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# Shiny wing scales cause spec(tac)ular camouflage of the angled sunbeam butterfly, *Curetis acuta*

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The angled sunbeam butterfly, *Curetis acuta* (Lycaenidae), is a distinctly sexually dimorphic lycaenid butterfly from Asia. The dorsal wings of female and male butterflies have a similar pattern, with a large white area in the female and an orange area in the male, framed within brown-black margins. The ventral wings of both sexes are silvery white, which is caused by stacks of overlapping, non-pigmented, and specular-reflecting scales. With oblique illumination, the reflected light of the ventral wings is strongly polarized. We show that the silvery reflection facilitates camouflage in a shaded, foliaceous environment. The ecological function of the silvery reflection is presumably two-fold: for intraspecific signalling in flight, and for reducing predation risk at rest and during hibernation. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **109**, 279–289.

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## INTRODUCTION

A tapestry of numerous small scales imbricates the wings of butterflies, often causing strikingly colourful patterns (Nijhout, 1991). In many species, the patterns differ strongly between the dorsal (upper) and the ventral (under) wing sides, because of opposite biological functions. The dorsal wings, which are exposed in active butterflies, for instance during flight, are often brightly coloured. These markings function in intra- and interspecific signalling: for example, in the radiant blue male *Morpho* butterflies and in the elaborately coloured peacock butterfly, *Inachis io* (Nijhout, 1991; Srinivasarao, 1999; Kinoshita, 2008). In most butterflies are at rest, have

a dull, inconspicuous colour, which then serves to camouflage the butterfly and decrease the risk of predation: e.g. the ventral sides of *I. io* are brownblack, presumably rendering the butterfly inconspicuous against the background when they rest or hibernate. In the green hairstreak butterfly, *Callophrys rubi*, the colour of the ventral wings matches that of plant leaves (Michielsen & Stavenga, 2008; Michielsen, De Raedt & Stavenga, 2010; Schröder-Turk *et al.*, 2011).

The colour of the wing scales can be mainly pigmentary (as in *I. io*), as a result of pigments deposited in the wing scale structures, or can have a structural basis (as in *C. rubi*), when the structure of the scales have periodicities in the nanometer range. Butterfly wing scales commonly consist of two layers: a flat basal lamina and a structured upper lamina. The two layers are joined by pillar-like trabeculae (Ghiradella, 1984; Ghiradella, 1998; Ghiradella, 2010). When the upper

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lamina is irregularly structured, the scale acts as a diffuser, and, in the absence of a light-absorbing pigment, thus becomes a white light reflector (Stavenga et al., 2004; Morehouse, Vukusic & Rutowski, 2007). For example, the wing scales of white pierids (cabbage butterflies) have highly elaborate, granular structures, which effectively scatter broadband light (Giraldo, Yoshioka & Stavenga, 2008). These granules contain a pterin pigment, leucopterin (Yagi, 1954), which absorbs light in the ultraviolet wavelength range (invisible for humans, but visible for insects). Xanthopterin and ervthropterin, other pterins common in pierid butterflies, also absorb in the blue and green wavelength ranges, respectively, and thus the wings have a yellow, orange, or red colour (Wijnen, Leertouwer & Stavenga, 2007).

Structural coloration occurs when periodic structures enhance light reflection in a specific wavelength range by constructive light interference and suppress light reflection at other wavelengths by destructive interference (Vukusic & Sambles, 2003; Kinoshita, Yoshioka & Miyazaki, 2008). The periodicity can be one-dimensional, as in the multilayers of the bluecoloured wing scales of various lycaenids (Wilts, Leertouwer & Stavenga, 2009), or three-dimensional, as in the gyroid-type photonic crystals in the greencoloured wing scales of the papilionid Parides sesostris (Land, 1972; Vukusic & Sambles, 2003; Michielsen & Stavenga, 2008; Wilts et al., 2012a). In many butterfly species the structural colours are tuned by filtering pigments: that is, pigmentary and structural colorations are combined, for instance in the green scales of P. sesostris (Wilts et al., 2012a) and in the purple wing tip scales of the male pierid Colotis regina (Wilts, Pirih & Stavenga, 2011).

