


RESEARCH ARTICLE

The wing pattern of *Hydriomena* Hübner, [1825] (Lepidoptera: Geometridae: Larentiinae) lacks a predictable relationship with venation

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Abstract

Two simple models have been successfully applied to predict the relationship between wing pattern and venation in various lineages of Lepidoptera. However, neither of these models holds for the geometrid genus *Hydriomena* Hübner, 1825. Wing patterns in *Hydriomena* were studied intensively during the 1920s after the description of the nymphalid groundplan, an idealized schematic that outlines the primary elements of butterfly wing patterns; geometrids strongly resemble butterflies and, until recently, were considered to be among their closest relatives. The evolution of wing pattern in Geometridae has been neglected since the 1930s. Here, the relationship between wing pattern and venation is examined for *Hydriomena costipunctata* Barnes and McDunnough, 1912 and the *Hydriomena speciosata* (Packard, 1873) group. These two lineages have some of the simplest wing patterns in *Hydriomena*, consisting of large, well-defined dark and light pattern elements. The relationship between wing pattern and venation varies considerably within and between these lineages and can even vary between the right and left wings on the same individual. Although many different wing patterns were observed among the individuals examined for this study, not one can be reconciled with either of the models that successfully predict the relationship between wing pattern and venation in many other groups of Lepidoptera. This suggests that bands occurring on the wings of *Hydriomena* are not homologous with those on the wings of butterflies or of Acronictinae (Macroheterocera: Noctuidae), the only other two obtectomeran lineages for which the relationship between wing pattern and venation has been examined in recent years.

KEYWORDS

color pattern, evolution, Macroheterocera, scale, venation

1 | INTRODUCTION

For decades, butterfly wing patterns have been studied intensively with little regard for any other superfamilies of Lepidoptera (Monteiro, 2015; Nijhout, 1978, 1991, 2001; Otaki, 2012; Sekimura & Nijhout, 2017). Because the phylogeny of lepidopteran superfamilies is rather pectinate in nature and because butterflies are not among

superfamilies that diverged earliest or most recently (Heikkilä, Mutanen, Wahlberg, Sihvonen, & Kaila, 2015; Regier et al., 2013), findings about their wing patterns do not necessarily inform the directionality of any higher-level evolutionary change. Butterflies are among the most early-diverging superfamilies in Obtectomera, a clade that also includes the more recently derived and highly speciose superfamilies Pyraloidea, Geometroidea, and Noctuoidea (Heikkilä

et al., 2015; Regier et al., 2013). Certain obtectomeran moths, most famously in the superfamilies Geometroidea and Bombycoidea, have long been recognized for their complex wing patterns consisting of many pattern elements with intricate hierarchical relationships (Nijhout, 1978).

In recent years, the relationship between wing pattern and venation has been used to identify potentially homologous pattern elements, primarily in Microlepidoptera (Baixeras, 2002; Brown & Powell, 1991; Schachat, 2017a, 2017b; Schachat & Brown, 2015, 2016, 2018). The predictive power of the relationship between wing pattern and venation was confirmed when the wing pattern of mandibulate moths was successfully used to predict the precise location of a plesiomorphic wing vein for Lepidoptera (Schachat & Brown, 2015, 2016; Schachat & Gibbs, 2016). Although few lineages of Microlepidoptera have yet been evaluated in this context, wing pattern in Obtectomera other than butterflies has received even less attention, with just two recent studies of moths in the family Noctuoidea (Gawne & Nijhout, 2019; Schachat & Goldstein, 2018), only one of which evaluated the role of venation along the entirety of the wing.

Of the many phylogenetic gaps in our knowledge of the relationship between wing pattern and venation in Lepidoptera, the absence of data for Geometroidea is especially striking. The Geometroidea have the greatest described species richness of any superfamily that has not yet been examined (van Nieukerken et al., 2011).

Furthermore, Geometridae were long believed to be the sister-group to butterflies (Nijhout, 1994) and in many cases their wings are highly reminiscent of those of butterflies, with which they often participate in mimicry rings (Beccaloni, 1997; Carpenter, 1946). Studies of geometrid wing patterns, particularly of the larentiine genus *Hydriomena* Hübner, [1825], were common during the 1920s and 1930s (Henke, 1928, 1933; Süffert, 1929) when the publication of the nymphalid groundplan revolutionized the study of butterfly wing patterns (Schwanwitsch, 1924; Süffert, 1927). However, wing patterns in *Hydriomena* cannot be discussed strictly in terms of the pattern elements seen on butterfly wings because various species of *Hydriomena* have wing patterns whose complexity lies beyond the bounds of the nymphalid groundplan (Nijhout, 1991; Süffert, 1929). The predictive power of the relationship between wing pattern and venation, noted in many lineages across the lepidopteran phylogeny, clearly warrants a reassessment of wing pattern in *Hydriomena*.

The role of wing venation in the development of wing pattern is easiest to evaluate in taxa whose wing patterns contain only two colors that form alternating dark and light transverse bands. Such patterns can be evaluated according to two models, both of which predict the development of wing pattern in different microlepidopteran and obtectomeran groups. Under the first model, the “alternating wing-margin model,” each band—whether dark or light—surrounds exactly one vein along the costal margin of the wing (Figure 1a). Under the second, the “uniform wing-margin model,” bands of the same color—

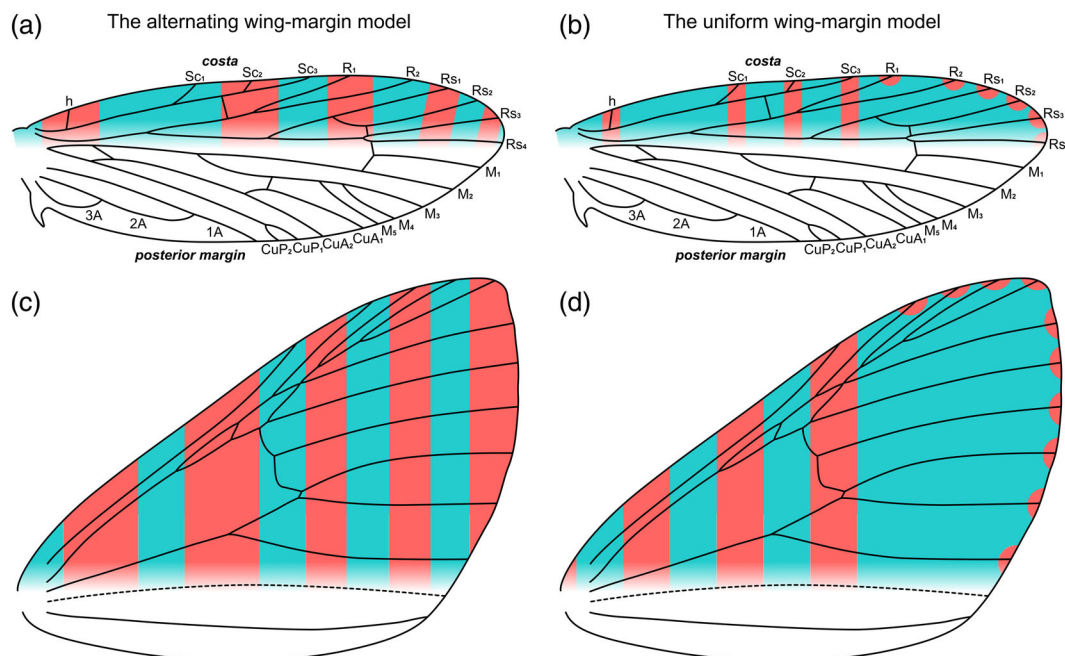


FIGURE 1 The two predictive “wing-margin” models for the relationship between wing pattern and venation. Spots and bands are interchangeable wing pattern elements, and either color seen here—red or blue—can develop into a darker color. Wing pattern is only illustrated for the costal portion of the wing because the role of wing venation along the posterior wing margin in pattern development is not entirely understood, however this matter is irrelevant to *Hydriomena* because no wing veins terminate along the posterior margin in this genus. (a) The “alternating wing-margin” model, plotted onto the hypothesized plesiomorphic groundplan for lepidopteran venation (Schachat & Gibbs, 2016). (b) The “uniform wing-margin model,” with the distribution of spots and bands based on observations of *Lichenaula* Meyrick, 1890 (Schachat, 2017a), plotted onto the hypothesized plesiomorphic groundplan for lepidopteran venation (Schachat & Gibbs, 2016). (c) The “alternating wing-margin” model, plotted onto the wing venation of *Hydriomena speciosata* specimen CASENT 8277789. (d) The “uniform wing-margin model,” plotted onto the wing venation of *Hydriomena speciosata* specimen CASENT 8277789

whether dark or light—straddle each vein along the costal margin of the wing, with bands of the other color reaching the costal margin between those veins (Figure 1b). Under either model, lack of expression can reduce the transverse bands to spots. The alternating wing-margin model was first described in Tortricidae (Baixeras, 2002; Brown & Powell, 1991), has been found to hold for the most early-diverging extant moths with wing patterns (Schachat & Brown, 2015, 2016), and has been used to identify homologies between butterfly wing patterns and the plesiomorphic wing pattern for crown Lepidoptera (Schachat & Brown, 2016). The uniform wing-margin model has been found to hold for most of the microlepidopteran genera examined thus far (Schachat, 2017a, 2017b; Schachat & Brown, 2018) and also for the noctuid subfamily Acronictinae (Schachat & Goldstein, 2018), which is far more closely related to Geometridae than butterflies are (Heikkilä et al., 2015; Regier et al., 2013).

Two North American species groups in *Hydriomena* have simple wing patterns that consist exclusively of dark and light pattern elements: *Hydriomena costipunctata* Barnes and McDunnough, 1912 and the species group that includes *Hydriomena speciosata* (Packard, 1873; Figure 2). The aims of this contribution are to describe a wing-pattern groundplan for these species groups, to evaluate whether either of the two wing-margin models predicts the relationship between pattern and venation on their wings, and more broadly, to document variation in wing pattern within individuals, between males and females, and between species.

