Chapter 26
Rapid Colour Change in Spiders

Judith Wunderlin and Christian Kropf

26.1 Introduction

Among the various ways of camouflage in the animal kingdom, rapid colour change belongs to the most impressive ones. In contrast to slow morphological colour change, the so-called physiological colour change occurs relatively fast (Holl 1987; Stuart-Fox and Moussalli 2009). It may take some hours but can also be finished within parts of a second.

Physiological colour change is generally enabled by movements of pigment granules within cells or by modifications of the morphology of the pigment-containing cells (Holl 1987). When pigment granules move within chromatophores, they either disperse or concentrate (Stuart-Fox and Moussalli 2009). Relatively well-known examples of animals being capable of physiological colour change are chameleons and cephalopods (Stevens and Merilaita 2009). Among the circa 1.1 million described (and presumably up to 3.7 million really existing arthropod species; Hamilton et al. 2010), there are only few examples of physiological colour change. Some crustaceans (Auerswald et al. 2008) and insects (Key and Day 1954; Hinton and Jarman 1972) are able to change their colour rather slowly. Rapid colour change (i.e. a physiological colour change within parts of a second) within arthropods is only known from spiders (Araneae).

These spiders show mostly a white or at least light opisthosomal pattern, made up by specialized midgut cells beneath the hypodermis, the so-called guanocytes (Millot 1926; Seitz 1972). These cells store the excretory product guanine that appears white and acts as a colourant (Oxford 1998). In all reported cases of rapid

J. Wunderlin • C. Kropf (✉)
Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

Natural History Museum, Bern, Switzerland
e-mail: judith.wunderlin@gmail.com; christian.kropf@iee.unibe.ch

W. Nentwig (ed.), *Spider Ecophysiology*,
DOI 10.1007/978-3-642-33989-9_26,

colour change in spiders, the white guanine markings on the opisthosomal surface diminish in size or disappear more or less completely. As a consequence, the general colouration of the spider's opisthosoma changes to the darker or greyish brown of the digestive mass. Recovery of the original colour pattern requires a few or several minutes (e.g. Blanke 1975; Holl 1987). Rapid colour change in spiders is always related to disturbances, especially when the spider has to drop from the web (Oxford and Gillespie 1998).

Up to now, it is not clear how this impressive phenomenon works. In a study on the araneid *Cyrtophora cicatrosa*, the importance of guanocytes for rapid colour change of spiders was recognized (Blanke 1975). This author proposed that movement of guanine within the guanocytes rather than the contraction of the cells is responsible for the colour change. On the other hand, Edmunds and Edmunds (1986) assumed that there should be contractile elements in the guanocytes in *Argiope flavipalpis*, also an araneid. However, their efforts to find such elements failed. In this context, Oxford and Gillespie (1998) concluded that guanine contraction or retraction seems to be the basis of all physiological colour change in spiders.

Bristowe (1941) was the first who documented the rapid colour change of the linyphiid spider *Floronia bucculenta* that is native to temperate regions of Europe and Russia. An ongoing study on this species gives new insights into the underlying mechanism of rapid colour change.

26.2 Spiders Capable of Rapid Colour Change

Up to now 21 spider species (most of them web-building) from five different families are known to be able to change their colour rapidly. They mainly belong to the Tetragnathidae (ten species) and Araneidae (eight species).

26.2.1 Tetragnathidae

Three species of the genus *Leucauge* are able to change colour rapidly. The name refers to the Greek *leukos* meaning "white" and points to the white guanine pattern on the opisthosoma of *Leucauge* species. Uyemura (1957) observed large flecks on the opisthosoma of *Leucauge subgemmea* becoming smaller and more separated when the spider is picked or shaken strongly. In the genus *Tetragnatha*, many Hawaiian species perform rapid colour change when dropping from the web (R. Gillespie, personal communication), so the species list given in Table 26.1 may have to be extended in the future.

