Nentwig · Ansorg · Bolzern · Frick · Ganske · Hänggi · Kropf · Stäubli

All You Need to Know About Spiders

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Preface

You are curious about spiders. Maybe you were previously indifferent to these animals or you are even afraid of them, or you belong to the (probably) small group of spider fans. In any case, you have been tempted by the book title to acquire the necessary knowledge about spiders which one should know, or have at hand, these days in as compact and comprehensive a form as possible. We are happy with your decision and draw the following conclusions:

First, we assume that previous disinterest or even fear towards spiders is not the best attitude. Maybe they are interesting animals after all, and maybe you don't need to fear them. In any case, you probably think the best way to reach such insights is to learn more about spiders. We share this attitude and this is why we have put together this book for you.

Second, you chose this book because no other on the market offers what we promise and what you were looking for. Indeed it is remarkable that there is no book that presents, in simple terms, the sometimes quite complex relationships and broadly explains everything that's important about the form and function of spiders, their importance in our environment, both locally in the house and garden but also globally, and the reasons for our fears. Spiders drink instead of eating? And have more sensory organs than humans? They move hydraulically? Despite venom glands, spiders are harmless to humans? Sex between spiders? One of the most diverse groups of animals in the world? Can spiders be removed with a vacuum cleaner? Or what about spiders as pets?

It would be great if our book attracts many curious readers and we are convinced that it is worth knowing more about spiders.

Wolfgang Nentwig Association for the Promotion of Spider Research

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The Association for the Promotion of Spider Research

Founded in Switzerland in 2016, the Association for the Promotion of Spider Research aims to inform the public about the importance of spiders and to promote scientific research. The Association works closely with natural history museums and professional arachnological bodies. Currently, three projects are in the fore-ground of our work: 1) support of the online identification site Spiders of Europe (https://araneae.nmbe.ch), which offers identification keys, descriptions, illustrations and distribution maps in an English and German version for all ca. 5000 European spider species; 2) support of the World Spider Catalog (https://wsc.nmbe.ch), which contains all taxonomically relevant information on the approximately 50,000 spider species occurring worldwide, as well as the corresponding scientific information (approximately 16,000 scientific articles); (3) imparting knowledge in book form, such as this book here, which is also available in German, in order to sustainably inform as many interested people as possible about spiders. The proceeds from this book will go entirely to the projects of the Association.

You can find more information here https://wsc.nmbe.ch/association/index. If you would like to support the Association for the Promotion of Spider Research, please contact us. Wolfgang Nentwig (President) (wolfgang.nentwig@iee.unibe. ch) Ambros Hänggi (Vice President) (ambros.haenggi@bs.ch).

Part I Facts on Structure and Function



1

Getting to Know You: A First Look at Spiders

Spiders do not live in our world. Why is that? "Our world" is what our sense organs report to us and what our brain makes of it. But spiders have different senses than we do. They produce complex mixtures of venom, make different types of silk as needed, and have a unique movement system. Their sex seems bizarre, and as predators they are feared. Their evolutionary success far eclipses that of mammals. One key to understanding the spider as a model of success is its body structure. So, let us take a look at this first.

1.1 Eight Legs and a Wasp Waist

The first thing that catches the eye when looking at a spider is its eight legs. In this way you can already distinguish spiders from the invariably six-legged insects. And what legs they are! In spiders, they are covered with hundreds to tens of thousands of the finest hairs, most of which are supplied with nerves and serve as sensory organs. Spiders can do much more with their legs than just walk: they can smell, taste and touch with them, they can sense air movements, vibrations, electrical charge differences, temperature and humidity with them. More about this can be found in Chap. 3. Five senses my ass!

If you look a little closer, you will always notice a **wasp waist** on a spider, such that its body appears constricted (Fig. 1.1). This is what distinguishes them from, for example, the harvestmen, mites, ticks, scorpions and other arachnids. This wasp waist makes it possible to distinguish at first glance a fore body (anterior part or prosoma) from a hind body (posterior part or opisthosoma) in spiders. The constricted area (the petiole or petiolus) is formed by the small anterior-most segment of the hind body. The other eleven segments of the hind body contain

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Fig. 1.1 Dorsal view of a male spider. Photo Yvonne Kranz-Baltensperger

most of the internal organs (digestive, respiratory and reproductive organs, heart and spinnerets).

But what is a **segment**? For this we have to go back a bit. Arachnids (Arachnida) belong together with insects, crustaceans and millipedes to the huge group of arthropods (Arthropoda), which all have a segmented body structure. In the other arthropods the segments are clearly visible from the outside, but in most spiders this is only the case in the embryo. However, in the post-embryonic developmental stages of spiders the internal anatomy still indicates their original segmented body structure.

