

Wolfgang Nentwig *Editor*

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# Spider Ecophysiology

 Springer

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# Preface

Spiders are among the most successful groups of terrestrial organisms. With more than 42,000 species, spiders are the most numerous predacious arthropod group, only seconded by some insect families such as carabids' beetles or ants. This gives spiders, omnipresent in all terrestrial habitats, a key position in ecological networks and ecosystem functioning. During their evolution of more than 300 million years, spiders developed and improved unique features, the combination of which is regarded as entry for their unrivalled success story. Among the key achievements of spiders at least four have to be mentioned.

First, spiders possess up to six different silk gland types that allow them to use silk for a variety of web types not only to catch their prey but also to wrap their victims until they are defenceless. Spiders build silken retreats, sperm webs, cocoons and draglines, thus demonstrating the remarkable material properties of one of the most resistant and elastic biomaterials. Second, spiders are venomous animals and inject defined venom quantities into a prey item to paralyse or kill it. Spider venom is a complex mixture of hundreds of components, consisting of low molecular compounds, peptides and proteins, which target the extracellular matrix, membranes and a variety of receptors, quite often located in the nervous or muscular system. Third, the locomotion of spiders is driven by a combination of muscles and a hydraulic pressure system, since some leg segments only possess flexor muscles. Instead of extensor muscles, the hydraulic pressure of their haemolymph is fine-tuned by a well-balanced system of valves, which provides the necessary back-pressure. This reduces in major parts of the long leg tubes of spiders the muscle system and allows at the same time larger flexors, so that spiders in general are more powerful than comparable insects. Fourth, the distal end of the male pedipalp developed into a complex structure composed of fixed and movable sclerites that are used to transfer sperm to the female seminal receptacles during mating. This key-lock mechanism guarantees safe sperm transfer within the species, largely preventing mating outside the own species, and probably represents a major driver for the fast species radiation we observe in spiders.

Ecophysiology is a bridge from functional and evolutionary aspects of morphology, physiology, biochemistry and molecular biology to ecology. Currently,

cutting-edge science in spiders focuses on the circulatory and respiratory system, locomotion and dispersal abilities, the immune system, endosymbionts and pathogens, chemical communication, gland secretions, venom components, silk structure, structure and perception of colours and colouration and nutritional requirements, to name only a few. Spiders became valuable indicator species in agroecosystems and for conservation biology. Modern transfer and application technologies consider spiders and their products with respect to biomimetics, material sciences and agrochemical and pharmaceutical industries.

It is now 26 years ago that I edited a first comprehensive book on ecophysiology of spiders, published also with Springer [Nentwig W (ed) (1987) *Ecophysiology of spiders*. Springer, Heidelberg]. Scientific progress since then was remarkable and an evaluation of the topics from that time and relevant publications over the last two decades showed the appearance of many new fascinating subjects. A new book on the old subject, therefore, is definitely not just a revised version but became something completely new. Seven subjects from the old book (on colouration, respiration system, reproductive glands, pheromones, venom, silk and dispersal) can also be found in this new book, most of them now represented by several much more detailed chapters and with a completely new content. Moreover, many additional and intriguing aspects are included. The innovative character of this book and of spider ecophysiology is also underlined by the fact that only two author teams from the old book contributed to this new book (Mark Townley with Ed Tillinghast and me, obviously dinosaurs in arachnology).

Special thanks go to Springer Publishers with Annika König and Jutta Lindenborn. I also want to acknowledge the support from Christian Kropf and Rita Schneider.

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*Wolfgang Nentwig*

# Contents

## Part I Respiration and Circulatory System

- 1 **Evolution and Adaptation of Hemocyanin Within Spiders . . . . .** 3  
Thorsten Burmester
- 2 **The Circulatory System of Spiders . . . . .** 15  
Christian S. Wirkner and Katarina Huckstorf
- 3 **Tracheae in Spiders: Respiratory Organs  
for Special Functions . . . . .** 29  
Anke Schmitz

## Part II Locomotion and Dispersal

- 4 **Hydraulic System of Locomotion . . . . .** 43  
Christian Kropf
- 5 **Functional Aspects of Spider Scopulae . . . . .** 57  
Senta Niederegger
- 6 **Cost–Benefit Balance of Dispersal and the Evolution  
of Conditional Dispersal Strategies in Spiders . . . . .** 67  
Dries Bonte

