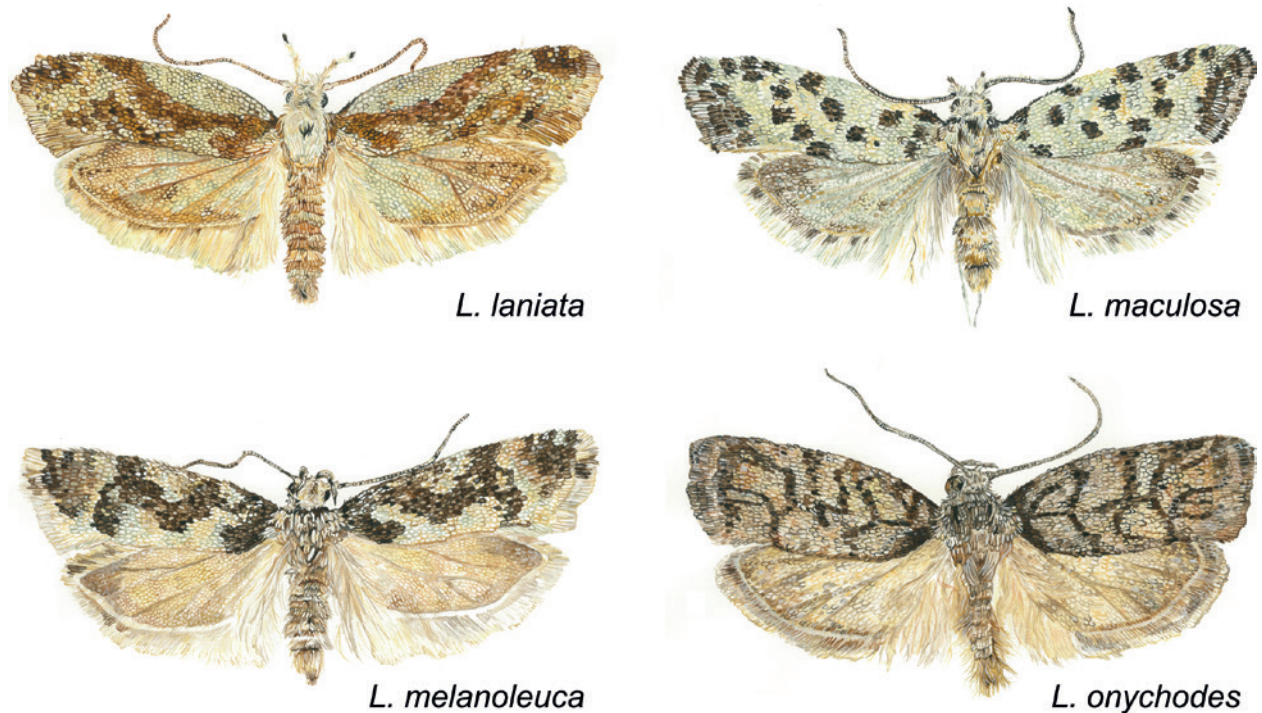


Fig. 2. Watercolor illustrations of *Lichenaula* specimens from four species, dorsal views. Courtesy of Celia L. Curtis.

wing-margin was inspired by derived, distantly related micropterigid species and is not yet known to hold for any other monotrysian moths, it likely represents a common homoplastic character state.

A number of unresolved issues remain with regards to the relationship between wing pattern and venation in microlepidoptera. No examination of any single lineage has yet found full and unequivocal support for the uniform wing-margin model. Furthermore, the frequency of wing patterns following the alternating and uniform wing-margin models is still not known. Lastly, many microlepidoptera have speckled or mottled wing patterns; such patterns were included in a broad overview of the Psychidae (SCHACHAT & BROWN 2017) but have otherwise received no attention.

