Matched Filter Properties of Infrared Receptors Used for Fire and Heat Detection in Insects

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Contents

Abstract

About 25 insect species are attracted by forest fires and thus 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. From a technical point of view, insect IR receptors can be classified into two classes: bolometer-like sensors innervated by thermoreceptors and so-called photomechanic sensors which are innervated by mechanoreceptors. Despite of their different functional principles, insect IR receptors all show the same built-in filter properties. Remarkably, these filters were already preset by the absorption spectra of the gases in the atmosphere and the chemical composition of the insect cuticle. The atmospheric windows can be regarded as valuable filters (Filter 1) because emission maxima of relevant IR sources like fires or warm-

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blooded creatures are located within the MW(mid-wavelength)IR and LW(long wavelength)IR windows. Filter 2 is given by cuticular absorption. Insect cuticle can be regarded as a composite material consisting of biopolymers that show strong IR absorption bands in the MWIR. Because both filters perfectly match, an IR-sensitive pyrophilous insect is able to efficiently sense MWIR radiation emitted by a forest fire. Thus, filters could be used without further modifications enabling the underlying sensory cells to perceive a maximum of temperature increase and/or thermal expansion.

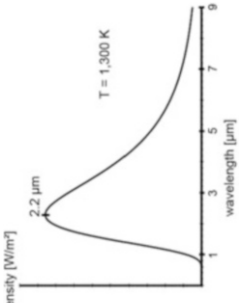## 8.1   Nature and Perception of Infrared Radiation

Independent from its condition of aggregation, every matter with a temperature above the absolute zero point emits electromagnetic radiation. This is caused by molecular movements starting above 0 K. In the context of this chapter, electromagnetic radiation significant for living organisms is considered. Here, the upper limit is represented by the surface temperature of sun at 5,800 K, the lower limit by objects at ambient temperature (cf. Table 8.1). Thus, under normal conditions, organisms are primarily subjected to a radiation spectrum ranging from high-level *ultraviolet* (UV) down to low-energy *infrared* (IR) radiation (Fig. 8.1). The spectral distribution of the radiation emitted, e.g., by a high-intensity forest fire with a temperature of 1,300 K, can be calculated according to Planck's radiation law (on the right in Table 8.1). At a given temperature, the wavelength at which most of the radiant energy is emitted (λ_{max}) can be easily calculated by the law of Wien:

$$\lambda max = \frac{2,897.8\,[\mu m*K]}{T[K]}$$

where T is the absolute temperature given in Kelvin [K]. Temperatures and values for λ_{max} are given in Table 8.1 for the sun, fires at high and low intensities, and a mouse.

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 appropriate sensor should have its highest sensitivity at λ_{max} of the radiation source. This is realized in, e.g., human photoreceptors, 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 (cf. Table 8.1). In general, the spectral sensitivity of photopigments 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. 2008)), (ii) in the *mid-wavelength infrared* (MWIR, 3–8 μm), or (iii) even in the *long wavelength infrared* (LWIR, 8–15 μm; Fig. 8.1).

Table 8.1 Characteristics of different thermal sources in view of emission of electromagnetic radiation

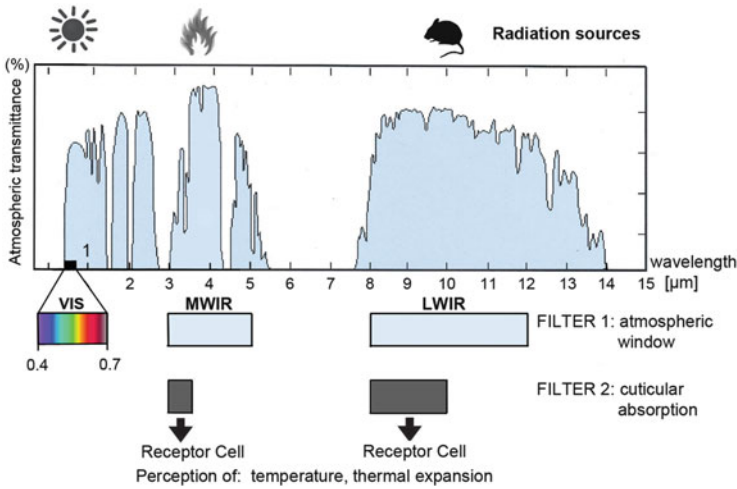| Source	T [K]	λ_{max} [μm]	Total energy emitted per m² (assuming an emissivity of 0.98)	Photon energy (1 photon)	Spectral distribution of radiation intensity emitted from a high intensity forest fire according to Planck's radiation law
Sun	5,800	0.5	62.89 MW	398 zJ 2.5 eV	
Fire	High int. 1,300 800 low int.	2.2 3.6	159 KW 22.8 KW	90 zJ (0.6 eV) 55 zJ (0.3 eV)	
Mouse	310	9.3	450 W	21 zJ (0.1 eV)	

Fig. 8.1 Atmospheric transmittance of electromagnetic radiation emitted from objects with biological relevance. Atmospheric windows 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. Maxima of cuticular absorption (After Vondran et al. 1995) are also indicated below. Transmission spectrum adopted from the Naval Air Warfare Center

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), "*long wavelength*" (LW) photoreceptors with absorption maxima beyond 670 nm (Douglas et al. 1998) are unknown. The first essential step in vision always is the cis-trans torsional isomerization of the rhodopsin chromophore (Schoenlein et al. 1991). This conformational switch at least requires a photon energy of more than 1.24 eV (the energy content of a 1 μm photon). As can be derived from Table 8.1, IR photons emitted by a fire or a warm-blooded creature do not carry enough energy to initiate the isomerization of a visual pigment.

Nevertheless, the IR photons must be absorbed efficiently to cause distinct effects in the receptor. Absorption will be maximal if the frequency of vibration of a chemical bond between two atoms and the frequency of an incoming photon match (so-called resonance condition). Most organic molecules show vibrational absorption bands in the MWIR region (Barth 2007). The insect cuticle consists of protein and chitin (N-acetylglucosamines) showing many C–H, N–H, and O–H groups (Chapman 1998; Neville 1975). Molecules with these groups oscillate with frequencies of about 100 THz and, therefore, show stretch or vibrational resonances around 3 μm (Herzberg and Huber 1950). In general, most organic molecules strongly absorb in the MWIR and LWIR region of the electromagnetic spectrum (Hesse et al. 1995). In case of absorption of an IR photon, the vibrational energy is converted within fractions of a millisecond into translational energy, i.e., heat, by non-radiative de-excitation processes. Any heating inevitably also causes thermal

deformation. The absorber of a thermal IR detector, therefore, has to be monitored by a temperature and/or a mechanical displacement sensor.

