

# Stable structural color patterns displayed on transparent insect wings

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Color patterns play central roles in the behavior of insects, and are important traits for taxonomic studies. Here we report striking and stable structural color patterns—wing interference patterns (WIPs)—in the transparent wings of small Hymenoptera and Diptera, patterns that have been largely overlooked by biologists. These extremely thin wings reflect vivid color patterns caused by thin film interference. The visibility of these patterns is affected by the way the insects display their wings against various backgrounds with different light properties. The specific color sequence displayed lacks pure red and matches the color vision of most insects, strongly suggesting that the biological significance of WIPs lies in visual signaling. Taxon-specific color patterns are formed by uneven membrane thickness, pigmentation, venation, and hair placement. The optically refracted pattern is also stabilized by microstructures of the wing such as membrane corrugations and spherical cell structures that reinforce the pattern and make it essentially noniridescent over a large range of light incidences. WIPs can be applied to map the micromorphology of wings through direct observation and are useful in several fields of biology. We demonstrate their usefulness as identification patterns to solve cases of cryptic species complexes in tiny parasitic wasps, and indicate their potentials for research on the genetic control of wing development through direct links between the transregulatory wing landscape and interference patterns we observe in *Drosophila* model species. Some species display sexually dimorphic WIPs, suggesting sexual selection as one of the driving forces for their evolution.

Generation of complex pigmentation patterns by insects is currently an active research front (1–3), with insights into the morphogenetic control of pigment spots in wings of a *Drosophila* model species (4) (Fig. 1 *J* and *K*) underpinning principles for coloration and repeated regulatory evolution that are potentially broadly applicable beyond insects (5–7). Parallel studies of structural insect colors with repeated functional morphology and multiple functions of simple structures (8–10) have recently expanded into a major research area (11–14) that is predominantly focused on larger organisms such as butterflies (14–16), beetles (17), and damselflies (18). Here we merge these two fields by showing structural wing color patterns in the transparent wings of small wasps (Hymenoptera) and flies (Diptera). Given favorable light conditions, they display a world of brightly patterned wings (Fig. 1) that are apparently unnoticed by contemporary biologists. The color patterns are the effect of thin film interference; about 20% of incoming light beams are reflected from a single extremely thin and transparent layer with a refractive index of chitin (13). The remaining 80% of the light goes through the wing. Any animal with color vision can see these color patterns when the wing reflections are not overpowered by strong background reflections. The strength of their appearance in natural conditions depends on the balance between light reflections from the wing and from the background. The intensity of the background reflections in nature varies from 0% (pitch black background, Fig. 1 *A*, *D*, and *E*) to 100% (pure white background or toward a light source), but will normally be similar to a green leaf, where the wing reflections are readily observed (Fig. 1 *B*, *C*,

and *F*). In laboratory conditions most wings are studied against a white background (Fig. 1 *G*, *H*, and *J*), or the wings are embedded in a medium with a refractive index close to that of chitin (e.g., ref. 19). In both cases the color reflections will be faint or invisible.

Insects are an exceedingly diverse and ancient group and their signal-receiver architecture of thin membranous wings and color vision was apparently in place before their huge radiation (20–22). The evolution of functional wings (Pterygota) that can be freely operated in multidirections (Neoptera), coupled with small body size, has long been viewed as associated with their extreme diversity (20). With selection acting to decrease the size of wing membranes that are reinforced for aerodynamic function by membrane corrugations, hair placement, and venation, there has been simultaneous reinforcement of an optically refracted and stable color reflection. This reflection, coupled with the early evolution of trichromatic UV-blue-green perception by the insect compound eye (22), has along with pigmentation (2, 4, 23), transformed wings into visual communication posters for those who can see their colors.

The color sequence reflecting from transparent insect wings was discovered and published before Darwin's theory of evolution (24), but it has later been disregarded as a soap bubble iridescence effect, with randomly changing colors flashing over the wing surface (25). Taxonomic monographs for Hymenoptera and Diptera typically describe wings as transparent, with or without pigmented areas, but with no mention of structural color patterns (e.g., refs. 26, 27). However, we have found that these small transparent wings almost universally display stable and essentially noniridescent structural color patterns that are often taxon-specific. The patterns are visible and stable at various angles of view in live insects in nature (Fig. 1 *A–F*) as well as on 100-year-old dry museum specimens (Fig. 1*K*).