The Australian genus *Lichenaula* Meyrick, 1890 belongs to the subfamily Xyloryctinae (Xyloryctidae), in the superfamily Gelechioidea (HODGES 1998; KAILA 2004; KAILA et al. 2011; HEIKKILÄ et al. 2011). This genus contains species with a variety of wing patterns: spots and bands, reminiscent of the wing patterns seen in microlepidopteran lineages examined previously, as well as mottled wing patterns with few discernible pattern elements comprised of adjacent, concolorous scales (Fig. 2). The wing patterns seen in *Lichenaula* are not typical for the superfamily Gelechioidea, but were chosen as the subject of the present study because they lend themselves to comparison with the predictive models and with the wing patterns of other microlepidoptera. Of the three largest superfamilies of microlepidoptera – Tineoidea, Tortricoidea, and Gelechioidea – Tineoidea and Tortricoidea have both been examined in multiple studies of the relationship between wing pattern and venation (BROWN & POWELL 1991; BAIXERAS 2002; SCHACHAT &

BROWN 2017; SCHACHAT 2017), but the Gelechioidea have not yet been examined in this context. *Lichenaula* therefore presents an opportunity to broaden the morphological and taxonomic scope of this growing area of inquiry.

2. Materials and methods

All species examined are listed in Table 1. All specimens examined here belong to the genus *Lichenaula* and are held in the Australian National Insect Collection in Canberra, Australia. Only forewings were examined because hindwings do not have any color pattern. The methods used here parallel those of recent studies (SCHACHAT & BROWN 2017; SCHACHAT 2017).

To observe the relationship between wing pattern and wing venation, the clearing agent Histolene was applied to individual forewings. Because Histolene leaves a residue that can only be removed by very careful application of acetone, this method may be destructive in some cases and therefore could only be carried out on a subset of the available specimens. Specimens considered to be “available” for study were those that had not been designated as types (including paratypes), had not been used in previous molecular studies such as the Barcode of Life Database, and whose wings were in sufficiently good condition that the relationship between venation and color pattern could be observed. For species represented by 10 or fewer available specimens, only one was chosen for examination. For species represented by 10–30 available specimens, three were chosen for examination. For species represented by more than 30 available specimens,

five were chosen for examination. One forewing was examined per specimen. A total of 34 wings were examined, representing 12 species of *Lichenaula* (Table 1).

Specimens were chosen for study based on the preservation of wing pattern; due to the limited number of specimens available, equal representation of males and females was not possible for many species. This is unlikely to impact the results presented here, as no differences in wing pattern were noted between males and females.

To produce illustrations, specimens were photographed twice using a Leica DSC 500 microscope/camera and the Leica Application Suite software (Version 4.4, Leica Microsystems, Germany). First, specimens were photographed while lit from above in order to record the natural state of the wing pattern. Then, Histolene was applied and the specimen was photographed from below, in order to see the wing veins. Illustrations were created by tracing the wing veins in each photo using Affinity Designer graphics software (Version 1.5.5, Serif Labs, United Kingdom), and then superimposing the venation onto the first photograph that showed the original wing pattern.

Terminology is used as follows. The “costal margin,” or “costa,” is the anterior margin of the wing and appears as the upper margin in all photographs and illustrations presented here. The “dorsal margin,” or “dorsum,” is the posterior margin of the wing and appears as the lower margin in all photographs and illustrations presented here. The term “band” is used for fasciae, or stripes, of color; the term “fascia” is not used here because of previous findings that individual colors do not reflect homology and can therefore be misleading in a macroevolutionary context (SCHACHAT & BROWN 2016). The term “pattern element” is used to refer to all discrete areas of color on the wing, including spots, bands, and what is referred to in other publications as the “ground color.” The abbreviations for wing veins are illustrated in Figure 1.

3. Results

3.1. The uniform wing-margin model

Lichenaula maculosa is the only species examined here with a wing pattern consisting entirely of spots, reminiscent of ermine moths such as *Yponomeuta* Latreille, 1796 (Yponomeutidae). In the three specimens examined, each vein that reaches the costa is surrounded by a dark spot (Table 1; Figs. 3A, S1A,B). The spots surrounding Rs_3 and Rs_4 become confluent along the wing margin and the spots surrounding R and Rs_1 are confluent, or very nearly so, in the interior of the wing.