Structural coloration commonly refers to reflections in a restricted wavelength band. Some structurally coloured butterfly species, however, have wing scales reflecting broadband light, for example the nymphalid *Argyrophorus argenteus*, where the wings are fully covered by silvery reflecting scales (Vukusic, Kelly & Hooper, 2009). Silvery reflecting wing scales also occur in patches at the ventral wings of several fritillary butterflies (Simonsen, 2007; Giraldo, 2008).

Another prominent example is the angled sunbeam butterfly *Curetis acuta*, which is a widespread Asian butterfly (Eliot, 1990). In central Japan, its flying period is between May and November, with a peak in the autumn on warm and sunny days. The ventral wings of both sexes of *C. acuta* are almost fully covered by silvery coloured scales, but the coloration of the dorsal wings is sexually dimorphic (see Fig. 1). To unravel the spectral and spatial reflection properties of *C. acuta* wings and wing scales, we have applied a variety of optical methods: among others microspectrophotometry, imaging scatterometry, and angle-dependent reflectance measurements. We discuss the biological function of the silvery-white coloration as an adaptive coloration strategy, serving for camouflage in a foliaceous environment and as an intraspecific signal during patrolling flights.

## MATERIAL AND METHODS

## ANIMALS

Specimens of *Curetis acuta* Moore, 1877 (Lycaenidae) were captured near Sokendai, Shonan Village, Kanagawa Prefecture, Japan. Micrographs of wing patches were taken with a Zeiss Universal Microscope (Carl Zeiss AG, Oberkochen, Germany) and an Olympus SZX16 stereomicroscope (Olympus, Tokyo, Japan), equipped with Kappa DX-40 (Kappa Optronics GmbH, Gleichen, Germany) and Olympus DP70 digital cameras, respectively.

## SCANNING AND TRANSMISSION ELECTRON MICROSCOPY

The ultrastructure of the wing scales was investigated with an XL-30 ESEM scanning electron microscope (Philips, Eindhoven, Netherlands). Prior to imaging, the wing scales were sputtered with palladium. For transmission electron microscopy (TEM) of the scales, wing parts were prefixed in 2% paraformaldehyde and 2.5% glutaraldehyde in  $0.1 \text{ mol } l^{-1}$ sodium cacodylate buffer (CB, pH 7.3) for ~45 min, then post-fixed in 2% osmium tetroxide in 0.1 M CB for 2 h at room temperature (25 °C), and further block-stained in 2% uranyl acetate in 50% EtOH for 1 h. After dehydrating with a graded series of ethanol and infiltration with propylene oxide, the tissues were embedded in Spurr's resin. The tissues were cut into 40–50-nm ultrathin sections, which were observed using a Hitachi H7650 (Tokyo, Japan) transmission electron microscope.

## Spectrometry

Reflectance spectra of the wings were measured with a bifurcated probe (Avantes FCR-7UV200; Avantes, Eerbeek, the Netherlands) and with an angledependent reflectance measurement (ARM) set-up, using an Avaspec 2048-2 CCD detector array spectrometer. The procedures were performed as described previously (Pirih, Wilts & Stavenga, 2011; Stavenga *et al.*, 2011). Transmittance spectra of single scales were measured with a microspectrophotometer (MSP), consisting of a Leitz Ortholux microscope, with an Olympus  $20 \times$  objective (NA 0.46), connected with the Avantes spectrometer. The reference was a diffuse white reflectance tile (Avantes WS-2).



**Figure 1.** Sexual dichromatism of the angled sunbeam butterfly, *Curetis acuta*, and reflectance spectra. A, dorsal side of the female *C. acuta* with large, white-coloured areas on the fore- and hindwing, framed by brown-black borders. B, dorsal side of the male, with large, orange-red-coloured areas. C, brilliant-white ventral side of the female. (The ventral wing side of the male is identical.) D, reflectance spectra measured with a bifurcated probe of the numbered wing areas in (A-C). Scale bar: 1 cm.

## IMAGING SCATTEROMETRY

For investigating the spatial reflection characteristics of the wing scales, we performed imaging scatterometry (Stavenga *et al.*, 2009). An isolated, single scale or a wing patch was glued at the pulled tip of a glass micropipette, and subsequently positioned at the first focal point of the ellipsoidal mirror of the imaging scatterometer. The object was illuminated with a narrow (or alternatively wide) aperture, focused light beam, and the spatial distribution of the far-field scattered light was then monitored. A flake of magnesium oxide served as a white diffuse reference object (for further procedural details, see Vukusic & Stavenga, 2009; Wilts *et al.*, 2009).

