

Symmetry systems and compartments in Lepidopteran wings: the evolution of a patterning mechanism

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SUMMARY

The wing patterns of butterflies are made up of an array of discrete pattern elements. Wing patterns evolve through changes in the size, shape and color of these pattern elements. The pattern elements are arranged in several parallel symmetry systems that develop independently from one another. The wing is further compartmentalized for color pattern formation by the wing veins. Pattern development in these compartments is largely independent from that in adjacent compartments. This two-fold compartmentalization of the color pattern (by symmetry systems and wing veins) has resulted in an extremely flexible developmental system that allows each pattern element to vary and evolve independently, without the burden of correlated evolution in other elements. The lack of developmental constraints on pattern evolution may explain why butterflies have diverged so dramatically in their color patterns, and why accurate mimicry has evolved so frequently.

This flexible developmental system appears to have evolved from the convergence of two ancient patterning systems that the butterflies inherited from their ancestors. Mapping of various pattern types onto a phylogeny of the Lepidoptera indicates that symmetry systems evolved in several steps from simple spotting patterns. Initially all such patterns were developmentally identical but each

became individuated in the immediate ancestors of the butterflies. Compartmentalization by wing veins is found in all Lepidoptera and their sister group the Trichoptera, but affects primarily the ripple patterns that form the background upon which spotting patterns and symmetry systems develop. These background patterns are determined earlier in ontogeny than are the symmetry systems, and the compartmentalization mechanism is presumably no longer active when the latter develop. It appears that both individuation of symmetry systems and compartmentalization by the wing veins began at or near the wing margin. Only the butterflies and their immediate ancestors evolved a pattern formation mechanism that combines the development of a regular array of well-differentiated symmetry systems with the mechanism that compartmentalizes the wing with respect to color pattern formation. The result was an uncoupling of symmetry system development in each wing cell. This, together with the individuation of symmetry systems, yielded an essentially mosaic developmental system of unprecedented permutational flexibility that enabled the great radiation of butterfly wing patterns.

Key words: symmetry, compartment, Lepidoptera, wing, pattern formation, butterfly

INTRODUCTION

The color patterns on the wings of butterflies are examples of pure pattern formation without morphogenesis. Cell movement and cell division play no role in pattern determination and differentiation in this system. Each surface of a wing is a monolayer of epidermal cells. The color pattern is a product of the interactions among intercellular signalling mechanisms that determine the spatially patterned synthesis of pigments (Nijhout, 1990, 1991). The color patterns that result are highly organized systems of discrete pattern elements, each with a species-characteristic position, size, shape and color. Not only is the arrangement and morphology of the pattern elements identical among the individuals of a species, but individual pattern elements can be traced from species to species, across genera, and often across families. Thus in the course of pattern evolution, each of the pattern elements that makes up the

overall wing pattern has become individuated and the elements of the color pattern adhere to a system of homologies that is every bit as consistent as that observed in the bones of tetrapod limbs and vertebrate skulls.

The system of homologies among pattern elements in butterflies is called the nymphalid groundplan (Schwanwitsch, 1924; Süffert, 1927; Nijhout, 1991). The nymphalid groundplan consists of three sets of paired bands called symmetry systems. Butterflies have three such symmetry systems on their wings, the basal symmetry system, central symmetry system and border symmetry system. In a few species, the bands of these symmetry systems run uninterrupted from the anterior to the posterior margin of the wing, but in the vast majority of species the bands are interrupted and their position is dislocated wherever they cross a wing vein. Each band is thus broken up into a series of short segments, or pattern elements, by the venation system of the wing.

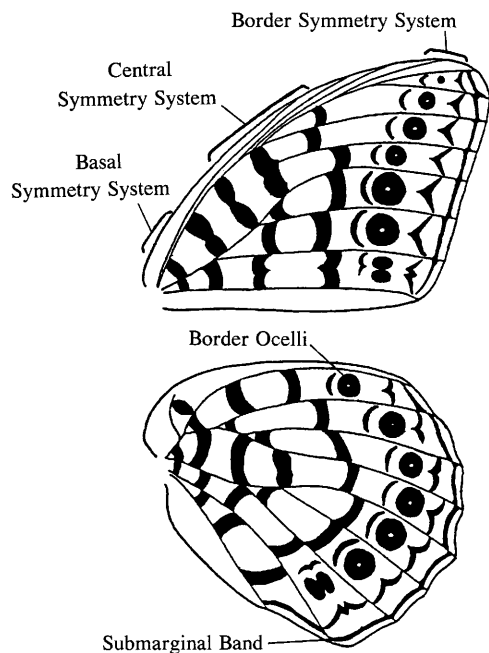


Fig. 1. The nymphalid groundplan. The butterfly wing pattern is compartmentalized into three developmentally independent symmetry systems of pigmented bands. The border symmetry system is usually the most elaborate with eyespot patterns developed along its midline; there is characteristically one such eyespot in each wing-cell. The wing pattern is also compartmentalized by the wing veins so that the elements of each symmetry system in a given wing cell develop largely independently from their homologs in adjacent wing-cells.

In butterflies, the wing veins in effect compartmentalize the color pattern, and the overall wing pattern is a serial repetition of fundamentally similar pattern elements in each wing-cell (the area between wing veins). Fig. 1 shows a version of the nymphalid groundplan that emphasizes this compartmentalization of the wing pattern by the veins. Each pattern element, then, can be viewed as a member of a rank of serial homologues that corresponds to one of the bands of the classical nymphalid groundplan.

