Article

The circadian rhythm and visual elements in scorpions: A review

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Abstract
The purpose of this paper is to review the state of research in this field and to outline future ways how to proceed. The term: "Zeitgeber", implies 'time giver' meaning: synchronizer when an external entrainment factor synchronizes the endogenous rhythm**.** Is this 'time', the chronological date in the sense that it is related to the time of day as reflected in the natural light-dark cycles? Or does it mean cyclic phases of activity as demonstrated in the laboratory? Moreover, is it totally independent of the animal's physiological condition? This subject was studied largely in buthid species (15) of a total of only 30 scorpion species. Moreover, many (over 25%) of the studies (19) were done on a single buthid species: *Androctonus australis*. Species diversity was observed only by one author's work who studied eye structure in seven species. Since he found variability in eye structure it would not be advisable to generalize. The fact that experimenting was carried out irrespective of species diversity, gender, ecological or physiological conditions, and was usually done on animals kept in captivity for some time before the experimenting had started, is a major drawback to this kind of study. The diurnal rhythms is triggered either directly through spontaneous arrhythmic activity in the central nervous system, or by neurosecretory material. It is possible that these differences arise from either different technical treatments or due to basic problems, and these need to be clarified.

Keywords Zeitgeber; structure of the eyes; photic entrainment; hormonal and neurosecretory entrainments.

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1 Introduction

In this study I shall discuss the subject of biological rhythms in scorpions. This would include only the rhythmic photic and chemosensory behaviors and not other physiological (Warburg, 2013a), nor the locomotory rhythmicity dealt separately (Warburg, 2013b). This report deals with the main 'Zeitgeber': the neurosecretory system which are dealt etc, and three kinds of entrainment systems: the photic, the extra ocular and the chemosensory.

This subject was studied largely in buthid species (16) of a total of 32 scorpion species, as listed below (Species (author/ year) of scorpions studied for their photic behavior and the sources):

Buthidae

1. *Androctonus australis* (Linnaeus, 1758)
Fleissner 1968, 1972, 1974, 1975, 1977a,b, 1983, 1986, Fleissner and Fleissner 1978, 1986, Fleissner and Heinrichs 1982; Heinrichs
and Fleissner 1987; Carricaburu 1968; Carricaburu et al. 1982; Carricaburu and Cherrak 1968; Carricaburu and Muñoz-Cuevas, A.
1986a,b; 1987; Schliwa and Fleissnr 1979
2. *A. funestus* Ehrenberg, 1828
Grenacher 1880; Lankester and Bourne 1883
3. *A. mauritanicus* (Pocock, 1902)
Goyffon et al. 1975
4. *Paruroctonus* (now *Smeringurus*) *mesaensis* (Stahnke, 1940)
Blass and Gaffin 2088
5. *P. utahensis* (Williams, 1968)
Blass and Gaffin 2088
6. *Centruroides vittatus* (Say, 1821)
Blass and Gaffin 2088
7. *C. sculpturatus* (Ewing, 1928)
Belmonte and Stensaas 1975; Machan 1967,1968
8. *C. marginatus* (Gervais, 1814)
Scheuring 1912
9. *Scorpio europeus* (Linnaeus, 1758)
Graber 1879; Haller 1912
10. *Buthus afer* (Linnaeus, 1758)
Graber 1879; Grenacher 1880
11. *B. occitanus* (Amoreux, 1789)
Müller 1828
12. *B. martensi* (Karsch, 1891)
Cheng-Pin, P. 1939-40
13. *Parabutus transvaalicus* Purcell, 1889
Spreitzer and Melzer 2003
14. *Lychas americanus* C. L. Koch, 1845
Grenacher 1880
15. *Leiurus quinquestriatus* (Ehrenberg, 1828)
Abushama 1964; Yinon 1969

Caraboctonidae

16. *Hadrurus arizonensis* (Ewing, 1928)
Belmonte and Stensaas 1975

Euscorpiidae

17. *Euscorpius italicus* (Herbst, 1800)
Grenacher 1880; Lankester and Bourne 1883; Police 1900
18. *E. carpathicus* (Linnaeus, 1767)
Grenacher 1880; Lankester and Bourne1883; Wuttke 1966; Kwartimikov 1980
19. *E. flavicaudis* (DeGeer, 1778)
Carricaburu and Muñoz-Cuevas 1986a, 1987
20. *E. europeus*, Latr
Hesse 1901

