Biology of Spiders

Rainer F. Foelix

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Harvard University Press
Cambridge, Massachusetts, and London, England 1982

Printed in the United States of America

Translated from the original German edition, *Biologie der Spinnen*
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Library of Congress Cataloging in Publication Data

Foelix, Rainer F., 1943–
Biology of spiders.

Translation of: Biologie der Spinnen.
Bibliography: p.
Includes index.
1. Spiders. I. Title.
QL458.4.F6313 595.4'4 81-13269
ISBN 0-674-07431-9 AACR2

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Preface

Not long ago the spiders were the most neglected of the most interesting animals . . .

T. H. Savory, 1962

SPIDERS have always been treated as a minority group. Oddly enough, spiders have been largely ignored by most biologists, although quite a few people are fascinated by them. Many universities have large entomology departments, but few have an arachnology section. One objective of this book is to demonstrate that the achievements of spiders can well compete with those of crustaceans and insects; in fact, their evolutionary success has been attained largely at the expense of the insects.

The most recent books on the biology of spiders were published by T. H. Savory in 1928 and by E. Nielsen in 1932. Needless to say, arachnology has progressed immensely since then. Although there exist some newer and quite excellent books on the natural history of spiders, such as W. S. Bristowe's *The World of Spiders* (1958) or W. J. Gertsch's *American Spiders* (1949, 1979), no recent author has really attempted to pull together the various biological facets of a spider's life. The present book tries to fill this gap. Nevertheless, its aim is not to serve as a condensed handbook or as a review for the already knowledgeable arachnologist. It is meant instead for anybody interested in biology, especially for those who already find spiders particularly intriguing creatures. Those who wish to probe

more deeply into specific subjects will be guided by the extensive bibliography.

The original version of this book appeared in German (*Biologie der Spinnen*, Stuttgart, Georg Thieme Verlag, 1979). The present book is a fairly close translation of that edition, although a few new paragraphs and pictures have been added and some findings reported in more recent literature have been incorporated into some chapters.

Many colleagues helped with the original edition and I want to give them credit here once again: F. G. Barth, L. Beck, R. R. Forster, W. W. Gettmann, P. Görner, M. Grasshoff, Å. Holm, H. Homann, J. S. Rovner, W.-D. Schröer, R. Wehner, and P. N. Witt. For reviewing chapters of the English translation I am grateful to D. J. Harris, H. W. Levi, P. J. Peters, N. I. Platnick, J. S. Rovner, and A. C. Whittle. Particular thanks go to my friend and colleague David Troyer, who critically checked the entire manuscript and eliminated most of my "Germanisms" as well as some inconsistencies. Rose M. Udics of Harvard University Press substantially improved the final draft, for which I am grateful. Chapter 5 was largely illustrated by Vernessa Riley; for all other drawings and diagrams I am responsible myself.

Finally, I would like to thank all those people who pointed out flaws in the original German edition. I have tried to make the appropriate corrections, but quite probably other shortcomings will come to light, for which I am, of course, fully responsible; I hope that these will not distract the reader.

Fall 1981 Rainer F. Foelix

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An Introduction to Spiders

SPIDERS are distributed all over the world and have conquered all ecological environments, with perhaps the single exception of the air. 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 solitary 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). With respect to functions the prosoma serves mainly for locomotion, for food uptake, and for 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.

