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Introduction: spider biology

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The introductory chapter has been written especially for readers unfamiliar with the finer details of spider systematics, terminology and biology. The introduction is by no means intended to be a complete account of spider biology, which can be found in the excellent *Biology of Spiders* by Rainer Foelix (1996). Instead, here we concentrate on those aspects of spider biology that prepare the reader for the behavioural chapters to follow. The sections on systematics, fossil record and evolutionary milestones will help place the various behaviours discussed into an evolutionary context. The biology section will familiarise the reader with the spider-specific terminology and reveal some of the peculiarities of spiders: did you know that in modern spiders females have two separate copulatory openings and that spiders can produce up to seven different types of silk? For readers already familiar with spiders, the introduction offers a succinct and up-to-date summary of spider biology.

1.1 Scope of this book

The aim of this book is to illustrate the incredible diversity and often bewildering complexity of spider behaviour. Researchers that regularly work with spiders are well aware of their behavioural potential, and yet spiders still surprise us constantly with behaviours and phenomena that are intriguing, often bizarre and uncommon in other animals. Here we aim to enthuse readers that may have not considered spiders as models for behavioural studies, perhaps assuming that they are limited in their behavioural repertoires. Behavioural variation can be found in all aspects of spider biology, including foraging,

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building webs, courtship and mating. While variation is high between different species, it is surprisingly high between individuals of the same species, and also within the same individual. This book highlights that spiders are not simple robots with a limited behavioural repertoire. Rather, they show great cognitive abilities, changing their behaviour to suit their situational needs. We hope that this book will serve two functions: first, encourage behavioural and evolutionary biologists to consider spiders as potential study models and, second, become a resource for researchers already working on spider behaviour. Most of all, we hope you enjoy the book!

1.2 Spider biology

1.2.1 *Systematics of the main spider groups*

Spiders (Order Araneae) belong to the Class Arachnida along with several other Orders including mites and ticks (Acari), scorpions (Scorpiones), harvestmen (Opiliones), whiptailed scorpions and vinegaroons (Thelyphonida), whipspiders (or tailless whipscorpions (Amblypygi)), micro whipscorpions (Palpigradi), false scorpions (Pseudoscorpiones), sun spiders (Solifugae) and windscorpions (Ricinulei) (Wheeler and Hayashi, 1998). There is strong evidence that the spiders form a monophyletic group based on the presence of chelicerae (mouthparts) with venom glands, modified legs for sperm transfer (pedipalps) and abdominal silk glands and spinnerets (Coddington, 2005, Coddington and Levi, 1991). In terms of arachnid diversity, spiders only trail the ticks and mites in the number of described species. Currently, there are 41 719 taxonomically recognised spider species from 3802 genera (Platnick, 2010).

The two main suborders of spiders are the basal Mesothelae and the more derived Opisthothelae (Figure 1.1). The Mesothelae, unlike the Opisthothelae, still exhibit external and internal segmentation of the opisthosoma. This group only occurs in South-East Asia and is represented by a single family (Liphistiidae) with five genera and 89 species (Coddington, 2005, 2010). The opisthothele spiders include the Mygalomorphae and the Araneomorphae. The former comprise the tarantulas, funnel-web and trapdoor spiders represented by 15 families with around 2600 species in 321 genera (Hedin and Bond, 2006, Platnick, 2010). Most mygalomorphs are relatively large, ground-dwelling spiders that live in permanent burrows. Their dispersal is limited as the spiderlings of most species do not balloon (Coddington, 2005, Hedin and Bond, 2006). Mygalomorph systematics is still somewhat problematic. Molecular data support the split of the mygalomorphs into two main groups: the atypoids (including the Atypidae, Antrodiaetidae and Mecicobothriidae) and the non-atypoids (the remaining 12 families). However, the remaining relationships between

