



PERGAMON

Micron 33 (2002) 211–225

micron

www.elsevier.com/locate/micron

Biological infrared imaging and sensing

Angela L. Campbell*, Rajesh R. Naik, Laura Sowards, Morley O. Stone

Air Force Research Laboratory, Materials and Manufacturing Directorate, MLPJ Building 651, Area B, 3005 P. Street, Suite 1, Wright-Patterson AFB, OH 45433-7702, USA

Abstract

A variety of thermoreceptors are present in animals and insects, which aid them in hunting, feeding and survival. Infrared (IR) imaging pit organs in Crotaline and Boid snakes enable them to detect, locate and apprehend their prey by detecting the IR radiation they emit. IR pit organs of common vampire bats (*Desmodus rotundus*) enable them to detect IR radiation emitted by blood-rich locations on homeothermic prey. The beetle *Melanophila acuminata* locates forest fires by IR-detecting pit organs in order to lay their eggs in freshly killed conifers. Thermoreceptors located in the wings and antennae of darkly pigmented butterflies (*Pachliopta aristolochiae* and *Troides rhadamathus plateni*) protect them from heat damage while sun basking. Blood-sucking bugs (*Triatoma infestans*) are speculated to possess thermoreceptors, which enable them to perceive the radiant heat emitted by homeothermic prey and estimate its temperature at a distance. This is a review of the diverse types of biological thermoreceptors, their structure and function, and how electron microscopy has been instrumental in determining their ultrastructure. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Boid snakes; Crotaline snakes; Vampire bats; Beetles; Sun-basking butterflies; Electromagnetic radiation; Infrared imaging; Infrared sensing; Morphology; Natural infrared detectors; Pit organ; Scanning electron microscopy (SEM); Scanning probe microscopy (SPM); Transmission electron microscopy; Thermoreceptors; Thermomechanical receptors

1. Introduction

The biological processes of many animals and insects are affected by the presence of thermal energy in their environment (Barrett et al., 1970). Many animals and insects have the ability to detect changes in thermal energy within their environment. Diverse types of thermoreceptors are found in nature, which aid animals and insects in hunting, feeding and survival. Crotaline and Boid snakes possess infrared (IR) imaging receptors called pit organs, which work along with their visual and other sensory systems to enable them to detect, locate and apprehend prey (Bullock and Diecke, 1956; Barrett et al., 1970). Vampire bats possess IR pit organs, which enable them to locate blood-rich locations on their prey by detecting the IR radiation they emit (Kishida et al., 1984; Kurten and Schmidt, 1985). Forest fire-seeking beetles (*Melanophila acuminata*), which lay their eggs in trees freshly killed by forest fires, detect forest fires with IR detecting pit organs (Evans, 1964; Schmitz and Beckmann, 1998). Certain butterflies possess thermoreceptors in their wings and antennae that protect them from heat damage during basking (Schmitz and Wasserthal, 1993; Schmitz, 1994). Blood-sucking bugs (*Triatoma infestans*)

are speculated to possess thermoreceptors, which enable them to perceive the radiant heat of a warm source and estimate its temperature at a distance, when seeking homeothermic prey (Lazzari and Nunez, 1989; Schmitz and Beckmann, 1998). This is a review of the various types of biological thermoreceptors, how their function enables each species to survive, and the role electron microscopy has played in determining their ultrastructure. Table 1 presents a summary.

2. Infrared imaging organs of snakes

2.1. Survival function

The pit organs of Crotaline and Boid snakes are radiant heat detectors, which aid them in survival by enabling them to detect, locate and apprehend warm-blooded prey and by warning them of the presence of predators (de Cock Buning, 1985) and other objects they must avoid (Molenaar, 1992). These enable them to image warm-blooded prey in the infrared (IR) region of the electromagnetic spectrum. Pit organs absorb IR radiation in two major atmospheric windows: the 3–5 μm range and the 8–12 μm range which matches the IR emission of targeted prey (Grace et al., 1999). In addition to detecting IR radiation emitted by warm objects in their environment, the pit organs are also sensitive to conducted

* Corresponding author. Fax: +1-937-255-3808, ext. 3124.

E-mail address: angela.campbell@ml.af.mil (A.L. Campbell).

Table 1
Properties of biological infrared imaging and sensing organs and thermoreceptors

Animal/Insect	Threshold energy ($\mu\text{W}/\text{cm}^2$)	Threshold temperature change ($^{\circ}\text{C}$)	Distance to detection	Type of receptor	Directional sensitivity	Reference
Boid IR receptor (<i>Boa constrictor</i>)	176.89	0.003	16.4 cm	Specific warm	No	Barrett et al. (1970); de Cock Buning (1983); Molenaar (1992).
Boid pit organ (<i>Python reticulatus</i>)	59.75	0.026	28.3 cm	Non-specific warm bimodal (IR and tactile)	Yes	Barrett et al. (1970); de Cock Buning (1983); Molenaar (1992)
Crotaline pit organ (<i>Agkistrodon rhodostoma</i>)	10.75	0.003	66.3 cm	Specific warm	Yes	de Cock Buning (1983); Molenaar (1992)
Beetle antennal thermoreceptors (<i>Melanophila acuminata</i>)	May detect fires at short range	2.0	N/A	Warm receptor	Yes	Evans (1964)
Beetle pit organ (<i>Melanophila acuminata</i>)	60–500	0.01	60–100 miles	Warm receptor	Yes	Schmitz and Bleckmann (1998)
Common vampire bat pit organs (<i>Desmodus rotundus</i>)	50	–	8–12 cm	Warm receptor	Yes	Kurten and Schmidt. (1985); Molenaar (1992)
Blood-sucking insect antennae (<i>Itratoma infestans</i>)	–	Orient toward objects between 30 and 32 $^{\circ}\text{C}$	4–10 cm	No receptor identified yet	Yes	Lazzari and Nunez (1989)
Butterfly wing vein thermoreceptors (<i>Troides r. plateni</i>)	–	Respond to heating rate of 2.4–4 $^{\circ}\text{C}/\text{s}$	N/A	type II receptors (warm)	Yes	Schmitz and Wasserthal (1993)
Butterfly antennal thermoreceptors (<i>Troides r. plateni</i>)	–	May measure ambient temperatures	N/A	Type I receptor (warm)	Yes	Schmitz and Wasserthal (1993)

heat as well as other types of microwave energy (Molenaar, 1992). The receptors in the pit organs are able to detect very small changes in temperature (Barrett et al., 1970; Newman and Hartline, 1982). Bullock and Diecke (1956) found that the rattlesnake pit organ is capable of detecting a 0.003°C change in the temperature of water flowing across the pit membrane. Boid snakes are able to detect changes in temperature as small as 0.026°C (Barrett et al., 1970). Stimuli warmer or colder than the background temperature of the snake's environment can be detected independently of the ambient temperature and the snake's own body temperature.

Crotaline snakes such as the rattlesnake, cottonmouth and copperhead possess two pits (facial pits) located on either side of the face between the eye and the nostril. Boids, such as the *Python*, possess as many as 13 pairs of labial pits located on their upper and lower jaws (Barrett et al., 1970; Newman and Hartline, 1982; Molenaar, 1992). Other Boids such as *Boa constrictor* and anaconda (*Eunectes muniras*) lack pit organs. However, they do possess IR-sensitive receptors in their labial scales (Barrett et al., 1970).

There are nine stages which describe the hunting and feeding behavior of snakes which include rest, alertness, head turnings, approach, preparation, strike, constriction (Boids) or re-approach (Crotalines), head searching and swallowing (de Cock Buning, 1983, 1985). Various combinations of the sensory systems (visual, infrared, chemical, and mechanical) are involved at some time during the feeding and hunting process. When snakes are in an environment where there is little visual stimulation, such as at night, or in a rodent's den, the hunting and feeding behavior is initiated by the presence of radiant heat from the prey in snakes with pits, such as rattlesnakes and pythons. Mechanical stimulation (substrate vibration) initiates the hunting and feeding process in snakes that do not possess pits, such as vipers and boa constrictors (de Cock Buning, 1983).

Pit organs, by sensing thermal stimuli, are utilized in many of the phases of the hunting and feeding behavior of snakes. However, they are most important during the strike phase where they trigger and guide the strike toward their prey (de Cock Buning, 1983). Like the eye, nose and ear, pit organs are telereceptors; meaning they detect specific features of objects at a distance (Molenaar, 1992). Newman and Hartline (1982) speculate that they may be able to locate objects that emit radiant heat in space with high accuracy in much the same way as the eye. Additionally, thermoreceptors that respond to thermal stimuli independently of the pit organs, are present in the oral mucosa of vipers and pit vipers. These receptors help to aim the strike when the mouth is opened and the fangs are extended (Molenaar, 1992).

In some species of snakes with IR receptors, other stimuli are detected, i.e. the receptors are multimodal. *Python reticulatus* has bimodal receptors that respond to touch in addition to a rise in temperature (de Cock Buning, 1983). These receptors can be classified as mechanoreceptors that are sensitive to changes in temperature. They also possess the

function of preventing mechanical stimulation of the receptors (de Cock Buning, 1983).

