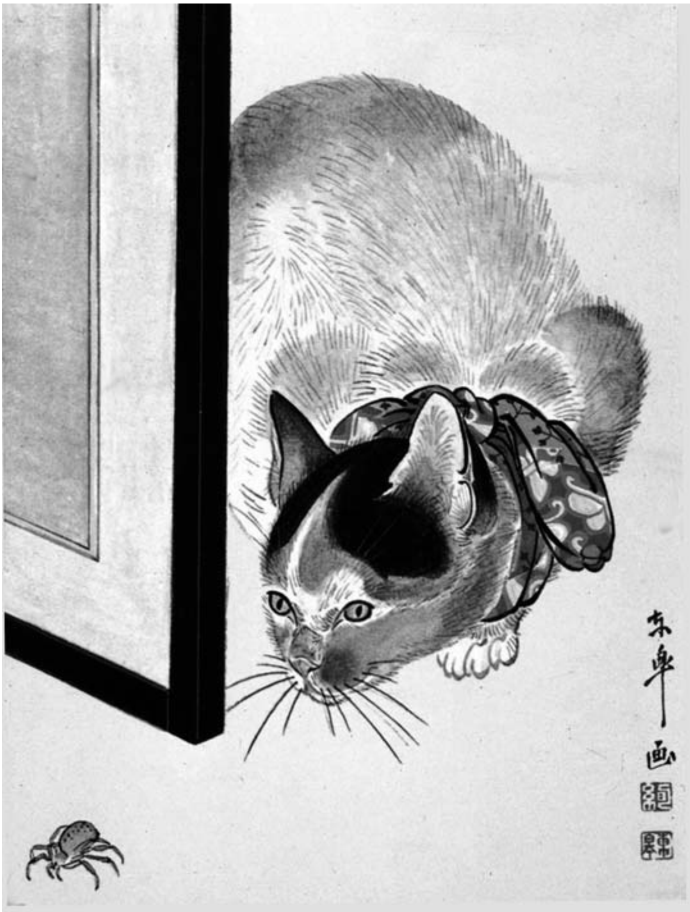
BIOLOGY OF SPIDERS

third edition

RAINER F. FOELIX

Biology of

SPIDERS



It is hoped that the reader approaches the subject of spiders with as much curiosity as this cat in this Japanese silk painting. Curiosity does not necessarily kill the cat—nor the spider. (“Cat and Spider” by Oide Makoto, 1836–1905; The Metropolitan Museum of Art, New York.)

RAINER F. FOELIX

Biology of
SPIDERS

Third Edition

OXFORD
UNIVERSITY PRESS

2011

OXFORD
UNIVERSITY PRESS

Oxford University Press
Oxford University Press, Inc., publishes works that further
Oxford University's objective of excellence
in research, scholarship, and education.

Oxford New York
Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto

With offices in
Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam

Published by Oxford University Press, Inc.
198 Madison Avenue, New York, New York 10016
www.oup.com

Library of Congress Cataloging-in-Publication Data

Foelix, Rainer F., 1943–
[Biologie der Spinnen. English]
Biology of spiders / Rainer F. Foelix. — 3rd ed.
p. cm.
ISBN 978-0-19-973482-5 (pbk.) 1. Spiders. I. Title.
QL458.4.F6313 2010
595.4'4–dc22 2010009511

1 3 5 7 9 8 6 4 2
Printed in the United States of America
on acid-free paper

Contents

Preface

It is now exactly 30 years that *Biology of Spiders* was first published, and I never expected nor planned to follow up with any further editions. When the science editor of Oxford University Press asked me last year whether I would prepare a third edition, I had at first strong reservations because I knew vaguely how much work would be in stock for me: 12 years had passed since the second edition, and literally thousands of articles about spiders had been published during that time. I took up the challenge anyway and subsequently spent an entire year working exclusively on this new edition. Going through the enormous amount of spider literature was only possible through the internet, rapid information exchange by e-mail, and the support of kind colleagues who sent me with their latest spider publications. Including the major results of arachnological research of the past decade, it was thus possible to update all ten chapters. This is not to say that it is a complete revision—of course, there will be omissions, deliberate and unconscious ones. My goal was always to provide a readable book on the biology of spiders, not an encyclopedia. The fact that this new edition nevertheless contains more than 500 new references gives some idea of how much of the recent literature has been incorporated.

Particular attention was paid to the illustrations. Since all the former drawings and photographs had to be scanned anew, this provided a good opportunity to improve and to correct any flaws in the 200 illustrations of the last edition. Almost 100 new pictures have been added to the present edition, often originals that were taken specifically for this book. Many unique photographs were contributed by fellow arachnologists, to whom I am most grateful.

My thanks go to the following colleagues for their help and support: Friedrich Barth, Jon Coddington, Paula Cushing, Bill Eberhard, Bruno Erb, Cheryl Hayashi, David Hill, Martin Huber, Yael Lubin, Peter Michalik, Wolfgang Nentwig, Martin

Nyffeler, Brent Opell, Bastian Rast, Robert Raven, Jerome Rovner, David Schürch, Karin Schütt, Paul Selden, Robert Suter, Rolf Thieleczek, George Uetz, Benno Wullschleger, and Samuel Zschokke. I also wish to express my gratitude to the following institutions: The Naturama Aargau for use of their computer and graphics facilities, the Neue Kantonsschule Aarau for letting me work on their electron microscopes, and the Smithsonian Institution in Washington, DC, for allowing access to the scientific literature. Finally, I´d like to thank my editor Phyllis Cohen and her colleagues Lisa Stallings, Karla Pace, and Jennifer Kowing at Oxford University Press and Anindita Sengupta at Glyph International for transforming my manuscript into an attractive book.

R. F. F.
Aarau
January 2010

Biology of
SPIDERS

An Introduction to Spiders

1

Most people dislike spiders. And, usually, they know very little about them. This lack of knowledge is also apparent when it comes to illustrations of spiders, which commonly look more like caricatures than real spiders. For instance, if we look at early illustrations, the only feature that is depicted correctly is the number of legs (fig. 1.1a). This rendering improved somewhat in the later Middle Ages, when naturalists developed a deeper interest in insects and spiders and started to look at them more closely (fig. 1.1b). What is typical for spiders, what makes them different from other arthropods, and why are they actually quite interesting? This first chapter provides a brief but concise introduction to spiders and their biology.

Spiders are distributed all over the world and have conquered all ecological environments, with perhaps the exception of the air and the open sea. Most spiders are relatively small (2–10 mm body length), yet some large tarantulas may reach a body length of 80–90 mm. Male spiders are almost always smaller and have a shorter life span than females.

All spiders are carnivorous. Many are specialized as snare builders (web spiders), whereas others hunt their victims (ground spiders or wandering spiders). Insects constitute the major source of prey for spiders, but certain other arthropods are often consumed as well.

A spider's body consists of two main parts: an anterior portion, the *prosoma* (or cephalothorax), and a posterior part, the *opisthosoma* (or abdomen). These are connected by a narrow stalk, the *pedicel* (fig. 1.2). The prosoma's functions are mainly for locomotion, food uptake, and nervous integration (as the site of the central nervous system). In contrast, the opisthosoma fulfills chiefly vegetative tasks: digestion, circulation, respiration, excretion, reproduction, and silk production.

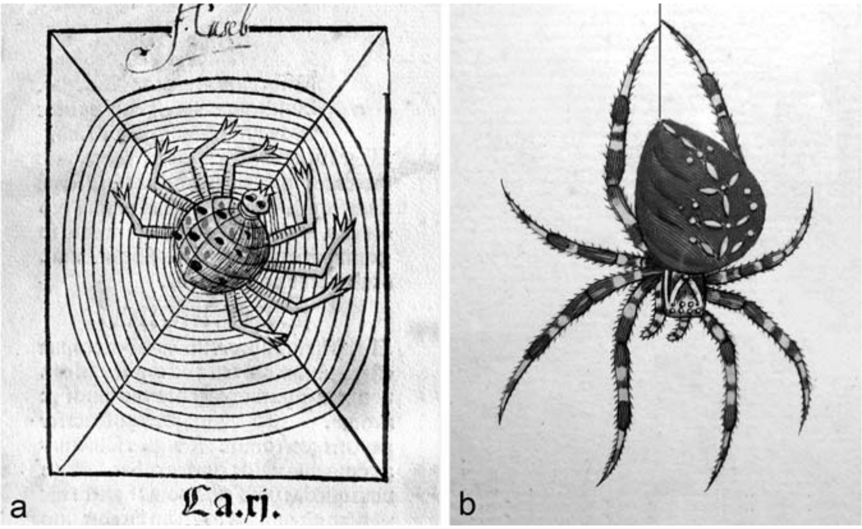


Figure 1.1
(*a*) In medieval times spiders were depicted rather crudely and anthropomorphic. Of all the typical spider features only the number of legs is correctly shown in this wood-cut from 1491 (*Hortis Sanitatis*; Mainz, Germany). (*b*) In contrast, all main characters of a spider are correctly pictured in this copperplate engraving of a garden spider: eight legs, eight eyes, two body parts, and most important, silk producing spinnerets (Rösel von Rosenhof, 1761).

The prosoma is covered by a dorsal and a ventral plate, the carapace and the sternum, respectively. It serves as the place of attachment for six pairs of extremities: one pair of biting chelicerae and one pair of leglike pedipalps are situated in front of four pairs of walking legs. In mature male spiders the pedipalps are modified into copulatory organs—a quite extraordinary feature, not found in any other arthropod. The opisthosoma is usually unsegmented, except in some spiders considered to have evolved from ancient species (Mesothelae). In contrast to the firm prosoma, the abdomen is rather soft and sacklike; it carries the spinnerets on its posterior end.

A Sketch of Spider Systematics

At present taxonomists recognize about 40,000 spider species, which they group into 110 families (Platnick, 2009). How this diversity should be arranged into a "natural" system of classification is still very much a matter of controversy. This is best illustrated by the fact that about 20 different spider classifications have been proposed since 1900.

The order of spiders, Araneae, is usually divided into three suborders, the Mesothelae, the Mygalomorphae, and the Araneomorphae. Until recently the Mygalomorphae were referred to as Orthognatha because of the nearly parallel

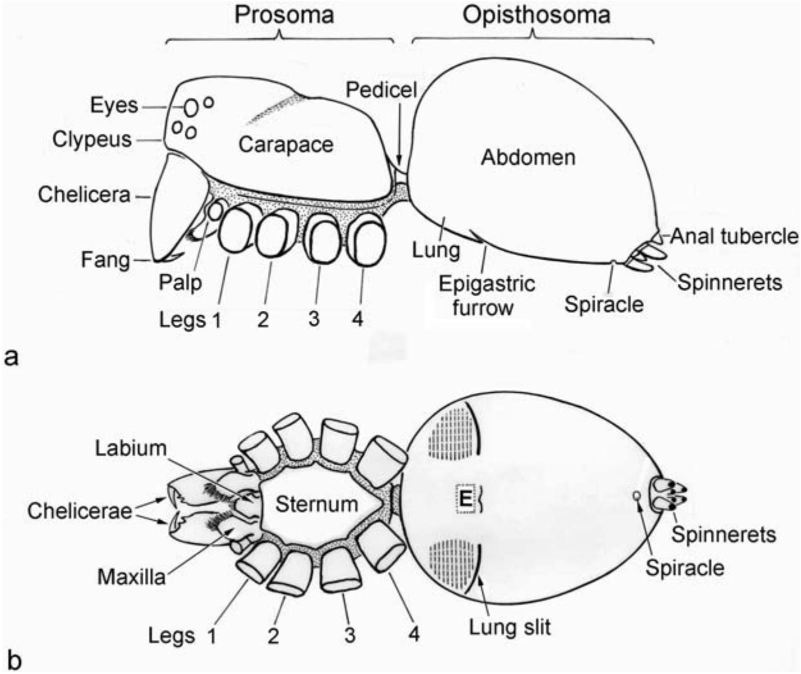


Figure 1.2
External appearance of a spider´s body: (*a*) side view, (*b*) ventral view. E = epigynum (in adult females).

alignment of their chelicerae, while the Araneomorphae correspond to the former Labidognatha, which possess vertical chelicerae opposing each other (fig. 1.3). The Mesothelae represent the phylogenetically oldest spiders because they exhibit a clearly segmented abdomen, as well as several other "primitive" characters. The Mygalomorphae comprise all the tarantulas; their chelicerae lie almost parallel to each other (fig. 1.4), and their spinnerets are often reduced. More than 90% of all spiders belong to the Araneomorphae (Labidognatha). Their classification into higher taxa is still problematic. Formerly, one classification separated the Cribellatae from the Ecribellatae, based on the presence of a spinning plate (*cribellum*) situated in front of the spinnerets as the distinguishing character of the Cribellatae. All Araneomorphae without such a cribellum were grouped together as Ecribellatae. Nowadays it is generally assumed that all spiders were originally cribellate, and that the ecribellate spiders evolved later by a reduction or loss of the cribellum. However, several aspects remain unclear, such as possible parallel evolutions (convergences) among cribellate and ecribellate spiders. This "cribellate problem" will be discussed briefly in chapter 10.