## RESULTS

#### SEXUAL DICHROMATISM OF CURETIS ACUTA

Both sexes of *C. acuta* have a wingspan of about 4 cm (Fig. 1). The dorsal wings of females and males have similar patterns, but are composed of different colour

sets. The dorsal fore- and hindwings in both sexes are framed within brown-black margins, whereas the central areas are white in the female and orange in the male (Fig. 1A, B). The ventral wings of both females and males are silvery white (Fig. 1C). We measured the reflectance spectra from the various wing areas with a bifurcated probe (Fig. 1D) and from single wing scales with a microspectrophotometer.

The white areas of the female dorsal wings contain a majority of silvery-whitish scales, intermingled with brown-black scales (Fig. 2A), with the ratio of the two scale types depending on the location. The orange areas of the male dorsal wings contain orange-red scales, mixed with brown-black scales (Fig. 2B). The latter scale type exclusively populates the brown wing margins. These scales are clearly coloured by melanin pigment, as is evident from the sharp rise in reflectance with increasing wavelength (Fig. 1D, curve 1).

The reflectance of the white areas in the female dorsal wings (Fig. 1D, curve 2) is low in the UV range, with a minimum at  $\sim 280$  nm, possibly because of absorption by uric acid (Wijnen *et al.*, 2007) and/or



**Figure 2.** Epi-illumination light microscopy of *Curetis acuta* wing patches. A, an area in the female dorsal hindwing showing silvery-white and brown-black scales. B, an area of the male dorsal forewing showing orange-red and black scales. Scale bar:  $100 \mu m$ .

proteins (Pace *et al.*, 1995); the reflectance is high in the visible wavelength range, and rises further above 600 nm. The latter rise is the result of melanincontaining brown-black scales (Fig. 2A). The reflectance of the orange areas in the male dorsal wings (Fig. 1D, curve 3) is very low in the short wavelength range, up to 500 nm, evidently because of a pigment that absorbs light in the violet-blue wavelength range, and then rises in two phases, between 500 and 600 nm, because of the decreasing absorption of the blue-absorbing pigment in the orange-red scales, and again above 600 nm because of the scattering caused by the melanin-containing brown-black scales (Fig. 2B).

The reflectance spectrum of the ventral wings of both females and males is broadband, with a minimum in the UV range, very similar as that measured in the white scales of the female dorsal wings (Fig. 1D, curve 4). In the visible wavelength range, the reflectance of the ventral wings exceeds that of the white areas of the female's dorsal wings, because of stacking in the white scales. Below the stacks of white scales there are some black scales, but their contribution to the overall reflectance remains minor. Measurements with an integrating sphere (not shown) yield reflectances of about 0.5 because of the large number of up to six overlapping scales, similar to pierid butterflies (Stavenga, Giraldo & Hoenders, 2006; Wilts *et al.*, 2011).

The reflectance spectra of the silvery-white areas indicate the absence of a pigment absorbing light in the visible wavelength range, but the orange-red and brown-black scales obviously do contain pigments. We characterized these pigments by measuring the



**Figure 3.** Absorbance spectra of single orange-red and brown-black scales in immersion, deduced from transmission measurements with a microspectrophotometer.

spectral transmission on single scales immersed in a fluid with refractive index 1.56; this value closely matches the refractive index of chitin, the material of butterfly scales (Leertouwer, Wilts & Stavenga, 2011). Figure 3 shows the absorbance spectra obtained. The pigment in the brown-black scales has a broad absorbance spectrum, very reminiscent of melanin (Stavenga *et al.*, 2012a). The pigment in the orangered scales absorbs maximally at ~455 nm, and therefore the pigment is presumably a mixture of different ommochromes (Nijhout, 1997).

## ANATOMY OF THE WING SCALES

Visual inspection showed that the dorsal and ventral wing sides not only strongly differ in coloration, but



Figure 4. Ultrastructure of the wing scales. A, scanning electron micrograph of an orange-red scale of the male dorsal wing, showing the basic bauplan of scales: ridges connected by cross-ribs; pigment is immersed throughout the scale material. B, scanning electron micrograph of a silvery scale from the ventral wing of a female: the windows in between the ridges and cross-ribs are closed, except for a few perforations. C, transmission electron microscopy of a cross section of a silvery scale. Scale bar:  $2 \mu m$ .

also in spatial reflection properties. Whereas the dorsal wings reflect light rather diffusely, the ventral wings are rather specular. This indicated a very different fine structure of the scales, and thus we performed scanning electron microscopy on the orange-red scales of the male dorsal wings, and on the silvery scales of the female ventral wings (Fig. 4A, B).