## Discussion

**Two-Beam Wing Interference Patterns (WIPs).** The wings of most insects are mainly composed of two layers of transparent chitin compressed to a single membrane (Fig. 2 *I–K*) with a refractive index of approximately 1.57 (14). In air, these dimensions are ideal for two-beam thin film interference, whereby light beams reflect from the upper and lower surfaces of the membrane (13). The thickness of the composite chitinous membrane varies with the topography of the wing, and the areas of different thickness reflect different interference colors that together produce a specific color pattern, the WIP. The sequence of colors in WIPs of Hymenoptera (Fig. 2 *F*, *G*, and *M*) and Diptera (Fig. 2*A*) is regular and identical to the Newton series reflected from a thin film

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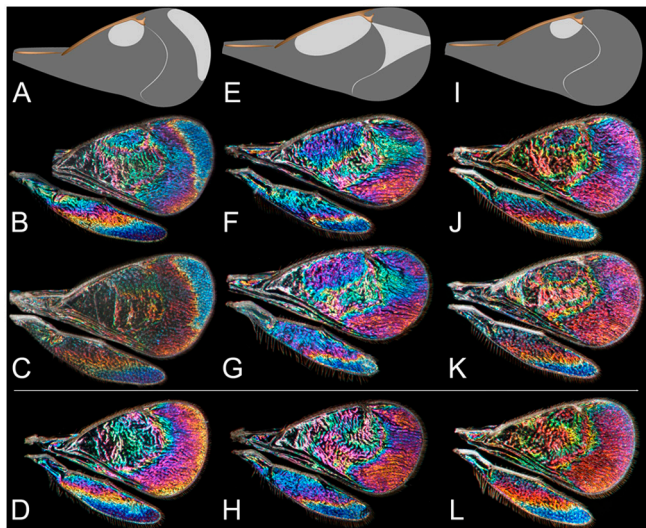
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of oil on water (25, 28). The Newton series is a very characteristic sequence of repeated color bands grouped into orders. The first three Newton orders (up to 550 nm wing membrane thickness, see Fig. 2H) display a near complete scale of spectral colors, except for pure red, whereas the next higher orders (with increasing wing thickness) reflect a repeated sequence of nonspectral (to the human eye) magentas and greens that gradually fade into uniform pale gray. Those of the second and third order are the brightest in the scale. This ordered color sequence makes it possible to reciprocally calculate and map membrane thickness in the range between *ca.* 50 and 1500 nanometres when compared with a Newton series scale (Fig. 2A, F–H, and M).

The fore- and hindwings of Hymenoptera are coupled together into one functional unit during flight and during what we suspect are WIP displays. The hindwing pattern usually forms an extension of the WIP from the forewing or sometimes displays its own characteristic details (Fig. 3), just as is the case with the pigment-based and scale-based patterns on Lepidoptera wings. In wings of small chalcidoid wasps (body length less than 3 mm) there are membrane corrugations that form regularly spaced parallel ridges about 20  $\mu\text{m}$  apart (Fig. 2B and D), with rows of setae along the tops of ridges. Diptera have only one pair of functional wings and the corrugation ridges usually occur in association with regular rows of microtrichia. These are typically spaced about 10–15  $\mu\text{m}$  apart in the middle of spherical cell structures, as in *Drosophila* (29). The more pebbled interference patterns suggest spherical reflection around each microtrichium (Fig. 2A).