In contrast to other arthropods, spiders do not have a clearly separated head. Instead, this is integrated into the fore body (prosoma). The prosoma bears the walking legs and (mostly) eight eyes, the function of which will be discussed in more detail in Chap. 2.

1.2 An Armoured Skin, Old Maids and Skeletal Sensing

Let's look a little closer at the two body parts of a spider. The fore body is quite robustly armoured. This armoured skin (also called the cuticle) is secreted by the



Fig. 1.2 Ventral view of a male (a) and a female (b) spider. The numbers 1–4 refer to the coxae of the walking legs 1–4. *Photo* Yvonne Kranz-Baltensperger

cells of the skin (the epidermis) to the outside. It is still soft at first, but hardens quickly and afterwards can no longer grow. As long as the spider grows in size, the cuticle has to be formed again at regular intervals and the old cuticle is shed in the course of a **moult** like a dress that has become too tight. This moulting process is described in more detail in Chap. 5.

Most spiders do not shed their skin after reaching **sexual maturity.** However, this is not the case with female tarantulas. They can remain sexually mature for many years and continue to shed their skin regularly during this time. Since the mating organs of female tarantulas are made of cuticle, they too are formed anew each time they moult. So even very old tarantula females enter the new mating season as virgins (old maids if you like) every time!

The cuticle contains a very solid protein, **sclerotin**, the content of which determines the hardness of the armoured skin. The sclerotin content of the cuticle is high in places where it is subjected to high stress, for example at muscle attachment sites. In other places, where the cuticle must be flexible or movable, for example at the joint membranes of the walking legs, it is very low. Further details on the structure of the cuticle can be found in Chap. 5. The underside of the fore body is armoured with a ventral plate (the sternum) (Fig. 1.2).

The cuticle protects the spider from harmful mechanical and chemical influences and from moisture loss. It also serves as an **exoskeleton**, to which numerous muscles attach. For comparison: In humans, the bony inner skeleton fulfils the same function. But that is not all: the countless sensory organs, which are distributed all over the body of the spider, especially frequently on the legs, are also made of cuticle material. This makes the spider's exoskeleton a tremendously complex system of thousands of different sense organs, in other words a skeletal sensory system! The cuticle can receive, amplify and transmit stimuli: a true miracle of evolution and a unique feature of arthropods.

1.3 Great Legs

The walking legs of spiders consist of seven joints which are movable against each other and are called (from body to tip) the coxa (hip), trochanter (thigh ring), femur (thigh), patella (kneecap), tibia (shin), metatarsus and tarsus (foot) (Fig. 1.3). At the end of each leg are two **claws**, usually covered with rows of teeth (Fig. 1.4).



Fig. 1.3 A spider leg. Photo Yvonne Kranz-Baltensperger



Fig. 1.4 a Web-building spiders have two toothed claws and a median claw on each foot, surrounded by several toothed bristles. **b** Adhesive hairs (scopulate hairs) on the tips of the legs, as seen here in the false wolf spider *Zoropsis spinimana* (Zoropsidae), enable many free-hunting spiders to run up smooth surfaces and hold on to wriggling prey. Each of these hairs is branched into hundreds of fine divisions, which have widened terminal feet at the end. *Photos* a Christian Kropf, b Benjamin Eggs

These enable spiders to hold on to uneven surfaces very well. Spiders that build webs for prey capture have an additional central claw between the two claws, which serves to hold and release the spider threads when building the web. Freely hunting spiders, such as jumping spiders, crab spiders or wolf spiders, lack this central claw or it is only rudimentarily present.

Many freely hunting spiders have numerous adhesive hairs (scopulate hairs) at the tips of their legs, which enable them to run up **smooth surfaces**. Each of these hairs branches into hundreds of fine divisions, each of which has a widened terminal foot at the end (Fig. 1.4). Theoretically, this allows a large spider to cling to a surface with millions of points of adhesion, while also supporting many times its own weight without falling off. Even large spiders can thus easily walk on the underside of a glass plate!

When a spider walks on a smooth surface, it is noticeable that the animal only touches down with the tips of its legs. In many species, however, not only the ends of the legs, but also other areas of the legs are covered with **adhesive hairs** that never come into contact with the surface when running. Why this happens could be clarified by high-speed recordings: The enormous adhesiveness of the scopulate hairs also serves to efficiently hold a wriggling prey animal (Fig. 6.7).

The exact adhesion mechanism of the scopulate hairs is still being researched. The main forces at work are electrical attraction (Van der Waals forces), but also capillary forces. The latter are caused by the fact that most surfaces are covered with an extremely thin film of water above a certain humidity. Therefore, the adhesion of the scopulate hairs also depends on the relative humidity.

