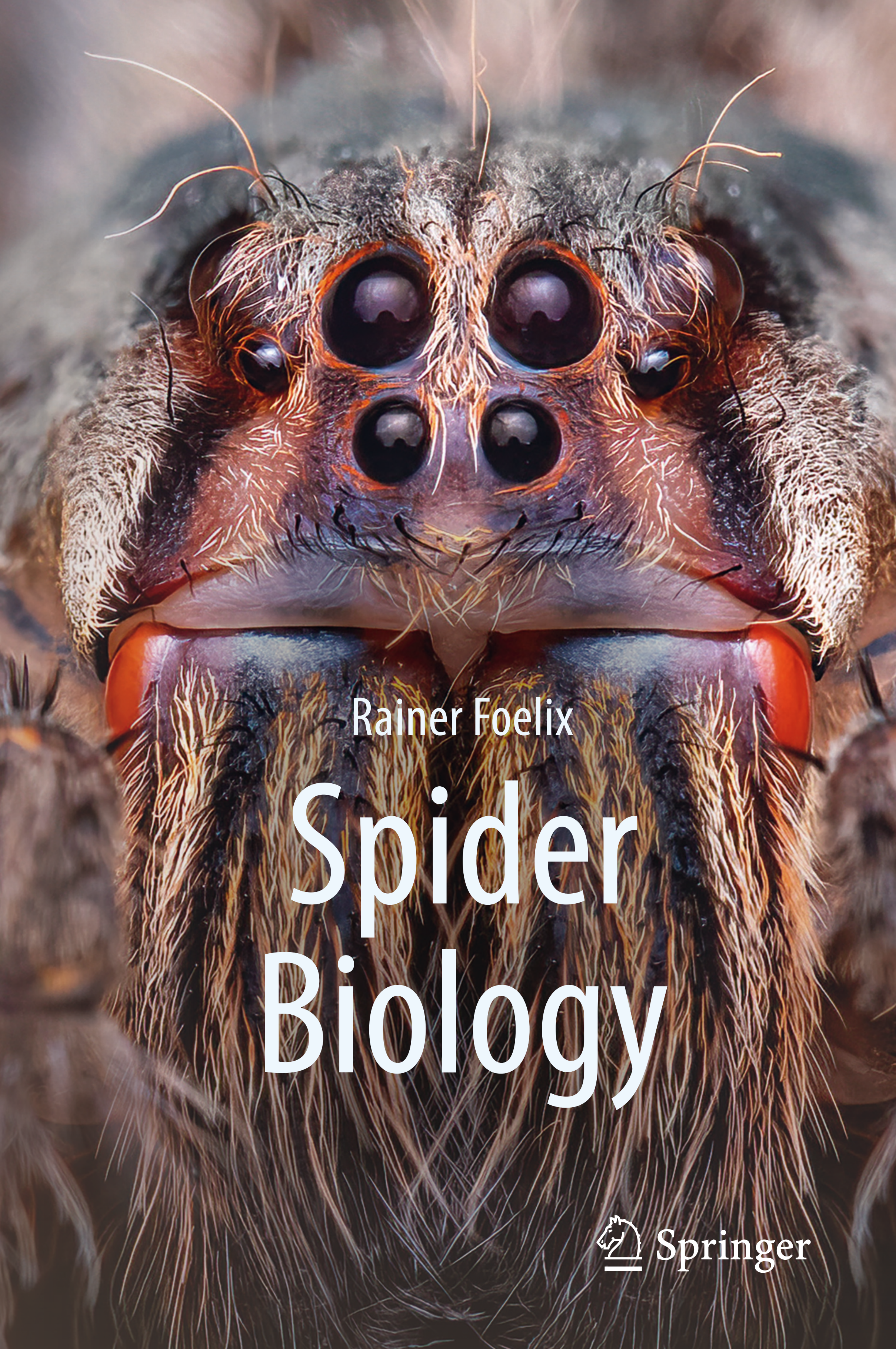

Rainer Foelix

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Nose ornament (or mask) worn in Pre-Columbian Peru, denoting high social status. Moche culture, 200-900 CE, gold, silver, shell and stone. Courtesy Metropolitan Museum of Art.

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A mortal maid by name of Arachne once did weave upon her loom visions of such gossamer beauty that they cast in pale shadow the works of the divine (D. E. Hill)

Preface

This book is based on the latest English (2011) and German (2015) editions of *Biology of Spiders*, but has been completely rewritten and updated (to 2024). It was initiated by my colleague David Hill and we worked together for more than a year to come up with this new version, now called *Spider Biology*. Unfortunately, I was not able to persuade him to be a co-author, although he has made substantial contributions to all the chapters, especially Chapter 10 (Phylogeny and Systematics), which was largely written by him. David Hill has also dealt with all the technical issues, including the entire layout of this book. So my first and most sincere thanks go to him. I am also grateful to many other colleagues and friends who have contributed their photographs, diagrams, or scientific data. In particular, I would like to mention Gordon Ackermann, Nicky Bay, Jillian Cowles, William Eberhard, Anka Eichhoff, Bruno Erb, Marshal Hedin, Anna-Christin Joel, Yael Lubin, Wolfgang Nentwig, Jürgen Otto, Bastian Rast, Ingo Rechenberg, Jerome Rovner, Wolfgang Schröer, Rolf Thieleczek, and Benno Wullschleger. I am also indebted to the Neue Kantonsschule Aarau (NKSA) for allowing me to use their electron microscope (EM) facilities - most of the EM images presented here originate from this lab. Finally, I want to thank Springer Verlag for the extensive preparations to get this book into print, and especially my editor Lars Koerner for his competent and patient collaboration.

As in my previous spider books, I have tried to focus on the essentials and not go into too much detail - after all, it should still be a readable book. However, since about 700 new spider publications had to be included and many new illustrations added, the volume of the new book has inevitably increased. It has always been my main concern to provide highly instructive and high quality illustrations, and therefore most figures are not simply copies of the originals, but have been altered to create a more consistent style throughout the book. It should also be emphasized that this book is intended primarily for the general reader interested in spiders, rather than for the specialist. However, for the more professional arachnologist, a reference list of about 2000 original articles should allow for further in-depth studies.

Contents

1 *Introduction to the Spiders*

Most people have a negative attitude towards spiders, but at the same time they know very little about them. This lack of knowledge is also evident in pictorial representations of spiders. In old historical prints, for example, many features are highly anthropomorphized (eyes, fingers, body) and often only the number of legs is correctly depicted (Fig. 1.1a). In other cultures, as among the Native Americans, pictures of spiders were anatomically correct from a very early time, as the ornament in Fig. 1.1b vividly demonstrates. It was not until the later Middle Ages, when naturalists like Maria Sibylla Merian or Rösel von Rosenhof began to study insects and spiders more closely, that illustrations became more lifelike (Fig. 1.2).

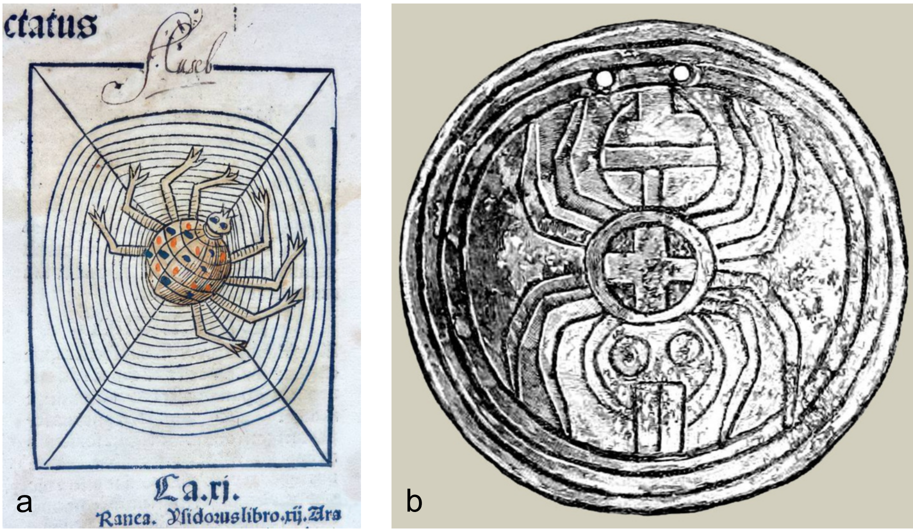

Fig. 1.1 (a) In medieval times spiders were depicted rather crudely and anthropomorphically. Of all the typical spider features only the number of legs is correctly shown in this woodcut from 1491 (*Hortis Sanitatis*, Mainz, Germany). **(b)** In contrast, all primary characters of a spider are correctly pictured in this *gorgette* from a prehistoric burial in eastern North America (Holmes 1883).

What characteristics are truly typical of spiders, and how do they differ from insects or other arthropods? And isn't the lifestyle, development, and behavior of spiders just as complex and interesting as in other animal groups? This chapter aims to provide a brief overview of spider characteristics as well as the most important spider families, before we delve into the actual biology of spiders.