**Fig. 3.** WIPs of three species of genus *Achrysocharoides* (Hymenoptera: Eulophidae). Male wings (above the line) and female wings (below the line). While sorting a collection of *Achrysocharoides*, several males with a distinct blue spot in the WIP were discovered. Further investigations revealed a case of two cryptic species (*A. acerianus* and *A. platanoideae*) and extending the investigation resolved another case of three cryptic species (*A. gahani*, *A. robiniae*, *A. robinicolus*) (38). All species were initially separated using male WIPs, but other morphological differences in combination with acquired new biological data confirmed the hypothesis of species delimitation. *A. platanoideae* and *A. robiniae* have sexually dimorphic WIPs despite having transparent wings without any pigmentation and from the classical point of view males and females have identical wings. (A–D) *A. platanoideae*. (A) Schematic illustration of the distinctive small spot in the corner between the marginal vein and the stigmal vein and the larger marginal spot along the apical edge, which is blue in the WIP. (B) WIP of male (UK, 1999). (C) WIP of male (Sweden, 2007). (D) WIP of female (Sweden, 1981). (E–H) *A. robiniae*; all collected in Hungary, 2002. (E) Schematic illustration of the distinctive large spot along marginal vein and the extended spot in the apical part, which is green in the WIP. (F–G) WIP of males. (H) WIP of female. (I–L) *A. robinicolus*; all collected in USA, 2002. (I) Schematic illustration of the distinctive small spot in the corner between the marginal and the stigmal veins and lack of pattern in the apical part. (J–K) WIP of males. (L) WIP of female.

Whereas the microstructures of the wing membrane are somewhat different in Hymenoptera and Diptera, the resulting effect is the same: essentially noniridescent coherent scattering (cf. 8). The old report (25) of highly variegated colorings randomly mingled, with housefly wing changing color as the angle of vision changes, is wrong. We find almost no iridescence unless the light is narrowly concentrated in one direction at a slight angle to the surface. The stable noniridescent patterns that we see can be explained by the convex ridges of a corrugated (Fig. 2C and I) or pebbled (Fig. 2A) wing membrane that act as diopters to stabilize the interference reflection and eliminate the iridescence effect over a large range of light incidences (8, 9). Contrary to the iridescence of a flat thin film, the strongly microstructured wing membrane appears noniridescent, both under different ring light illuminations and in natural outdoor light.

Pigmented areas and the rigidity of wing veins contribute to stabilize the wing color pattern, contributing frames for the WIPs of different wing segments and the wing overall. The WIPs may reciprocally display the vein system and emphasize the pigment patterns (Figs. 1, 4, 5, and 6). In species with smoky or semitransparent pigmented wings, the WIP loses its characteristic metallic shine (e.g., Fig. 6G), and it may not appear if pigments are capturing the light (e.g., Fig. 5P–R). In species with large individuals, the reticulate system of veins compartmentalizes and supports the wing such that it remains strong while simultaneously being thin enough to produce WIPs in the areas framed by the veins. For example, wings of some Braconidae and Ichneumonidae wasps display cell-specific WIPs that are different from those of other adjacent compartments (Fig. 6N–P). As a species evolves smaller individuals, the wing vein system is commonly reduced. In the smallest wasps, but those having a wing large enough to display a WIP, the veins are confined to the anterior wing margin, leaving the wing membrane as a seemingly large empty space (about the size of a wing cell on a larger wasp or fly). To stabilize such a vein-free wing there are extensive supporting corrugations and thickenings of the membrane (Fig. 2B–E). These features form structural patterns that display WIPs based on the three first Newton orders, which are created by membrane thickness from 100 to about 600 nm (Fig. 2H). In sum a taxon-specific WIP reflects a complex of micromorphological features of the wing (uneven membrane thickness, corrugations, setae arrangement, pigmentation, venation) framed by a specific wing shape (Fig. 5, 6).

**Genetic Control of the WIP.** The complex black pigment patterns that are repeatedly evolved in many groups of Diptera are formed and controlled by a set of spatiotemporal on/off switches for the single gene *yellow* (6, 7) and sometimes also involve other genes and physical wing traits (2, 4). An increasing body of evidence demonstrates direct parallels between development and regulation of wing patterns in distantly related groups such as *Drosophila* and butterflies (2, 7, 23, 30).

