



# Diversity of UV Reflection Patterns in Odonata

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Dragonflies and damselflies (Odonata) are large-eyed diurnal insects that exhibit a variety of color patterns on their wings and/or bodies. Because Odonata can perceive light with wavelengths extending from ultraviolet (UV) to red, the color patterns with UV reflection can be visually recognized by each other. The UV reflection patterns of Odonata have been investigated by using a UV camera and optically measuring the reflectance of body and wing surfaces. The UV reflection of Odonata can be classified into three classes, namely, iridescent UV reflection, wax-based UV reflection, and UV reflection by epidermal granules. In this review, I present UV images of these three classes and representative examples of reflectance. Among the Odonata with colorful iridescent wings consisting of multilayer structures, some species (e.g., *Chalcopteryx scintillans*) predominantly reflect UV light, whereas other species (e.g., *Calopteryx japonica*) mostly reflect light at wavelengths above 400 nm. Whitish wax (called pruinescence) on the body and/or wing surface strongly reflects light including UV, due to the light-scattering fine structures produced by the wax. The chemical composition of the dragonfly's abdominal UV-reflective wax differs from previously identified waxes of other organisms. The blue-tailed damselflies *Ischnura* species exhibit immature-adult-specific UV reflection by the pteridine pigment-based selective light scattering and absorption. Iridescent coloration and wax-based color changes are generally important for mate recognition and male–male competition in Odonata, although the ecological importance of UV reflection remains largely unknown except for few examples in damselflies.

**Keywords:** Odonata, dragonfly, damselfly, color, UV reflection, multilayer, wax, pigment

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## INTRODUCTION

Dragonflies and damselflies (Odonata) are large-eyed diurnal insects, and adults exhibit a variety of color patterns on their wings and/or bodies. These color patterns often represent sexual color dimorphism, color transition via sexual maturation, and intraspecific color polymorphisms within the same sex (Tillyard, 1917; Corbet, 1999; Bybee et al., 2016; Futahashi, 2016). Both dragonflies (suborders Anisozygoptera and Anisoptera) and damselflies (suborder Zygoptera) possess a remarkably large number of visual opsin genes (Futahashi et al., 2015; Suvorov et al., 2017), and electrophysiological studies have shown that Odonata species can perceive light with wavelengths extending from ultraviolet (UV) to red (Meinertzhagen et al., 1983; Yang and Osorio, 1991; Labhart and Nilsson, 1995; Huang et al., 2014; Futahashi et al., 2015), suggesting that the UV reflection patterns can be visually recognized by each other.

The UV reflection pattern of Odonata has been classically investigated using a UV camera, and it has been reported that several Libellulidae dragonflies coated with a whitish wax consistently exhibit UV reflection (Robey, 1975; Silberglied, 1979; Harris et al., 2011; Futahashi et al., 2019). Hilton (1986) comprehensively investigated UV reflection using dried specimens preserved in a museum. Even though 343 species belonging to 16 families were investigated, UV reflection was detected only in one damselfly species, namely *Euphaea amphicyana* (Euphaeidae). As pointed out in this paper, one of the reasons that UV reflection was not observed in almost all the species was that their body color was changed and the surface wax was destroyed by acetone treatment for preparing the dried specimens. Harris et al. (2011) used fresh specimens of 10 species belonging to 4 families and found that the UV reflection pattern often differed between species and sexes, although it was difficult to evaluate the intensity of the UV reflection due to the low UV sensitivity of the equipment.

Aside from the observation using a UV camera, optical measurements of the reflectance of wing and body surfaces have been conducted, and UV reflection has been detected in several Odonata species (Robertson, 1984; Schultz and Fincke, 2009; Guillermo-Ferreira et al., 2014, 2015, 2019; Nixon et al., 2015, 2017; Futahashi et al., 2019; Henze et al., 2019). The UV reflection of Odonata can be classified into the following three classes: iridescent UV reflection, wax-based UV reflection, and UV reflection by epidermal granules. In this review, I show UV photographs of these three classes taken with a high-sensitivity camera (Sony A7S, IDAS UV-VIS mod) and a UV filter (IDAS-U) in the field, as well as representative examples of reflectance from previous reports. I also aim to review the mechanism underlying the UV reflection and its ecological significance.