1.1 | Relevance of the nymphalid groundplan

The nymphalid groundplan contains three “symmetry systems”: pattern elements comprised of multiple colors that are self-symmetrical along the proximal-distal axis of the wing, in terms of color but not necessarily shape (Nijhout, 1991; Otaki, 2012; Schwanwitsch, 1924; Süffert, 1927). These symmetry systems undoubtedly arose from simpler pattern elements consisting of a single color (Lemche, 1935, 1937; Nijhout, 1994; Schachat & Brown, 2016). Species with simple wing patterns were deliberately chosen for this study because this is the first in nearly a century to examine the morphology of geometrid wing patterns. The wings of *Hydriomena* do not have any pattern elements of sufficient complexity to fit the definition of a symmetry system; by focusing on geometrid wing patterns that are far simpler than

those described by the nymphalid groundplan, the hope is that the straightforward nature of this study will facilitate more informed comparisons of nymphalid and geometrid symmetry systems when the latter are reexamined.

Differing, and sometimes conflicting, vocabularies have emerged to describe pattern elements on the wings of Lepidoptera. Studies of Microlepidoptera have traditionally treated wing pattern as a taxonomic character. These studies discuss “bands” or “fasciae” that occur between fields of “ground color.” Some authors use “fasciae” to describe the darkest pattern elements on the wing (Baixeras, 2002; Brown & Powell, 1991; Meyrick, 1914), whereas others use this term for the lightest pattern elements (Philpott, 1927; Zeller-Lukashort, Kurz, Lees, & Kurz, 2007). The consensus in the microlepidopteran literature appears to be that the “ground color” is that which occupies the most space on the wing, typically comprising one or a few contiguous areas that are interrupted by smaller pattern elements such as spots or fasciae. The only universal criterion for the ground color appears to be that it is not the most iridescent, or “metallic,” color on the wing (Braun, 1923). Just like the fasciae, the ground color can be dark (Zeller-Lukashort et al., 2007) or light (Kaila, 1995). In contrast to Microlepidoptera, studies of wing pattern in butterflies are typically motivated by developmental considerations rather than the search for taxonomic characters. In the nymphalid groundplan (Nijhout, 1991), pattern elements such as symmetry systems are surrounded by a “background color” that, unlike the microlepidopteran “ground color,” need not occupy the most space on the wing or comprise the largest contiguous marking on the wing. There may be an explicit expectation that the “background color” of the nymphalid groundplan is lighter than the pattern elements that it surrounds (Otaki, 2017), but this is not the case for many Microlepidoptera in which the darkest area of the wing best fits the definition of “ground color” (Zeller-Lukashort et al., 2007). These contrasting traditions minimize the possibility that a marking described as “ground color” in the Microlepidoptera literature would be described as “background color” in the butterfly literature. Furthermore, as noted above, homologous pattern elements within the same genus (Schachat & Brown, 2018) or family (Schachat & Brown, 2016) can “flip” between light and dark, rendering color meaningless in the context of ancestral states and leaving venation and the contrast boundaries between pattern elements as the only characters that reflect homologies.

FIGURE 2 Photos of *Hydriomena speciosata*. Left: pinned specimen, copyright Jim Vargo, used with permission. Right: live moth, sample ID AVBC 256-10, by CBG Photography Group, Centre for Biodiversity Genomics (CC-BY-NC-SA license)



While the expected vocabulary for discussion of wing pattern in Macroheterocera may be that of the nymphalid groundplan, due to the historical misconception that butterflies fall within this clade, this vocabulary simply does not apply to the species of *Hydriomena* examined here. These species lack most, if not all, characteristic features of the nymphalid groundplan: symmetry systems, a discal spot, eyespots, and so forth. The most salient feature of the nymphalid groundplan that can be designated in the species examined here is the background color. However, because this feature also fits the typical definition of “ground color” as used in the microlepidopteran literature, and because the term “ground color” is used inconsistently between taxa and authors, the terms “background color” and “ground color” are avoided here.

For certain butterflies, the concepts that underlie the nymphalid groundplan have been employed to describe wing patterns that do not contain symmetry systems, such as the wing patterns of *Heliconius Kluk*, 1802 (Nijhout, 1978). In the case of these butterflies, sufficient information is available about their close relatives to confidently infer that they arose from an ancestor whose wing patterns did indeed contain symmetry systems that conform to the nymphalid groundplan (Nijhout, 1991, 2003). Use of the nymphalid groundplan to describe wing pattern in *Heliconius* makes sense because wing pattern in this genus is likely a highly modified version of the nymphalid groundplan. However, it is not yet known whether the species examined here—or any other Obtectomera outside the superfamily Papilionoidea, for that matter—arose from an ancestor whose wing pattern contained the symmetry systems described by the nymphalid groundplan.

For these reasons, this contribution uses language that is as simple and neutral as possible. Pattern elements are not described with terminology traditionally used in the Microlepidoptera literature because these terms have been used inconsistently, and are not described with terminology traditionally used in the butterfly literature because the wing patterns examined here lack the symmetry systems that form the basis of the nymphalid groundplan. Instead, markings on the wings of *Hydriomena* are described here as “dark pattern elements” or “light pattern elements.” The reader is left to conceptualize these dark and light pattern elements as fasciae, ground color, background color, symmetry systems, and so forth, according to the framework of their choosing.

2 | MATERIALS AND METHODS

Material was examined from the Essig Museum of Entomology, University of California Berkeley, California, USA (EMEC) and the California Academy of Sciences, San Francisco, California, USA (CAS). Five males and five females collected between 11 and 20 July, 1973 from the same *H. speciosata* population in Arcata, California, USA were examined. Four specimens assigned to the “*H. speciosata* group” were examined. According to the most recent checklist that includes North American species in this genus (Pohl, Patterson, & Pelham, 2016), *Hydriomena* group IV McDunnough, 1954 consists of *H. speciosata*; *Hydriomena morosata* Barnes & McDunnough, 1917; *Hydriomena*

barnesata Swett, 1909; *Hydriomena cyriadoides* McDunnough, 1954; and *Hydriomena sperryi* McDunnough, 1952. These five species were also grouped together in the previous checklist of North American moths (Hodges, 1983). Lastly, nine specimens of *H. costipunctata* were examined. The phylogenetic relationship between *H. costipunctata* and the *H. speciosata* group has not been examined (Öunap et al., 2016; Sihvonen et al., 2011), but because *H. costipunctata* has been assigned to *Hydriomena* Group II (Pohl et al., 2016), it appears that *H. costipunctata* does not fall within the sister group to the *H. speciosata* group.

Only forewings are illustrated because the hindwings of these species do not contain any discernible pattern elements. Only the dorsal wing surfaces are illustrated because there are no pattern elements on the ventral surface. Both the right and left forewing are illustrated for each specimen.

2.1 | Illustrations

The original versions of all vector illustrations in this publication are freely available at <https://purl.stanford.edu/hk239bf3472> with a CC BY-NC Attribution-NonCommercial license. The illustration of each wing pattern is based on two photographs. First, the wing was photographed while lit from above, to view the color pattern. Second, the clearing agent Histo-clear was applied and the wing was photographed while lit from below, to view the venation. All photographs were taken with a Leica M165 C microscope and the Leica Application Suite software, version 4.4. The wing pattern and venation were traced from the two photographs in the Affinity Designer vector graphics software, version 1.6.1. The wing pattern and venation were then combined into a single composite illustration so that these features can be viewed simultaneously.

Veins known to occur in *Hydriomena* that could not be clearly observed on certain specimens were inferred, and are illustrated with dashed lines. The wing margin is folded or broken on a number of wings, preventing visualization of wing pattern at the points where certain veins terminate. A black outline is used around all intact areas of the wing margin, permitting differentiation of the regions where the margin was not examined. When the wing margin is folded or broken, this is noted in the figure caption.

Wing pattern in these species of *Hydriomena* contains dark brown and light green bands. On many wings, bright white spots punctuate the light green bands. With museum specimens, it is often impossible to discern the boundaries between the white and green areas because the green coloration fades with time—some museum specimens have labels that say “was green.” To avoid conveying the false impression that a green region of the wing is white, or vice-versa, all wings were illustrated in grayscale: the dark brown regions are illustrated in dark gray, and the green and white areas are illustrated in light gray. Because the white spots are overwhelmingly confined to the interior of the wing, rarely reaching the margin, the inability to distinguish between green and white regions in older specimens is not an obstacle to interpretations of the relationship between wing pattern and venation along the costa.

2.2 | Terminology

The term “model” is used here for the alternating and uniform wing-margin models because these predict the location of pattern elements and have been evaluated in a phylogenetic context. The term “groundplan” is used here to describe the majority-rule exercise of describing common features, the same sense in which the term “nymphalid groundplan” has been used (Nijhout, 1991). “Groundplan” is used in the absence of phylogenetic information and with no intended implications for homology or ancestral states.

The term “crown Lepidoptera” describes the clade that includes all extant Lepidoptera plus all extinct descendants of their most recent common ancestor. “Crown Lepidoptera” excludes the lineages that originated after the divergence between Lepidoptera and Trichoptera but are not descended from the most recent common ancestor of all extant Lepidoptera.

“Costa” refers to the costal, or anterior, margin of the wing; “termen” to the distal margin of the wing; “posterior margin” to the anal margin of the wing, which is referred by some authors as the “dorsum” (Carter, Kristensen, & Fischer, 1998). The terminology used for venation follows conventions that are widely accepted in studies of all winged insect orders (Wootton, 1979). Although the Radius and Radial sector veins are often referred to as branches of “R” in the Macroheterocera literature, Wootton’s terminology, which has been used in many large-scale studies of Lepidoptera (Carter et al., 1998), is used here. According to Wootton’s terminological scheme, geometrids have one “R” vein followed by four “Rs” veins: Rs_1 , Rs_2 , Rs_3 , and Rs_4 . Rs_4 terminates along the termen on the wings of *Hydriomena*, and this is believed to be the ancestral state for Lepidoptera (Schachat & Gibbs, 2016). However, Rs_4 terminates along the costa in two of the groups of Microlepidoptera that were previously examined (Schachat, 2017b; Schachat & Brown, 2015), and in those groups the relationship between Rs_4 and wing pattern occurs as predicted by the wing-margin models. Therefore, Rs_4 is discussed here in conjunction with the veins that terminate along the costa.