WIPs add an additional dimension and morphological diversity palette to the now emerging “repeated regulating evolution” model (5). WIPs mean that wing pigmentation (4) is only a part of the story. Other morphogenetic elements are responsible for the regulation of membrane thickness, formation of membrane corrugations, hair placement (29), venation pattern (31), and other traits. The transregulatory wing landscape (32, 33) illustrates how different genes, *cis*-regulatory elements (33), and wing landmarks (4) (e.g., veins, bumps, troughs, slopes, hairs) may work together to form the wing and create/stabilize the size, location and nature of a specific WIP. A specific WIP may be the analogue to a pigment field or complex that performs a specific function, such as are false eye spots (34). For example, the longitudinal division of the wing disc into the anterior-posterior compartments associated with the regulators *engrailed* (32) and *hedgehog* (23), is directly reflected in WIPs. There is a distinct color shift indicating a transition line in membrane thickness



**WIP Diversity and Stability.** The majority of the more than 17,000 species of butterflies can be distinguished by their wing color patterns (16, 30), though it is also the case that many of these seemingly species-specific color patterns may be in common throughout complexes of visually “identical” sibling species (36). Our observations of WIPs suggest that species identification in many groups of Hymenoptera and Diptera is enhanced if WIPs are added to the set of taxonomic characters. These two orders are estimated to contain far more than twenty times the number of butterfly species (21, 37). This diversity remains unknown partly due to difficulties in distinguishing morphologically similar species (e.g., ref. 37), also known as “cryptic species” (which often means “not readily distinguishable by a large diurnal mammal with a microscope”). In a recent paper (38) we described cryptic species in the chalcidoid genus *Achrysocharoides* (wasp family Eulophidae). Five species, three of which were described as new, were initially separated by relying exclusively on distinctive male WIPs (Fig. 3) and subsequently confirmed as distinct species through finding additional differences in morphology and biology. Wings of chalcidoid wasps have long been regarded as poor in features because most species lack pigment patterns. WIPs as morphological characters will aid their identification and species discovery.

The fly family Drosophilidae ranks among the most studied organisms and displays excellent interspecific variation in WIPs (Fig. 4) and low intraspecific variation. When we compared WIPs from closely related *Drosophila* species, we found the overall pattern to be interspecifically similar but with distinct features for each species (Fig. 4 *A–E* and *L*). A superficial visual survey of Diptera (Fig. 5) and Hymenoptera (Fig. 6) wings encounters a diverse colorful array in all small wings (and to some degree in individual wing cells of large wings). There is a wide variety of kinds of WIPs from unicolored to elaborate patterns and spots. The claim that fly (e.g., ref. 2) and wasp wing patterns are no match for the incredible diversity of colorful butterfly wing patterns is obsolete.

WIPs, just as are other traits, are intraspecifically variable and phenotypically plastic. However, our preliminary impression is that they are largely uniform among conspecifics and often appear to be characteristic of a species, at least to the degree encountered in other insect color patterns. An evolutionary or environmentally induced change in wing size may affect the thickness of the membrane, thereby displacing the sequence of colors within the same WIP. The stable pattern may be more relevant to taxonomy and the insect than is the hue or color sequence. For example, the intraspecific variation of WIP in a sample ( $n = 20$ ) from a laboratory bred Canton-S strain of *D. melanogaster* is small with a moderate size-dependent color displacement (Fig. 4 *A* and *B*). In this case, the wings of males had less variable WIPs than did those of females, despite the larger variation in size of male wings.

We have encountered sexual dimorphism in WIPs in species with completely transparent wings such as parasitic *Achrysocharoides* wasps and in those with pigment patterns (e.g., *Drosophila*, Fig. 4*L*). This dimorphism may either be a result of difference in size (usually large female, small male) affecting the hue but with the same pattern in both sexes or, the more indicative, with different patterns between the sexes (Fig. 3 *A–H*). The latter case, with species-specific and sexually dimorphic patterns, suggests that sexual selection is one of the driving forces for the evolution of these patterns. When the males and females of the same species have identical WIPs (Fig. 3 *I–L*), but differ in other external morphological characters, the WIPs can be used to match the sexes.

**WIP Perspectives for Biodiversity Studies.** WIPs are an additional and overlooked trait for identifying and discovering (especially cryptic) species, just as have been DNA barcodes (e.g., ref. 36). Two-dimensional patterns on a flat wing are technically straight-

forward to document and analyze with pattern recognition software tools (39) and couple well with wing morphometrics (40). For phylogenetic classifications, WIPs are promising unexplored traits that can be used to visually map wing topography and measure wing membrane thickness. WIPs may reflect different types of microstructural arrangements in the wing such as nearly flat or strongly corrugated membranes and attendant membrane gradients (Fig. 5 *A*, *S*, and *L*). Alternatively they may independently cross over venation patterns (Fig. 5 *M* and *R*). The strong demarcation of the vein system via narrow color transitions along vein margins (e.g., Fig. 5 *B* and *H*) has been unrecognized and offers a unique functional and phylogenetic perspective to wing venation; it may even indicate the location and extension of wing veins that have been lost during evolution (Fig. 5*E*).

