Biologically-Inspired Systems

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Functional Surfaces in Biology III

Diversity of the Physical Phenomena

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Motto: Structure and function of biological systems as inspiration for technical developments
Throughout evolution, nature has constantly been called upon to act as an engineer in solving technical problems. Organisms have evolved an immense variety of shapes and structures from macro down to the nanoscale. Zoologists and botanists have collected a huge amount of information about the structure and functions of biological materials and systems. This information can be also utilized to mimic biological solutions in further technical developments. The most important feature of the evolution of biological systems is multiple origins of similar solutions in different lineages of living organisms. These examples should be the best candidates for biomimetics. This book series will deal with topics related to structure and function in biological systems and show how knowledge from biology can be used for technical developments in engineering and materials science. It is intended to accelerate interdisciplinary research on biological functional systems and to promote technical developments. Documenting of the advances in the field will be important for fellow scientists, students, public officials, and for the public in general. Each of the books in this series is expected to provide a comprehensive, authoritative synthesis of the topic.

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Preface: Diversity of the Physical Phenomena in Biological Surfaces

In 2009, in two volumes of "Functional Surfaces in Biology I and II", we quite naively tried to cover the diversity of the physical phenomena in biological surfaces (Gorb 2009a, b). However, it turned out that the field of functional biological surfaces is a very rapidly growing one with an increasing number of subfields, which are difficult to comprise even within several issues. The "Functional Surfaces in Biology III" continues the idea of the two previous issues and presents a new collection of chapters written in form either of topical reviews or original papers and devoted to structure-property relationships of biological surfaces.

Meanwhile it is well known that this kind of studies can inspire further technological developments (Heepe et al. 2017); however, the present book is primarily concentrated on interesting aspects of biological systems rather than on the development of technical systems inspired by mechanisms observed in biological systems. In other words, this issue aimed at revealing novel functional aspects of biological surfaces rather than implementing this knowledge in biomimetics.

The "Functional Surfaces in Biology III" shows a broad variety of facets of structural and experimental research on various biological surfaces in general. It covers a wide range of biological systems (from infrared receptors, photonic systems, moisture harvesting microstructures, water/oil absorbing surfaces, gas exchanging interfaces to adhesion enhancing and friction reducing systems) and their structure-function relationships and can be therefore interesting for biologists, physicists, chemists as well as materials scientists and engineers fascinated by the idea of biomimetics.

The first chapter by Anke Schmitz and Helmut Schmitz is devoted to the role of the cuticular surfaces in infrared reception of pyrophilous ('fire-loving') insects that rely on forest fires for their reproduction. In these insects, both the navigation towards a fire and short-range orientation on a freshly burnt material depend on a variety of specialized infrared sensors located on the thorax and abdomen. The chapter reviews the studied insect infrared receptors with an emphasis on the cuticle role in infrared perception. The authors distinguish three designs of receptors based on two different functional principles, which in turn rely on specialized types of cuticle serving as an interface between incoming radiation and sensory cells.

The Chap. 2 by Mikhail Kryuchkov, Artem Blagodatski, Vsevolod Cherepanov, and Vladimir L. Katanaev opens biophotonic section of the book. It provides an overview of the diversity of arthropod corneal nanostructures, which can be of nipple-, ridge-, maze-, or dimple-type with various transitions among them. With a diameter being thinner than the wavelength of the visible light, these structures provide a variety of functions ranging from reflection reduction to the enhancement of water-repellence. Interestingly, the entire diversity of these structures can be described by simple reaction-diffusion models that can explain formation of arthropod corneal nanostructures during eye development. The authors' vision is that real molecular identities, responsible for these reactions, can be revealed in model insect organisms and potentially used in bioengineering of novel nanocoatings.

In the Chap. 3, Villads Egede Johansen, Olimpia Domitilla Onelli, Lisa Maria Steiner, and Silvia Vignolini discuss biological structural colours caused by pigments organized in specific nano-scale architectures. Interestingly, these architectures in biological systems are very often not perfectly ordered, and such a disorder provides a broad range of functional optical effects. The authors discuss the influence of disorders on the photonic effects of biological surfaces by taking an example of the blue-winged *Morpho* butterfly. The role of hierarchical organization and pixelated surfaces is also demonstrated in the context of their role in tuning optical appearances of biological surfaces. Finally, this chapter provides mathematical tools for disorder analysis and using them describes examples of completely disordered structures having white appearance, such as in the dorsal surface of *Cyphochilus* beetle.

The Chap. 4 by Anna-Christin Joel, Gerda Buchberger, and Philipp Comanns opens section on the surface wettability by the review of structure-function relationships in moisture-harvesting reptiles that live in arid environments. The authors reveal special microstructural adaptations of the reptile integument enabling additional moisture-harvesting from various sources. Interestingly, this ability is often accompanied by a specific animal behavior. Most of these reptiles possess highly-specialized skin structures in form of microscopical capillary channels facilitating water flow in the anterior direction of the body. The authors discuss biomimetic potential (especially in the field of microfluidics) of these structural and experimental studies on reptiles.

The Chap. 5 by Anita Roth-Nebelsick, Frank Hauber, and Wilfried Konrad on porous structures for water absorption and gas exchange in orchids continues the wettability section. It is known that epiphytic orchids possess aerial roots with a special outer tissue layer, so called the velamen radicum, aiding in water condensation from the air and its absorption. The velamen radicum presumably played a very important role in successful radiation of epiphytic orchids. The authors show here that this tissue consists of dead cells building up a porous material with highly adapted surface and underlying tissues with interesting water draining behavior strongly depending on the thickness and structure of the tissue. They also provide comparison of velamen radicum in various orchid taxa and discuss structure-function relationships of this system.