2.2. Infrared receptor structures

In general, pit organs whether labial or facial are open external cavities, 1–5 mm in diameter, located in the soft tissue and bone of either the face or the upper and/or lower jaws of IR-sensitive snakes (Terashima et al., 1968; Barrett et al., 1970; Newman and Hartline, 1982). The cavities of the facial pit organs contain an inner chamber that is separated by a thin (15 µm), concave, heavily innervated, IR-sensitive membrane (Terashima et al., 1968; Barrett et al., 1970; de Cock Buning et al., 1981; Newman and Hartline, 1982; Molenaar, 1992). The IR-sensitive membrane of facial pits is characterized by a high concentration of terminal nerve masses (TNMs) situated between two cornified epidermal layers and a dense capillary bed located directly beneath the membrane (Barrett et al., 1970; Newman and Hartline, 1982; Molenaar, 1992). Boid pit organs are shallow depressions or cavities located within or between the labial scales (Amemiya et al., 1998a). The shapes of the labial pits in pythons for example, vary according to their positioning. Pits in the upper labial scales can be in the shape of vertically elongated ovals, sickles, or triangles. The pits facing forward in the upper lip of the snakes are deeper than those facing to the side. Pits in the lower labial scales are round or square and are never vertically elongated. Caudal pits in the lower labial scales are usually deeper than those facing to the side. Labial pits lack the membrane present in the facial pits (Barrett et al., 1970; de Cock Buning, 1985). However, they do have a dense capillary bed beneath the floor of the pit in the epidermis and are heavily innervated (Barrett et al., 1970). Both facial and labial pits have a nervous layer that contains very high concentrations of oxidative enzymes (adenosine triphosphatase, succinic dehydrogenase and lactic acid dehydrogenase), and a high concentration of mitochondria, which change their configuration in the presence of IR radiation (Molenaar, 1992; Barrett et al., 1970; Amemiya et al., 1998a).

The sensitivity to IR radiation is much greater in Crotaline snakes than in Boid snakes due to the pit structure. Although pit organs are more sensitive to IR than the thermoreceptors in mammals, their threshold sensitivity to temperature is not much different. The close proximity of the receptors to the surface of the sensory epithelium (2–30 µm below the surface) (Barrett et al., 1970; Newman and Hartline, 1982; Molenaar, 1992; Amemiya et al., 1998b) in the pit organs makes them much more sensitive. Thermoreceptors in mammals lie much deeper (300 µm below the skin) which require 20 times as much heat energy to warm the receptors than it would for a Crotaline pit organ (Newman and Hartline, 1982). In addition to the difference in the depth of the receptors, anatomical differences make the Crotaline receptors more sensitive. The 15 µm thick pit

membrane is surrounded by air on both sides, insulating it from heat loss by conduction to surrounding tissues, thus causing nearly all IR radiation incident on the pit to heat the membrane (Newman and Hartline, 1982). In addition, the pit membrane of Crotaline pit organs has a higher degree of innervation of nerve fibers than the receptors in the floor of labial pits or scales (Newman and Hartline, 1982; de Cock Buning, 1985).

The membrane of facial pits is innervated by 6000–7000 (Newman and Hartline, 1982; de Cock Buning, 1985) myelinated fibers 2.5–3.5 μm in diameter which project from the maxillary and ophthalmic branches (de Cock Buning, 1985; Molenaar, 1992; Amemiya et al., 1998b) of the trigeminal nerve system (TNS). According to Amemiya et al. (1998b), these nerve fibers enter the inner layer of the pit membrane and then begin to branch repeatedly and bend toward the outer membrane surface. As they bend and branch, the fibers lose their myelin sheaths and terminate in expanded processes just beneath the outer epithelial and cornified layers of the pit (Amemiya et al., 1998a,b). The terminal processes of these fibers aggregate into separate bundles called terminal nerve masses (TNMs), which are associated with specialized Schwann cells. Instead of forming a myelin sheath around the nerve fibers like normal Schwann cells, these Schwann cells extend their cytoplasmic processes between the TNMs and are believed to provide physical support and containment of their components (Amemiya et al., 1998b). A dense capillary bed projecting throughout the network of TNMs supplies the blood necessary to provide the cooling, extremely high energy and the high level of oxygen required for the TNMs to function (Amemiya et al., 1998b). The TNMs are each about 40 μm in diameter and contain several bulbs, which are densely packed with mitochondria (Molenaar, 1992; Amemiya et al., 1998b).

In Boid snakes, the TNMs (50 μm in diameter) are located at the bottom of the labial pits or in the labial scales (in Boids without pits), in the outer epithelium of the labial scales where they are supported by the epithelial cells (Molenaar, 1992; Amemiya et al., 1998a). Since they are supported within the epithelium they are shed and renewed periodically with each molting cycle (Amemiya et al., 1998a,b). About 400 myelinated nerve fibers (2.5–6.4 μm in diameter) (de Cock Buning, 1985) located just beneath the pit floor, bend and branch in much the same way as in the facial pits of Crotaline snakes, to form identical TNMs (Molenaar, 1992). The TNMs are also densely packed with mitochondria, are closely associated with a capillary network, which supplies energy, oxygen and cooling, and they are located 5–10 μm beneath the surface of the pit floor (Molenaar, 1992; Amemiya et al., 1998a). The nerve fibers, which make up the TNMs, originate from the maxillary branch of the trigeminal nerve (*Corallus caninus* and *Morelia spilotes*) in the upper labial pits or scales and from the mandibular branch of the trigeminal nerve in the lower labial pits or scales (Barrett et al., 1970; Molenaar, 1992).

Python reticulatus has a more complicated innervation by the trigeminal nerve system (de Cocking Buning, 1985; Molenaar, 1992). The ophthalmic branch innervates the first two pits of the upper labial scales. The deep branch of the maxillary nerve innervates maxillary pits two–five. Pits five–seven are innervated by nerve fibers from the superficial branch of the maxillary nerve. Rostrally located mental mandibular pits are innervated by the mental branches of the mandibular nerve and caudally located mandibular pits are innervated by the superficial ramus of the mandibular nerve (Molenaar, 1992).

The trigeminal nerve system (TNS) of Crotaline and Boid snakes is composed of two separate parts which include the common sensory trigeminal system which is equivalent to that found in other vertebrates, and the lateral descending trigeminal system. The lateral descending trigeminal sensory tract and its nucleus are placed lateral to the common sensory tract in the medulla (Newman and Hartline, 1982; Kishida et al., 1984; Molenaar, 1992). It relays impulses resulting from thermal stimuli in the snakes' environment, from the terminal nerve masses in the pit organs to specialized structures (nuclei) in the brain which are unique only to these IR sensitive snakes. Cobalt chloride staining of the nerves innervating the pit membrane in rattlesnakes and pythons showed that the trigeminal nerve fibers end in a nucleus called the nucleus of the lateral descending trigeminal tract (LTTD) (Newman and Hartline, 1982). In Crotaline snakes, heat stimuli are successively transferred from the TNMs to the nucleus of the lateral descending trigeminal tract (LTTD), to the nucleus reticularis colaris (RC), and to the optic tectum of the midbrain (Newman and Hartline, 1982; Kishida et al., 1984; de Cock Buning, 1985; Molenaar, 1992). In Boid snakes, heat stimuli successively transferred from the TNMs to the nucleus of the lateral descending trigeminal tract (LTTD) and the stratum griseum centrale of the mesocephalic tectum just below the visual projection in the tectum (de Cock Buning, 1983, 1984, 1985; Kishida et al., 1984; Molenaar, 1992).

2.3. Infrared sensory system

In mammals, the trigeminal nerve is associated with relaying sensory messages such as touch, pressure, temperature and pain from the facial area to the brain. As outlined above, the facial and labial pit organs in Crotaline and Boid snakes are also innervated by the trigeminal nerve system (TNS). In other vertebrates, the optic tectum plays a role in visual image formation and in spatial representation of other sensory information. It is known to integrate sensory input from various types of stimuli (sight, sound, touch, and pressure) within an animal's environment (Newman and Hartline, 1982). According to Newman, the optic tectum in IR-sensitive snakes combines IR impulses from pit organs and visual impulses from the eyes to provide them with an imaging system that allows them to compare and contrast visual and IR images. The connection between the

pit organ, trigeminal nerve system, LTDD, RC and optic tectum may serve a similar function in the formation of an IR map of the snake's environment, as does the connection between the retina, the optic nerve and the optic tectum in the formation of a visual map. In both imaging systems, the connections are made in such a way that a map of IR and visual space is formed on the tectal surfaces. The IR and visual maps represent space as it is viewed by the pit organ and the eye, respectively (Newman and Hartline, 1982). In the visual imaging system, the front part of the tectum represents the visual space in front of the animal and the back part of the tectum represents the visual space in the back and to the sides of the animal. Similarly, in the IR imaging system the front part of the tectum responds to IR stimuli originating from the front of the snake. However, in contrast to the visual image system, the back part of the optic tectum in the IR imaging system represents the visual space originating from the sides of the snake (Newman and Hartline, 1982).

There is a difference in the orientation of the map of IR space on the tectum in IR-sensitive snakes (rattlesnake, *Python reticularis*) when compared to the general vertebrate pattern of connections in the somatic sensory system (Newman and Hartline, 1982). In most other vertebrates, the front part of the tectum corresponds to the front part of the body. In rattlesnakes and in pythons, the front part of the tectum represents the back of the pit membrane; the portion of the pit membrane farthest away from the nose of the snake. Each of the 26 pits of the reticulated python is an inverted optical system that requires an inverted tectal map. When all of the pits are considered as a combined unit, the front pits project to the front of the tectum and the back pits project to the back. The IR field of view from adjacent pits overlaps substantially and this overlapping projection extends to regions in the tectum. According to Newman and Hartline (1982), all of this combined, is speculated to create a coherent representation of IR space on the python tectal surface, which may correspond, register and integrate with the visual representation.