1.1 Body division and segmentation

A brief characterization of spiders is as follows: The body is divided into two parts: The anterior body (prosoma or cephalothorax) is connected to the abdomen (opisthosoma or abdomen) by a narrow stalk (pedicel) (Fig. 1.3). The prosoma is covered by single dorsal and ventral plates (carapace and sternum, respectively); segmentation of the carapace is not evident when viewed from above. Six pairs of

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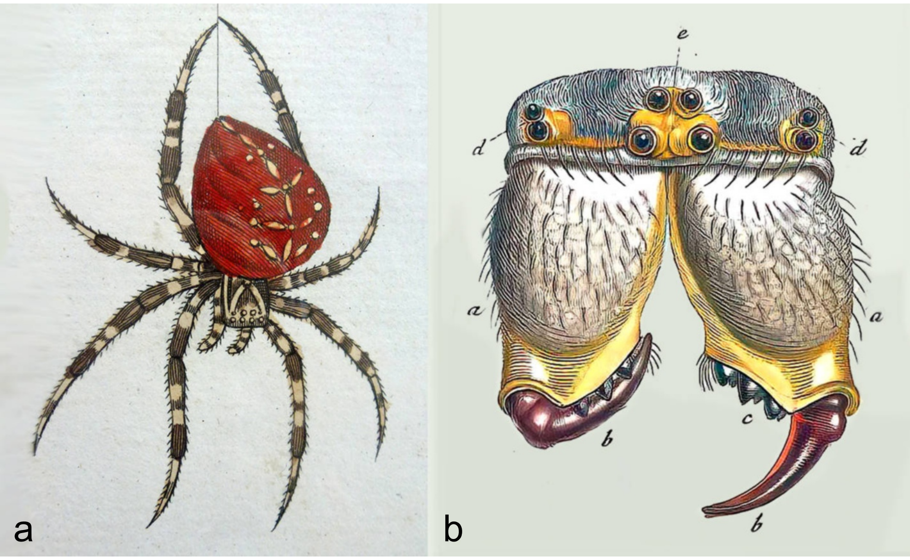

Fig. 1.2 **(a)** Etchings of spiders were increasingly more life-like in the 18th century, as in this common garden spider *Araneus diadematus* by Rösel von Rosenhof (1761). **(b)** He even portrayed microscopical details of the mouth parts correctly (for clarity the original image has been rotated by 180°).

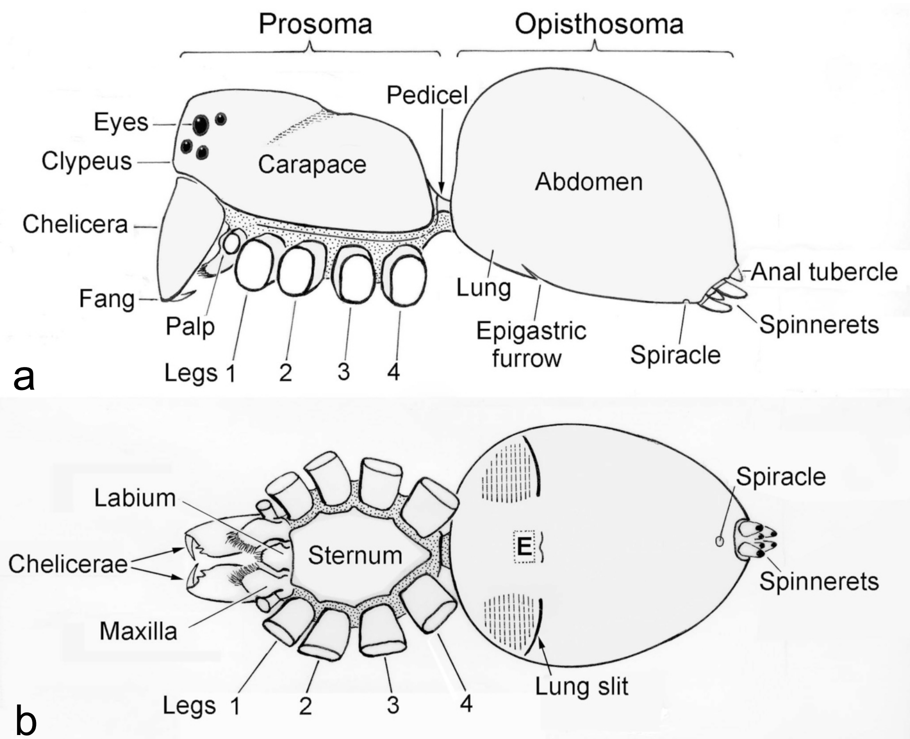

Fig. 1.3 External appearance of a spider´s body. **(a)** Side view. **(b)** Ventral view. E = epigynum (in adult females).

appendages are associated with the prosoma. In front of the four pairs of walking legs are the leg-like pedipalps (or simply palps) and in front of them are the two-segmented chelicerae, mainly used to capture prey. In mature male spiders, the pedipalps are modified into copulatory organs - a unique feature that is absent in other arthropods. Except for the *segmented trapdoor spiders* of the suborder Mesothelae, segmentation of the sack-like opisthosoma is not obvious.

Functionally, the prosoma mainly serves for locomotion, feeding, and nervous integration (the location of the central nervous system). In contrast, the opisthosoma fulfills important vegetative functions: digestion, circulation, respiration, excretion, reproduction, and silk production. The opisthosoma also serves as an additional appendage for the deposition of silk lines.

All spiders have a predatory lifestyle, i.e. they are carnivorous. Many have specialized as stationary snare builders (web spiders), while others actively hunt for their prey (ground or wandering spiders). Their prey mainly consists of insects, but other arthropods may also be eaten.

Spiders have a worldwide distribution and have colonized all habitats except for the air and sea. Most spiders are relatively small (2-10 mm body length), but the largest tarantulas can reach 80-90 mm in body length. Males are almost always smaller and shorter-lived than females.

1.2 Systematic overview

Systematists currently distinguish over 50,000 different spider species, which they assign to more than 130 different families (WSC 2025). Regarding the systematic classification, there are naturally different opinions - over 20 different systems have been proposed since 1900 alone. However, in recent years there has been a great deal of study of the evolutionary relationships of spider families, and there is now more general agreement on the placement of most.

The order of spiders (Araneae) is divided into two suborders, the basal Mesothelae (Liphistiidae) and the Opisthothelae, based on the relative position of spinnerets on the underside of the opisthosoma (Wheeler et al., 2017). The Opisthothelae, representing the great majority of extant spider species, is further divided into the Mygalomorphae (tarantulas and their allies, with orthognath chelicerae that move side by side in a vertical plane) and the Araneomorphae (all remaining spiders, with labidognath chelicerae that oppose each other in a transverse plane) (Figs. 1.4 -1.6).

Most spider species (>90%) belong to the Araneomorphae (Labidognatha). In the past, two infraorders were distinguished, namely the Cribellatae and the Ecribellatae. In cribellate spiders the most anterior of four pairs of spinnerets is fused into a single, median plate (the cribellum) with numerous tiny ducts that release very fine (cribellate) silk. Ecribellate araneomorphs lack the cribellum and, in its place, have a small projection known as the colulus. Today it is widely thought that araneomorph spiders were originally cribellate and that many ecribellate spiders later emerged through reduction or loss of the cribellum (Correa-Garhwal et al. 2022).

The renowned French arachnologist Eugène Simon separated ecribellate spiders with a simple female genital apparatus as Haplogynae from those with a more complicated genital apparatus, the Entelegynae (Fig. 1.7). This classification has existed for over a century (Simon 1892, 1903) but has not remained without controversy (Brignoli 1975, 1978; Lehtinen 1975; Platnick 1975). Nevertheless, some families can still be considered "classic" Haplogynae today, such as the Scytodidae (spitting spiders), the Pholcidae (cellar spiders), and the Dysderidae (woodlouse hunters).

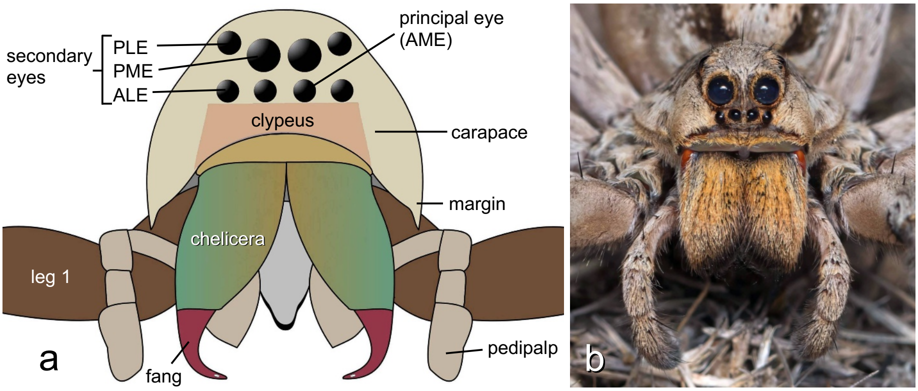

Fig. 1.4 (a) Diagrammatic front view of a spider's prosoma showing the arrangement of the eight eyes and the chelicerae (D. E. Hill). **(b)** Portrait of a wolf spider (♀ *Hogna carolinensis*) (© Luis Fernando Valdez Ojeda, CC BY 4.0).

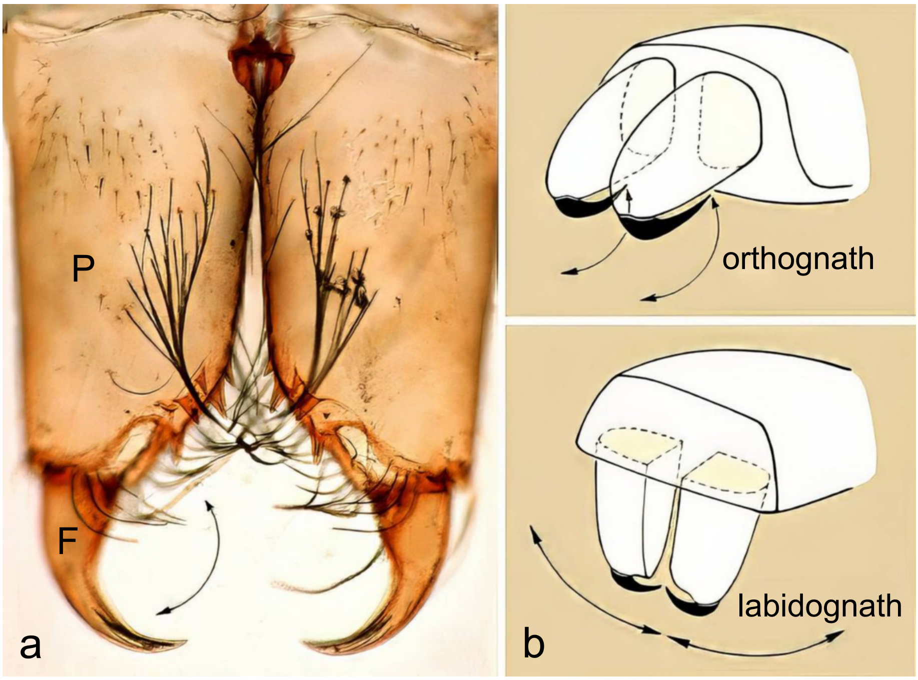

Fig. 1.5 (a) Chelicerae of the house spider *Eratigena*, frontal view. The cheliceral fangs (F) have moved out from their resting position in the cheliceral base, or paturon (P). **(b)** Movement of the chelicerae in orthognath and labidognath spiders (after Kaestner 1969).