The Chap. 6 by Elena V. Gorb, Philipp Hofmann, Alexander E. Filippov, and Stanislav N. Gorb deals with the adsorption ability of epicuticular wax coverages in plants that have been often shown to be impeding locomotion and reducing attachment of insects. One of mechanisms responsible for these effects, a possible adsorption of insect adhesive fluid by highly porous wax coverage, has been previously proposed. This chapter reports on experimental tests proving the adsorption ability of different fluids by plant wax blooms. Using a cryo scanning electron microscopy approach, high-speed video recordings of fluid drops behavior and numerical analysis of experimental data, the authors show that the wax coverage in the waxy zone of *Nepenthes alata*pitcher can strongly adsorb oil, but not water, which is a strong evidence that three-dimensional plant wax coverages will be anti-adhesive for insects relying on wet adhesion by oily substances.

The Chap. 7 by Janek von Byern, Carsten Müller, Karin Voigtländer, Victoria Dorrer, Martina Marchetti-Deschmann, Patrick Flammang, and Georg Mayer provides an overview of biological adhesives utilized by more than 100 marine and terrestrial organisms for defence and predation. These functions require specific combination of particular behaviours and properties of the adhesive, such as fast curing process, squirting over distance, bonding to various substrates, but organisms' protection against own glue. These organisms have a very wide environmental and phylogenetic diversity: hagfish, comb jellies, centipedes, salamanders, spiders, glowworms, velvet worms, etc. The review collects scattered published information about the composition, production, secretion mechanisms and mechanical properties of these glues, however, it concludes that only little is known about their functional principles. We are very much convinced that this chapter will facilitate new experimental studies on biological adhesives.

A case study from bioadhesion research is provided in the Chap. 8 by Lars Heepe, Constanze Grohmann, and Stanislav N. Gorb. This chapter deals with the visualization of tarsal adhesive setae in contact during normal and ceiling walk in the ladybird beetle. These setae form an intimate contact with the substrate and generate adhesion supporting insect walk on vertical walls or even on the ceiling. Previous adhesive force measurements at the level of individual setae provided estimation of the maximum adhesive capability of animals by assuming all setae being in contact. However, these values do not coincide with the results of adhesion measurements performed at the level of the whole animal. This discrepancy is due to the fact that not all setae are simultaneously applied during locomotion and this chapter deals with quantification of the beetle adhesive setae used during locomotion. It turned out that beetles use considerably more setae in contact during ceiling walk than during normal walk. The authors conclude that in order to control adhesion, animals are capable of controlling not only the amount of tarsal setae in contact, but also the type of setae depending on the type of substrate.

Another example of an effective high-speed biological adhesion is an adhesive tongue of frogs, which is an efficient tool capable of capturing fast moving prey. It is obvious that the interaction between the tongue surface and an adhesive mucus coating is crucial for generating strong pull-off forces with the prey surface. The Chap. 9 by Thomas Kleinteich and Stanislav N. Gorb is a comparative study of tongue surfaces in nine frog species bearing microscopical papillae of different size and shape. The specific microstructure presumably contributes to the particular adhesive performance of different frog species and may correlate with the prey spectra between the taxa studied. This study also opens an interesting possibility of combining surface microstructure with adhesive fluids to enhance dynamical performance of the next generation of adhesives.

In fish, the combination of the scale surface structure with mucus leads to the friction reduction and generation of slippery surfaces. Dylan K. Wainwright and George V. Lauder discuss this system in detail in the Chap. 10 called "Mucus matters". The authors describe different categories of scales (cycloid, crenate, spinoid, ctenoid) and discuss structure-function relationships of sub-scale features, such as spines, ctenii, radii, and circuli. The authors suggest that three-dimensionality of these features is crucial for their hydrodynamic and protective functions. Additionally, fishskin is covered by mucus which was often ignored in previous studies. This chapter presents three-dimensional analyses of intact fish skin surfaces from seven species and compares them to the skin with the removed epidermis and mucus. This approach allowed demonstrating how mucus and epidermis interact with the scale surface and result in the functional surface texture, which remains a largely unexplored area. A very important feature of this chapter is the discussion on techniques for investigation and imaging the structure of fish surface, such as for example gel-based surface profilometry.

Another friction-related study is the book final Chap. 11 by Yoko Matsumura, Alexander E. Kovalev, Alexander E. Filippov, and Stanislav N. Gorb. It is devoted to the friction reduction mechanism during the super-long penis propulsion in beetles. There is no doubt that surface interactions of the male and female genitalia during copulation play a key role in evolution, but the morpho/physical diversity of interacting surfaces and their biomechanics in sexual intercourse of the vast majority of animals are not well studied. The authors take male and female genitalia in cassidinebeetles as a model system and using microscopical analysis of material composition reveal stiffness gradient in male penis. Furthermore, they numerically model its propulsion into the female duct. This simulation demonstrates that the type of the stiffness gradients observed in the real male (softer at the tip and stiffer at the base) aids in the faster propulsion than other types. This chapter indicates that previously ignored physical properties of genital surfaces may aid in understanding physical interactions of sexes and shed light on the evolution of genitalia.

In general, this book discusses numerous experimental methods for the characterization of the mechanical and optical properties of biological surfaces at the micro- and nanoscale. It combines approaches from biology, physics, chemistry, materials science, and engineering and therefore represents a good example of modern interdisciplinary science. Due to this latter reason, we hope that the contributions from this book will be of interest to both engineers and physicists, who use inspirations from biology to design technical surfaces and systems, as well as to biologists, who apply physical and engineering approaches to understand how biological systems function.