Among the Ecribellatae, some spider families with simple genital structures (the so-called Haplogynae) were separated from those with complex genital structures, the Entelegynae (fig. 1.5). This classification dates back to Eugène

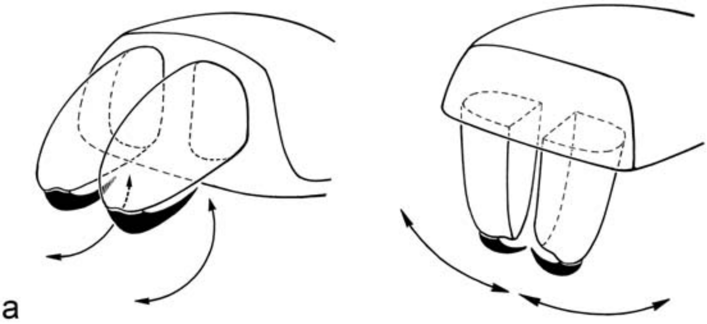


Figure 1.3
Movement of the chelicerae in orthognath (*a*) and labidognath spiders (*b*). (After Kaestner, 1969.)

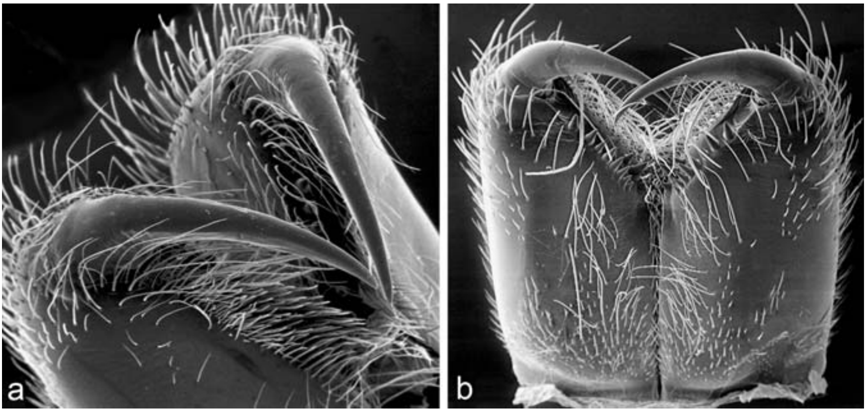


Figure 1.4
(*a*) Orthognath chelicerae (*Brachypelma*, ventral view), having a roughly parallel alignment. (*b*) labidognath chelicerae (*Tegenaria*, posterior view), opposing each other.

Simon's "Histoire Naturelle des Araignées" (1892–1903). Over the past years, however, several arachnologists have voiced the opinion that the Haplogynae are not really a homogenous group (Brignoli, 1975; Lehtinen, 1975; Platnick, 1975; Platnick et al., 1991). Some haplogynes have quite complex genital structures (Burger et al., 2006a, b), and some haplogynes seem to be secondarily reduced entelegynes. Despite all these arguments, there are still some families that represent "classical" haplogyne spiders, such as the Scytotidae, the Pholcidae, and the Dysderidae.

Following Simon's classification, the Entelegynae were further divided into Dionycha and Trionycha, depending on whether the legs have two or three tarsal claws (fig. 1.6). Although this subdivision also became questionable, there is again some justification to maintain at least some classical Dionycha, such as the Salticidae, the Clubionidae, and the Thomisidae.

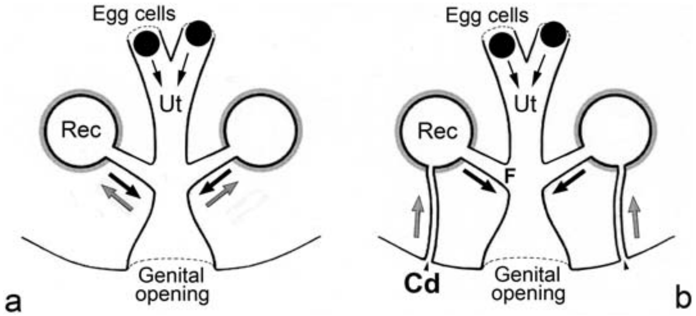


Figure 1.5
Comparison of the female reproductive tracts in (*a*) *haplogyne*, and (*b*) *entelegyne* spiders. Gray arrows indicate the direction of sperm transfer into the spermathecae (Rec), black arrows denote the sperm transfer toward the egg cells prior to fertilization. Cd = copulatory ducts, F = fertilization duct, Ut = Uterus. (After Uhl et al., 2009.)

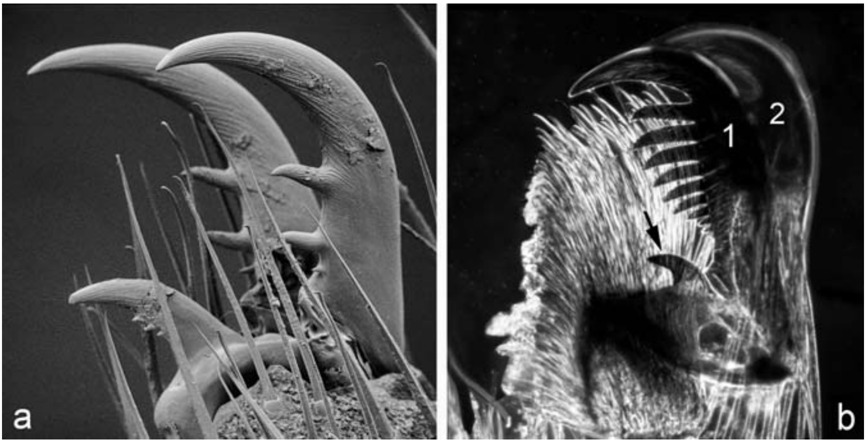


Figure 1.6
(*a*) Ancient spiders probably had three tarsal claws on each leg, as seen here in the "primitive" spider *Liphistius*. (*b*) In some spider families, the *Dionycha*, the middle claw was supposedly lost. However, a reduced middle claw (arrow) is often still present, like in this tarsus of a young jumping spider. The two main claws (1, 2) are serrated like a comb.

Since the following text will often refer to certain spider families, the main families and their systematic position are listed below (for more details of modern spider systematics, see chapter 10).

Order Araneae

1. Suborder Mesothelae (1 family)
   Family Liphistiidae (85 species)
2. Suborder Mygalomorphae (Orthognatha) (15 families)
   Family Atypidae (45 species)
   Ctenizidae (120 species)
   Dipluridae (180 species)
   Theraphosidae (900 species)
3. Suborder Araneomorphae (Labidognatha) (90 families)
   Family Dysderidae (560 species)
   Pholcidae (1000 species)
   Scytotidae (220 species)
   Amaurobiidae (750 species)
   Dictynidae (550 species)
   Eresidae (100 species)
   Clubionidae (560 species)
   Gnaphosidae (2100 species)
   Salticidae (5200 species)
   Thomisidae (2100 species)
   Lycosidae (2350 species)
   Pisauridae (340 species)
   Oxyopidae (420 species)
   Agelenidae (500 species)
   Araneidae (3000 species)
   Linyphiidae (4300 species)
   Theridiidae (2300 species)
   Uloboridae (260 species)

To familiarize the uninitiated reader with this seemingly abstract system, the following natural history of some spider families will serve as an introduction.

Funnel-web Spiders (Agelenidae)

Funnel-web spiders are familiar to most of us. In European houses, for example, we usually find *Tegenaria* in the bathroom, often trapped in the tub, where it cannot scale the smooth walls. Aside from its considerable size (10 mm body length), *Tegenaria* is quite conspicuous because of its long, hairy legs (12–18 mm) and the two long spinnerets protruding from its abdomen (fig. 1.7). Outdoors we can readily find the somewhat smaller *Agelena* in short grass or low bushes. The sheet webs of agelenids usually cover vegetation or bridge the corners of buildings. The flat web narrows like a funnel on one end, forming a small silken tube. This retreat is open

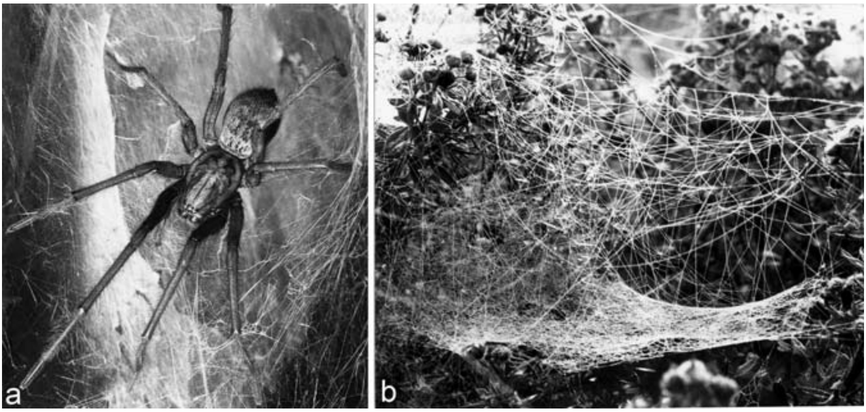


Figure 1.7
(*a*) Juvenile house spider (*Tegenaria*) sitting at the entrance of her retreat. (*b*) Agelenid funnel web, covered with early morning dew. (Photo: Paas.)

on both ends, and most of the time the spider sits there in ambush, its outstretched front legs poised to receive vibrations from the web. When an insect blunders onto the web, the spider quickly darts out from its hideout, bites the victim, and carries it back. The actual feeding process always takes place inside the retreat. During the return to the tube the spider shows remarkably good orientation. For this reason funnel-web spiders have been a favorite subject for sensory physiologists (see chapter 4).

The water spider *Argyroneta aquatica* was long considered to be a member of the agelenid family, but is now placed in its own family (Argyronetidae). It is the only spider that lives constantly under water. Rather than build a web, it attaches an air bubble to a water plant and uses it as a residence. It hunts mostly fly larvae or small crustaceans, which it catches while swimming about freely under water. To eat the prey the spider must return to its diving bell. The abdomen of the water spider is always encased in a shiny air bubble, and this silvery reflection has earned it the scientific name *Argyroneta* (Greek, *argyros* = silver). From time to time the air bag is replenished at the water surface. Thus the respiration of a water spider does not differ in principle from that of its land-living relatives.

Orb-Web Spiders (Araneidae)

The most impressive web design belongs to the orb weavers. The orb web of the common garden spider certainly represents the best-known type of all webs (figs. 5.23, 5.25). The spider either sits right in the center of the web or hides in a retreat outside of it. Insects flying into the web become stuck to the sticky threads long enough for the spider to rush out from the hub to bite or wrap its victim. Araneids are among the most successful spider families, as the enormous diversity of their species (3000) testifies. Thus it comes as no surprise to find that there are hundreds of structural variations on the orb-web design as well. Some examples are given in chapter 5. The body structures of araneids also varies considerably; most notable are the tropical orb weavers, which can be very colorful and exotically shaped (fig. 1.8).