## Part III Immune System and Pathogens

- 7 **The Immune System of Spiders . . . . .** 81  
Lucia Kuhn-Nentwig and Wolfgang Nentwig
- 8 **Endosymbiont Infections in Spiders . . . . .** 93  
Sara L. Goodacre and Oliver Y. Martin
- 9 **Fungal Pathogens of Spiders . . . . .** 107  
Harry C. Evans



## Part IV Chemical Communication and Reproduction

- 10 Chemical Communication and Contact Cuticular Compounds in Spiders** . . . . . 125  
Marie Trabalon
- 11 Spider Olfaction: Attracting, Detecting, Luring and Avoiding** . . . . 141  
Gabriele Uhl
- 12 Karyotypes, Sex Chromosomes, and Meiotic Division in Spiders** . . . . . 159  
Tereza Kořínková and Jiří Král
- 13 Male Reproductive System of Spiders** . . . . . 173  
Peter Michalik and Elisabeth Lipke

## Part V Venom

- 14 Main Components of Spider Venoms** . . . . . 191  
Wolfgang Nentwig and Lucia Kuhn-Nentwig
- 15 The Neurotoxic Mode of Action of Venoms from the Spider Family Theraphosidae** . . . . . 203  
Volker Herzig and Glenn F. King
- 16 The Cytotoxic Mode of Action of the Venom of *Cupiennius salei* (Ctenidae)** . . . . . 217  
Lucia Kuhn-Nentwig and Wolfgang Nentwig
- 17 The Evolution of a Toxic Enzyme in Sicariid Spiders** . . . . . 229  
Greta Binford
- 18 Predation by Spitting Spiders: Elaborate Venom Gland, Intricate Delivery System** . . . . . 241  
Robert B. Suter and Gail E. Stratton
- 19 Spider Venoms Potentially Lethal to Humans** . . . . . 253  
Wolfgang Nentwig and Lucia Kuhn-Nentwig

## Part VI Silk

- 20 Spider Silk: Molecular Structure and Function in Webs** . . . . . 267  
Todd A. Blackledge
- 21 Aggregate Silk Gland Secretions of Araneoid Spiders** . . . . . 283  
Mark A. Townley and Edward K. Tillinghast
- 22 Cribellar Thread** . . . . . 303  
Brent D. Opell

**Part VII Colouration**

**23 Insect View of Orb Spider Body Colorations . . . . . 319**  
 I-Min Tso

**24 Structural Colors in Spiders . . . . . 333**  
 Rainer F. Foelix, Bruno Erb, and David E. Hill

**25 UV and Camouflage in Crab Spiders (Thomisidae) . . . . . 349**  
 Marie E. Herberstein and Felipe M. Gawryszewski

**26 Rapid Colour Change in Spiders . . . . . 361**  
 Judith Wunderlin and Christian Kropf

**Part VIII Nutrition**

**27 Nutritional Aspects of Spider Feeding . . . . . 373**  
 Søren Toft

**28 Herbivory in Spiders . . . . . 385**  
 Dirk Sanders

**29 Artificial Diets for Spiders . . . . . 393**  
 Divina M. Amalin

**Part IX Ecotoxicology**

**30 Effects of Heavy Metal Contamination . . . . . 403**  
 Paweł Migula, Grażyna Wilczek, and Agnieszka Babczyńska

**31 Side Effect of Synthetic Pesticides on Spiders . . . . . 415**  
 Stano Pekár

**32 Side Effects of *Bacillus thuringiensis* Toxins on Spiders . . . . . 429**  
 Michael Meissle

**33 Effects of Neem on Spiders . . . . . 441**  
 John D. Stark

**Part X Applications**

**34 Modelling and Application of the Hydraulic Spider Leg Mechanism . . . . . 451**  
 Lena Zentner

**35 Adhesion to Flat Surfaces: From Spiders to Stickers . . . . . 463**  
 Tobias Seidl and Renato Vidoni

**36 Technical and Biomedical Uses of Nature’s Strongest Fiber:  
Spider Silk** . . . . . 475  
Christina Allmeling, Christine Radtke, and Peter M. Vogt

**37 Spider Venom Components as Drug Candidates** . . . . . 491  
Vera Oldrati, Estelle Bianchi, and Reto Stöcklin

**Appendix. Spider Phylogeny** . . . . . 505

**Subject Index** . . . . . 511

# Part I

## Respiration and Circulatory System

Different from insects, spiders do not transport aerial oxygen directly to the cells, but use their hemolymph as intermediate transport system, thus they more resemble crustacean, molluscs, or even vertebrates. Such a respiratory system demands structures to saturate carrier proteins with oxygen (hemocyanin) and a circulatory system for the hemolymph. Starting with a not very efficient ancestral type, spiders tuned their systems considerably: they reorganized their lung system, modified their circulatory system, and experimented with their tracheal system. Spiders did not really reach the high performance of many insects, but considering the evolutionary constraints, they did the best they could.