Pattern evolution and diversification in butterflies has occurred via the modification of individual pattern elements. While in some species all members of a homologous series are identical and can be readily recognized as belonging to a single system, in most species individual pattern elements in one or more wing cells have become greatly modified in color, shape or size, and frequently even lost (see Nijhout, 1991, for illustrations). Morphometric and quantitative genetic analyses of pattern variation have revealed that there are no phenotypic or genetic correlations between pattern elements that belong to different homologous series, even when they are adjacent to each other in a wing-cell. (Paulsen and Nijhout, 1993; Paulsen, 1994). These findings suggest that adjacent symmetry systems share few if any genetic determinants. There are small to moderate phenotypic and genetic correlations among the members of a homologous series; these correlations are strongest among elements that have not diverged in morphology and weakest among elements that have diverged greatly (Paulsen and Nijhout, 1993; Paulsen, 1994). Experimental perturbation studies likewise indicate that the development of each

pattern element is uncoupled from that of other elements on the wing, insofar as surgical perturbations of the wing typically only affect the morphology of a single pattern element, leaving the morphology of its immediate neighbors unaffected (Nijhout, 1981, 1991). The genetic and phenotypic evidence thus indicates that the wing pattern is composed of semi-independent pattern elements whose position, size, shape and color can be individually modified to achieve a particular optical effect.

It appears at present that there are few genetic constraints on the independent evolution of pattern elements. The developmental basis of this lack of internal constraint is that the position and morphology of each pattern element is determined by signalling sources whose effects extend only over short distances, and whose signal does not appear to pass across wing veins except in a few instances (Nijhout, 1990, 1991). The evolutionary consequence of this lack of constraint is that it enables natural selection to act on small portions of the pattern, and the response of those parts to selection is not constrained by the correlated evolution of other parts. Pattern formation on butterfly wings apparently exist at or near one of the extremes of a spectrum of developmental constraints. It is a system with relatively little internal fabricational constraint, and this lack of constraint has enabled not only the vast morphological radiation of color patterns we see today, but also the ability of butterfly patterns to easily evolve camouflage and mimicry of great accuracy and detail (Nijhout, 1994a).

The reason this developmental system is so highly flexible is that the wing pattern is compartmentalized in two ways. First, there is a proximodistal compartmentalization by independent symmetry systems, each organized around a discrete set of signalling sources. Second, there is an anteroposterior compartmentalization of the wing surface by the wing veins into compartments, the wing-cells, in which pattern development proceeds autonomously or nearly so. This highly compartmentalized, essentially mosaic, developmental system is to my knowledge unique, and it is therefore of interest to investigate how it might have arisen in evolution.

THE EVOLUTION OF A DEVELOPMENTAL SYSTEM

Molecular evidence

The molecular biology of wing pattern development is still in its infancy. There is preliminary evidence from Sean B. Carroll and his associates (Carroll et al., 1994; Nijhout, 1994b) that the organizing center of developing eyespots in *Precis coenia* is marked by the expression of the *Distal-less* gene. Carroll et al. (1994) hypothesize that the gradients that give rise to eyespots (and by analogy, to the bands of symmetry systems) may be generated by a process similar to, and perhaps evolved from, the proximodistal pattern formation system in insect appendages (Williams and Carroll, 1993). If this hypothesis is correct, then the multiple organizing centers for the color pattern on a butterfly wing may all be derived from the replication and patterned re-expression of the proximodistal axis determining system later in development.

Phylogenetic background

Evidence about the evolutionary origin of a particular feature, when this feature may have originated only once and in the

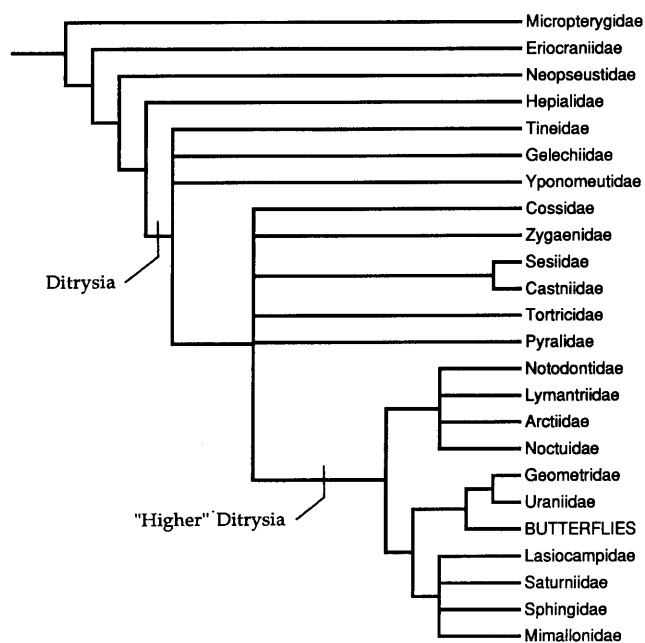


Fig. 2. Phylogenetic relationships among the major families of Lepidoptera. The position of the butterflies (Superfamily Papilionoidea) is indicated. (Based on Nielsen, 1989; Scoble, 1992; Kristensen, 1984).

distant past, must come from comparative studies. The steps involved in the evolution of a particular character from an ancestor that did not possess that character can often be reconstructed by examining how different states of the character are distributed in sister taxa of the group of interest. In the case of butterfly wing patterns, then, we need to ask what evidence we can find for the evolution of this double compartmentalized system from the way in which wing patterns are organized in the moths that constitute the sister taxa to the butterflies.

The basis of all comparative studies is a good phylogeny of the group in question. Whether one interprets a particular character state as primitive or derived in a particular taxonomic group depends on whether or not that character state occurs in the sister group (the out-group rule: Hennig, 1965; Wiley, 1981). Constructing a phylogeny is itself a major task and, while our understanding of the detailed phylogeny of the Lepidoptera is still incomplete, systematists are gradually converging on a common interpretation of its broad outlines. It is fortunate that lepidopteran systematists have not used color pattern characters in their phylogenetic reconstruction, because this means that the existing phylogenies are not loaded, or biased, in favor of a particular model of color pattern evolution.