Temperature stimuli warmer or colder than background temperatures are detected by the pit organs of Crotaline and Boid snakes. The background temperatures are dependent upon the heat emitted by the surfaces of solid objects present within the field of view of the snake (Barrett et al., 1970). The maximum sensitivity of the receptors depends on the temperature of the snake's natural habitat. According to Molenaar (1992) physiological investigations show that the IR receptors in Crotaline and Boid snakes are warm receptors. Upon detecting a positive change in temperature, warm receptors exhibit an increase in the frequency of response, in contrast to cold receptors, which exhibit an increase in the frequency of response when a negative change in temperature is detected. When an increase in temperature above the background temperature is encountered, the receptor exhibits an increase in the neuronal firing frequency above the baseline frequency. When the receptor detects a decrease in temperature

below the background temperature no increase in the frequency of firing occurs. Nonspecific bimodal IR and tactile receptors are found in the python (Barrett et al., 1970). When there is an absence in stimulus (an absence of change in temperatures) a spontaneous or 'resting' discharge is found in warm receptors which is characterized by continuous irregular and fluctuating activity and is present in the IR receptors of all IR sensitive snake families.

Pit organ receptors are also phasic, (Barrett et al., 1970) meaning that once an IR stimulus is encountered the frequency of the neuronal impulses in the receptors returns to the original level in spite of the maintained stimulus. In other words, the receptor adapts to the stimulus. These receptors have a fast adaptation to weak stimuli and a slow adaptation to strong stimuli (Barrett et al., 1970). They are very sensitive to small changes in temperature and much less sensitive to maintained temperatures. Bullock and Diecke (1956) found that IR receptors in the rattlesnake exhibit markedly increased firing within 100 ms of irradiation with a strong IR source. The stimulus remained for a short time and then slowly decayed to the 'resting' discharge (Bullock and Diecke, 1956; Newman and Hartline, 1982).

2.4. Image formation in IR pits

When pit organs encounter IR radiation, receptive areas in the pit floor are stimulated. A receptive area is a distinct portion of the sensory surface of the pit floor that elicits a neural response in a single unit (de Cock Buning, 1984; Molenaar, 1992), which corresponds to a terminal nerve mass. Each terminal nerve mass is connected to a single peripheral nerve which is in turn connected to a higher order neuron. Associated with each receptive area is a receptive field that projects conically into space (Molenaar, 1992). It is the part of the surrounding space in which an IR source elicits a neural response in a single unit (de Cock Buning, 1984).

The facial pits of Crotaline snakes and the labial pits of pythons can be modeled to operate as pinhole cameras with an aperture (A) and a projection depth (D). Image formation in pit organs is possible only by means of diffraction patterns around the edges of the pit. The quality of image formation in a pin hole camera is determined by the resolving power of the system (Molenaar, 1992), which is determined by its geometry. If an IR source is assumed to be an extended source whose radiation covers a broad band of wavelengths, and is not affected by diffraction, the illumination pattern on the pit floor can be characterized as having a central part with maximum intensity and a surrounding part which has an intensity of zero (de Cock Buning, 1985; Molenaar, 1992).

The geometry of the pit organs determines their resolving power. Facial pits have a peculiar asymmetrical shape, which can be approximated by a half circle representing the pit floor, and an aperture, which is shifted upward out

of center. Supralabial pits of *Python reticulatus* have a small opening, wider sensitive floor and the deepest pits projecting ahead when compared to other labial pits. Python supralabial pits have flat pit floors and sidewalls that bulge inwardly (de Cock Buning, 1984) which can be modeled by approximating the aperture opening as two half-circles. The pit floor of the python rostral infralabial pits can be modeled as a half circle with an aperture equal to twice its radius (de Cock Buning, 1984).

2.5. Electron microscopy and scanning probe microscopy

Transmission electron microscopy (TEM), scanning electron microscopy (SEM), and scanning probe microscopy have been instrumental in the investigation of the structure and morphology of the pit organs of IR-sensitive snakes. Barret et al. (1970) utilized electron microscopy to observe the configurational changes in the mitochondria present within the IR-sensitive receptors of the cottonmouth moccasin, when exposed to IR radiation as outlined previously, and to observe the mitochondria-packed terminal nerve masses within the pit floor of the labial pits of the reticulated python. They also utilized SEM to image the surface of the cornified epidermis of the pit membrane. Amemiya et al. (1998b) used advanced SEM techniques in the first direct three-dimensional observation of the TNMs in Crotaline snakes and the first evidence of their spatial arrangement within the pit membrane. Prior to this SEM study, TEM and light microscopy had been used to infer the three-dimensional ultrastructure of the TNMs using theoretical reconstructions of ultrathin sections (Amemiya et al., 1998b). The images obtained by SEM provided three dimensional views of all structures previously reported to be present within the pit membrane in addition to the TNMs, which include the supporting Schwann cells, unmyelinated and myelinated nerve fibers, the capillary bed, and vacuole cells.

The ultrastructure of the surfaces of pit organs in Boid and Crotaline snakes scatter or reflect electromagnetic radiation of specific wavelengths (Amemiya et al., 1995; Campbell et al., 1999) and may aid the pit organs in their function as IR detectors. Pit organ epidermal surfaces of IR-sensitive snakes are covered with arrays of pore-like structures called micropits (Amemiya et al., 1995; Campbell et al., 1999). In a previous study, we performed the first detailed three-dimensional examination of Boid scale surface morphology by SEM and scanning probe microscopy (SPM) (Figs. 1–3) (Campbell et al., 1999). In contrast to a previous study by Amemiya et al. (1995) we found that micropits were also present on the epidermal surfaces of maxillary non pit organs, spectacle and ventral scales. We also found that each of these scale surfaces contain major surfaces features of overlapping plate-like structures. Scanning probe microscopy measurements of micropit dimension varied as a function of location on the snake's body and the pit organ surface is distinct from all other surfaces containing similar morphology. Mean micropit widths,

depths and distances between the micropits observed in the pit organ scales, were significantly larger than those found in all other scale types scales. Pit organ micropits averaged 319 nm in width, 46 nm in depth and were spaced an average of 808 nm. Mean micropit widths for maxillary non pit, spectacle and ventral scales were 249, 179, and 151 nm, respectively. Mean micropit depths for these respective scales were 16, 6 and 6 nm and mean micropit distances were 677, 529 and 525 nm. In addition, the size distributions of the micropit widths and depths were found to be very broad in pit organ scales and very narrow in non pit organ scales. We hypothesized that these size distribution differences contribute to differences in the scatter of visible light as a function of scale type. The broad distribution of micropit widths and depths in the pit organ micropits may be responsible for enhanced visible light scatter over other scale types and may enhance absorption of infrared radiation. The differences in the micropit dimensions as a function of scale type presented evidence that the arrays of micropit and plate surface structures may function as spectral filters or anti-reflective coatings with respect to incident electromagnetic radiation.

Amemiya et al. (1995) investigated the surface architecture of Crotaline pit organs utilizing TEM and SEM. They observed micropits on the outer and inner surfaces of the pit membrane and on the epithelium of the wall of the inner chamber, which also has a closely packed array of large and small domed structures. The array of domes were speculated to function as a light trap that prevents IR rays, which are transmitted into the inner chamber, from being reflected back onto the receptors in the pit membrane.

3. Infrared sensing organs of vampire bats

Common vampire bats (*Desmodus rotundus*) feed on the blood of homeothermic vertebrates in order to survive. They possess three IR sensing facial pit organs located within their nasal structure which enable them to detect their prey and to select locations on their prey that are rich in blood. Experiments by Kurten and Schmidt (1985) suggest that these animals are able to detect temperature differences. The authors demonstrated a propensity of two bats toward a warm object. Two signal units (one warm and one at ambient temperatures) were mounted on the front wall of the arena and separated by a heat insulating partition. During a trial a bat was released into the chamber and allowed to make a choice between the two signal units. If the bat chose the heated signal unit he was rewarded with food by a feeding tube inserted through an opening below the signal unit. In both animals a threshold intensity of radiant heat of $50 \mu\text{W}/\text{cm}^2$ was needed to be emitted for them to choose the warm signal unit. Calculations based on the radiation emitted by human skin suggested that the vampire bat should be able to detect warm-blooded animals at a distance of up to 16 cm (Kurten and Schmidt, 1985).

