

# Chapter 24

## Structural Colors in Spiders

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### 24.1 Introduction

The finely color'd Feathers of some Birds, and particularly those of Peacock Tails, do, in the very same part of the feather, appear of several Colours . . . after the very same manner than thin Plates were found to do . . . and therefore their Colours arise from the thinness of the transparent parts of the Feathers. . . . and to the same purpose it is, that the Webs of some Spiders, by being spun very fine, have appear'd color'd . . . and by varying the Position of the Eye, do vary their Colours.

Isaac Newton (1730)

It is quite remarkable that almost 300 years ago Isaac Newton already knew that certain colors are not due to pigments but are caused by the microstructure of an object. The “thin plates” he was referring to were later found to be an essential part for light interference, which is mostly responsible for such “structural colors.” Newton’s correct assumption is even more astonishing, if we consider that those “thin plates” are in the nanometer range (or the wavelengths of visible light) and therefore could not be resolved with a light microscope.

Interference of light often occurs in stacks of thin plates, mostly in alternating materials with different optical densities (refractive index). At the border of each layer, a light ray is transmitted but also reflected; due to their different path lengths, a phase shift occurs (varies as a function of wavelength), and the reflected light will appear of a different color than the incoming light (Land 1972; Kinoshita et al. 2008).

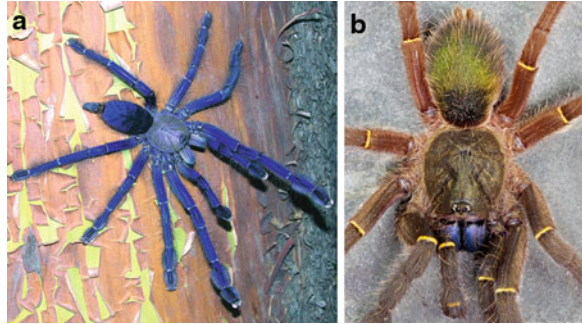
Structural colors may also be produced if a surface is scored by fine parallel ridges (and grooves) which act as diffraction gratings. Incident light is separated

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**Fig. 24.1** Colorful theraphosids. (a) A deep-blue *Cyriopagopus* resting on a tree trunk (Photo: Rick West). (b) A juvenile *Ephebopus cyanognathus* with the typical blue chelicerae, a green-golden opisthosoma, and yellow fringes on the distal femora (Photo: Bastian Rast)



into its component wavelengths and reflected into different directions (Parker and Martini 2006). This effect is commonly seen on the surface of some beetle wings (Hinton 1968) and also on compact disks.

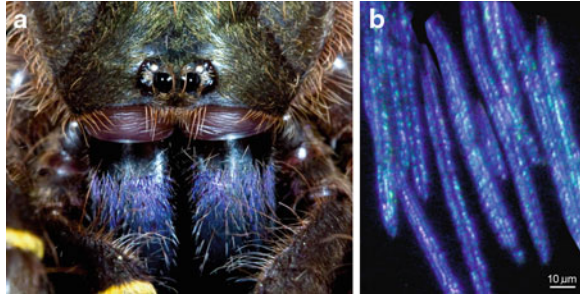
The most conspicuous structural (or physical) colors are known as *iridescence*, which means the colors change, depending on the angle of the incident light—or the angle an observer is viewing an iridescent object (Doucet and Meadows 2009; Meadows et al. 2009). Iridescent colors are caused on layered or crystalline nanostructures by coherent scattering (Prum 2006). Well-known biological examples of iridescence are certain feathers of birds (e.g., in peacocks and hummingbirds), certain insect wings (e.g., in butterflies and beetles), sea shells (mother of pearl), and even plant petals (Glover and Whitney 2010). Inanimate objects such as minerals (e.g., opal and labradorite), thin oil films on water, or soap bubbles may also display distinct interference colors (Kinoshita 2008; Vukusic 2004).

Among animals, structural colors have been extensively studied in birds (e.g., Durrer 1977; Prum 2006) and in insects (e.g., Ghiradella 1998, 2010; Prum et al. 2006), but spiders have received relatively little attention (Foelix et al. 2009; Ingram et al. 2009, 2011; Parker and Hegedus 2003). It is true that most spiders are rather drab and inconspicuously colored, yet there are notable exceptions. For instance, many jumping spiders (Salticidae) are quite colorful and even the nocturnal theraphosid may have brightly colored species (Fig. 24.1). This chapter will focus on structural colors found in these two families. Structural colors in these spiders reside mostly in special hairs and scales but may occur also in the solid body cuticle, for instance, of the chelicerae and the lenses of the eyes (Homann 1985).