Behavioural, ecological, morphological, and evolutionary studies of insects with small wings will benefit from the discovery of WIPs in that they probably function in intra- and interspecific signaling. If so, they may be one more of the functionally dependent traits that may block evolutionary changes being driven by quite unrelated selective forces, such as wing aerodynamics, speed of wing hardening following adult eclosion, wing weight and durability. There is a definite possibility that some of the variation in membrane thickness, corrugations, pigmentations and venation reticulations has its adaptive value partly or solely in the WIPs they produce. If WIPs are truly important in the biology of insects, rather than being a byproduct of other physical traits (as is the case with inanimate oil slicks), they may in turn be one of the driving evolutionary processes affecting the nature of wing venation reticulation, with all its seemingly nonsensical variation among insects (which is commonly attributed to need for wing strength).

Wing displays play a central role in visual courtship communications in several families of Diptera (3, 19, 32, 41–44) as well as many other insects, and have been suggested as one of the drivers of the initial evolution of the insect wing (45). However, all research to date on the evolution of Diptera wings and courtship has focused solely on pigment patterns—phrased by the authors as “evolution in black and white” (3, 6, 19). Butterflies, where females may prefer males with bright structural ornamentations, emphasizing intraspecific selection as the driving force (46), reveal one intriguing difference when compared with Hymenoptera and Diptera. Whereas only a few larger species of these two orders are known to have red eye receptors, such receptors are much more common in the Lepidoptera, especially among butterflies (22), as are red butterfly scales produced by multilayer interference or red pigments (9). The Newton series color sequence displayed in single layer WIPs excludes pure red and fits most small insects’ trichromatic UV-blue-green color vision (22), including those with transparent wings. Among flies, attraction to blue and green light in the dark may be stronger than attraction to UV light and red light (47). These observations suggest that the biological significance of WIPs is for visual signaling, including intraspecific recognition by their bearers.

Some peculiar behavior involving wings in small species of Hymenoptera may be explained through WIP display. For instance, why do females of pollinating fig wasps hold their unpigmented wings straight up in the air (48), like billboards, when walking on the fig as they arrive? When the female enters the fig’s fruit-like reproductive structure (syconium) through the very tight opening (ostiole), the wings break off. A drop of liquid is excreted from the end of the abdomen and glues the wings into a protruding and visible position. This may be a species-specific signal that the syconium is now occupied, and the WIPs of these wings may be a part of the signal. Newly eclosed 2–3 mm long tropical microgastrine braconid wasps (37) raise their seemingly pattern-free transparent wings and wave them when encountering a sib while walking in the rearing container. Again, the WIPs may be part of the signal.

WIPs appear to be cheap visual signals, though wing thickness, setae, or other traits that modify a WIP may have strategic as

well as materials costs. Unlike moths and butterflies, where color patterns are made with complex scales and pigments, the WIPs of transparent wasp and fly wings appear to be of low cost. For the receiver of the signal, developing and maintaining photoreceptor systems are believed to be very energy consuming and demonstrate clear trade-offs between energy consumption and performance (49, 50). Crepuscular to nocturnal insects use dim light (51) and have evolved attraction to dark or contrasting dark/white swarm markers (e.g., ref. 52). WIPs perceived by insects may be a cheap complement to the unavoidable cost of having a color-sensitive receiving system (49).

WIPs offer opportunities for evo-devo studies that connect wing biophysics and topography to morphogenetics and regulatory evolution. Colorful species-specific WIPs are, in contrast with DNA barcodes from highly conserved genes (36), traits that may have major behavioural importance to the insects bearing them, as well as be serendipitous byproducts of other traits. Wasps and flies are very species-rich and small (53), and their extremely thin wings are therefore ideal for displaying WIPs. The WIP is potentially a major contribution to the toolbox for evolution of small insects with transparent wings and thus an important piece of the evolutionary puzzle.

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