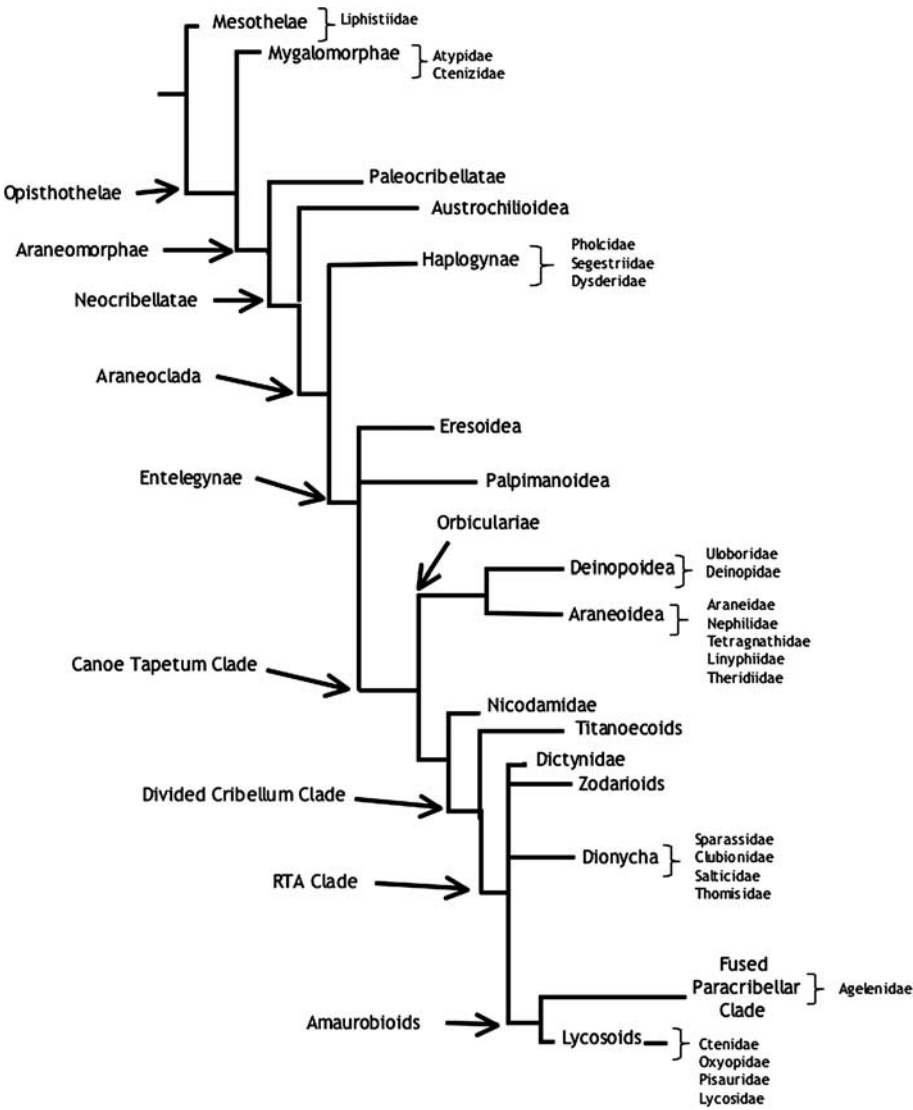


Figure 1.1 Phylogeny of the Araneae, simplified from Coddington (2005). The listed families are not exhaustive but predominantly include those that are also frequently referred to throughout the book.

families and the monophyly of some families remain contentious (Ayoub *et al.*, 2007, Hedin and Bond, 2006).

By far the most diverse suborder of spiders is the Araneomorphae, the sister group to the Mygalomorphae. It contains more than 38 000 described species in 3407 genera and 90 families (Platnick, 2010). There are several synapomorphic characters common to all araneomorphs, including the cribellum – a sclerotised

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plate bearing thousands of silk extruding spigots (secondarily lost in many araneomorph families). Other synapomorphies are the major ampullate glands, the piriform glands and diaxial chelicerae (Coddington, 2005).