## 24.2 Structural Colors in Hairs of Theraphosid Spiders

Even most arachnologists are not aware that there are quite a few brightly colored theraphosids; yet among pet spider keepers, these are highly prized, for instance, *Avicularia versicolor*, *Cyriopagopus* spp., *Ephebopus cyanognathus*, *Euathlus* spp.,

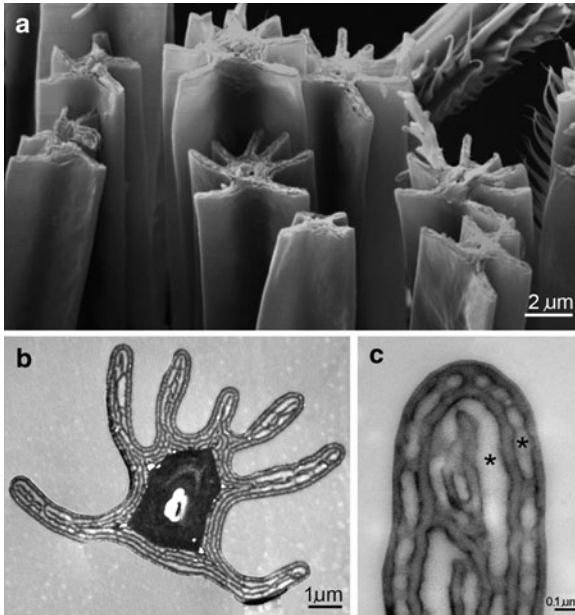
**Fig. 24.2** Blue hairs on the chelicerae of *E. cyanognathus*. (a) The blue color resides entirely in the hairs, not in the cuticle. (b) Epi-illumination with a weak LED light source yields deep-blue and purple color hues (from Foelix et al. 2009)



*Haplopelma lividum*, *Heterothele gabonensis*, *Holothele* spp., *Iridopelma* spp., *Pamphobeteus* spp., *Phormictopus* spp., *Poecilotheria metallica*, and *Xenesthis immanis*, to name just a few. Since most of them are iridescent, it is clear that the coloration is due (at least in part) to structural colors. But where exactly are the structural colors of those theraphosids localized, and how are they produced? In the few species we have examined so far, the bright colors were always restricted to specialized hairs and were not found in the body cuticle. The two species which we studied closely were *E. cyanognathus* and *P. metallica*.

### 24.2.1 *Ephebopus cyanognathus*

This spider from Brazil, Guyana, and Suriname is known under the vernacular name “blue fang tarantula” because of its metallic blue chelicerae (Figs. 24.1b and 24.2). A closer inspection under a dissecting microscope reveals that the blue color comes from deep-blue hairs covering the cheliceral basal segment (Fig. 24.2). Under epi-illumination the color may change from a deep violet blue to lighter blue or even turquoise, depending on the direction of the incident light. Under transmitted light these hairs appear completely transparent and colorless. They measure 100–200 μm in length and only 5–6 μm in diameter. The hair shaft bears several rows of fine extensions near the base, which fuse into solid laterally projecting fins along the distal hair shaft. Cross sections of the hair shaft appear star-shaped; only the central core consists of solid cuticle, whereas the peripheral part is layered (Fig. 24.3). The solid core probably absorbs non-reflected light and may function like the dark backing of a mirror. The peripheral lamellation is barely visible with the scanning electron microscope (Fig. 24.3a) but is clearly seen with the transmission electron microscope: about six cuticular lamellae (50–70 nm) alternate with narrow air spaces (60–120 nm) (Fig. 24.3 b, c). Due to the different refractive indices of cuticle (1.58) and air (1), incoming light rays will be split into refracted and reflected rays at each border line of cuticle and air. Depending on the different distances, these light waves have traveled into this air/cuticle stack, the reflected rays will show phase shifts, and the resulting interference shows up in different colors (Fig. 24.4a). Many thin layers (lamellae) cause “constructive