The wing patterns of various species include both spots and bands, with the spots generally appearing to-

ward the apex and the margin of the wing and the bands generally appearing toward the base and the interior of the wing. Along the costa, each vein is surrounded by a discrete pattern element in *Lichenaula comparella* (Table 1; Figs. 3B, S1C) and *L. melanoleuca* (Fig. 3C), with many of these pattern elements becoming confluent in the interior of the wing. In one *L. comparella* specimen, the pattern elements surrounding Rs_1 and Rs_2 are confluent along the costa and comprise the margin of a band (Fig. S1D). In *L. melanoleuca*, the spot surrounding R is greatly reduced in one specimen (Fig. S1E) and occurs strictly within the wing fringe – beyond the wing margin – in another (Fig. S1F).

The pattern elements surrounding Sc and R on along the costa in *Lichenaula laniata* are barely discernible from each other in one specimen, but each vein is surrounded by a discrete pattern element along the costa with confluence often occurring in the interior of the wing (Table 1; Fig. 3D). In other specimens, the pattern elements surrounding Sc and R are fully confluent and the spot surrounding Rs_1 is either: reduced in size (Fig. S2A), so reduced that it occurs only beyond the wing margin (Fig. S2B), fully confluent with the pattern elements surrounding the other branches of Rs (Fig. S2C), or entirely absent (Fig. S2D).

In one specimen of *Lichenaula calligrapha*, all veins are surrounded by discrete pattern elements along the costa (Table 1; Fig. 3E). In other specimens, the spot surrounding Rs_3 is either greatly reduced (Fig. S2E) or absent (Fig. S2F), or the spot surrounding R is absent (Figs. S2G,H). In most specimens of *L. lichenea*, all veins are surrounded by a discrete pattern element along the costa (Table 1; Figs. 3F, S3A–C); in one specimen, this one-to-one relationship between veins and pattern elements appears to hold not only for the costa but for the entirety of the wing margin (Fig. S3B). In one specimen, the spots surrounding Rs_3 and Rs_4 have been reduced such that they appear only in the wing fringe, beyond the wing margin (Fig. S3D).

The only specimen of *Lichenaula callispora* that was examined (Fig. 3G) has a wing pattern similar to those of *L. melanoleuca* (Fig. S1F) and *L. laniata* (Fig. S2B) in that all veins except for R are surrounded by pattern elements along the costa; a spot occurs near R, but is of very small size and occurs only in the wing fringe, past the wing margin.

3.2. A banded wing pattern

The wing pattern of *Lichenaula* nr. *arisema* consists of two alternating series of bands: three light and three dark bands (Fig. 3H). The first three bands – two light and one dark – reach the costa in a region of the wing where no veins terminate. The following two bands surround Sc and R, respectively. A final dark band occurs between the apex of the wing and the point where Rs_1 reaches the costa, and surrounds Rs_2 , Rs_3 , and Rs_4 .

Table 1. The species of *Lichenaula* examined for the present study, the pattern type / pattern elements observed, conformity with the “uniform wing-margin” model, number of specimens examined, and figure references.

Species	Authority	Pattern type	“Uniform”	# examined	Figures
<i>L. nr. arisema</i>	—	Bands	No	1	Fig. 3H
<i>L. calligrapha</i>	Meyrick, 1890	Bands & spots	Yes	5	Figs. 3E, S2E–H
<i>L. callispora</i>	Turner, 1904	Bands & spots	Probably	1	Fig. 3G
<i>L. choriodes</i>	Meyrick, 1890	Mottled	Probably	3	Figs. 4C, S3E,F
<i>L. comparella</i>	(Walker, 1864)	Bands & spots	Yes	3	Figs. 3B, S1C,D
<i>L. laniata</i>	Meyrick, 1890	Bands & spots	Yes	5	Figs. 3D, S2A–D
<i>L. lichenea</i>	Meyrick, 1890	Bands & spots	Yes	5	Figs. 3F, S3A–D
<i>L. maculosa</i>	(Turner, 1898)	Spots	Yes	3	Figs. 3A, S1A,B
<i>L. melanoleuca</i>	Turner, 1898	Bands & spots	Yes	3	Figs. 3C, S1E,F
<i>L. musica</i>	Meyrick, 1890	Mottled	Yes	1	Fig. 4A
<i>L. onychodes</i>	Turner, 1898	Mottled	Probably	3	Figs. 4D, S3G,H
<i>L. phloeochroa</i>	Turner, 1898	Mottled	Yes	1	Fig. 4B