## EXAMPLES AND MECHANISMS OF IRIDESCENT UV REFLECTION

Some Odonata species have colorful iridescent wings and/or bodies (Figures 1A–C), and the spectral reflectance and cuticular structures of the iridescent coloration have been reported (Fitzstephens and Getty, 2000; Vukusic et al., 2004; Hariyama et al., 2005; Schultz and Fincke, 2009; Kuitunen and Gorb, 2011; Stavenga et al., 2012; Nixon et al., 2013, 2015; Guillermo-Ferreira et al., 2014, 2015, 2019; Appel et al., 2015). In the iridescent coloration of the wings, some species (e.g., *Chalcopteryx scintillans*, Polythoridae) predominantly reflect UV light (Figures 2A,B), whereas other species (e.g., *Calopteryx japonica*, Calopterygidae, Figures 1C,D) mostly reflect light at wavelengths above 400 nm (Figure 2B; Stavenga et al., 2012; Guillermo-Ferreira et al., 2019). In the flutterer dragonfly *Rhyothemis fuliginosa* (Libellulidae), bluish male wings strongly reflected UV light (Figure 1A), while greenish female wings scarcely reflected UV light (Figure 1B). Like other insects, the difference in reflectance of the iridescent coloration is primarily attributed to the difference in the multilayer structure that contains several layers with alternating high and low electron density near the wing surface. The resulting reflected

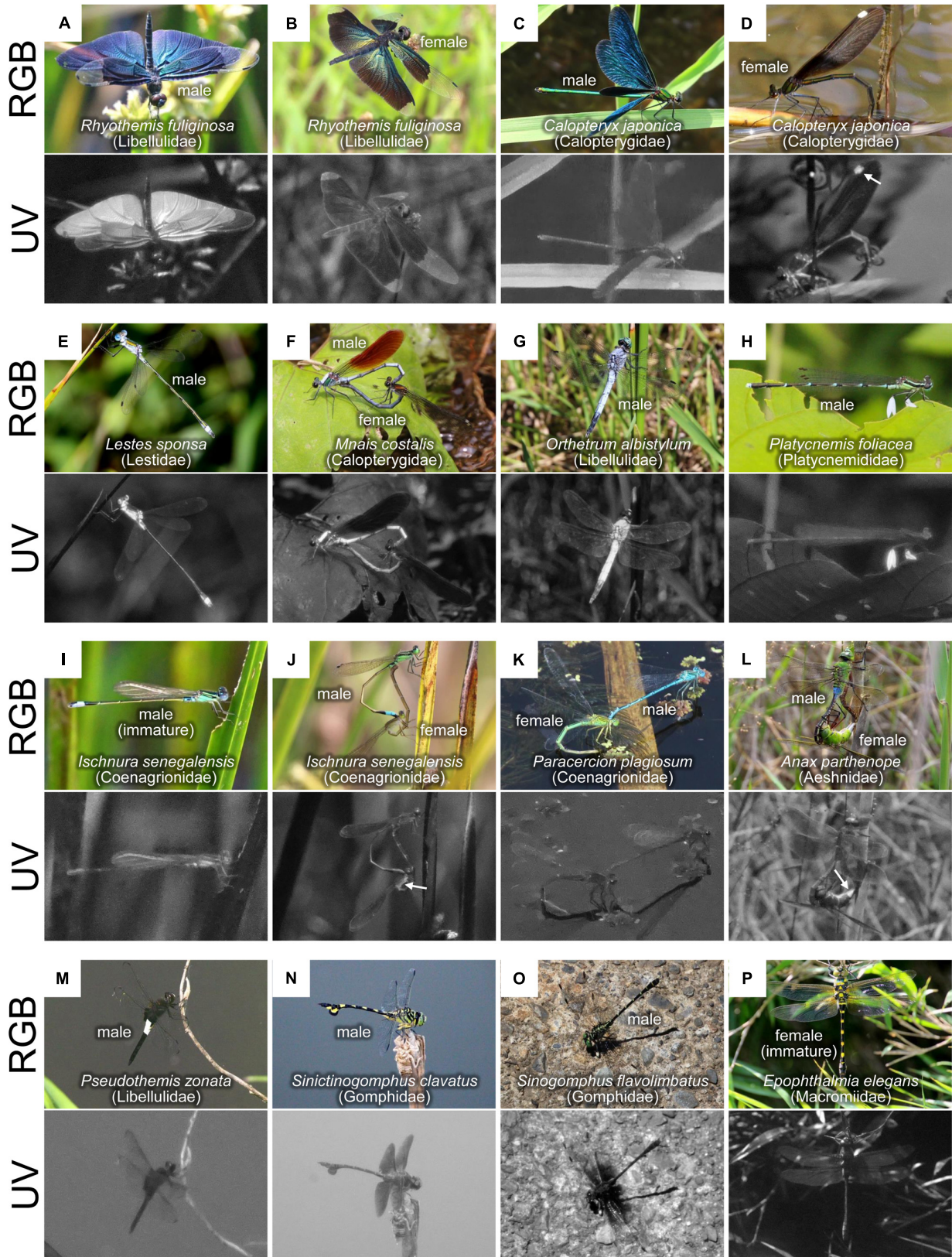
wavelength is dependent on several factors, such as the thickness of the dense layers, the interval between layers, the refractive index of the layers, and the angles of refraction in layers (Kinoshita and Yoshioka, 2005; Stavenga et al., 2011). In general, a thinner multilayer interval produces shorter peaks in the reflected light. In the black-winged damselfly *Calopteryx maculate* (Calopterygidae), the iridescent coloration of male wings can be manipulated experimentally by the changes in diet. The bluish males (resulting from higher food consumption) have thinner layers than the greenish males (Fitzstephens and Getty, 2000). In the damselfly *Matronoides cyaneipennis* (Calopterygidae), males have bluish iridescent coloration on the dorsal hindwings and greenish iridescent coloration on the ventral hindwings (Nixon et al., 2013). There are five layers at both surfaces of the wings; the only difference is that the second layer of the dorsal surface is thinner than that of the ventral surface. Theoretically modeled reflectance shows that this small difference results in a significant change in the peak reflection wavelength (Nixon et al., 2013).