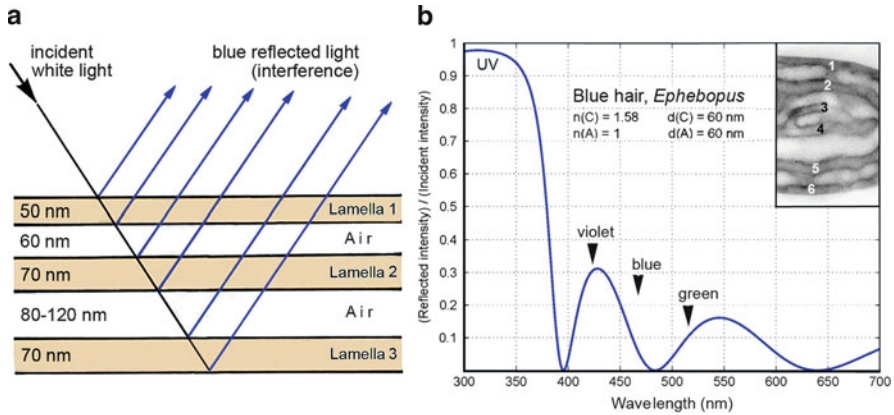


**Fig. 24.3** Fine structure of the blue cheliceral hairs in *E. cyanognathus* (Theraphosidae). (a) Hair shafts, clipped with a razor blade, exhibit a typical cogwheel shape in cross section. The lamellar structure of the hair wall is barely visible in this scanning electron micrograph. (b) Cross section of a blue hair as seen in a thin section in the transmission electron microscope. Only the center of the hair shaft consists of solid cuticle, whereas the lateral fins are distinctly layered. (c) High magnification of a lateral fin showing several cuticular lamellae of 50–70-nm thickness, alternating with equally narrow air spaces (*asterisk*) (from Foelix et al. 2009)

interference,” that is, the intensity of the interference colors is enhanced. About ten alternating layers yield an almost complete reflection of a given wavelength (Land 1972); in the case of the blue hairs in *Ephebopus*, we found 5–6 alternating layers (Fig. 24.3b, c). The color of the reflected light is mostly a deep blue, with shades of violet and green. This is confirmed, when the theoretical reflectance spectra are calculated, based on measurements of the optical thickness and the geometrical dimensions of the lamellae (Huxley 1968; Fig. 24.4b). In addition to a strong UV reflectance, there is a distinct peak in the blue and violet (maximum at 430 nm) and a smaller one in the green (maximum at 540 nm) in the calculated spectrum.

### 24.2.2 *Poecilotheria metallica*

Another deeply blue-colored theraphosid is *P. metallica* from India, the “Gooty Sapphire Ornamental Tree Spider,” or simply “Gooty Sapphire,” which is among the most treasured spiders among pet spider keepers. All legs, palps, and chelicerae are covered by deep-blue hairs, and the proximal tibiae show a patch of bright

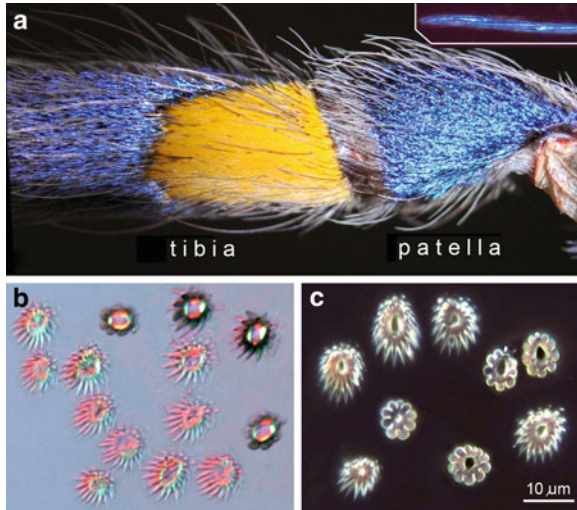


**Fig. 24.4** Blue iridescent colors in theraphosid hairs. (a) Diagram showing the reflection of incoming *white light* at the border lines of cuticular lamellae and air spaces. Measurements were taken from cheliceral hairs in *E. cyanognathus* (Fig. 24.3c). (b) Theoretical spectral reflectance of six cuticular lamellae of high refractive index  $n(C) = 1.58$  separated by five gaps of low refractive index  $n(A) = 1$ , based on measurements taken from the *inset* picture. Note that the largest peaks lie in the UV, *violet* and *blue* part of the spectrum, and a smaller one in the *green* (courtesy of Rolf Thieleczek)

yellow hairs (Fig. 24.5a). Whereas the blue hairs are clearly iridescent, the yellow hairs hardly change their hue when the angle of the incident light varies.