8.2   IR Receptors in the Animal Kingdom

True IR receptors are relatively rare in animals. In vertebrates, receptors especially evolved for the detection of LWIR (8–15 μm (D'Amico et al. 2008)) can be found in vampire bats of the species *Desmodus rotundus* (Kürten and Schmidt 1982) and in three families of snakes: in the Boidae, the Pythonidae, and – within the family of Viperidae – in the subfamily Crotalinae, commonly known as pit vipers (Molenaar 1992; Bullock and Barrett 1968). Although the vertebrate IR organs have a very diverse appearance, receptors are all located on the head close to the mouth and are innervated by highly thermosensitive fibers of the trigeminal nervous system. When crawling on a warm-blooded host (e.g., a cow), the nocturnal blood-feeding vampire bats use their IR receptors for the localization of a rewarding biting site well supplied with blood (Kürten and Schmidt 1982). Large numbers of thermoreceptors were found in the central nose leaf yielding strong evidence that this facial area is responsible for the IR-receptive capabilities of the vampire bats (Kürten et al. 1984b). Receptors are sensitive to weak IR radiation down to an intensity of 50 μW/cm^2 enabling the bat to detect thermal radiation emitted from human skin up to a distance of 13 cm (Kürten and Schmidt 1982; Kürten et al. 1984b). Terminal sensory units for the perception of temperature differences are free nerve endings of warm and cold fibers ramifying directly under the epidermis (Kürten et al. 1984a). The molecular bases for IR reception in vampire bats most probably are specialized TRPV1 channels (transient receptor potential cation channel V1) (Gracheva et al. 2011).

The IR-sensitive snakes preferentially also hunt at night and use their IR receptors to locate warm-blooded prey. From outside, IR receptors are hard to detect at the heads of most boid snakes. Receptors are much better to discover in most pythons as small labial pits in the supra- and infralabials bordering the jaw and easy to identify in pit vipers as a pair of prominent holes in the loreal region located between the eyes and the nostrils (Molenaar 1992). As in vampire bats, the outer IR-absorbing surfaces are innervated by thermosensitive trigeminal fibers. The terminal endings of these fibers, however, show a unique feature increasing the sensitivity of the snake IR systems: so-called *terminal nerve masses* (TNMs). In brief, a TNM can be regarded as inflated terminus of a fine free nerve ending that contains enormous masses of mitochondria. The overall diameter of a TMN is about 30–50 μm (Terashima et al. 1970; Bullock and Fox 1957; Amemiya et al. 1996). TNMs are supplied with blood by a rich capillary network that also can afford rapid cooling of irradiated spots within the receptor. Among IR-sensitive snakes, pit vipers possess the most sophisticated IR receptors showing the highest sensitivity. Because the TMNs are embedded in a very thin membrane of only about 15 μm thickness providing a strongly reduced heat capacity, the sensitivity threshold has been determined to be only 3.35 μW/cm^2 in the western diamondback

rattlesnake, *Crotalus atrox*. This remarkable sensitivity enables the rattlesnake to detect a mouse from a distance of 1 m in complete darkness (Ebert and Westhoff 2006). The ion channels most probably responsible for the high sensitivity are modified TRPA1 channels (Gracheva et al. 2010).

A look at the IR receptors in invertebrates reveals a higher diversity. Although IR receptors hitherto have been found only in very few insects, they are very different from each other and can be located at different parts of the body.
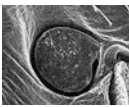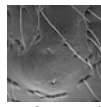
At first it is reasonable to suppose that – like in IR-sensitive snakes – also many nocturnal blood-feeding insects like mosquitoes could possess IR receptors for the detection of LWIR emitted by their warm-blooded prey. So far, however, IR sensory capabilities have only been demonstrated in certain blood-sucking triatomine bugs. These predatory insects search for a blood meal at night and for close range orientation in the centimeter range also use IR radiation given off by their warm-blooded hosts (Lazzari and Núñez 1989; Schmitz et al. 2000b; Guerenstein and Lazzari 2009). According to the current knowledge, however, IR reception in triatomine bugs is accomplished by highly sensitive antennal thermoreceptors (Insausti et al. 1999; Bernard 1974; Lazzari and Wicklein 1994; Guerenstein and Lazzari 2009). The response of thermoreceptors is ambiguous with regard to the temperature source, because convective as well as radiant heat results in a temperature increase of the cuticular portion of the receptors. Nevertheless, because thermoreceptive sensilla appear as conical, cylindrical, or hairlike structures, the transfer of radiant heat, which is limited to the surface area exposed to the radiation source, will be less important than convection (Gingl and Tichy 2001). On the other hand, flat extended areas on the body surface should be optimal for the transfer of radiant heat. Most probably, antennal thermoreceptors can be found on every insect antenna (Altner and Loftus 1985). Until now, additional extra-antennal IR receptors have not been described morphologically and/or physiologically for blood-sucking bugs or any other insect supposed to use IR radiation for the detection of low temperature IR sources.

In contrast, IR receptors developed in addition to the antennal thermoreceptive sensilla have only been found in very few insect species. These receptors are used for the detection of MWIR radiation (3–8 μm (D'Amico et al. 2008)) emitted from fires. Thus, insects equipped with extra-antennal IR receptors belong to a small group of specialists that are associated with forest fires. These "fire-loving" (pyrophilous) insects generally depend on forest fires for their reproduction and, therefore, approach ongoing fires and immediately invade freshly burnt areas to start reproduction.

8.3   Advantages of Detecting Forest Fires by IR Radiation

All pyrophilous insect species depicted in Table 8.2 and described below in more detail are attracted by forest fires. The main reason for this unusual behavior is that these insects as well as their offspring make use of the food resources made available by the fire. After a fire, the freshly burnt area becomes immediately

Table 8.2 Infrared receptors in pyrophilous insects

	"Little ash beetle"	"Australian fire beetle"	"Black fire beetle"	"Pyrophilous flat bugs"
	Acanthocnemus nigricans	*Merimna atrata*		*Aradus spec.*
	Only species in the genus	Only species in the genus	*Melanophila spec.* 11 species	4 IR-sensitive species in the genus *Aradus* (200 species)
Systematic position	*Beetle* (family: Acanthocnemidae)	Jewel *beetles* (family: Buprestidae)		Flat *bugs* (family: Aradidae)
Ventral habitus				
IR organs/ receptors indicated in yellow				
Legs omitted L: 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 (sensory disk with numerous tiny sensilla)	Left anterior IR organ (trough-shaped cuticular depression)	Single IR sensillum (about 70 dome-shaped sensilla in a sensory pit)	Single IR sensillum (dome-shaped sensilla interspersed between hair mechanoreceptors)
Mode of operation	Bolometer (in *Merimna* with additional photomechanic unit)	Photomechanic receptors		

populated by the insects because it initially serves as a safe meeting place for the sexes; potential predators are efficiently kept away by heat and smoke. Consequently, fire detection is an essential precondition for the survival of pyrophilous insects. The outbreak of a forest fire, however, is highly unpredictable. Therefore, pyrophilous insects should be able to detect fires from distances as large as possible. It is reasonable to suppose that the sensory organs, which are used for fire detection, have been subjected to a strong evolutionary pressure with regard to sensitivity. Additionally, when flying over a burnt area in search for a landing ground, the insect has to avoid to land on "hot spots" with dangerous surface temperatures of more than 60 °C. These two different requirements therefore request a rather large dynamic range of perception.