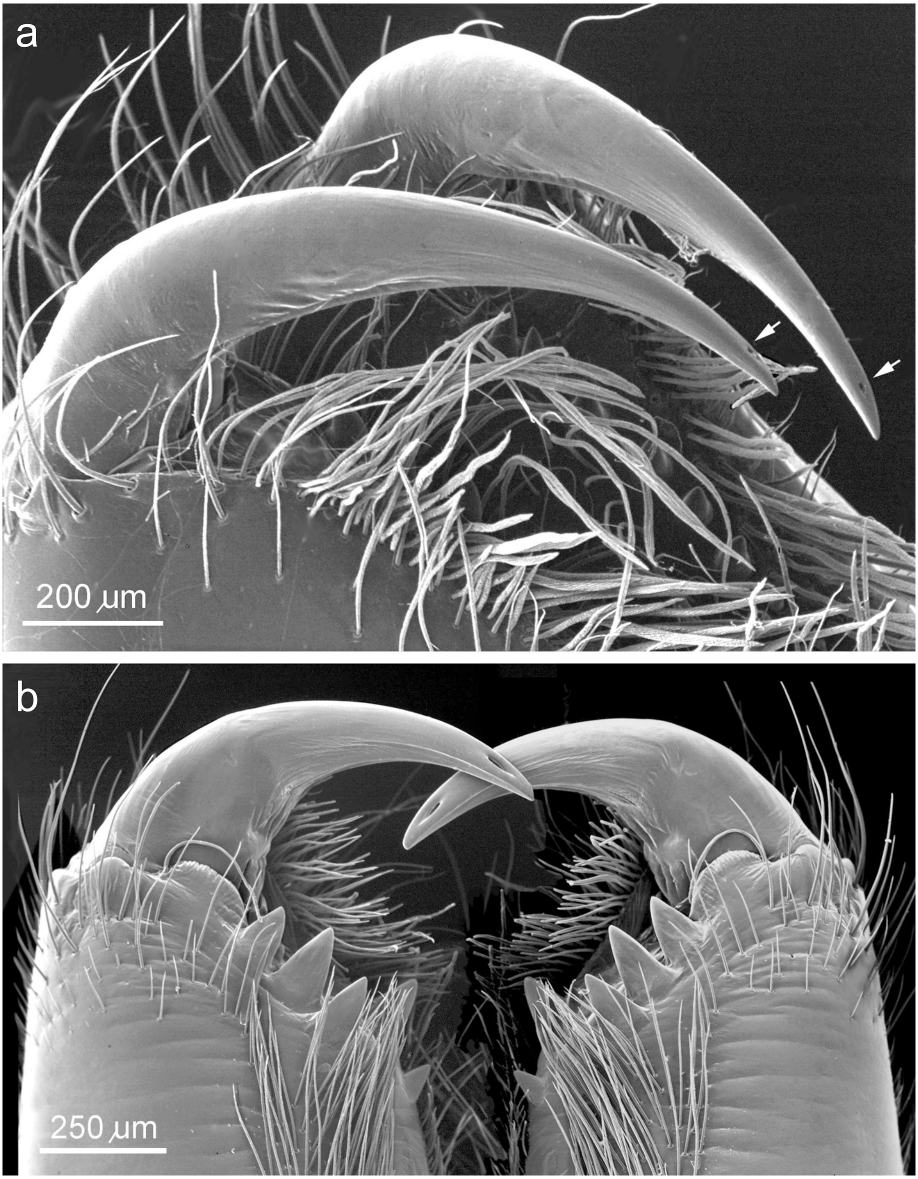

Fig. 1.6 **(a)** Orthognath chelicerae (*Dolichothele*, ventro-lateral view), with fangs having a roughly parallel alignment. Small arrows indicate the openings of the venom ducts near the tip of the cheliceral fangs. **(b)** Labidognath chelicerae (*Lycosa*, posterior view), opposing-each other. Note the venom openings and the prominent retromarginal cheliceral teeth.

Furthermore, the Entelegynae were divided into the Dionycha (two-clawed) and the Trionycha (three-clawed), depending on whether the walking legs had two or three tarsal claws (Fig. 1.8). This classification was soon questioned, but at least some "classic" Dionycha can still be recognized, to include the Salticidae (jumping spiders) and the Clubionidae (sac spiders).

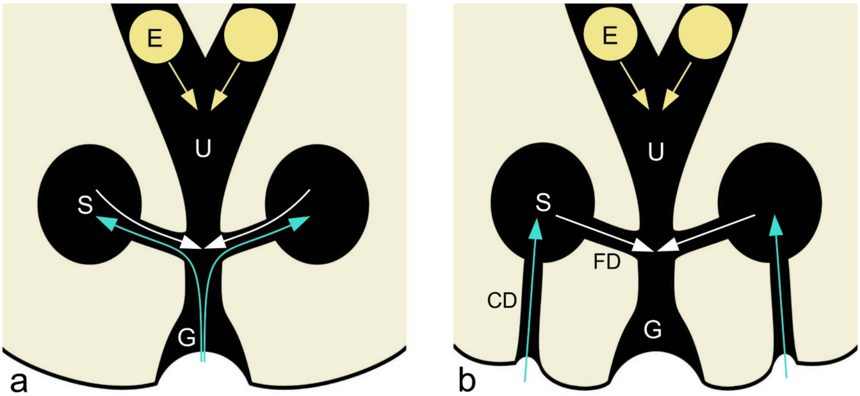

Fig. 1.7 Female reproductive tracts in **(a)** haplogyne and **(b)** entelegyne spiders. Green arrows depict collection of sperm in the spermathecae (S) when mating. White arrows depict release of sperm to fertilize the eggs (E). CD = copulatory duct, FD = fertilization duct, G = genital pore (*gonopore*), U = uterus. (© D. E. Hill, CC BY 4.0)

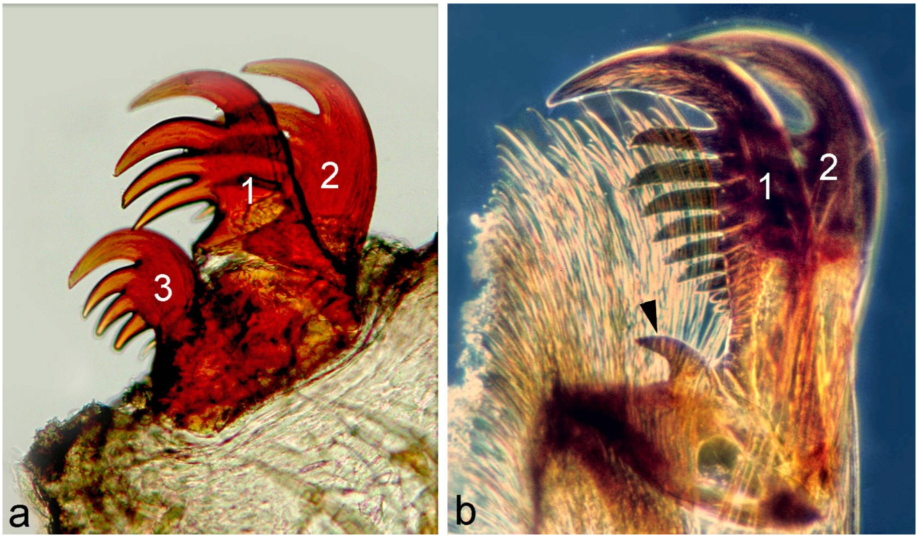

Fig. 1.8 **(a)** Ancient spiders probably had three pretarsal claws on each leg, as seen here in the "primitive" spider *Liphistius*. **(b)** In the Dionycha, the middle claw was supposedly lost. However, a reduced middle claw (arrow) is often still present, as in this tarsus of a young jumping spider. The two main claws (1, 2) are toothed, like a comb.

Since we refer to certain spider families frequently, some of the more important families and their systematic classification will be briefly listed here (Wheeler et al. 2017; WSC 2025). A more detailed picture of today's spider systematics is provided in Chapter 10.