The editors would like to thank all the authors for contributing their first-class work to this book. We are also grateful to all referees Harvey B. Lillywhite (University of Florida, USA), Wolfgang Böhme (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany), Uwe Erb (University of Toronto, Canada), Dennis LaJeuness (The University of North Carolina at Greensboro, USA), Bodo Wilts (Adolphe Merkle Institute, Fribourg, Switzerland), Vladimir V. Tsukruk (Georgia Institute of Technology, Atlanta, USA), Akira Saito (Osaka University, Japan), Shinya Yoshioka (Tokyo University of Science, Japan), Douglas S. Fudge (Chapman University, Orange, USA), Mason Dean (Max Planck Institute of Colloids and Interfaces, Potsdam, Germany), Doekele G. Stavenga (University of Groningen, The Netherlands), Victor Benno Meyer-Rochow (Research Institute of Luminous Organisms, Tokyo, Japan), Lloyd Graham (CSIRO, North Epping, Australia), and Robert B. Suter (Vassar College, USA) for their constructive reports, which facilitated the high quality of the manuscripts and also allowed us to publish in a timely manner. Finally, we thank the Editorial Team at Springer-Nature for their continuous great support of biology- and biomimetics-related topics within BISY book series.

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Part I
Receptors

Chapter 1
Cuticle as Functional Interface in Insect Infrared Receptors

Anke Schmitz and Helmut Schmitz

Abstract Pyrophilous (‘fire-loving‘) insects depend on forest fires for their reproduction. Therefore, such insects approach ongoing fires and invade the freshly burnt area immediately. In beetles members of two genera of jewel beetles (Buprestidae) and one species of the genus *Acanthocnemus* (Acanthocnemidae) show a highly pyrophilous behaviour. Additionally, pyrophilous behaviour has also been described for four species of the large flat bug genus *Aradus* (Aradidae). For the long-range navigation towards a fire as well as for the short-range orientation on a freshly burnt area these insects have developed special sensors for the smell of burning and for infrared (IR) radiation. Whereas the olfactory receptors for smoke are located on the antennae, the IR receptors are housed in extraantennal sensory organs. Although the community of pyrophilous insects is rather small, no ‘standard’ IR receptors exist. Receptors are located on the thorax or on the abdomen and show a stunning diversity with respect to structure and function. Two functional principles and three fundamentally different designs have been described. Nevertheless, in all receptors the cuticle plays an important role as interface between incoming radiation and the associated sensory cells. The cuticular apparatus of an IR receptor, therefore, has to manage effective absorption and subsequent fast transformation of photon energy into a state variable which can be perceived by the sensory cells. The chapter provides an overview about the known insect IR receptors with a focus on the impact of the cuticle in IR perception.

1.1 Introduction

About 25 insect species are attracted by forest fires and can be found on freshly burnt areas after fires. In three genera of pyrophilous beetles and one genus of pyrophilous bugs infrared (IR) receptors have been discovered. Although the number of IR sensitive insects is extremely small, no standard insect IR receptor exists. At least in three of the four IR sensitive genera receptors look totally different and

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are located on different parts of the body. As a result, at least two different functional principles can be distinguished: bolometer like receptors and so-called photomechanic receptors. Consequently, insect IR receptors can be innervated by thermo- or mechanosensitive cells. However, in all insect IR receptors the IR absorbing cuticle is the very important interface ensuring effective absorption of IR photons and subsequent conversion of the photon energy into a stimulus detectable by the corresponding sensory cell. Insect cuticle can be regarded as a composite material consisting of biopolymers that show strong IR absorption bands in the mid infrared radiation region (MWIR). During the independent evolution of insect IR receptors in the four genera the cuticular components of the receptors have undergone profound structural and functional modifications to be able to fulfill their respective sensory tasks.

In this chapter the infrared organs of pyrophilous insects are outlined. Especially the IR absorbing cuticular apparatus of the different IR receptors and how absorbed IR quantum energy is transformed into a signal perceivable for the inherent sensory cells is in the focus of interest. After a short introduction in the nature of infrared radiation the pyrophilous behavior and the bolometer like IR receptors of the Australian Little Ash Beetle *Acanthocnemus nigricans* and the Australian Firebeetle *Merimna atrata* are described. Then the behavior and the so-called photomechanic IR receptor of buprestid beetles of the genus *Melanophila* and flat bugs of the genus *Aradus* are introduced. In the discussion the cuticle as effective IR absorber is dealt with and finally the different routes of converting IR quantum energy into bioelectric signals are highlighted.

1.2 Physical Properties of Infrared Radiation

Every body with a temperature above 0 K (−273.15 °C) emits IR radiation. This is caused by molecular movements starting at temperatures slightly above 0 K. In nature and engineering IR radiation can be used for the detection of objects with a temperature higher or lower than the ambient temperature. This is especially useful in complete darkness. Detection of IR radiation requires special detectors. Two classes of IR detectors are currently used: uncooled bolometer sensors and much more sensitive cooled quantum detectors. In a bolometer the temperature of an IR absorbing surface is measured with a temperature sensor; in a quantum detector the energy of an absorbed IR photon induces an electrical effect in a semiconductor material which can be read out with an integrated circuit. To suppress the thermal noise in the semiconductor, sensors routinely are cryogenically cooled. In this chapter electromagnetic radiation significant for living organisms is considered. Here the upper limit is represented by the surface temperature of sun at 5800 K; the lower limit by objects at ambient temperature. In their natural environment organisms are primarily subjected to a radiation spectrum ranging from high-level ultraviolet (UV) down to low-energy infrared (IR) radiation (Fig. 1.1). The spectral distribution of the radiation emitted e.g. by a high intensity forest fire with a temperature of 1300 K can be calculated according to Planck's radiation law. At a given temperature the wavelength at which most of the radiant energy is emitted (λ_{max}) can be calculated by the law of Wien:

$\lambda \max = \frac{2,897.8\left[\mu \mathrm{m} * K\right]}{\mathrm{T}\left[\mathrm{K}\right]}$,where T is the absolute temperature given in Kelvin [K].