# Chapter 1

## Evolution and Adaptation of Hemocyanin Within Spiders

Thorsten Burmester

### 1.1 Introduction

The transport and storage of oxygen in animals are mediated by three distinct types of respiratory proteins (hemoglobins, hemerythrins or hemocyanins). In many arthropod and mollusc species, oxygen is bound to large copper proteins referred to as hemocyanins, which occur freely dissolved in the hemolymph (Markl and Decker 1992; van Holde and Miller 1995). However, arthropod and mollusc hemocyanins belong to different protein families and evolved from distinct types of copper-containing enzymes already in the Precambrian (Burmester 2001). Arthropod hemocyanins originated from the phenoloxidases, which are  $\text{Cu}^+$ -containing enzymes involved in immune response and cuticle sclerotisation (Burmester 2002). Some arthropod taxa have lost hemocyanin and rely on hemoglobin for oxygen supply (Weber and Vinogradov 2001) or lack any respiratory protein. In some decapod crustaceans and in the hexapods, hemocyanin-related proteins that do not bind  $\text{O}_2$  occur. These proteins, referred to as pseudo-hemocyanins (cryptocyanins) or hexamerins, respectively, are considered mainly as storage proteins but may also have other, non-respiratory functions (Burmester 1999a, b; Terwilliger et al. 1999).

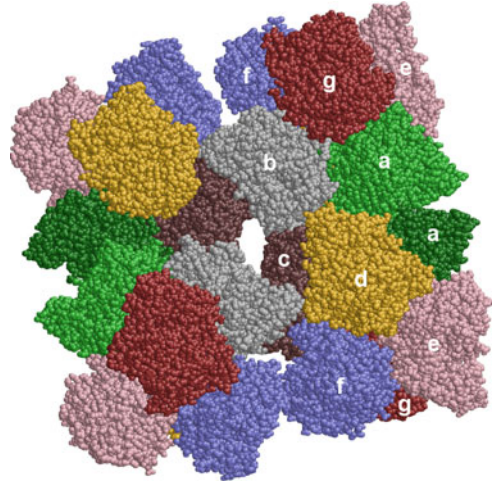
The general structure of an arthropod hemocyanin is highly conserved. The protein is built by hexamers or oligo-hexamers of subunits in the range of 70–85 kDa (Markl and Decker 1992; van Holde and Miller 1995). Each subunit can bind one  $\text{O}_2$  molecule by the means of two  $\text{Cu}^+$  ions, each of which being coordinated by three conserved histidines of the polypeptide chain (copper A and copper B binding sites). The arthropod hemocyanins may assemble to large structures (Fig. 1.1), which consist of up to 48 subunits ( $8 \times 6$ -mer structure) and have a mass of up to 3,600 kDa (Markl and Decker 1992). The subunits that build an

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**Fig. 1.1** Structure of *Aphonopelma hentzi*  $4 \times 6$ -mer hemocyanin. The seven subunit types are labeled on the two right-hand side hexamers and displayed in different colors: (a) *green*; (b) *gray*; (c) *brown*; (d) *yellow*; (e) *pink*; (f) *blue*; (g) *red*