The ancestral state for crown Lepidoptera includes three branches of Sc and two branches of R (Schachat & Gibbs, 2016). However, *Hydriomena* has only one branch of Sc and one branch of R. It is necessary to identify homologous branches between *Hydriomena* and ancestral Lepidoptera in order to evaluate the alternating wing-margin model. Examinations of various families, from micropterigids (Schachat & Brown, 2015) to tortricids (Baixeras, 2002; Brown & Powell, 1991) have found that “Sc,” in groups that have only one branch of this vein, corresponds to the plesiomorphic lepidopteran Sc_3 , and that “R,” in groups that have only one branch of this vein, corresponds to the plesiomorphic lepidopteran R_2 .

3 | RESULTS

A total of 46 wings were examined for this study. Every one of these wings violates the predictions of both the alternating wing-margin model and the uniform wing-margin model (Figure 3). There is also

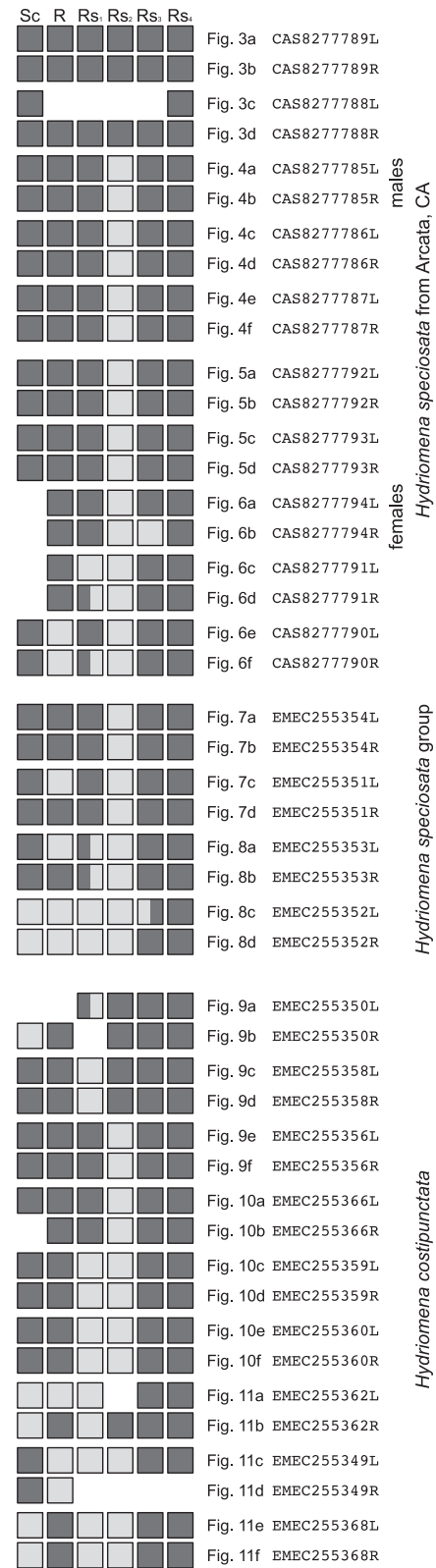


FIGURE 3 A grid showing whether dark or light scales surround veins Sc through Rs_4 along the wing margin in all specimens examined here, with specimen numbers and references to illustrations

notable variation in the relationship between wing pattern and venation at all scales—within individuals, within sexes, between sexes, and between species—which precludes the formulation of a generalized

schematic of the relationship between wing pattern and venation in *Hydriomena*.

3.1 | Violation of predictive models

All of the wings examined violate the uniform wing-margin model. On 42 of the 46 wings examined, at least one vein along the costa is surrounded by a dark pattern element and at least one vein is surrounded by a light pattern element (Figures 5–12). On three of the wings examined, belonging to males from the Arcata population of *H. speciosata*, all veins along the costa are surrounded by dark pattern elements (Figure 4a–b,d). However, none of these three wing patterns conform to the uniform wing-margin model: on all of these wings, R and Rs_1 are surrounded by the same dark pattern element and Rs_2 – Rs_4 are surrounded by the same dark pattern element. These wing patterns therefore violate the uniform wing-margin model because there is not a one-to-one correspondence between wing veins and dark pattern elements along the costa.

All of the wings examined violate the alternating wing-margin model as well. The alternating wing-margin model predicts that Rs_1 and Rs_3 will be surrounded by concolorous pattern elements and that Rs_2 will be surrounded by a pattern element of a different color; this is not the case for the majority of the wings examined (Figures 4, 7b,c, 9c,d, 10a–d, 11c–f, and 12). On the remaining wings, Rs_1 and Rs_3 are surrounded by dark pattern elements and Rs_2 is surrounded by a light pattern element (Figures 5–7a,d–f, 8–9a,b, 10e,f, and 11a,b). However an examination of Sc and R shows that these patterns violate the alternating wing-margin model. Because Sc in *Hydriomena* corresponds to the plesiomorphic lepidopteran Sc_3 , and because R in

Hydriomena corresponds to the plesiomorphic lepidopteran R_2 , the alternating wing-margin model predicts that both of these veins should be surrounded by the same color pattern element that surrounds Rs_2 —in this instance, a light pattern element. However, this is not the case for any of the wings in which Rs_1 and Rs_3 are surrounded by dark pattern elements and Rs_2 is surrounded by a light pattern element: either Sc (Figures 7e,f, 8c, and 9A) or both Sc and R (Figures 5–6, 8a,b,d, 9b, 10e,f, and 11A) are surrounded by dark pattern elements. On such wings for which the Sc vein cannot be observed, R is surrounded by a dark pattern element (Figures 7a,d and 11b).

3.2 | Pattern variation at different scales

The relationship between wing pattern and venation varies around every vein that terminates along the costa. The first four veins that terminate along the costa in *Hydriomena*—Sc, R, Rs_1 , and Rs_2 —are surrounded by a dark pattern element along the costa on at least four specimens and by a light pattern element on at least three specimens. Sc is typically surrounded by a dark pattern element (Figures 4–7e,f, 8–9a,b, 10c–f, 11, and 12c,d), with one exception in the *H. speciosata* species group (Figure 9c,d) and with three exceptions in *H. costipunctata* (Figures 10a,b and 12a,b,e,f). In moths belonging to the *H. speciosata* group that are not from the Arcata population, R is equally likely to be surrounded along the costa by a dark pattern element (Figures 8a,b,d and 9b) or by a light pattern element (Figures 8c and 9a,c,d). In the *H. speciosata* population from Arcata and in *H. costipunctata*, R is most commonly surrounded by a dark pattern element (Figures 4–7a–d, 10–11, and 12b,e,f), with just a few exceptions (Figures 7e,f and 12a,c,d). Rs_1 is the vein whose relationship with

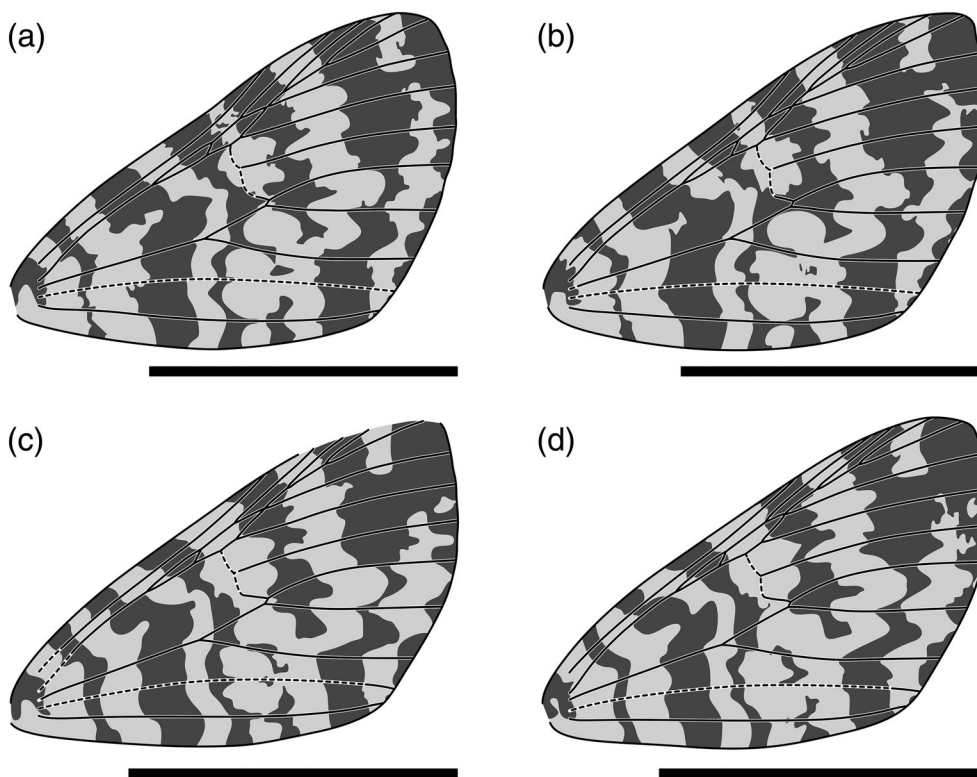
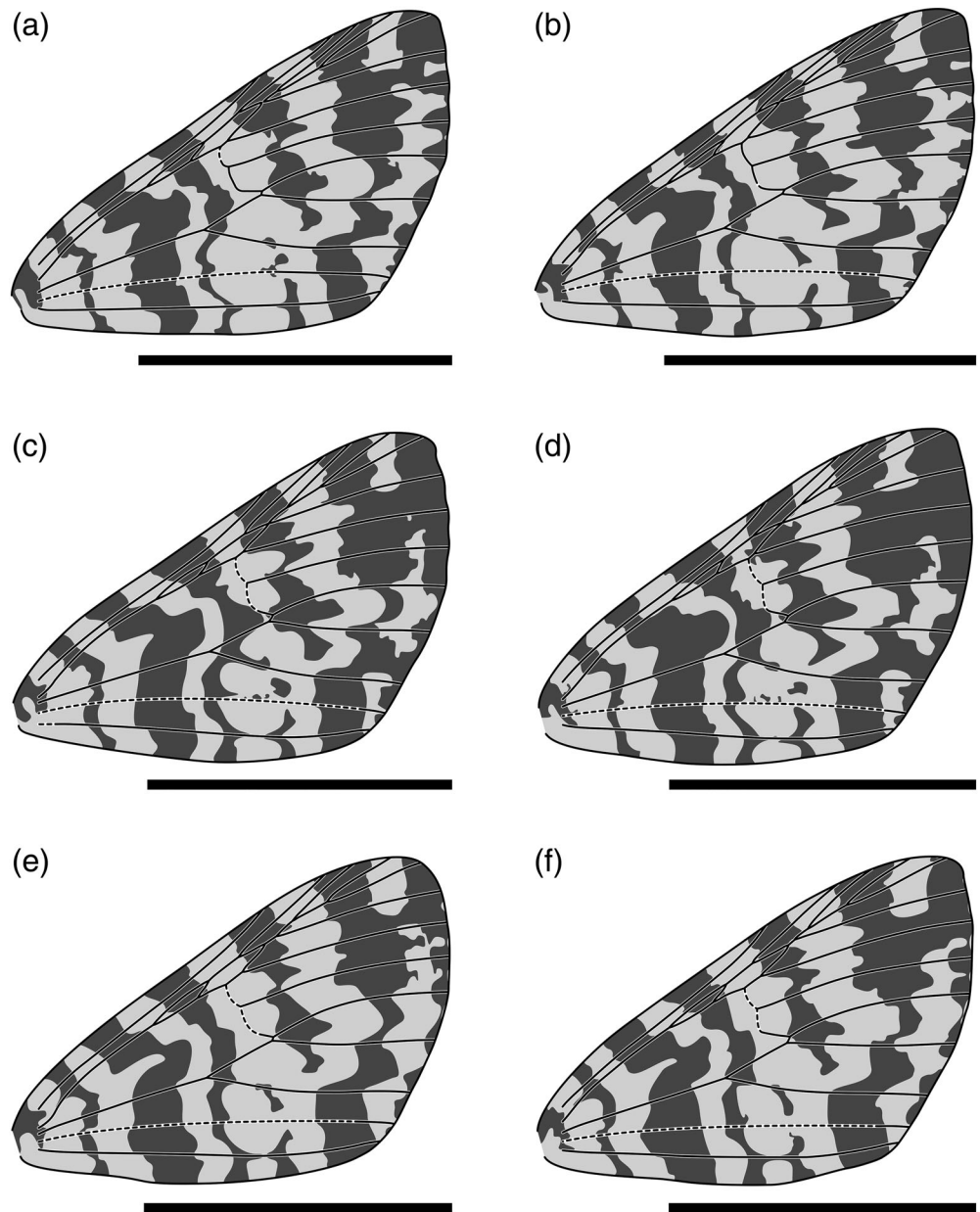