The orange-red scales have the standard, basic structure of butterfly wing scales (Fig. 4A). The upper lamina is formed by numerous parallel ridges, with spacing of about 1.3 µm, and connecting cross-ribs, with spacing of about 0.6 µm. The windows in between the cross-ribs are open, and trabeculae support the upper lamina onto the more or less flat, continuous lower lamina (Ghiradella, 1989; Ghiradella, 2010). The silvery scales of the ventral wings have a different structure (Fig. 4B). The distance between the ridges is  $\sim 1.8 \,\mu m$ , and that between the just-visible cross-ribs is  $\sim 3 \,\mu m$ . The windows are virtually fully closed, except for some small, irregular perforations. Transmission electron microscopy revealed that the silvery scales are slight modifications of the standard butterfly wing scale. The upper lamina is characteristically marked by pronounced ridges, and the lower lamina is basically a thin film (Fig. 4C). The trabeculae connecting the upper and lower laminae are irregularly spaced.

# SPECTRAL AND SPATIAL SCATTERING PROPERTIES OF THE SILVERY SCALES

The nearly flat laminae of the silvery scales suggest that these scales act as thin-film reflectors. A scale of the ventral wing of *C. acuta* observed with an epiillumination microscope, using a high-power objective, reveals a colourful, speckled image (Fig. 5A). The local speckles average out at low magnification (Fig. 2A), merging into the silvery-white colour observed overall (Fig. 1C).

We investigated the spatial scattering properties of the silvery scales by imaging scatterometry (Fig. 5B-D). Figure 5B presents a scatterogram of a single white scale, oriented nearly perpendicular to the horizontal axis of the scatterometer: the ridge direction made a small angle with the vertical axis. The light source was a narrow-aperture  $(5^{\circ})$  white-light beam, and the illuminated area was a spot with diameter of  $10 \,\mu\text{m}$ . The resulting scattering pattern is a coloured line perpendicular to the ridges. It is caused by diffraction at the grating created by the prominent scale ridges, which interrupt the plane of the reflecting window panes (Kinoshita, 2008; Kinoshita et al., 2008; Stavenga et al., 2009). Figure 5C shows the scatter diagram when a wing patch area of 140 µm in diameter (approximately three to four wing scales) was illuminated with the same narrow-aperture beam. The resulting scatter pattern is a broadened white line on top of a white, diffuse background. The broad white line is the average of the diffraction lines created by the individual scales. By opening the aperture, so that the illuminating light source becomes hemispherical, a diffuse, hemispherical scatter pattern was obtained (Fig. 5D).



**Figure 5.** Epi-illumination light microcopy and imaging scatterometry of silvery wing scales. A, a scale of the ventral wing observed with an epi-illumination light microscope. Scale bar:  $20 \,\mu$ m. B, scatterogram resulting from a narrow aperture axial light beam illuminating a small part of a single scale. A diffraction pattern emerges perpendicular to the ridges, which are slightly oriented obliquely. C, off-axis illumination on several scales yields a more diffuse scatter pattern. D, illumination by a hemispherical light source results in a diffuse scatter pattern.

## ANGLE- AND POLARIZATION-DEPENDENT REFLECTANCE

The ventral wing scales consist of reflecting plates, suggesting that at large angles of light incidence the reflected light may become strongly polarized. We therefore performed a detailed angle- and polarization-dependent analysis of the reflectance of the whole wing (see also Fig. S1). Figure 6 shows the angle-dependent reflectance measured for incident linearly polarized light, i.e. transverse electric (TE, or s) and transverse magnetic (TM, or p) polarized light, averaged over the wavelength range of 300–700 nm. The plane of light incidence, which contains the