An orb web is typical not only of the Araneidae but also of two other spider families, the Tetragnathidae and the Uloboridae. Uloborids build an orb web that is very similar to the webs of the araneids, but that differs from them in one important aspect: the catching threads are not studded with glue droplets but are decorated instead with an extremely fine mesh of cribellate silk ("hackle band"; fig. 5.18).

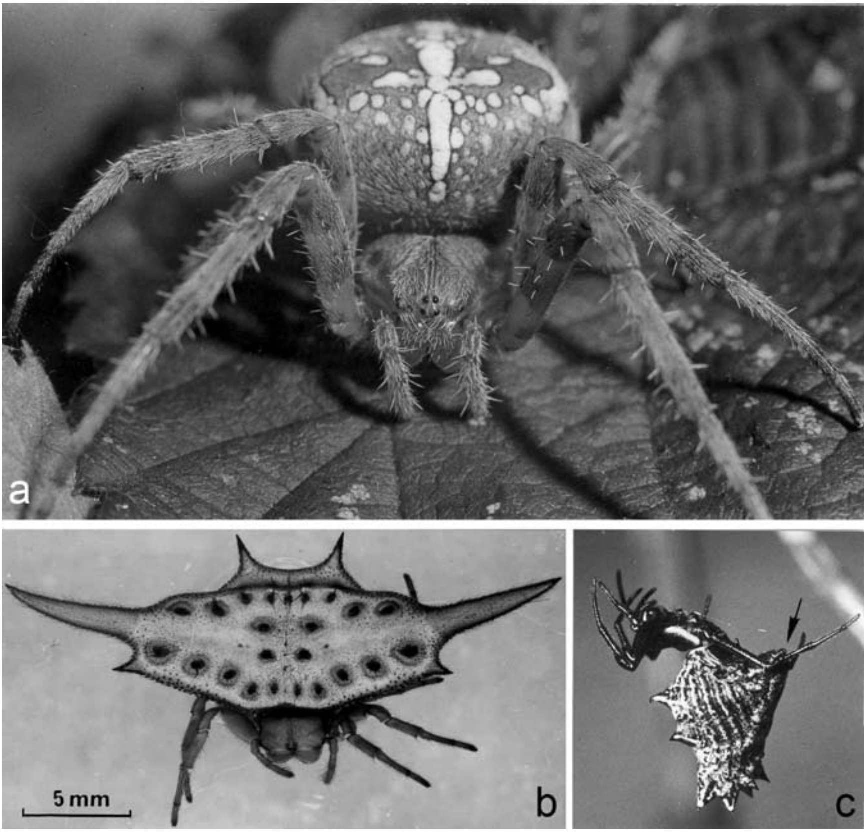


Figure 1.8
Orb web spiders. (*a*) The best known of all orb weavers, the garden spider *Araneus diadematus* (Photo: Grocki and Foelix.) (*b*) This *Gasteracantha versicolor* from Madagascar is armored with long spines on its hard abdomen (Photo: Emerit.) (*c*) A North American orb weaver, *Micrathena gracilis*, hanging on a horizontal thread. Note the position of the spinnerets (arrow).

Wolf Spiders (Lycosidae)

Wolf spiders are vagabonds that lie in ambush or freely hunt their prey. They are best recognized by their characteristic eye arrangement of four uniformly small eyes in the anterior row of eyes and two large median eyes in the posterior row (fig. 2.2). About 2300 different species occur all over the world, and they vary quite a bit in size. Smaller wolf spiders (4–10 mm body length) roam freely among stones or low vegetation; only the larger representatives (*Arctosa*, *Trochosa*, *Alopecosa*; 10–20 mm) dig burrows. Certain species live close to the water and can even walk on its surface (fig. 6.11). Members of the aptly named genus *Pirata* hunt insects on the water surface, or even dive after tadpoles or small fish (Gettmann, 1978). A few species of wolf spiders (*Aulonia*, *Hippasa*, *Sosippus*, *Aglaoctenus*), thought to be more primitive varieties, build webs reminiscent of the sheet webs of agelenids (Brady, 1962, 2007; Job, 1968, 1974).

The most famous wolf spider is certainly the Mediterranean tarantula (the name being derived from the Italian town of Taranto). True tarantulas (*Lycosa*, *Hogna*) can reach an impressive 30 mm of body length (fig. 1.9), but they are not related to the big tropical “tarantulas,” the mygalomorphs, also known as bird spiders. Although tarantulas have long had a reputation as dangerous spiders, the ancient fear of their dangerous bite has been proven to be unfounded. Probably any bites alleged to be from a tarantula were in fact inflicted by black widow spiders. Tarantulas live in silk-lined burrows in the soil. Some species even construct a sort of lid to close the tube, creating a burrow similar to that of the trapdoor spiders (Ctenizidae). At night tarantulas leave their burrows to prowl in search of insects. However, wolf spiders generally do not actively run down their prey, as their name might suggest, but sit quietly and wait until a victim happens to come by (Ford, 1978; Stratton, 1985).

Wolf spiders react mainly to vibrations caused by the wing beat or by the characteristic walking pattern of the prey. Visual cues also play a role in detecting prey, but the eyes of wolf spiders perceive only a rather coarse image, and thus only objects close by can serve as visual stimuli. This becomes apparent during courtship, when the dark palps or front legs of the male are waved in a species-specific manner to attract the attention of the female. Female wolf spiders are well known for their brood care. After laying their eggs, they attach the egg case to their spinnerets and carry it around wherever they go (fig. 7.35). Some weeks later, just before the young spiderlings are ready to leave the cocoon, the mother rips the cocoon wall so that the young can emerge. As soon as the spiderlings have crawled out, they clamber onto their mother’s back (figs. 7.35, 7.36). Since there may be more than 100 spiderlings, they huddle in several layers. They ride on their mother’s abdomen for about a week, then gradually disperse and take in food for the first time.

Another group of spiders, the Ctenidae, is often considered as a separate family but could also be classified as a subfamily of the Lycosidae (Homann, 1971). The most notorious ctenid spider is the extremely venomous and aggressive *Phoneutria* (fig. 3.7). A less ferocious ctenid spider, which will be mentioned in many of the following chapters, is *Cupiennius salei* from Central America (fig. 6.17; Barth, 2002).

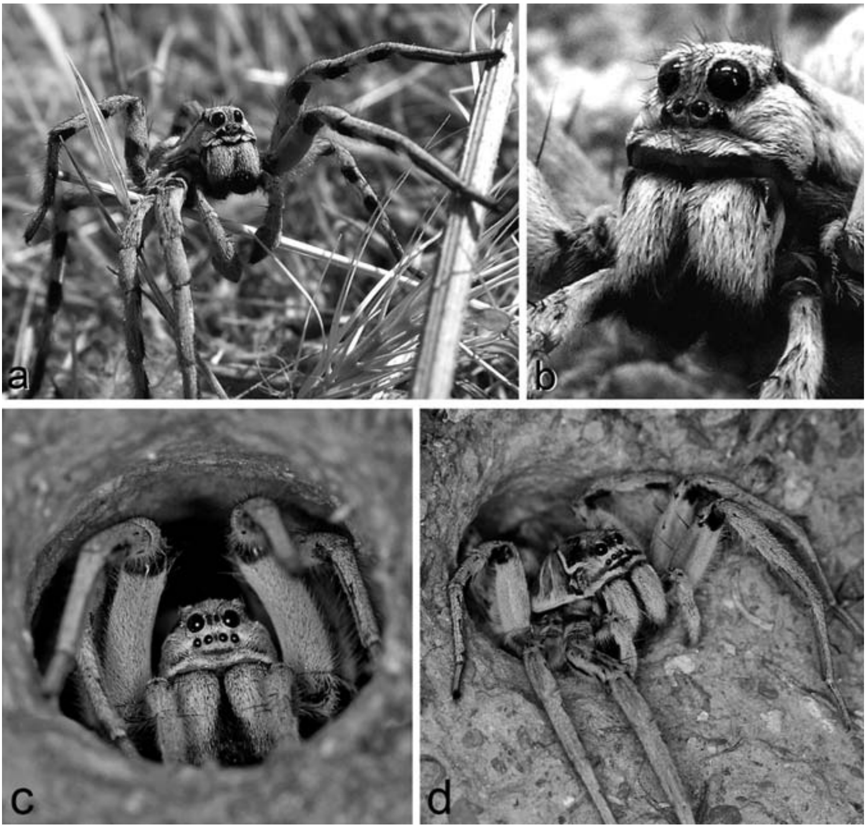


Figure 1.9
Wolf spiders. (*a*) A young male of the famous European tarantula, *Lycosa tarentula.* (*b*) Portrait showing the four small eyes of the front row and the large Posterior Median Eyes (Photos: Ortega-Escobar.) (*c*) The Australian wolf spider *Tasmanicosa* lives in silk-lined tubes in the soil. (*d*) At dusk the spider sits at the entrance of its burrow waiting for prey to pass by. (Photos *c*, *d*: Rast.)

Crab Spiders (Thomisidae)

Crab spiders lie quietly in ambush and do not build webs (fig. 1.10). They sit motionless on leaves or in blossoms where, with attentively outstretched legs, they await landing insects. Their small eyes can produce sharp images only at very short distances, yet they perceive motions as far as 20 cm away (Homann, 1934). If prey comes within reach (0.5–1 cm), it is seized by the spider's strong front legs and then paralyzed by its poisonous bite. Even large insects, such as butterflies or bumblebees, are successfully attacked (fig. 9.5). The victim is sucked out through the tiny

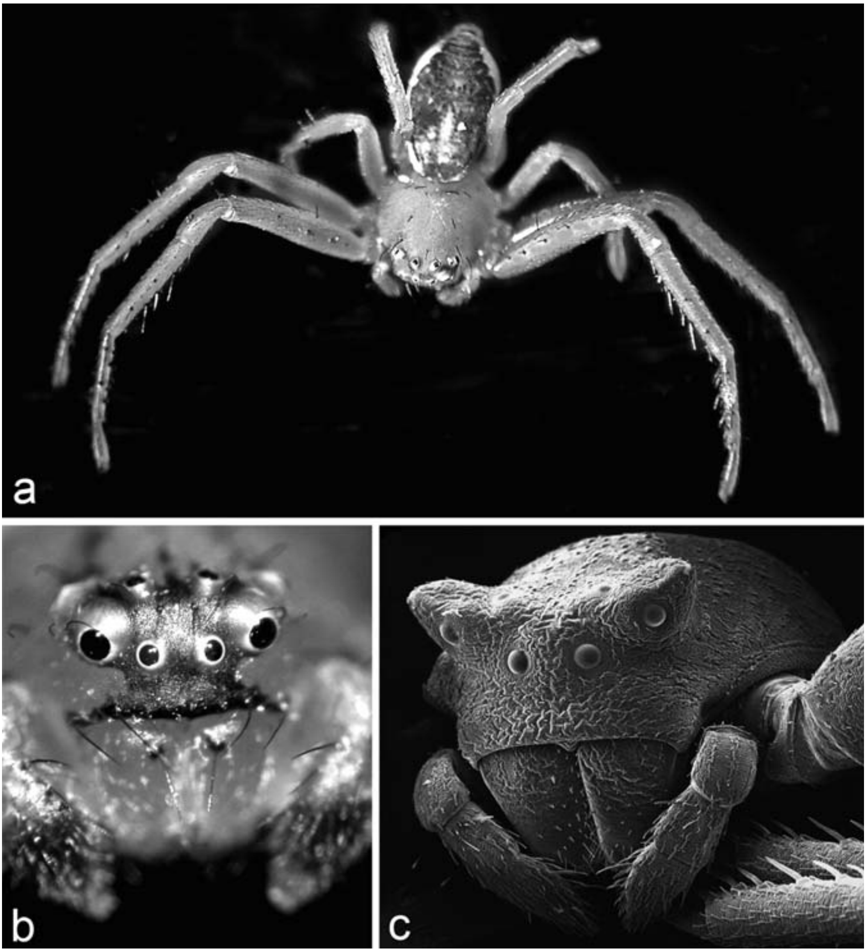


Figure 1.10
Crab spiders. (*a*) A small *Diaea* with the typical "over-sized" front legs that are used for grasping prey. (*b*) Portrait of *Diaea* showing the well developed eyes. (*c*) Portrait of a large *Thomisus* with exotic processes in the head region; also note the strong spines on the front legs. (Photos: Erb and Foelix.)

bite holes (fig. 3.1). Since its exoskeleton remains intact, the victim appears practically unharmed when the spider has finished its meal (Foelix, 1996).