FIGURE 4 Wing pattern in males from the *Hydriomena speciosata* population from Arcata, California. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) CASENT 8277789. (c, d) CASENT 8277788; the apex is folded in (c), denoted by the break in the black outline of the wing

FIGURE 5 Wing pattern in males from the *Hydriomena speciosata* population from Arcata, California, continued. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) CASENT 8277785. (c, d) CASENT 8277786. (e, f) CASENT 8277787



wing pattern differs most between the *H. speciosata* group and *H. costipunctata*. This vein is typically surrounded by a dark pattern element for the *H. speciosata* group (Figures 4–7a,b,e, and 8) with unambiguous exceptions on only two specimens (Figures 7c and 9c,d). For *H. costipunctata*, Rs_1 is most commonly surrounded by a light pattern element (Figures 10c,d, 11c–f, and 12) with unambiguous exceptions on only two specimens (Figures 10e,f and 11a,b).

Rs_2 is the only vein that is typically surrounded by a light pattern element. This finding holds both for the *H. speciosata* species group (Figures 5–9) and for *H. costipunctata* (Figures 10e,f, 11, and 12c–f). In *H. speciosata*, the only wings on which Rs_2 is surrounded by a dark pattern element are those on which all veins along the costa are surrounded by dark pattern elements (Figure 4). It is slightly more common for Rs_2 to be surrounded by a dark pattern element on the wings of *H. costipunctata* (Figures 10a–d and 12a,b).

Of the veins that occur along the costa, Rs_3 has the most consistent relationship with wing pattern. It is surrounded by a dark pattern element in all *H. costipunctata* specimens (Figures 10–12). This is also typically the case for the *H. speciosata* species group (Figures 4–7a,c–f, 8, and 9a,b,d), with one unambiguous exception (Figure 7b) in which Rs_3 is surrounded along the costa by a minute light pattern element that interrupts a far larger dark pattern element, and with one ambiguous exception in which Rs_3 terminates at the boundary between a dark and a light pattern element (Figure 9c).

The relationship between wing pattern and venation can differ between the right and left forewings of a single individual. Of the 23 specimens examined, 12 have an identical relationship between pattern and venation on the right and left wings, and four do not. For the remaining seven specimens, no definitive statements can be made because the relationship between wing pattern and venation could

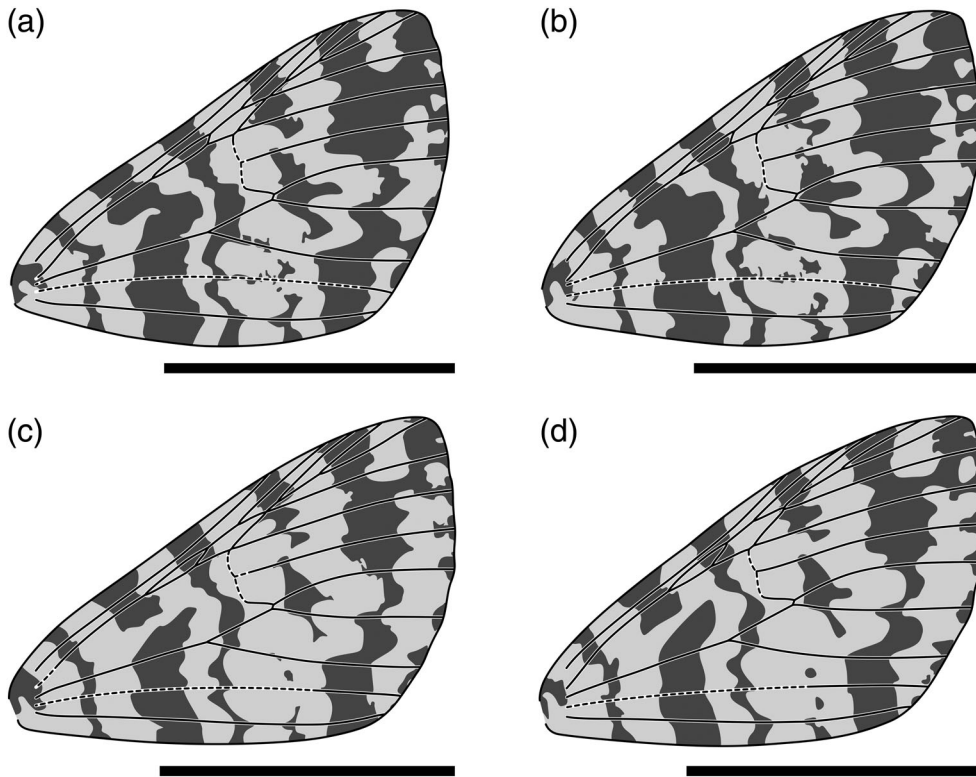


FIGURE 6 Wing pattern in females from the *Hydriomena speciosata* population from Arcata, California. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) CASENT 8277792. (c, d) CASENT 8277793

not be observed for all veins that terminate along the costa or because a vein terminates along the costa at the boundary between two pattern elements. Sixteen of the specimens examined have wings whose costa is intact, allowing comparison between the left and right wings. The relationship between wing pattern and venation is identical on 12 of these 16 specimens (Figures 4a,b, 5–6, 8a,b, 10c–f, 11c–f, and 12e,f). Four specimens have unambiguously dissimilar relationship between wing pattern and venation on the right versus left wings (Figures 7a,b, 8c,d, 9a,b, and 12a,b). In five specimens this relationship appears identical, but a tear or fold along the costa precludes any more definitive statements to this effect (Figures 4c,d, 7c,d, 10a,b, 11a,b, and 12c,d). Two specimens have intact wings for which it is impossible to make a definitive statement because one vein terminates along the margin between a dark and a light pattern element (Figures 7e,f and 9c,d).