For the perception of radiation in the mentioned wavelength range the photon energy is of special importance. When trying to detect an object by electromagnetic radiation (either emitted or reflected by the object) an ideal sensor should have its highest sensitivity at λ_{max} of the radiation source. This is realized in e.g. in photoreceptors of most diurnal animals, where the rhodopsin of the light-sensitive rods enabling scotopic vision exhibits its λ_{max} at about 0.5 μm (Schoenlein et al. 1991; Bowmaker and Hunt 2006), perfectly matching the emission maximum of the sun. In general, the spectral sensitivity of photo pigments is determined by the interaction of retinal with specific amino acids lining the ligand-binding pocket within the opsin (Bowmaker and Hunt 2006). Thus, the ability to see in the IR requires pigments showing sufficient absorption (i) in the *near infrared* (NIR, 0.75–1.4 μm (D'Amico et al. 2009)), (ii) in the *mid wavelength infrared* (MWIR, 3–8 μm) or (iii) even in the *long wavelength infrared* (LWIR, 8–12 μm; Fig. 1.1). The corresponding frequency f of an IR photon of a given wavelength λ can be calculated according to $f = c/\lambda$ with c = speed of light. Although some animals, e.g. some fish living in turbid waters, are obviously able to see in the NIR (Meuthen et al. 2012; Shcherbakov et al. 2013) by *"long-wavelengths"* (LWS) photoreceptors. However, LWS receptors with absorbance spectra beyond 800 nm are unknown (Douglas et al. 1998). The first essential step in vision always is the cis-trans torsional isomerization of the

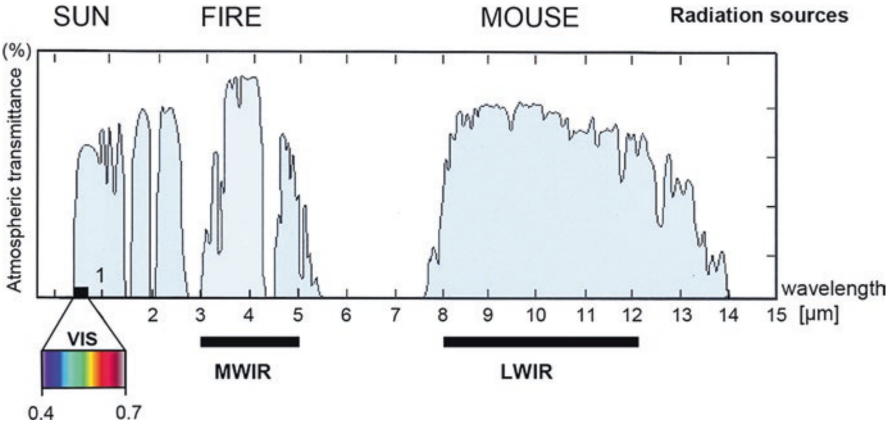


Fig. 1.1 Atmospheric transmittance of electromagnetic radiation emitted from objects with biological relevance. Atmospheric windows (indicated in blue) exist for visible light (VIS) radiated from the sun, MWIR radiated from high temperature sources like forest fires, and LWIR radiated from low temperature sources like warm-blooded creatures

rhodopsin chromophore (Schoenlein et al. 1991). This conformational switch requires a photon energy of more than 1.24 eV (the energy content of a 1 μm photon). However, IR photons emitted by a fire or a warm-blooded creature do not carry enough energy to initiate the isomerization of a visual pigment.

Consequently, in technical and biological IR receptors other mechanisms for converting the energy of an absorbed IR photon into an appropriate signal have to be realized. After absorption at the surface of a biological IR receptor thermal and/or mechanical effects initiated in the absorber material could be measured by underlying sensory cells. Thus it is proposed that the absorbing surfaces as well as the structuring of the absorber material have been improved by evolution to maximize these processes.

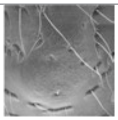
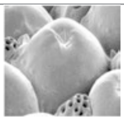
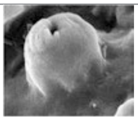
1.3 IR Receptors in Pyrophilous Insects

A fire not only devastates a forest but also creates a very interesting ecological niche within minutes: the burnt area (Bond and Keeley 2005). On a freshly burnt area, most biotic as well as many abiotic factors have changed dramatically. For insect species which feed on dead wood or fungi, such a place is of great interest (Saint-Germain et al. 2008). However, the area has to be approached quickly before more and more competitors arrive. In this regard it is of interest that ecological investigations have shown that a small community of insects can be found more frequently on burnt than on unburnt areas. This particular group of so-called pyrophilous insects consists of about 40 species out of the orders of Coleoptera, Hemiptera, Diptera, and Lepidoptera (Wikars 1997). It can be proposed that pyrophilous insects have developed sensory and behavioral adaptations to detect and approach fires and burnt areas. This is especially true for species which can be found on freshly burnt areas immediately after a fire.

In contrast to an approach by olfactory cues which can be considerably impeded by the wind, especially over longer distances, an orientation by electromagnetic radiation in the visible and in the infrared (IR) spectrum allows a straight approach to the source. This is also promoted by an atmospherical window transparent for MWIR (mid wavelength IR) radiation between 3 and 5 μm (Fig. 1.1). So it is evident that pyrophilous insects appear to be predestined to have evolved IR receptors.

At present 17 insect species out of four pyrophilous genera are known to possess IR sensory organs (Table 1.1). Compared to the amount of known insect species (roughly one million) this is a negligible number. Even though IR receptors are very rare in insects, no “standard” IR receptor seems to exist. At least three fundamentally different types of receptors could be identified: a pair of prothoracic discs covered with numerous tiny sensilla in *Acanthocnemus nigricans*, pairs of roundish abdominal IR organs in *Merimna atrata*, and the so-called photomechanic IR sensilla in *Melanophila* beetles and in a few species of pyrophilous *Aradus* bugs. With regard to the functional principles, two categories exist: bolometer-like receptors in *Acanthocnemus* and *Merimna* and photomechanic sensilla in *Melanophila* and