Fig. 2 shows the phylogenetic relationships among the major families of moths and the placement of the butterflies within the moths. There is a gradually building recognition that the butterflies may share a most recent common ancestor with the geometrid and uraniid moths (Nielsen, 1989), and not with a group of day-flying moths, the Castniidae, as was once thought (Brock, 1971; Common, 1975). The relationships among many of the major groups and families of moths remains unresolved, as can be seen from the many polychotomies in Fig. 2, and lepidopteran systematists continue to disagree on which characters contain useful phylogenetic information (Nielsen, 1989; Scoble, 1992). The major groups of Lepidoptera belong to the

Ditrysia (having two genital openings). Within this group, most authors isolate a large lineage variously called the Higher Ditrysia (shown in Fig. 2) or Obtectomera (Minet, 1991; Nielsen, 1989; Scoble, 1992). There is some disagreement on the placement of the Pyralidae. They are here placed outside the Higher Ditrysia, as suggested by Scoble (1992). The sister group to the order Lepidoptera is the Trichoptera (caddis flies).

Below, I will take note of the distribution of various features of the color pattern in the families shown in this phylogeny. My conclusions are based on many years of comparative studies involving thousands of species of moths. While I have examined species in all families, it is also clear that my studies have not taken in all the species that exist and, insofar as I may have missed some key species, some of the conclusions presented below may be subject to revision. In general, I will assume that if a character is found in a single species of a family, that character is at least potentially present in all members of that family and in all families more distal in the phylogeny, even if it is not expressed in any of them. Many wing pattern characters are expressed sporadically (and apparently erratically) in single species or genera of distantly related families. This observation suggests that the development and expression of many color pattern characters can be readily turned on and off, much in the way a threshold character can disappear and reappear by successively raising and lowering the threshold for its expression. Such evolutionary reversals can be accomplished relatively easily and rapidly.

Not all moths have symmetry systems, nor do all moths have their color pattern compartmentalized by wing veins, and the occurrence of these two features is not correlated in the phylogeny. The question of the evolutionary origin of the butterfly patterning system can therefore be divided into two separate questions: when do symmetry systems first appear, and when does compartmentalization by wing veins first appear? As we will see below, neither of these two simple questions has a simple answer.

The evolution of symmetry systems

Clear examples of multiple, parallel symmetry systems, that run from the anterior to the posterior margin of the wing, are found in all the Higher Ditrysia and in the Pyralidae. The remaining families have either only a single symmetry system or have a foreground pattern of multiple irregular spots or circles. These spots, in turn, may remain isolated or may be fused with one another to various degrees. Families that are most basal in the phylogeny, such as the Micropterygidae (mandibled moths) and many of the 'lower' Ditrysia, have a much simplified banding pattern. In some species there is a single color partition across the wing so that the proximal half is a different color from the distal half. Other species have an irregular band that is either Y-shaped, or broad near both the anterior and posterior margins and constricted or broken near the middle of the wing.

There is no single pattern type that is unambiguously basal or primitive for the Lepidoptera as a whole. There is, not unexpectedly, an overall tendency for patterns to become more complex (i.e. to be composed of more parts, with more morphological diversity among those parts) as one goes up the phylogeny. There is also a general tendency for the number of parallel bands that make up the pattern to increase in number, and a trend from irregular spotting patterns to regular banding

patterns. But there are exceptions (reversals) to all these trends in many families. The detection of trends or transition series is complicated by the fact that the pattern is scale dependent. Small moths have simpler wing patterns than large ones, composed of fewer parts and with less detail in the differentiation of those parts. Some apparent reversals of evolutionary trends in the color pattern are no doubt due to the fact that some families contain many species of small body size. Conversely, in some families with relatively 'primitive' patterns such as the Hepialidae (swift moths), the patterns of species with unusually large body sizes can be surprisingly complex. In order to correctly interpret this diversity of patterns it is necessary to understand the developmental origin of symmetry systems.

Symmetry systems develop around discrete organizing centers. This has been experimentally demonstrated by the work of Kühn and Von Engelhardt (1933), Henke (1933), Wehrmaker (1959), Schwartz (1962), and Toussaint and French (1988). These organizing centers act as sources that establish a gradient whose local value determines the synthesis of different pigments within its field. A point source then gives rise to a pattern of concentric circular bands such as is seen in the eyespots of butterflies; around a row of closely spaced point sources the bands fuse, producing the pattern of parallel bands that we recognize as a symmetry system. The position of a symmetry system is therefore specified by the positions of these organizing centers: in species with a single symmetry system there is a single array of organizing centers; in species with three symmetry systems there are three parallel rows of organizing centers (Nijhout, 1991). In the butterflies there is potentially one such organizing center per wing-cell, but this is not true in the moths. In Pyralidae there are two or three organizing centers for the central symmetry system (Kühn and Von Engelhardt, 1933; Schwartz, 1962; Nijhout, 1991). In the Saturniidae and Lymantriidae too, there appear to be at least two organizing centers (Henke, 1933; Nijhout, 1978). In the Geometridae there appear many centers of origin for the central symmetry system. In some species there is possibly one per wing-cell at the center of a well-developed symmetry system (Fig. 3A), while in others there is no clear symmetry system and the pattern appears to originate from a handful of source scattered across the wing (Fig. 3B). The developmental physiology of these geometrid patterns has not yet been investigated experimentally.

In the ditrysian moths that have well-developed patterns but do not have symmetry systems, such as the Zygaenidae, the wing pattern is composed of roughly circular patterns, often with concentric bands of different colors. These spots may fuse with each other to different degrees and in different combinations, depending on the species. When two spots merge their bands become smoothly continuous. Individual variability and species diversity show that any pair of neighboring spots can fuse (Fig. 4), which implies that all the spots are developmentally equivalent. It is reasonable to assume that these circular patterns represent the precur-

sors (or ancestors) of symmetry systems and that each is organized around a point source of pattern determination, much like the eyespots of butterflies (a proposition that can be tested by ablating the centers of these spots early in development). If this interpretation is correct, then the fact that any pair of spots can fuse implies that the primitive wing pattern develops around an assortment of identical signalling sources. I assume here that these spots develop around organizing centers similar to those described by Kühn and Von Engelhardt (1933), though this proposition has yet to be tested experimentally in the Zygaenidae and most other families of moths.