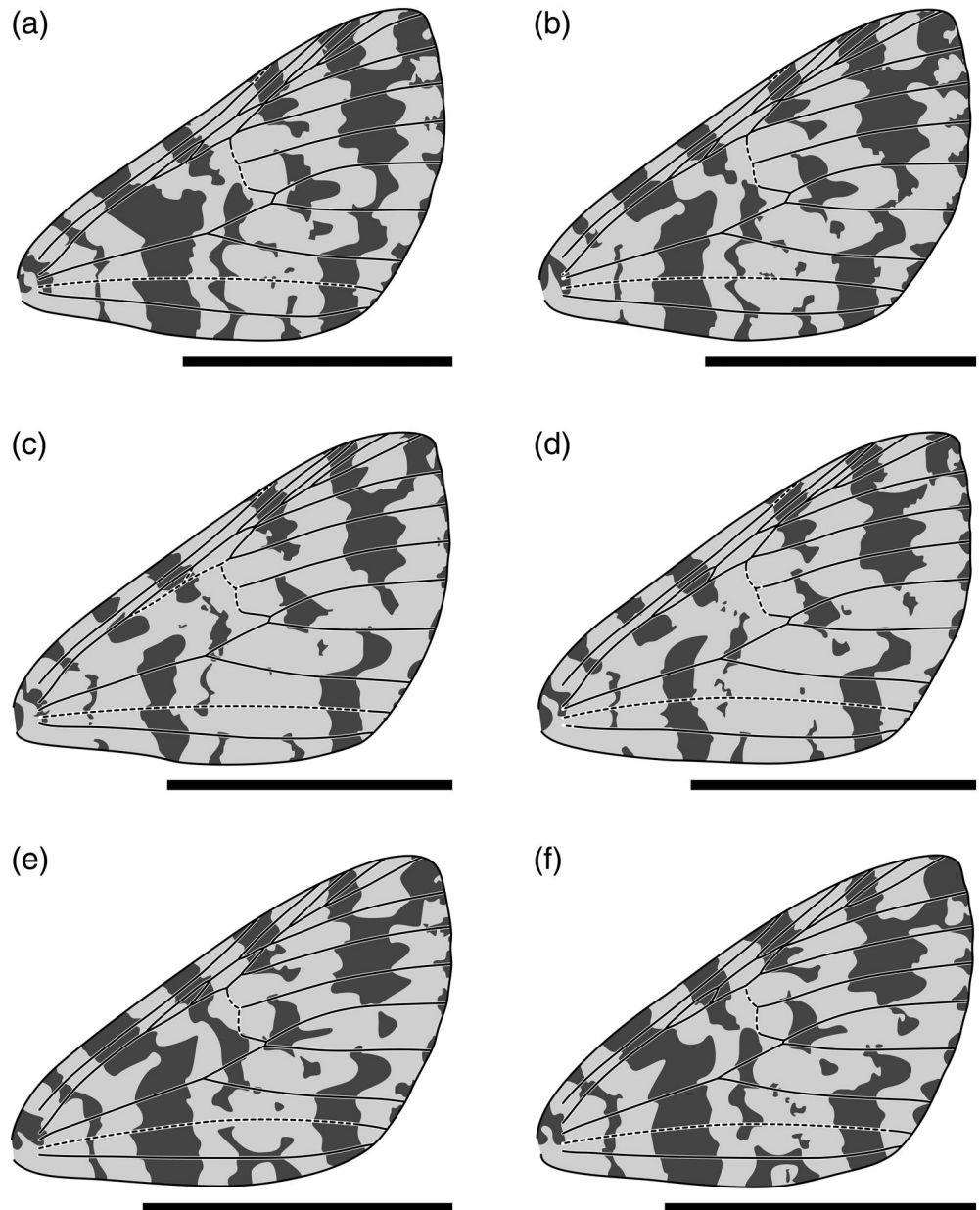
In the *H. speciosata* population from Arcata, there is variation within and between sexes. The darkest wing patterns belong to males and the lightest to females. Males tend to have more veins surrounded by dark pattern elements. The only two specimens on which veins Sc–Rs₄ are all surrounded by dark pattern elements along the costa, are male (Figure 4). On the remaining three males from this population, Rs₂ is surrounded by a light pattern element along the costa, with Sc–Rs₁ and Rs₃–Rs₄ all surrounded by dark pattern elements (Figure 5). Rs₂ is also surrounded by a light pattern element along the costa in all females from this population. On half of the wings belonging to females, it is again the case that all other veins are surrounded by dark pattern elements (Figures 6 and 7A). On the other wings, either R (Figure 7e,f), Rs₁ (Figure 7c,d), or Rs₃ (Figure 7b) is surrounded by a light pattern element.

Pattern elements also tend to be larger, and are more likely to become confluent, on the wings of males than on the wings of females. The wings of all males from the *H. speciosata* population from Arcata contain various transverse bands that run from the costa to the dorsum (Figures 4 and 5) but this is only the case for three of the five females that were examined—the same three females for which Rs₂ is the only vein that is surrounded by a light pattern element along the costa (Figures 6 and 7a,b). On another female from Arcata, the most distal of the transverse bands, which surrounds Rs₁ along the costa, is fragmented (Figure 7e,f). The other female from Arcata does not have a single intact transverse band anywhere on either wing (Figure 7c,d).

The dark pattern elements on the wings of *H. speciosata* tend to be larger than those of *H. costipunctata*. The wings of *H. speciosata* from Arcata typically have complete transverse bands (Figures 4–7a,b) and the other wings examined from the *H. speciosata* group contain dark pattern elements that are at least as large (Figures 8 and 9c,d) if not noticeably larger (Figure 9a,b). In contrast, not one of the nine *H. costipunctata* specimens examined here has a single complete transverse band (Figures 10–12).

However, the relationship between wing pattern and venation is not fundamentally different between *H. costipunctata* and the *H. speciosata* species group. On the wings of two of the nine *H. costipunctata* specimens examined (Figures 10e,f and 11a,b), all veins except Rs₂ are surrounded by dark pattern elements along the costa, as is often the case for *H. speciosata*. On the wings of another specimen (Figure 10c,d), all veins except Rs₁ are surrounded by dark pattern elements along the costa. On the wings of the other specimens, either two veins (Figures 11c–f and 12b) or three veins

FIGURE 7 Wing pattern in females from the *Hydriomena speciosata* population from Arcata, California, continued. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) CASENT 8277794. (c, d) CASENT 8277791. (e, f) CASENT 8277790



(Figure 12a,c-f) are surrounded by light pattern elements along the costa. However the only specimens examined for which four veins are surrounded by dark pattern elements belong to the *H. speciosata* group (Figure 9c,d). Specimens from the *H. speciosata* group account for the majority of wings examined for this study (14/23, 61%), and have the wings with the most veins surrounded by dark pattern elements and with the fewest veins surrounded by dark pattern elements. Although wings from the *H. speciosata* group tend to have a higher proportion of surface area covered by dark pattern elements, the relationship between wing pattern and venation observed in this group is not distinguishable from that observed in *H. costipunctata*.

3.3 | Wing pattern along the termen

On the wings of *Hydriomena*, no veins reach the posterior margin. Eight veins reach the termen: Rs_4 , M_1 , M_2 , M_3 , CuA_1 , CuA_2 , CuP , and A . The

first five of these— Rs_4 , M_1 , M_2 , M_3 , and CuA_1 —are nearly always surrounded by dark pattern elements (Figures 4a,c,d, 5–9a–c, 10–11, and 12), with rare exceptions in which M_3 (Figure 4b) and CuA_1 (Figure 9d) are surrounded by small, light pattern elements. In the *H. speciosata* species group, Rs_3 and Rs_4 are typically surrounded by the same large, contiguous pattern element (Figures 5a,b,e, 6a,b, 7f, 8b,c, and 9a,b,d) that occasionally extends posteriorly past M_1 (Figure 4) or even past M_3 (Figures 5c,d). A light pattern element sometimes appears along the margin between Rs_3 and Rs_4 (Figures 5f, 6c,d, 7a,c–e, and 8a,d). In *H. costipunctata*, the pattern elements that surround Rs_3 and Rs_4 are usually separate (Figures 10a,d–f, 11a,b,e,f, and 12), and when they do meet in the interior of the wing there is still a light pattern element along the margin between the points where these two veins terminate (Figures 10c and 11c,d), with one exception (Figure 10b).

In the *H. speciosata* species group, dark spots occur on either side of CuA_2 . These spots are usually confluent along the margin,

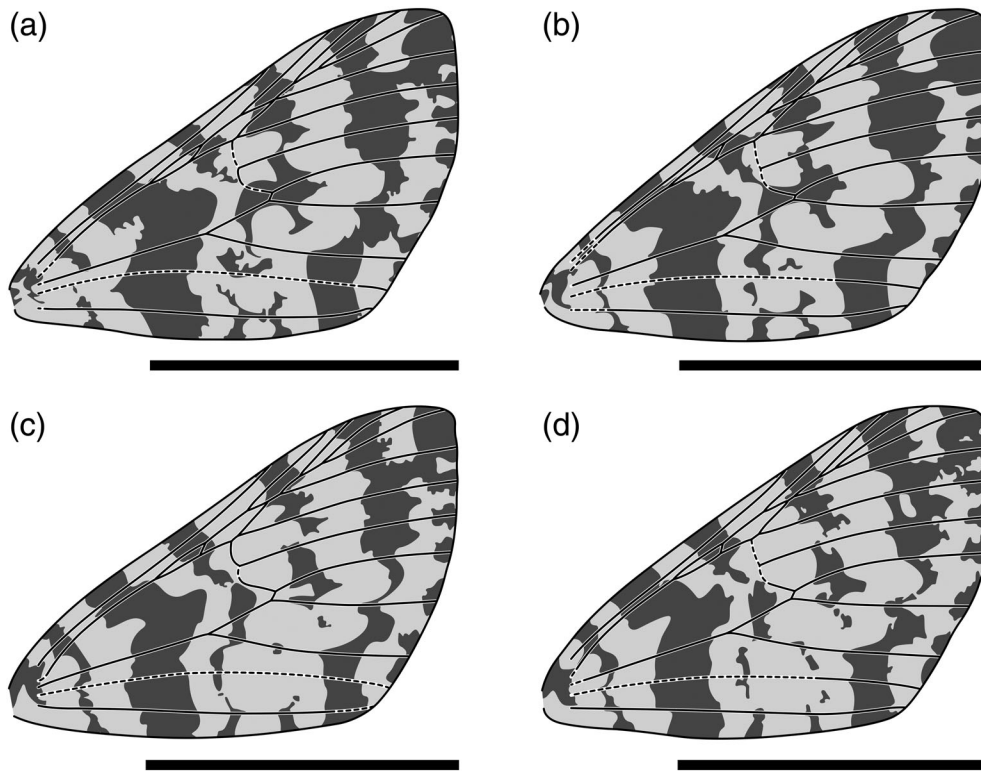


FIGURE 8 Wing pattern in the *Hydiomena speciosata* group. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) EMEC 255354. (c, d) EMEC 255351

such that CuA_2 is surrounded by dark scales at the point where it terminates (Figures 4–7a,b,d,f, 8c,d, and 9b). However, the spots on either side of CuA_2 occasionally remain separate, leaving this vein surrounded by light scales (Figures 7c,e, 8a, and 9a,c,d). On one wing, the two spots remain separate and one of them surrounds

CuA_2 (Figure 8b). In *H. costipunctata*, CuA_2 is always surrounded by a single dark spot (Figures 10c,d and 11a,b,e,f), although the shape of this spot often appears consistent with the premise that two separate dark spots became confluent along the termen (Figures 10a,b,e,f, 11c,d, and 12). CuP and A are typically