In a first approach to understand the phenomenon how a small insect could be able to approach a fire over distances of many kilometers, it is obvious to propose that olfaction plays a major role. However, there is no experimental evidence that flying pyrophilous insects could be lured to an odor source by the smell of smoke. A recent study has shown that pyrophilous *Melanophila* beetles can be attracted by certain volatiles emitted by burning or smoldering wood (Paczkowski et al. 2013). In the study, beetles were tested crawling around in a two-arm olfactometer at temperatures of 30 °C. No information about the sex and mating state of the beetles is provided. So these data are more likely suited to show that beetles (e.g., mated females?), once having landed on a burnt tree, can detect a suitable spot for oviposition by olfactory cues. Furthermore, evaluations of satellite images very often yielded the result that the large smoke plume from a forest fire initially is driven away from the fire by the wind in a narrow angle over distances of many kilometers, meanwhile slowly ascending to higher altitudes. Only beetles closer to the ground and inside the smoke plume would have a chance to become aware of the fire solely by olfactory cues. In contrast, beetles that are already close to the fire but outside the smoke plume most probably can see the plume but cannot smell the smoke. Also the light of the flames – generally only visible at night – may not play an important role, because *Melanophila* beetles, as nearly all jewel beetles, are active during the day (Evans et al. 2007).

According to the current conception of how pyrophilous insects may be able to become aware of a fire from large distances, these IR-sensitive insects most probably use a combination of visual cues (view of a big "cloud" against the horizon) and IR radiation (Schmitz and Bousack 2012). To make sure that a smoke plume and not a cloud bank is approached over many kilometers, a zone of IR emission has to exist at the base of the cloud just above treetop level. It is proposed that pyrophilous insects carefully screen the place of origin of the potential smoke plume for additional IR emission before they start to approach the fire. In contrast to an approach by olfactory cues which can be considerably impeded by the wind, especially over longer distances, an orientation by electro-magnetic radiation in the visible and in the infrared spectrum allows a straight approach to the source. This is also promoted by an atmospherical window transparent for MWIR radiation between 3 and 5 μm (Fig. 8.1).

8.4   Diversity of IR Receptors in Pyrophilous Insects: An Overview

Currently, only 17 insect species out of four genera are known to possess IR sensory organs (Table 8.2). Compared to the amount of known insect species (roughly one million), this indeed is a negligible number. Nevertheless, a closer look at the IR receptors in the different genera reveals a surprising diversity. At least three fundamentally different types of receptors could be identified: a pair of prothoracic disks covered with numerous tiny sensilla in *Acanthocnemus nigricans*, one to three pairs of roundish abdominal IR organs in *Merimna atrata*, and the so-called

photomechanic IR sensilla in *Melanophila* beetles and in a few 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 *Aradus* (cf. Table 8.2). The different shapes as well as the location at different spots on the thorax or the abdomen already provide evidence that IR receptors in the four genera have evolved independently from each other. Therefore, it can be stated that no "standard" IR receptor seems to exist in insects. This becomes especially evident when comparing the IR receptors in *Melanophila* beetles and in *Merimna atrata*. Although both beetles belong to the family of jewel beetles, make use of the same ecological niche after fires, and show the same biology and pyrophilous behavior, their IR receptors are totally different from each other as will be explained below in more detail. In contrast, a striking similarity exists between the photomechanic IR sensilla found in *Melanophila* beetles and *Aradus* bugs. Because the lineages of beetles and bugs most probably have already separated in the Permian about 270 mya, there is little doubt that IR sensilla in both genera have developed independently. In this particular case, the independent evolution has led to more or less the same type of mechanoreceptor-based IR sensillum.

The sensory ecology and the IR receptors of the mentioned pyrophilous insects will be described in more detail in the following.

8.4.1 The "Little Ash Beetle" *Acanthocnemus nigricans*

8.4.1.1 Biology and Behavior

A. nigricans is the only species within its family. Originally, the "little ash beetle" *A. nigricans* (family Acanthocnemidae, Table 8.2) was endemic to Australia (Champion 1922). In the last decades, however, this beetle has been exported out of Australia and nowadays can be found in several European countries like Spain, Italy, and Portugal (Alonso-Zarazaga et al. 2003; Mayor 2007; Liberti 2009; Valcárcel and Piloña 2009; Kovalenko 2011). In 2011 it was also found in Russia (Kovalenko 2011). The inconspicuous beetle is only 3–5 mm long and is attracted by forest fires (own observations in the last 10 years). Immediately after a fire, *A. nigricans* can be found on freshly burnt areas, preferably close to spots of hot ashes. However, its biology is nearly unknown. It has been speculated that the sexes meet around the hot spots in order to mate. 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. In summary, 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 behind the head on the first segment of the thorax (Kreiss et al. 2005).
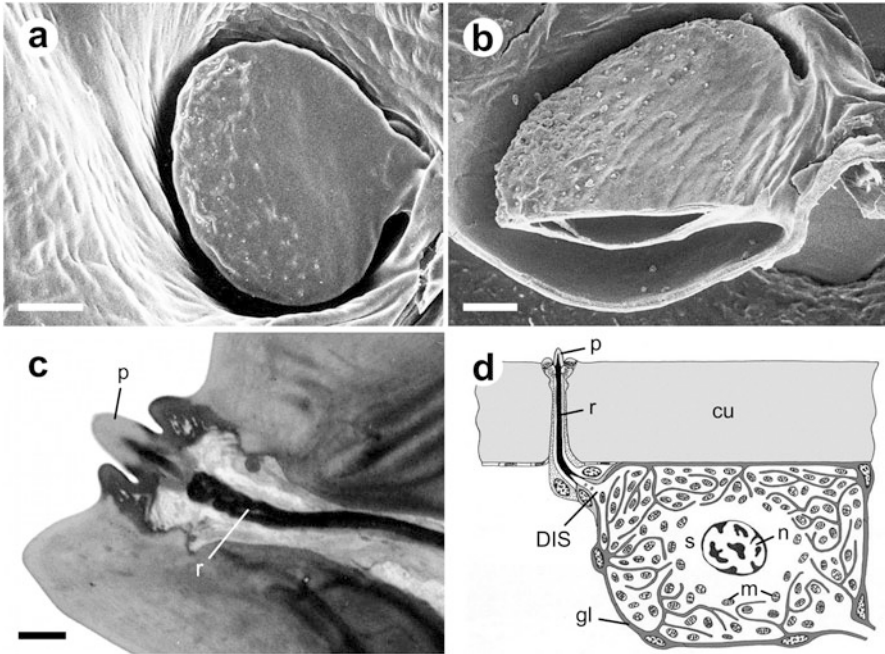
Fig. 8.2 (**a**) Left IR organ of *Acanthocnemus nigricans* (head is located on the *left*). A little cuticular disk (diameter 150 μm) is situated on the lateral prothorax directly in front of the coxa of the foreleg. About 90 tiny sensilla are located on the anterior half of the disk. *Bar*: 30 μm (**b**) Cut through the ventral part of the disk and the underlying cavity shows the composition of the organ. The disk 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 disk. 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 disk 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)