Families of moths differ in the number and distribution of organizing centers on their wings. The more basal families of moths have relatively few such centers. Most patterns in the Micropterygidae, Gelechiidae and related families, for instance, appear to be derived from a small number of such centers spaced around the periphery of the wing (Fig. 5). These centers can expand to form spots or elongate to form bands, and the spots and bands can fuse in various ways, producing large areas of contrasting color, interdigitating bands and Y-shaped patterns. Each family of these primitive moths tends to have a characteristic pattern of organizing centers and a limited diversity of ways in which the spots and bands that these centers produce expand and fuse with one another. In the Hepialidae, for instance, there are a larger number of sources distributed in what appears to be an haphazard arrangement (Fig. 6), although this arrangement is very consistent throughout the family and produces an array of color patterns that is highly distinctive of this family. In the Hepialidae we also see incipient symmetry systems made up by the fusion of rings that develop around rows of adjoining sources.

The colorful and complex wing patterns of the Arctiidae (tiger moths) are likewise composed of irregular spots and bands that fuse in various patterns. In the Arctiidae we also see the first appearance of a multiple parallel banding pattern (Fig. 7). These bands are derived from the irregular banding pattern, presumably by some process that causes the sources to become aligned in relatively straight and parallel rows. There can be as many as six parallel bands evenly spaced on the wing, all self-symmetrical, and all identical in color. Each of these bands can now be seen as a symmetry system. In the species with such parallel bands there is often a partial local fusion between

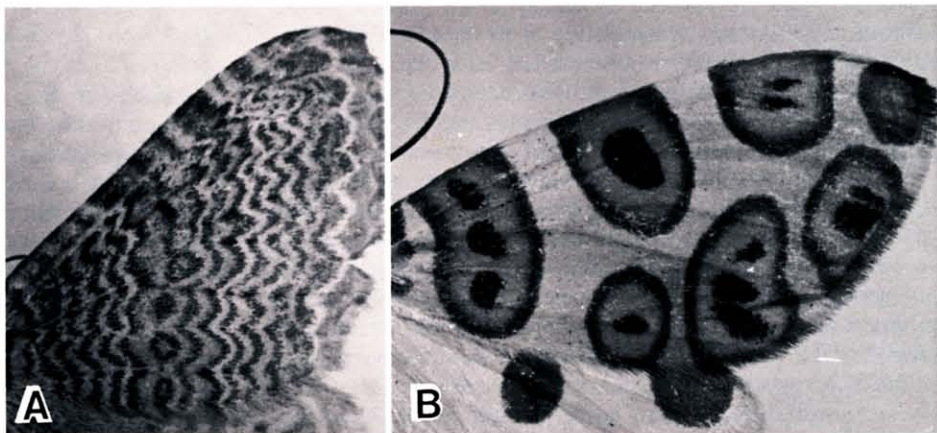


Fig. 3. Wing patterns of two moths in the family Geometridae. (A) *Hydria undulata*; (B) *Pantheroides pardaclis*.

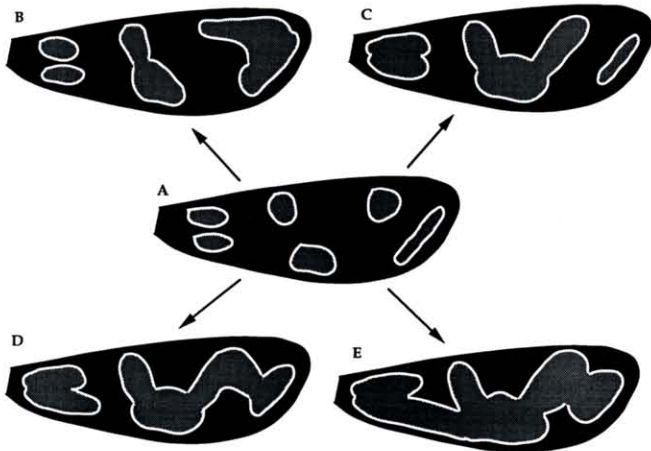


Fig. 4. Wing pattern diversity in the Zygaenidae (B-E) arises from different degrees of enlargement and fusion among roughly circular pattern elements that arise from some six centers of origin scattered across the wing (A).

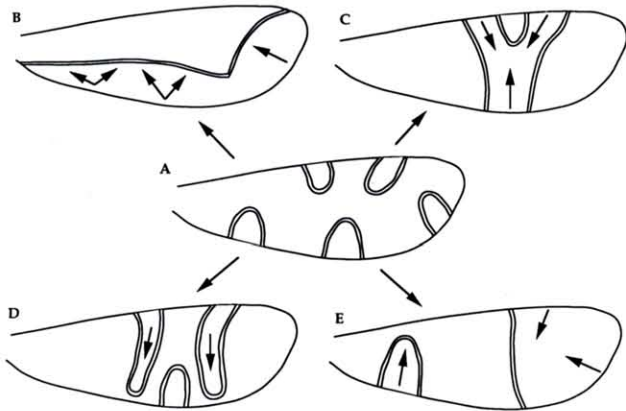


Fig. 5. A sampler of wing pattern diversity found in the 'primitive' moth families. Various banding patterns arise from differential expansion and fusion among patterns emerging from a limited number of origins (arrows).

neighboring bands (Fig. 7C), further demonstrating that all the bands are developmentally equivalent.