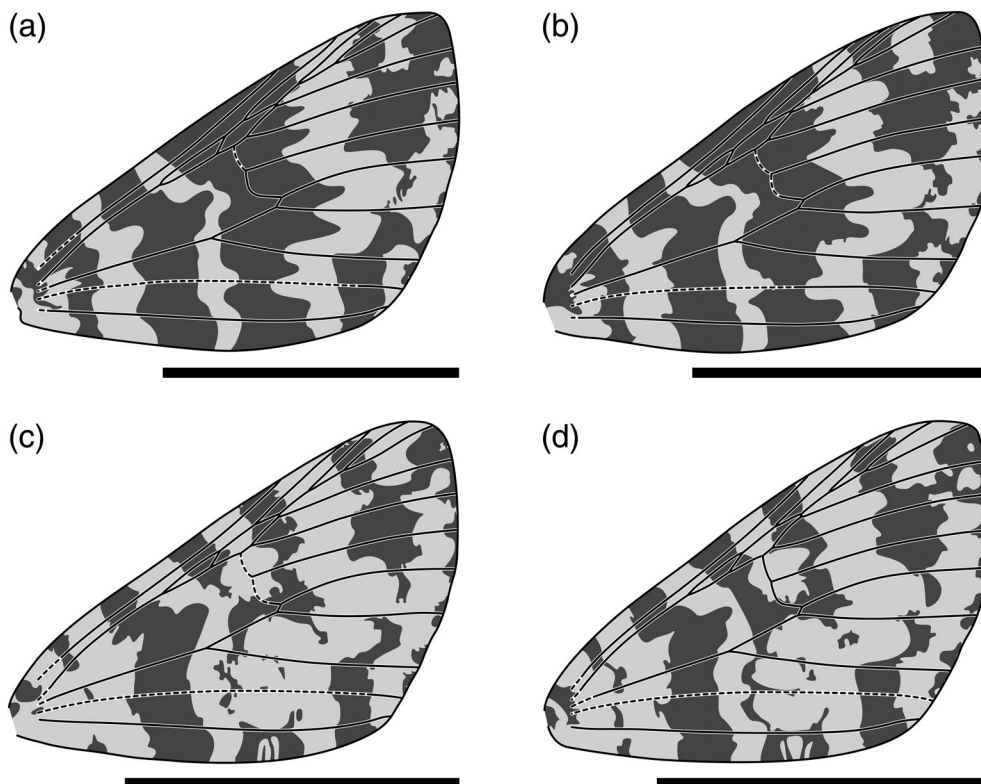
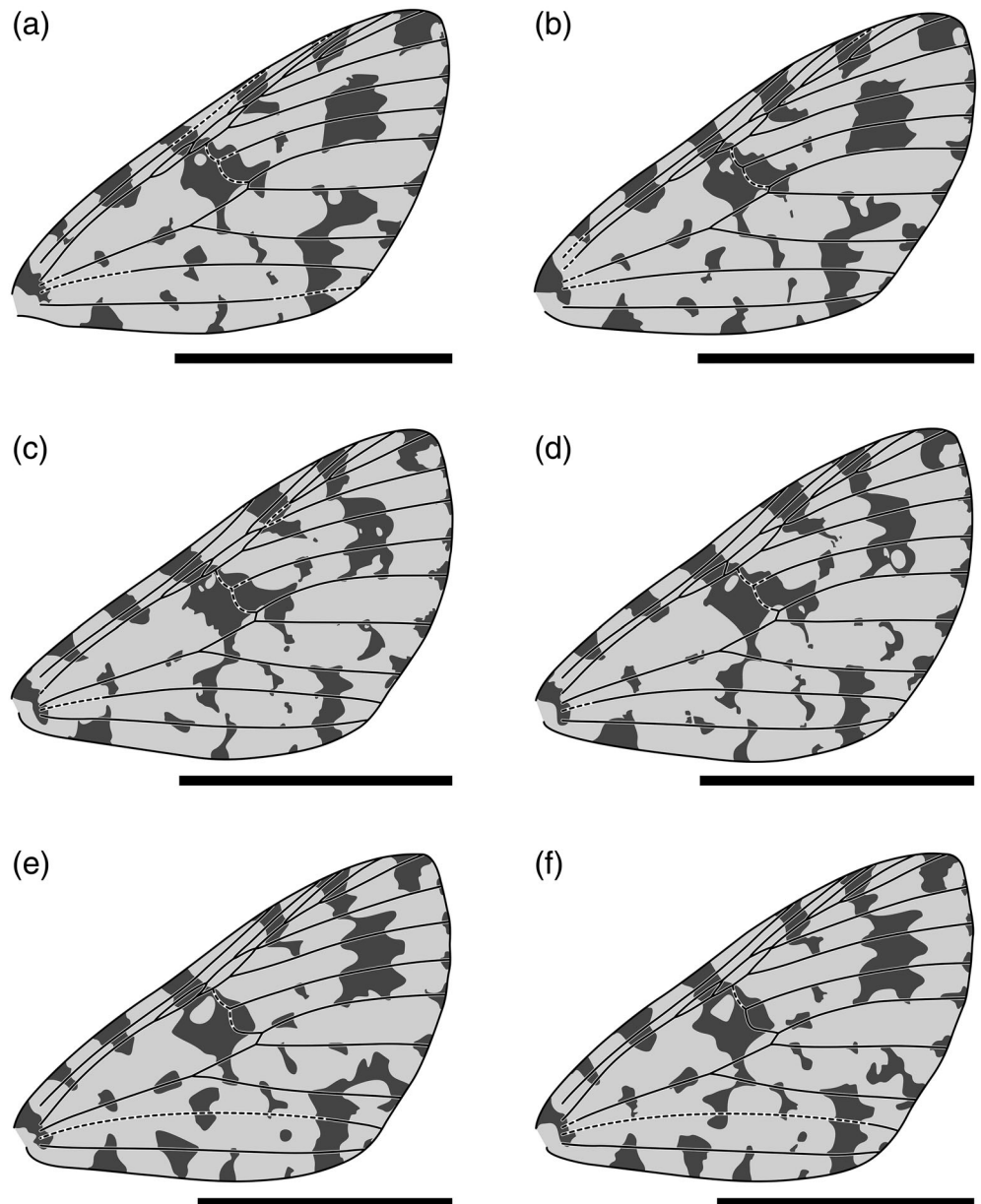


FIGURE 9 Wing pattern in the *Hydiomena speciosata* group, continued. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) EMEC 255353. (c, d) EMEC 255352

FIGURE 10 Wing pattern in *Hydriomena costipunctata*. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) EMEC 255350. (c, d) EMEC 255358. (e, f) EMEC 255356



surrounded by the same light pattern element (Figures 4–5a–c,e,f, 6–10a,c,d, 11a–d,f, and 12a,f). There is a rare exception in which CuP is surrounded by a dark pattern element in *H. speciosata* (Figure 5d). A more common exception for A to be surrounded by a dark pattern element in *H. costipunctata* (Figures 10b,e,f, 11e, and 12b–e).

3.4 | A wing pattern groundplan for *Hydriomena*

Despite the lack of a predictable relationship between wing pattern and venation, pattern elements occur on the wings of the *H. speciosata* species group and *H. costipunctata* with sufficient consistency to allow the description of a wing pattern groundplan for these species. Seven dark bands occur along the costa. The most distal of these reaches the apex and can become reduced in

H. costipunctata, leaving it confined to the apex (Figure 11a,b). The wings of only one individual appear to have fewer than seven dark transverse bands that reach the costa, and it is quite clear that the fourth and fifth transverse bands have become confluent (Figure 9a, b). A spot often occurs at the base of the wing in the *H. speciosata* species group and either is confluent with the first transverse band that reaches the costa (Figures 4–5b–f, 6–7a,b,d–f, 8c,d, and 9b) or reaches a small portion the costa while remaining separate from that band (Figures 7c, 8a,b, and 9a,c,d).

In the *H. speciosata* species group, five of the seven transverse bands mentioned above reach the posterior margin of the wing (Figures 4–9c,d). The only exception is the specimen in which the fourth and fifth transverse bands have become confluent; these are the third and fourth transverse bands that reach the posterior margin (Figure 9a,b). Five pattern elements occur along the posterior margin