Hemiscorpiidae

21. *Opistacanthus validus* Thorell, 1876
Machan 1968a

Scorpionidae

22. *Didymocentrus lesueurii* (Gervais, 1844)
Carricaburu and Muñoz-Cuevas 1986b, 1987

23. *Heterometrus swammerdami* E. Simon, 1872
Rao and Habibulla 1973; Habibulla 1971, 2004
24. *H. longimanus* (Herbst, 1800);
Scheuring 1912
25. *H. gravimanus* (Pocock, 1894)
Geethabali and Rao 1973
26. *H. fulvipes* (C.L. Koch, 1837)
Uthaman and Reddy 1985; Vasantha et al. 1977; Venkatachari 1971; Geethabali 1976, 1977; Geethabali and Rao 1973
27. *U. novaehollandiae* Peters, 1861
Zwicky 1968, 1970a,b
28. *Scorpio europaeus* (Schroeder, 1908)
Graber 1879; Haller 1912
29. *Pandinus imperator* (C.L. Koch, 1841)
Scheuring 1913

Vaejovidae

30. *Vaejovis spinigerus* (Wood, 1863)
Machan 1967, 1968a

2 The Endogenous Hormonal Entrainmment

The central nerve system of *Euscorpius italicus* (Herbst, 1800) was described by Police (1900) and later by Haller (1912) in *Scorpio europaeus* (Linnaeus) (see Figs. 1-3 there).

The central nervous system consists in *Buthus martensi* (Karsch, 1891), of a supra-oesophageal ganglion and a ventral nerve cord which consists of a sub-oesophageal ganglion, a pair of connective cords, three mesosomal ganglia and five metasomal ganglia (Cheng-Pin –1939-1940). A detailed study on the segmental origin of the nerves in scorpions is by Henry (1949). She provides three detailed schemes (Figs 68-70 there).

In a study on the nervous system of *Heterometrus fulvipes* (C.L. Koch, 1837), Venkatachari (1971) recorded the spontaneity rhythmicity in electrical activity in various regions of the nerve chord as well as in peripheral nerves. The rhythm was minimal at 4 AM and maximum at 4 PM.

Goyffon et al. (1975) described the spontaneous rhythmic electrical activity in the buthids *Androctonus mauretanicus* (Pocock, 1902), *Androctonus australis* (Linnaeus, 1758), and *Buthus occitanus* (Amoreaux, 1789), as well as in the scorpionid *Pandinus imperator* (C.L. Koch, 1841).

Effect of Carbaryl (an anticholinesterase drug) on the spontaneous and evoked potentials of the scorpion prosomian nervous system, was studied in *A. australis* by Carricaburu et al. (1982) who found that it increased both the amplitude as well as the frequency of electric activity thereby modifying the median eye (not the lateral eye) response. Carricaburu and Muñoz-Cuevas (1986a, b) found that periodic waves were observed only during night marking the activity of the suboesophageal pace-maker in *Euscorpius flavicaudis* (DeGeer, 1778).

In *E. flavicaudis* and *Didymocentrus lesueurii* (Gervais, 1844) injection of Octopamine reversed their locomotory circadian rhythm, whereas the injection of Phentolamine resulted in normalizing the rhythm (Carricaburu and Muñoz-Cuevas 1987).

Habibulla (2004) studied the brain modulation of circadian rhythms in the scorpionid *Heterometrus swammerdami* E. Simon, 1872. The neuronal components of the circadian clock were studied in the 'buthid' scorpion *A. australis* (Heinrichs and Fleissner 1987).

3 Neurosecrtetory Activity

Neurosecretory activity of scorpions was studied by Habibulla (1971) who studying *H. swammerdami*, found that the brain contains in the cephalothoracic nerve mass lipoproteins as well as alanine, arginine, aspartic and glutamic acids. Rao and Habibulla (1973) correlated diurnal activity of neurosecretory cells (NSC) in the lateral cells of groups numbers 3, 4 and 5, with the circadian type of locomotory activity phase which took place between 6 PM to about midnight.