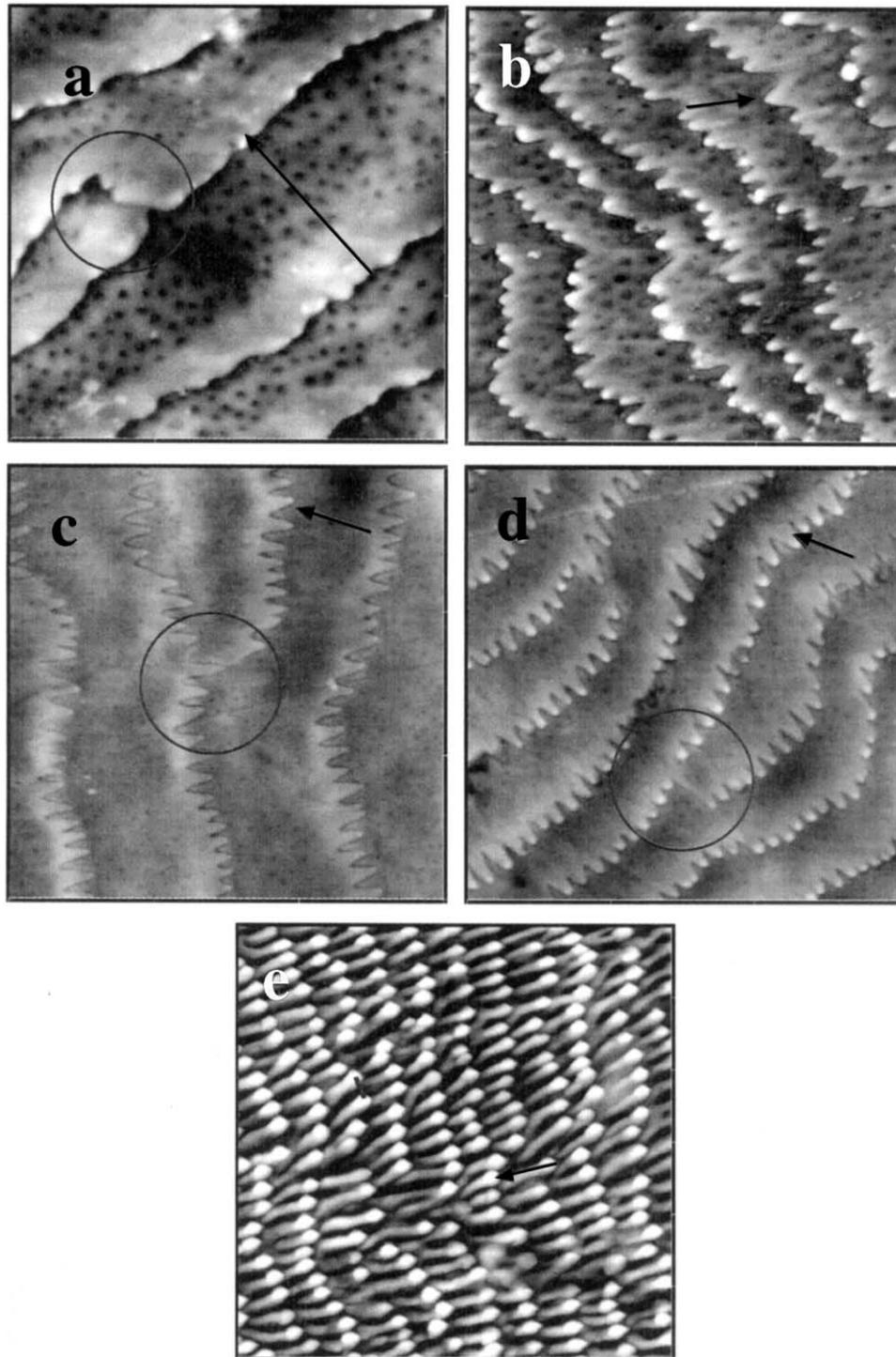


Fig. 1. TappingMode AFM (TMAFM) images ($15 \times 15 \mu\text{m}$) from the center portion of each scale type of carpet python shed skin. (a) Maxillary pit scale showing wide plate structures, a plate junction point (encircled area) and deep micropits. Arrow indicates distance between plate structures ($3.5 \mu\text{m}$). (b) Maxillary non-pit scale showing narrow plate structures, rounded plate-edge projections (arrow) and micropits. (c) Ocular spectacle scale showing wide plate structures, plate junction point in the center (encircled), shallow micropits and pointed plate-edge projections (arrow). (d) Ventral scale showing plate structures, plate junction points, rounded plate-edge projections (arrow) and shallow micropits. Black bar in the image illustrates the distance between plate-edge projections (620 nm) present on the edge of the plate structures. (e) Dorsal scale showing ridge features. Arrow indicates the tip-to-tip distance between ridges ($1.6 \mu\text{m}$). Black line to the left of the image indicates the side-to-side distance between ridges (597 nm).

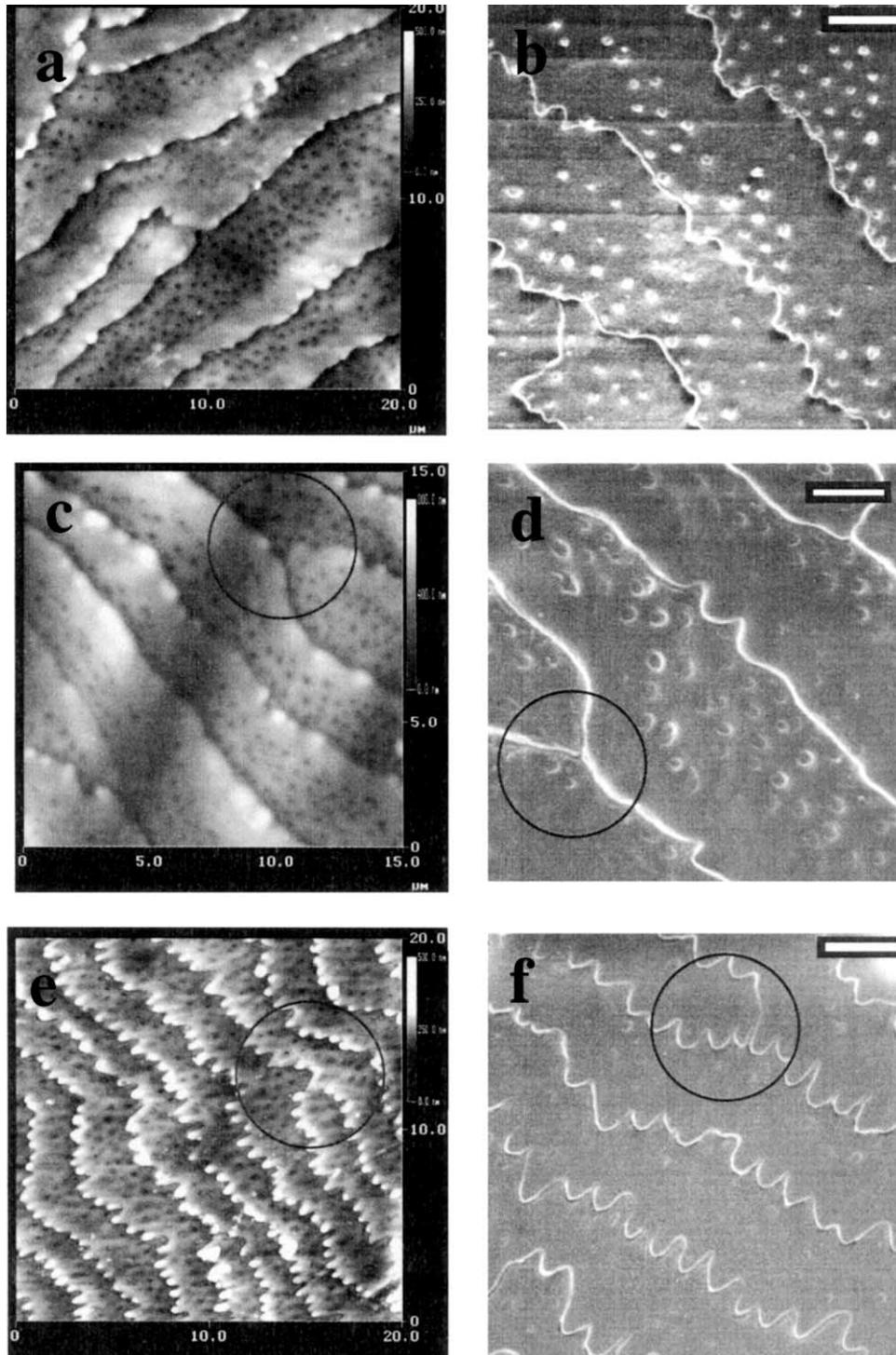


Fig. 2. TappingMode AFM ($15 \times 15 \mu\text{m}$) (a, c, e) and SEM (b, d, f) images of several types of scales from carpet python shed skin. Images (a) and (b) show the center portions of mandibular pit scales while (c) and (d) show the center portions of maxillary pit scales. The center portions of maxillary non pit scales are shown in images (e) and (f). The image scale in (e) and (f) were directly adjacent to the maxillary pit scale in the specimen used. Images (a–d) show plate structures and deep spherical micropits. Images (e) and (f) show plate structures which are narrower than those in (a–d), plate-edge projections with narrow tips and micropits. The micropits in images (e) and (f) are less spherical and more shallow than those found in the mandibular and maxillary pit scales. Encircled areas indicate plate junction points. Images (a–d) clearly show that arrays of micropits cover only one-half to two-thirds the width of the plate structures followed by an area free of micropits in an anterior to posterior direction. (In (b) anterior is at the top right of the image.) In contrast, images (e) and (f) show that the micropits in the maxillary non pit scale cover the entire plate structure surface. The edges of plate structures in SEM image has irregularly shaped and spaced projections. Bright areas in the TMAFM images indicate taller features while dark areas indicate deeper features. b, d, f: Bar = $1.5 \mu\text{m}$.