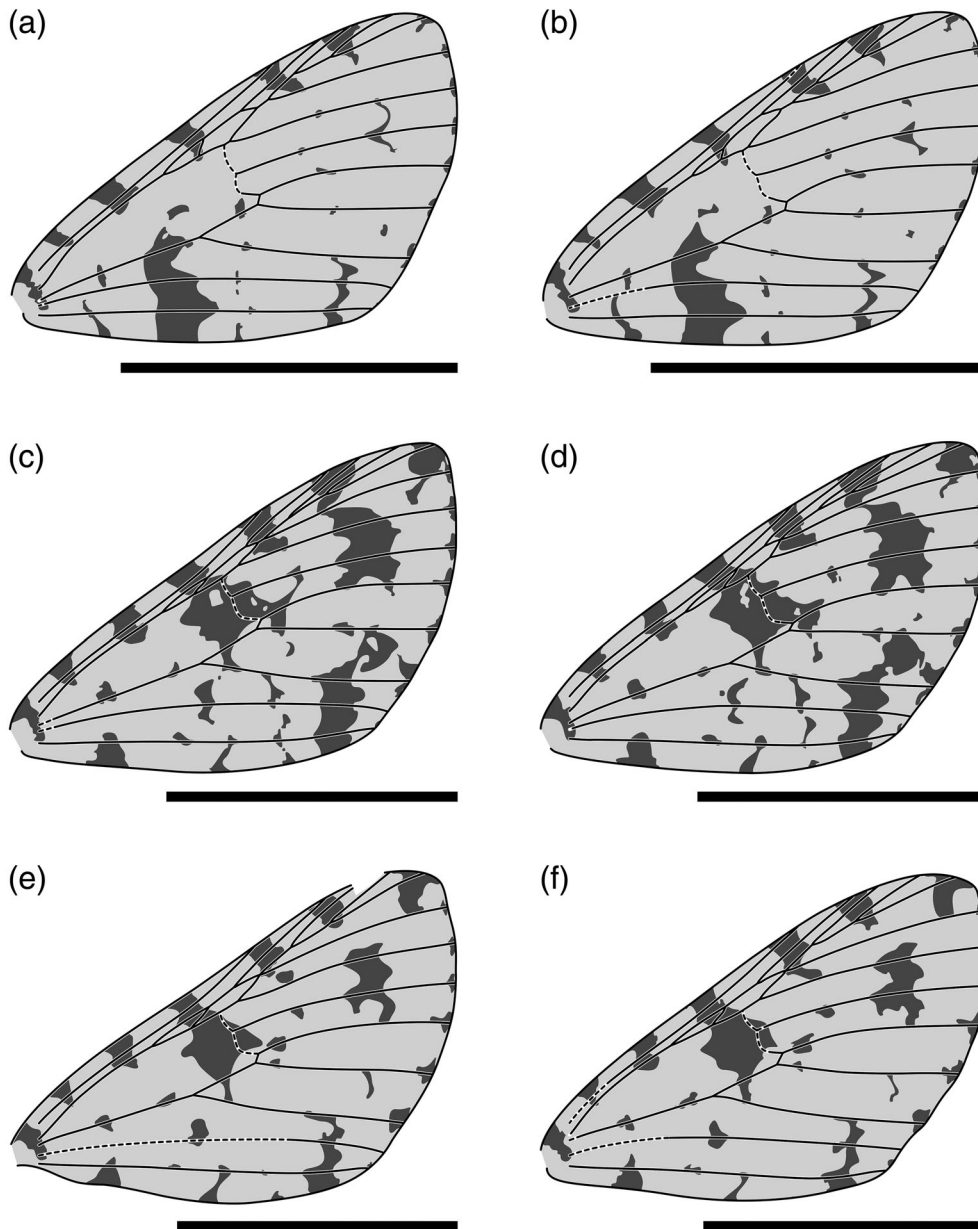


FIGURE 11 Wing pattern in *Hydiomena costipunctata*, continued. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) EMEC 255366. (c, d) EMEC 255359. (e, f) EMEC 255360; the wing is broken near the apex in (e), denoted by the break in the black outline of the wing

in four of the *H. costipunctata* specimens examined (Figures 10e,f and 12), but these never form complete transverse bands that extend uninterrupted from the costa to the posterior margin. In the other *H. costipunctata* specimens, only four (Figures 10a–d and 11a–e) or even just three (Figure 11f) pattern elements occur along the posterior margin.

The same number of pattern elements can be identified on the costa and on the posterior margin for the two species groups examined here, allowing the enumeration of a wing pattern groundplan for these taxa. *H. costipunctata* always has many small pattern elements that occur in the interior of the wing and do not reach the margin (Figures 10 and 12). This is often the case for the *H. speciosata* species group as well (Figures 6a,b, 7–8c,d, and 9c,d), however on many wings there are only one or two pattern elements that do not reach the costa (Figures 4–6c,d, and 8a,b). The only specimen that does not

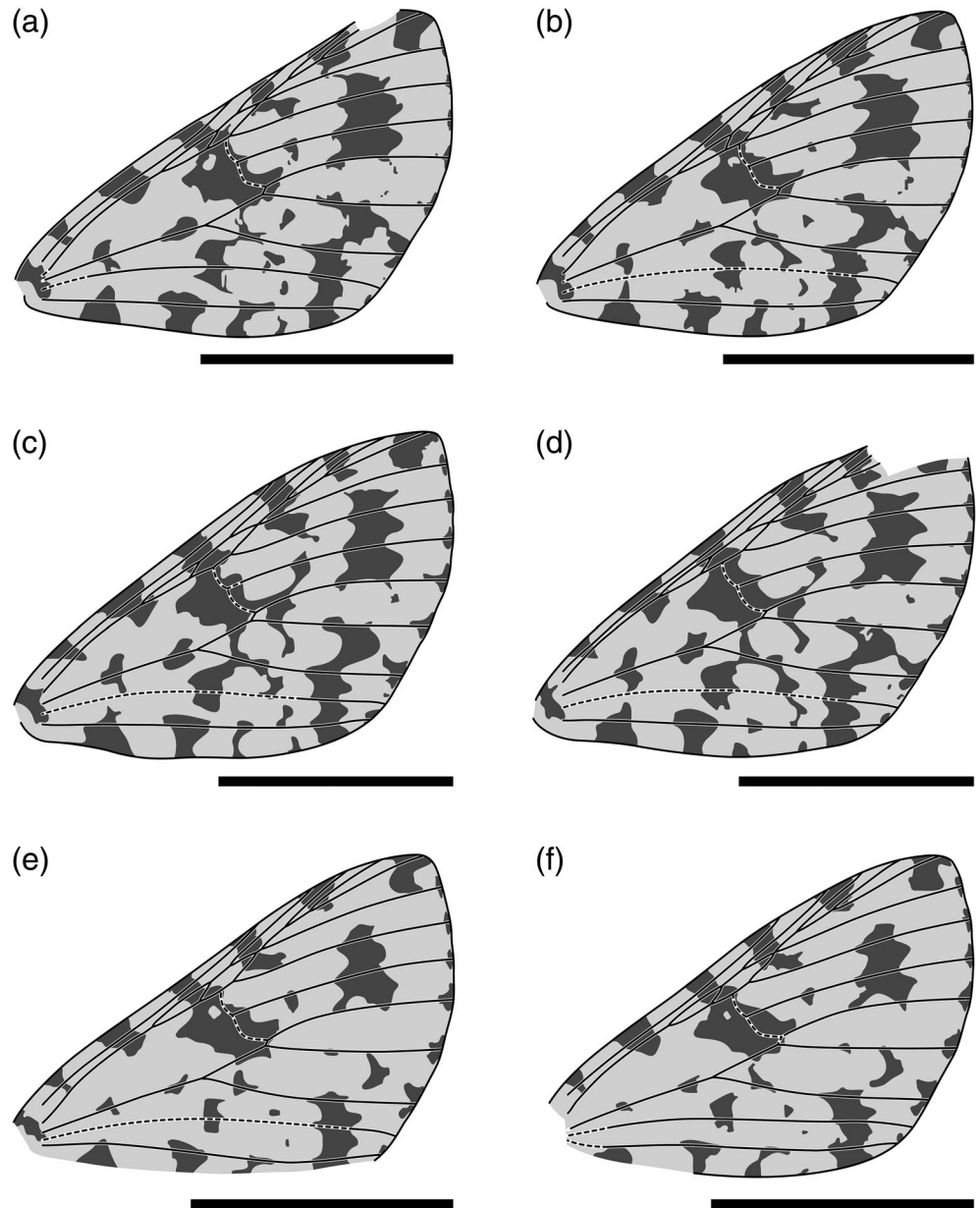
have a single pattern element confined to the interior of the wing is the specimen with confluent transverse bands (Figure 9a,b). When pattern elements occur in the interior of the wing and do not reach the margin, they appear to be fragments of the transverse bands seen in the *H. speciosata* group.

The wing patterns shown in Figures 7a and 12f are illustrated without venation in Figure 13 because these typify the wing patterns of the *H. speciosata* species group and of *H. costipunctata*, respectively.

4 | DISCUSSION

Hydiomena is the first genus of Lepidoptera documented to violate both the alternating wing-margin model and the uniform wing-margin model. The relationship between wing pattern and venation along the

FIGURE 12 Wing pattern in *Hydriomena costipunctata*, continued. Scale bars represent 1 cm. Wings in the left column are left wings that have been flipped horizontally for ease of comparison. Specimen numbers are as follows. (a, b) EMEC 255362; the wing is broken near the apex in (a), denoted by the break in the black outline of the wing. (c, d) EMEC 255349; the apex is broken in (d), denoted by the break in the black outline of the wing. (e, f) EMEC 255368; the wing is folded along the posterior margin in both (e) and (f), denoted by the break in the black outline of the wing



costa is as variable as possible in that all five veins that terminate along the costa—Sc, R, Rs_1 , Rs_2 , and Rs_3 —are surrounded by light pattern elements on some of the wings examined and by dark pattern elements on others.

Whenever 20 or more representatives of a genus or family have been examined in this context, various individuals violate both of the wing-margin models. These models emerged as archetypes, discerned after the examination of many individuals (Baixeras, 2002; Brown & Powell, 1991). However, all other lineages that have been examined to date differ from *Hydriomena* in two ways. First, a majority of specimens examined follow one of these two models in the other lineages examined, whereas in *Hydriomena*, not a single specimen follows either model. Second, in the other lineages, violations of the models tend to occur in systematic, predictable ways. In *Micropterix* Hübner, 1825 and in species of *Sabatinca* Walker, 1863 that occur in

New Zealand, the majority of specimens examined have wing patterns that conform to the alternating wing-margin model, with violations of this model attributable to confluence or lack of expression (Schachat & Brown, 2015, 2016). The uniform wing-margin model typically holds for the tineid genus *Moerarchis* Durrant, 1914, and violations of this model can be attributed to transitions to the alternating wing-margin model (Schachat, 2017b). The uniform wing-margin model also predicts the relationship between wing pattern and venation in various psychid genera from Australia and for the xylocyctid genus *Lichenaula* Meyrick, 1890. Violations of this model in both lineages tend to occur as spots diminish in size toward the apex of the wing, sometimes becoming so small that they are confined to the wing fringe and therefore cannot overlap with any veins (Schachat, 2017a; Schachat & Brown, 2018). In Acronictinae, the only other macroheteroceran lineage examined to date, the relationship between