Table 1.1 Infrared receptors in pyrophilous insects

	'Little Ash Beetle' *Acanthocnemus nigricans* Only species in the genus	'Australian Fire Beetle' *Merimna atrata* Only species in the genus	'Black Fire Beetles' *Melanophila spec.* 11 species with IR receptors	'Pyrophilous Flat Bugs' *Aradus spec.* 4 species with IR receptors
Systematic position	**Beetle** (family: Acanthocnemidae)	Jewel **beetles** (family: Buprestidae)		Flat **bugs** (family: Aradidae)
Ventral habitus IR organs/receptors indicated in yellow Legs omittedL: body length	 L: 4 mm	 L: 20 mm	 L: 10 mm	 L: 4 mm
Position of IR receptor	Prothorax	Abdomen	Metathorax	Pro−/mesothorax
Picture of IR organ or single sensillum	 Left IR organ (diameter 150 μm)	 Left anterior IR organ (trough-shaped cuticular depression, diameter 500 μm)	 Single IR sensillum (about 70 sensilla in a sensory pit, diameter 20 μm)	 Single IR sensillum (sensilla located between hair mechanoreceptors, diameter 20 μm)
Mode of operation	Bolometer (in *Merimna* with additional photomechanic unit)		Photomechanic receptors	

Aradus (cf. Table 1.1). The different configuration as well as the location at different spots on the thorax or the abdomen already provides strong evidence that IR receptors in the four genera have evolved independently from each other.

In all insect IR receptors, the cuticle of the exoskeleton constitutes the IR receiving interface interconnected between the environment and the interior sensory cells. Cuticle can be regarded as a biopolymer and, therefore, is a highly effective IR absorber. As already delineated in a previous publication (Schmitz and Bleckmann 1998a), chitin and protein molecules contain many C-H, N-H, and O-H groups swinging with frequencies in the range of 100 THz. As a result, cuticle shows distinctive stretch resonances in the range of 3 μm which corresponds to the emission maximum of a forest fire. The existence of stretch resonances is an ideal prerequisite for maximal absorption of photons in an absorber material inevitably causing a rise in temperature. Therefore, the cuticle plays a very important role in the different insect IR organs.

1.4 Bolometer Like IR Receptors in *Acanthocnemus* and *Merimna*

1.4.1 The 'little ash beetle' Acanthocnemus nigricans

1.4.1.1 Pyrophilous Behavior

Originally, the "little ash beetle" *A. nigricans* (family Acanthocnemidae, Table 1.1) was endemic to Australia (Champion 1922) and represents the only species within its family. In the last decades this beetle has been exported out of Australia and nowadays can also be found in several countries of the Palearctic ecozone (Alonso-Zarazaga et al. 2003; Mayor 2007; Liberti 2009; Valcárcel and Piloña 2009; Kovalenko 2011). The inconspicuous beetle is only 3–5 mm long and is strongly attracted by forest fires (own observations during the last decade). Immediately after a fire, *A. nigricans* can be found on freshly burnt areas, preferably close to fields of hot ashes. However, its biology is largely unknown. It has been speculated that the sexes meet around hot spots for mating. Observations of the behavior are very difficult because after landing on the ash and a short period of hectically running around the beetles dive into the ash and become invisible. So the substrate to which the eggs may be deposited is unknown. Nevertheless, there is strong evidence that *Acanthocnemus* depends on fires for its reproduction. As special adaptation to its pyrophilous way of life the beetle is equipped with a pair of complex IR receptors located on the first segment of the thorax (Kreiss et al. 2005).

1.4.1.2 The Prothoracic IR Organs

The IR organs of *A. nigricans* are unique in insects. As depicted in Table 1.1 and Fig. 1.2a one pair of IR organs is located on the prothorax (Schmitz et al. 2002; Kreiss et al. 2005). The main component of each organ is a little cuticular disc which is situated over a cavity (Fig. 1.2b). The air within the cavity beneath the disc communicates with the ambient air by a small gap around the disc. By this construction the thermal mass of the disc is considerably reduced and the underlying air layer thermally insulates the disc from the thorax. On the anterior surface of the disc about 90 tiny cuticular sensilla are situated. This is the part of the disc with the lowest thermal mass. A single disc sensillum consists of a small cuticular peg (diameter about 1.5 μm, length about 2 μm) which is connected to an unusual electron dense rod (Figs. 1.2c, d). The rod most probably represents the extremely hypertrophied dendritic sheath normally ensheathing the outer dendritic segment (DOS) in other mechanosensory sensilla (Kreiss et al. 2005). In the *A. nigricans* IR sensillum the outer peg effectively is connected to the inner dendritic segment (DIS) of the sensory cell, which is situated under the cuticle (Fig. 1.2d). However, the function of the rod remains enigmatic. Recently computer simulations have shown that rods may serve as heat conducting structures channeling heat to the underlying sensory