3.3. Mottled wing patterns

Though *Lichenaula phloeochroa* has a mottled wing pattern, the relationship between venation and color pattern along the costa is clear: each vein is surrounded by a single dark spot (Fig. 4A). *L. musica* has a similar wing pattern, but the boundaries of the spots are not as distinct (Fig. 4B). In one specimen of *L. choriodes*, each vein is surrounded by dark scales along the costal margin of the wing, but the boundaries between pattern elements become less clear toward the apex (Fig. 4C). In other specimens belonging to this species, the boundaries between dark pattern elements and the light ground color are unclear and certain veins are not surrounded by dark pattern elements (Figs. S3E,F). On the wings of *L. onychodes*, veins are always surrounded by dark scales along the costa but the boundaries between pattern elements and the ground color can be impossible to distinguish (Table 1; Figs. 4D, S3G,H).

4. Discussion

Of all moth genera whose wing patterns have been examined in this context, *Lichenaula* provides the strongest support for the uniform wing-margin model. In every species of *Lichenaula* for which three or more specimens were examined, at least one specimen has one-to-one relationship between wing veins and dark pattern elements along the costa, conforming precisely to the predictions of the uniform wing-margin model.

Lichenaula provides novel insights into the ways in which wing patterns can deviate from the uniform wing-margin model. On wings that conform precisely to this model, the spots that occur along the costa are often uniform in size. When spots become greatly reduced in size, they may continue to surround the same vein along the costa (Figs. S1E, S2A,E) and, upon further reduction in size, the spots will occur only on the wing fringe (Figs.

3G, S1F, S2B,F, S3D). Of note, this phenomenon also appears to occur in the genus *Izatha* (HOARE 2010), which is distantly related to *Lichenaula* within the Xyloryctidae (KAILA et al. 2011).

4.1. The dorsal wing margin

The relationship between pattern and venation along the dorsal margin of moth wings is poorly understood. In studies of the family Micropterigidae, the relationship between pattern and venation was noted only along the costal margin of the wing because few discrete pattern elements could be discerned along the dorsum (SCHACHAT & BROWN 2015, 2016). For Psychidae, no conclusions were drawn regarding the dorsum because the relationship between pattern and venation was sometimes ambiguous even along the costa (SCHACHAT & BROWN 2017). The tineid genus *Moerarchis* provides strong evidence that a relationship between pattern and venation exists along the dorsum in addition to the costa (SCHACHAT 2017).

In *Lichenaula*, the relationship between pattern and venation along the dorsum is generally ambiguous. In species with mottled wing patterns, pattern elements are especially indistinct beyond the costa (Figs. 4A–D). *L. maculosa* provides the strongest evidence for a consistent relationship between pattern and venation along the entire wing margin, with dark spots surrounding all veins except CuP and A at the wing margin (Figs. 3A, S1A,B). Along the dorsum of *L. comparella* and *L. lichenea*, the pattern-venation relationship is consistent with that of *L. maculosa* but confluence of pattern elements causes some ambiguity (Figs. 3B,F). *L. melanoleuca* and *L. laniata* have multiple, discrete light and dark pattern elements along the dorsum, but in these species, no strong relationship between pattern and venation is evident (Figs. 3C,D). Overall, various species of *Lichenaula* have wing patterns that suggest a relationship between pattern and venation along the dorsum, but no definitive conclusions can be drawn at this time.