8.4.1.2 Structure and Function of the Prothoracic IR Organs

The IR organs are unique in *A. nigricans*. As depicted in Table 8.2 and Fig. 8.2a, b, 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 disk which is situated over a cavity. The air within the cavity beneath the disk communicates with the ambient air by a small gap around the disk (Fig. 8.2a, b). By this construction, the thermal mass of the disk is considerably reduced and the underlying air layer thermally insulates the disk from the body. On the anterior surface of the disk, about 90 tiny cuticular sensilla are situated. This is the part of the disk with the lowest thermal mass. A single disk 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 (Fig. 8.2c, d). The rod most probably represents the extremely hypertrophied dendritic sheath normally ensheathing the outer dendritic segment (DOS) in other
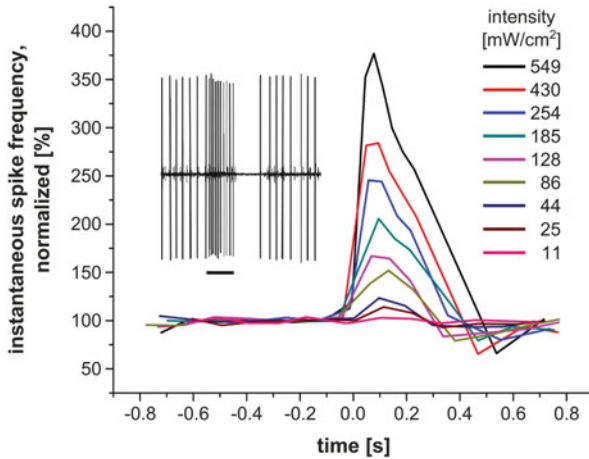
Fig. 8.3 Single unit recording from an IR sensillum on the sensory disk of *Acanthocnemus nigricans*. *Inset* shows the typical phasic-tonic response pattern to a stimulus applied by a red helium-neon laser (380 mW/cm^2). Increase in spike frequency (normalized to the frequency without stimulus which was set to 100 %) depended on stimulus intensity (11–549 mW/cm^2 tested). *Black bar* indicates duration of stimulus (250 ms) (Adapted from Kreiss et al. 2007)

mechanosensory sensilla. 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. 8.2d). However, the function of the rod remains enigmatic. 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. 8.2d).

Electrophysiological recordings from single disk sensilla have shown that sensilla responded with a phasic-tonic increase of neuronal activity to increasing temperature (Fig. 8.3; Kreiss et al. 2007). In principle, this corresponds to the typical response pattern of a 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 8.2). In a bolometer, absorbed IR radiation heats up a thin absorber that corresponds to the outer surface of the disk. The resulting increase in temperature is measured by the sensory cells inside the disk. 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 for thermal imaging, the sensitivity 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 has to be shown experimentally. More likely, beetles use their thoracic IR organs for navigation on freshly burnt areas that still show many hot spots. *Acanthocnemus* is active during the day and most hot spots cannot be seen with eyes under bright 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 their IR receptors. Furthermore, IR receptors could serve as early warning systems to avoid a landing on a hot spot.

8.4.2 IR Receptors in *Merimna atrata*

8.4.2.1 Biology and Behavior

M. atrata is the only species within the genus *Merimna* and is distributed all over Australia (Hawkeswood 2007). Up to now, *Merimna* has not been found outside the Australian mainland. *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 (own observations). Beetles rapidly spread over the burnt area and can be observed flying around relatively low or running over the ground, trees, and shrubs (Schmitz and Schmitz 2002; Poulton 1915). 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 extensively uses 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.

8.4.2.2 Structure and Function of 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 (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. 8.4a–c, Schmitz et al. 2001).

The absorbing area is a roundish and shallow dint 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. 8.4a, e, Schneider and Schmitz 2013). It is characterized by the following special features: (i) a lack of dark pigments within the exocuticle
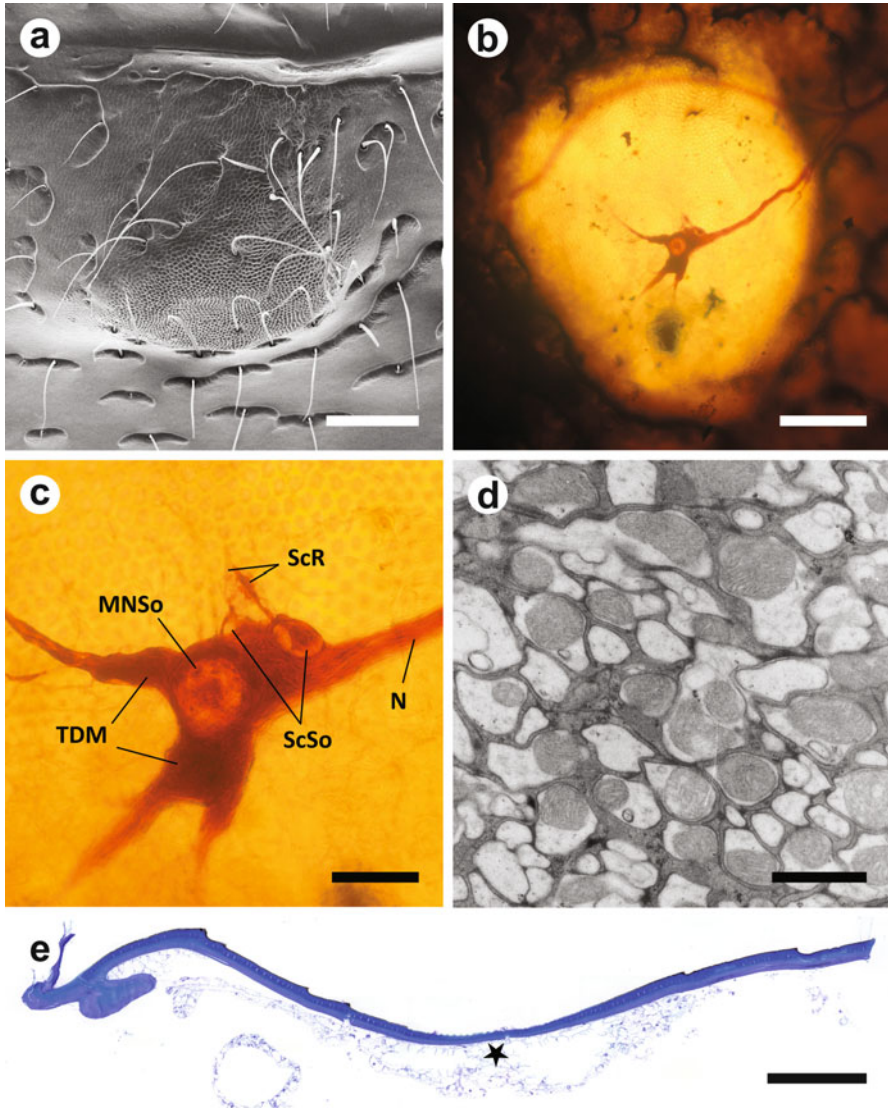
Fig. 8.4 IR organ of *Merimna atrata*. (**a**) SEM image of the absorbing area showing its three-dimensional shape and honeycomb-like surface structure. *Bar*: 200 μm. (**b**) LM micrograph of the sensory complex stained with cobalt/nickel innervating the *yellowish* absorbing area. *Bar*: 200 μm. (**c**) Sensory complex shown in (**b**) at higher magnification. *MNSo* soma with nucleus of multipolar neuron, *N* nerve, *SCSo* somata of the sensory cells of two scolopidia, *ScR* scolopale rods, *TDM* terminal dendritic mass of the multipolar neuron. *Bar*: 50 μm. Orientation in (**a–c**): *top* = anterior, *bottom* = posterior, *left* = lateral, *right* = medial. (**d**) TEM micrograph of the TDM of the thermosensitive multipolar neuron. *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, *left* = anterior, *right* = posterior. *Bar*: 100 μm (**a** and **d** modified after Kahl et al. (2014, **b** and **c** modified after Schneider and Schmitz 2013)