Crab spiders may be very colorful—they are often white, pink, or bright yellow, and some are green. To some degree adult females can adapt their coloration to the background on which they sit. Even the less colorful species are usually well camouflaged and are hard to detect among the vegetation.

The name “crab spider” comes from their ability to walk sideways very adroitly. The family Philodromidae was formerly grouped together with the Thomisidae, although they bear only a superficial resemblance to crab spiders (Homann, 1975). Most notably, their legs are all of equal length, a feature typical of wandering spiders. Also, recent molecular phylogenetic analyses exclude the Philodromidae from the Thomisid family (Benjamin et al., 2008).

Jumping Spiders (Salticidae)

At least for an arachnologist, the “jumpers” are among the most attractive, if not most congenial, spiders. They are all rather small (3–10 mm) with short, stout legs and a square prosoma (fig. 1.11). Most conspicuous are the anterior eyes, which occupy the entire front of the carapace (fig. 4.17). Jumping spiders react very definitely to visual stimuli such as passing insects or the approaching finger of an observer: first they turn to face the object, then they walk closer. They can distinguish different shapes at a distance of less than 10 cm; this limit can be observed while the spider stalks prey and also during courtship. Males often possess conspicuously marked legs, which they use for display toward females (fig. 7.24). The hunting behavior of jumping spiders reminds one of cats: they stalk and pursue their prey until it is close enough for a final pounce. Long jumps up to 16 cm can be seen when a jumping spider flees. Before it jumps, the spider always attaches a safety thread to the ground, so that if it falls off an edge it will simply be held back by the thread and can quickly climb back the few centimeters to the point of takeoff (fig. 6.8).

Jumping spiders are most active during the day. They prefer sunshine; in cloudy or rainy weather they withdraw inside small silken nests. These shelters not only protect them from the environment but also permit them to molt safely, to build egg cases, and to hibernate.

Tarantulas (Theraphosidae)

These often large and hairy spiders (fig. 1.12) usually occur in tropical and subtropical regions. Most species lead a hidden life on the ground in crevices or tubes, but some are arboreal, building silken retreats in the trees. They are typical sit-and-wait predators, mostly active at night, except for the adult males, which can be seen wandering around in broad daylight. Most tarantulas do not venture far from their retreat; often they leave it only briefly for capturing prey.

Typical morphological features are the nearly parallel chelicerae (orthognath), two pairs of book lungs, little differentiated palpal coxae, and reduced anterior spinnerets. Because of their size, tarantulas have a reputation of being highly poisonous. This is not true for most species. The actual bite may be painful due to the large chelicerae (they can actually penetrate through fingernails!), but the effects of the venom are in most cases comparable to a wasp´s sting. In some genera (e.g., *Hysterocrates*, *Poecilotheria*), however, the bites can be more severe, causing painful muscle cramps that may last for several weeks (Ezendam, 2007; Höfler, 1996).

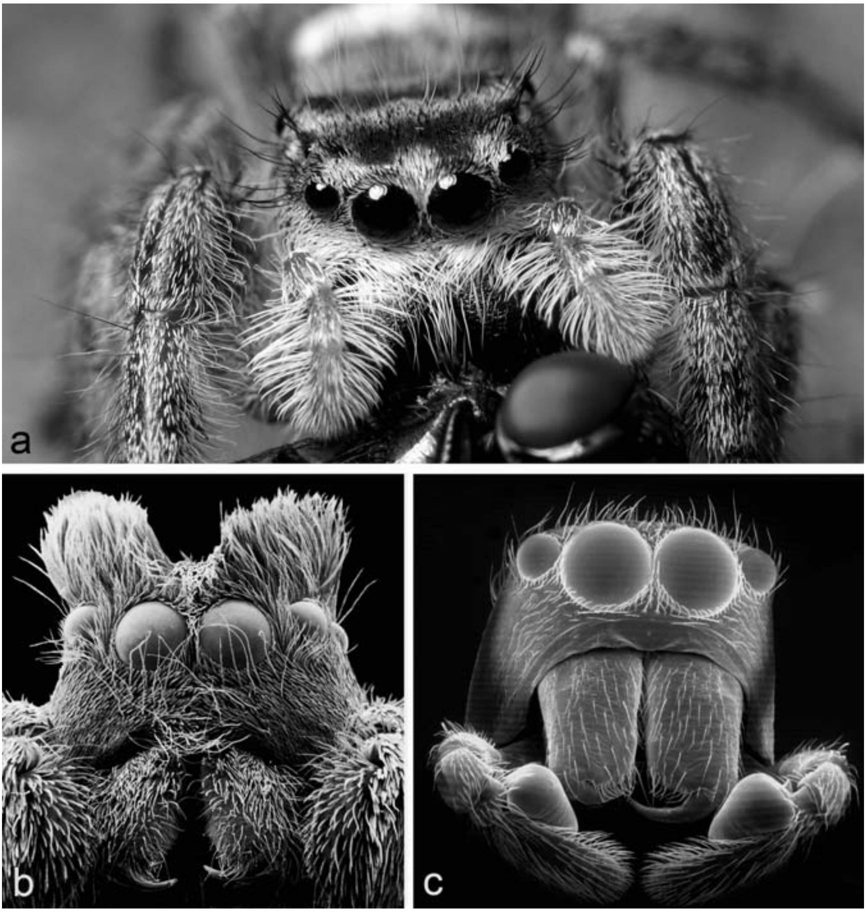


Figure 1.11
Jumping spiders are easily recognized by their large eyes, especially the main eyes in the middle. Frontal views of (*a*) *Phidippus*, (*b*) *Habronattus* (Photos: Hill) and (*c*) *Heliophanus*. (Photo: Chu and Foelix.)

Most tarantulas are shy and take to flight rather than inflicting a bite. Interestingly, Old World tarantulas are a bit more aggressive (or better said, more defensive) than their New World counterparts. There is another difference between those two groups: Many New World tarantulas defend themselves by brushing off *urticating hairs* from their abdomen (fig. 4.5). These tiny, barbed hairs can penetrate the skin or get into the eyes or the respiratory tract, where they cause strong irritations and allergies. Such hairs are lacking in Old World tarantulas.

Tarantulas can live for many years;more than 25 years have been recorded for some females. Males live much shorter (2–10 years). In contrast to most other

Figure 1.12
The large tarantula *Pterinochilus* from Central Africa lives in silken tubes under stones and is most active at night. A bite may be painful but has no severe effects. (Photo: Rast.)

spiders, tarantulas can still molt after becoming mature. This is quite common in females but happens very rarely in males.

Tarantulas play an important role in basic research because substantial quantities of venom or hemolymph can be obtained due to their size. Toxicologists have studied about 60 different tarantula venoms (Bode et al., 2001; Escoubas and Rash, 2004), and pharmacologists unravel antimicrobial peptides in tarantula blood, which inhibit the growth of bacteria and fungi (Lorenzini et al., 2003).

Some people are highly afraid of large tarantulas and consider them ugly and creepy creatures. Some others find them fascinating and keep them as pets. As a famous tarantula expert has aptly put it, “To anyone who has learned to know this spider, it is as handsome as a goldfinch and fully as interesting” (Baerg, 1958, p. 1). For those who are particularly interested in tarantulas, there are many books that describe how to keep and breed them; a recent comprehensive treatise, for instance, is *The Tarantula Keeper´s Guide* by Schultz and Schultz (2009).

Functional Anatomy

2

Prosoma

The dorsal plate of the prosoma is called the *carapace*. It bears a distinct indentation along its midline (fig. 2.1). This indented area extends on the inside of the carapace as a solid cuticular ridge, which serves as the attachment site for the dorsal muscles of the sucking stomach. Several furrows radiate from the dorsal groove: two shallow, diverging lines separate an anterior cephalic part from a posterior thoracic part. Even fainter subdivisions may be recognized laterally, pointing from the center of the carapace toward the coxae of the legs. It seems doubtful whether these furrows correspond to the original segmentation of the prosoma, although embryological studies indicate that the prosoma is formed by six fused segments.

The "head" part of the prosoma bears the eyes and the chelicerae. Most spiders have eight eyes, which are arranged in specific patterns in the various families. Usually the eyes lie in two rows (sometimes in three), and accordingly they are referred to as anterior lateral eyes (ALE), anterior median eyes (AME), posterior lateral eyes (PLE), and posterior median eyes (PME) (fig 2.2). The relative position of the eyes is very important for the systematic classification of spiders. Just by looking at the arrangement and relative size of the different eyes, one can often immediately determine the family of a particular spider. For example, all jumping spiders (Salticidae) possess one row of large frontal eyes, with the AME being the largest; wolf spiders have four uniformly small frontal eyes, but rather large PLE and PME (figs. 1.9, 2.2). The area between the anterior row of eyes and the edge of the carapace is called the *clypeus*.

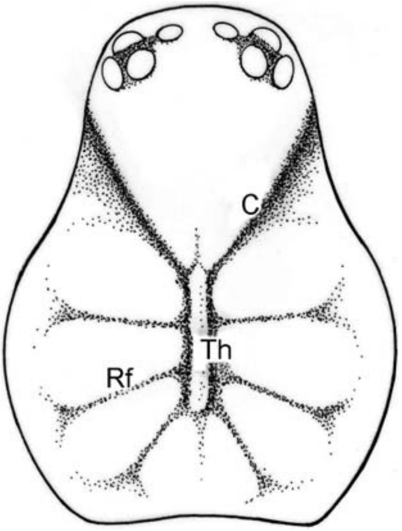


Figure 2.1
Carapace of the "primitive" spider *Hypochilus*, dorsal view. Two grooves (c) extend from the thoracic furrow (Th), separating the carapace into a "head" and a "thoracic" portion. The latter is further subdivided by radial furrows (Rf).

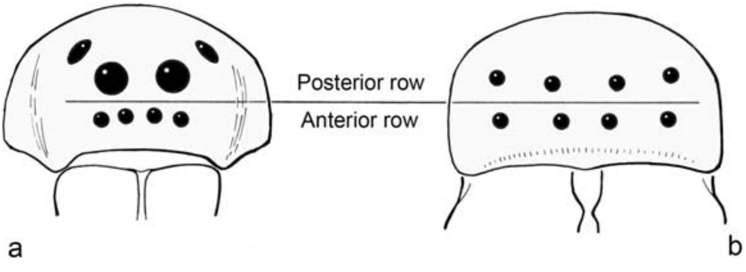


Figure 2.2
Eye pattern in (*a*) the wolf spider *Lycosa* and (*b*) the orb weaver *Tetragnatha*. The wolf spider has uniformly small eyes in the anterior row, the orb weaver has relatively small eyes in both rows of eyes. (*a*, After Kaston, 1972; *b*, After Bristowe, 1958.).