Table 26.1 List of spider species with rapid colour change (adapted from Oxford and Gillespie 1998, distribution mainly from Platnick 2012)

Species	Family	Distribution	References
Leucauge blanda	Tetragnathidae	Russia, China, Korea, Taiwan, Japan	Feng (1990)
Leucauge celebesiana	Tetragnathidae	India to China, Laos, Japan, Sulawesi, New Guinea	Yaginuma (1986), Feng (1990); both sub *Leucauge magnifica*
Leucauge subgemmea	Tetragnathidae	Russia, China, Korea, Japan	Uyemura (1957)
Tetragnatha eurychasma	Tetragnathidae	Hawaii	Gillespie (personal communication)
Tetragnatha filiciphilia	Tetragnathidae	Hawaii	Gillespie (personal communication)
Tetragnatha paludicola	Tetragnathidae	Hawaii	Gillespie (personal communication)
Tetragnatha sp. A, B, C	Tetragnathidae	Hawaii	Oxford and Gillespie (1998)
Tylorida striata	Tetragnathidae	China to Australia	Feng (1990)
Argiope flavipalpis	Araneidae	Africa, Yemen	Edmunds and Edmunds (1986)
Argiope reinwardti	Araneidae	Malaysia to New Guinea	Bristowe (1976)
Argiope sp.	Araneidae	Malaysia or Sumatra	Bristowe (1976)
Argiope sp.	Araneidae	W. Africa	Bell (1893)
Cyrtophora cicatrosa	Araneidae	Pakistan to Northern Territory	Blanke (1975)
Gasteracantha "*fornicata*"	Araneidae	Sumatra	Bristowe (1976)
Gea heptagon	Araneidae	USA to Argentina, South Pacific Islands, Australia	Sabath (1969)
Phonognatha graeffei	Araneidae	Australia	Roberts (1936, sub *Araneus wagneri*)
Chrysso scintillans	Theridiidae	Myanmar, China, Korea, Japan, Philippines	Uyemura (1957, sub *Argyria venusta*)
Floronia bucculenta	Linyphiidae	Europe, Russia	Bristowe (1941, 1958)
Philodromus spinitarsis	Philodromidae	Russia, China, Korea, Japan	Ikeda (1989)

Gasteracantha "*fornicata*" is probably misidentified as this species should occur only in Queensland (Platnick 2012).

26.2.2 Araneidae

In the genus *Argiope*, two identified (*A. flavipalpis*, *A. reinwardti*) and two unidentified species are able to change colour rapidly. Edmunds and Edmunds (1986) assumed contractile elements to be responsible for the contraction of guanocytes in *A. flavipalpis*. They observed the darkening of the opisthosoma in the moment when the spider dropped from the web. The spiders remain dark during thanatosis but start to become bright soon when climbing back into the web. Recovery of the original white pattern needs considerably more time than darkening.

One of the first observed spider species with rapidly changing colour was *Phonognatha graeffei* where the creamy mottled pattern disappears when it falls out of the web (Roberts 1936). *Gasteracantha* "*fornicata*" (probably misidentified, see, Table 26.1) changes its colour from red to black; this should be caused by a contraction of pigment-containing cells (Bristowe 1976). *Gea heptagon* is patterned with bright dots and immediately turns to brown when dropping (Sabath 1969); recovery of the original white markings takes several minutes. In the same way, *Cyrtophora cicatrosa* changes its colour (Blanke 1975). Blanke found new white guanine dots after the recolouring, not observed previously to colour change, and therefore, he proposed a guanine relocation to be the underlying mechanism of the colour change.

26.2.3 Other Families

The theridiid spider *Chrysso scintillans* changes the abdominal pattern from a continuous golden yellow colouration to starlike flecks when disturbed (Uyemura 1957). The opisthosomal pattern of the philodromid *Philodromus spinitarsis* is less conspicuous; the colour changes partially from pale brown to almost black when the spider drops (Ikeda 1989).

26.3 Guanocytes

The midgut fills a great part of the spider's opisthosoma with its folded diverticula. Midgut tissue basically consists of four cell types: secretory cells, resorption cells, basal cells, and guanocytes (Foelix 2011). Guanocytes are specialized midgut cells whose main function is to store the purine excretory product guanine (Millot 1926). They support the tissues responsible for excretion as they absorb purine-containing metabolic products (Seitz 1972, 1987).

Guanine is stored in anhydrous crystalline form and therefore made nonhazardous. Most guanine is present just after the reproductive phase. Subsequently, guanine starts to be discarded and the so-called guanine-storing minimum is reached at the end of the life cycle (Seitz 1972).