Vasantha et al. (1977) found that the neuro-hormones modulate enzyme activity. Enzyme activity in the ventral nerve chord shows diurnal rhythmicity maximum at 4 PM and at 4 AM. Similar diurnal rhythmicity was seen in the spontaneous electrical activity of the central nervous system.

In a study of cardiac rhythmicity in *Hadrurus arizonensis* (Ewing, 1928) a cyclic pattern was noticeable (Ziganow, 1976). This could be related to cyclic events in oxygen consumption (Warburg, 2013a).

Uthaman and Srinavasa Reddy (1980) studying *H. fulvipes*1found that neural factors regulate oxygen consumption rhythm in isolated hepatopancreatic tissue of the scorpion.

It appears that the efferent neurosecretory fibers mediate the signal. The role of the neurosecretory cells in the circadian-clock system of the scorpion has been described by Fleissner and Heinrichs (1982). They found that the efferent neurosecretory fibers in the median eye control the circadian rhythm. Fleissner (1983) studying the buthid *A. australis* described the pacemaker in central nervous system. He has proven that the NSC fibres are a central part of the circadian clock system by mediating circadian signals from the CNS to the median eye. The transmission of circadian rhythms from the CNS to the eye is via the neurosecretory efferent fibers.

In a later study, Uthaman and Srinavasa Reddy (1985) studying *H. fulvipes* found the rhythmic changes in the activity of neurosecretory cells of the scorpion to be of bimodal nature peaking both at noon and at midnight. These two peaks lie 6h in advance of the locomotory peaks. Carricaburu and Muñoz-Cuevas (1986 a,b) described in the scorpion *E. flavicaudis* the periodic electrical waves observing them only at night when they mark the activity of the sub-oesophageal pace-maker. The signal travels through the optic nerve by nervous rather than by hormonal stimulus. Therefore, the visual pace-maker is located in the supraoesophageal ganglion. The 2nd pace-maker lies in the suboesophageal ganglion and sends axons to the legs (Habibulla, 1971). Later Habibulla (2004) found the maximal brain serotonin to occurs at midnight and minimum at 4 AM.

4 The Structure of Eyes

One of the earlier accounts on the structure of the scorpion's eye (*B. occitanus*) can be found in Dufour (1856). Grenacher (1879) examined eyes of *Buthus afer* (Linnaeus, 1758), and *Lychas americanus* C. L. Koch, 1845. He laid the foundations of the study of minute structure of the arthropod eye. Nevertheless, he has not given an account of scorpion's eye structure. Moreover, his observations were confined to the central eye and did not extend to the lateral eye. Graber (1880) studied the eyes of *Scorpio europaeus* ((Schroeder, 1908) and of *B. afer*. He was the first who observed the scorpion's retina and to describe the lens. Lankester and Bourne (1883) studied eyes of *Androctonus funestus* Ehrenberg, 1828, *Euscorpius italicus*, and *E. carpathicus* (Linnaeus, 1767). They described five lenses composing the lateral eyes: three larger ones and two smaller ones. Each lens is an enlargement of the cuticle (hypodermis). They proposed to call it "ommateum". The ommateum of the scorpion's lateral eye consists of a single layer of larger (nerve-end cells) and smaller (interneural cell). The central eyes of *A. funestus* are two to three times larger than the lateral eyes. The authors distinguished between a lens (a laminated mass of cuticle) and an ommateum. The ommateum consists of two cell layers: the vitreus body (cells devoid of pigment) and the retina (layer of nerve-end cells that divides the vitreus body from the retinal body, and a layer of nerve fibers). Each group of five nerve-end cells is a retinula each of which is provided by a rhabdom. The pigment granules are in the branches of the interstitial cells.

Parker (1886) recognized three layers the triplostichous nature of the median eyes and the monostichous (single layered) nature of the lateral eyes of *Centrurus* sp.:

1. Lentigen layer called the ‘vitreous’ layer that produces the lens.
2. Retina contains two kinds of cells: retinal (or nerve-end) cells, and pigment cells.
3. Post-retinal layer (intimately fused with the retina).

Parker considered the lateral eyes to be the ancestral type of the median eyes.