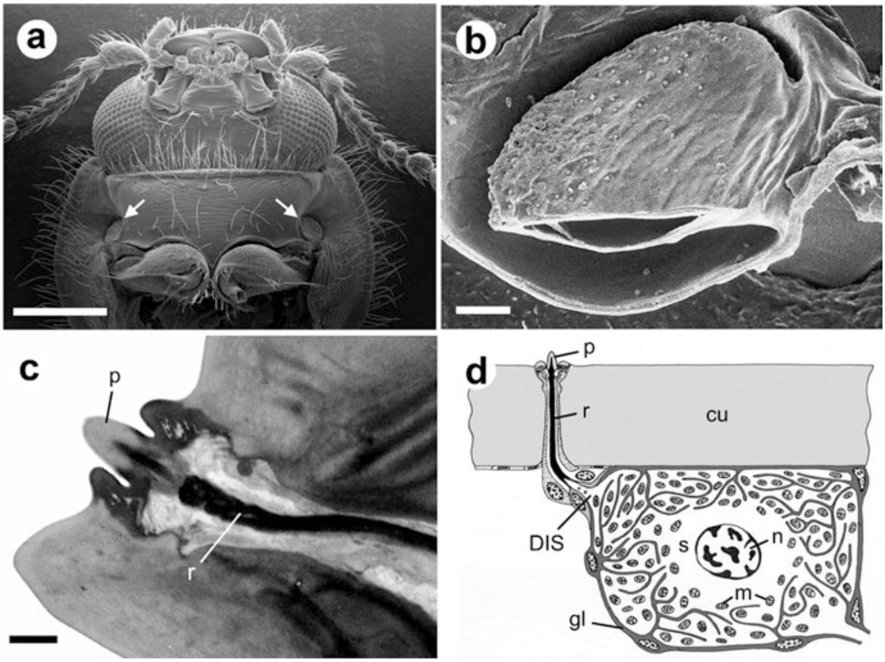


Fig. 1.2 (**a**) Head and prothorax of *Acanthocnemus nigricans*. The prothoracic IR organs are discernible as little cuticular discs (diameter 150 μm) located directly in front of the coxa of the forelegs. Bar: 500 μm. (**b**) Cut through the ventral part of the disc and the underlying cavity shows the composition of the organ. The disc is held above the cavity by a small posterior stalk. Bar: 20 μm. (**c**) Section through a single sensillum at the anterior rim of the disc. An electron dense rod (r) is connected to the outer peg (p) and continues through the dendritic canal down to the soma of a sensory cell located below the cuticle. Bar: 1 μm. (**d**) Schematic drawing of a disc sensillum. Note that numerous mitochondria (m) are housed inside the soma. DIS: short dendritic inner segment gl: glial cells, n: nucleus, p: peg, r: rod, s: soma. (**d**) Modified after Kreiss et al. (2005)

cells (Zhou et al. 2016). The soma of the sensory cell as well as the DIS is characterized by many deep invaginations of the cell membrane. The narrow extracellular spaces enclosed by the invaginated membranes are filled by darker glial cells. Especially the peripheral intracellular compartments inside the soma are densely filled with mitochondria (Fig. 1.2d).

Electrophysiological recordings from single disc sensilla have shown that sensilla responded with a phasic-tonic increase of neuronal activity to increasing temperature (Kreiss et al. 2007). In principle this corresponds to the typical response pattern of a thermoreceptive warm cell (Gingl and Tichy 2001). Threshold sensitivity has been determined to be between 11 and 25 mW/cm^2 tested with a red helium-neon laser (Kreiss et al. 2007).

Due to its morphology and response behavior the IR organs of *Acanthocnemus* can be classified as microbolometer-like IR sensors (cf. Table 1.1). In a bolometer, absorbed IR radiation heats up a thin absorber that corresponds to the outer surface of the disc containing the cuticular parts of the sensilla. The resulting increase in temperature is measured by the sensory cells inside the disc. Commonly the absorbers of a technical microbolometer are coated with e.g. vanadium oxide whose electrical resistance strongly changes with temperature. This can be easily measured by an appropriate readout circuit (Rogalski 2002). Compared to microbolometer sensors used nowadays e.g. for thermal imaging, the sensivity of the *Acanthocnemus* IR receptors is rather low. Current technical microbolometers have sensitivities of a few μW/cm^2 (Budzier and Gerlach 2011) and, therefore, it is unlikely that *Acanthocnemus* uses its IR organs for fire detection from larger distances. Theoretical calculations suggest that *Acanthocnemus* might be able to detect a large fire of e.g. 10 ha from distances of a few kilometers. However, this still has to be shown experimentally. More likely beetles use their thoracic IR organs for the navigation on freshly burnt areas still showing many hot spots. *Acanthocnemus* is active during the day and most hot spots cannot be seen with their complex eyes by daylight. Because it has been frequently observed by the authors that beetles seem to aggregate very close to smaller hot spots (e.g. patches of hot ashes around a burnt stump) it can be concluded that the beetles are able to detect those hot spots from distances of some meters by IR reception. Furthermore, IR receptors could serve as early warning systems to avoid a landing on a hot spot.

1.4.2 IR receptors in Merimna atrata

1.4.2.1 Pyrophilous Behavior

The buprestid beetle *M. atrata* is the only species within the genus *Merimna* and is distributed all over Australia (Hawkeswood 2007). *Merimna* exclusively breeds in different species of fire-killed eucalyptus trees (Myrtaceae (Hawkeswood and Peterson 1982; Kitchin 2009)). Immediately after a fire, first *Merimna* beetles arrive at the border of the freshly burnt area where they can be observed resting or running around on the vegetation. However, to the earliest time when a human is able to enter the burnt area the beetles also start to invade the scorched terrain (Schmitz et al. 2015). Beetles rapidly spread over the burnt area and can be observed flying around relatively low or running over burnt ground, trees and shrubs (Poulton 1915; Schmitz and Schmitz 2002). Males primarily are in search for females. After copulation the females start to deposit their eggs under the bark of fire-scorched eucalyptus trees by inserting their ovipositor in small crevices. After hatching, the larvae start to feed inside the wood of the fire-killed trees; the new generation of beetles will emerge 1 or 2 years later (Kitchin 2009).

Additionally, *Merimna* also perceives the opportunity to forage on the burnt area. All material potentially edible is investigated and, if consumable, eaten up. Also carcases of small fire-killed vertebrates are devoured (Schmitz et al. 2015).

1.4.2.2 The Abdominal IR Organs

In *M. atrata* one pair of IR organs is located ventrolaterally on the second, third and sometimes also on the fourth abdominal sternite each (cf. Table 1.1) (Mainz et al. 2004). The IR organs consist of an external cuticular part – the radiation absorbing area – and an internal sensory complex innervating this area (Fig. 1.3a, c) (Schmitz et al. 2001).