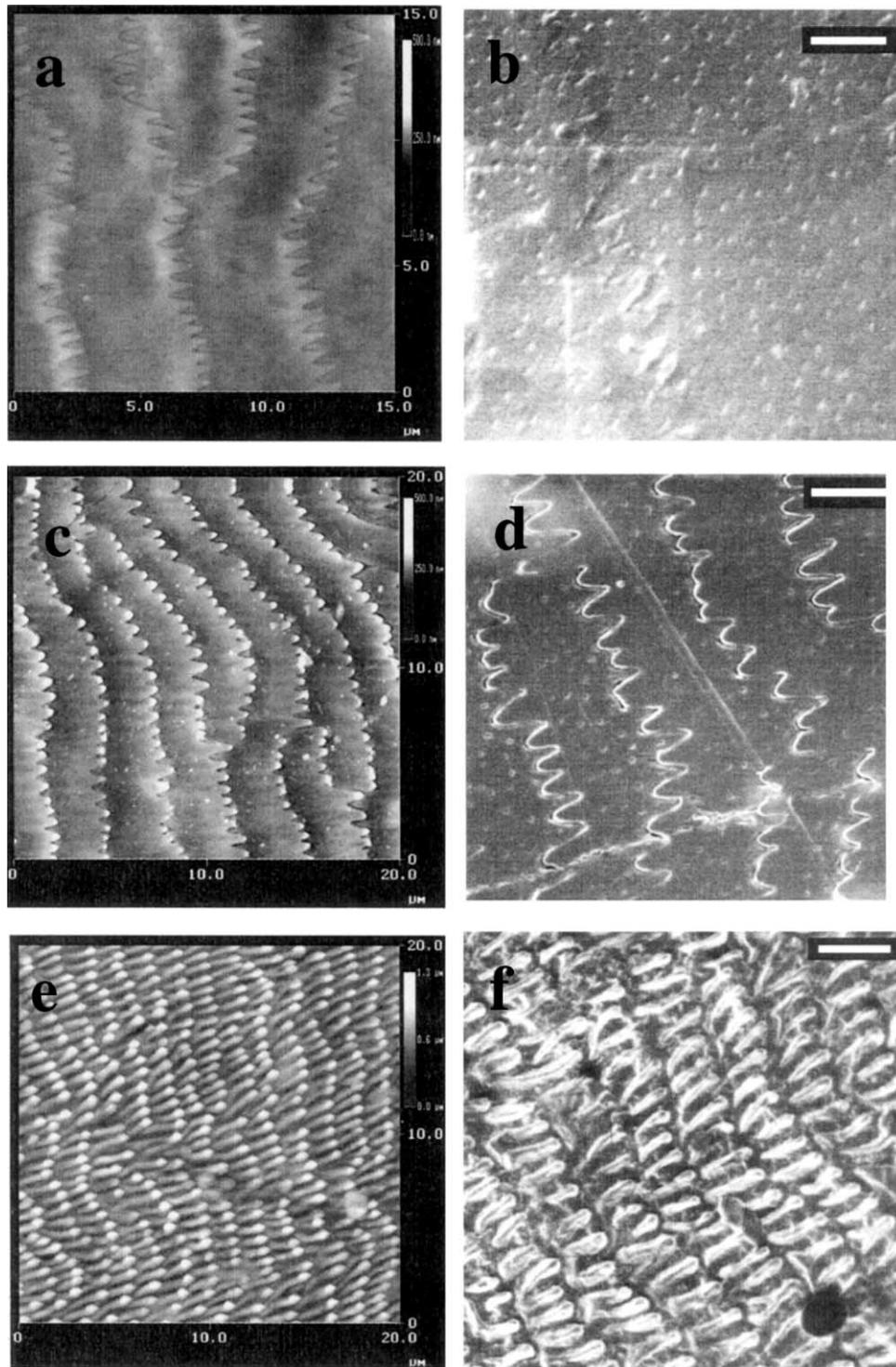


Fig. 3. TappingMode AFM ($15 \times 15 \mu\text{m}$) and SEM images of spectacle (a) and (b), ventral (c) and (d) and dorsal (e) and (f) scales of carpet python shed skin. In contrast to the maxillary non pit scale the tips of the plate-edge projections on the spectacle plate structures are more pointed as opposed to rounded. Spectacle scale plate structures are considerably wider than those in the pit organ and maxillary non pit organ scales, and possess micropits within plate structures that are more shallow, spaced at smaller distances and are smaller in width than those found in the pit organ and maxillary non pit organ scales. Ventral scale plate structures, plate-edge projections and micropits are shown in images (c) and (d). Micropits in the ventral scales appear similar to those in the spectacle scales in terms of widths, depths and spacing. However, the plate-edge projections are more rounded than pointed. Dorsal scales shown in images (e) and (f) have a unique surface structure when compared to the other scales, showing overlapping parallel rows of parallel elongated ridges. b, d, f: Bar = $1.5 \mu\text{m}$.

The nasal structure of the vampire bat has two distinct regions, which include a central nose leaf, which contains the nostrils, and a semicircular ring of pads separated from the nose leaf by a depression (Kurten and Schmidt, 1985). The depression is bridged by tissue in two places. This bridging divides the depression into an apical pit and two lateral pits. The lateral pits are approximately 1 mm wide and 1 mm deep. They are situated at an angle of approximately 45° to the right and to the left of the median plane of the animal. The apical pit rises slightly toward the nose leaf so that it is directed upward and forward. Thus, each pit opening faces in a different direction. The nose leaf is extremely flexible and is continually in motion when seeking prey enabling the bat to change the apertures of the nasal pits as necessary (Kurten and Schmidt, 1985). The arrangement of the three nasal pits could be instrumental in providing directionality in the detection of radiant heat.

Kurten and Schmidt (1985) found that the floor of the pit organs has an extremely dense network of connective tissue that lies immediately beneath the skin. In contrast to the floor snake pit organs, the pit floor of the vampire bat has no blood vessels. Histological studies detected no nerves present. However, they could have been masked by the presence of the dense connective tissue network, which has an appearance similar to nerve fibers when treated by the histological methods utilized in their study. Studies with SEM and TEM would be necessary to image the sensory system of these nasal pit organs since these structures are of ultrastructural dimensions. The dense connective tissue provides excellent insulation for the pit organs. Thermography studies suggest that the nose and pit organs are thermally isolated. The nose and pits were 9°C cooler than the surrounding tissues, thus preventing the body temperature of the bat from interfering with the ability of the pits to detect temperature changes in the environment. Similarly, in our studies with infrared video analysis of the head of a ball python, we observed that the nose region containing the pit organs was much cooler than other regions on the face of the snake (our unpublished observations).

The vampire bat has an infrared sensory system similar to that of IR sensitive snakes (Kishida et al., 1984). Kishida et al. (1984) examined the brains of three species of bats and found that only the vampire bat possessed a nucleus situated lateral to the common descending trigeminal tract similar to that found in the lateral descending trigeminal tract of Crotaline and Boid snakes. The nucleus was located in relatively the same place as the nucleus of the lateral descending trigeminal tract in IR-sensitive snakes and possessed a similar morphology. They therefore classified this nucleus as the vampire bat lateral descending tract nucleus. The presence of this nucleus may suggest that the vampire bat may have the ability to image their homeothermic prey in the same way that IR-sensitive snakes can.

4. IR detectors in *Melanophila acuminata*

Melanophila acuminata is a species of beetle that is able to locate forest fires from great distances. They detect IR radiation emitted by forest fires as far as 60–100 miles away, utilizing two IR detecting pit organs located on either side of their thorax near their middle legs (Evans, 1964, 1966; Hart, 1998; Schmitz and Beckmann, 1998; Gronenberg and Schmitz, 1999). In order to reproduce, they must lay their eggs in the bark of freshly killed conifers (Vondran et al., 1995; Hart, 1998; Gronenberg and Schmitz, 1999). Male and female *Melanophila* approach forest fires in great numbers (Schmitz and Beckmann, 1998). While the trees are still burning, the male and female beetles mate and the females lay their eggs under the bark of the conifers, just after the flames of the forest fire have extinguished and temperatures are tolerable to sustain the eggs (Vondran et al., 1995; Hart, 1998; Schmitz and Beckmann, 1998; Gronenberg and Schmitz, 1999). After the eggs hatch, the larvae remain in the dead trees and feed on them for a year or more, then tunnel out, pupate and emerge as adults (Hart, 1998). The larvae feed on the bark of the dead trees because they are unable to survive the defense reaction of a living tree to insect feeding (Schmitz and Beckmann, 1998).

Forest fires burn at temperatures between 729 and 2100°F (435–1150°C) (Vondran et al., 1995; Hart, 1998; Schmitz and Beckmann, 1998). This corresponds to IR wavelengths in the range of 2–4 μm at which forest fires have a peak emission of IR radiation (Schmitz and Beckmann, 1998; Gronenberg and Schmitz, 1999). *Melanophila* are able to detect and respond to IR wavelengths in the range of 2.4–4.0 μm with a peak response at 3.0 μm (Evans, 1966; Hart, 1998; Schmitz and Beckmann, 1998). Detection of these wavelengths at great distances is possible because the atmosphere readily transmits IR wavelengths ranging from 3 to 5 μm (Schmitz and Beckmann, 1998).