On the basis of the presence of two rather than one pair of book lungs, the Paleocribellatae (with only one family, the Hypochilidae) are sister to the Neocribellatae, which include all other araneomorphs. The large Neocribellatae group is split into the Haplogynae and Entelegynae clades (Figure 1.1). Entelegyne females have fertilisation ducts that are separate from the copulation ducts, which are lacking in haplogynes (Figures 1.2, 1.5). In most entelegynes (but also some haplogynes), a sclerotised plate, the epigynum, covers the genital opening (Coddington, 2005, Coddington and Levi, 1991). The monophyly of the Entelegynae is supported by morphological and genetic evidence, but the monophyly of the Haplogynae is contentious (Ayoub *et al.*, 2007, Coddington, 2005).

Among the Entelegynae two major clades are responsible for most of the current spider diversity: the RTA clade (with over 21 000 species in 39 families) and the Orbiculariae (over 11 000 species in 15 families; Blackledge *et al.*, 2009, Coddington, 2005). The retrolateral tibial apophysis (RTA) located on the tibia of the male pedipalp is the synapomorphy that defines the RTA clade. The function of this structure is to anchor the male pedipalp to the female genital opening during copulation (Coddington, 2005, Coddington and Levi, 1991). Many families within this clade have mostly lost the ability to build webs, such as the wolf spiders (Lycosidae), crab spiders (Thomisidae) or the jumping spiders (Salticidae), although some wolf and jumping spider species still build webs (Coddington, 2005, Coddington and Levi, 1991).

The Orbiculariae, the orb-web spiders, consist of two main groups distinguished by the type of silk they produce. The Deinopoidea produce dry cribellate silk while the Araneoidea spin ecribellate, sticky silk. Despite this fundamental difference in silk type, the monophyly of the Orbiculariae and the single origin of the orb-web spiders have recently received molecular support (Blackledge *et al.*, 2009, Garb *et al.*, 2006). Within the Araneoidea, the orb web has subsequently been lost in favour of three-dimensional space webs such as the sheet webs of the Linyphiidae or the tanglefoot/cob webs of the Theridiidae (Blackledge *et al.*, 2003, Coddington, 2005).

1.2.2 External morphology

Spiders have two major body regions, the prosoma and the opisthosoma (also called the cephalothorax and abdomen respectively) joined by a pedicel (Figure 1.2). The prosoma carries six pairs of appendages: the chelicerae, the pedipalps and four pairs of walking legs. The main podomeres (articles) of the