Police (1908) published some beautiful drawings based on micrographs which have been reproduced there (see Taf .I, Fig.3 the retina cells in the median eye, and Taf. II sections through the lateral eyes there).

A detailed description of scorpion eye structure can be found in Scheuring (1913). He was first to describe difference of structure in several scorpion species. The variability in eye structure appears to be greater than thought. Moreover he describes differences in scorpion fields of sight.

The fine structure of the retina cells is given in *A. australis* by Schliwa and Fleissner (1979). They found that the retina of the median eye is composed of retinula and pigment cells. However, the lateral eye consists of a lens but lacks the viterous body.

Farley (1999) briefly reviewed this subject (pp 194-195). Recently, Spreitzer and Melzer (2003) described a nymphal eye in *Parabuthus transvaalicus* Purcell, 1889. They consider it to be an accessory lateral eye devoid of both lenses and pigment cells.

5 The ‘Zeitgeber’ and Entrainment

This term "Zeitgeber" implies ‘time giver’ meaning synchronizer when an external entrainment factor synchronizes the endogenous rhythm. What exactly are we to understand by using this term? Is it the chronological date in the sense that it is related to the time of day as reflected in the natural light-dark cycles? Or, does it mean cyclic phases in activity as demonstrated in the laboratory? Moreover, is it totally independent of the animal's physiological condition? Both the photic and non-photic ‘Zeitgebers’ stimuli will be discussed here.

6 The Photic Entrainment System

Abushama (1964) was first who demonstrated experimentally that 72% of the 200 *Leiurus quinquestriatus* (Ehrenberg, 1828) scorpions he studied preferred the lowest light intensity (see Table I there).

Wuttke (1966) was one of the earliest to experiment with the rhythmic activity of the scorpion *E. carpathicus*. He used artificial illumination and described a bimodal curve of activity rhythm.

The photoreceptors are of great importance for entrainment of circadian rhythms in scorpions (Ramakrishna and Pampathi Rao, 1971). Belmonte and Stensaas (1975) found that repetitive firing to light is a normal response of photorecetors. The sensitivity of the scorpion eye to light is controlled by the central nervous system (CNS) (see Fleissner, 1986; Fleissner and Fleissner, 1986).

7 Light Wavelength Biases of Scorpions

The spectral sensitivity of the scorpions’ eyes was studied in three scorpion species: *Centruroides sculpturatus* (Ewing), *Vaejovis spinigerus* (Wood), and *Opistacanthus validus fulvipes* (Thorell, 1876) by Machan (1968a,b). Moreover, he found that the lateral eyes show a maximum in the UV and another peak in the blue-green area (Machan, 1968a). In addition the medium eye is many folds less responsive compared with the lateral eye (Machan, 1968b).

This subject of the effect a particular wavelength (IR, red, green, UV) has on the locomotory activity, was studied in *Paruroctonus utahensis* (Williams, 1968) and in *Centruroides vittatus* (Say, 1821) by Blass and Gaffin (2008). They found a highest activity when animals moved more rapidly was in the UV light followed by the green light.

The eyes of the buthid scorpion *A. australis*. C.L.Koch, consist of one pair of ocelli-like median eyes and three pairs of lateral eyes (Carricaburu, 1968). Carricaburu and Cherrak (1968) analyzed the electro-retinogram of the scorpion *A. australis*. They found that the electrical response of the median eye consists of a quick negative on-wave followed by a positive wave then a quick positive off-wave followed by a long negative wave.

The circadian sensitivity changes in the median eyes of the North African scorpion *A. australis* was based on pigment migration within the eye (Fleissner, 1972). This is undoubtedly the most important mechanism involved in the circadian sensitivity change (Fleissner, 1974). It is entirely synchronous in both median eye pairs (Fleissner, 1977a). In constant darkness the median eyes change their sensitivity endogenously (Fleissner, 1977b).

Interruption of the visual pathway abolishes the circadian sensitivity of the median eyes (Fleissner, 1983; Fleissner and Fleissner, 1978). This would indicate a neuronal pathway rather than a by way of the haemolymph (Fleissner and Fleissner, 1978, 1986); 'or' rather than a blood-borne factor as was suggested previously by Rao and Reddy (1967).