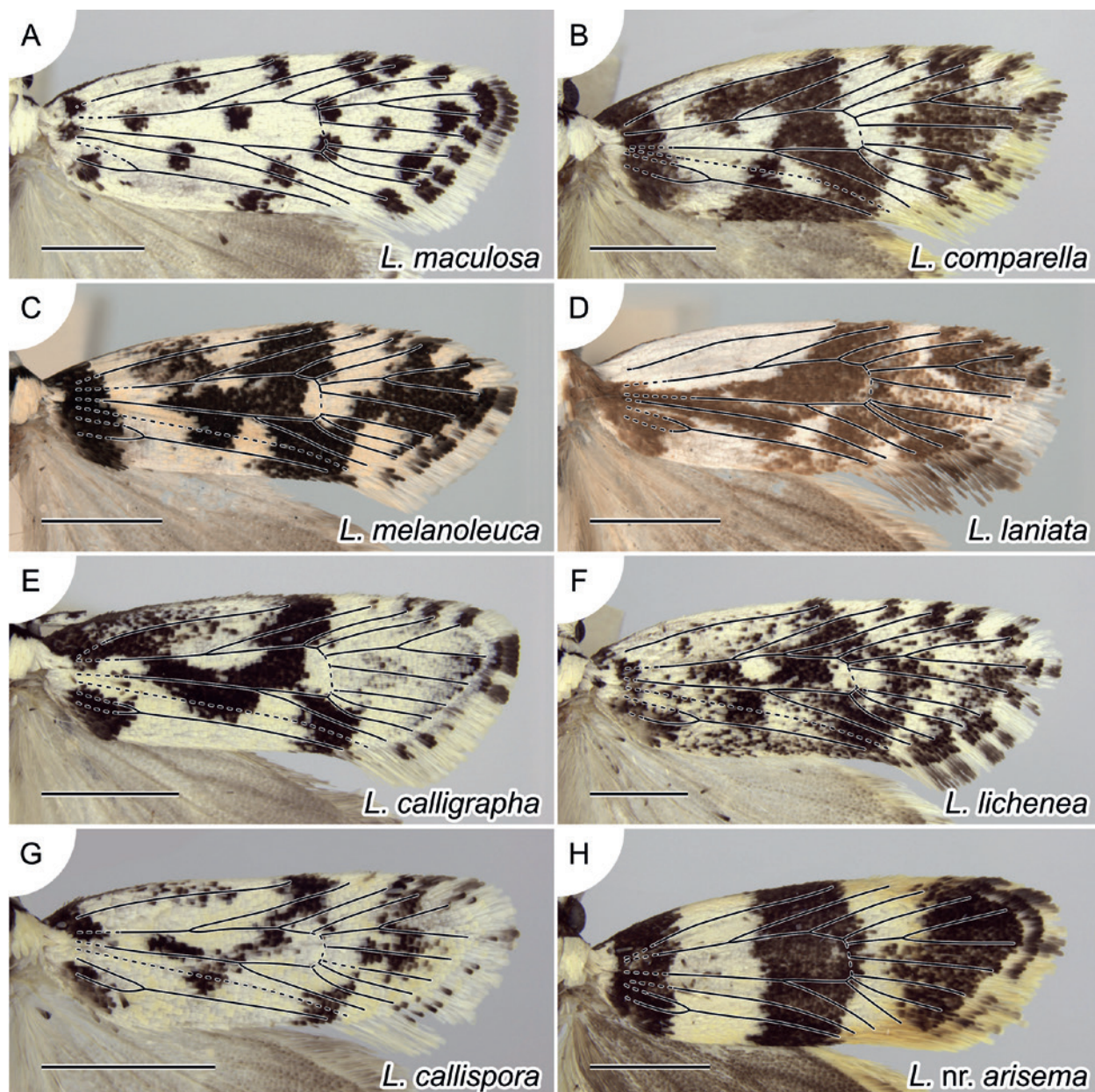


Fig. 3. Wing pattern and wing venation in moths belonging to the genus *Lichenaula*. **A:** *L. maculosa* (Turner, 1898). **B:** *L. comparella* (Walker, 1864). **C:** *L. melanoleuca* Turner, 1898. **D:** *L. laniata* Meyrick, 1890. **E:** *L. calligrapha* Meyrick, 1890. **F:** *L. lichenea* Meyrick, 1890. **G:** *L. callispora* Turner, 1904. **H:** *L. nr. arisema*. (Scale bars: 2 mm.)