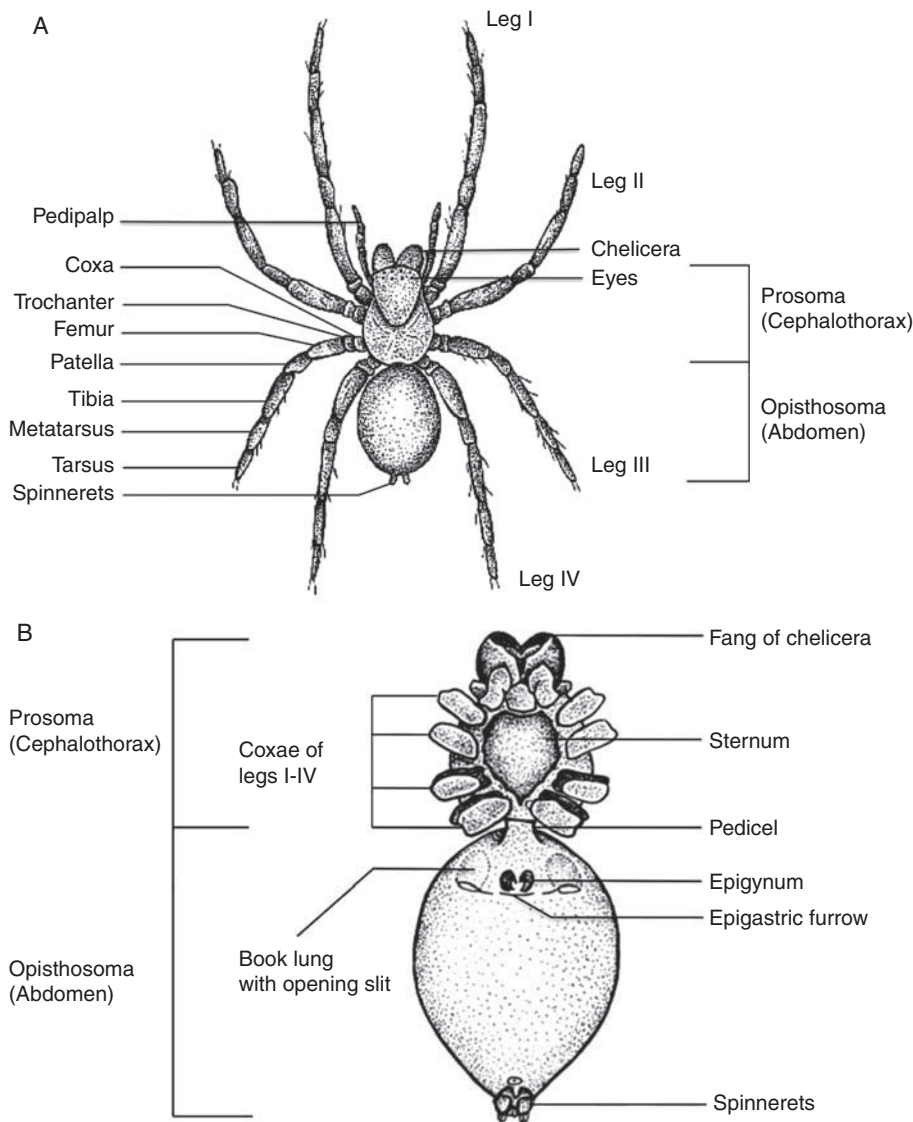


Figure 1.2 External morphology of spiders (A, dorsal view; B, ventral view).
(Redrawn from Jocqué and Dippenaar-Schoeman, 2007, by Monika Hänel with kind permission from Rudy Jocqué and Ansi Dippenaar-Schoeman.)

walking legs are the coxa, trochanter, femur, patella, tibia, metatarsus and tarsus (from proximal to distal end of the legs). The pedipalps contain similar podomeres to the walking legs, but are missing the metatarsus and have at their base a maxilla that surrounds the mouth and connects to the coxa (McGregor *et al.*, 2008). The chelicerae, however, consist of only two segments, with a

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movable distal fang that sits inside a groove in the basal segment when not being used (Yigit *et al.*, 2009). The distal segment of the male pedipalp, the palpal bulb, is modified for sperm transfer and appears to be derived embryologically from the tarsal claw (see Eberhard and Huber, 2010, for a review). Also located on the prosoma are four pairs of eyes (in some groups the number of eyes may be reduced or even lacking).

The opisthosoma also has remnants of four pairs of appendages: two pairs develop into breathing organs called the book lungs while the other two pairs develop into spinnerets. The male and female genital openings are situated on the ventral opisthosoma in the epigastric furrow.

1.2.3 Locomotion

Spiders use their eight legs and their silk as a means of locomotion. The lifestyle (i.e. cursorial or sedentary web building) can usually be deduced from the morphology of the spider, particularly the structure of the tarsal claws (Vollrath and Selden, 2007).

Locomotion on silk

Web-building spiders tend to remain motionless for long periods of time at a hidden or central location in the web. Movement is initiated by stimuli (usually vibratory) indicating the presence of prey, a potential mate or a predator (Harwood, 1974, Venner *et al.*, 2000, Zschokke, 1996). Spiders that build webs have morphological adaptations for walking on silk, such as modifications of the median tarsal claws that grip the silk thread, absent in cursorial spiders (Schütt, 1995). The median tarsal claw hooks onto the silk thread while serrated bristles on either side hold the thread in place (Foelix, 1970b, 1996). Orb-web spiders tend to grip the radial threads when traversing their webs rather than the sticky spirals (Yoshida, 1987).