The diphasic electroretinogram was described in the median and lateral eyes of *L. quinquestriatus* by Yinon (1969). Only three pairs of lateral eyes were found to be functional.

8 The Extra-occular Non-visual Photoreceptors Entrainment System

There are extra-ocular neural photoreceptors in the metasoma of the scorpions *H. fulvipes* and *Heterometrus gravimanus* (Pocock, 1894). These structures seem to mediate the metasomal light sense of scorpions as shown by electrophysiological recordings (Geethabali and Rao ,1973; Zwicky, 1968).

Scorpions are photopositive during the period between 6 PM and midnight and photonegative during the rest of the day (Geethabali, 1977). This is in part due to the neural metasomatic photoreceptors.

There are three different types of non-image producing photoreceptors. These are next to the optic lobes, in the last ganglia of the ventral cord, and in the scorpion's lateral eyes (Fleissner and Fleissner, 2003).

The maximal activity of *D. lesueuri*i took place at midnight (Carricaburu and Muñoz-Cuevas, 1986a, b).

The effect that the spontaneous electrical activity of the suboesophageal ganglion had on the circadian rhythms in the scorpion *E. flavicaudis* was described by Carricaburu ans Muñoz-Cuevas (1986a). They found four kinds of waves with one of them the 'periodic wave' kind was found only during night. They suggest the significance of the suboesophageal 'pace maker' in triggering the onset of locomotory activity.

Zwicky (1968) recorded spike activity in the nerve cord having revealed an extraocular light sense in the tail of the scorpion *Urodacus novae-hollandiae* Peters, 1861. He localized a light response in the tail of *U. novae-hollandiae* in the form of a burst of activity that began at sunset and lasted the first few hours of the night (Zwicky, 1970a). The spectral sensitivity of the tail of *U. novae-hollandiae* was to long UV and green peaking at the blue-green region (Zwicky, 1970b)

9 Conclusion

The fact that experimenting was carried out irrespective of species diversity, gender, ecological or physiological conditions, and was usually done on animals kept in captivity for some time before the experimenting had started, is a major drawback to this kind of study.

Moreover, the variability in eye structure is greater than thought before and ought to be taken into account.

The diurnal rhythms is triggered either directly through spontaneous arrhythmic activity in the central nervous system, or by neurosecretory material. These discrepancies need further work.

References

Abushama FT. 1964. On the behaviour and sensory physiology of the scorpion *Leiurus quinquestriatus* (H. & E.). Animal Behaviour, 12(1): 140-153

Belmonte C, Stensaas LJ. 1975. Repetitive spikes in photorerceptor axons of the scorpion eye. Invertebrate eye structure and Tetradoxin. Journal of General Physiology, 66: 649-655

Blass GRC, Gaffin DD. 2008. Light wavelength biases of scorpions. Animal Behaviour, 76: 365-373

Carricaburu P. 1968. Dioptrique oculaire du scorpion *Androctonus australis*. Vision Research, 8: 1067-1072

Carricaburu P, Biwer G., Goyffon M. 1982. Effect of carbaryl on the spontaneous and evoked potentials of the scorpion prosomian nervous system. Comparative Biochemistry and Physiology, 73C(1): 201-204

Carricaburu P, Cherrak M. 1968. Analysis of the electroretinogram of the scorpion *Androctonus australis* (L.). Zeitschrift für vergleichende Physiologie, 61: 386-393

Carricaburu P, Muñoz-Cuevas A.1986a. Spontaneous electrical activity of the suboesophageal ganglion and circadian rhythms in scorpions. Journal of Experimental Biology, 45: 301-310

Carricaburu P, Muñoz-Cuevas A. 1986b. Visual circadian rhythm in the scorpion *Didymcentrus lesueurii* (Gervais)(Arachnida). Actas X Congr. Int. Aracnol. Jaca/España, I: 7-12

Carricaburu P, Muñoz-Cuevas A. 1987. La modulation du rhythme visuel circadien par l'octopamine chez les Scorpions et l'adaptation a la vie souterraine. Comptes Rendus Academie des Science Paris 305, III: 285-288