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. 8.4b, Schmitz et al. 2001), (ii) a honeycomb-like microstructure in the central region of the absorbing area (Fig. 8.4a, Schmitz et al. 2000a), and (iii) a reduced thickness of the cuticle in the center (Fig. 8.4e, 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 sensory complex comprises a large multipolar type 1 neuron with a specialized dendritic region called terminal dendritic mass (TDM, Fig. 8.4c) and in close proximity to that a chordotonal organ (CO), represented by two scolopidia (Fig. 8.4c, Schneider and Schmitz 2013). The thermoreceptive function of the multipolar neuron has been confirmed by electrophysiological recordings (Schmitz and Trenner 2003). Like the disk sensilla in *Acanthocnemus*, the neuron responds in a phasic-tonic way with an increase of its spike frequency to increasing temperature (Fig. 8.5). Thus, the thermoreceptive modality of the multipolar neuron also allows a classification of the *Merimna* IR organ as a bolometer. However, because of the
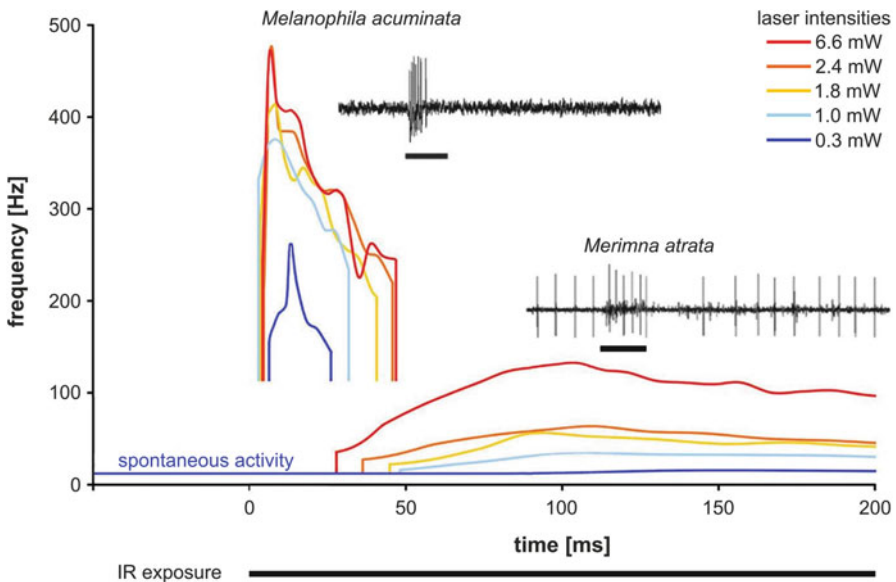
Fig. 8.5 Electrophysiological recordings from a single IR sensillum in the pit organ of *Melanophila acuminata* (*left*) and from the thermosensitive multipolar neuron in the *Merimna* IR organ (*right*). Receptors were stimulated with a red laser at different intensities from 0.3 to 6.6 mW. Stimulation always started at 0 ms and lasted 200 ms (*black bar* indicates IR exposure). Note the fast and strictly phasic response pattern of the *Melanophila* sensillum with very short latencies and the long-lasting phasic-tonic response of the *Merimna* receptor with considerable longer latencies. Insets are examples of single original recordings (Adapted from Schmitz and Trenner 2003)

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 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 also involved in IR perception, which may enable the beetle to detect also remote forest fires (Schneider and Schmitz 2013). The CO represents a mechanosensory unit, consisting of two mononematic monodynal scolopidia, located in direct proximity to the multipolar neuron in the center of the absorbing area (Fig. 8.4c, 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 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. 8.4e). 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). Other probable benefits provided by the additional mechanoreceptive innervation of the IR organ by the CO could include, e.g., faster response times, a larger dynamic range, higher reliability or improved filter properties. In summary, this could increase the overall performance of the whole IR organ (Schneider and Schmitz 2014). However, unambiguous electrophysiological recordings from the CO are missing so far.

8.4.3 IR Receptors in Pyrophilous *Melanophila* Beetles

8.4.3.1 Biology and Behavior

Beetles of the genus *Melanophila* inhabit nearly all continents except Australia and Antarctica and use fire-killed trees as food for their larvae (Table 8.3, Bellamy 2008; Evans 1964, 1966b; Linsley 1933, 1943; Manee 1913; Ricksecker 1885; Sharp 1918; Sloop 1937; VanDyke 1926; Wikars 1997). As far as it is known, nearly 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, it has been reported that *Melanophila* species breed in a variety of burnt conifers as well as in several species of scorched deciduous trees (Apel 1991; Horion 1955). Thus, it can be stated 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!

Table 8.3 Recent species of the genus *Melanophila* according to Bellamy (2008), distribution, and early records of pyrophilous behavior and/or IR organs

Recent *Melanophila* species	Distribution	Pyrophilous behavior described by	IR organs described by
M. acuminata	African; Nearctic; Neotropical; Oriental; Palearctic	Ricksecker (1885), Manee (1913), Sharp (1918), and Linsley (1933)	Sloop (1937) and Evans (1964)
M. atra	Neotropical	–	Evans (1966a)
M. atropurpurea	Nearctic	Linsley (1933)	Sloop (1937)
M. caudata	Nearctic	–	Sloop (1937)
M. consputa	Nearctic	Ricksecker (1885), VanDyke (1926), and Linsley (1933)	Sloop (1937)
M. coriacea	Oriental	Wikars (1997)	Evans (1966)
M. cuspidata (syn.: *M. nigrita*)	African; Palearctic	Wikars (1997)	Evans (1966)
M. gestroi	African; Palearctic	–	–
M. ignicola	Oriental; Palearctic	Champion (1918)	Sloop (1937)
M. notata	Nearctic; Neotropical; Palearctic; oriental	Manee (1913) and Linsley (1933)	Sloop (1937)
M. obscurata	Palearctic	–	–
M. occidentalis	Nearctic	Obenberger 1928 in Linsley (1943)	Sloop (1937)
M. unicolor	African	–	Evans (1966)