The absorbing area is a roundish and shallow indentation of the cuticle. Depending on the size of the beetle, the average diameter is about 500 µm and the depth is about 150 µm (Fig. 1.3a, c, e) (Schneider and Schmitz 2013). An absorbing area is characterized by the following special features: (i) a lack of dark pigments within the exocuticle resulting in a yellowish color of the IR organ in contrast to the glossy dark brown color of 'normal' cuticle surrounding the absorbing area (Fig. 1.3c) (Schmitz et al. 2001); (ii) a honeycomb-like microstructure in the central region of the absorbing area (Fig. 1.3a, b) (Schmitz et al. 2000); (iii) and a reduced thickness of the cuticle in the center (Fig. 1.3e) (Schneider and Schmitz 2013, 2014)) under which the sensory complex is situated. It can be proposed that the lack of dark pigments in the cuticle of the absorbing area significantly reduces the absorption of visible light and subsequent heating, because dark pigments like melanins have their absorption maxima within the range of visible light (Stark et al. 2005). The reduction in thickness decreases the thermal mass of the cuticle which most probably allows faster heating and cooling of the cuticle above the sensory complex.

The sensory complex comprises a large multipolar Type1 neuron with a specialized dendritic region called terminal dendritic mass (TDM, Fig. 1.3d) and in close proximity to that a smaller chordotonal organ (CO), represented by two scolopidia (Schneider and Schmitz 2013). The thermoreceptive function of the multipolar neuron has been confirmed by electrophysiological recordings (Schmitz and Trenner 2003). Like the disc-sensilla in *Acanthocnemus*, the neuron responds in a phasic-tonic way with an increase of its spike frequency to increasing temperatures. Thus the thermoreceptive modality of the multipolar neuron also allows a classification of the *Merimna* IR organ as a bolometer. However, because of the rather low threshold sensitivity of 40 mW/cm^2, determined in the electrophysiological experiments conducted so far (Schmitz and Trenner 2003), it has been concluded that the *Merimna* IR organ is not suitable for remote sensing of forest fires but rather serves for short-distance sensing, e.g. to prevent the beetle from landing on hot surfaces (Schmitz and Trenner 2003). More recent investigations have concentrated on the CO as a second, putative receptor system involved in IR perception, which may increase the sensitivity of the IR organs (Schneider and Schmitz 2013). The CO represents a mechanosensory unit, consisting of two mononematic scolopidia, located in direct proximity to the multipolar neuron in the center of the absorbing area (Fig. 1.3c) (Schneider and Schmitz 2013)). Just like other scolopidia of this type, they are supposed to respond to axial stress or bending (Field and Matheson 1998). In general scolopidia function as proprioceptors or specialized mechanoreceptor organs, capable of detecting mechanical displacements over several orders of magnitude (Field and Matheson 1998) down to 0.6 nm (Michelsen and Larsen 1985). Therefore, it has

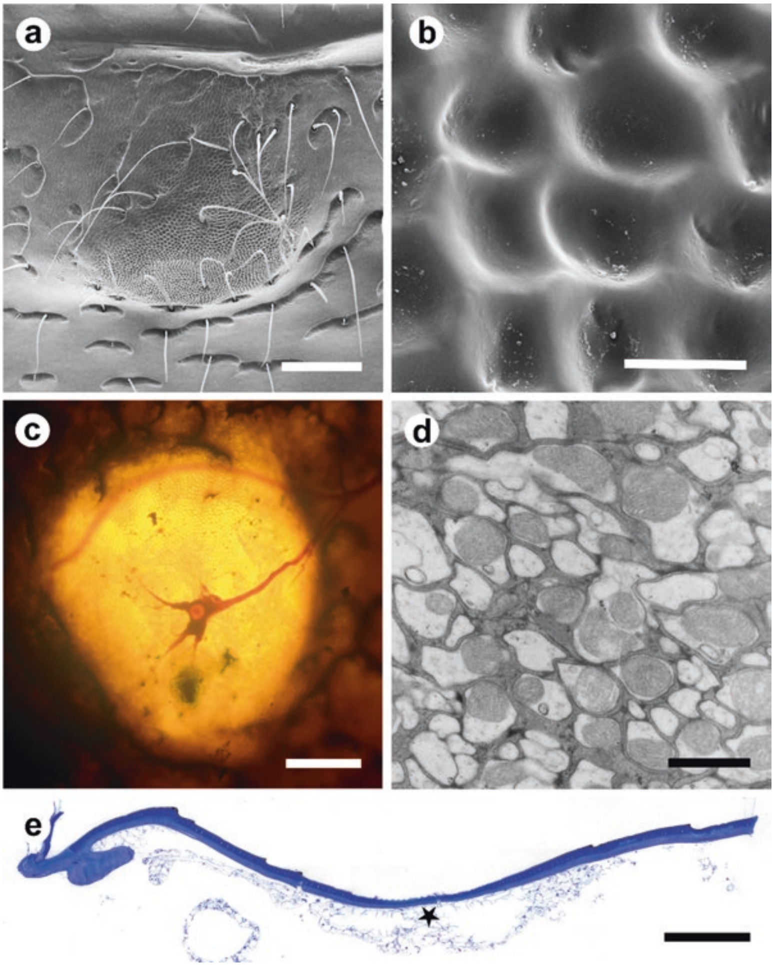


Fig. 1.3 IR-organ of *Merimna atrata*. (**a**) SEM-image of the absorbing area showing its three-dimensional shape and honeycomb-like surface structure. Bar: 200 μm. (**b**) Detail of the surface of the IR absorbing area showing a somewhat irregularly honeycomb microstructure. Bar: 10 μm. (**c**) LM-micrograph of the sensory complex stained with cobalt/nickel innervating the yellowish absorbing area. Bar: 200 μm. (**d)** TEM-micrograph of the terminal dendritic mass (TDM) of the thermosensitive multipolar neuron. Dendrites are densely filled with mitochondria. Bar: 1 μm. (**e**) Longitudinal section through the center of the absorbing area stained with toluidine-blue/borax (LM-image). Asterisk indicates position of the sensory complex. Orientation: top = exterior, bottom = interior. Bar: 100 μm. (**c**) and (**e**) Modified after Schneider and Schmitz (2013)

been proposed that the absorption of IR radiation could also lead to minute deformations of the absorbing area with its highest extend in the central region, corresponding to the attachment site of the CO (see asterisk in Fig. 1.3e). The CO could perceive these mechanical events and thus probably extend the measuring range, thereby increasing the sensitivity of the IR organ (Mainz et al. 2004; Schneider and