In the remaining Ditrysia, the number of symmetry systems is reduced. In most families there is only a single symmetry system in the middle of the wing. More seldom there is a second symmetry system near the margin (as in the Saturniidae), and at the base of the wing (as in some Geometridae). In some members of these families all three systems are present. In almost all families of moths that have multiple symmetry systems, the pigmentation of all symmetry systems is identical. The Saturniidae are a notable exception as they have a border symmetry system that is distinctively different in pigmentation from the central symmetry system. Distinctively colored borders also occur in some Notodontidae, Noctuidae and Geometridae. The wing pattern of the butterflies evolved from these ancestral systems by stabilizing the number of symmetry systems to three, and by a significant further differentiation of the individual symmetry systems. In the butterflies each symmetry systems have become individu-

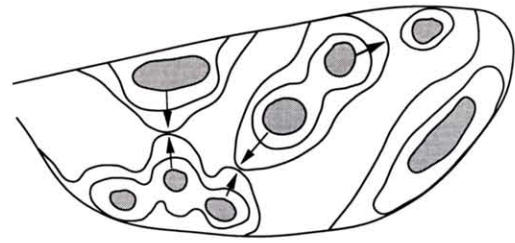


Fig. 6. Groundplan of the wing pattern of the Hepialidae. Species differ from each other in differential expansion of patterns from scattered centers of origin (gray); several possible contours are shown.

ated, as evidenced by the fact that each system develops a distinctive pigmentation, the bands of adjacent systems can no longer fuse with each other, and variation in each system is completely uncorrelated with that of adjacent systems (Nijhout, 1978, 1991; Paulsen and Nijhout, 1993).

The evolution of symmetry systems, then, appears to have occurred in the following five stages. The first stage is found in the most primitive Lepidoptera where a small number of sources for pattern determination on the wing produce a pattern of spots and bars. The pattern-determining system of these moths is doubtless derived from that of their pre-lepidopteran ancestors and may be related to the systems that also produce banding and spotting patterns on the wings of other insects. In the second stage, the number of these sources increases, dependent at least in part on the evolution of large body size; although the arrangement of these sources is constant and characteristic for each family, they are not aligned in any systematic or regular pattern. In the third stage, the sources become arranged in parallel rows and now produce a number of parallel symmetry systems. In the fourth stage, the number of rows is reduced and stabilized to three. The fifth stage is the differentiation and individuation of the symmetry systems produced by each row of sources, so that each system develops a distinctive form and pigmentation. If there was no evolution in the signal sources (the more parsimonious assumption), then the last step presumably involved the evolution of a distinctive environment in the regions of the wing where each symmetry system develops, so that in each region the signal interacts differently with its environment and induces a different pigment.

Evolution of pattern compartmentalization by the wing venation system

In butterflies, compartmentalization of the color pattern by wing veins uncouples pattern development in adjoining wing-cells and, as a consequence of this developmental uncoupling, allows evolution of the color pattern in different wing cells to become uncoupled as well. One of the consequences of compartmentalization, then, is that pattern elements in adjoining wing-cells can diverge morphologically. To discover when during lepidopteran phylogeny compartmentalization first appeared, we can search for species whose wings exhibit sharp differences of the pattern in adjacent wing cells. Such differences could be the dislocation of a band where it crosses a wing vein, the elimination of segments of a band in one or more wing-cells, or an abrupt change in the morphology or pigmentation of a band segment from one wing-cell to the next.