8.4.3.2 Structure, Function, and Possible Detection Range of the Metathoracic IR Organs

The IR receptors are situated in two pit organs which are located on the metathorax (cf. Table 8.2). Each IR organ houses about 70 IR sensilla which are closely packed together at the bottom of the pit (Fig. 8.6a, Evans 1966a; Vondran et al. 1995). From the outside, a single sensillum can be recognized by a hemispherical dome with a diameter of about 12–15 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 10 μm (Fig. 8.6b). 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, (ii) an intermediate layer of unstructured cuticle revealing many irregularly arranged microcavities (mc in Fig. 8.6b), 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. The narrow gap surrounding the sphere is filled out by leaflike extensions of at least two enveloping cells (not visible in the dried cuticular specimen shown in Fig. 8.6b). From below, the sphere is innervated by a single sensory cell (Fig. 8.6c). As a prominent feature, it has been found that the outermost
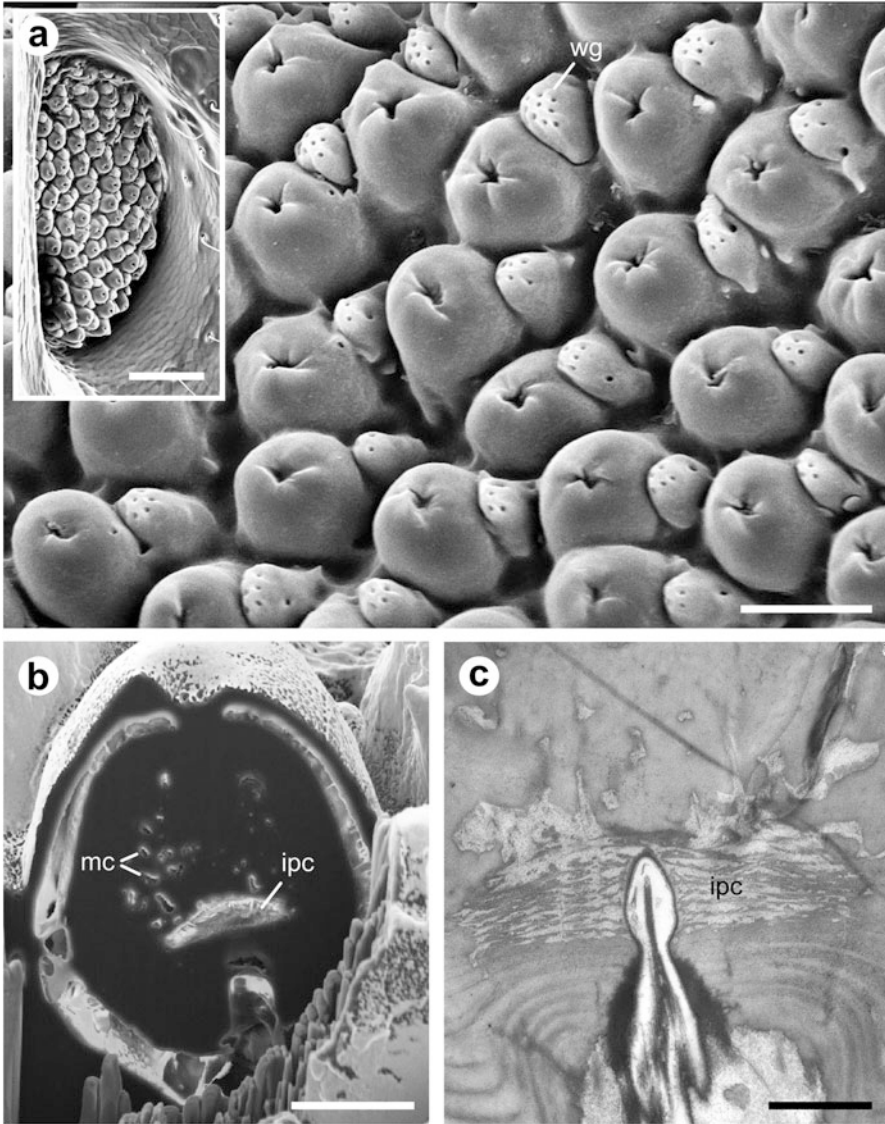
Fig. 8.6 Morphology of the IR organ of *Melanophila acuminata*. (**a**) Dome-shaped IR sensilla at the bottom of a pit organ (shown in the *inset*). Each sensillum is accompanied by a smaller wax gland (*wg*) characterized by tiny pores. SEM micrographs, *Bar*: 15 μm (*Inset* 100 μm) (**b**) Single IR sensillum centrally opened by focused ion beam (FIB) in a SEM. Specimen was air-dried; therefore, only the cuticle is preserved. Microcavities (*mc*) of the intermediate layer and the inner pressure chamber (*ipc*) can be discerned inside the sphere. *Bar*: 5 μm. (**c**) Outermost tip of the ciliary dendrite of the mechanosensitive cell inside the inner pressure chamber (*ipc*). The tip is suspended by fine filaments inside the fluid-filled chamber which communicates with the fluid in the microcavities. Any increase in fluid pressure is transferred onto the dendritic membrane. TEM micrograph, *Bar*: 1 μm (**c** adapted from Schmitz et al. 2007)

tip of the dendrite is located inside an inner pressure chamber in the sphere (IPC in Fig. 8.6c). 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 and Bleckmann 1998; Schmitz et al. 1997).

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), the only compliant structure in the sphere is the olive-shaped tip of the dendrite in the inner pressure chamber which becomes slightly squeezed by the increasing pressure. This lateral compression of the dendritic tip is the adequate stimulus for the mechanoreceptor (French 1992; Thurm et al. 1983).

Up to now the crucial question from which distances *Melanophila* beetles can detect a fire by IR reception cannot be answered satisfactorily. Extracellular electrophysiological recordings obtained by inserting a metal electrode between the IR sensilla have revealed a fast and strictly phasic response to heating (Fig. 8.5) (Schmitz et al. 1997), and a threshold sensitivity of 500 μW/cm^2 has been estimated (Schmitz and Bleckmann 1998). It has been calculated that this sensitivity would enable a beetle to detect a larger forest fire of 10 ha with a temperature of 700 °C from a distance of about 10 km (Schmitz and Bleckmann 1998). However, because the metal electrode may have sucked considerable amounts of heat energy away from the sensilla, this threshold most probably is underestimated. A recent in-depth modeling of a big historic oil-tank fire, which attracted untold numbers of *Melanophila consputa* in California 90 years ago (VanDyke 1926), suggested a much higher 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 a crucial cue used by the beetles to detect the fire, this would result in a sensitivity of 40 nW/cm^2 (Schmitz and Bousack 2012). In principle this would mean that the IR receptors of *Melanophila* beetles can compete even with technical high sensitivity quantum IR sensors that have to be cooled, e.g., with liquid nitrogen, to suppress the thermal noise. However, additional mechanisms like active amplification, which, already has been described for auditory hearing organs in insects (Göpfert and Robert 2001, 2003; Mhatre and Robert 2013), and effective noise suppression have to be postulated to make this unbelievable sensitivity imaginable.

8.4.4 IR Receptors in Pyrophilous *Aradus* Bugs

The family of Aradidae (flat bugs) comprises about 200 species (Heiss and Pericart 2007). Within this large family, only eight species have been described to be associated with forest fires because these species were found on burnt areas relatively soon after a fire (Table 8.4; (Baena and Torres 2013; Johansson

Table 8.4 *Aradus* species found shortly after a fire on a burnt area and/or their IR receptors

Aradus species	Distribution	Pyrophilous behavior described by	IR receptors existing (+); missing (−); no data available (n.a.); according to Schmitz et al. (2010)
A. albicornis	Australian	Schmitz et al. (2008)	+
A. anisotomus = *anullicornis*	Eurasian	Wikars (1997) and Wyniger et al. (2002)	n.a.
A. crenaticollis	Eurasian	Wikars (1997) and Johansson et al. (2010)	−
A. flavicornis	Eurasian, African	Baena and Torres (2013)	+
A. fuscicornis	Australian	Schmitz et al. (2010)	+
A. laeviusculus	Eurasian	Lappalainen and Simola (1998)	−
A. lugubris	Eurasian, North-American	Wyniger et al. (2002) and Johansson et al. (2010)	+
A. signaticornis	Eurasian, North-American	Wikars (1997) and Wyniger et al. (2002)	n.a.

et al. 2010; Lappalainen and Simola 1998; Schmitz et al. 2008, 2010; Wikars 1997; Wyniger et al. 2002)). Also in *A. gracilicornis* and *A. gracilis*, a pyrophilous behavior has been described (Deyrup and Mosley 2004). However, both species were found more than 1 year after the fire. Thus, the time of arrival of the pioneer generation and, hence, a pronounced pyrophilous behavior is uncertain (see also next section). Within this small group of pyrophilous flat bugs, IR receptors so far were only found in four species: namely, in *A. albicornis*, *A. flavicornis*, *A. fuscicornis*, and *A. lugubris* (cf. Tables 8.2 and 8.4; Schmitz et al. 2010).