In the flutterer dragonfly *Rhyothemis resplendens* (Libellulidae), the multilayer structure is obviously wrinkled, which causes the light to be scattered at a broader angle than the unwrinkled multilayer structure (Nixon et al., 2015). In addition, the surface wax plays an important role in color tuning and angle-dependent light scattering (Kuitunen and Gorb, 2011; Guillermo-Ferreira et al., 2015, 2019). In the neotropical morpho dragonfly *Zenithoptera lanei* (Libellulidae), the surface wax of the dorsal wings increases brightness and reduces chroma (Guillermo-Ferreira et al., 2015). In the Amazonian damselfly *C. scintillans*, the surface wax of the dorsal wings provides specific angle-dependent light scattering and antireflective properties (Guillermo-Ferreira et al., 2019).

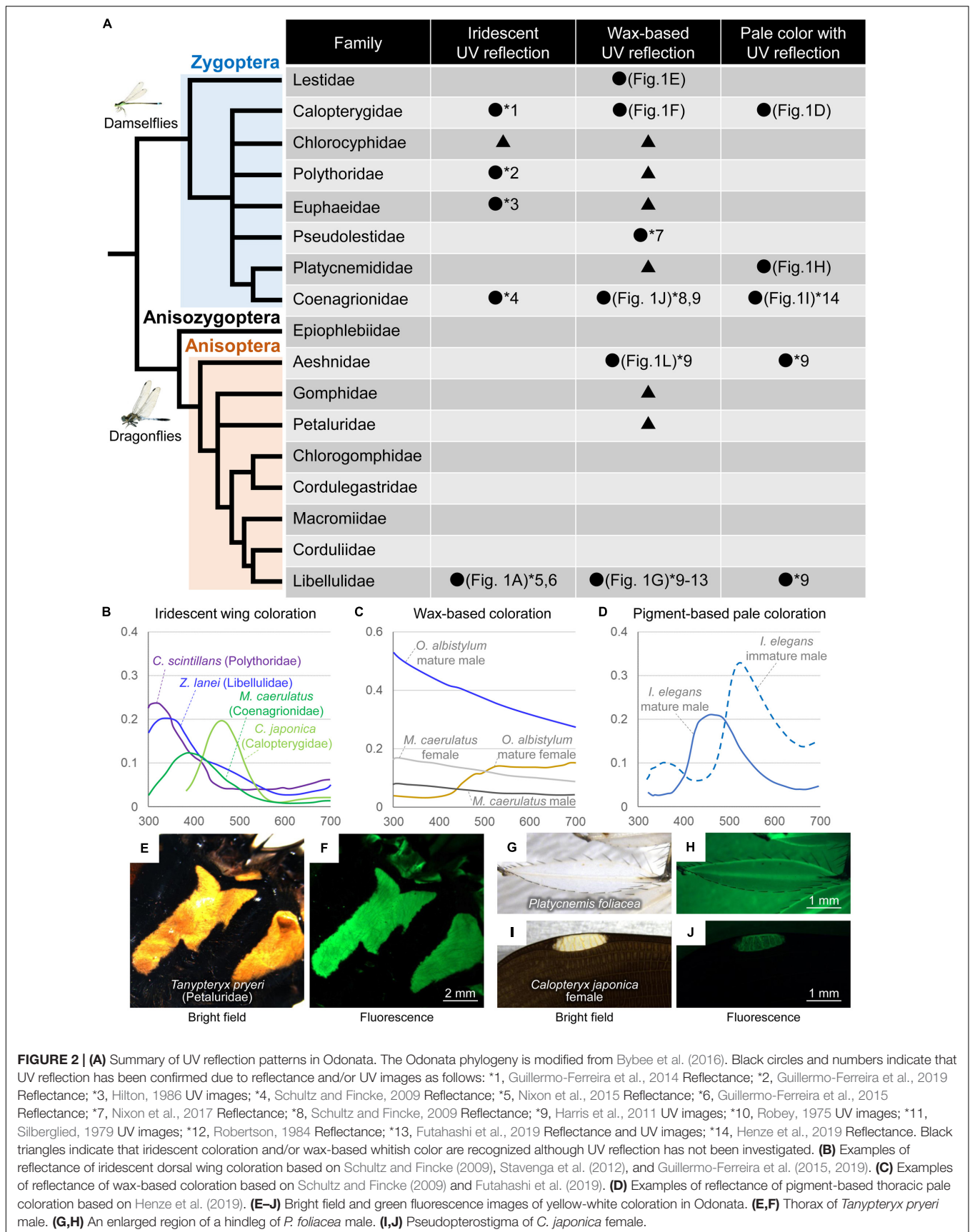
## EXAMPLES AND MECHANISMS OF WAX-BASED UV REFLECTION

A wide variety of Odonata species are partly coated with whitish or pale bluish wax (called pruinescence) on body surfaces of the abdomen, thorax, head, and wings (Figures 1E–G, 2A). Wax secreted from numerous fine ducts penetrating the cuticle layer increases during adult maturation and is generally well-developed in males than in females, resulting in wax-based, sex-specific color changes (Tillyard, 1917; Jacobs, 1955; Robey, 1975; Gorb, 1995; Corbet, 