The pit organs of *Melanophila* are located next to the hip (coxal) cavities of the middle (mesothoracic) legs (Evans, 1964, 1966; Schmitz and Beckmann, 1998). They are elliptical in shape and are on average 450 μm long by 200 μm wide and 108 μm deep. Each pit organ consists of 50–100 densely packed (350/mm²) (Vondran et al., 1995) dome shaped sensory organs or sensilla present in the pit floor (Fig. 4a). The sensilla are thin, transparent, lens-like cuticular structures, which are 12–18 μm in diameter (Evans, 1964, 1966; Vondran et al., 1995; Schmitz and Beckmann, 1998). The overall body of *Melanophila* is composed of an exoskeleton that has two layers, which include a tough exocuticle and a soft endocuticle (Evans, 1966; Hart, 1998). Within the pit organ, no exocuticle is present on the sensilla, however, they consist of a mesocuticle (Vondran et al., 1995), which forms a distinct layer above the endocuticle (Hart, 1998). Each sensillum has a small apical depression (Vondran et al., 1995) and is associated with an adjacent wax gland, which also consists of mesocuticle (Evans, 1966). These wax glands secrete wax filaments

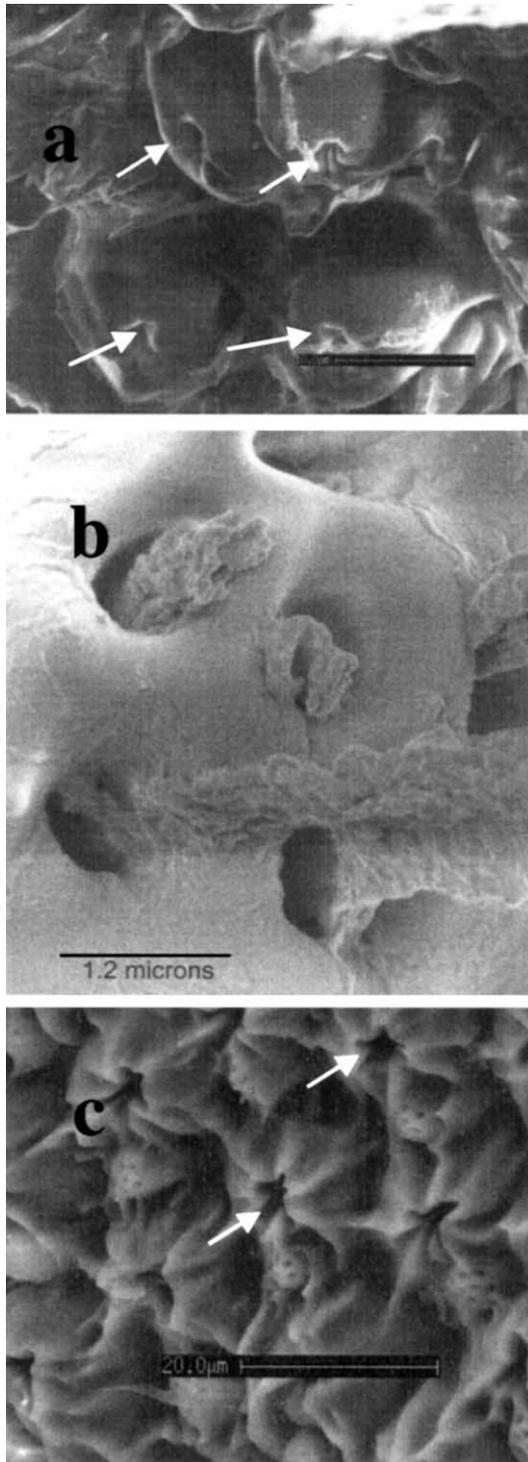


Fig. 4. SEM images of sensilla (a), wax gland (b), and collapsed sensilla (c) within the sensor pit organs of *Melanophila acuminata* which are located next to the coxal cavities of the mesothoracic legs. Image (a) shows several sensilla with apical depressions as indicated by the arrows. Several wax filaments are also shown on the sensilla. Image (b) shows a wax gland with wax filaments protruding from several pores. Sensilla in image (c) are collapsed or deflated as a result of pit organ samples being subjected to a vacuum of 10^{-7} torr during SEM acquisition. There is a dramatic change in sensilla volume and morphology as a result of the vacuum.

(Fig. 4b), which cover the sensilla and are believed to protect them from smoke, dirt accumulation and desiccation (Evans, 1964, 1966, 1975).

The spherule of each sensillum is innervated by a single ciliary neuron present in the epidermis (Vondran et al., 1995). The central cavity of each sensillum is connected to the nerve cell by axons in canals, which run through the endocuticle. The distal end of the dendrite of the sensory cell ends at the base of the cavity of the sensillum, whereas the proximal end of the nerve cell, which innervates the sensillum, is connected to the mesothoracic ganglion (Evans, 1966; Vondran et al., 1995).

Scanning electron microscopy and TEM have been utilized to study the ultrastructure of the IR-sensitive pit organ of *Melanophila acuminata* (Evans, 1975; Vondran et al., 1995). The outer surface morphology of the pit organ has been studied by SEM. The detailed structure of the sensilla was observed from ultrathin sections imaged by TEM in a study by Vondran et al., (1995). Scanning electron microscopy was also utilized in a study by Gronenberg and Schmitz (1999) to observe the afferent projections of the infrared sensitive neurons in the central nervous system of *Melanophila acuminata*. The structure, morphology and distribution of the wax fibers present on the pit organ surfaces have also been determined by SEM (Evans, 1975; Vondran et al., 1995).

Ultrathin sections of sensilla imaged by TEM displayed a lens-like mesocuticular spherule structure covered by a $1 \mu\text{m}$ thick cuticle. The spherule is connected to the outer cuticle by a stalk that runs from the apical depression of the sensilla into the spherule. With the exception of this stalk, a protoplasmic layer composed of the projections of two enveloping cells (trichogen cell and tormogen cell) envelops the entire spherule (Vondran et al., 1995).

In our SEM studies, beetles were air dried, dissected and coated with 40 \AA of tungsten on a dual ion beam sputter coater (VCR Group, Inc., South San Francisco, CA). Samples were stored in a vacuum overnight before testing. Scanning electron microscope images were captured with a Leica Stereoscan 360FE (Leica Microsystems Inc., Deerfield, IL) operated at 10 kV with a working distance of 25 mm or with a cold field emission scanning electron microscope (Hitachi S-900, Nissei Sangyo America Ltd, Gaithersburg, MD) operated at 1 or 10 kV. Fig. 4a shows several sensilla within the pit organ of *Melanophila acuminata* which are covered with wax filaments and Fig. 4b shows a wax gland with protruding wax strands.

During SEM data acquisition, the samples were subjected to a vacuum of 10^{-7} torr. Under these conditions, the upper portion of the sensilla of some samples collapsed or deflated (Fig. 4c). The dramatic change in sensilla volume is evident when compared to the sensilla in Fig. 4a. This likely indicates that these sensilla have a large hollow chamber, which expands with infrared absorption and contracts afterwards. Therefore, the degree of expansion of these membrane components seems to be the sole contributing factor for

the photomechanical portion of infrared detection. These findings support other research, which indicates a photomechanical mechanism.

Melanophila pit organs are thermomechanical receptors, which convert IR electromagnetic radiation to mechanical energy. The deformation of the nerve innervating the thermomechanical receptors triggers a nerve impulse in the sensory system (Hart, 1998; Schmitz and Beckmann, 1998). When IR radiation from forest fires in the 3 μm range impinges the pit organs, it is absorbed by the cuticular spherules of the sensilla. The cuticle tissue is composed of a protein matrix embedded with long-chained chitin (*N*-acetylglucosamines) molecules (Hart, 1998; Schmitz and Beckmann, 1998). Chitin contains C–H, N–H, and O–H bonds which are bonds that have stretch resonances in the range of 3 μm . When IR radiation comes in contact with these bonds their vibrational energy is converted into translational energy producing heat by non-radiative de-excitation processes.

According to Schmitz and Beckmann (1998) the heating of these bonds within the cuticle is proposed to cause a small change in the spherule volume (swelling and distortion) (Hart, 1998) and in turn produce a deformation of the dendritic tip of the mechanosensory cell. They also speculate that the spherule is designed to exert an adequate amount of mechanical impact on the dendrite tip to trigger nerve impulses. TEM image of ultrathin sections of sensilla showed that the cuticle of the spherule is composed of three components. An amorphous core of approximately 6 μm in diameter which shows scattered insertions of cuticle of greater electron density, an unstructured cuticle displaying some irregular lacunae, and an outer mantle of helically arranged cuticle formed in a fountain-like structure which has a lamellar appearance (Vondran et al., 1995). Schmitz and Beckmann (1998) proposed that the third component of the spherule has a coefficient of thermal expansion that is greater than the first and second components. In addition, they speculate that the middle component could help to promote the displacement of the outer mantle layer relative to the amorphous core.

Although many studies provide evidence that *Melanophila* are attracted to forest fires solely by the detection of the emitted IR radiation and not by visual, auditory or olfactory cues (Evans, 1964; Vondran et al., 1995; Hart, 1998; Schmitz and Beckmann, 1998), a recent study shows that they may be attracted to forest fires by a combination of olfactory cues and IR radiation (unpublished results).

Schmitz and Beckmann (1998) found that a stimulus intensity of 5 mW/cm^2 was sufficient to elicit a neural response (2–3 action potentials) when the pit organs were exposed to IR radiation in the wavelength range from 1.65 μm to the far IR. They conducted an electrophysiological study where the pit organs were stimulated with a thermal radiator that emitted IR radiation within the wavelength range of a forest fire. The pit organs responded exclusively to IR radiation and not to a flash of visible light,

sound, or moderate air movements. Mechanical stimulation was observed however when the thermal radiator was inserted too far into the cuticle of the sensilla. Linear extrapolation of the results in this study indicated that a radiation power of 500 $\mu\text{W}/\text{cm}^2$ might elicit a neural response (Schmitz and Beckmann, 1998).