Dislocations of, or gaps in, symmetry system bands are

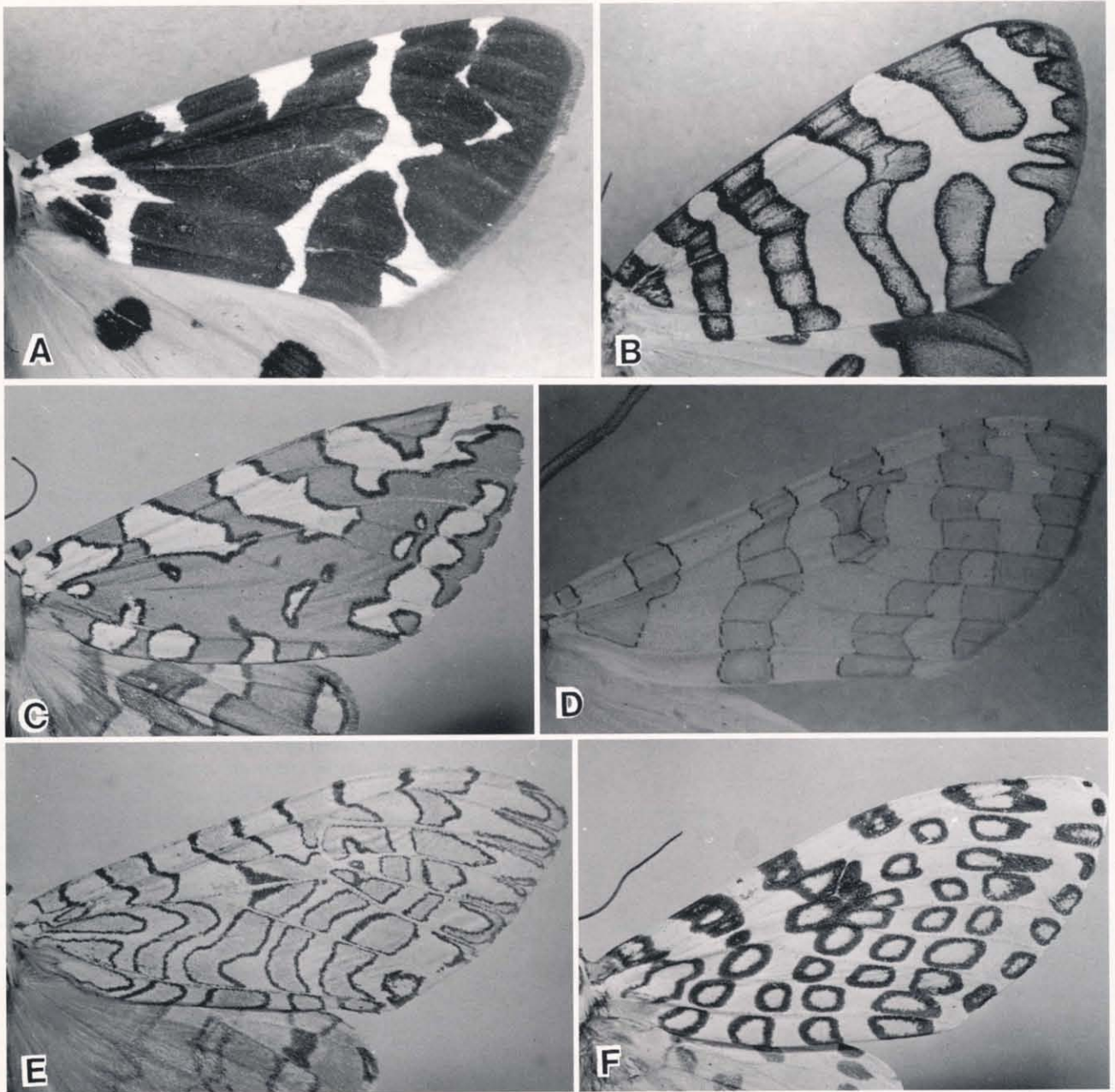


Fig. 7. The wing patterns of various Arctiidae illustrating broadly fused patterns (A), well-defined bands (B, D), lateral fusions among bands (C), dislocated bands (D), and bands broken by wing veins to various degrees (E, F). (A) *Arctia caja*; (B) *Callimorpha thelwalli*; (C) *Arachnis aulea*; (D) *Halisidota tessellaris*; (E) *Arachnis picta*; (F) *Epantheria scribonia*.

found rarely outside of the butterflies. There are a few cases in the Arctiidae (*Halisidota*; Fig. 7D) and the Geometridae (where the genus *Dysphanis* has a very butterfly-like wing pattern), and the occurrence in these two families suggests that the potential for dislocation must exist in most of the Ditrysia, although this potential is seldom expressed. The wing veins do, however, play important roles in other aspects of pattern formation in many families of moths, in ways that reveal much about how the compartmentalization of butterfly wing patterns may have evolved. In the moths, two pattern systems are affected by the wing veins. First, symmetry system bands are often deflected proximally or distally where they cross a wing

vein (Fig. 8). Second, ripple patterns, very primitive patterns that are not part of the nymphalid groundplan, are almost always dislocated at the wing veins (Fig. 9), even in the most basal families of moths. Below I will attempt to interpret the significance of each of these morphological features for pattern development and evolution.

Distortions of symmetry system bands near a wing vein can be found in all families of the Ditrysia and in the Pyralidae and Hepialidae. In most cases, the bands are continuous across the wing but are deflected into proximally or distally pointing peaks where they cross the wing veins, giving the band a scalloped appearance (Figs 3, 8C). If each band represents a

threshold on a gradient (Toussaint and French, 1988), then one can obtain scalloped bands if the threshold changes in the vicinity of a wing vein, or if the gradient has a different shape near a wing vein than it does in the middle of a wing-cell. If patterns are produced as thresholds on gradients of a diffusible signalling substance that moves from cell to cell through gap junctions (Nijhout, 1990), then a change in the density of gap junctions (which would affect the local rate of diffusion) near the wing veins could account for the observed deviations in the positions of the bands. Since developmental uncoupling of color pattern formation in adjoining wing-cells could be accomplished by abolishing communication between them, then a mechanism for modulating the density of gap junctions at the wing veins of these moths would provide the necessary preconditions for the evolution of compartmentalization of the pattern in their descendants, the butterflies.

There are also a number of cases, particularly common in the Arctiidae, where the band is constricted and fully interrupted at a wing vein. In species such as *Ecpantheria scribonia* (Arctiidae), each band forms rings that are squared off or flattened on the sides that face the wing veins (Fig. 7F). If there is a simple blockage of intercellular diffusional coupling at the wing veins then it must extend some distance away from the wing veins. If there is an organizing center at the middle of each spot (it must be remembered that each band in the Arctiidae is a symmetry system) then computer simulation suggests that the shapes of patterns found in Arctiidae could be obtained if the wing veins either absorbed or destroyed the diffusing signal (Nijhout, 1991). Such a mechanism would also inhibit communication across wing veins and could, therefore, also provide an adequate precondition for the evolution of compartmentalization.

Ripple patterns are a different case. Ripples are believed to be patterns of the 'background' unrelated to the symmetry systems of the nymphalid groundplan (Nijhout, 1991). They are composed of short irregular lines that run across the wing-cell perpendicular to the wing veins. These ripples are connected in random branching patterns. A consequence of this stochastic structure is that no two wings (even those of a single specimen) have an identical ripple pattern. The scale of this branching pattern varies from species to species; large scale ripples give the overall wing pattern a striated appearance, small scale ripples give a reticulated appearance (Fig. 9). At all scales, the ripples are sharply interrupted at the wing veins; there is no bending near the veins, as we see in the bands of symmetry systems.

Ripple patterns on the wing are older than the Lepidoptera; they are found also in the Trichoptera, Homoptera and Orthoptera, which

suggests that they may well represent one of the oldest color patterns in the insects. In the Lepidoptera they are either the exclusive wing pattern, as in most Cossidae, Neopseustidae

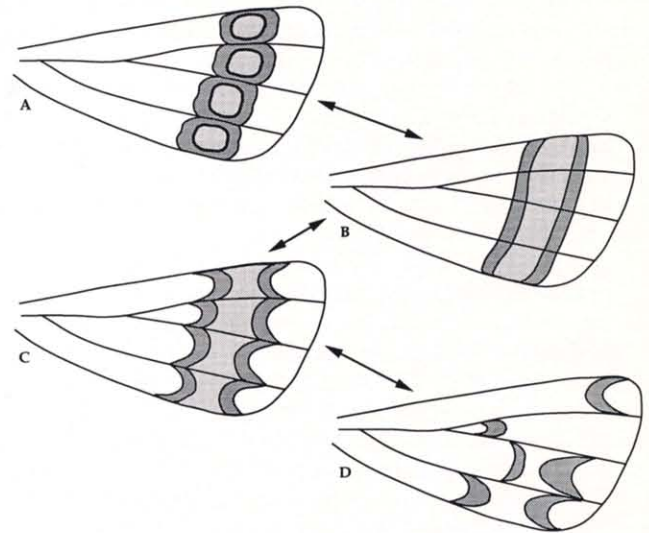


Fig. 8. Evolution of symmetry system bands. Bands can be constricted to circles (A), or deflected at wing veins (C). In butterflies the bands become dislocated and may even be lost in certain wing-cells (D). Double-headed arrows indicate possible evolutionary interconversions.