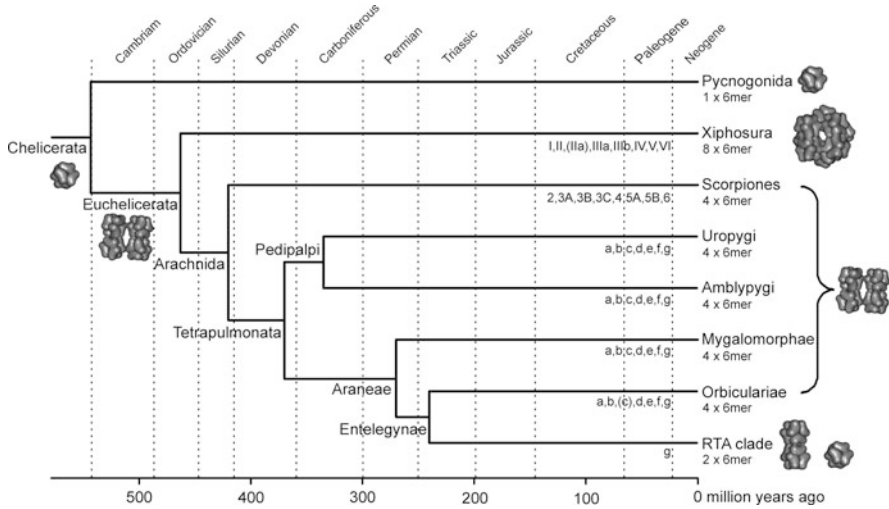


oligomer may either be identical, deriving from the same gene, or structurally related and thus coded by distinct genes. Subunit composition and assembly in each hemocyanin is essentially taxon specific (Markl 1986; Markl et al. 1986). While in some decapod crustaceans, subunit composition and structure may change during development or in response to environmental challenges (Durstewitz and Terwilliger 1997a, b), the hemocyanins in the other arthropod taxa appear to be more conservative, without any known variations throughout the life cycle. Moreover, subunit compositions of the oligomeric hemocyanins in many chelicerate taxa have remained unchanged for several 100 million years (Markl 1986; Markl et al. 1986; Rehm et al. 2012).

## 1.2 Evolution of Chelicerate Hemocyanins

### 1.2.1 Occurrence and Evolution of Hemocyanins in Chelicerates

A typical chelicerate hemocyanin subunit comprises 620–630 amino acids (70–75 kDa). The evolutionary rate is comparatively low and in the range of  $0.5\text{--}0.6 \times 10^{-9}$  amino acid replacements per site per year, which is about two- to threefold lower than in the crustacean hemocyanins (Burmester 2002). Biochemical and structural studies showed that a chelicerate hemocyanin may consist of up to eight distinct subunit types, which assemble to oligomers of either  $1 \times 6$ ,  $2 \times 6$ ,  $4 \times 6$  or  $8 \times 6$ mers (Markl 1986; Markl et al. 1986). Each of the single subunits occupies a defined position in the native protein, which mirrors up to 520 million years of independent evolutionary history (Rehm et al. 2012). Hemocyanin proteins or cDNA sequences have been identified in the Pycnogonida (sea spiders or



**Fig. 1.2** Timescale of the evolution of chelicerates and evolution of hemocyanin structures. Adapted from Rehm et al. (2012). Note that only taxa for which hemocyanin sequences are available are displayed

Pantopoda), Xiphosura (horseshoe crabs), Scorpiones (scorpions), Amblypygi (whip spiders), Uropygi (whip scorpions) and Araneae (true spiders). By contrast, no hemocyanin has been found in the Opiliones (harvestmen), Pseudoscorpiones (false or book scorpions), Solifugae (camel or sun spiders) and Acari (mites and ticks) (Markl 1986; Markl et al. 1986; Rehm et al. 2012). There is at present no information on the hemocyanin status of the Palpigradi (microwhip scorpions) and Ricinulei (tickspiders).

Most studies agree that the Pycnogonida are the closest relatives of the Euchelicerata. A single hemocyanin subunit cDNA was found in the sea spider *Endeis spinosa*, indicating that the hemocyanin protein of this species is a homohexamer (Rehm et al. 2012) (Fig. 1.2). However, there are no biochemical studies to confirm this notion. Phylogenetic analyses identified this sequence in a sister group position to all other chelicerate hemocyanin subunits, indicating that the hemocyanins of the stem group chelicerates had a similar simple, possibly homohexameric structure. The horseshoe crabs (Xiphosura) have the largest hemocyanin molecules. These  $8 \times 6$ mers consist of seven or eight distinct subunit types (Markl 1986; Markl et al. 1986). The *Limulus polyphemus* hemocyanin, which is the best investigated hemocyanin of the Xiphosura, is composed of  $6 \times$  subunit type I,  $8 \times$  II,  $2 \times$  IIA,  $8 \times$  IIIA,  $8 \times$  IIIB,  $8 \times$  IV,  $4 \times$  V,  $4 \times$  VI. Orthologous subunits have been identified in other xiphosurans (Sugita and Shishikura 1995), which have only seven subunit types and no subunit IIa. The complete subunit sequences are available from *Carcinoscorpius rotundicauda* (GenBank acc. nos. DQ090469–DQ090484), which have, however, not been formally published.