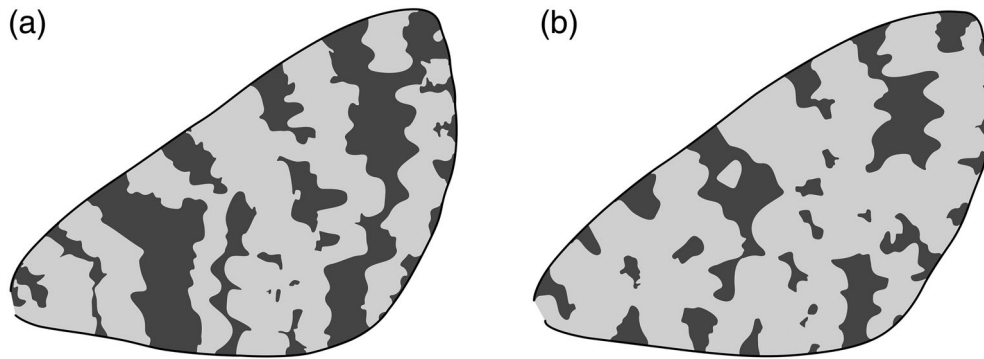


FIGURE 13 Exemplars of wing pattern groundplans for the two species groups examined here, illustrated without venation because the relationship between wing pattern and venation is so inconsistent in *Hydriomena*. (a) A representative of the *Hydriomena speciosata* group: the left wing of specimen CASENT 8277794, illustrated with venation in Figure 7a. (b) A representative of *Hydriomena costipunctata*: the left wing of specimen EMEC 255368, illustrated with venation in Figure 12f

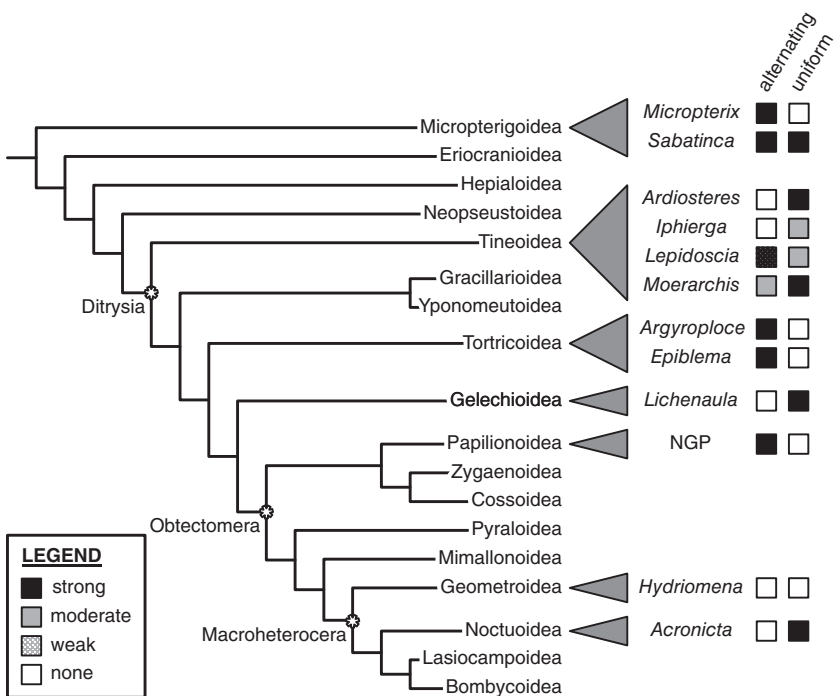


FIGURE 14 Support for the “alternating” and “uniform” wing margin models, in phylogenetic context. Modified from Schachat & Goldstein, 2018

wing pattern and venation was not found to violate the uniform wing-margin model (Schachat & Goldstein, 2018).

Hydriomena is therefore the only lineage examined thus far for which not a single wing conforms to either model and for which no conclusions can be drawn as to whether either model represents an ancestral state for this genus. Because the nymphalid groundplan conforms to the alternating wing-margin model, Acronictinae conform to the uniform wing-margin model, and *Hydriomena* does not conform to either, the relationship between wing pattern and venation in Obtectomera appears to be as variable as possible given that data are available for only three disparate taxa (Figure 14). The wing patterns of Nymphalidae and Acronictinae have clear developmental commonalities with wing patterns in different groups of Microlepidoptera, but the wing patterns of *Hydriomena* appear to be governed by entirely different developmental constraints.

The lack of any consistent relationship between wing pattern and venation along the costa of *Hydriomena* is somewhat surprising given the consistent relationship observed along the termen. In groups that conform to the alternating wing-margin model, the implications of this model for the termen and for the posterior margin are obscured by the confluence of pattern elements (Schachat & Brown, 2015, 2016) and by the lack of expression of plesiomorphic veins (Schachat & Gibbs, 2016). In microlepidopteran groups that conform to the uniform wing-margin model, one spot tends to surround each vein along the termen and along the posterior margin, with the consistent exception of CuP (Schachat, 2017b) and the occasional exception of A (Schachat, 2017a). Acronictinae also conform to the uniform wing-margin model, but along the termen in this group, dark spots occur between veins instead of on them (Schachat & Goldstein, 2018). The relationship between wing pattern and venation along the termen of

Hydriomena is most reminiscent of that seen in the microlepidopteran genera *Moerarchis* and especially *Lichenaula*. This finding suggests that wing pattern in *Hydriomena* is more consistent with the uniform wing-margin model than the alternating wing-margin model, but no definitive statements can be made because neither model has any predictive power for the costa in this genus.

The inconsistent relationship between wing pattern and venation along the costa of *Hydriomena* is also surprising given the consistency with which this genus conforms to the groundplan articulated above, which applies to wing pattern alone. The number of pattern elements and their relative positions in both species groups can be predicted for the entirety of the wing margin, and the size of those pattern elements can also be predicted for each species group—the smaller, more numerous dark pattern elements on the wings of *H. costipunctata* appear to be fragments of the larger, contiguous transverse bands that occur on the wings of the *H. speciosata* species group. The lack of a relationship between wing pattern and venation in *Hydriomena*, despite the relative uniformity of the size and position of pattern elements, suggests that the degree of variability in the appearance of pattern elements has no relationship with the degree of variability in the relationship between wing pattern and venation. In the tineid species *Moerarchis clathrata* (Felder and Rogenhofer, 1875) there is a consistent relationship between wing pattern and venation, but wing pattern is nevertheless variable in the number of pattern elements, their size, and their location on the wing (Schachat, 2017b). In contrast, *Hydriomena* shows no consistent relationship between wing pattern and venation along the costa but the size and location of pattern elements is highly predictable.

4.1 | The importance of wing venation in Obtectomera

The relevance of wing venation along the costa has been a key feature of the nymphalid groundplan from its inception. The two authors who independently described the nymphalid groundplan in the 1920s both discerned the same relationship between wing pattern and venation along the costa: the entirety of the central symmetry system reaches the costa proximal to the point where Sc terminates, and the marginal band system reaches the costa proximal to the point where Rs₂ terminates (Schwanwitsch, 1924; Süffert, 1927). The relationship of the border symmetry system to the costal margin is obscured somewhat because Schwanwitsch illustrated pattern elements between R/Rs₂ and A, rather than between the costal and posterior margins as Süffert did, but Süffert's version of the nymphalid groundplan shows the border symmetry system reaching the costa around Rs₁, between R and Rs₂, and Schwanwitsch's version does not contradict this. More recent renditions of the nymphalid groundplan (Nijhout, 1991; Otaki, 2012) show a relationship between wing pattern and venation along the costa equivalent to that seen in the micropterigid genus *Sabatinca* (Schachat & Brown, 2016), suggesting that the role of venation in the development of butterfly wing patterns may reflect the ancestral state for crown Lepidoptera.

Furthermore, a feature of the nymphalid groundplan noted in one of the two original descriptions (Süffert, 1927) and in recent iterations (Nijhout, 1991; Otaki, 2012) is the ongoing role of plesiomorphic venation that does not occur on the wing of an adult butterfly. One eyespot occurs between each pair of adjacent veins along the termen, except between CuA₂ and A, where two eyespots occur. The ancestral state for crown Lepidoptera includes a vein in this location, CuP. Although this vein does not occur on the adult wing of nymphalid butterflies, it nevertheless constrains the development of their wing patterns. This phenomenon, through which plesiomorphic veins constrain wing pattern development even if absent from the adult wing, has also been documented in the other lineages that follow the alternating wing-margin model (Baixeras, 2002; Brown & Powell, 1991; Schachat & Brown, 2015, 2016). It is therefore no surprise that individual mutant butterflies that lack wing veins still have color patterns that follow the trajectories of ancestral veins (Reed & Gilbert, 2004).

Before the description of the nymphalid groundplan, various authors incorporated phylogenetic information into their studies of lepidopteran wing pattern (Braun, 1914; Eimer, 1889; von Linden, 1902). However, studies of the nymphalid groundplan overwhelmingly eschewed phylogenetic context, treating macroheteroceran wing patterns as variants of the nymphalid groundplan without interrogating any purported phylogenetic justification for doing so (Henke, 1928, 1933; Schwanwitsch, 1956; Süffert, 1929). At present there is no *a priori* reason to expect any features of the nymphalid groundplan, including the relationship between wing pattern and venation that it describes, to represent an ancestral state for Obtectomera or for Macroheterocera. Nothing akin to the nymphalid groundplan has been found in any ditrysian lineages that diverged before Obtectomera (Baixeras, 2002; Braun, 1914, 1923; Brown & Powell, 1991; Schachat, 2017a, 2017b; Schachat & Brown, 2018); studies of wing pattern in butterflies' closest relatives, such as zygaenoid and cossoid moths (Heikkilä et al., 2015; Regier et al., 2013), are lacking; and the relationship between wing pattern and venation outlined in the nymphalid groundplan does not hold for either of the macroheteroceran lineages in which this relationship has been examined.

4.2 | Future directions

The scant available data for Obtectomera suggest that the relationship between wing pattern and venation is highly variable in this clade, casting doubt on the possibility that any one model, such as the nymphalid groundplan, holds across all obtectomeran superfamilies. The variation documented thus far precludes any predictions of what the relationship between wing pattern and venation will be in other obtectomeran superfamilies, highlighting the need for many additional studies.

In addition to the need for preliminary documentation of the relationship between wing pattern and venation in other obtectomeran superfamilies, there is also a need for further studies of Geometridae. *H. costipunctata* and the *H. speciosata* species group were chosen for this study because their simple wing patterns are straightforward, leaving as little room as possible for subjective judgments on the relevance of predictive models. Now that a wing pattern groundplan has

been inferred for two species groups within *Hydriomena*, the relationship between wing pattern and venation should be examined in geometrid lineages with more complex wing pattern elements: symmetry systems reminiscent of the nymphalid groundplan, and the higher-level symmetry systems that initially brought attention to wing pattern in Larentiinae (Süffert, 1929).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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