1999; Futahashi et al., 2019). In general, mature males secrete dense wax predominantly on the dorsal region, whereas mature females secrete pruinose wax mostly on the ventral region and often become slightly whitish with aging (Gorb, 1995; Harris et al., 2011; Futahashi et al., 2019). In the suborder Zygoptera, species with whitish wax are found in most families, whereas in the suborder Anisoptera, species with conspicuous whitish wax are found predominantly in the family Libellulidae (Corbet, 1999). River-dwelling dragonfly species (e.g., Epiophlebiidae, Gomphidae, Chlorogomphidae, Cordulegastridae, and Macromiidae) scarcely secrete whitish wax with a few exceptions like *Gomphurus lynnae* (Gomphidae) (Paulson, 1983; Figure 2A). Weak pruinose wax on the ventral





**FIGURE 1** | Color pattern diversity in dragonflies as visualized in red, green, blue (RGB), and ultraviolet (UV) light. **(A–P)** Each image was photographed normally (upper) or through a UV filter (lower) in the field. Sex and species names are provided for each image.





thorax and abdomen is detected in several families, such as Aeshnidae (Harris et al., 2011; **Figures 1J,L**, arrows). The surface wax can be removed by rubbing and dissolves completely in chloroform (Schultz and Fincke, 2009; Guillermo-Ferreira et al., 2015, 2019; Futahashi et al., 2019).