Often the eyes stand close together in pairs, sometimes clearly raised above the surrounding cuticle, as in the Theraphosidae and Filistatidae. In their most extreme arrangement, the eyes are perched on the ends of eye stalks, as in some midget spiders (Micryphantidae; fig. 2.3). Often the males of Micryphantidae have prosomal glands, which open through tiny pores onto the head region. The secretion of these glands is sucked up by the females during courtship and apparently serves a special

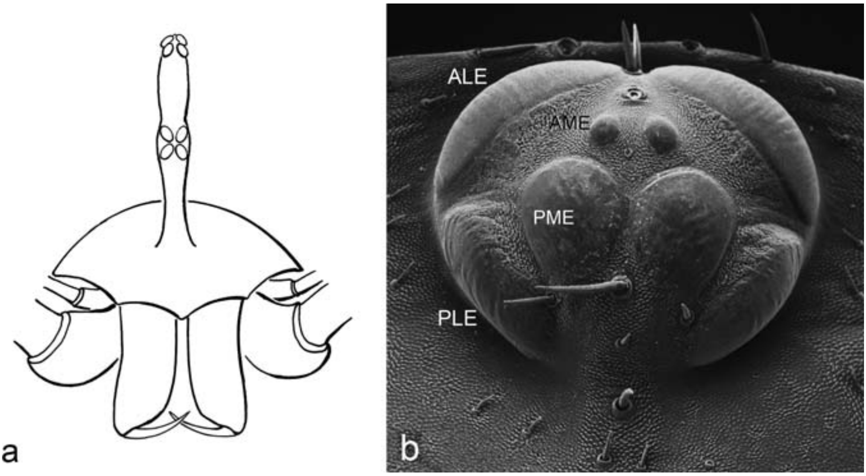


Figure 2.3
Aberrant position of the eyes in a male midget spider, *Walckenaeria acuminata*. (*a*) Front view of the prosoma with eye stalk (after Crome, 1957). (*b*) Orthognathous spiders (like this *Liphistius bristowei*) have their eyes close together on a small tubercle. Note the almost panoramic field of vision that results from the arrangement of the individual eyes on the eye hill (ALE = Anterior Lateral Eyes, AME = Anterior Median Eyes, PME = Posterior Median Eyes, PLE = Posterior Lateral Eyes).

function in sexual behavior (Blest and Taylor, 1977; Schaible et al., 1986). Some spiders have fewer than the usual eight eyes. The so-called six-eyed spiders (Dysderidae), the spitting spiders (Scytodidae), and some daddy-longlegs spiders (Pholcidae) have only six. In some species we find a reduction to four (*Tetrablemma*, Theridiidae) or even to two eyes (*Nops*, Caponiidae), and some cave-dwelling spiders have lost their eyes altogether (Millot, 1949; Sanocka, 1982). In some wolf spiders from Hawaiian caves, for instance, the eyes have either been reduced in size (*Lycosa howarthi*) or they have disappeared completely (*Adelocosa anops*) (fig. 2.4; Howarth, 1972; Gertsch, 1973).

Sternum

An undivided sternal plate (sternum) lies on the ventral side of the prosoma (fig. 1.2b). Developmentally it is derived from four fused sternites; the partition lines can sometimes just be discerned in very young spiders. Anteriorly, a small medial plate, the labium, is attached to the sternum. In most spiders, the labium and sternum are hinged together by a cuticular membrane (fig. 2.5). Both the sternum and carapace are rather stiff parts of the prosomal exoskeleton. They are, however, connected by a soft pliable area, the *pleurae* (the stippled area of fig. 1.2a), which enables them to move in relation to each other. A small shift of the carapace toward the sternum

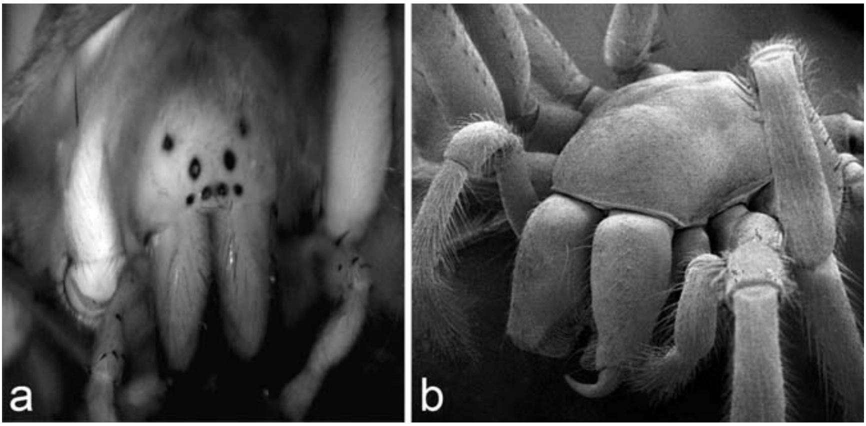


Figure 2.4
Eyes in cave spiders. (*a*) The wolf spider *Lycosa howarthi* from a Hawaiian cave shows a reduction in eye size, especially in the posterior row of eyes (Photo: Foelix and Howarth.) (*b*) The dysderid spider *Parastalita stygia* from a Slovenian cave has no eyes at all. (Photo: Foelix and Kuntner.)

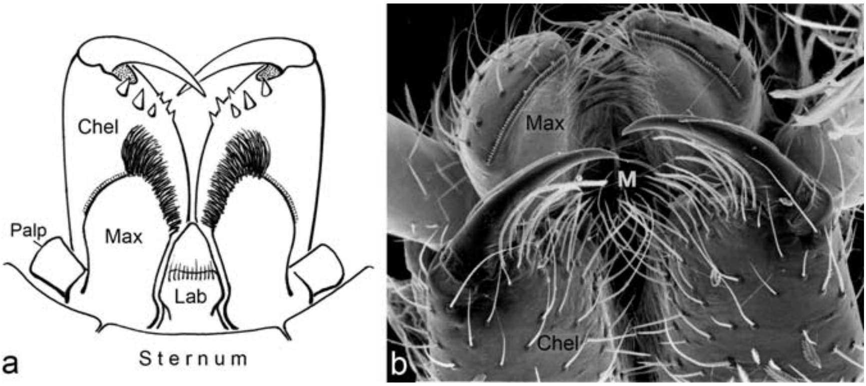


Figure 2.5
(*a*) Mouth parts of a wolf spider (*Lycosa*) as seen ventrally. Chel = chelicerae, Lab = labium, Max = maxilla (endite). (After Kaston, 1972.) (*b*) Mouthparts of a jumping spider (*Portia*), frontal view. The mouth opening (M) lies between the two maxillae (Max) and behind the chelicerae (Chel). 200 x.

(caused by connecting lateral muscles) increases the hemolymph pressure in the prosoma and in the legs; this in turn leads to the stretching of certain leg joints (see chapter 6).

Chelicerae

The chelicerae are the first appendages of the prosoma. In the spider embryo they lie behind the mouth opening, but during subsequent development they migrate to an anterior position, as do the antennae of other arthropods (fig. 8.4). Each chelicera consists of two parts, a stout basal part and a movable articulated fang. The inner edge of the fang is finely serrated and is apparently used to clip silk threads (H. M. Peters, 1982). Normally the fang rests in a groove of the basal segment like the blade of a pocket knife. When the spider bites, the fangs move out of their groove and penetrate the prey. At the same time, venom is injected through a tiny opening at the tip of the fang (fig. 2.6). It is interesting that this opening is never located at the very tip but always subterminally, which is mechanically more stable and also prevents clogging of the tip. The same technically superior solution has evolved independently in other animals (e.g., in the stinger of scorpions or the fangs of venomous snakes; fig. 2.7).

Movement of the cheliceral fang is achieved by two antagonistic muscles within the basal segment: a rather weak extensor muscle that opens the fang, and a much

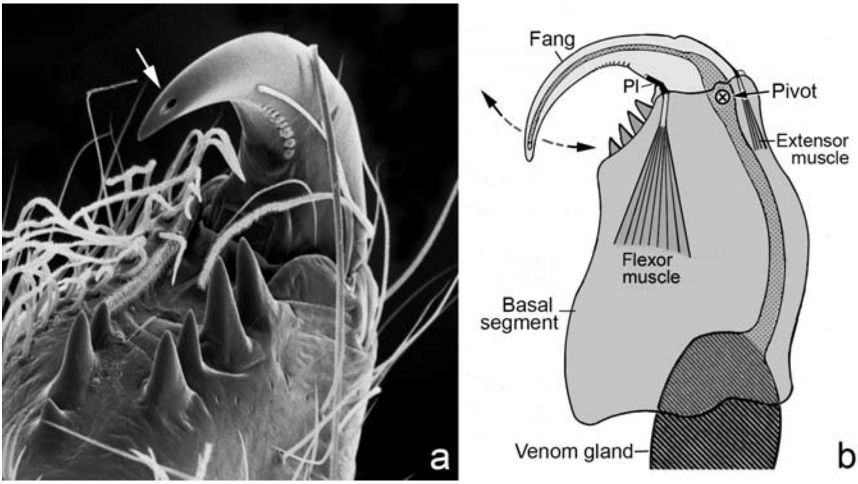


Figure 2.6
(*a*) The movable cheliceral claw (fang) normally rests between the cheliceral teeth of the basal segment. Note the serrated edge of the fang and the opening of the venom gland (arrow) (*Cupiennius*, 250 x). (*b*) Schematic drawing of a chelicera. Arrows indicate the movements of the fang, caused by the action of the flexor and the extensor muscle. Pl = plagula sklerite. (After Millot, 1949; Foelix et al., 2005.)

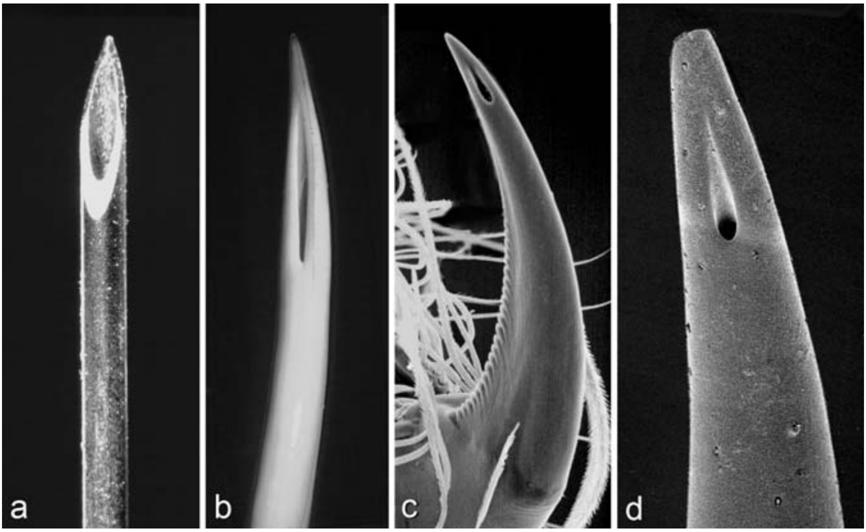


Figure 2.7
Optimal technical solution for drug or venom injection: (*a*) hypodermic needle, (*b*) venom tooth of a viper, (*c*) cheliceral fang of a spider, (*d*) stinger of a scorpion. (Photos: Foelix and Erb.)

larger flexor muscle that pulls it back (Foelix et al., 2005). This strong closing muscle is important when holding a struggling prey after the initial bite, because all the legs are then quickly withdrawn.

Both sides of the cheliceral groove are often armed with cuticular teeth (fig. 2.6a). These act as a buttress for the movable fang. Spiders whose chelicerae are equipped with such teeth mash their prey into an unrecognizable mass. Spiders without such teeth (e.g., thomisids) can only suck out their victims through the small bite holes (fig. 3.1; Homann, 1985; Foelix, 1996). The number and size of the cheliceral teeth are important diagnostic characteristics for the taxonomist. Mesothelae and most tarantulas have many teeth (up to 15), but only in a single row (Raven, 1985; Haupt, 2003). Most labidognath spiders have two rows of just a few teeth, but set in a specific pattern. A single row of cheliceral teeth is considered to be the ancient (plesiomorphic) condition.