Order Araneae (*spiders*)

1. Suborder Mesothelae (*segmented trapdoor spiders*, 1 family)
    - Fam. Liphistiidae (194 species)

2. Suborder Opisthothelae
2.1 Infraorder Mygalomorphae (31 families)
Fam. Atypidae (*purse-web spiders*, 56 species)
Fam. Idiopidae (*armored trapdoor spiders*, 446 species)
Fam. Barychelidae (*brushed trapdoor spiders*, 284 species)
Fam. Theraphosidae (*tarantulas*, 1134 species)
Fam. Nemesiidae (*funnel-web trapdoor spiders*, 188 species)
Fam. Dipluridae (*curtain-web spiders*, 146 species)
2.2 Infraorder Araneomorphae (104 families)
Fam. Filistatidae (*crevice weavers*, 192 species)
Fam. Segestriidae (*tube-dwelling spiders*, 181 species)
Fam. Oonopidae (*goblin spiders*, 1962 species)
Fam. Dysderidae (*woodlouse hunters*, 653 species)
Fam. Scytodidae (*spitting spiders*, 253 species)
Fam. Pholcidae (*cellar spiders*, 2029 species)
Fam. Theridiidae (*cobweb spiders*, 2586 species)
Fam. Araneidae (*orb-weavers*, 3144 species)
Fam. Tetragnathidae (*long-jawed orb-weavers*, 990 species)
Fam. Linyphiidae (*sheet weavers*, 4940 species)
Fam. Eresidae (*velvet spiders*, 106 species)
Fam. Uloboridae (*hackled orb-weavers*, 283 species)
Fam. Zodariidae (*ant spiders*, 1306 species)
Fam. Amaurobiidae (*hackled-mesh weavers*, 202 species)
Fam. Agelenidae (*funnel-web spiders*, 1420 species)
Fam. Dictynidae (*mesh-web weavers*, 460 species)
Fam. Sparassidae (*huntsman spiders*, 1523 species)
Fam. Ctenidae (*wandering spiders*, 605 species)
Fam. Oxyopidae (*lynx spiders*, 448 species)
Fam. Pisauridae (*nursery web spiders*, 236 species)
Fam. Lycosidae (*wolf spiders*, 2489 species)
Fam. Thomisidae (*crab spiders*, 2169 species)
Fam. Clubionidae (*sac spiders*, 667 species)
Fam. Anyphaenidae (*ghost spiders*, 649 species)
Fam. Gnaphosidae (*ground spiders*, 2479 species)
Fam. Corinnidae (*ant-mimic spiders*, 876 species)
Fam. Cheiracanthiidae (*yellow sac-spiders*, 376 species)
Fam. Philodromidae (*running crab spiders*, 527 species)
Fam. Salticidae (*jumping spiders*, 6808 species)

Here I introduce some of the better-known spider families.

1. Funnel-web spiders (Agelenidae). Funnel-web spiders are familiar to everyone. In our houses, we most commonly encounter the house spider *Eratigena* (formerly *Tegenaria*), usually in the bathroom, where it cannot climb the smooth walls of the bathtub. In addition to their body size (10 mm), they stand out because of their long, hairy legs (12-18 mm in length) and two protruding spinnerets at the end of the abdomen. The dorsal side of their abdomen bears a typical chevron pattern (Fig. 1.9b).

Fig. 1.9 (a) A female funnel web spider (*Agelenopsis*) sitting at the entrance of her retreat (photo: D. E. Hill). **(b)** The abdomen of *Agelena* shows a typical chevron pattern and long spinnerets (photo: B. Erb). **(c)** A female *Agelena* sitting on top of her star-shaped egg case (photo: W. Schröer).

Outdoors, we can easily find the North American *Agelenopsis* or the slightly smaller Eurasian *Agelena* in low grass or bushes (Fig. 1.9a, c). The sheet webs of funnel-web spiders usually span wall corners or low plant cover. These spiders owe their name to the manner in which their flat web funnels into a tube at one end; there, the spider waits and usually extends its front legs to feel vibrations on the surface of the web. Only when an insect lands on the web does it quickly run out, bite the prey, and carry it back to its tubular retreat. The actual feeding process always takes place inside the retreat. These spiders exhibit surprisingly good orientation, both on their way to the prey and on their way back to the retreat. Funnel-web spiders have therefore been a preferred subject for sensory physiologists.

The water spider *Argyroneta aquatica*, the only spider that lives permanently under water, was long classified as a funnel-web spider. Later it was placed in its own family, the Argyronetidae, then assigned to the Cybaeidae, and now to the Dictynidae. Instead of a web, it uses silk lines to build a submersed air bubble on aquatic plants and this bubble then serves as her residence (Fig. 6.15). Mostly fly larvae or small crustaceans that swim freely under water are hunted and then eaten inside the air bubble. The abdomen of a water spider is always encased by a silvery, shiny air envelope that is renewed from time to time at the water surface. Therefore, the water spider can breathe in principle just like an ordinary spider on land (Heinzberger 1974; Seymour & Hetz 2011).

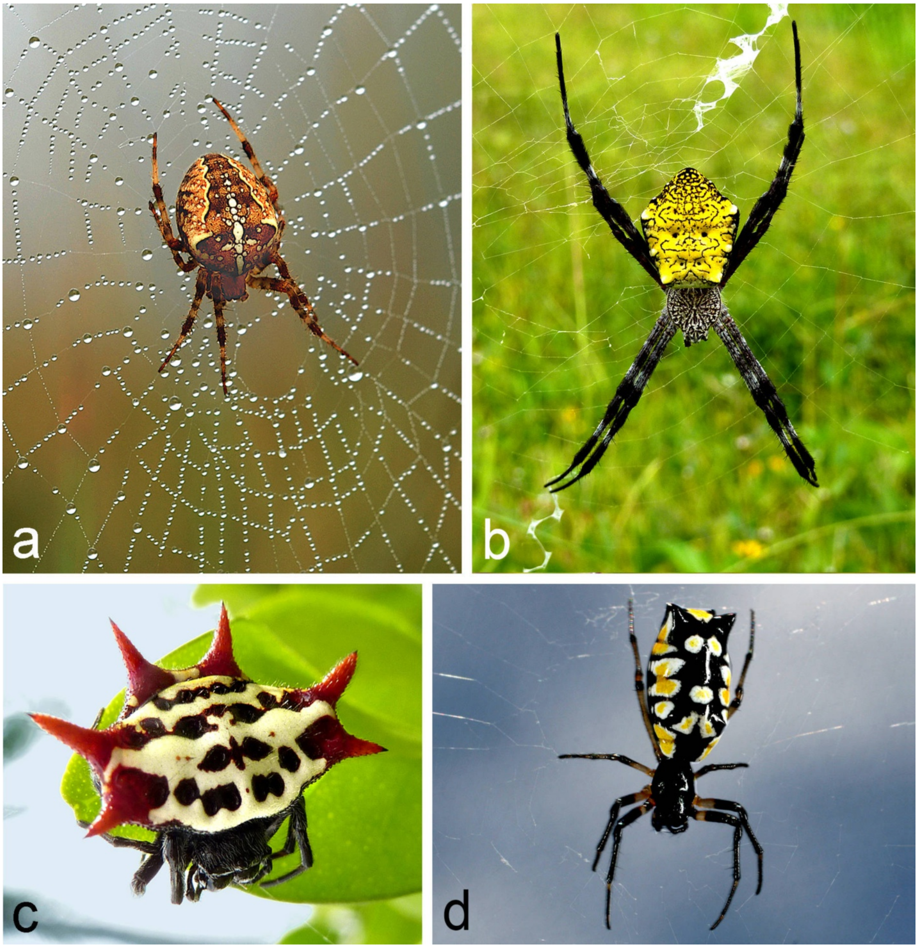

Fig. 1.10 Orb-web spiders. **(a)** The best known of all orb-weavers, the garden spider *Araneus diadematus* (photo: B. Erb). **(b)** The Hawaiian garden spider *Argiope appensa* with the typical black, white and yellow striation of its abdomen and the four pairs of legs held in an X-pattern. **(c)** A spinybacked orb weaver (*Gasteracantha cancriformis*) that was introduced to Kauai (Hawaii). **(d)** Another spiny orb weaver (*Micrathena funebris*) from North America (photo: J. Cowles).

2. Orb-web spiders (Araneidae). The ability to build elaborate capture webs is most impressively realized in the orb-weaving spiders. The webs of the domestic garden spider (Fig. 5.26) are probably the best-known web type of all spiders. This spider sits either at the center (hub) of the web or hides in a retreat outside of the web. Insects that get caught in the web are held by the sticky capture threads - at least until the spider rushes out of the hub to wrap or bite it.

With an enormous number of species (>3300), orb-weaving spiders are among the most successful of spider families. Accordingly, there are also hundreds of different designs of the orb web; some examples are discussed in more detail in Chapter 5. The body shape of the Araneidae also varies greatly (Fig. 1.10). Particularly in the tropics, many species are very colorful and their abdomens may have fantastic shapes and spiny extensions.

In addition to the Araneidae, we also find an orb-web in the Tetragnathidae (*long-jawed orb-weavers*) and in the Uloboridae (*hackled orb-weavers*). The latter build a similar orb-web, but the capture threads are covered not with liquid glue droplets, but with extremely fine cribellate silk that is also very sticky.

3. Wolf spiders (Lycosidae). Wolf spiders are vagabonds that usually lie in ambush or freely hunt their prey. They are best recognized by their typical eye arrangement, with four uniformly small eyes in the front row and two large medial eyes in the posterior row (Figs. 1.4b, 1.11).

The approximately 2400 species of wolf spiders are widespread around the world and vary greatly in size. The best known are the large "tarantulas" (*Lycosa tarantula*) of the Mediterranean countries, whose name derives from the Italian town of Taranto. They are wrongly reputed to be dangerously venomous. These tarantulas are large (3 cm body length) and live in the earth, in tubes that they line with silk. Some wolf spiders make complex entrances or even a lid at the opening of their burrow (Framenau 2009), similar to trapdoor spiders (Ctenizidae). At night, they leave their tubes to prowl for insects. However, wolf spiders generally do not actively pursue their prey, as their name suggests. Rather, they usually sit motionless in one place and wait for a victim to walk by, so to speak (Ford 1978; Stratton 1985).

European wolf spiders (about 70 species) are usually only 4-10 mm in body length and live freely in low vegetation or among stones. Only the larger representatives (*Arctosa, Trochosa, Lycosa*; 1-2 cm body length) dig burrows. Certain species prefer to live near water and can run skillfully on the water surface (Fig. 6.11) which has earned some of them the scientific name *Pirata*. These hunt insects on the water surface, but they can also dive and catch tadpoles or small fish. Wolf spiders primarily respond to vibrations emitted by the prey (running, wing beats), but also to visual stimuli. The eyes of wolf spiders allow for relatively coarse visual perception (Homann 1931), but visual stimuli are only effective from a few centimeters away. This is also evident in the courtship behavior of male wolf spiders. The often dark-colored pedipalps or front legs are waved in a species-specific manner to attract the attention of the female. Female wolf spiders are well-known for their brood care. They attach their lentiform egg sac to their abdomen and carry it with them wherever they go. Shortly before the young hatch, the mother provides "midwifery" by slightly tearing the firm shell of the egg sac. When the young emerge from this sac they immediately climb onto the mother's back (Fig. 7.35). They sit tightly packed, often in several layers, and are carried around by their mother for about a week. Only gradually do they scatter and then take in food for the first time.