Schmitz 2013). Investigations of the mechanical properties of the IR absorbing area have revealed that – despite of the reduced thickness – the cuticle in the center of the absorbing areas is significantly stiffer and harder than the surrounding normal cuticle (Schneider and Schmitz 2014). This may result in a thermal deformation behavior specially adapted for the perception by mechanosensory units. Other probable advantages provided by the COs could include e.g. faster response times, a larger dynamic range, higher reliability or improved filter properties. However, unambiguous electrophysiological recordings from the CO are missing so far.

1.5 Photomechanic IR Receptors in *Melanophila* Beetles and Pyrophilous Flat Bugs of the Genus *Aradus*

There is considerable evidence that the so-called photomechanic IR receptors have developed from common mechanosensitive bristles. A possible evolutionary scenario can be outlined as follows: in insects, which already had started to develop a pyrophilous way of life, heat from hot surfaces on a burnt area may have stimulated external mechanoreceptors (see Discussion). This can be exemplified by looking at the photomechanic sensilla in *Melanophila* beetles and *Aradus* bugs. As discussed by Schmitz et al. (2007, 2010), there is strong evidence that in both pyrophilous species the IR sensilla have evolved directly from hair mechanoreceptors (sensilla trichodea). However, because photomechanic IR sensilla so far have only been found in recent species of the genus *Melanophila* within the beetles and in very few pyrophilous species of the genus *Aradus* within the bugs, sensilla must have developed independently in both genera. It is imaginable that e.g. the dome-shaped area provides a good surface to volume ratio allowing enhanced absorption of IR photons; the diameter of the sphere could reflect the penetration depth of IR photons into the cuticle of 3–4 μm (Schmitz et al. 2010).

1.5.1 IR Pit Organs in Melanophila *Beetles*

1.5.1.1 Pyrophilous Behaviour

Buprestid beetles of the genus *Melanophila* inhabit nearly all continents except Australia and Antarctica, and use fire killed trees as food for their larvae (Ricksecker 1885; Manee 1913; Sharp 1918; Van Dyke 1926; Linsley 1933; Sloop 1937; Linsley 1943; Evans 1964, 1966b; Wikars 1997; Bellamy 2008). As far as it is known, all recent species show the same pyrophilous biology and behavior as reported above for *Merimna* in Australia. Of course both genera use different tree species. Whereas *Merimna* breeds in scorched eucalyptus trees, *Melanophila* species breed in a variety of burnt conifers as well as in several species of scorched deciduous trees (Horion 1955; Apel 1991). Thus, it can be concluded that the two buprestid genera have occupied the same ecological niche and have developed a nearly identical pyrophilous way of life on different continents. Surprisingly, their IR receptors are totally different.

A possible reason for the different type of construction of the *Melanophila* IR organ could be that the *Melanophila* IR receptors are more sensitive than the *Merimna* IR organs. It has been reported that untold numbers of *Melanophila consputa* were attracted to a burning 750,000-barrel oil storage tank near Coalinga in California in 1924 (Van Dyke 1926). A recent modeling of this historic oil tank fire suggested a remarkably high sensitivity of the IR receptors (Schmitz and Bousack 2012). The analysis of the geographical conditions around the tank fire yielded the result that most beetles must have become aware of this fire from a distance of 130 km. If IR radiation really was an important cue used by the beetles to detect the fire, this would result in a sensitivity of the IR pit organs of 4-13nW/cm^2 (Schmitz and Bousack 2012).

1.5.1.2 The Metathoracic IR Organs

The IR receptors are situated in two pit organs which are located on the metathorax (cf. Table 1.1). Each IR organ houses about 70 IR sensilla which are closely packed together at the bottom of the pit (Fig. 1.4a, (Evans 1966a; Vondran et al. 1995)). From the outside, a single sensillum can be recognized by a hemispherical dome with a diameter of about 15–20 µm. The dome is built by a thin cuticle which represents the outer boundary of a spherical internal cavity. The cavity is almost completely filled out by a tiny cuticular sphere with a diameter of about 12 µm (Fig. 1.4b, c). Based on transmission electron microscopic (TEM) observations, Vondran et al. (1995) described that the sphere consists of three different zones: (i) an outer lamellated mantle, also confirmed by scanning probe microscopy (Hazel et al. 2001), (ii) an intermediate layer of unstructured cuticle revealing many irregularly arranged microcavities (mc in Fig. 1.4c), and (iii) an innermost central zone where the cuticle appears uniform except for some spots of higher electron density. The sphere is connected to the vertex of the outer cuticular dome by a small cuticular stalk (Fig. 1.4b, c). The narrow gap surrounding the sphere is filled out by leaf-like extensions of at least two enveloping cells (not visible in the dried cuticular specimen shown in Fig. 1.4c). From below, the sphere is innervated by a single sensory cell (Fig. 1.6a). As a prominent feature it has been found that the outermost tip of the dendrite is located inside an inner pressure chamber in the sphere (ipc in Fig. 1.4c). All morphological as well as all physiological data available so far have demonstrated that this cell is a ciliary mechanoreceptor (Vondran et al. 1995; Schmitz et al. 1997; Schmitz and Bleckmann 1998b).

According to the current conception of how IR radiation may be converted into a mechanical event perceivable by the mechanoreceptive cell, absorbed IR radiation heats the sphere and causes an increase in pressure in the fluid filled system of communicating microcavities inside the sphere. Because the outer lamellated mantle consists of hard exocuticle reinforced by layers of chitin fibers (Schmitz et al. 2007),