The chelicerae are used not only for subduing prey or for defense, but also serve as "pliers" for all kinds of grasping; therefore they have been referred to as the spider's "hands." The versatility of the chelicerae is best demonstrated when we look at their main tasks in various spider families. Trapdoor spiders (Ctenizidae) use their chelicerae to dig burrows, nursery-web spiders (Pisauridae) to carry egg cocoons, and orb weavers (Araneidae) to transport small prey. In the long-jawed orb weavers (Tetragnathidae) and the cribellate Dictynidae, the males and females interlock their chelicerae during mating. Some spiders, such as the small Archaeidae

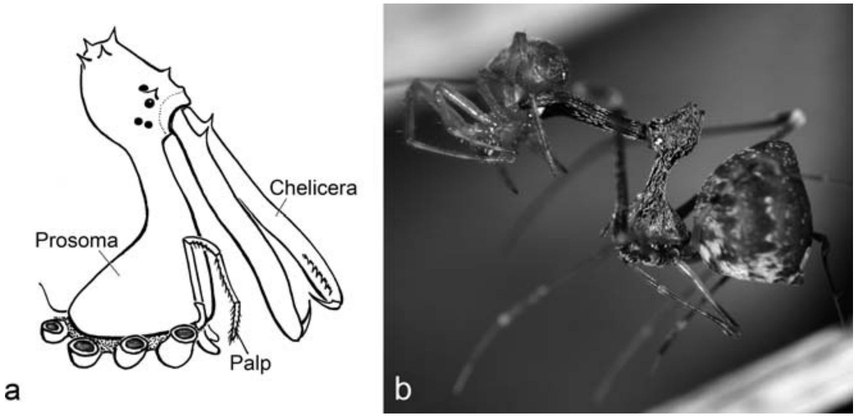


Figure 2.8
(*a*) Extreme development of the chelicerae in the assassin spider *Archaea* from Madagascar (After Legendre, 1972.) (*b*) The higly elongated chelicerae are used to literally spear prey, often other spiders. This is usually done while the spider is hanging upside down; for clarity this picture has been turned by 180° (Photo: Hormiga.)

from Madagascar, possess extremely long chelicerae (fig. 2.8), and they literally spear their prey with these enormous appendages. Often male spiders have larger chelicerae than the females (fig. 2.8). The common zebra spider, *Salticus scenicus* (fig. 6.20), is a typical example of such sexual dimorphism. In another jumping spider (*Myrmarachne*), the male's chelicerae are five times larger than the female's, but the male's chelicerae lack a fang duct and therefore they cannot envenom prey (Pollard, 1994). Instead they skewer their victims on their elongated cheliceral fangs. Finally, some money spiders (Linyphiidae) possess chelicerae with stridulatory organs for producing sounds (see chapter 9).

It has already been noted that Orthognatha and Labidognatha move their chelicerae in quite different manners (fig. 1.3). The opposed chelicerae of Labidognatha supposedly have the advantage of a much larger span, so that even rather large prey could be overpowered (Kaestner, 1952). However, direct observation and experiments do not support this theory. Many orthognath (mygalomorph) spiders subdue quite large prey, sometimes even twice their own size (Nentwig and Wissel, 1986). This is due to other factors than the cheliceral span (e.g., an aggressive wrapping behavior).

It should also be pointed out that orthognath chelicerae do not simply move up and down but can also be spread sideways. Likewise, labidognath chelicerae do not only extend laterally but can also move forward. This is very noticeable in the assassin spiders (Archaeidae), which spear other spiders with their elongated chelicerae (fig. 2.8).

There is another commonly held belief that has been challenged: the strict division into "primitive" orthognath and "higher" labidognath spiders (Kraus and Kraus, 1993). Some ancient spiders (e.g., Mesothelae or Hypochilidae), have their chelicerae neither parallel nor opposing each other, but in an intermediate position termed *plagiognath* (fig. 1.4). It is conceivable that this condition actually represents the older arrangement from which orthognathy and labidognathy was derived. Actually, only few orthognath spiders have strictly parallel chelicerae (e.g., *Atypus*; fig. 5.22); most theraphosids (tarantulas) conform more to the plagiognath position.

Pedipalps and Mouth Parts

The second pair of appendages are the *pedipalps*. Their segmentation corresponds to that of the legs, except that one segment, the metatarsus, is lacking (fig. 2.9). Despite their general resemblance to legs, the palps are usually not used for locomotion. Instead, they often play a role during prey catching, when they constantly touch and manipulate the prey.

The most notable modification of the palps is found in male spiders. Male palps act as copulatory devices, and they also have an important signaling function during courtship (fig. 7.20a). The coxae of the pedipalps represent another specialization, for these have been transformed into chewing mouth parts (*maxillae* or *endites*). In “primitive” spiders, such as Mesothelae and tarantulas, the maxillae are only slightly modified, whereas in the Labidognatha they are broadened laterally. In most Labidognatha, the anterior rim of each maxilla is clearly serrated; this rim, the *serrula* (fig. 2.10), is used as a saw for cutting into the prey. The inner sides of the maxillae are fringed by a dense cover of hair that acts as a filter while the spider is sucking in the liquefied food. The mouth opening is bordered laterally by the maxillae, in front by the rostrum, and in the back by the labium. These four mouth parts form the mouth proper, which leads into a flattened pharynx. The pharynx consists of a movable, hinged front (*rostrum*) and a back wall (*labium*) and is lined by cuticular platelets. These contain very fine grooves covered by small teeth, which together function as a microfilter. The pharyngeal lumen can be widened by the

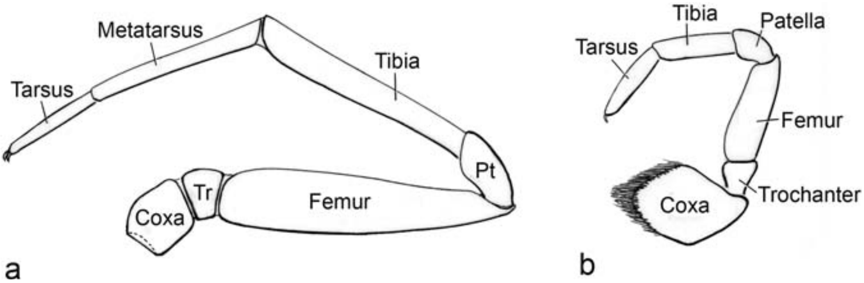


Figure 2.9
Segmentation of (*a*) a leg and (*b*) a pedipalp. Pt = patella, Tr = trochanter. (After Kaston, 1972.)

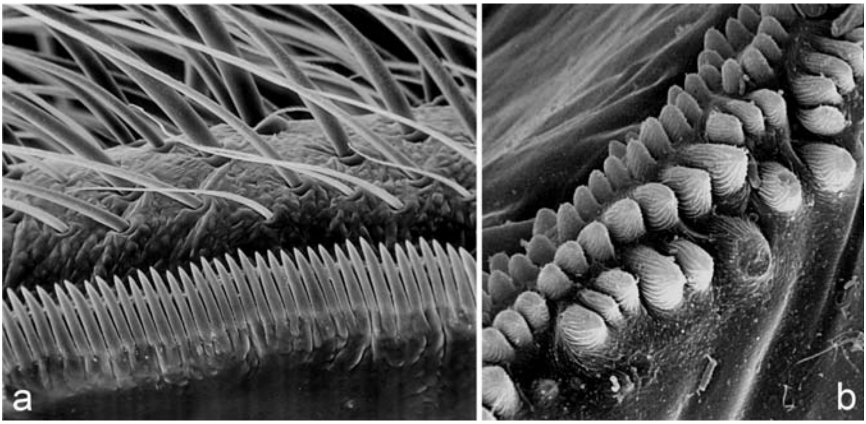


Figure 2.10
The serrula, a cuticular ridge on the palpal coxae, (*a*) sawlike in the wandering spider *Cupiennius*, and (*b*) more like a rough file in *Hypochilus*. 220 x.

action of several muscle bands (see fig. 2.23). Thus the pharynx acts as a suction pump.

Walking Legs

Four pairs of legs fan out radially from the pliable connection (*pleura*) between carapace and sternum. Each leg has seven segments: a coxa and a trochanter, which are both short; a long femur and a kneelike patella; a slender tibia and metatarsus; and, finally, a tarsus with two or three claws (fig. 2.9). Usually the front legs (1 and 2) are relatively long, and the first pair of legs in particular is often used as feelers to probe the environment. The sensory capacity of the legs stems from a variety of sensory hairs that densely cover the distal leg segments.

Tarsal Claws

The tip of the tarsus bears two bent claws, which are generally serrated like a comb (figs. 2.21, 2.22). Some spiders (Trionycha) have an additional middle claw. All claws arise from a single cuticular platelet (pretarsus). They can be lifted or lowered as a unit by the action of two antagonistic muscles, the *musculus levator praetarsi* and the *musculus depressor praetarsi* (see fig. 2.20). The middle claw is important for web spiders, because they use it to catch hold of the silk threads of their webs; in fact, only the middle hook and not the large main claws grasps the thread (Foelix, 1970a). The thread is pushed by the middle claw against serrated bristles situated opposite the claws (fig. 2.12). There it is held, snagged in the little notches of these bristles. To release the thread, the middle claw is lifted by the *musculus levator praetarsi*; the inherent elasticity of the thread simply causes it to spring back out of the clasp of the claw (Wilson, 1962b).

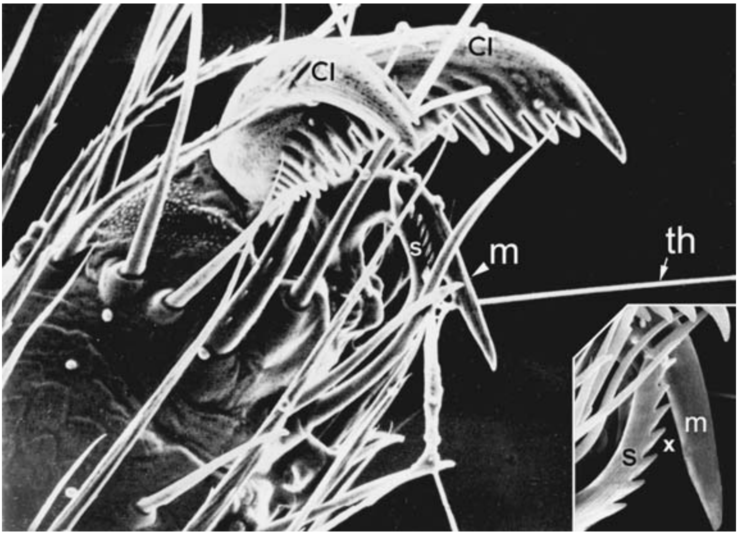


Figure 2.11
Most web spiders exhibit three tarsal claws: two combed main claws (Cl) and a smooth middle hook (m). The silk thread (th) is grasped only with the middle hook and pushed against serrated bristles (s). 600 x. *Inset*: Detail of the middle hook (m) opposing a serrated bristle (s); the silk thread fits into the notches (x) of the serrated bristle. 1,000 x.

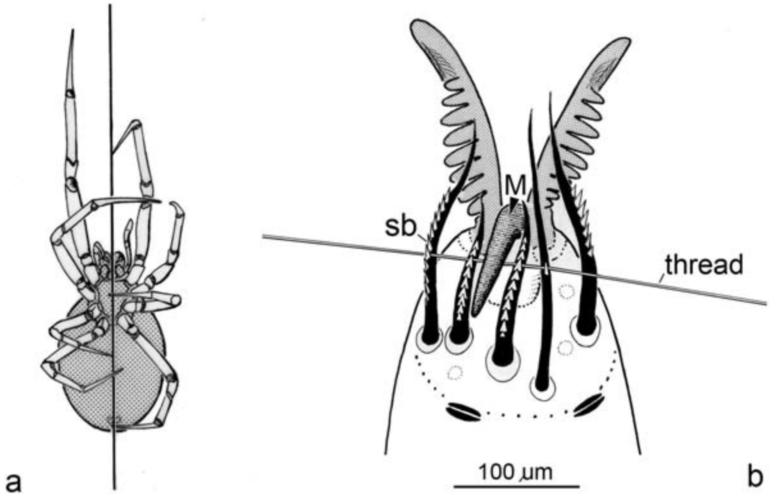


Figure 2.12
(*a*) The orb weaver *Zygiella* climbing a vertical thread. (After Frank, 1957.) (*b*) Grasping a thread: interaction of the middle hook (M) and the opposing serrated bristles (sb). (After Foelix, 1970a.)