8.4.4.1 Biology and Behavior

There is strong evidence that pyrophilous *Aradus* bugs listed in Table 8.4 are lured to burnt trees by fire-specific cues like smoke, heat, and – after the fire has ceased – persisting smell of burning. Attracted by these cues, those fire-adapted species arrive early on a burnt area. The behavior of *Aradus* species in general is hard to observe because the tiny flat bugs conceal themselves under the bark of the burnt trees. According to the current knowledge, the adult bugs and their larvae feed on the mycelia of fast-growing post-fire fungi, which start to grow on burnt wood immediately after a fire (Froeschner 1988; Wikars 1992). Sporadic own observations on *A. albicornis* in Western Australia revealed that bugs arrive on freshly burnt areas a few hours after a fire has raged over a forest. Apparently, bugs prefer to colonize weak moisture-loving eucalyptus trees growing near creeks or

lakes like *Eucalyptus rudis*. After copulation, the females deposit their eggs at the base of the stem already hidden a few centimeters in the soil. In this so-called collar region, lignotuber bulges were frequently observed. These are specialized woody storage organs with an active cambium layer, therefore still having a high moisture content, that are capable of resprouting after a fire even if the above-ground part of the tree is totally burnt. This obviously is the zone where the fungi find good conditions and start to grow. If the collar region is carefully excavated about a week after the fire, groups of adults and first larvae can be found between the superficial roots sucking on the mycelia. There is evidence that the pyrophilous *Aradus* species continue to reproduce at these favorable spots as long as the fungi stay alive.

8.4.4.2 Structure and Function of the Prothoracic IR Organs

Photomechanic IR receptors are mainly located on both propleurae of the prothorax (Table 8.2). The propleurae extend behind the bulges of the prothoracic leg bases and are developed as thin winglike duplications of the body wall. Accordingly, the thermal mass is rather low. Very few IR sensilla were also found directly posterior to the bases of the mesothoracic legs (cf. Table 8.2, Schmitz et al. 2010). At a first glance, a single IR sensillum strongly resembles an IR sensillum located in the pit organs of *Melanophila* (cf. Table 8.2, Figs. 8.6a, 8.7a, and 8.8). However, numbers of sensilla are much lower in *Aradus* (one or two dozen on each propleura) and the sensilla are loosely interspersed between the bollard-like hair mechanoreceptors (Fig. 8.7a). TEM micrographs show that two further differences to the *Melanophila* sensilla exist: a distinct cleft around the sphere is missing in the *Aradus* sensillum (Figs. 8.7b and 8.8), and the outermost tip of the mechanosensitive dendrite anchored in the cuticle of the sphere remains only about 500 nm below the bottom of the indentation in the center of the sphere (Fig. 8.7b, c). On the other hand, the same basic components of a photomechanic IR sensillum described in *Melanophila* beetles are present: an outer lamellated shell enclosing a microfluidic core which is innervated by one ciliary mechanosensory cell. At its outermost tip, the dendrite of the mechanoreceptor is in direct contact to the fluid inside the sphere (Figs. 8.7b, c). Thus, the IR sensilla of pyrophilous *Aradus* bugs also can be classified as photomechanic IR receptors.

First electrophysiological recordings revealed that the sensillum responds to heating in a phasic-tonic way. At high stimulation intensities, first spike latencies were only 3–7 ms like in the *Melanophila* sensilla (Fig. 8.7d). However, the sensitivity seems to be considerably lower. So far a threshold sensitivity of 11 mW/cm^2 has been determined by extracellular recordings (Schmitz et al. 2008). As in the beetle *Acanthocnemus*, it cannot be completely ruled out that the bugs may use their IR receptors for the detection of fires from distances of some kilometers. Because the pyrophilous *Aradus* species are also very small and appear to be weak flyers, it seems unlikely that they use their IR receptor for fire detection from larger distances. Most probably, bugs also use the IR sensilla for the localization of hot spots prior to landing.
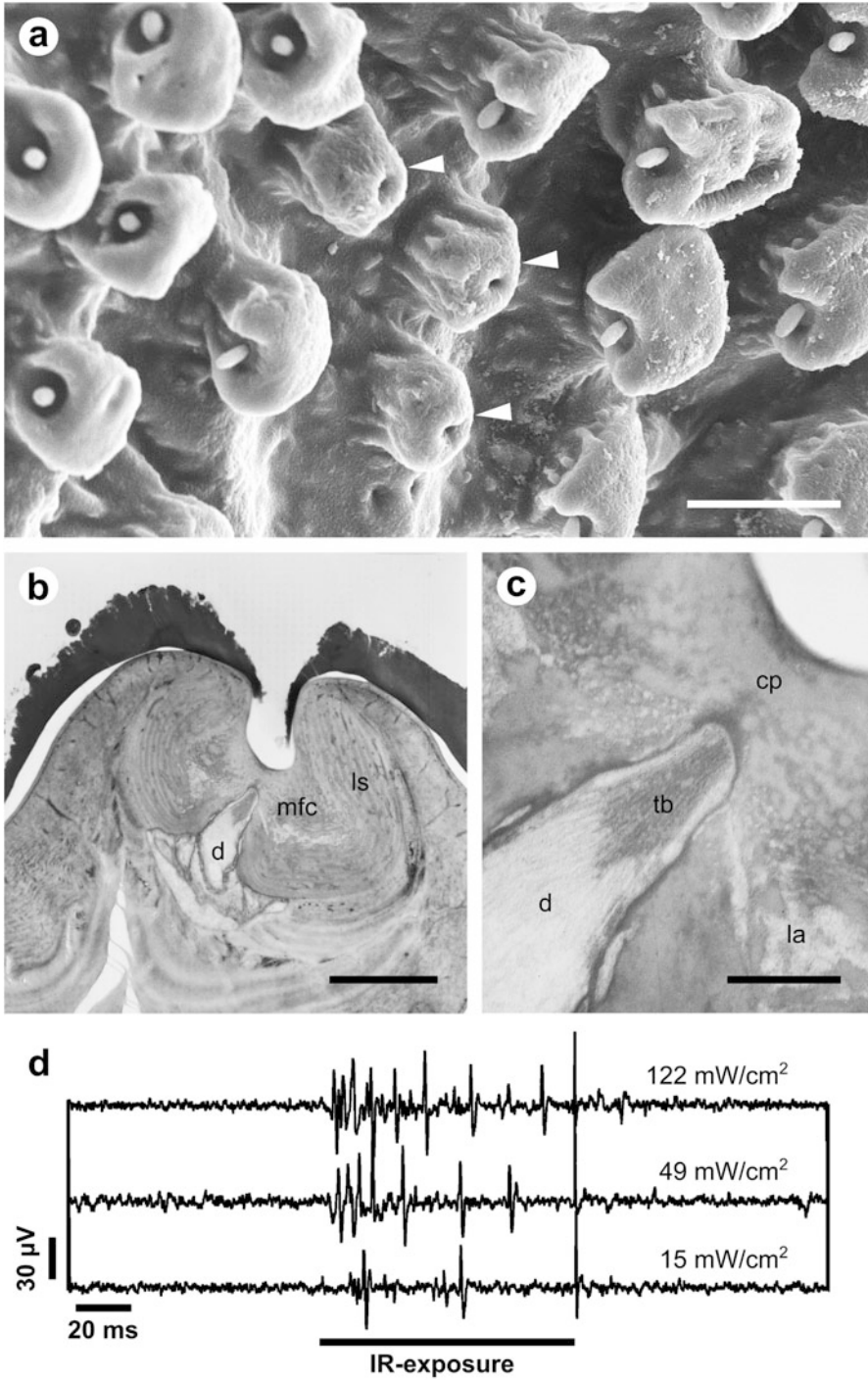
Fig. 8.7 (**a**) Detail from the right propleura of *Aradus albicornis*. Between several bollard-like hair mechanoreceptors with short bristles, three IR sensilla are interspersed (*white arrowheads*,
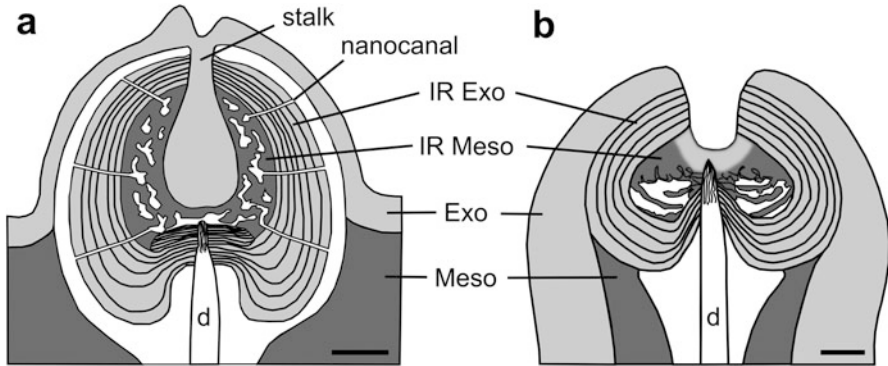
Fig. 8.8 Schematic drawings of photomechanic IR sensilla in (**a**) *Melanophila* beetles and (**b**) pyrophilous *Aradus* bugs. In both receptors, the expansion of the fluid encapsulated inside an inner microfluidic center is measured by a ciliary mechanosensitive cell (**a** adapted from Schmitz et al. 2007, **b** adapted from Schmitz et al. 2008)