4.2. Ancestral wing veins

The strong support for the uniform wing-margin model found in *Lichenaula* provides an opportunity to address questions about the evolution of wing patterns that conform to this model.

On wings that follow the alternating wing-margin model (Fig. 1A) – belonging to moths in the families Micropterigidae and Tortricidae – plesiomorphic lepidopteran wing veins continue to influence the development of wing pattern, even if those veins are not expressed in the adult wing. For example, moths' ancestral 3-branched subcostal vein is known today in the family Agathiphiagidae (SCHACHAT & GIBBS 2016), and the first branch of the radius vein is not expressed in *Micropterix* or in any

Tortricidae; however, the ancestral 3-branched subcostal vein and 2-branched radius vein continue to influence the development of wing pattern in both Micropterigidae and Tortricidae (BROWN & POWELL 1991; BAIXERAS 2002; SCHACHAT & BROWN 2015, 2016).

For wing patterns that follow the uniform wing-margin model, the role of plesiomorphic veins is not nearly as clear. The psychid genus *Ardiosteres* and the tineid genus *Moerarchis* both generally conform to the uniform wing-margin model (SCHACHAT & BROWN 2017; SCHACHAT 2017). In these genera, a number of pattern elements reach the costa before Sc terminates along the margin; this could be interpreted as evidence that plesiomorphic lepidopteran veins – the humeral vein and the first two branches of the subcostal vein – continue to

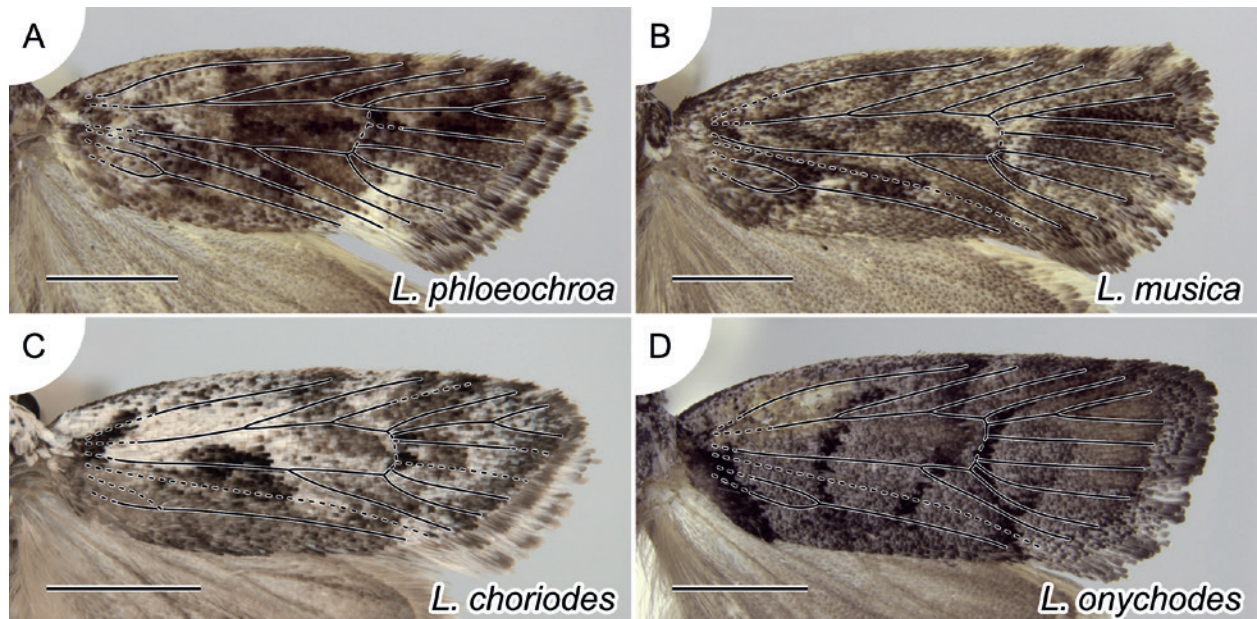


Fig. 4. Wing pattern and wing venation in moths belonging to the genus *Lichenaula*, continued. A: *L. musica* Meyrick, 1890. B: *L. phloeochroa* Turner, 1898. C: *L. choriodes* Meyrick, 1890. D: *L. onychodes* Turner, 1898. (Scale bars: 2 mm.)

constrain the development of wing pattern in these taxa. However, none of the psychid or tineid specimens examined showed strong evidence of continued influence of a 2-branched radius vein.