The ultrastructure of the sensory cells that innervate the spherules is similar to that of typical insect mechanoreceptors. These sensory cells show all the features of the ciliary neurons found in mechanoreceptors (Schmitz and Beckmann, 1998). Typical mechanoreceptors have a long whisker-like bristle with a ball-and-socket joint at its base (Hart, 1998). The dendrite of the sensory neuron that innervates the mechanoreceptor bridges the distance between the socket and base of the bristle. If the bristle moves a distance of 1 nm with respect to the socket the dendrite bends and triggers the sensory neuron to fire (Hart, 1998). Similarly, Schmitz and Beckmann (1998) estimated that IR radiation at a wavelength of 3 μm and intensity of 5 mW/cm^2 would heat and swell the spherule enough to deform it by 1 nm, which would bend the dendrite and trigger impulses in the sensory neuron (Hart, 1998).

5. Thermoreceptors in butterflies

Certain butterflies (*Pachliopta aristolochiae*, *Pieris brassicae*, *Gonepteryx rhamni*, *Troides rhadamathus plateni*, *Aristolochia tagala*, *Vanessa io* and *Argynnis paphia*) must maintain a body temperature between 30 and 40°C in order to sustain their flight and feeding activity (Schmitz and Wasserthal, 1993; Schmitz, 1994). Sun-basking and behavioral thermoregulation are utilized to achieve the required temperature range. As they bask in the sun, solar radiation is absorbed by their body and wings causing heating of their temperature above ambient. The wings play a very important role in thermoregulation, specifically in gaining heat from the sun, and protecting the butterfly from overheating and undesirable convection (Schmitz, 1994), which can cause cell damage in the wings and thorax, as well as desiccation and brittleness. The amount of exposure to the sun and the amount of heat gain can be varied by adjusting their wing position (Schmitz and Wasserthal, 1993; Schmitz, 1994). According to the Lambert cosine law, maximum exposure (or maximum radiant heat gain) occurs when the wings are fully opened and positioned perpendicular ($\cos \alpha = 1$) to the incident radiation from the sun's rays, while minimum exposure occurs when the wings are fully closed and positioned parallel ($\cos \alpha = 0$) with the sun's rays. The latter positioning is known as the heat protection posture. Intermediate positioning can achieve intermediate amounts of exposure and heating (Schmitz and Wasserthal, 1993; Schmitz, 1994).

Thermal characteristics of sun-basking butterflies vary as a function of the type of basking and wing coloration (Schmitz, 1994). There are three basking types: dorsal,

lateral and body. *Pachliopta aristolochiae* and *Troides rhadamathus plateni* are dorsal basking butterflies with black wings. During basking, the dorsal surface of their forewings intercepts sunlight. Their wings are highly absorbing because of the dark pigmentation and their absorption is directly proportional to the amount of heat gain (Schmitz, 1994). The heat gained as a result of absorption is conducted to the bodies of these butterflies, along the wing veins and by additional convection of warm air between and beneath the heated wings. *Pieris brassicae* is a body basking butterfly with white wings. Wing positioning is very important in these butterflies which assume intermediate wing opening angles (10–60°) (Schmitz, 1994). In contrast to dorsal basking butterflies, their wings are unable to trap warm air. It is speculated that the dorsal surfaces of the forewings of *Pieris brassicae* may act as solar reflectors, which focus sunlight onto the thorax by diffuse reflection, thus increasing their body temperature (Schmitz, 1994). Precise orientation to the sun is also observed in basking pierids, which implies that their wings may be involved in trapping radiation to elevate their body temperature. *Gonepteryx rhamni* are lateral basking butterflies with yellow wings (Schmitz, 1994). Their wings are tightly closed when they bask. As a result, a layer of trapped air is present between their fore- and hindwings and above the thorax between the forewings. Ninety-five percent of the solar radiation transmitted through the wings is absorbed by the hairy black thorax thus providing additional heating (Schmitz, 1994).

According to Schmitz (1993), when butterflies bask, their wings, antennae and thorax heat at different warming rates and reach different equilibrium temperatures as a result of differences in their masses. The temperature of the wings of freshly killed *Pachliopta aristolochiae* increased by a factor of more than 30 times faster than the thorax during the initial 12 s of exposure to moderate solar radiation of an intensity of 54 W/cm², at an average ambient temperature of 26°C. The temperature increased in the ‘medium-mass’ wings of *Pachliopta aristolochiae* by 20–25.5°C after 30 s of exposure causing them to reach equilibrium temperatures in the range of 46–51.5°C. Under the same conditions, the thorax of these butterflies reached equilibrium temperatures in the range of 40–43°C (which represents optimum physiological temperatures) after 6–8 min of exposure, representing an increase in temperature of 14–17°C above the ambient temperature. The ‘low-mass’ antennae heated only 2–4°C above ambient temperature after 15–30 s of exposure to moderated solar intensity.

Schmitz (1993) analyzed the wing thermosensitivity of live, free-resting *Troides rhadamathus plateni* by slow step-wise scanning of the wing veins of the forewing with a calibrated light beam of 1 mm diameter. Within the first second of exposure, the light beam elicited slow wing closing reactions at discrete locations along the veins, when a heating rate in the range of 2.4–4°C/s was reached, suggesting the existence of a sensory system that is able to detect

increases in temperature. Equilibrium temperatures in the range of 36–42°C were reached in the A2 and A3 basal wing veins after irradiation for 12 s. When the radiation intensity of the light beam was increased, to produce an equilibrium temperature of 46°C or more, immediate violent wing fluttering or beating was elicited and the butterfly escaped the beam by either crawling or tilting away from the beam (Schmitz and Wasserthal, 1993), thus exhibiting a pain response.

Butterflies with darkly pigmented wings such as *Pachliopta aristolochiae* and *Troides rhadamathus plateni* are believed to have thermoreceptors that regulate their wing positioning and thus the amount of heating. These thermoreceptors, classified as warm receptors (Schmitz and Wasserthal, 1993), are believed to detect a steepness in warming rate ($\Delta T/\Delta t$), which triggers an initial response of slow wing closing movements when exposed to moderate intensity solar radiation (54 mW/cm²). Faster steepness of warming rates result when the wings are exposed to higher intensity solar radiation up to 100 mW/cm² and elicit violent wing fluttering movements known as the pain reaction. It is believed that overheating of the wings is avoided by the ability of the wings to detect rapid changes in temperature, and adjust the wings accordingly to minimize the amount of exposure to damaging radiation as outlined above.

Thermoreceptors in *Troides* are located along the anal veins A2 and A3 of the wings. Schmitz (1993) used axonal filling with CaCl₂ and silver-intensification to detect the interior structures of the thermoreceptors. A few single nerve-cell bodies were found in vein A3 which appear to be multipolar subepidermal neurons, which are so called ‘Type II receptors’ without accessory structures. No visible connections to cuticular sensillar structures were found, in contrast to those seen in mechanoreceptors. Serial sections of the internal sensory cells in the anal veins A2 and A3 showed that the branching dendrites of one single cell could terminate at different sites. In one case, one branch ended in the haemocoel adjacent to the vein nerve and the other terminated below the hypodermis. Dendrites viewed by light microscopy contained a glial sheath. TEM images of ultrathin sections showed that a glial sheath did not surround the fine ends of the branching dendrites. These unmyelinated dendritic endings were found directly beside the vein nerve.

Troides also have thermo/hygroreceptors located at the top of the antennal club called sensilla basiconica, which are believed to measure ambient temperatures (Schmitz and Wasserthal, 1993). The ultrastructure of the sensilla was determined from ultrathin sections of the antennal clubs analyzed with TEM and whole sensilla analyzed with SEM. The morphology of the sensilla is similar to that found in other insects (Schmitz and Wasserthal, 1993; Anton and Tichy, 1994). They contain three dendritic outer segments (DOS). Two of the DOS, which extend into the peg are cylindrical-unbranched and suspected to be hygroreceptors. The third

DOS is located beneath the peg socket and is presumed to be a thermoreceptor. The thermoreceptor dendrite can either be branched or lamellated.

6. Thermoreception in humans and other animals and insects

Humans possess heat receptors in the epidermis and dermis, which are distributed in a punctate fashion over the entire body. The receptors are unspecialized free nerve endings, which detect changes in temperature, as well as steady state temperatures (Barrett et al., 1970). Myelinated cold receptors that exhibit a steady state response to continuous stimuli (tonic) are also present in the skin of the hand in humans, are sensitive to pressure and are innervated by radial nerve (Barrett et al., 1970). Thermoreceptors are also located in other areas in the human body. Warm and cold receptors are distributed along the gastrointestinal tract of humans. In a study by Villanova et al. (1997), these thermoreceptors were shown to induce specific sensory and reflex responses when they detected warm and cold stimuli. When the stomach and small intestine were stimulated with warm and cold stimuli, cold stimuli induced an abdominal cold sensation and a reflex contraction of the stomach, and warm stimuli induced a warm sensation and a reflex gastric relaxation.