Spiders leave behind dragline silk (extruded from the anterior spinnerets) as they move about. This acts as a safety line, or a means of communication between individuals such as to locate mates and competitors (e.g. Clark and Jackson, 1994, Leonard and Morse, 2006). The strength of the dragline is altered depending on whether the spider is moving across a vertical or horizontal surface (Garrido *et al.*, 2002). Draglines are also used for dispersal via ballooning. Ballooning spiders release a line of silk into the airstream, release the substrate and are lifted into the air (Suter, 1999a). Ballooning spiders can move distances from a few metres to kilometres (Reynolds *et al.*, 2006). Ballooning is a common method of spiderling dispersal in most spider groups, although rarer in mygalomorphs (Coddington, 2005, Coyle *et al.*, 1985, Hedin and Bond, 2006).

Locomotion on land

Many cursorial spiders use scopulae on the leg tips (claw tufts) to help them walk and climb smooth, steep surfaces. These claw tufts comprise many setae covered with small extensions that end in spatula-shaped tips (Foelix and Chu-Wang, 1975, Niederegger and Gorb, 2006, Roscoe and Walker, 1991).

Jumping spiders have, as indicated by their name, the ability to jump great distances, up to several times their own body lengths. The thrust for the jump is almost entirely generated from the sudden hydraulic straightening of the fourth pair of legs (Parry and Brown, 1959). Jumping is not only an efficient means to bridge gaps but also an effective tool for prey capture (e.g. Bartos, 2002).

Locomotion on water

Spider species that are found in regular association with water may rely on water for foraging (Shultz, 1987a), predator evasion (Johnson and Sih, 2007) and mate location (Arnqvist, 1992). Water is a denser medium than air, and hence requires particular adaptations for locomotion. Spiders that traverse the surface of the water have hydrophobic exoskeletons and cuticular hairs that prevent the animal breaking the surface tension (Suter *et al.*, 1997). The main forms of aquatic locomotion by spiders are rowing, walking, galloping, sailing and diving under the water surface (Barnes and Barth, 1991, Shultz, 1987b, Suter *et al.*, 2003). Sailing is probably one of the least energetically expensive forms of aquatic locomotion, although direction cannot be controlled. It involves the spider using wind currents close to the surface of the water to propel it across the water surface by extending and elevating either the first pair of legs or the entire body from the surface (Suter, 1999b).

Spiders that associate consistently with water are cursorial spiders, particularly the wolf spiders (Lycosidae), while only two species of jumping spiders have been observed to move on water (Stratton *et al.*, 2004). Some spiders, such as the semi-aquatic *Dolomedes* fishing spiders (Lycosidae), are very good at walking, running or rowing on water (Stratton *et al.*, 2004). *Dolomedes* has even been observed jumping vertically on the water surface, a behaviour that has only recently been discounted as an anti-predator behaviour (Suter and Gruenwald, 2000). Only one species of spider, *Argyroneta aquatica* (Cybaeidae), spends its whole life in water (Schütz and Taborisky, 2003). Occasionally, web-building spiders will walk on water, most notably tetragnathids (Suter *et al.*, 2003).

1.2.4 Silk production

Silk plays a central role in the life of spiders. Its function in foraging through webs is obviously best known, but silk is also used to build egg sacs and