In Libellulidae dragonflies, the abdominal surface wax strongly reflects both UV and visible light (Robey, 1975; Silberglied, 1979; Robertson, 1984; Harris et al., 2011; Futahashi et al., 2019). UV photographs confirmed that the whitish surface wax caused UV reflection in all examined species (**Figures 1E–G**). Based on its fine structure, the abdominal surface wax can be classified into two types, lamellar type (detected in Lestidae and Libellulidae) and filamentous type (detected in Calopterygidae and Euphaeidae) (Gorb, 1995). The sizes of wax lamellae on the abdomen differ between the dorsal and ventral regions as well as between species and sexes (Gorb, 1995; Futahashi et al., 2019). The whitish color of the wax-secreted region temporarily blackens when light scattering is disturbed by the application of acetone, while it irreversibly blackens when the wax is removed by chloroform treatment, suggesting that wax-based fine structures are responsible for the whitish color with UV reflection (Futahashi et al., 2019). The whitish wax also appears on the wing surface of several Odonata species, forming micropillar or filamentous structures (Gorb et al., 2000; Schultz and Fincke, 2009; Guillermo-Ferreira et al., 2015, 2019; Nixon et al., 2017). In the neotropical helicopter damselfly *Megaloprepus caerulatus* (Coenagrionidae, formerly known as Pseudostigmatidae), white bands on the wings are coated with longer and thicker structures compared to the bluish iridescent and hyaline wing regions (Schultz and Fincke, 2009). Chloroform treatment removes the wax on the wing surface, turning white color into transparent (Schultz and Fincke, 2009).

The reflectance of the dorsal abdomen of Libellulidae species shows that mature males with whitish wax represent a spectrum that decreases gradually from 300 to 700 nm (**Figure 2C**; Robertson, 1984; Futahashi et al., 2019). Meanwhile, the dorsal abdomen of mature females (without the pruinose wax) exhibits little UV reflection and mainly reflects light at wavelengths above 500 nm (**Figure 2C**; Futahashi et al., 2019). The reflectance of the whitish wing markings shows a flat spectrum (Schultz and Fincke, 2009; Xu and Fincke, 2015; Nixon et al., 2017). In *M. caerulatus*, sex-specific white bands appear on the wings, and white bands on females exhibit stronger reflection than those on males (**Figure 2C**; Schultz and Fincke, 2009; Xu and Fincke, 2015).

In the Libellulidae species, chemical analysis has revealed that very long-chain aldehydes and very long-chain methyl ketones are the major components of the abdominal wax. The chemically synthesized compound of very long-chain methyl ketone, which is the main UV-reflective wax component of mature males of *Orthetrum albistylum* (Libellulidae) (**Figure 1G**), spontaneously forms light-scattering fine structures with strong UV reflection (Futahashi et al., 2019), suggesting that the secreted very long-chain methyl ketones play a crucial role in UV reflection. The comparative transcriptome in different stages, sexes, and abdominal regions of *O. albistylum* has revealed that the *ELOVL17* gene, a member of the elongation of the very long-chain fatty acid (ELOVL) protein family,

is specifically expressed in the region where very long-chain methyl ketones are present, suggesting that this gene is involved in the production of very long-chain methyl ketones (Futahashi et al., 2019). Wax-based UV reflection has been also reported in several other organisms (Byers, 1975; Pope, 1979); however, the chemical composition of dragonfly abdominal wax differs from previously identified waxes of other organisms. Because the wax-based body color changes in the Libellulidae dragonflies are likely to have evolved independently of those in other Odonata (**Figure 2A**), further research is needed to determine whether the wax component and the genes involved in wax production are the same in other Odonata species.