Guanocytes in spiders may cause a matt white or a silvery colouration. In the first case, the cells are packed with prismatic guanine crystals. In the second case, plates of doublet crystals are formed within guanocytes that are stacked with cytoplasm between the plates. The two crystals of each plate are cemented by layers of amorphous guanine. Crystal morphology and stack dimensions determine the light-reflective properties of a guanine stack (Levy-Lior et al. 2010).

Already Millot (1926) discerned the function of guanine as a colourant. However, Seitz (1972) disputed this in the case of *Araneus diadematus*. Nowadays, the importance of guanine as a biochrome in spider colouration is generally acknowledged (Holl 1987; Oxford 1998). The white or silvery colour shines through the thin and transparent opisthosomal cuticle. The amounts of white, for example, range from only few stripe-like markings (e.g. in *Linyphia* species) to a totally white opisthosoma as found in the thomisid *Misumena vatia*. In many spider species, conspicuous colours like red are brightened by the white guanine, whereas in dark spider species, guanine plays no role for the colouration of the integument (Holl 1987).

Guanine storage obviously is one precondition for developing colour change in spiders (Oxford 1998). Almost all colour-changing spider species are representatives of the families with many guanine-storing species: Araneidae, Tetragnathidae, Theridiidae, and Philodromidae. However, maintaining stored guanine is costly (Oxford 1998), and this might be a reason why so few species developed rapid colour change.

26.4 Colour Change in *Floronia bucculenta* (Linyphiidae)

26.4.1 Life Observations

The colour pattern of *F. bucculenta* consists of many white dots on a brownish background. The white dots are relatively diverse in their shape; only few are truly circular. Dots close to the dorso-median line are bigger than lateral ones. During colour change, the dots seemingly become very small or disappear completely (Fig. 26.1). *F. bucculenta* changes its colour from white to a dark brown the moment it drops from the web. The change can also be induced when the spider is shaken in a tube. During colour change, the white dots are almost instantaneously pulled inwards. Often, the spider will exhibit thanatosis after dropping. This presumably makes it even more difficult for predators to find it.

The darkening of the opisthosoma takes place no matter if the spider lands on a dark or a light surface. In the lab, the spiders changed their colour to dark although they landed on a white ground and were even better visible then. Therefore, the spider probably is not able to control the reaction. Under natural conditions, the spider lands on the dark forest floor, where it is well camouflaged.

Whereas the disappearance of the guanine dots happens instantaneously, the dots reappear in approximately one to two minutes. This looks as if the white dots were slowly coming out of the deep. Similar observations were made in other colour-changing spiders (see Sect. 26.2).

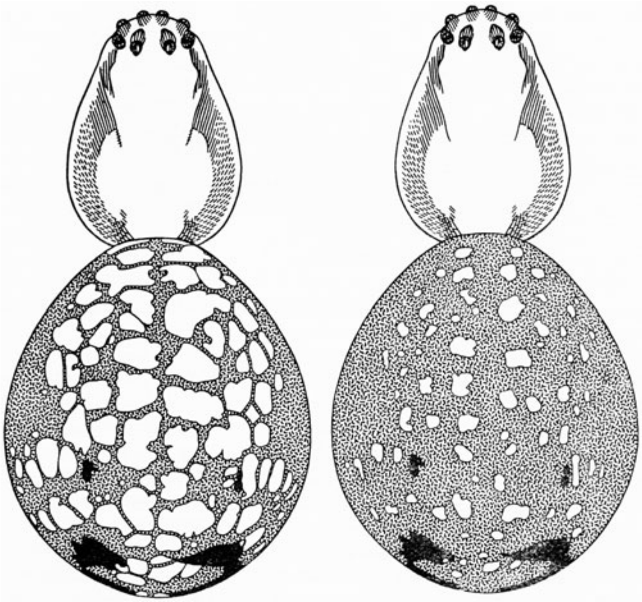

Fig. 26.1 Two states of colouration in *Floronia bucculenta* (taken from Bristowe 1958). *Left*: normal colouration with a lot of extended white dots. *Right*: dark state just after colour change

26.4.2 Guanocytes

The white dots on the surface of the opisthosoma of *Floronia bucculenta* have different forms. Therefore, the shape of guanine accumulations varies also in histological sections. Generally, they are about 50 μm in diameter and up to 100 μm in length (Fig. 26.2). Towards the outside, the white accumulations are normally wider than at the proximal end. One guanine accumulation that is visible from the outside as one white point consists in fact of several elongate guanocytes with a diameter of 5–10 μm and a length of 50–100 μm.