Cheng-Pin P. 1939-40. Morphology and anatomy of the Chinese scorpion *Buthus martensi* Karsch. Peking Natural History Bulletin, 14 (2): 103-117

Dufour L. 1856. Histoire anatomique et physiologique des scorpions. Mémoires de l'Academie des sciences. Science Mathematique Physique, 14: 561-656

Farley RD. 1999. Scorpiones. In: Microscopical Anatomy of Invertebrates. Vol. 8A. Chelicerata Arthropoda (Harrison FW, Foelix RF, eds). 117-222, Wiley-Liss, New York, USA

Fleissner G. 1972. Circadian sensitivity changes in the median eyes of the North African scorpion, *Androctonus australis*. 133-139 In: Wehner R. (ed.). Information processing in the visual systems of arthropods. Springer Verlag, Berlin, Germany

Fleissner G. 1974. Circadiane Adaptations und Schirmpigmentverlagerung in den Sehzellen der Medianaugen von *Androctonus australis* L. (Buthidae, Scorpiones). Journal of Comparative Physiology, 91: 399-416

Fleissner G. 1977a. Entrainment of the scorpion's circadian rhythm via the Media eye. Journal of Comparative Physiology, 118: 93-99

Fleissner G. 1977b. Differences in the physiological properties of the median and lateral eyes and their possible meaning for the entrainment of the scorpion's circadian rhythm. Journal of Interdisciplinary Cycle Research, 8: 15-26

Fleissner G. 1983. Efferent neurosecretory fibers as pathways for circadian clock signals in the scorpion. Naturwissenschaften, 70: 366-368

Fleissner G. 1986. Die innere Uhr und der Lichtsinn von Skorpionen und Käfern. Naturwissschaftten, 73: 78-88

Fleissner G, Fleissner G. 1978. The optic nerve mediates the circadian pigment migration in the median eyes of the scorpion. Comparative Biochemistry and Physiology, 61A: 69-71

Fleissner G, Fleissner G. 1986. Neurobiology of a circadian clock in the visual system of scorpions. In: Neurobiology of Arachnids (Barth G, ed).351-375, Springer, Heidelberg, Germany

Fleissner G, Fleissner G. 2003. Nonvisual photoreceptors in arthropods with emphasis on their putative role as receptors of natural zeitgeber stimuli. Chronobiology International, 20(4): 593-616

Fleissner G, Heinrichs S. 1982. Neurosecretory cells in the circadian-clock system of the scorpion, *Androctonus australis*. Cell and Tissue Research, 224: 233-238

Geethabali. 1977. Photic behaviour in scorpion *Heterometrus fulvipes.* Indian Journal of Experimental Biology, 15: 384-385

Geethabali, Rao KP. 1973. A metasomatic neural photoreceptor in the scorpion. Journal of Experimental Biology, 58: 189-196

Goyffon M, Luyckx J, Vachon M. 1975. Sur l'existence d'une activite electrique rhythmique spontanee du systeme nerveux cephalique de scorpion Comptes Rendus Academie des Science Paris, 280: 873-876

Graber V. 1880. Über das unicorneale Tracheatenauge- und speciell das Arachnoideen- und Myriapoden-Auge. Archiv für Mikroskopische Anatomie, 17: 58-93

Grenacher H. 1880. Über die Augen einigen Myriapoden. Archiv für Mikroskopische Anatomie, 17: 415-467

Habibulla M. 1971. Neurosecretion in the brain of a scorpion *Heteromentrus swammerdami*-a histochemical study. General and Comparative Endocrinology, 17: 253-255

Habibulla M. 2004. Studies on the brain modulation of circadian rhythms in the scorpion *Heterometrus swammerdami*. 28th Annuual Meeting of the American Arachnological Society Norman, Oklahoma, USA

Haller B. 1912. Über das Zentralnervensystem des Skorpions und der Spinnenn. Ein zweiter Beitrgag zur Stammesgeschichte der Arachnoideen. 504-524, Archiv fur Mikroskopische Anatomie LXXIX abt 1, 4th Heft, Germany

Henry LM. 1949. The nervous system and the segmentation of the head in a scorpion (Arachnida). Microentomology, 14(4): 121-126