Only a few representatives of wolf spiders (*Aglaoctenus*, *Aulonia, Hippasa, Sosippus, Venonia*) build flat ground webs that resemble the sheet webs of funnel spiders (Agelenidae); they are therefore considered relatively basal species (Brady 1962, 2007; Job 1968, 1974; Eberhard & Hazzi 2017; Gonzáles et al. 2013, 2014).

The wandering spiders (Ctenidae) were temporarily assigned to the subfamily Cteninae of the Lycosidae (Homann 1971), but are now again placed in their own family. They include the extremely venomous and supposedly aggressive *Phoneutria fera* as well as *Cupiennius salei* (now Trechalidae), which has been studied extensively (Barth 2002) and therefore will be mentioned quite often in later chapters.

Fig. 1.11 Large wolf spiders. **(a)** Lateral view of a female European tarantula (*Lycosa tarantula*) with an egg sac attached to her spinnerets. **(b)** A female tarantula with her newly hatched spiderlings sitting on her back. **(c)** The two-colored Australian wolf spider *Hoggicosa* lives in silk-lined tubes in dry soil. **(d)** Another Australian lycosid (*Tasmanicosa*) sitting at the entrance of its burrow waiting for prey to pass by. (Photos: B. Rast)

4. Crab spiders (Thomisidae). Crab spiders are pure ambush predators that do not spin webs. They sit motionless on flowers or leaves, waiting with their extended front legs for insects to land. The relatively small eyes only allow for shape recognition at close range, but movements can be detected from as far away as 20 cm (Homann 1934). When prey comes within reach (0.5-1 cm), it is seized with the two pairs of powerful front legs (Fig. 1.12) and paralyzed with a venomous bite. Even large flower visitors such as bumblebees or butterflies are successfully attacked (Fig. 9.5). Their prey is only sucked out through the tiny bite holes, leaving an almost intact shell (Foelix 1996; Fig. 3.2).

Crab spiders are often brightly colored, usually pure white, pink or yellow, less commonly green. Mature females may adapt their coloring to some extent to match the color of the background (often a flower!). Even the less colorful species are usually well camouflaged and hardly noticeable among vegetation. Crab spiders owe their name to their ability to move very adroitly sideways.

The running crab spiders (Philodromidae) were long classified as crab spiders but are not closely related to them (Ch. 10; Homann 1975; Benjamin et al. 2008; Wheeler et al. 2017). Philodromid spiders differ from thomisids in having four pairs of legs of similar length. Accordingly, their method of prey capture is different: they chase their prey in rapid runs.

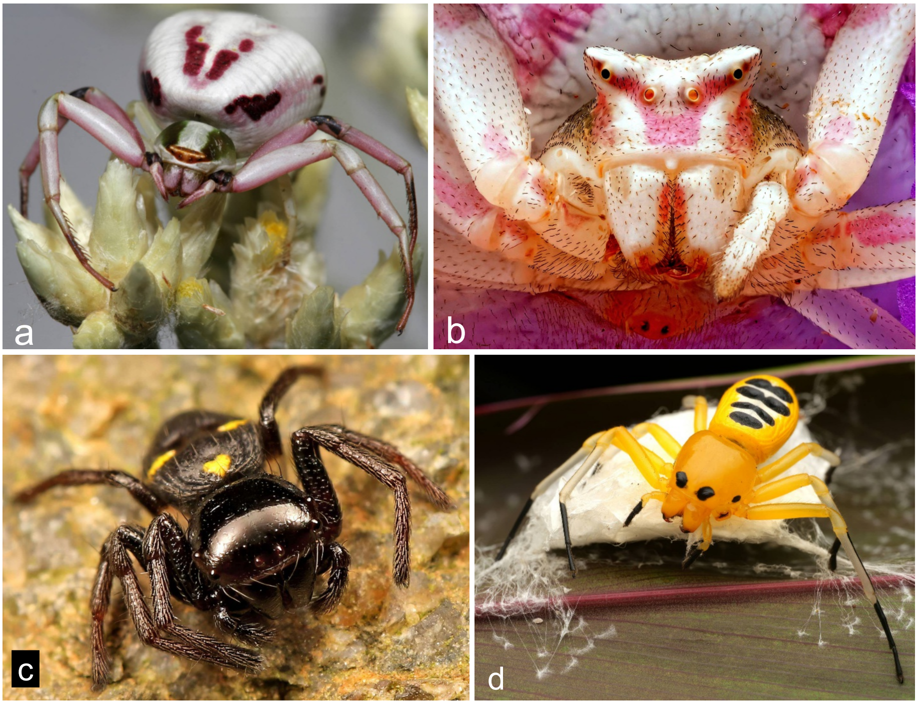

Fig. 1.12 Crab spiders are sit-and-wait predators with over-sized front legs. **(a)** *Misumenoides formosipes*, South Carolina (photo: D. E. Hill). **(b)** *Thomisus onustus*, Germany (© Alexis, CC BY 4.0). **(c)** *Pactactes trimaculatus*, South Africa (© Wynand Uys, CC BY 4.0). **(d)** *Platythomisus* sp., Papua New Guinea.

5. Jumping spiders (Salticidae). These are among the most attractive, if not to say "most congenial" spiders, at least for spider enthusiasts. They are mostly small animals (body length 3-10 mm) with relatively short, strong legs and a cephalothorax that is squared off to form a distinct face at the front. Particularly striking are the four eyes of the front eye row, which span the anterior part of the carapace (Fig. 1.13).

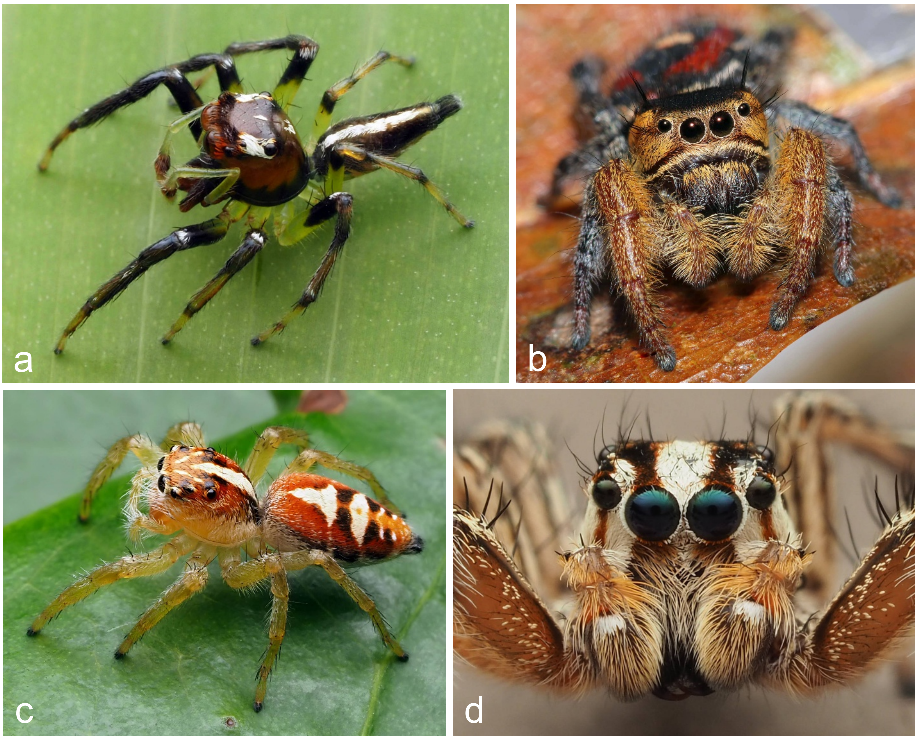

Fig. 1.13 Jumping spiders (Salticidae) can be recognized by their large principal eyes (AME). **(a)** ♂ *Acragas longipalpus*, Belize. **(b)** ♀ *Phidippus cruentus*, Mexico (D. E. Hill). **(c)** ♀ *Frigga pratensis*, Mexico. **(d)** ♂ *Plexippus paykulli*.

Jumping spiders react strongly to visual stimuli, whether it's a passing fly or the approaching finger of an observer. They usually turn to face the object head-on before running closer. These spiders may recognize shapes at a distance of more than 10 cm. This is evident in both hunting behavior and courtship. Even more striking than in wolf spiders, many male jumping spiders have especially colored leg pairs that signal their readiness to mate to the female (Fig. 7.24).

Jumping spiders sneak up on their prey like a cat and even pursue them - then jump on them from a short distance away (Fig. 6.20). Larger jumps (up to 16 cm in some species) may occur when the spider is fleeing. A safety thread is always attached to the substrate before jumping. If the jump leads to nothing, the spider can immediately climb back to the starting point after having fallen a few centimeters.

Jumping spiders are not only diurnal animals but are also particularly fond of sunlight. At night, or during periods of inclement weather, they may retreat into silken nests or shelters. This is also where molting, egg laying, and hibernation take place. Many species in temperate, seasonal climates construct elaborate silk nests in which they overwinter. However, by far the greatest diversity of jumping spiders can be found in the tropics, where many species construct simple nests, often comprised of a single sheet of silk threads deposited under a leaf.

6. Tarantulas (Theraphosidae). These mostly large and hairy spiders occur in the tropics and subtropics (Fig. 1.14). Most live on the ground and hide during the day in their burrows, but some are genuine tree-dwellers. They can inhabit various habitats, from the humid rainforest to dry steppe areas and high mountain regions, e.g. in the Andes, where they occur at over 4700 meters above sea level (Rast & Hüsser 2022, pers. comm.). Virtually all are typical ambush predators that move very little and become active only with the onset of dusk. Only the males undertake extensive wanderings, even in broad daylight.