The shape of the guanocytes and consequently the form of the whole guanine accumulations of *F. bucculenta* are different as compared to other species. Generally, guanocytes in other spiders are about 30–50 μm long and show an elongated cubic form which varies from species to species (Millot 1926). For example, *Araneus diadematus* has relatively broad clubbed guanocytes that are about 60 μm long (Seitz 1972). In *A. diadematus,* there are much larger parts made out of normal resorption cells fitted in between the proximal ends of the guanocytes than it is the case in *F. bucculenta*. *Misumena vatia* shows guanocytes with a cubic form (Insausti and Casas 2008). The possible function of the elongated shape of the guanocytes in *F. bucculenta* probably has to do with their ability to retract (see below) but needs to be explored in more detail.

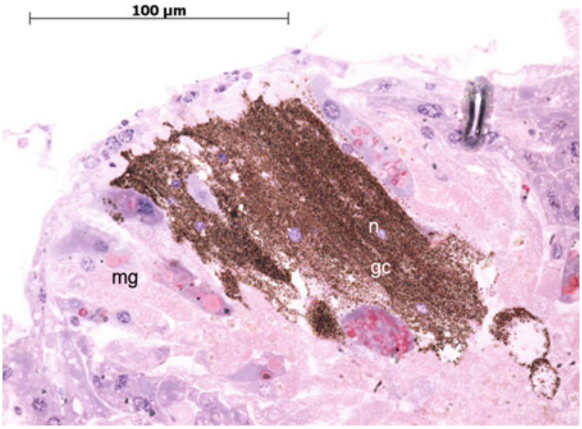

Fig. 26.2 Longitudinal section of a midgut diverticulum of *Floronia bucculenta* with the longish guanocytes. Staining: hematoxylin–eosin. *gc* guanocytes, *mg* midgut, *n* nucleus

In *F. bucculenta*, no tight connection between guanocytes and hypodermis can be found, which seems to be a precondition for a rapid colour change (see below). However, according to Seitz (1972), the guanocytes in *A. diadematus* (that is not able to change its colour) are tightly interconnected to the hypodermis by protuberances and invaginations of cell membranes. These connections may be important for the stability of the colour pattern as the possible signal function should be independent of the feeding state of the spider.

26.4.3 Muscles

Fine striated muscles lie above the guanine-containing parts of the midgut diverticula. Looking at a midgut diverticulum from above, the muscle fibres are arranged like a dense grid (Fig. 26.3a). Each muscle strand is about 2–3 µm wide. The muscles are mainly present at the apical parts of the diverticula. Further inside, their number decreases rapidly (Fig. 26.3b). Here, the muscles lie mainly at the side of the guanine accumulations. At the proximal ends of the guanocytes and of the whole guanine accumulation, no muscles are visible any more. The position of the muscle grid within the surrounding tissues is illustrated in a model drawing (Fig. 26.4). A contraction of the muscle grid in *Floronia bucculenta* will likely lead to the observable colour change during which the white guanocytes retreat within the spider's opisthosoma. However, the exact mechanism is still part of ongoing studies.

The guanine-storing areas of another linyphiid spider, *Linyphia triangularis*, were investigated. This species shows white guanine markings on its opisthosoma too; however, it is not able to change its colour pattern. *L. triangularis* has broader and shorter guanocytes than *F. bucculenta*, and no muscles connected to the midgut cells or the guanocytes are visible.