The prosoma is covered by a dorsal and a ventral plate, the cara-

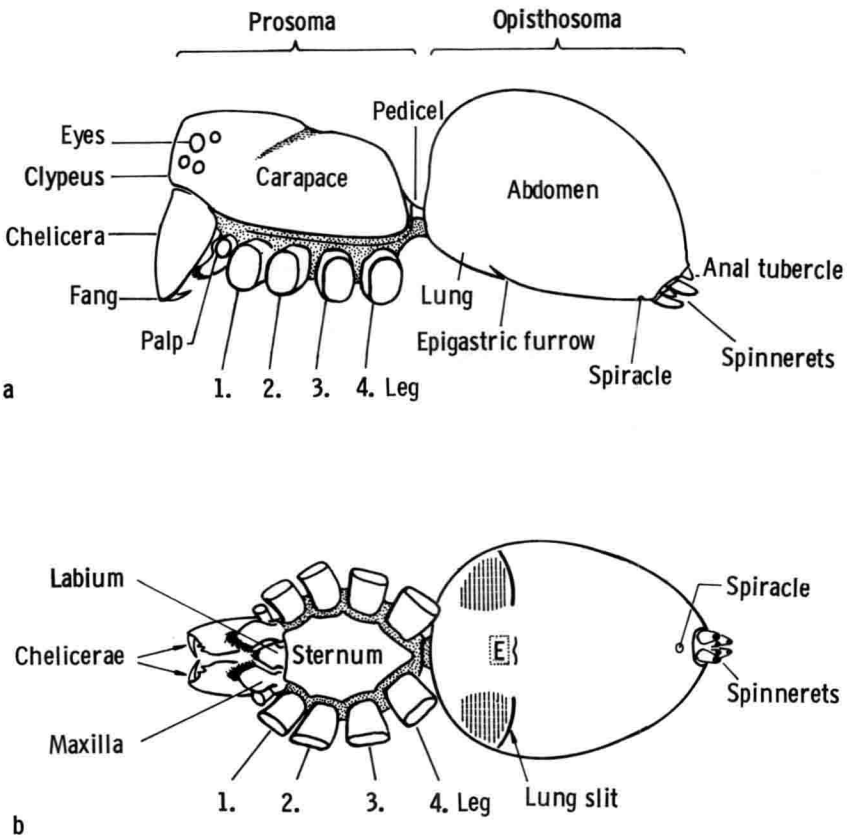


Fig. 1. External appearance of a spider's body: (*a*) Lateral view; (*b*) Ventral view; E = epigynum.

pace 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 more than 30,000 spider species, which they group into approximately 60 families. 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 more than 18 different spider classifications have been proposed since 1900.

The order of spiders (Araneae) can be divided broadly into two suborders, the Orthognatha and the Labidognatha, on the basis of the different position of the chelicerae. Whereas all Orthognatha (for example, "tarantulas") possess horizontally directed chelicerae, which work approximately parallel to each other, the Labidognatha ("modern" spiders, considered to be more recently evolved) have vertical chelicerae, which oppose each other (Fig. 2).

Another group, the Mesothelae, although orthognath, is often regarded as a distinct suborder of its own. They constitute only the single family Liphistiidae, which represents the phylogenetically oldest spiders. In contrast to all other spiders the Mesothelae exhibit a clearly segmented abdomen, as well as several other "primitive" characters.

A division of the Labidognatha into higher taxa is somewhat problematical. The common division of this suborder into *Cribellatae* and *Ecribellatae* is based on the presence of a spinning plate (cribellum) situated in front of the spinnerets as the distinguishing character of the Cribellatae. All labidognath spiders without such a cribellum are grouped together as Ecribellatae. However, there now seems to be general consensus that Ecribellatae have evolved

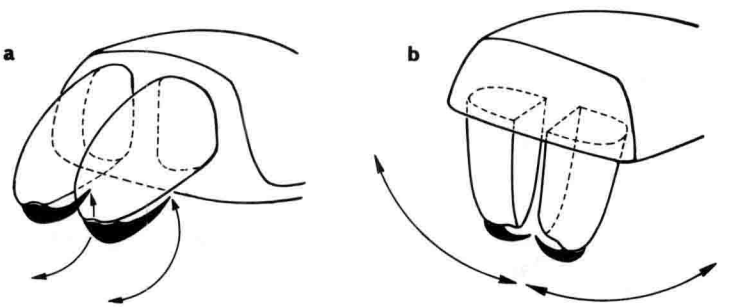


Fig. 2. Movement of the chelicerae in (*a*) orthognath and (*b*) labidognath spiders. (After Kaestner, 1969.)

independently several times from Cribellatae and that a clear-cut phyletic division can no longer be maintained. The cribellate-ecribellate problem will be discussed in more detail in more detail in chapter 10.

Among the Ecribellatae, some spider families with simple genital structures, the so-called *Haplogynae,* can be separated from those which have complex genital structures, the *Entelegynae.* This classification dates back to Eugène Simon's *Histoire Naturelle des Araignèes* (1892–1903). Recently, however, some have voiced the opinion that the Haplogynae are not really a uniform group (Brignoli, 1975; Lehtinen, 1975; Platnick, 1975). If one accepts Simon's classification, the Entelegynae could be divided into *Dionycha* and *Trionycha,* depending on whether the walking legs have two or three tarsal claws.