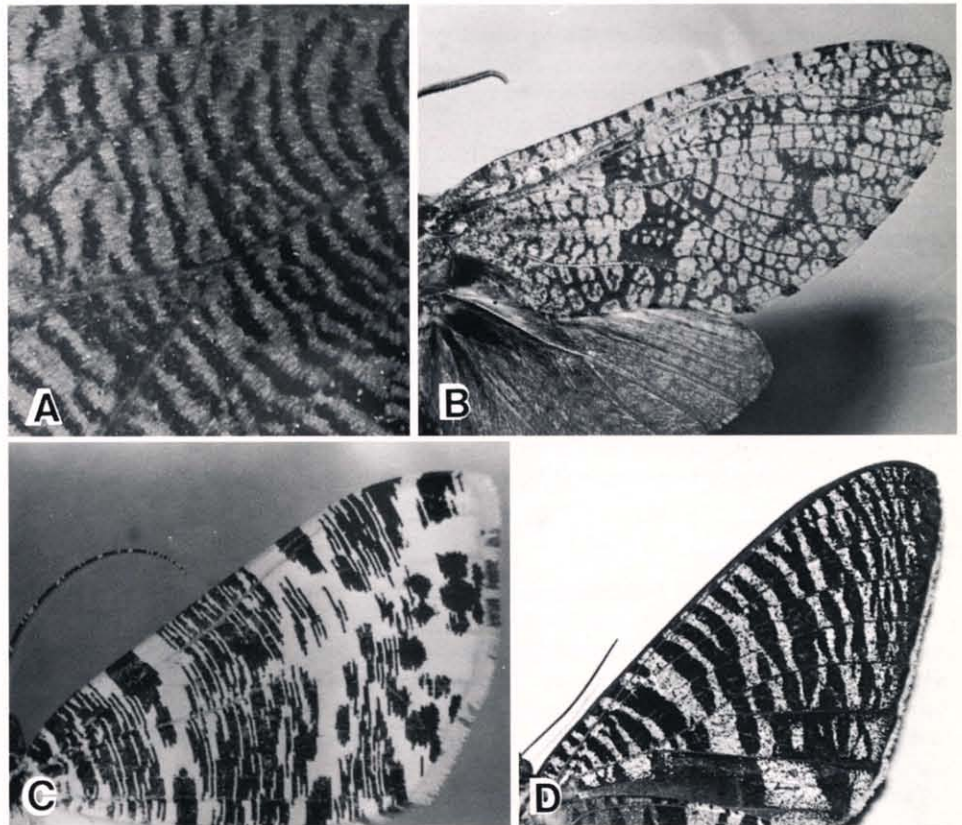


Fig. 9. Various examples of ripple patterns. (A) *Cercyonis pegala* (Satyridae); (B) *Prionoxystus robiniae* (Cossidae); (C) *Durbana tricoloraria* (Geometridae); (D) *Chrysidia madagascarensis* (Uraniidae).

and many other non-ditrysians, or they co-occur with the symmetry systems in many Ditrysia. In the butterflies and many Ditrysia, the ripple patterns are clearly part of the background and the elements of the nymphalid groundplan develop 'on top' of the ripples without interacting with them (illustrations in Nijhout, 1991). On the basis of comparative and experimental studies, Nijhout (1991) suggested that during color pattern development ripple pattern determination precedes that of the elements of the nymphalid groundplan.

Sharp discontinuities of ripple patterns at the wing veins suggest that barriers to pattern determination exist at the veins. But in moth species that have *both* symmetry bands and ripple patterns, the former are almost always smoothly continuous across wing veins while the latter are not. Clearly the veins have a different function during the determination of these two pattern systems. The simplest interpretation of this difference is that the veins change their properties during development, so that they act as barriers during early stages of development when the ripple patterns are determined, and become 'transparent' to intercellular signals later in development when the banding pattern is determined. Presumably this could happen by having epidermal cells coupled through gap junctions early in development, but not later. Gap junctions can be controlled dynamically and are known to change during development in other systems (Fraser, 1985). If this is a correct interpretation, then this implies that compartmentalization of the wing is actually a very ancient character that is expressed early in development in many and perhaps all Lepidoptera. The butterflies (and probably some arctiids and geometrids) then differ from the moths only in the evolution of a delay in the time at which the venous barrier is lost during development, so that the compartmentalization mechanism that formerly was only active during ripple pattern determination remains active and now also affects symmetry system determination.

Intermediate stages in the transformation from a completely un-compartmentalized to a completely compartmentalized wing can actually be found sporadically throughout the moths. In the Zygaenidae, for instance, there are species in which the spots, particularly those near the wing margin, are indented where they cross a wing vein. Similar indentations and discontinuities of the pattern at or near the distal wing margin are found in other moth families as well. These observations suggests that at least the distal portions of the wing may have venous compartments in some species. A proximodistally graded 'activity' of the wing veins, such as is found in some butterflies (Nijhout, 1991), may thus have its origin fairly early in lepidopteran phylogeny.

Putting it all together

The patterning system of butterflies with its two-fold compartmentalization, appears to have evolved through the convergence of two very ancient pattern-determining mechanisms, illustrated diagrammatically in Fig. 10. My hypothesis is that there were two independent primitive patterning mechanisms which the Lepidoptera inherited from their phylogenetic ancestors.