### 24.2.2.1 Blue Hairs

We selected the proximal tibia, where blue and yellow hairs are juxtaposed (Fig. 24.5a). Unexpectedly, cross sections of blue and yellow hairs often appear very similar in the light microscope (Fig. 24.5b). This is because the blue hairs have the same spiny extensions along the basal hair shaft as the yellow hairs do. The more distal part of the shaft in blue hairs lacks these spines and has only smooth longitudinal ridges (Fig. 24.6a). Cross sections show about nine such ridges (Figs. 24.5c and 24.6c) which are made up of a cuticular meshwork. High magnification reveals a solid cuticle in the core of the hair shaft and a distinct lamellation in the periphery (Fig. 24.7a). This lamellation of 6–7 stacked cuticular layers and intervening air spaces is well developed in the longitudinal ribs but changes into an irregular meshwork toward the center of the hair shaft. Interestingly, the same irregular meshwork is present in the spiny extensions of the basal hair shaft. This is most likely the reason why these hairs appear blue over the entire length of the hair shaft. Calculations of the spectral reflectance give essentially the same results as shown for the blue hairs in *Epehebopus* in Fig. 24.4b; the peak for violet blue has the maximum at 445 nm, and the smaller green peak at 540 nm (13 layers of cuticle/air, 65-nm thickness).



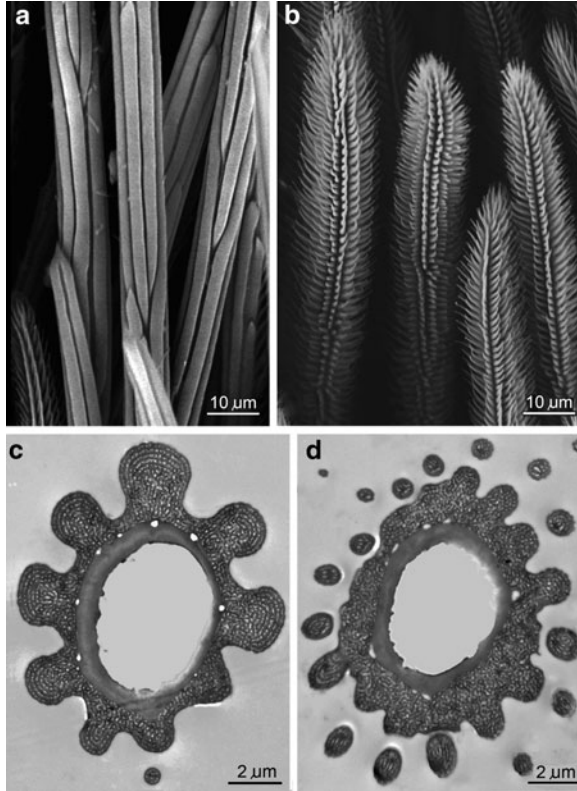
**Fig. 24.5** Blue and yellow hairs of the theraphosid *P. metallica*. (a) Note the difference of the blue color hues on tibia and patella, depending on the angle of the reflected light. *Inset*: higher magnification of a blue hair showing longitudinal ridges along the hair shaft. (b) Cross sections of ten spiny (yellow) hairs, which appear pinkish under polarized light; four darker (blue) hairs are seen in the upper right. (c) Cross sections of nine blue hairs under dark-field illumination. The hair shafts bear spines toward the hair base, but are smooth with longitudinal ridges in the distal part

#### 24.2.2.2 Yellow Hairs

The yellow hairs occur on all the legs (more pronounced on legs 1 and 2) but are restricted to lateral patches on the proximal tibia (Fig. 24.5a). Each hair is brushlike, with 10–14 rows of cuticular extensions along the entire hair shaft (Fig. 24.6b). Cross sections of the hair shaft show only an irregular cuticular meshwork (Fig. 24.6d; 24.7b) but no lamellation as in the blue hairs. This meshwork is probably responsible for the yellow interference color. Unfortunately, no precise measurements could be obtained from this irregular meshwork. Nevertheless, using an approximation of 140 nm for the lamellar thickness, the calculated reflectance curve showed a peak in the yellow (maximum at 560 nm) and also a strong reflection in the UV. No pigment is present in these hairs, because sections appear colorless under transmitted white light. This is surprising, since a yellow coloration is generally based on ommochrome pigments (Holl 1987).