## EXAMPLES AND MECHANISMS OF PIGMENT-BASED PALE COLOR WITH UV REFLECTION

Recently, another type of UV reflection has been reported, namely, UV reflection by epidermal granules containing pteridine pigments. UV reflection is generally weak or undetectable in the blue-green, yellow, and white thoracic and abdominal markings of most Odonata species (**Figures 1H–P**; Hilton, 1986). Notably, UV reflection has been sometimes confirmed in pale-colored regions without whitish wax (**Figure 2A**; Harris et al., 2011; Henze et al., 2019). For example, in the blue-tailed damselflies *Ischnura* species (Coenagrionidae), remarkable UV reflection has been recognized in the blue-green thoracic regions of males and andromorphic females only during the immature adult stage, and UV reflection decreases rapidly as they mature (**Figures 1I,J, 2D**; Henze et al., 2019). Such non-iridescent light blue-green coloration of dragonflies can be explained by coherent scattering due to light-scattering granules containing pteridine pigments in the distal layer of the epidermis and light-absorbing granules containing ommochrome pigments in the proximal layer of the epidermis (Veron, 1974; Prum et al., 2004; Henze et al., 2019). Some pteridine pigments (e.g., leucopterin and xanthopterin) absorb light predominantly in the UV range, and the amount and composition of pteridine pigments cause sex- and species-specific differences in UV reflection in the wings of pierid butterflies (Makino et al., 1952; Stavenga et al., 2004; Rutowski et al., 2005; Giraldo and Stavenga, 2007; Morehouse et al., 2007). In *Ischnura* damselflies, reflectance at different adult developmental stages is associated with changes in pteridine pigments (probably erythropterin and xanthopterin) within epidermal nanospheres (Henze et al., 2019). The calculated reflectance spectra show that erythropterin-containing nanospheres reflect light with two peaks in the green and UV wavelength range, whereas xanthopterin-containing nanospheres reflect light in the blue wavelength range (Henze et al., 2019), corresponding to the reflectance of immature or mature males, respectively (**Figure 2D**).

In males of the featherleg damselfly *Platycnemis foliacea* (Platycnemididae), UV reflection was observed on the white petal-like enlarged regions of the legs, although the central lines of the white legs, whitish thoracic, and abdominal

markings scarcely reflected UV light (**Figure 1H**). Moreover, UV reflection was also prominent at the white spot called the pseudopterostigma on the female wings of *C. japonica* (Calopterygidae) (**Figure 1D**, arrow). Yellowish pigments in Odonata have been considered to be pteridine pigments (Krieger, 1954; Vilela et al., 2017), and pteridine pigments often emit strong fluorescence under UV light (Kayser, 1985). Fluorescence signals were generally observed with yellowish markings (**Figures 2E,F**), the edge and central line of the white legs of *P. foliaceae* (**Figures 2G,H**), and the wing veins of the pseudopterostigma region of *C. japonica* (**Figures 2I,J**), probably due to pteridine pigments. Meanwhile, the fluorescence signals were weak in the UV-reflective regions, such as white petal-like regions on the legs of *P. foliaceae* (**Figures 2G,H**) and the whitish wing membranes in the pseudopterostigma of *C. japonica* females (**Figures 2I,J**), suggesting that UV-reflective white colors are probably due to substances other than pteridine pigments. Identification of pigments in various Odonata species deserves future study.