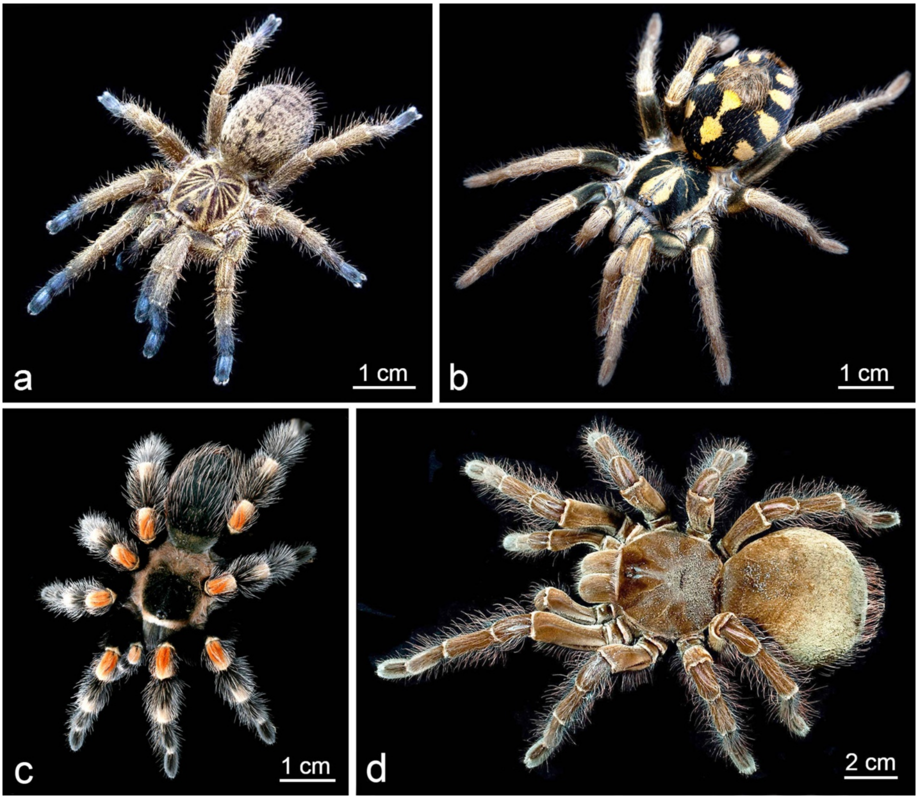

Fig. 1.14 Tarantulas (Theraphosidae). **(a)** *Idiothele mira* or "sp. blue foot", a small ground spider (2-3 cm) from South Africa. **(b)** A somewhat larger ground spider (3-4 cm) from Venezuela. **(c)** *Brachypelma smithi*, the Red Knee tarantula (3- 4 cm) from Mexico, is the most popular pet among tarantula keepers. **(d)** *Theraphosa blondi*, the largest tarantula of all, from South America – with extended legs it may span 30 cm. (Photos: B. Rast)

Typical characteristics of Theraphosidae are the large, nearly parallel, chelicerae (Fig. 1.6a), two pairs of book lungs, leg-like pedipalps, and reduced anterior spinnerets. Probably due to their considerable size, many people believe tarantulas to be particularly dangerous or venomous. However, this is not the case for most species. The bite itself can be quite painful due to the large cheliceral fangs (5-6 mm), but the toxicity is usually harmless, similar to that of a wasp sting. However, in some genera (*Hysterocrates, Poecilotheria*), more caution is advised because their venom can cause strong muscle cramps that can last for days or even weeks (Ezendam 2007; Höfler 1996). Most tarantulas are rather shy and prefer to retreat rather than bite offensively. It is often claimed that South American tarantulas are relatively docile and harmless, while tarantulas from the Old World (Africa, Asia) are more aggressive and therefore more dangerous. In fact, it seems that African tarantulas simply assume a defensive posture more quickly than their South American relatives. Tarantula experts therefore prefer to speak of "defensive" tarantulas rather than "aggressive" ones. Many South American tarantulas also have a defense weapon that is lacking in Old World tarantulas: They defend themselves with *urticating* hairs that they brush off their abdomen when threatened (Fig. 4.6). These tiny, barbed hairs are prickly and can penetrate deeply into the skin, causing intense itching. It gets even more unpleasant if they get into the eyes or respiratory tract, where they can cause inflammation and allergies.

Tarantulas can live surprisingly long, up to 25 years in females. Males, on the other hand, live only a few years (2-10). A peculiarity of tarantulas is that they can molt even after reaching adulthood, in contrast to most other spiders. This is the rule for females, while it is more of an exception for males. Another peculiarity of tarantulas has proven to be a misconception: a few years ago, it was claimed that tarantulas could produce silk threads with their feet (tarsi), allowing them to attach themselves to vertical, smooth surfaces, like glass (Gorb et al. 2006; Rind et al. 2011). Morphological and behavioral studies have since shown that this is not the case, as the alleged spinning organs turned out to be contact chemoreceptors (Foelix et al. 2011, 2012c, 2013b; Pérez-Miles et al. 2009, 2012).

Tarantulas play an important role in basic research, as their size provides relatively large amounts of venom or hemolymph (blood). Toxicologists have now investigated over 60 different tarantula venoms (Bode et al. 2001; Escoubas & Rash 2004). Pharmacologists are interested in the antimicrobial peptides in spider blood, which inhibit the growth of bacteria and fungi (Lorenzini et al. 2003).

Many people are afraid of tarantulas or at least find them creepy. However, some find them fascinating and keep hundreds of them as pets in terraria at home. As a great tarantula expert rightly noted over 60 years ago: "*To anyone who has learned to know this spider, it is as handsome as a goldfinch, and fully as interesting*" (Baerg 1958). Many tarantulas are extremely colorful and the blue iridescent species, in particular, are highly priced among tarantula keepers (Fig. 2.38). Interestingly, the color pattern can vary greatly between juvenile and adult tarantulas, even within the same species (Fig. 1.15).

Fig. 1.15 Some tarantulas may look quite different during juvenile stages and in the adult stage. **(a)** A young *Chromatopelma cyaneopubescens* from Venezuela with orange legs, yellow prosoma and a black and red pattern on the abdomen. **(b)** In the adult stage (6-7 cm). The legs and prosoma are bright blue, the abdomen red and orange. (Photos: B. Rast)

7. ***Other spiders.*** The Antrodiaetidae (Fig. 1.16a) is one of five families of basal or *atypoid* mygalomorphs, living in burrows much like the primitive Mesothelae. Uloborids (Fig. 1.16b) are cribellate web spiders, but are more closely related to the wolf spiders and jumping spiders than they are to the more primitive cribellates (e.g., hypochilids, filistatids).

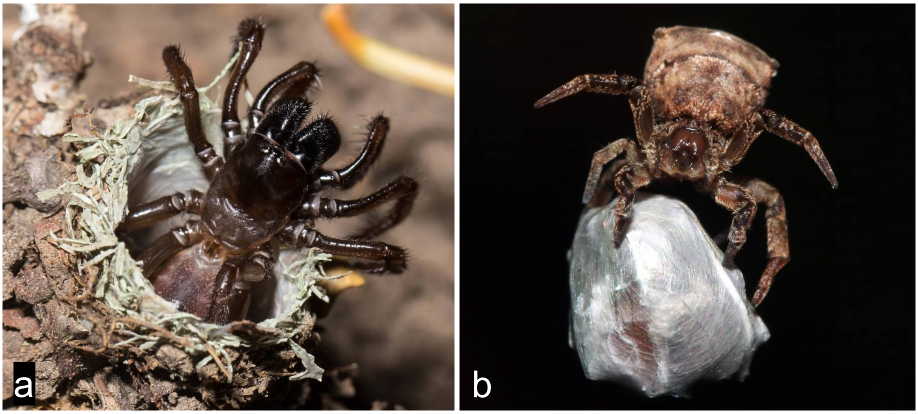

Fig. 1.16 (a) Folding trapdoor spider (Antrodiaetidae: *Atypoides riversi*), California (© Ken-ichi Ue da, CC BY 4.0). **(b)** Triangle spider (Uloboridae: *Hyptiotes* sp.) with prey, South Carolina (© D. E. Hill, CC BY 4.0).

Representatives of several other large spider families are shown in Fig. 1.17. Cellar spiders (Pholcidae) and cobweb spiders (Theridiidae) are most often encountered in temperate regions, with many species living in and around houses and other buildings. The sheetweb weavers (Linyphiidae) are small, but often abundant in Holarctic grasslands and prairies. In tropical or subtropical regions, the large, freeliving huntsman spiders (Sparassidae) are commonly encountered, often on walls or tree trunks. Ground spiders (Gnaphosidae) do not make webs, but run very quickly in pursuit of their prey. Corinnid sac spiders were once included in the Clubionidae. The are small to medium sized running spiders, often found in leaf litter.