### 24.3 Structural Colors in Scales of Jumping Spiders (Salticidae)

The most colorful spiders are certainly found among the jumping spiders. Their structural colors arise mostly from modified hairs (scales) but also from solid cuticle (see Sect. 23.4). Scales are defined as flattened hairs (setae) that have a pedicel bent

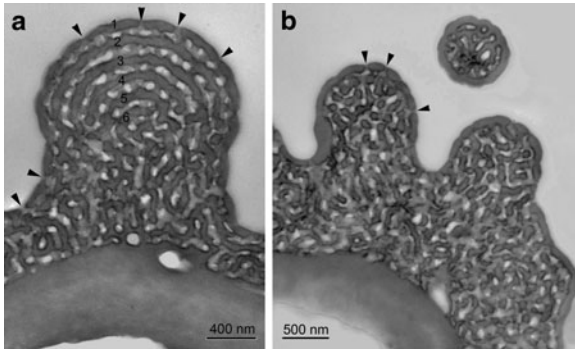


**Fig. 24.6** Fine structure of blue and yellow tibial hairs in *P. metallica* (Theraphosidae). (a) The blue hairs have longitudinal ridges along the distal hair shaft. (b) The yellow hairs bear many fine extensions along the entire hair shaft. (c) Cross-section of a blue hair (TEM) showing a hollow center, surrounded by a thin cuticular tube and nine distinct ridges that consist of a highly lamellated cuticle. (d) Cross-section of a yellow hair showing a solid cuticle ring in the center surrounded by a loose cuticular meshwork that is also present in the peripheral extensions

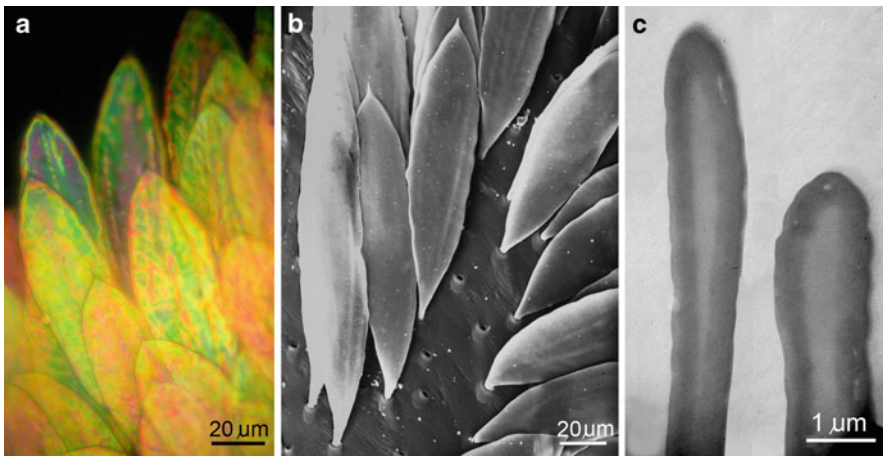
near the socket, so that the scale lies close and parallel to the surface cuticle (Hill 1979; Townsend and Felgenhauer 1998). Although the size and shape of scales vary a great deal among the 5,000 species of salticids, they may be roughly grouped into three types: lanceolate, spatulate, and lamelliform (Roth 1993). Most studies on salticid scales have covered morphological, functional, or phylogenetic aspects, but only a few dealt with the structural colors of these scales (Land et al. 2007; Taylor and McGraw 2007). We shall focus here on two examples, the golden scales of *Habronattus hallani* and the blue scales of *Maratus splendens* and *Maratus volans*.

### 24.3.1 *Habronattus hallani*

The genus *Habronattus* contains about 100 different species, the males of which are very colorful. We picked *H. hallani* (from Arizona, USA) which is renowned for



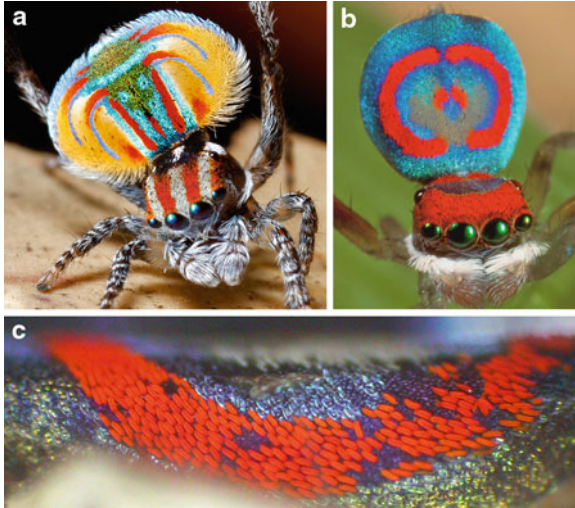
**Fig. 24.7** Cross sections of a blue hair (a) and a yellow hair (b) in *P. metallica* (Theraphosidae) at high magnification. (a) Only the innermost part of the hair shaft is solid; the outer cuticle consists of six regular lamellae (1–6), alternating with light air spaces. They connect through pores (arrowheads) to the outside. (b) An irregular cuticular meshwork occupies the peripheral part of yellow hair shafts. Note the pores (arrowheads) on the surface