Barrett et al. (1970) cited a number of thermoreceptors found in various vertebrates (Humans, Crotaline and Boid snakes, cat, and hamster). Thermoreceptors in humans and snakes were previously discussed. Cats have thermoreceptors located in various locations. Myelinated cold receptors (tonic) and warm receptors (phasic), innervated by the lingual nerve of the mandibular branch of the trigeminal nerve system (TNS), located in the tongue of cats, are able to detect a 1°C change in temperature. Unmyelinated cold (tonic) and warm (phasic) receptors are located in the leg skin of cats, which are innervated by the saphenous nerve and are able to detect a change in temperature of 0.2°C. Phasic thermoreceptors (myelinated and unmyelinated), present in the cornea of cats, are both specific warm and cold receptors, which are also sensitive to touch and pain. They are sensitive to changes in temperature in the range of 0.058–7.47°C. The facial skin of hibernating hamsters has tonic cold-pressure receptors, which are innervated by the infra-orbital nerve of the TNS.

Lazzari and Nunez (1989) presented behavioral evidence that the blood-sucking insect *Triatoma infestans* perceives the radiant heat of a warm source and can estimate its temperature at a distance when seeking homeothermic prey. It has also been speculated that convection currents and warm-air gradients may be involved in the orientation of these insects to a food source (Lazzari and Nunez, 1989). The typical behavioral response of these insects to a food source involves antennal movements followed by locomotor activity and proboscis extension when they are near the source. Since proboscis extension is not affected by covering the insects' eyes, it is

speculated that they can estimate the distance to the food source using thermal information only, possibly by performing a triangulation with their antennae (Lazzari and Nunez, 1989). The antennae of *Triatoma infestans* are believed to be involved in thermoreception at close range to an IR source whose temperature is the same as its normal food source (32°C). However, they seem to not be significant in thermoreception when in contact with the source. Lazzari and Nunez (1989) believe that rostral receptors could be involved with mechano- and thermoreception during contact with the surface of the source.

7. Summary

Several animals and insects possess thermoreceptors, which aid them in hunting, feeding and survival. Imaging IR pit organs in Crotaline and Boid snakes enable them to apprehend prey by detecting the IR radiation they emit in the 8–10 µm range of the electromagnetic spectrum. Common vampire bats (*Desmodus rotundus*) may be able to image blood-rich locations on homeothermic prey with three facial pit organs located within their nasal structure. They have an infrared sensory system that includes a nucleus situated lateral to the common descending trigeminal tract similar to that found in Crotaline and Boid snakes. Forest fire-seeking beetles (*Melanophila acuminata*) detect forest fires from 60–100 miles away using pit organs, which detect IR wavelengths in the 2–4 µm range. These beetles can only reproduce by laying their eggs in the bark of freshly killed conifers found in extinguished forest fires. Darkly pigmented sun-basking butterflies possess wing vein thermoreceptors, which detect steep changes in temperature which elicit a heat protection response that protects them from heat damage while sun basking. Blood-sucking bugs (*Triatoma infestans*) are speculated to possess thermoreceptors, which enable them to perceive the radiant heat emitted by homeothermic prey and estimate its temperature at a distance. Electron microscopy has been instrumental in determining the ultrastructure of biological thermoreceptors. Transmission electron microscopy, scanning electron microscopy, and scanning probe microscopy have been instrumental in the investigation of the structure and morphology of the pit organs of IR-sensitive snakes. The outer surface of the morphology of the pit organ of *Melanophila acuminata* has been studied by SEM, while the detailed structure of sensilla within the pit organ has been observed from ultrathin sections imaged by TEM. The ultrastructure of the sensilla of thermo/hygroreceptors located in the tips of the antennal clubs of *Troides rhadamathus plateni* butterflies has been determined by TEM and SEM.

Acknowledgements

This work was supported by the United States Air Force Office of Scientific Research (AFOSR).

References

- Amemiya, F., Goris, R.C., Masuda, Y., Kishida, R., Atobe, Y., Ishii, M., Kusunoki, T., 1995. The surface architecture of snake infrared receptors. *Biomedical Research* 16, 411–421.
- Amemiya, F., Goris, R.C., Atobe, Y., Ishii, N., Kusunoki, T., 1998a. The ultrastructure of infrared receptors in a boid snake, *Python regius*: evidence for periodic regeneration of the terminals. In: Terashima, S., Goris, R.C. (Eds.). *Infrared Receptors and the Trigeminal Sensory System*. Harwood Academic Publishers, Japan, pp. 35–46.
- Amemiya, F., Ushiki, T., Goris, R.C., Atobe, Y., Kusunoki, T., 1998b. Ultrastructure of the crotaline snake infrared pit receptors: SEM confirmation of TEM findings. In: Terashima, S., Goris, R.C. (Eds.). *Infrared Receptors and the Trigeminal Sensory System*. Harwood Academic Publishers, Japan, pp. 1–12.
- Anton, S., Tichy, H., 1994. Hygro- and thermoreceptors in tip-pore sensilla of the tarsal organ of the spider *Cupiennius salei*: innervation and central projection. *Cell Tissue Research* 278, 399–407.
- Barrett, R., Maderson, P.F.A., Meszler, R.M., 1970. The pit organs of snakes. In: Gans, C. (Ed.). *Biology of Reptilia*, vol. 2. Academic Press, London, pp. 277–314.
- Bullock, T.H., Diecke, F.P.J., 1956. Properties of an infra-red receptor. *Journal of Physiology* 134, 47–87.
- Campbell, A.L., Stone, M.O., Church, D., Grace, M.S., 1999. Surface ultrastructure of pit organ, spectacle, and not pit organ epidermis of infrared imaging boid snakes: a scanning probe and scanning electron microscope study. *Journal of Structural Biology* 126, 105–120.
- de Cock Buning, T., 1983. Thermal sensitivity as a specialization for prey capture and feeding in snakes. *American Zoology* 23, 363–375.
- de Cock Buning, T., 1984. A theoretical approach to the heat sensitive pit organs of snakes. *Journal of Theoretical Biology* 111, 509–529.
- de Cock Buning, T., 1985. Qualitative and quantitative explanation of the forms of heat sensitive organs in snakes. *Acta Biotheoretica* 34, 193–206.
- de Cock Buning, T., Terashima, S., Goris, R.C., 1981. Crotaline pit organs analyzed as warm receptors. *Cellular and Molecular Neurobiology* 1, 69–85.
- Evans, W.G., 1964. Infra-red receptors in *Melanophila acuminata* DeGeer. *Nature* 4928, 211.
- Evans, W.G., 1966. Morphology of the infrared sense organs of *Melanophila acuminata* (Buprestidae: Coleoptera). *Annals of Entomological Society of America* 59, 873–877.
- Evans, W.G., 1975. Wax secretion in the infrared sensory pit of *Melanophila acuminata* (Coleoptera: Buprestidae). *Quaestiones Entomologicae* 11, 587–589.
- Grace, M.S., Church, D.R., Kelly, C.T., Lynn, W.F., Cooper, T.M., 1999. The python pit organ: imaging and immunocytochemical analysis of an extremely sensitive natural infrared detector. *Biosensory & Bioelectronics* 14, 53–59.
- Gronenberg, W., Schmitz, H., 1999. Afferent projections of infrared-sensitive sensilla. *Cell Tissue Research* 297, 311–318.
- Hart, S., 1998. Beetle mania: an attraction to fire. *BioScience* 48, 3–5.
- Kishida, R., Goris, R.C., Terashima, S.-L., Dubbeldam, J.L., 1984. A suspected infrared-recipient nucleus in the brainstem of the vampire bat, *Desmodus rotundus*. *Brain Research* 322, 351–355.
- Kurten, L., Schmidt, U., 1985. Thermoperception in the common vampire bat (*Desmodus rotundus*). *Journal of Comparative Physiology* 146, 223–228.
- Lazzari, C.R., Nunez, J.A., 1989. The response to radiant heat and the estimation of the temperature of distant sources in *Triatoma infestans*. *Journal of Insect Physiology* 35, 525–529.
- Molenaar, G.J., 1992. Anatomy and physiology of infrared sensitivity of snakes. In: Gans, C. (Ed.). *Biology of Reptilia*. Vol. 17, Neurology. The University of Chicago Press, Chicago, pp. 367–453.
- Newman, E.A., Hartline, P.H., 1982. The infrared 'vision' of snakes. *Scientific American* 20, 116–127.
- Schmitz, H., 1994. Thermal characterization of butterfly wings 1. Absorption in relation to different color, surface structure and basking type. *Journal of Thermal Biology* 19, 403–412.
- Schmitz, H., Beckmann, H., 1998. The photomechanic infrared receptor for the detection of forest fires in the beetle *Melanophila acuminata* (Coleoptera: Buprestidae). *Journal of Comparative Physiology A* 182, 647–657.
- Schmitz, H., Wasserthal, L., 1993. Antennal thermoreceptors and wing-thermosensitivity of heliotherm butterflies: their possible role in thermoregulatory behavior. *Journal of Insect Physiology* 39, 1007–1019.
- Terashima, S., Goris, R.C., Katsuki, Y., 1968. Generator potential of crotaline snake infrared receptor. *Journal of Neurophysiology* 31, 682–688.
- Villanova, N., Azpiroz, F., Malgelada, J.-R., 1997. Perception and gut reflexes induced by stimulation of gastrointestinal thermoreceptors in humans. *Journal of Physiology* 502, 215–222.
- Vondran, T., Apel, K.-H., Schmitz, H., 1995. The infrared receptor of *Melanophila acuminata* De Geer (Coleoptera: Buprestidae): ultrastructural study of a unique insect thermoreceptor and its possible descent from a hair mechanoreceptor. *Tissue and Cell* 27, 645–658.