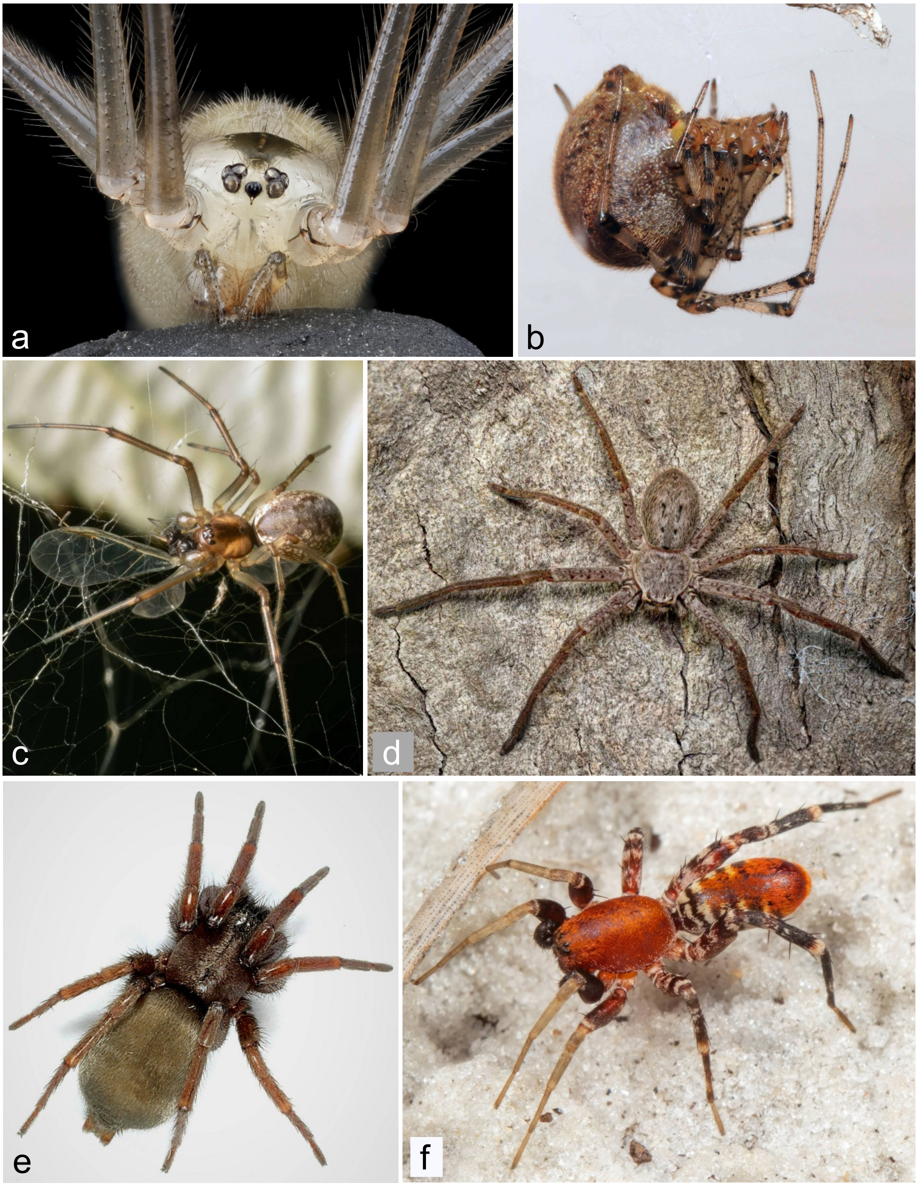

Fig. 1.17 Representatives of other large spider families. **(a)** Cellar spider (Pholcidae: *Pholcus phalangioides*), Maryland. **(b)** Cobweb spider (Theridiidae: *Parasteatoda tepidariorum*), South Carolina (D. E. Hill). **(c)** Sheetweb weaver (Linyphiidae: *Neriene peltata*), Sweden. **(d)** Huntsman (Sparassidae: *Isopedella leai*), South Australia. **(e)** Mouse spider (Gnaphosidae: *Scotophaeus blackwalli*), England. **(f)** Corinnid sac spider (Corinnidae: *Castianeira amoena*), Florida.

2 *Functional Anatomy*

2.1 Segmentation

Although their bodies are markedly divided between a *prosoma* (cephalothorax) and *opisthosoma* (abdomen), spiders have generally retained the body segmentation of their chelicerate ancestors (Hill 2024), summarized here in Table 2.1. For example, the gonopore is always found on the venter of segment O2 (Dunlop & Lamsdell 2017).

Table 2.1 Segmentation of the spider body, compared to that of an insect (D. E. Hill, after Damen 2002; Schaeper et al. 2010; Sharma et al. 2014; Dunlop & Lamsdell 2017; Janssen & Pechmann 2023). Only the ocular segment (Oc) or *acron* is preoral. The narrow pedicel (O1) connects the prosoma to the rest of the opisthosoma. The spider *carapace* is a single structure that covers the entire prosoma. Some writers refer to segments by their *number*, from front to rear, others by a standard abbreviation (*abbr.*). *Corresponding* (or homologous) segments are identified by the regulatory genes that control the partitioning of segments during development.

spiders (Araneae)				***insects (Insecta)***	
body division	**segment number**	**abbr.**	**description or attached appendages**	**corresponding segment**	**body division**
prosoma	0	Oc	ocular or *acron*, all preoral structures including eyes	Oc (ancient, dates back to early protostomes)	**head**
	1	Ch	chelicerae, with base and fang	Ant, antenna	
	2	Pp	pedipalps, with coxal endites	Int, intercalary, second antenna (absent)	
	3	L1	legs 1	Ma, mandibles	
	4	L2	legs 2	Mx, maxilla, maxillary palp	
	5	L3	legs 3	La, labium, labial palp	
	6	L4	legs 4	T1, prothorax with legs 1	**thorax**
opisthosoma	7	O1	pedicel	T2, mesothorax with legs 2, forewings	
	8	O2	first pair of book lungs, gonopore	T3, metathorax with legs 3, hindwings	
	9	O3	second pair of book lungs or tracheal spiracle	A1-A8 or more, abdomen, A2 forms the petiole of Hymenoptera	**abdomen**
	10	O4	anterior spinnerets		
	11	O5	posterior spinnerets		
	12-16	O6-10	segments evident only in Mesothelae and embryos		
	17	011		Tel, telson, anus	
	18	012	anal tubercle		

2.2 Prosoma

2.2.1 Carapace. The dorsal shield (*carapace*) of the prosoma often shows a distinct depression in the median line. This is a keel-like indentation (*apodeme*) of the exoskeleton, which serves as an attachment site for the dorsal muscles of the

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underlying sucking stomach. Two flat grooves diverge forward from this indentation, dividing the carapace into an anterior *head section* and a posterior *thoracic section*. In addition, when viewed from above, less distinct radial grooves may be present (Fig. 2.1). However, it is doubtful whether these grooves indicate the former segment boundaries of the prosoma. It is assumed that the prosoma originated from the fusion of about seven segments: one anterior segment or *acron* (0) with no external appendages, and six posterior segments (corresponding to *somites* I-VI), each bearing one pair of appendages (Dunlop & Lamsdell 2017).

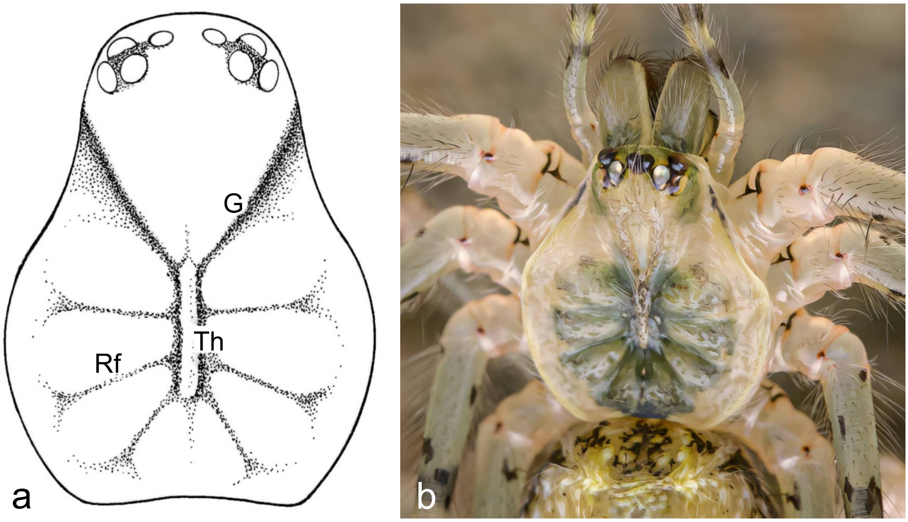

Fig. 2.1 **(a)** Carapace of the "primitive" spider *Hypochilus*, dorsal view. Two grooves (G) extend from the thoracic furrow (Th), separating the carapace into a "head" and a "thoracic" portion. The latter is further subdivided by radial furrows (Rf). **(b)** Dorsal view of carapace, ♂ *H. bernardino* (photo: Marshall Hedin).

The head section of the carapace carries the eyes and chelicerae. Most spiders have eight eyes, which are arranged in a characteristic way in each family (Fig. 2.2). The eyes are aligned in two, rarely three or four, rows one behind the other. Two quite different kinds of eyes are usually present, one pair of primary or anterior medial eyes (AME), and three pairs of secondary or lateral eyes (Fig. 1.4). Based on their relative position on the carapace, the secondary eyes are designated as either anterior lateral eyes (ALE), posterior medial eyes (PME; in jumping spiders these have been better described as mesolateral eyes, or MLE), or posterior lateral eyes (PLE).

Eye arrangement is very important for systematic identification. Based on the position and relative size of the various eyes, one can often immediately recognize the family affiliation. For example, all jumping spiders have a typical row of large front eyes (AME and ALE), with the AME being particularly prominent. Wolf spiders have small, relatively uniform eyes in the front row, but large PME and PLE (Fig. 2.2a). The region between the front row of eyes and the lower edge of the carapace is called the *clypeus* (Figs. 1.3, 1.4).

Having eight eyes certainly denotes the original state. Some spiders have only six eyes, such as the six-eyed spiders (Dysderidae), the recluse spiders (Sicariidae), and some cellar spiders (Pholcidae). In some species, there is even a reduction to four (Theridiidae: *Tetrablemma*) or two eyes (Caponiidae: *Nops*), and in some cave-dwelling forms, the eyes are completely absent (Millot 1949). In certain wolf spiders from Hawaiian caves, only the posterior row of eyes is clearly reduced (*Lycosa howarthi*, Fig. 2.3a), while in others (*Adelocosa anops*), the eyes are completely absent (Fig. 2.3b) (Gertsch 1973; Howarth 1972). Other eyeless spiders (Ctenidae: *Ciba*; Barychelidae: *Trichopelma*) have been reported from caves in various Caribbean islands (Bloom et al. 2014). *Troglobionts* (obligate cave-dwellers) or *troglobiomorphs* (adapted for life in caves) have been identified in 34 spider families (Mammola & Isaia 2017). In the nesticid *Kryptonesticus eremita*, the extent of eye development (retinal pigmentation) can even vary within a local population, depending on distance from a cave entrance (Dresco & Huber 1967).