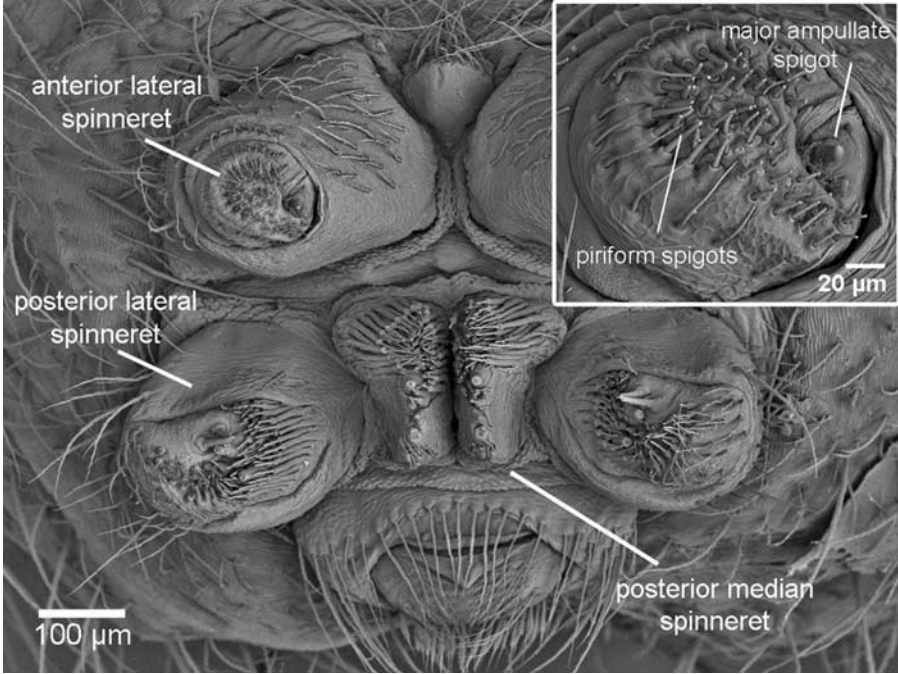


Figure 1.3 Ventral view of orb-web spider spinnerets (*Araneidae: Telaprocera maudae*). Inset: anterior lateral spinneret. Dragline silk is produced from the major ampullate spigot. (Photo credit: Aaron Harmer.)

to line burrows; it facilitates communication between the sexes, and aids in the dispersal of spiderlings (see Craig, 1997, 2003, for review). The silk-spinning apparatus consists of one or more types of silk glands within the opisthosoma that lead via a duct to the numerous spigots located on the external spinnerets (up to four pairs; Craig, 1997, 2003; Figure 1.3).

Silks are semi-crystalline biopolymers, characterised by repeated sequences of amino acids, such as alanine, glycine and serine (Craig, 1997, Kishore *et al.*, 2002). Silk consists of crystalline regions that are dominated by alanine, forming structured β -sheets, and non-crystalline regions. It is thought that β -sheets are responsible for the renowned strength of spider silk. The non-crystalline region is rich in glycine, somewhat less structured and thought to provide the elastic properties of spider silk (see Craig, 1997, Vollrath and Knight, 2001, for review). However, recent models suggest that spider silk may contain various conformations challenging the perhaps simplistic crystalline–amorphous silk concept (Vollrath and Knight, 2001).

The production of a solid silk strand from a liquid protein solution is very complex and generally not very well understood but is best studied in the

dragline silk from the major ampullate gland (see Vollrath and Knight, 2001, for a review). Dragline silk is produced as a liquid in the major ampullate glands and collects in the central lumen (Vollrath, 1999). The liquid is then drawn into a looped duct where water is successively removed. At the distal end of this duct, cells pump hydrogen ions into the duct, thereby increasing the pH within the lumen. The acidic conditions in the distal duct may assist the formation of the silk's β -sheets. An internal valve grips the thread when it passes to the outside via the elastic lips of the spigots, which remove the final coating of water from the silk. The spigots are also important for putting the emerging silk thread under pressure during the air-drawn phase that finalises the transformation from liquid to the solid silk thread (see Vollrath, 1999, Vollrath and Knight, 2001, Vollrath *et al.*, 1998, for a summary).

What distinguishes spider silk from other arthropod silk is the sheer diversity of silk glands and the silk types they produce. For example, orb-web spiders (Araneidae) maintain up to seven different gland types (aciniform, tubuliform, piriform, major ampullate, minor ampullate, flagelliform and aggregate glands; Craig, 1997, Vollrath and Knight, 2001). Silk types are characterised by different fibre compositions and chemical profiles as well as physical properties (Vollrath and Knight, 2001; Figure 1.4).