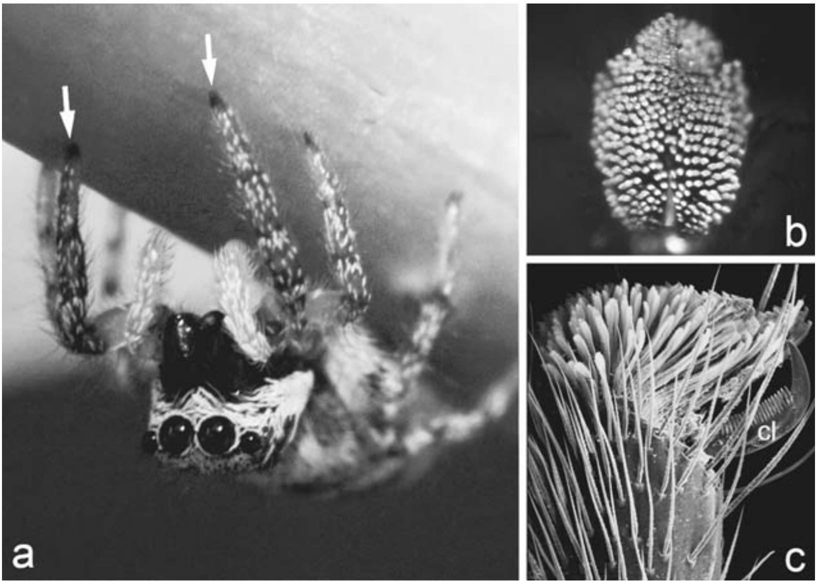


Figure 2.13
Claw tufts. (*a*) The jumping spider *Salticus scenicus* walking upside down on a plant stem. Only the claw tufts (arrows) make contact with the substrate. (Photo: Schulte.) (*b*) The claw tufts consist of two patches of scopula hairs, located on the ventral side of the pretarsus, directly beneath the claws. (Photo: Erb.) 160x. (*c*) lateral view of a claw tuft of the jumping spider *Marpissa*. 300 x.

Scopulae and Claw Tufts

Many hunting spiders possess dense cushions of hair on their feet, the *scopulae*; those lying directly under the claws are called claw tufts (fig. 2.13). In some spiders, especially in tarantulas (mygalomorphs), the entire ventral side of the tarsus and metatarsus may be covered by such scopula hairs.

All spiders that have claw tufts on the tips of their legs can easily walk on smooth vertical walls, and even on window panes. Under experimental conditions, *Cupiennius* could hold about 10 times its own body weight when sitting on a vertical glass plate (Seyfarth, 1985; personal communication). This remarkable ability can be explained if we look at the fine structure of the scopula hairs. The ventral surface of each hair splits into thousands of fine cuticular extensions (“end feet”), giving the hair the appearance of a hand broom (*scopa* means broom in Latin). A crab spider with only about 30 scopula hairs on each foot can nevertheless achieve 160,000 contact points with the substrate because each scopula hair has 500–1000 end feet (Foelix and Chu-Wang, 1975). Thus, the actual contact between the foot and the substrate is mediated by the thousands of microscopic end feet (fig. 2.14).

The commonly held belief that the scopulae function like suction cups is erroneous. Electrostatic forces are not involved either. The spider’s surefooted grip

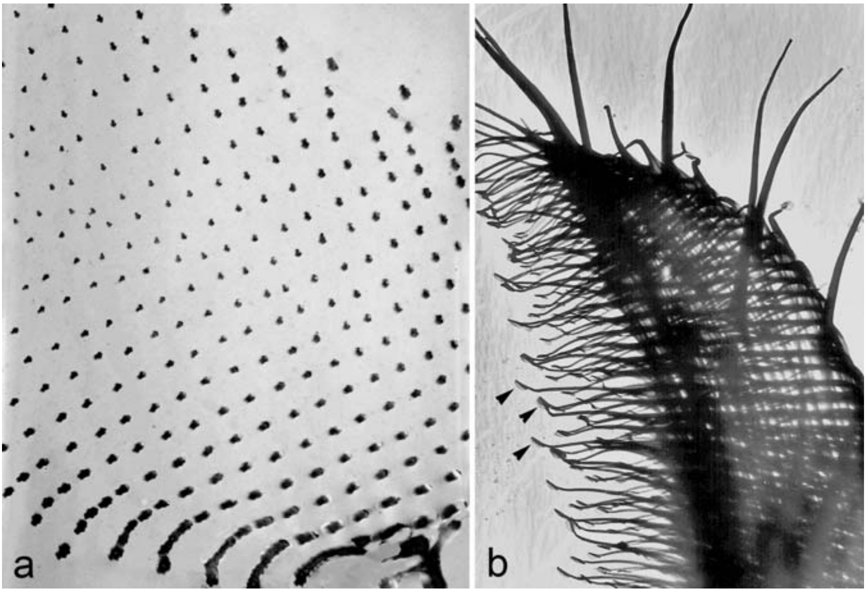


Figure 2.14
(*a*) Horizontal section of a scopula hair (*Lycosa*) illustrating the "footprint" that a single scopula hair produces when in contact with the substrate, 4,800 x. (Photo: Chu and Foelix.) (*b*) Side view of a single scopula hair from a tarantula showing the numerous extensions on the ventral side, terminating in little "end feet" (arrowheads). 6,000 x.

is achieved merely by the forces of physical adhesion. Adhesion is enhanced by the capillary forces of an extremely thin water film on the substrate (Homann, 1957; Roscoe and Walker, 1991). If the water film is absent, as with Teflon foil, then even scopulae-equipped spiders begin to slide or fall off, although normally they can easily walk upside down on glass plates. It has been calculated that a spider weighing 3 g would have 70 ponds (or 0.7 N) of capillary force available, provided that all possible contact points are established (Homann, 1957). Using an atomic force microscope, the adhesive force (van der Waals forces) of a single end foot was determined as 38 nN for a scopula hair in the jumping spider *Evarcha* (Kesel et al., 2003). If all end feet on all legs made contact, such a spider (body mass 15 mg) could theoretically hold 2.4 g, which corresponds to a safety factor of 160! This explains why a spider can still hold fast when some legs are lifted during walking. Incidentally, the same phenomenon of highly efficient adhesion forces is known in some reptiles, such as in skinks, which can walk surefootedly on walls and ceilings (Hiller, 1968).

One problem that is not fully resolved is how such a grip is loosened again. It has been suggested that a spider can, by degrees, detach its scopula hairs hydraulically by gradually increasing the hemolymph pressure (Rovner, 1978). Slow-motion pictures of moving salticids show clearly that the entire pretarsus (claws plus claw tufts) can be flexed or raised (Hill, 2006a). Apparently the adhesive hairs are pressed in a controlled fashion against the substrate, mostly by the action of the musculus depressor praetarsi. The release seems to be caused by the contraction of the musculus levator praetarsi (fig. 2.20a), resulting in gradually "peeling off" from the substrate. Additionally, hydraulic forces may also be involved, since an increase of the hemolymph pressure will lift the tarsus and bend the pretarsus (Speck and Barth, 1982).

In their natural surroundings, spiders with scopulae certainly have the advantage of being able to climb securely on overhanging rocks or leaves. Thus certain environments that normally would be inaccessible become available. The contact with a smooth substrate is always made by the distal claw tufts, not by the hairs covering the ventral sides of tarsi and metatarsi. A close inspection shows that the adhesive side of those scopulate hairs normally does not point toward the substrate but actually faces the leg surface. However, their adhesive function comes into play during prey capture (i.e., when a struggling victim needs to be held down securely; (Rovner and Knost, 1974; Rovner, 1978). Just before seizing a prey, the scopulate hairs can be erected hydraulically, thereby exposing their adhesive sides (Foelix et al., 1984).

Recent studies found that the leg scopulae exert strong friction only when pushed against a substrate, but not when pulled toward the body (Niederegger and Gorb, 2006). This is because the adhesive end feet lie on the inside of the scopulate hair and can only make contact when pushed onto a surface (fig. 2.15). Similarly, when a spider sits on a vertical wall facing down, gravity pushes against the scopulae of the forelegs, thereby bringing the end feet into contact with the wall and increasing the adhesive forces.

Leg Joints and Musculature

The movability of the seven leg segments is determined not only by the extensive musculature but also by the different types of joints. Most joints are *dicondylous*; that

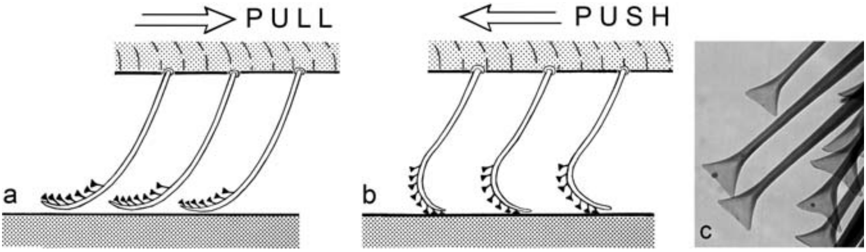


Figure 2.15
Scopula hairs covering the tarsus and metatarsus bear the adhesive end feet on the internal side. (*a*) When the leg is pulled toward the body, only the external, non-adhesive side touches the ground. (*b*) When the leg is pushed distally, the flexible scopula hairs bend backwards and the end feet come in contact with the substrate. (After Niederegger and Gorb, 2003). (*c*) Triangular end feet seen at high magnification. 8,000 x.

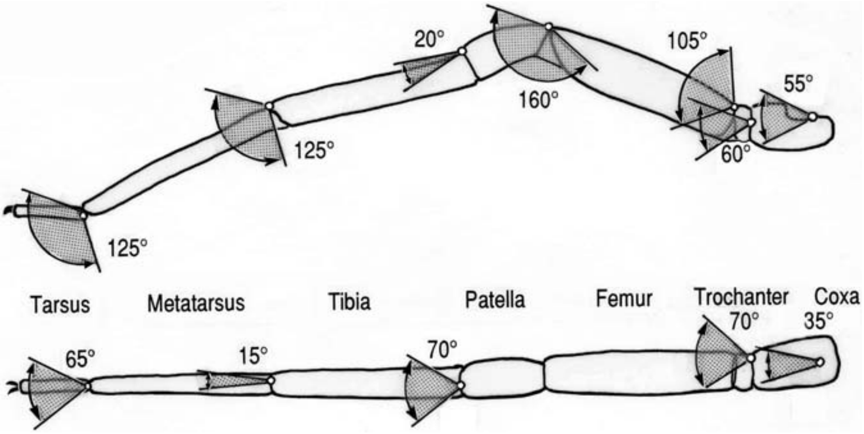


Figure 2.16
Range of movements for the leg joints in the wandering spider *Cupiennius*. The angles that each joint can move were measured on a live animal. Top: Lateral view of leg 1. Bottom: Dorsal view. (After Seyfarth, unpublished.)

is, they can move only in one plane (vertical movements; fig. 2.16). In contrast, the coxa-trochanter joint represents a kind of "saddle joint" (like in our thumb) and thus can be moved up and down as well as forward and backward (laterally). This lateral movability is absolutely necessary for locomotion and is most important for legs 2 and 3 (see chapter 6). The joint between patella and tibia also moves laterally and assists in positioning the leg tip precisely (Frank, 1957). A so-called passive joint lies between the tarsus and metatarsus; although a hinge is present, muscles are not involved in the movement between the two segments (figs. 2.17, 2.20).

There is little variation in the leg musculature of different spider families. For instance, 33 different leg muscles have been described for the orb weaver *Zygiella* (Frank, 1957); the tarantula *Eurypelma* (synonym *Dugesiella*), with 30, has just about as many (Dillon, 1952; Ruhland, 1976). Cursory spiders, which need to hold down their struggling prey, tend to have better developed muscles than web spiders, which subdue their prey by wrapping (Clarke, 1986). Most joints are equipped with several muscles (fig. 2.17) that either bend the joint (the flexors) or stretch it (the extensors). Two remarkable exceptions are the femur-patella joint and the tibia-metatarsal joint, both of which lack extensors (Petrunkevitch, 1909). How these joints can be stretched at all puzzled arachnologists for a long time. Later it was shown that the extension is caused by a hydraulic mechanism, that is, an increase in the hemolymph pressure (Ellis, 1944; Parry and Brown, 1959a, b; R. S. Wilson, 1970; R. S. Wilson and Bullock, 1973; Anderson and Prestwich, 1975).