**Figure 6.** Angle-dependent reflectance measured from a ventral wing of a male *Curetis acuta* for transverse electric (TE) and transverse magnetic (TM) polarized light averaged over the wavelength range of 300–800 nm. The plane of light incidence was normal to the wing and parallel with the scale ridges. The angle of light incidence, determined by the angle of the fibre delivering the illumination, was varied in steps of 5°, and the angle of the detection fibre was varied mirrorwise. The reflectance of TE-polarized light increases with increasing angle; the reflectance of TM-polarized light decreases with increasing angle, but goes through a minimum at ~50° (see blue arrows), as expected for a mirror-like dielectric surface. The minimum reflectance of the TM-polarized light is not zero, because of a background of diffusely scattered light.

incident light rays, was set perpendicular to the wing and parallel with the scale ridges. The angle of illumination, delivered by a focused light fibre, was varied in steps of 5°, and the angle of the detection fibre was varied mirror-wise. The reflectance of TE-polarized light increases monotonically with increasing angle; the reflectance of TM-polarized light decreases with an increasing angle of incidence up to ~55°, but above this angle, the reflectance rises again. This behaviour resembles that of an ideal, flat chitin layer, where the reflectance of TM-polarized light goes to zero at Brewster's angle (see the blue arrows in Fig. 6). The substantial background reflectance of ~0.45 is presumably caused by incoherent scattering induced by irregularities in the scale structures and in the scale stacking (indicated in Fig. 6 by the dashed green line).

## DISCUSSION

## Comparison of the scales of *Curetis Acuta* with those of *Graphium sarpedon*

Female and male *C. acuta* differ substantially in the coloration of the dorsal wings, which have orange

central areas in the males and white central areas in the females (Figs 1, 2). The displayed colours are the result of pigments and/or wing scale structuring. In a study on the swordtail butterfly *Graphium sarpedon* we found that the white scales of *G. sarpedon* have the standard papilionid scale structure (Stavenga *et al.*, 2012b), which is a slight modification of the basic butterfly scale structure (Ghiradella, 2010). The standard papilionid scale structure results in diffuse scattering (Wilts *et al.*, 2012b), and the same occurs with the orange-red scales of the male *C. acuta*, which have the basic nymphalid butterfly scale structure (Fig. 4A).

The ventral wings of both females and males are silvery white, and are essentially identical. The silvery scales somewhat resemble the glass scales of G. sarpedon (Stavenga et al., 2012b), which have fully closed, flat windows and act as strong polarizing reflectors for large angles of light incidence. The silvery scales of the ventral wings of C. acuta investigated here similarly act as polarizers; however, diffusely scattered light on the prominent ridges and the window perforations of the stacked silvery scales creates a substantial background (compare Fig. 5C with Fig. 6), which reduces the polarization contrast (see Fig. S1) as well as the specularity of the silver reflectors.

The chitin layers of the scale laminae of G. sarpedon each have a thickness of ~200 nm (for similar values of other butterflies, see Ghiradella, 1998). Like the glass scales of G. sarpedon, the membranes in the closed windows of Figure 4B will act as optical thin films. Thin films have coloured reflections, which rapidly change in colour upon slight changes in thickness. This is the reason why the silvery scales of C. acuta, when observed with an epi-illumination microscope, create a colourful, speckled image. It shows that the local thickness of the scale cuticle varies (Fig. 5A). The overall optical behaviour of the glass scales of G. sarpedon and the silvery scales of C. acuta is quite different. Whereas the reflections of the glass scales of G. sarpedon are strongly coloured and polarized overall, depending on the angle of illumination and observation, the specular reflections of the silvery scales of C. acuta are whitish and only a little polarized. The latter is the result of additive colour mixing of light reflected by multiple small domains of different thin-film thicknesses (see Figs 4C, 5A).

## The function of the silvery scales – not to be seen in the shade

Whereas the dorsal wing sides are displayed only when the animals are active (Fig. 7A), the ventral wing sides are exposed when they are at rest (Fig. 7B,



**Figure 7.** *Curetis acuta* perching on leaves. A, a female exposing the dorsal wings. B, exposed ventral wings, showing a distinct silvery-white reflection resulting from direct illumination by the sun. C, dorsal wings observed from an angle substantially deviating from the mirror angle of the sun, so that the wing reflections are the result of light emerging from the leaves (cropped photo by Oleg Kosterin.

C). When the butterflies rest on the leaves of shrubs and trees in the shade or under overcast skies, the ventral wing sides assume a green colour, thus serving as camouflage in a shaded environment



**Figure 8.** Diagram of light reflected from a *Curetis acuta* butterfly resting on a leaf. The letters (a, b, and c) refer to the panels presented in Figure 7.