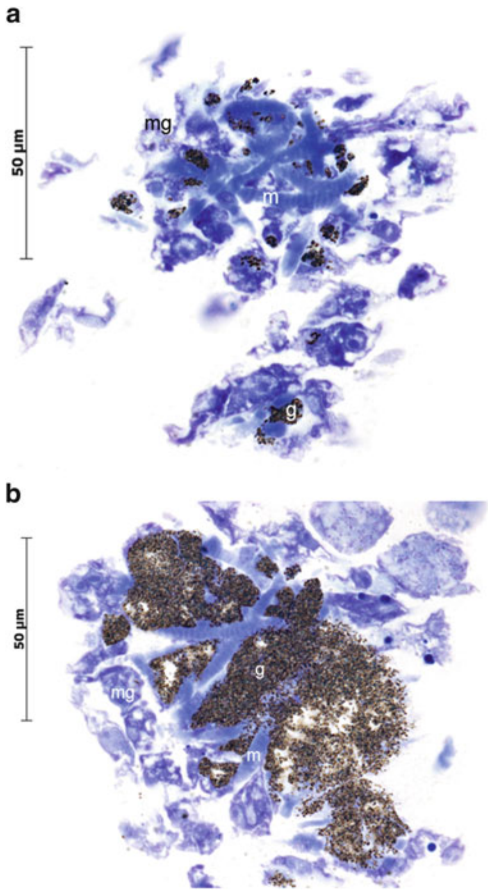

Fig. 26.3 Cross section of the outer part of a midgut diverticulum of *Floronia bucculenta* with guanine and striated muscles. Staining: toluidine blue. (**a**) Section right under the hypodermis, note the dense muscle grid and little guanine. (**b**) Section from further inside, less muscles and more guanine are visible. *g* guanine, *m* muscle, *mg* midgut tissue

At first glance, the described muscle grid may be confused with the abdominal sac (Whitehead and Rempel 1959), especially in longitudinal sections of midgut diverticula. However, the abdominal sac consists of smooth muscles, whereas the newly found muscle grid is clearly striated.

Physiological colour change was proposed to be a process by either migration of chromatic inclusions within cells or alteration of the chromatocyte morphology (Blanke 1975; Holl 1987). The findings in *F. bucculenta* are compatible with the second mechanism, a change of form and position of guanocytes. Such a mechanism was also proposed by Edmunds and Edmunds (1986) and by Oxford and Gillespie (1998). Our study is the first to present morphological support for this idea.

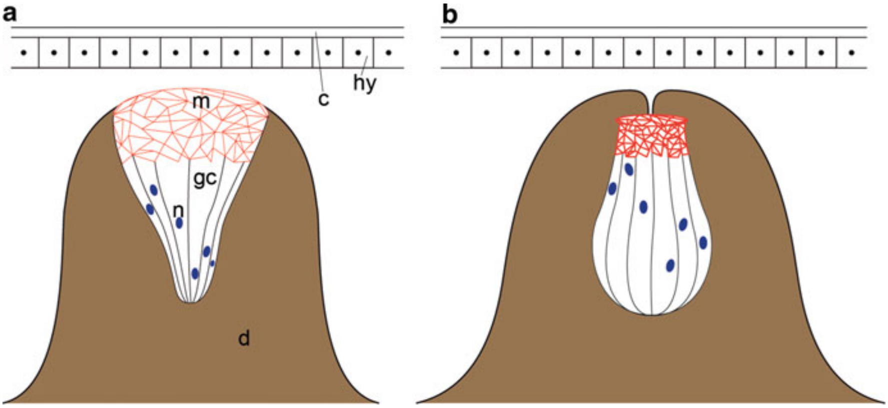

Fig. 26.4 Model of a midgut diverticulum in *Floronia bucculenta*. The white guanine is visible through the hypodermis and cuticle. Fine muscles (in red) cover the guanocytes like a grid. (**a**) Muscle grid relaxed, guanocytes beneath hypodermis; (**b**) muscle grid contracted, guanocytes retreated. *c* cuticle, *d* midgut diverticulum (brown), *gc* guanocytes, *hy* hypodermis, *m* muscles, *n* nucleus

26.5 Conclusions

Rapid physiological colour change is a rare phenomenon in animals. Among arthropods, it is known only from 21 spider species. Guanine markings are always involved when colour change can be observed. However, no studies dealing with the mechanism of the colour change have existed until now. In *Floronia bucculenta,* a set of fine striated muscles was discovered that is associated with the guanocytes. Contraction of these muscles probably leads to colour change by a retreat of the white guanocytes within parts of a second. No similar muscles are present in a related species that is not able to change its colour. The exact mechanism has still to be explored.

Acknowledgements Thanks go to R. Gillespie (Berkeley, USA) for giving valuable unpublished information and to H. Ono (Tokyo, Japan) for translating a Japanese text.