The first mechanism is one that generates spot patterns such as those illustrated in Figs 4, 5 and 6. This mechanism may be related to those that generate spotting patterns on the wings of flies and beetles, and possibly to those that generate spotted patterns in the Neuroptera (e.g. Fulgoridae) and Orthoptera. In

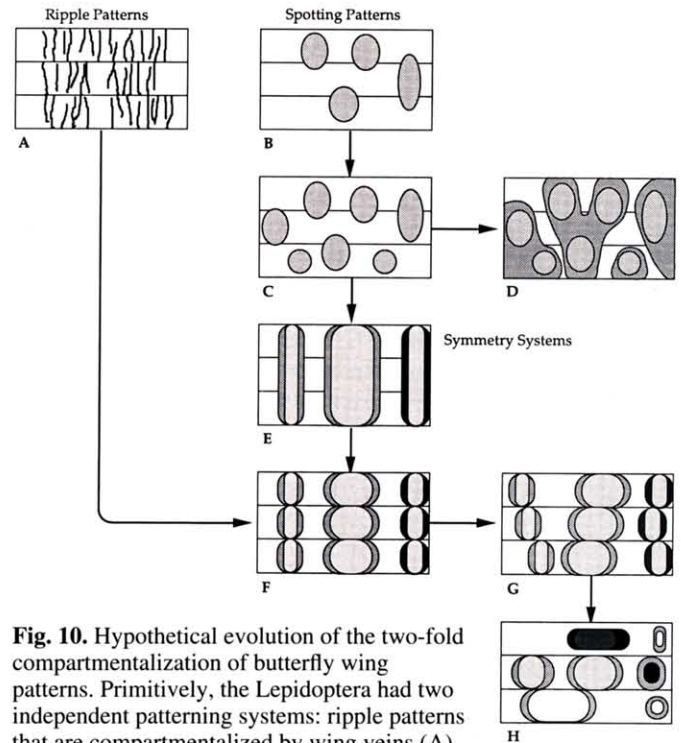


Fig. 10. Hypothetical evolution of the two-fold compartmentalization of butterfly wing patterns. Primitively, the Lepidoptera had two independent patterning systems: ripple patterns that are compartmentalized by wing veins (A), and spotting patterns (B). Spotting pattern evolved through multiplication of centers of origin (C), and diversification in the patterns of fusion between the spots (D). In the Ditrysia the centers of origin became well aligned to form discrete symmetry systems, and the symmetry systems became differentiated from each other (E). In the immediate ancestors of the butterflies the two patterning systems combined to produce a compartmentalization of symmetry systems (F). This compartmentalization enables bands of butterfly symmetry systems to become displaced independently in each wing-cell (G) and the elements in each wing-cell to evolve unique differentiation (H).

the primitive moths, all spots are generated by the same physiological mechanism, so that any two spots can fuse smoothly. These spots are not aligned in parallel rows, though they are often arranged in regular arrays that are characteristic for a genus of a family. In the Ditrysia there evolved a mechanism that aligns the spots into parallel rows. In the lineage that gave rise to the butterflies the number of these rows became limited to three. Primitively each symmetry system on a wing is composed of identical pigmented bands. It is not until the evolution of the butterflies (or their immediate ancestors) that we see a divergence in the morphology and pigmentation of different symmetry systems.

The second mechanism is that of compartmentalization by the wing veins. This too is an ancient mechanism the Lepidoptera inherited from their ancestors. In nearly all moths, compartmentalization is restricted to the ripple patterns and does not affect the spot patterns and symmetry systems. Compartmentalized ripple patterns and un-compartmentalized symmetry systems occurred side-by-side during most of the phylogenetic evolution of the Lepidoptera. During development, ripple pattern determination precedes symmetry system determination, and this suggests that in moths compartmentalization with respect to color pattern determination may be restricted to certain times of development. If this is correct,

then a simple way of compartmentalizing symmetry systems would be to extend the time during which compartmentalization is in effect into the period of symmetry system determination. This is what appears to have happened in the butterflies and their immediate ancestors.

In the butterflies we then see the coincidence of a mechanism that has evolved to produce a regular array of three symmetry systems with a mechanism that compartmentalizes the wing with respect to color pattern formation. The result is an uncoupling of development of the symmetry systems in different wing cells. The butterflies also inherited from their immediate ancestors the capacity to develop differences in the pigmentation of each of their symmetry systems, and further evolved these differences to the degree that adjacent symmetry systems no longer share a significant number of developmental determinants. Now, small portions of the bands of each symmetry system can move around within a wing-cell and be molded by natural selection into new alignments and new forms, without affecting the position, size, shape or color of any of the other segments.

It is interesting to ask at this point whether the evolution of a diurnal habit and the enormous radiation of wing color patterns as instruments for visual communication were cause or consequence of the evolution of this versatile patterning mechanism. The preconditions for the evolution of a highly compartmentalized and flexible pattern development system appear to be present in all the Ditrysia, but probably in few if any of the non-Ditrysia. A diurnal habit has clearly evolved several times in the Lepidoptera (for instance in the Castniidae, Sesiidae, Zygaenidae and Arctiidae). The comparative morphological evidence shows that indentation of distal patterns by the wing veins, and dislocation of symmetry bands occur occasionally in collateral lineages such as the Zygaenidae and Arctiidae, and this suggests that the conjunction of symmetry systems and compartmentalization of the wing long preceded the evolution of a diurnal habit by the butterflies' ancestors. Neither the Zygaenidae, nor the Arctiidae or Geometridae, however, appear to express a system that allows their symmetry systems to differentiate independently. Such a system probably evolved relatively early in the Ditrysiian phylogeny, however, since it is expressed in the Saturniidae and a few Notodontidae. Thus all the individual elements necessary for the evolution of a highly flexible and adaptable developmental system for color pattern formation (symmetry systems, their individuation and their compartmentalization) existed long before the butterflies evolved. Yet, while some families of moths express one or two of these elements, only in the butterflies have all three converged. With the evolution of a diurnal habit one might expect that the needs and opportunities for visual communication would favor the developmental system that can provide the broadest vocabulary of visual signals. This may have been the selective environment that favored the evolution of an interaction among the three existing patterning systems in the butterflies. The resulting integrated developmental system enabled their color patterns to diversify to a degree unprecedented in the phylogenetic history of the Lepidoptera.

This work was supported by grant IBN-9220211 from the National Science Foundation.

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