(Figs 7C, 8); however, when the butterflies are illuminated by direct sun, their distinct, silvery-white reflections start to contrast with the surrounding leaves (Fig. 7B). Interestingly, the vegetation of the coastal regions of central Japan contains numerous sclerophyllous plants with waxy leaves (e.g. the Japanese oak Quercus acuta), which produce green reflections with white specularity when exposed in the sun. In this environment the silvery-white ventral side of C. acuta appears to blend with the background, even when exposed to direct sunlight. Indeed, when chased C. acuta flee into dense sclerophyllous shrubs and sit on the twigs, where they are virtually impossible to detect from the background, both under overcast conditions and under clear skies. To a human observer, the resting butterflies resemble a half-eaten dead leaf, both in shape and in colour. As C. acuta survives the winter in the imago form, the individuals conceivably increase their chance of survival by actively searching for evergreen trees and shrubs with waxy vegetation before they start hibernation (and possibly the white colour helps for hiding in times of snow). The sparse dark scales present on the ventral wings may well add to the blending of the coloration with the twigs and dead leaves.

The white coloration of the ventral wings may in addition function in intraspecific signalling. When in

flight, at up to 10 m above the ground, *C. acuta* flashes when reflecting direct sunlight, especially against clear blue skies. In males this flashing signal may be enhanced by the black and orange of the dorsal wings, which are visible during the wingflap. We conclude that the silvery-white coloration of *C. acuta*, a combination of diffuse and specular reflectance, serves both to conceal and to reveal.

Given that *C. acuta* has a broad geographical distribution, ranging from India to North Japan, its forest habitats are likely to be very diverse. Furthermore, other species of the genus *Curetis*, which comprises 16 species, are likely to live in even more diverse environments (from the Philippines to the Himalayas), yet they all have silvery-white ventral wings (Eliot, 1990). It would therefore be very interesting to learn how well the silvery-white camouflage performs in environments with different optical properties, and what is the primary evolutionary drive to become silvery white, i.e. for camouflaging or for signalling purposes.

#### SILVER COLORATION IN NATURE

A metallic silver coloration occurs frequently in the animal kingdom, and is mostly caused by multilayered structures in the outermost organismal layers. A silvery reflection is often used for camouflage as it allows blending in with the environment with diffuse illumination from the surroundings (see above). This is the case in some butterfly pupae (Steinbrecht, 1985), for example. Also, many fish and cephalopods use a silver coloration as a ubiquitous camouflage strategy, i.e. by reducing contrast with the surrounding light conditions (Denton, 1970; Denton, Gilpin-Brown & Wright, 1972; Mäthger et al., 2009; Holt et al., 2011; Jordan, Partidge & Roberts, 2012). Silver reflectors can, for example, be found in the skin of herrings and sardines (Jordan et al., 2012), and around the eyes of squids and cephalopods (Mäthger et al., 2009; Holt et al., 2011). In fish, the silver reflectors are made of multilayers, consisting of a large stack of layers (of more than ten), which is in contrast to C. acuta where two air-separated layers of chitin create the silvery appearance. Fish reflectors can therefore be specialized for high reflectance and low polarization at all angles of light incidence (Jordan et al., 2012). In other animals, like birds, butterflies, and beetles, silver coloration is often employed for a contrastful, highly visible display (Vukusic et al., 2009). In the bird of paradise Parotia lawesii (Lawes' parotia), silver-coloured occipital feathers act as a unique visual cue in the mating ritual (Laman & Scholes, 2012; D. G. Stavenga, H. L. Leertouwer, D. Osorio & B. D. Wilts, unpubl. data). Curetis acuta may be unique in that the silvery wings combine two functions, acting for display when the butterflies are active and for camouflage when the butterflies are at rest.

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# SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Spatial reflectance maps for (A) unpolarised, (B) TE-(s)-polarized and (C) TM-(p)-polarized light measured of the ventral wing of a female *Curetis acuta*. The polarization contrast, i.e. the s/p reflectance ratio map is shown in (D). The polarization contrast is highest under large angle of illumination and detection. Black dots represent measurement points used for the interpolation. The procedure and analysis of these plots is as explained in Pirih *et al.* (2011).