References

Auerswald L, Freier F, Lopata A, Meyer B (2008) Physiological and morphological colour change in Antarctic krill, *Euphausia superba*: a field study in the Lazarev Sea. J Exp Biol 211: 3850–3858

Bell HHJ (1893) Notes on a spider. Nature 47:557–558

Blanke R (1975) Die Bedeutung der Guanozyten für den physiologischen Farbwechsel bei *Cyrtophora cicatrosa* (Arachnida: Araneidae). Ent Germ 2:1–6

Bristowe WS (1941) The comity of spiders II. Ray Society, London

Bristowe WS (1958) The world of spiders. Collins, London

Bristowe WS (1976) Rare arachnids from Malaysia and Sumatra. J Zool 178:7–14
Edmunds J, Edmunds M (1986) The defensive mechanisms of orb weavers (Araneae: Araneidae) in Ghana, West Africa. In: Eberhard WG, Lubin YD, Robinson BC (eds) Proceedings of the 9th International Congress of Arachnology, Panama, 1983. Smithsonian Institution Press, Washington
Feng Z-Q (1990) Spiders of China in colour. Hunan Science and Technology Publishing House, Hunan
Foelix RF (2011) Biology of spiders. Oxford University Press, Oxford
Hamilton AJ, Basset Y, Benke KK, Grimbacher PS, Miller SE, Novotny V, Samuelson GA, Stork NE, Weiblen GD, Yen JDL (2010) Quantifying uncertainty in estimation of global arthropod species richness. Am Nat 176:90–95
Hinton HE, Jarman GM (1972) Physiological colour change in the Hercules beetle. Nature 238: 160–161
Holl A (1987) Coloration and chromes. In: Nentwig W (ed) Ecophysiology of spiders. Springer, Berlin
Ikeda H (1989) Instantaneous colour change in *Philodromus spinitarsis* Simon. Atypus 93:7–9
Insausti TC, Casas J (2008) The functional morphology of color changing in a spider: development of ommochrome pigment granules. J Exp Biol 211:780–789
Key KHL, Day MF (1954) The physiological mechanism of colour change in the grasshopper *Kosciuscola tristis* (Sjöst) (Orthoptera, Acrididae). Aust J Zool 2:340–363
Levy-Lior A, Shimoni E, Schwartz O, Gavish-Regev E, Oron D, Oxford G, Weiner S, Addadi L (2010) Guanine-based biogenic photonic-crystal arrays in fish and spiders. Adv Funct Mater 20:320–329
Millot J (1926) Contributions à l'histophysiologie des Aranèides. Bull Biol France Belg Suppl 7:1–238
Oxford GS (1998) Guanine as a colorant in spiders: development, genetics, phylogenetics, and ecology. In: Selden PA (ed) Proceedings of the 17th European Colloqium of Arachnology, Edinburgh, 1997. British Arachnological Society, Burnham Beeches, Bucks
Oxford GS, Gillespie RG (1998) Evolution and ecology of spider coloration. Annu Rev Entomol 43:619–643
Platnick NI (2012) The world spider catalog, version 13.0. American Museum of Natural History. Online at http://research.amnh.org/iz/spiders/catalog. doi:10.5531/db.iz.0001
Roberts NL (1936) Colour change in the leaf-curling spider (*Araneus wagneri*). Proc R Zool Soc NSW 1936:28–29
Sabath LE (1969) Color change and life history observations of the spider *Gea heptagon* (Araneae: Araneidae). Psyche 76:367–374
Seitz KA (1972) Elektronenmikroskopische Untersuchungen an den Guanin-Speicherzellen von *Araneus diadematus* Clerck (Araneae, Araneidae). Z Morph Tiere 72:245–262
Seitz KA (1987) Excretory organs. In: Nentwig W (ed) Ecophysiology of spiders. Springer, Berlin
Stevens M, Merilaita S (2009) Animal camouflage: current issues and new perspectives. Phil Trans R Soc B 364:423–427
Stuart-Fox D, Moussalli A (2009) Camouflage, communication and thermoregulation: lessons from colour changing organisms. Phil Trans R Soc B 364:463–470
Uyemura T (1957) Colour change of two species of Japanese spiders. Acta Arachnol 15:1–10
Whitehead WF, Rempel JG (1959) A study of the musculature of the black widow spider, *Latrodectus mactans* (Fabr). Can J Zool 37:831–870
Yaginuma T (1986) Spiders of Japan in color—new edition. Hoikusha, Osaka