The hydraulically mediated extension of these joints can be elicited by carefully and gently squeezing a leg with forceps. In contrast, no such movement occurs if the leg is squeezed after its tip has been cut off. An important question is where the

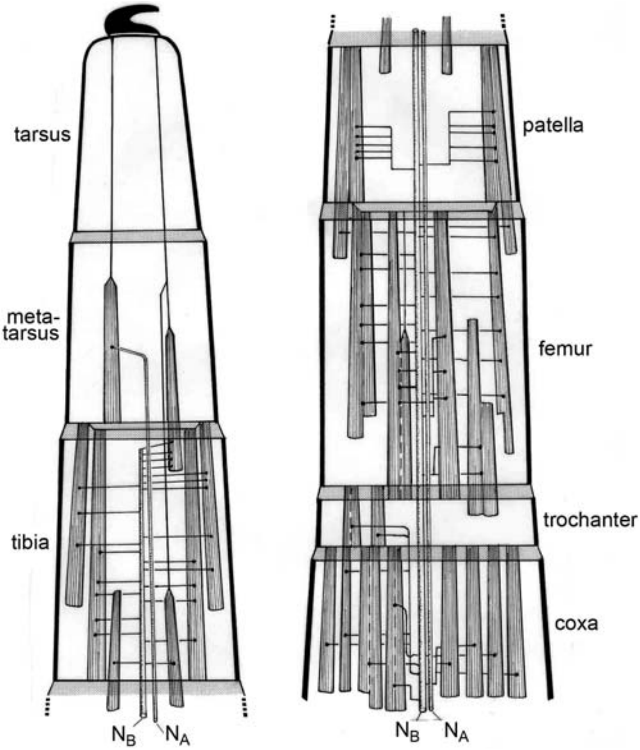


Figure 2.17
Diagram of the leg musculature and its innervation in the tarantula *Dugesiella*; N_A, N_B = motor nerves A and B. (After Ruhland and Rathmayer, 1978.)

"pressure pump" is located within the living spider. It turns out that a contraction of prosomal muscles (fig. 2.34; Shultz, 1991), which traverse the carapace vertically, leads to a reduction in the volume of the prosoma and thus to increased pressure there (fig. 2.18). This hemolymph pressure has been measured directly in several spiders (Homann, 1949; Parry and Brown, 1959a, b). In a tarantula, pressures of 40–60 mm of mercury (Hg) were measured during rest and 100 mm Hg during walking. At maximal activity (struggling), values of 480 mm Hg were observed (Stewart and Martin, 1974). These values are generally comparable to human systolic and diastolic blood pressures, which for a 20-year old are normally 120 and 80 mm Hg, respectively.

Histologically, all spider leg muscles are typical striated skeletal muscles. Each cell consists of many myofibrils, with light I-bands (isotropic) and darker A-bands (anisotropic). The Z-disks, which define the functional unit of a myofibril (the *sarcomere*), can be seen clearly under the light microscope. The ultrastructure of the contractile elements (actin and myosin) is similar to that of skeletal muscles of other

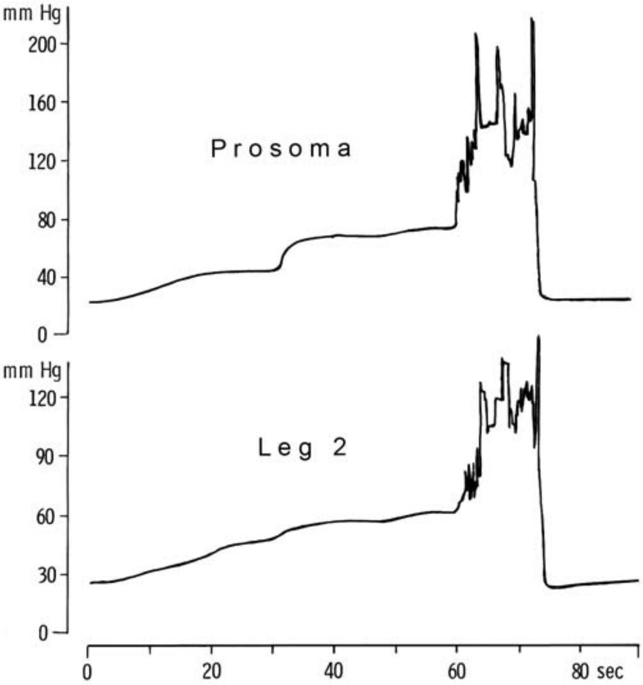


Figure 2.18
Synchronous recording of blood pressure in the prosoma and leg 2 of the tarantula *Dugesiella*. In the resting state the blood pressure is about 30 mm Hg. The onset of activity is marked by a concomitant increase of blood pressure in the prosoma and in the leg. (After Stewart and Martin, 1974.)

arthropods (fig. 2.19; Zebe and Rathmayer, 1968; Sherman and Luft, 1971; Fourtner, 1973). However, spider muscles contain only few mitochondria (Linzen and Gallowitz, 1975), and since mitochondria ultimately provide the energy for the cell, it is not surprising that spider muscles fatigue rapidly. It has been known for many years that, although spiders can achieve high levels of momentary activity, they usually become exhausted after a few seconds of exertion (Bristowe, 1932). During activity, mainly anaerobic energy sources (phosphate, glycogen) are used, whereas fat is burned during rest (Prestwich, 1988a, b; Paul, 1990; Eschrich and Paul, 1991). After a period of high activity, a long period of recovery follows with an elevated aerobic metabolism. D-Lactate accumulates as an end product in the muscle tissue, then spreads into the hemolymph, causing a drop in pH. This metabolic acidosis contributes to the rapid exhaustion in spiders.

Some muscles are elongated at one end into long "tendons." These tendons consist of fine cuticular tubes covered by a thin epithelium (hypodermis). Every time a spider molts, the cuticular part of the tendon is discarded along with the shed skin (exuvium). A typical example for such tendons is provided by the claw muscles

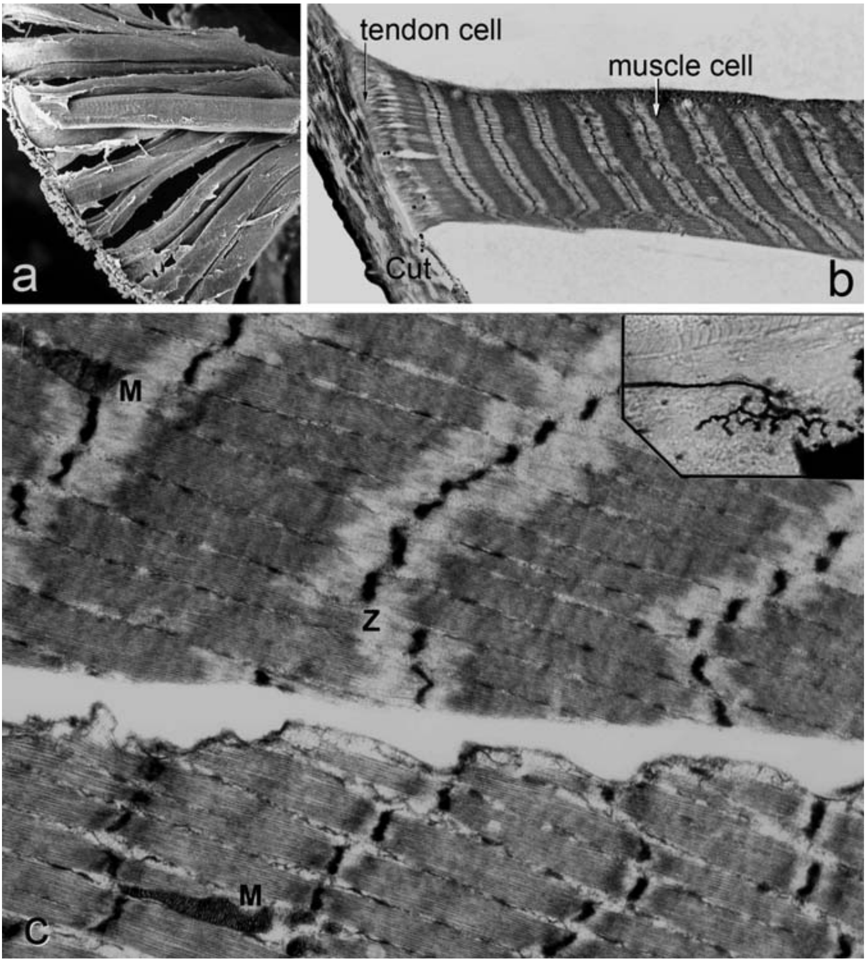


Figure 2.19
(*a*) A bundle of muscle fibers from the prosoma; the previous attachment to the cuticle was on the left side. 160 x. (*b*) Longitudinal section of a muscle cell still attached to the cuticle (Cut). The actual connection is made by an intercalated tendon cell. 600 x.
(*c*) Longitudinal section of two leg muscle fibers (*Pholcus*). The muscle fiber pictured in the upper half is in the relaxed state. It clearly shows dark A-bands and light I-bands with distinct dark Z-lines. The lower muscle fiber is contracted, hence the light I-bands have almost disappeared. Mitochondria (M) are rare. 7,000x . *Inset*: motor nerve endings branch on the surface of the muscle and form multiple synapses (Golgi preparation) 340 x.

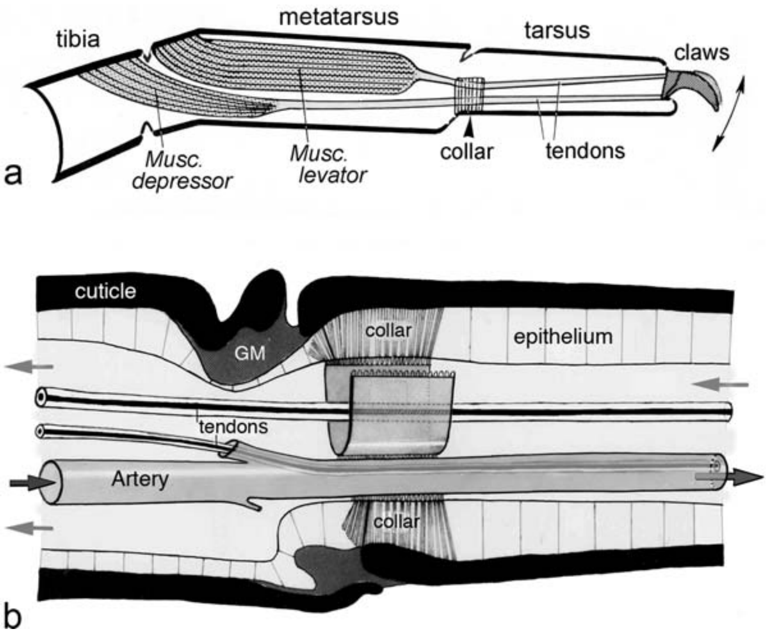


Figure 2.20
Muscles and tendons of the tarsal claws. (*a*) The *m. levator praetarsi* lifts the claws; the *m. depressor praetarsi* lowers them. The long tendons of both muscles pass through a "collar" near the metatarsal joint. (After Sherman and Luff, 1971.) (*b*) Detailed view of the metatarsal joint region and the collar: whereas the tendon of the levator muscle runs freely through the hemolymph, the tendon of the depressor muscle enters the leg artery. Arrows indicate the direction of the blood flow. (After Pack and Foelix, 1983, unpubl.)

located in the metatarsus and tibia. Their long tendons operate the claws as reins manipulate a bridle (Fig. 2.20). It is beyond the scope of this book to list all the different muscles in a spider's body. I shall give just one example to show how complex the muscle arrangement can be: the pedicel alone is provided by 36 muscles, 17 paired and 2 unpaired (Dierkes and Barth, 1995). Readers with a deeper interest in spider myology are referred to the detailed works of Palmgren (1978, 1981).

Innervation

The innervation of spider muscles is polyneuronal, that is, each muscle cell is supplied by several (usually three) motor nerve fibers (Rathmayer, 1965b). The nerve endings are distributed over the entire length of a muscle fiber, where they form numerous neuromuscular contacts (synapses; fig. 2.19c). Each spider leg is traversed by three main nerves (A, B, C). Nerve A is the smallest and contains sensory as well as motor fibers (Rathmayer, 1965a). The many thousands of nerve fibers