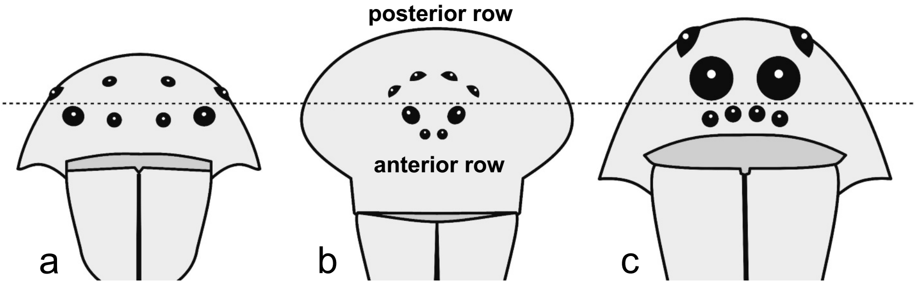

Fig. 2.2 Anterior and posterior eye rows of **(a)** the crab spider *Diaea* (Thomisidae), **(b)** the lynx spider *Peucetia* (Oxyopidae) and **(c)** the wolf spider *Hogna* (Lycosidae), viewed from the front (D. E. Hill). *Diaea* and *Peucetia* have larger anterior lateral eyes, while *Hogna* has large posterior eyes. Each eye row may be curved (e.g., b, anterior eyes, and c, posterior eyes), sometimes described as two separate transverse rows.

Fig. 2.3 Eyes in cave spiders. **(a)** The wolf spider *Lycosa howarthi* from a Hawaiian cave shows a reduction in eye size, especially in the posterior row. **(b)** The wolf spider *Adelocosa anops* (Hawaii) has no eyes at all. (Photos: Foelix & Howarth)

The eyes are often closely paired or slightly raised above the surrounding cuticle, for example, as eye mounds in *Liphistius* (Fig. 2.4a, b) and tarantulas. Occasionally, completely bizarre eye arrangements arise, as in some dwarf spiders (Micryphantidae; Fig. 2.4c), where the eyes are literally sitting on stalks. In addition, male dwarf spiders often have so-called pit or pore fields in the head region, on which glands open. The secretion of these glands has a special function in sexual behavior: It is actively absorbed by the female during mating (*gustatory courtship*) (Blest & Taylor 1977; Schaible et al. 1986).

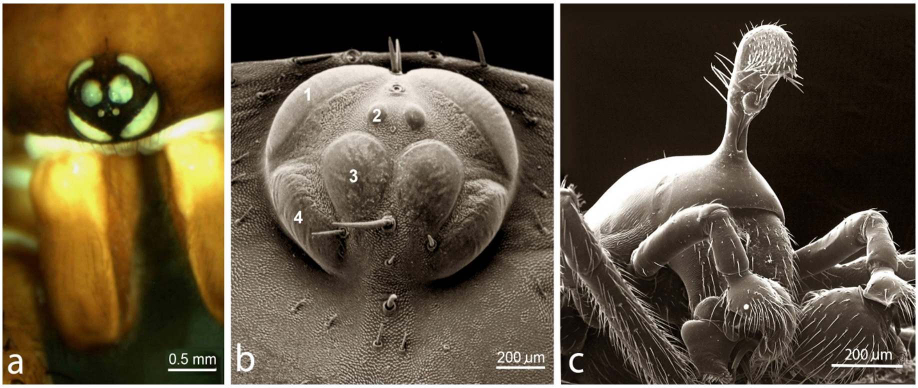

Fig. 2.4 (a, b) Orthognath spiders (like this *Liphistius*) have their eyes close together on a small tubercle. Note the almost panoramic field of vision that results from the arrangement of the four pairs of eyes (1-4). **(c)** Aberrant position of eyes on a stalk of the prosoma in a male dwarf spider (Linyphiidae: *Caracladus*).

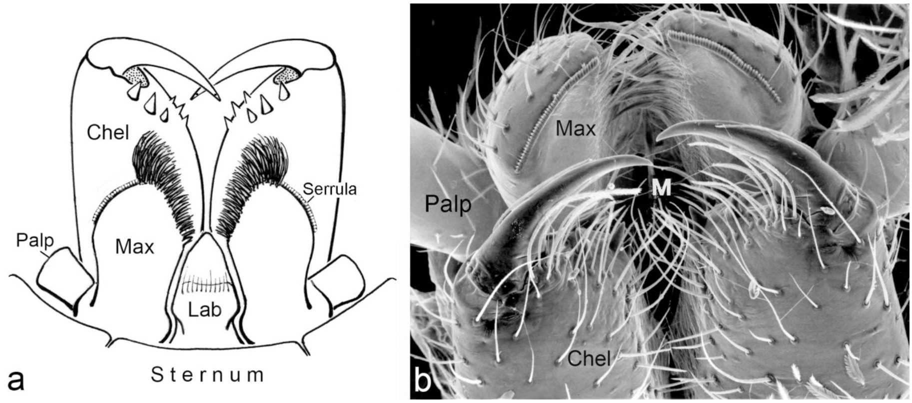

Fig. 2.5 (a) Mouth parts of a wolf spider (*Hogna*) seen from below (after Kaston 1972). Chel = chelicera, Lab = labium, Max = maxilla (or *endite*). **(b)** Mouth parts of a jumping spider (*Portia*) seen from the front. The small mouth opening (M) is located between the two maxillae; note the toothed edges (serrulae) on the maxillae.

2.2.2 Sternum. The single ventral plate, or *sternum* (Fig. 1.3b), develops in the embryo from the fusion of a series of *sternite primordia*; they arise from segments corresponding to the pedipalps and walking legs (Wolff & Hilbrant 2011). In very young spiders, at least four of these sternites may sometimes be recognized, separated by fine grooves. The evolutionary origin of the spider sternum is not known (Huber & Haug 2021). A median plate, the *labium*, which is usually movably separated by a membrane, adjoins the sternum anteriorly (Fig. 2.5a). Sternum and carapace are relatively rigid parts of the prosomal exoskeleton, but can be moved against each other due to the connecting soft *pleura* (Fig. 1.3, dotted areas).

2.2.3 Chelicerae. The chelicerae are the first pair of appendages on the prosoma. In the embryo, they are initially positioned behind the mouth (Fig. 8.4b), but during development, they move to the front of the mouth, like the antennae of other arthropods. The chelicerae always consist of two segments: a massive basal segment (*paturon*) and a movable *fang* that is articulated to it, near the tip of which opens a venom canal (Fig. 2.6). The terminal fang is normally folded like a blade of a pocket knife into a groove (*fang groove*) of the basal segment. When biting, the two fangs move out of this groove and are thrust into the prey, injecting venom at the same time. The actual venom opening is never at the fang tip, as in a pipette, but always just before it, as in a syringe needle. This is not only mechanically more stable but also prevents the venom opening from becoming clogged during penetration of the prey. It is noteworthy that this same technically optimal solution occurs in very different animals, such as the stinger of scorpions and the venomous fangs of snakes (Fig. 2.7).

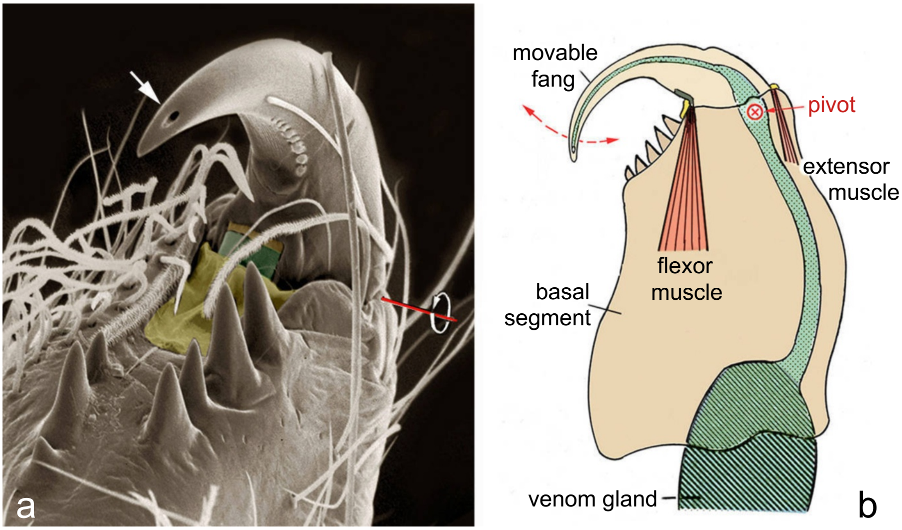

Fig. 2.6 (a) The movable cheliceral fang normally rests between the cheliceral teeth of the basal segment (*paturon*). Note the serrated edge of the fang and the opening of the venom duct (arrow) (*Cupiennius*). The articulating membrane of the cheliceral fang is marked in yellow, the sclerite of the flexor muscle in green. **(b)** Schematic drawing of a chelicera. Arrows indicate the movements of the fang, caused by the action of the flexor and the extensor muscle. (After Millot 1949 and Foelix et al. 2005)

In most spiders the venom opening lies on the backside of the fang (*retrograde*) and only rarely in front (*anterograde*). In some spiders (e.g. in tarantulas and Mesothelae) the venom opening takes up a middle position (*ventral*) and therefore cannot be seen from in front or from the back. This has led to the erroneus belief that *Liphistius* fangs lack venom openings (Haupt 2003) and that Mesothelae in general had no venom glands. However, those venom openings are clearly present when