Even more remarkable is the intraspecific and even intra-individual variation in structure, composition and properties of spider silk. Amino acid composition can vary with diet (Craig *et al.*, 2000, Tso *et al.*, 2005) and the mechanical properties of silk vary with environmental conditions such as climate (Craig *et al.*, 2000, Vollrath, 1999), prey availability (Tso *et al.*, 2007), diet (Zax *et al.*, 2004), spider condition (Crews and Opell, 2006, Madsen *et al.*, 1999) and the speed at which the silk is reeled from the spinneret (Madsen and Vollrath, 2000). The muscular and nervous control over spigots and spinnerets allows the spider to further adjust the diameter of the thread as well as the rate at which it is drawn, affecting the mechanical properties of the finished silk (Craig, 1997). This incredible variation in silk structure and mechanics between and within species

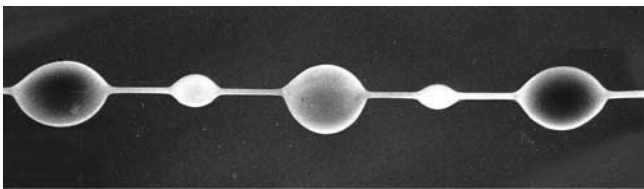


Figure 1.4 SEM of a sticky capture thread in an orb web. Sticky droplets are arranged along an axial fibre. (Reprinted with kind permission from Rainer Foelix.)

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and especially within an individual is a fascinating but not well understood phenomenon.

1.2.5 *Genitalia, mating and reproduction*

Spider internal and external genitalia are extremely variable across taxa but several elements are common to most spiders. The male internal system consists of paired testes in the abdomen that fuse and open through the ventral genital pore in the epigastric furrow (Figure 1.2B). A variety of associated glandular structures may nourish the sperm but may also produce substances that are transferred to the female during mating (e.g. Michalik and Uhl, 2005; see also Chapter 7).

Males do not possess copulatory organs that are directly connected with the testes. Instead the sperm is transferred indirectly via modified appendages, the pedipalps. The male ejaculates sperm through the genital pore onto a specially constructed sperm web. He then dips his pedipalps into the sperm droplet and takes the sperm up into a reservoir in the distal pedipalps. This process is called sperm induction. With the pedipalps charged, males search for females, although in some sheet-web spiders (Linyphiidae) males only fill their pedipalps once they have located a female (Eberhard and Huber, 2010, Foelix, 1996, Weygoldt, 1996).

Spider sperm itself shows very interesting characteristics and variation in morphology across taxa (Alberti, 1990). Unlike most animal sperm, spider sperm is inactive, with a rolled-up tail, when transferred into the female. After a period of storage, the female apparently activates the sperm, which then swim actively to fertilise the eggs. The process responsible for sperm activation is currently unknown. In the more basal spider groups (Mesothelae and Mygalomorphae) sperm is transferred in large aggregates of more than 20 individual sperm encapsulated by a common secretion sheath (coenospermia). Cleistospermia, where each sperm is enclosed and transferred individually, occurs in the more derived araneomorphs, such as the entelegynes and haplogynes. Some haplogynes also transfer completely fused sperm cells (syngametes) that are no longer separated by cell membranes but are surrounded by a common sheath (Michalik *et al.*, 2004). The adaptive value of the different sperm morphologies is intriguing but not well understood.

The female internal reproductive system consists of paired ovaries that fuse to form the uterus externus, which opens in the epigastric furrow. In the Mygalomorphae and Haplogynae (Araneomorphae) the female external genitalia consist of a single opening located near the anterior book lungs leading to a genital cavity (Figure 1.5). A single duct connects the genital cavity with single or multiple sperm storage organs, the spermatheca. Eggs travel from the ovary via