**Fig. 24.8** Golden iridescent scales in the salticid *Habronattus hallani*. (a) The femora are densely covered by overlapping, golden scales (Photo: Lisa Taylor). (b) These scales appear very smooth, with hardly any surface structure. (c) This is confirmed in thin sections; the wall thickness of a scale is only 0.2–0.3  $\mu\text{m}$

having iridescent scales on the front legs and also on the prosoma and clypeus. The femora and patellae are covered by overlapping lanceolate scales that have a distinct golden shine (Fig. 24.8a). The surface of these scales is very smooth, even at high magnification under the scanning electron microscope (Fig. 24.8b). Each scale measures only about 1  $\mu\text{m}$  in thickness, the actual wall being around 300 nm thick, which leaves a narrow air space in the center (Fig. 24.8c). A calculation of the reflectance spectrum shows a peak in the green (at 545 nm) and another one in the red



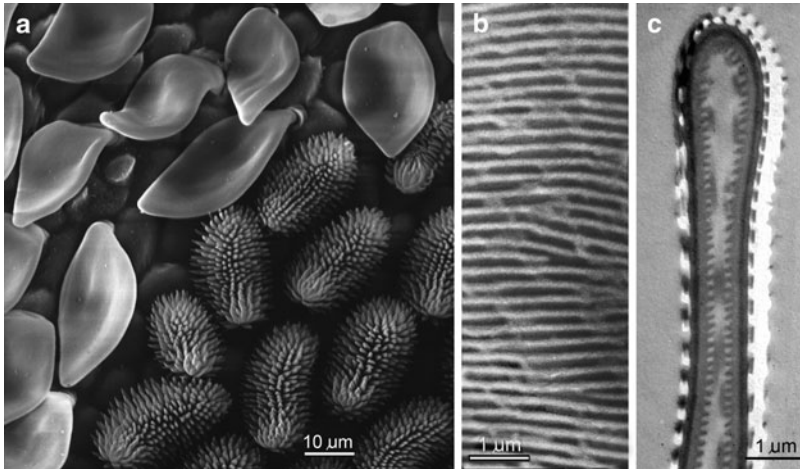


**Fig. 24.9** The most colorful jumping spider is the Australian salticid genus *Maratus*. (a) A courting male of *M. volans*, displaying its iridescent opisthosomal fan (Photo: Jürgen Otto). (b) A courting male of *M. splendens* demonstrating his blue and red opisthosomal flap; the *blue scales* may change to green, depending on the angle of illumination. The red hairs do not vary in color (Photo: Jürgen Otto). (c) Detail from the lateral opisthosoma of *M. splendens* showing a band of red brush hairs, flanked on both sides by blue or green scales

(at 700 nm), which together may account for the observed golden hue. Overall, the structure of these golden scales is surprisingly simple and resembles that of UV-reflecting scales of the jumping spider *Cosmophasis* (Land et al. 2007).

### 24.3.2 *Maratus splendens* and *M. volans*

Some of the most colorful jumping spiders belong to the genus *Maratus* from Australia. The vernacular name of these tiny salticids is “peacock spiders,” because the males elevate and extend an opisthosomal flap to display their striking colors (Fig. 24.9a). From our preliminary observations, it seems that blue and green are due to a variety of iridescent scales, whereas red (and perhaps yellow) is due to pigmented, brushlike hairs (Fig. 24.9b). The blue scales—which may also appear green depending on the angle of illumination (Fig. 24.9c)—are leaf-shaped, about 40  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide (Fig. 24.10a). At high magnification the scale surface reveals a regular pattern of fine cuticular ridges (Fig. 24.10b) that probably act as a diffraction grating (Parker and Hegedus 2003). Sections of these thin scales (1  $\mu\text{m}$ ) show a double-layered cuticle of different densities below the surface ridges (Fig. 24.10c). Another set of fine ribs lines the inner side of the scale wall bordering the narrow, air-filled central lumen. These blue scales are structurally much more