The wing patterns of many *Lichenaula* species follow the uniform wing-margin model more definitively than those of some *Moerarchis* specimens and many psychid species. *Lichenaula* does not provide strong evidence that plesiomorphic wing veins continue to influence the uniform wing-margin model when these veins are not expressed in the adult wing. In the species examined here that follow the uniform wing-margin model, only one (Figs. 3B,E,F) or two (Figs. 3A,C,G) dark pattern elements reach the costa before Sc terminates. However, there are three ancestral veins in this part of the wing: the humeral vein and the first two branches of the subcostal vein. Furthermore, none of the *Lichenaula* specimens examined here have any pattern elements that correspond to the ancestral branch of the Radius that is not visible on the adult wing.

The one-to-one relationship between pattern elements and ancestral lepidopteran wing veins, observed for the alternating wing-margin model in both Micropterigidae and Tortricidae, appears not to hold for the uniform wing-margin model.

4.3. Phylogenetic context

At present, the relationship between wing pattern and venation along the costa has been examined in representatives of five families of Lepidoptera: Micropterigidae (SCHACHAT & BROWN 2015, 2016), Psychidae (SCHACHAT & BROWN 2017), Tineidae (SCHACHAT 2017), Tortricidae (BROWN & POWELL 1991; BAIXERAS 2002), and now Xyloryctidae. Wing pattern in the family Nymphalidae

(Papilionoidea) is described by the nymphalid groundplan, which was recently updated (MARTIN & REED 2010; OTAKI 2012), and the relationship between wing pattern and venation for this family was extrapolated from the groundplan (SCHACHAT & BROWN 2016).

The alternating wing-margin model most likely represents the ancestral state for Lepidoptera. Recent phylogenies have recovered either Micropterigidae (HEIKILÄ et al. 2015; BAZINET et al. 2016) or Micropterigidae + Agathiphagidae as sister to all other Lepidoptera (REGIER et al. 2013, 2015). The Agathiphagidae have a lightly mottled wing pattern with no discrete pattern elements (SCHACHAT & GIBBS 2016), and most Micropterigidae follow the alternating wing-margin model – the few species that conform to the uniform wing-margin model fall into derived lineages of the genus *Sabatinca* (SCHACHAT & BROWN 2015, 2016). When viewed in a preliminary phylogenetic context, the results available thus far suggest that multiple transitions between the alternating and the uniform wing-margin model have occurred: represented by *Sabatinca*, various Tineoidea, and, now, *Lichenaula* (Fig. 5). However, Micropterigidae is the only family of moths for which the relationship between wing pattern and wing venation has been examined in an exhaustive and complete manner; additional representatives of the tineoid and gelechioid superfamilies should be examined in order to verify and refine the preliminary phylogenetic hypothesis presented here.

No insects outside of the Lepidoptera are known to have wing patterns that follow the alternating wing-margin model. In contrast, insects belonging to various orders have wing patterns that follow the uniform wing-margin model. *Drosophila guttifera* Walker, 1849 is perhaps the best-known insect whose wings have spots at the points where veins terminate along the margin (WERNER et al. 2010). Furthermore, spots also occur on the wings of