8.5   The Development of IR Receptors in Pyrophilous Insects

For several reasons, pyrophilous insects appear to be predestined to develop IR receptors. First of all, the flames and hot surfaces of a fire emit additional quantities of MWIR radiation, which is well transmitted through the corresponding atmospheric window into the surroundings (Fig. 8.1). Thus, this invisible electromagnetic radiation can serve as a valuable source of information permitting the detection of a fire from larger distances as well as the early contactless detection of unfavorable hot spots. The existence of IR receptors, therefore, is a clear advantage for a pyrophilous insect.

A fire creates a very interesting ecological niche within a few minutes: the burnt area (Bond and Keeley 2005). On a burnt area, most biotic as well as many abiotic factors have changed dramatically. For insect species which feed on dead wood or fungi, this spot is a kind of paradise (Saint-Germain et al. 2008). However, the area has to be approached quickly before competitors, also appetent to colonize the dead

Fig. 8.7 (continued) Bar: 20 μm). IR sensilla are characterized by a central indentation. SEM micrograph. (**b**) Section through the center of an IR sensillum at the position of the indentation. The sensillum is covered by an electron dense superficial layer. The internal sphere with a diameter of 10 μm shows a lamellated shell (*ls*) and contains a microfluidic core (*mfc*). In the center of the core, the dendritic tip (*d*) of the mechanosensory neuron is situated. TEM micrograph, *Bar*: 3 μm. (**c**) Detail of the insertion site of the dendrite. The dendrite contains a well-developed tubular body (*tb*), which is characteristic for insect mechanoreceptors, and ends in a cuticular plug (*cp*) about 500 nm below the bottom of the central indentation of the sphere. *la* lacuna of the fluidic core. TEM micrograph, *Bar*: 0.5 μm. (**d**) Electrophysiological recordings from a single IR sensillum with different radiation intensities applied with a red helium-neon laser. At high irradiation intensities, first spike latencies were only 3–7 ms (**d** adapted from Schmitz et al. 2008)

wood, arrive. The group of pyrophilous insects consists of about 40 species from the orders of Coleoptera, Hemiptera, Diptera, and Lepidoptera (Wikars 1997). In general, it can be proposed that this specialized group of insects has developed sensory and behavioral adaptations to master this task. There is evidence that adaptations in the jewel beetles *Melanophila* and *Merimna* toward a pyrophilous biology have advanced to an extent that successful reproduction obviously is impossible without a fire. Thus, the development of IR sensory capabilities is plausible in both genera.

The driving forces fostering the development of IR receptors can be summarized 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 unspecifically some peripheral receptors. Primarily, this may have affected external mechanoreceptors exposed to incoming IR radiation that were stimulated by thermal expansion of nearby cuticle or water in the respective receptor lymph cavities. By this, an evolutionary pressure came into play and – as a first important step – the IR-absorbing outer cuticular apparatus of the evolving IR sensillum had to be optimized. This can be exemplified by looking at the photomechanic sensilla in *Melanophila* beetles and *Aradus* bugs (Fig. 8.8). 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 surface 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).

Nevertheless, the routes of evolution toward an IR receptor in pyrophilous insects have found at least two other ways. IR receptors in *Merimna atrata* and *Acanthocnemus nigricans* are very different from each other and also from the photomechanic IR receptors. Currently, there is no concept available to trace back IR receptors in all genera of pyrophilous insects to a common ancestral form. Most probably, all receptors have evolved independently.

8.6 Matched Filters Permit the Best Possible Function of IR Receptors in Pyrophilous Insects

Despite of their independent evolution, insect IR receptors depicted in this chapter all show the same built-in filter properties! Remarkably, these filters were already preset by the absorption spectra of the gases in the atmosphere and the chemical composition of the insect cuticle. As depicted in Table 8.2, filters could be used (integrated into the sensor) without modifications enabling the underlying sensory cells to perceive a maximum of temperature increase and/or thermal expansion.

The atmospheric windows can be regarded as valuable filters (Filter 1) because emission maxima of relevant IR sources like fires or warm-blooded creatures are located within the MWIR and LWIR windows. These windows can be regarded as matched band-pass filters also accounted for in all technical IR sensors (Budzier and Gerlach 2011; Gaussorgues 1994).

Filter 2 is given by cuticular absorption. As pointed out in previous publications (Schmitz et al. 2007; Vondran et al. 1995; Schmitz and Bleckmann 1997), insect cuticle per se can be regarded as a composite material consisting of biopolymers that show strong IR absorption bands in the MWIR. This may have been a very important prerequisite for the evolution of all insect IR receptors. Because both filters perfectly match, an IR-sensitive pyrophilous insect is able to efficiently sense MWIR radiation by using its IR receptors that consist of optimized cuticular absorbers combined with appropriate sensory cells.

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