## ECOLOGICAL SIGNIFICANCE OF UV REFLECTION AND ABSORPTION

Since individuals of Odonata species visually recognize each other, body color patterns are generally important for mate recognition and male–male competition. Species with iridescent wings are found mainly in Zygoptera species (**Figure 2A**). This is likely because Zygoptera species fly more slowly than Anisoptera species (Rüppell, 1989), and species with colored wings often pause their wings during encounters (Hilfert-Rüppell and Rüppell, 2013). Also, courtship behavior is found predominantly in Zygoptera species (e.g., Calopterygidae), as males usually display their iridescent wings to females and rival males (Waage, 1973, 1988; Siva-Jothy, 1999; Hariyama et al., 2005; Nixon et al., 2013; Günther et al., 2014). The reflectance patterns suggest that the UV reflection seems to be important for some Odonata species, such as *C. scintillans* and *Z. lanei* (**Figure 2B**). In *C. scintillans*, the winners of territorial fights have higher values for the wing pigmentation and the hue of the wing's dorsal surface (Guillermo-Ferreira et al., 2019). In *Z. lanei*, males with distal half of their dorsal wings painted black reduce aggression from rivals, suggesting that iridescent wing coloration is important for male-male competition (Guillermo-Ferreira et al., 2015).

In *M. caerulatus*, both males and females have UV-blue iridescent markings and UV-reflective white bands on their wings (**Figures 2B,C**), although the position of white bands differs between sexes. Behavioral experiments suggest that the white band pattern on females helps males to distinguish potential mates from rivals (Schultz and Fincke, 2009). When UV reflection is artificially suppressed by using a UV-absorbing sunscreen agent, males with white bands that are less UV-reflective are more likely to lose territorial fights, although the UV reflectivity of the female's white bands does not affect the male's mate recognition (Xu and Fincke, 2015). In the damselfly *Mnesarete pudica* (Calopterygidae), both

mature males and mature females have UV-reflective coloration on their wings. Behavioral experiments with reducing UV reflection on their wings show that UV reflection enhances both sexual and aggressive responses, while male-specific red wing pigmentation is important for mate recognition (Guillermo-Ferreira et al., 2014).

Wax-based abdominal color changes are also important for mate recognition and male–male competition in many Odonata species (Jacobs, 1955; Robey, 1975; Corbet, 1999), although it remains unclear whether UV reflection itself is important. Moreover, a wax-based whitish color may help thermoregulation and provide protection against UV-induced damage by reflecting UV radiation (Paulson, 1983; Ubukata, 1985; Futahashi et al., 2019). Species that prefer sunny habitats tend to show stronger UV reflection, like mature males of *O. albistylum* (**Figures 1G, 2C**; Paulson, 1983; Futahashi et al., 2019). Given that most dragonfly species with ventral wax in females mate in sunny places without flying (**Figure 1F**; Sugimura et al., 2001; Ozono et al., 2017), it seems plausible that the UV-reflective wax in females protects the ventral abdomen, including ovaries, from UV damage (Futahashi et al., 2019).

Compared with iridescent coloration and the wax-based whitish color, little study has been conducted about the pigment-dependent differences in UV reflection. It should be noted that males of *I. elegans* prefer mature females with little UV reflection to immature females (Van Gossum et al., 2001). Males of *P. foliaceae* display their enlarged white legs to females, as well as to rival males, and *C. japonica* males first grab white pseudopterostigmas on the female's wings when connecting with a female (Sugimura et al., 2001; Ozono et al., 2017). The importance of UV reflection in these behaviors should be confirmed experimentally, like *M. caerulatus* and *M. pudica*.

Other than reflection, UV light is absorbed by pigments or transmitted due to absence of pigments. Hilton (1986) reported that the wings transmitted UV light without absorbing or reflecting it in about half of the species examined, and yellow, orange, and brown wing markings generally exhibited UV absorption (**Figures 1B–D,F,M–O**). Notably, conspicuous UV absorption has been observed in the almost hyaline (very faint yellow to human eyes) wings in some dragonflies, especially in Gomphidae species (**Figures 1N,O**; Hilton, 1986). Also, these UV absorption patterns often differ between sexes and species. For example, in the dragonfly *Phanogomphus hodgesi* (Gomphidae), UV light is absorbed in male wings and transmitted in female wings, although both males and females have similar hyaline wings (Hilton, 1986). In the male of *Sinogomphus flavolimbatus* (Gomphidae), a UV absorption pattern was detected at the base of the wings (**Figure 1O**), which is reminiscent of a UV-absorbing flower nectar guide. These examples suggest that sex- and species-specific UV absorption should also be considered for examining the importance of body color.

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The author confirms being the sole contributor of this work and has approved it for publication.

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**Conflict of Interest:** The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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