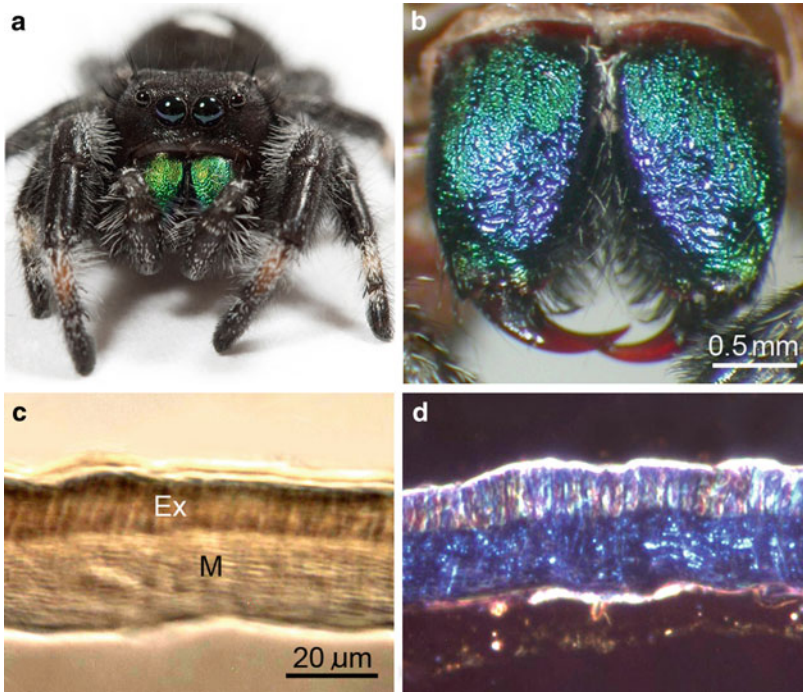
**Fig. 24.10** Fine structure of blue scales on the opisthosoma of *M. splendens* (Salticidae). (a) Leaflike (blue) scales are seen on the upper left and (red) hairs on the lower right. (b) High magnification of a blue scale showing fine ridges on the surface. (c) Thin sections reveal a narrow scale wall with surface ridges and a cuticular meshwork inside (*M. volans*)

complex than the golden scales in *H. hallani*. We surmise that the iridescent blue color results from a combination of surface diffraction and interference effects within the layered scale wall.

## 24.4 Iridescence in the Integument

Many male spiders, again mostly among salticids, are known for having shiny, colorful chelicerae (Fig. 24.11). These interference colors are caused by a multilayered body cuticle rather than by hairs or scales (Ingram et al. 2009, 2011). Among jumping spiders the genus *Phidippus* is probably best known for its green-to-blue (and also red to violet) chelicerae; for most *Phidippus* species, even juveniles and females exhibit colorful chelicerae, sometimes in different colors than in the males (Foelix et al. 2010). Ingram et al. (2009, 2011) assumed that the cheliceral cuticle lamellae contained intermittent air spaces that would provide a multi-reflector system. We did not see evidence for any air spaces and believe that the variation of refractive index between adjacent cuticular layers would be sufficient to cause interference.

Many close-up pictures of jumping spiders show the large eyes (front row) in either a green or red color hue (Fig. 24.9b). This color effect is due to interference in the multilayered lens cuticle, as was nicely demonstrated by Homann (1985). When eye preparations were soaked in lactic acid, the cuticle layers would slightly swell,



**Fig. 24.11** Colorful chelicerae in jumping spiders of the genus *Phidippus*. (a) A female *Phidippus regius* with dark-green chelicerae (Photo: Bastian Rast). (b) Even juveniles exhibit brightly colored chelicerae (exuvium). Note the change of color from green to blue to purple. (c) Semi-thin section of the cheliceral cuticle in *Phidippus audax*, unstained. Note the brown exocuticle (Ex) and the lighter, multilayered mesocuticle (M). (d) Same cuticle as in (c) but stained with methylene blue, dark-field illumination. Note the different optical properties of exo- and endocuticle

and a color shift from green to red could be induced. Similarly, when cuticular layers are compressed, a color change towards shorter wavelengths will result (Steinbrecht 1985). The observation that iridescence in a live spider (or in an exuvium) may change over time, or even disappear, can be explained by a slight change in the dimensions of the cuticle layers (or air spaces, if present).