1.4 Two Groping Penises on the Face

In front of the eight walking legs we see a small pair of additional, leg-like projections, the palps (pedipalps) (Fig. 1.2). They are never used for walking, but in juvenile spiders and females they serve mainly for touching the ground or prey. But they can also smell and taste with their sensory organs, as well as those on their legs, and sense air currents, temperature, and humidity. In the sexually mature male, the last joint of the palp is transformed into a **copulatory organ**, which is used to transfer sperm into the female during mating. Functionally, the two palps of males thus (also) serve as penises. At first glance, these organs often look like a pair of small boxing gloves in front of the face (Fig. 1.2). This makes it easy to distinguish males and females in spiders, usually even with the naked eye.

The copulatory organ on the male palp of spiders can be relatively simple, as in tarantulas, but can also be very complex in construction. In fact, some spiders have developed the most complex copulatory organs in the animal kingdom. In these species, which include our garden spiders and sheet web spiders, for example, the copulatory organ consists of numerous intricately shaped hard parts, adventurous projections, and inflatable membranes that connect these hard parts (Fig. 1.5). Inside the copulatory organ is a tube into which the sperm is taken before mating.

Almost always, the male mating organ is **species-specific** in construction. During mating, body fluid is pumped into the copulatory organ, causing the membranes to swell strongly and the hard parts to move from their resting position in a complicated, predetermined path. In this way they hook perfectly onto the mating plate on the female's hind body, the epigyne, which is also often intricately constructed (Fig. 1.5). The sperm is then transferred from the pedipalp via the epigyne to special storage organs called spermathecae. There it is stored by the female until the eggs are ripe.

The part of the palp that is closest to the body is transformed into a mouthpart, the gnathocoxa. It carries dense tufts of feathery hairs and a row of teeth (serrula). The function of these teeth is still unclear, possibly they serve to cut spider threads. The gnathocoxae delimit the **mouth opening** laterally. In front of this lies a soft-skinned upper lip (the labrum), while the rear edge of the mouth opening is formed by a firm lower lip (the labium) (Fig. 1.6). With these demarcations, the spider creates a space that allows it to digest its food in front of its mouth. If you want to know more about this, you will find it in Chap. 9.



Fig. 1.5 a Male pedipalp of an adult spider with the femur, patella and tibia as well as (above) the complex mating organ, which consists of numerous hard parts and membranes that become hooked onto the female. **b** the heart-shaped epigyne of an adult female spider. *Photos* Yvonne Kranz-Baltensperger

1.5 Poisoners and Drinkers

At the very front of the fore body (prosoma) are the jaws (chelicerae), which consist of a basal element close to the body and a movable **venomous fang** attached to it (Fig. 1.7). The base of the chelicera contains a **venom gland**, which in most spiders extends far into the fore body. The venom is a highly complex mixture of many components. It emerges, as in a syringe, from an opening just in front of the tip of the fang. Venom's main purpose is to paralyze prey, and in an emergency it is also used for defence, as will be explained in Chap. 6.

In the fore body there are numerous muscles. They allow movement of the legs and palps and the movements of a highly specialized **pumping stomach** (often inaccurately called a "sucking stomach"). With this organ, spiders can pump digestive enzymes into a prey animal and suck the liquefied parts of the prey back in. The stomach is located in a small bowl-shaped internal skeletal part, the **endosternite**, which serves, among other things, as an attachment site for the stomach muscles (Fig. 9.5). Tufts of feathery hairs in front of the mouth opening and a fine filter plate in the gullet prevent larger solid components of the prey from being sucked in. In fact, only particles smaller than a thousandth of a millimetre enter the gut! Spiders therefore do not actually eat, they drink, and there is more information about this in Chap. 9.



Fig. 1.6 Area around the mouth opening of a spider. Photo Yvonne Kranz-Baltensperger

1.6 Why Spiders Do not Eat Dumplings

The large spider brain is also located in the fore body, from which numerous nerves extend to all regions of the body. The brain has a special feature: it is penetrated by the oesophagus, which is only a thin tube because of the liquid food intake (Fig. 9.5). Imagine the spider taking in a thick chunk of food: This would therefore have to be transported through the brain—a headache guaranteed! This is probably why spiders started ingesting exclusively **liquid food** very early in their evolutionary history. Or to look at it another way: Because spiders only eat liquid food, they can afford to have a slender oesophagus. We will come back to this point in Chap. 9.



Fig. 1.7 Front view of a spider. Photo Yvonne Kranz-Baltensperger

1.7 About Blue-Blooded Starvelings and Why You can't Strangle Spiders

The hind body (opisthosoma) is not armoured like the front body, but **soft-skinned**. This makes it very stretchable, which benefits the spider when it takes in a large amount of food or when the eggs are maturing in a mated female. The foremost segment of the hind body forms the aforementioned wasp waist of the spider. This makes the hind body extremely **mobile** compared to the fore body. This is useful for spinning complex webs, overpowering prey, and for the various mating positions, which we will discuss in more detail in Chap. 10.