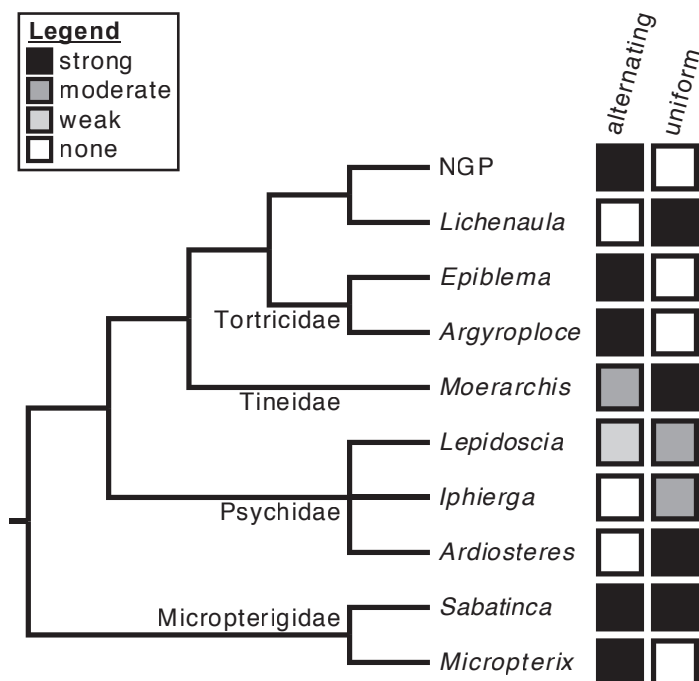


Fig. 5. Support for the “alternating” and “uniform wing-margin” models in the major moth genera examined so far and in the nymphalid groundplan (NGP), viewed in phylogenetic context. Genera that occur within the same family are rendered as polytomies. The family-level phylogeny is adopted from recent analyses (REGIER et al. 2013).

Drosophila guttifer at the points where veins bifurcate. These are reminiscent of the spots that occur at the points where Rs and M/CuP bifurcate in *L. maculosa* (Figs. 3A, S1A,B). Such spots have been noted in other moth taxa ranging from Micropterigidae (SCHACHAT & BROWN 2016) to Macroheterocera (LEMCHÉ 1935). Other non-lepidopterans whose wing patterns follow the uniform wing-margin model include the world’s largest known cicada species, *Megapomponia imperatoria* (Westwood, 1842) (LEE & SANBORN 2010), and cicadas from various other genera (e.g., LEE 2014). In *Megapomponia imperatoria*, additional spots occur on crossveins.

Among the sister-group to Lepidoptera, the Trichoptera, various genera in the family Phryganeidae have wing patterns with spots that straddle many veins along the wing margin (REDELL et al. 2009). In the phryganeid species *Oligostomis ocelligera* (Walker, 1852), additional spots occur at the points where veins bifurcate (REDELL et al. 2009). But, unlike the moths, flies, and cicadas mentioned above, *Oligostomis ocelligera* also has markings that occur between adjacent vein branches, rather than being centered on individual veins. This suggests that the wing patterns of Lepidoptera and Trichoptera may be constrained by different developmental mechanisms.

A recent contribution posited that the wing pattern elements of Lepidoptera are not homologous to the wing pattern elements of other insect orders, because the wing patterns of Lepidoptera do not resemble those of Trichoptera and because the wing patterns seen in Lepidoptera originate from the scales whereas the wing patterns of other insects originate from the wing membrane (SCHACHAT & BROWN 2016). The prevalence of the uniform wing-margin model within and beyond Lepidoptera is a suitable test case for the exploration of developmental mechanisms that underlie similar wing patterns across insect orders.

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File 1: schachat-lichenaulawingpattern-asp2017-electronicsupplement.pdf — **Fig. S1.** Intraspecific variation in wing pattern and wing venation of *Lichenaula*. **A,B:** *L. maculosa*. **C,D:** *L. comparella*. **E,F:** *L. melanoleuca*. (Scale bars: 2 mm.) — **Fig. S2.** Intraspecific variation in wing pattern and wing venation of *Lichenaula*, continued. **A–D:** *L. laniata*. **E–H:** *L. calligrapha*. (Scale bars: 2 mm.) — **Fig. S3.** Intraspecific variation in wing pattern and wing venation of *Lichenaula*, continued. **A–D:** *L. lichenea*. **E,F:** *L. choriodes*. **G,H:** *L. onychodes*. (Scale bars: 2 mm.)