Since the following text will often refer to certain spider families, the main families and their systematic position are listed here:

Order Araneae	
1. Suborder Mesothelae	9 species
2. Suborder Orthognatha	
Family Theraphosidae	800
Ctenizidae	700
Atypidae	20
3. Suborder Labidognatha	
a. Infraorder Ecribellatae	
Haplogynae	
Scytotidae	200
Dysderidae	250
Pholcidae	500
Entelegynae	
Dionycha (2 tarsal claws)	
Clubionidae	2,000
Thomisidae	3,000
Salticidae	4,000
Trionycha (3 tarsal claws)	
Lycosidae	2,500
Oxyopidae	500
Theridiidae	2,500
Linyphiidae	3,500
Agelenidae	1,000
Araneidae	2,500

b. Infraorder Cribellatae

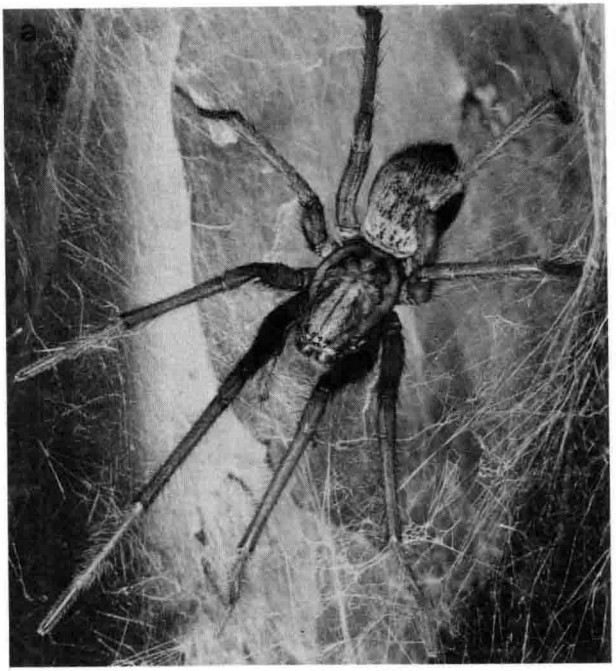
Amaurobiidae	350
Dictynidae	500
Eresidae	100
Uloboridae	200

In order to familiarize the uniniated reader with this seemingly abstract system, the following natural history of some selected 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 find *Tegenaria* usually 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. 3). 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 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* is also considered to be a member of the agelenid family. It is the only spider that lives constantly under water. Rather than build a web, she attaches an air bubble to a water plant and uses it as a residence. She hunts mostly fly larvae or small crustaceans which she catches as she swims about freely under water. To eat the prey the spider must return to her diving bell. The abdomen of the water spider is always encased in a shiny air bubble, and this silvery reflection has earned her 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 her land-living relatives.


a


b

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 (Fig. 98). The spider either sits right in the center of the web or hides in a retreat outside 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 (>2,500) testifies. Thus it comes as no surprise to find as well hundreds of structural variations on the orb-web design. Some examples will be given in chapter 5. The body structures of araneids may also vary considerably; most notable are the tropical orb weavers, which can be very colorful and exotically shaped (Fig. 4).

An orb web is typical not only for the Araneidae but also for 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").

Wolf Spiders (Lycosidae)

Wolf spiders are vagabonds which 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 (Figs. 5, 9). About 2,500 different species occur all over the world, and they may 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. 116). Members of the aptly named genus *Pirata* hunt insects on the water surface, or even dive after tadpoles or small fish

Fig. 3. (*a*) Juvenile female house spider (*Tegenaria*) sitting at the entrance of her retreat. (*b*) Typical agelenid sheet web, covered with early morning dew. (Photo *b*: Paas.)