Finally, another type of structural coloration should be mentioned, namely, the white or silvery reflection seen in several spider families (e.g., Araneidae, Tetragnathidae, Theridiidae). This is caused by guanine deposits in the peripheral cells of the midgut (guanocytes). If the stored crystals are small and cuboid, a matt white will result, but if the guanine forms very thin platelets ( $0.1 \mu\text{m}$ ), a shiny silver reflection is produced (Oxford 1998). It seems that the matt guanine represents the ancestral type, whereas the silver form is phylogenetically derived (Oxford and Gillespie 1998) (see also Wunderlin and Kropf 2013).

## 24.5 Structural and Functional Considerations

### 24.5.1 Structural Variation

Although we have looked at only a few colorful theraphosids, it is our impression that they have only special hairs—but no scales—that cause structural colors. These hairs may vary morphologically, but the basic design of having a lamellar structure in the nanometer range seems consistent. We also did not find any body cuticle that would exhibit structural colors.

In contrast, in araneomorph spiders we found no hairs but several types of scales that yield structural colors. Those scales may be structurally very simple, like the golden scales in *Habronattus*, or highly complex, combining surface diffraction gratings with internal multilayer reflectors, as in the blue scales of *Maratus*. Surface diffraction is apparently a very old mechanism for producing structural colors, already known from the Cambrian (Parker 1998). There may be many more variations on structural colors in spiders—only a few species have been studied so far and the picture is far from complete.

### 24.5.2 Behavioral Significance

Until now we have not yet posed the decisive question: what is the biological significance of structural colors in spiders? In the case of diurnal spiders with good color vision (as in salticids), the obvious answer is that these colors ought to play a role in communication, for example, during male–male contests or courtship (Fig. 24.9a; Hill and Otto 2011). There is indeed good evidence that body coloration is important during the courtship display of some spiders, regardless whether the colors are due to pigments or to interference (Lim et al. 2007; Taylor and McGraw 2007). Both immature and adult *Phidippus* flash their iridescent chelicerae with rapid movements of their pedipalps, while facing either sighted prey or a human observer (Fig. 24.12). During male–male contests or courtship, these chelicerae are displayed, but not flashed. The limited directional impact of this intense flickering color may insure that the signal is sent only to the intended recipient and not to undetected predators nearby.

It is much more difficult to interpret structural colors in the nocturnal theraphosids. Since their communication does not rely on visual signals, it is hard to say what kind of advantage any coloration might afford. Under twilight conditions it is conceivable that they may have an aposematic function, for instance, when *Poecilotheria* assumes its typical defense posture, raising its front legs and exposing the blue and yellow undersides. However, it may also be that bright colors in theraphosids are of no particular advantage (e.g., neutral)—perhaps comparable to colorful organisms living in the abyss of the oceans.



**Fig. 24.12** Three sequential images of a subadult female *Phidippus pulcherrimus* (Salticidae), flashing its iridescent blue-green chelicerae at the photographer at a rate of 2–4/s. This palp flicking also occurs when stalking certain kinds of prey

## 24.6 Conclusions

Structural colors are described and analyzed in theraphosid and salticid spiders. Some theraphosids are brightly blue: this is caused by special hairs with a lamellated wall that causes an interference of the incoming light. The incident white light is then reflected as a deep blue. In some cases, the hairs are bright yellow: there the hair wall exhibits a fine cuticular meshwork of slightly different dimensions than in the blue hairs but also results in interference, and the reflected light appears yellow. In salticids, iridescent colors are produced by flattened hairs (scales). Golden scales have a rather simple structure of two thin cuticular layers on the outside and a narrow air space in between. Blue iridescent scales are more complex, with multilayered scale walls and fine ridges on the surface that act as a diffraction grating. The body cuticle (e.g., chelicerae and eye lenses) may also be brightly colored due to light interference on many thin cuticular layers. The biological significance of structural colors in spiders is well understood in the diurnal salticids where optical signals are exchanged in courtship, usually in bright daylight. In contrast, theraphosids are mostly active at night and visual communication hardly plays any role. Their coloration may be of advantage at dawn during their defensive behavior, when the brightly colored blue and yellow legs are raised toward an aggressor.

**Acknowledgements** We are grateful to several colleagues who have helped us with this study: Bastian Rast and Benno Wullschleger, for supplying us with theraphosid material, and Judith Kastenmeier, Jürgen Otto, and Lisa Taylor for sending us salticids. Rolf Thieleczek kindly calculated the reflectance spectra of iridescent spider hairs and scales for us; Jerome Rovner and Benno Wullschleger critically read our manuscript. The Neue Kantonsschule Aarau generously let us use their electron microscope facilities. Digital photographs with the transmission electron microscope were kindly taken by Karin Boucke and Sherry Vinsant.

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