Near the end of the hind body are typically three pairs of jointed **spinnerets**, which can be easily moved individually with muscles and on which the **spinning glands** open. These glands are located inside the hind body—up to eight different varieties of spinning glands can be found in a spider! They produce different kinds of spider threads and also the glue that many spiders use to catch prey, more on this in Chap. 7.

Most of the hind body is occupied by the huge **midgut**, which branches and ramifies many times (Fig. 9.5). This super organ is not only the central metabolic organ, but also serves as a food store. This explains the astonishing capacity of spiders to starve for a very long time after a substantial meal. In some spiders,

certain midgut cells, the guanocytes, are specialized to store **guanine**, a crystalline metabolic end product, more on this in Chap. 9. These guanocytes are located just under the skin. Depending on the crystal form of the guanine, the silvery or white content of these cells shimmers through the skin. The white cross of the garden spider, for example, comes about in this way, but also colour patterns and colour changes, which we will discuss further in Chap. 12.

The heart is a muscular tube, open at the front and back. It lies just under the skin on the back of the hind body (Fig. 1.8). It can therefore pump body fluid both forward and backward. To this it must be said that spiders do not possess blood in our sense. Whereas we humans possess blood in a closed vascular system as a separate body fluid alongside lymph and other fluids, the spiders' only body fluid, **haemolymph**, is pumped through the aorta leading away from the heart and several arteries into the major regions of the body. It then leaves these vessels and flows freely between the organs to the lungs and then back to the heart. A finely distributing capillary system, such as we possess, and a returning venous system are absent. Spiders, unlike humans and many other animals, thus have an **open circulatory system** (Fig. 1.8).

The original respiratory organs of spiders are two pairs of **book lungs** in the hind body. This condition is shown for example by the tarantulas. In most spiders, however, the posterior pair of lungs has been replaced by tracheae (Fig. 1.8). These



Fig. 1.8 Longitudinal sectional diagram through a female spider body showing the cardiovascular system, reproductive organs and spinning apparatus. The central nervous system is given in blue, the blood vessel system in red, the air volume in the book lung in light blue. In the case of paired organs, only the parts of the left half of the body are drawn in each case. For reasons of clarity, the digestive organs have not been included here. These are shown in Fig. 9.5 in Chap. 9. *Figure* Wolfgang Nentwig

are cuticular tubes through which oxygen can be transported to the organs through a small opening, the stigma, and conversely carbon dioxide can be transported back out. Some very small spiders even breathe only through tracheae.

The book lungs consist of numerous hollow lamellae, which lie on top of each other like the pages of a book. Haemolymph flows in the hollow lamellae and air between the lamellae. Oxygen from the air enters the haemolymph through the wafer-thin wall of the lamellae, and carbon dioxide from the haemolymph enters the air. The oxygenated haemolymph is transported to the pericardial sinus through a channel (the pulmonary sinus). It then flows into the heart through several wide openings equipped with one-way valves, the ostia. The air enters the book lungs and trachea through small breathing openings on the hind body. Therefore, it would be futile to try to strangle a spider and squeeze its throat shut. It could continue to breathe through its breathing openings on the hind body without any problem.

Just like humans, spiders have a special transport molecule in their body fluid that transports oxygen to the tissues. For us, it is haemoglobin, which contains iron and therefore colours our blood red. Spiders bind oxygen with their coppercontaining **haemocyanin**, which looks blue because of the copper. Spiders can therefore be described as blue-blooded.

1.8 Love on and for Oneself: Why Spider Males Masturbate Before Sex

In the hind body are also the sexual organs: the **ovaries** or **testicles**. The genital opening is located on the underside in the second segment and is usually covered by an often complicated and species-specific mating plate (or epigyne) in the female. The genital opening of the male is, by contrast, quite inconspicuous. The male spider fills its mating organ on the palps (pedipalps) with sperm before mating. But how does the sperm get from the hind body into the palps? First, the male builds a simple **sperm web**. Then he massages his sexual opening with his legs until a sperm drop emerges—he masturbates, so to speak. The sperm drop is placed on the sperm web, after which the male dips the tips of his palps in it and sucks the sperm into his mating organ. This perfectly matches the shape of the female's sexual orifice. Only after this bizarre male foreplay does copulation take place, more on this in Chap. 10.

We still do not understand all the peculiarities of the spider's body plan. But we know from unquestionable fossil findings that it has existed since at least the Carboniferous period, thus for over 300 million years. Long before the dinosaurs came into being, spiders developed a body plan that has defied all the catastrophes of Earth history and is still found today in at least 50,000 species—a successful model of **evolution**!