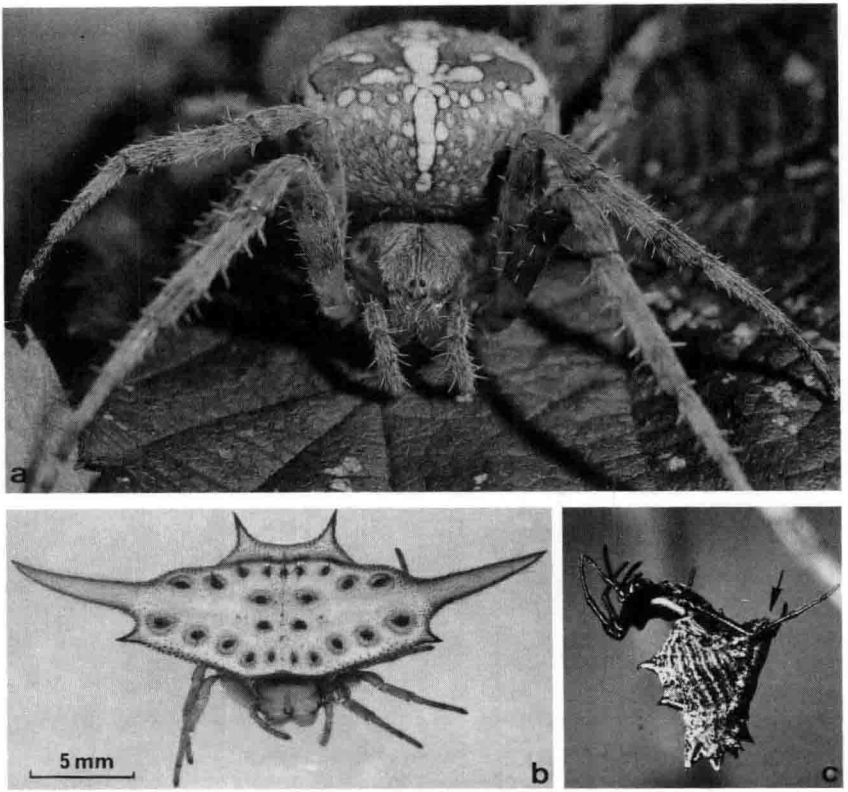


Fig. 4. (*a*) The best known of all orb weavers, the garden spider *Araneus diadematus*. (Photo: Grocki and Foelix.) (*b*) This *Gasteracantha versicolor* from Madagascar bears long spines on its abdomen, as exotic araneids often do. (Photo: Emerit, 1969.) (*c*) A North American orb weaver, *Micrathena gracilis*, hanging on a horizontal thread. Note the position of the spinnerets (arrow).

(Gettmann, 1978). A few species of wolf spiders (*Aulonia, Hippasa*), thought to be more primitive varieties, actually build webs reminiscent of the sheet webs of agelenids.

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, but they are not related to the big tropical "tarantulas," the mygalomorphs, also known as bird spiders. Although tarantulas have long had a bad reputation as dangerous spiders, the ancient fear of their poisonous bite has been proven to be quite

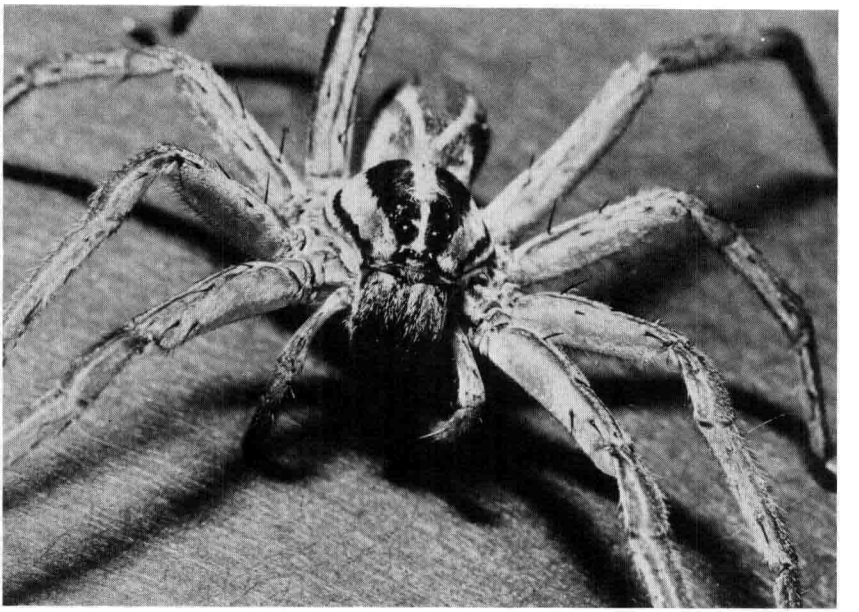


Fig. 5. A female wolf spider (*Lycosa rabida*) in an attentive posture.

wrong; 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 quite similar to that of the trapdoor spiders. 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).

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 coarse image, and thus only objects very 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. 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 spi-

derlings have crawled out, they clamber onto their mother's back (Fig. 151). Since they may number more than one hundred, they huddle there in several layers. They ride 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, was formerly considered a separate family, but recently has been reclassified as a subfamily of the Lycosidae (Homann, 1971). The most notorious ctenid spider is the extremely poisonous and aggressive *Phoneutria fera* (Fig. 38d). A less ferocious ctenid spider, which will be mentioned in many of the following chapters, is *Cupiennius salei* from Central America (Fig. 118).

Crab Spiders (Thomisidae)

Crab spiders lie quietly in ambush and do not build webs (Fig. 6). 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 gets seized by the spider's strong front legs and then paralyzed by its poisonous bite. The victim is sucked out through the tiny bite holes. Since its exoskeleton remains intact, the victim appears practically unharmed when the spider has finished its meal.

Crab spiders may be very colorful—they are often white 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 is often 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.

Jumping Spiders (Salticidae)

At least for an arachnologist the "jumpers" are among the most attractive, if not congenial, spiders. They are all rather small (3–10 mm), with short stout legs and a square prosoma. Most con-