Heinrichs S, Fleissner G. 1987. Neuronal components of the circadian clock in the scorpion, *Androctonus australis*: Central origin of the efferent neurosecretory elements projecting to the median eyes. Cell and Tissue Research, 250: 277-285

Lankester ER, Bourne AG. 1883. The minute structure of the lateral and central eyes of *Scorpio* and *Limulus*. Quarterly Journal of Microscopical Science, 23: 177-212

Machan L. 1967. Studies on structure and electrophysiology of scorpion eyes. South African Journal of Science, 63(12): 512-520

Machan L. 1968a. Spectral sensitivity of scorpion eyes and the possible role of shielding pigment effect. Journal of Experimental Biology, 49: 95-105

Machan L. 1968b. The effect of prolonged dark adaptation on sensitivity and the correlation of shielding pigment position in the median and lateral eyes of the scorpion. Comparative Biochemistry and Physiology, 26: 365-368

Müller J. 1828. Beiträge zur Anatomie des Scorpions. Archive für Anatomie und Physiologie, 13: 29-70

Parker GH. 1886. The eyes in scorpions. Bulletin of the Museum of Comparative Zoology, 13 (6): 173-204

Police G. 1900. Ricerche sul sistema nervosa dell' *Euscorpius italicus*. Atti della R Academia delle Scienze Fisiche e Matematiche Napoli 10, 2(7): 1-11

Police G. 1908. Sugli occhi dello Scorpione. Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere, 25: 1-70

Rao PK, Habibulla M. 1973. Correllation between neurosecretion and some physiological functions of the scorpion *Heterometrus swammerdami.* Proceedings of the Indian Academy of Science Section B., 77: 148-155

Rao K, Reddy TG. 1967. Blood borne factors in circadian rhythms of activity. Nature, 213(104): 7-8

Ramakrishna T, Pampathi Rao K. 1971. State determined system of a circadian rhythm in scorpion. Proceedings of the Indian Academy of Science, 73(4): 202-207

Scheuring L. 1912. Über ein neues Sinnesorgan bey *Heterometrus longimanus* Hbst. Zoologischer Anzeiger 40: 370-374

Scheuring L. 1913. Die Augen der Arachnoideen. Zoologische Jahrbücher Abteilung Anatomie und Ontogenie der Tiere, 33: 545-588

Schliwa M, Fleissner G. 1979. Arhabdomeric cells of the median eye retina of scorpions. Journal of Comparative Physiology, 130: 265-270

Spreitzer A & Melzer, R.R. 2003. The nymphal eyes of *Parabutus transvaalicus* Purcell, 1889 (Buthidae): An accessory lateral eye in scorpion. Zoologischer Anzeiger, 242: 137-143

Uthaman M, Srinavasa Reddy Y. 1980. Neural factors in the regulation of oxygen consumption rhythm in the tissues of the scorpion, *Heterometrus fulvipes* (C Koch). Chronobiologia, 7: 533-537

Uthaman M, Srinavasa Reddy Y. 1985. Rhythmic changes in the activity of neurosecretory cells of the scorpion, *Heteromertrus fulvipes* (C. Koch). Chronobiologia, 12: 331-338

Vasantha N, Venkatachari SAT, Murali Mohan P, Sasira Babu K. 1977. On the possible mode of action of neurohormones on cholinesterase activity in the ventral nerve cord of scorpion, *Heteromentrus fulvipes*. Experientia, 33(2): 238-239

Venkatachari SAT. 1971. Analysis of spontaneity in the nervous system of the scorpion, *Heterometrus fulvipes*. Indian Journal of Experimental Biology, 9: 338-344

Warburg MR. 2013a. A review on the diel rhythmic activities in physiological functions of scorpions. Entomological Science, 16 (3): 278-283

Warburg MR. 2013b. The locomotory rhythmic activity in scorpions with a review. Arthropods, 2(3): 95-104

Wuttke W. 1966. Untersuchungen zur Aktivitätsperiodik bei *Euscorpius carpaticus* L. (Chactidae). Zeitschrift für vergleichende Physiologie, 53: 405-448

Yinon U. 1969. The electroretinogram of scorpion eyes. Comparative Biochemistry and Physiology, 30: 989-992

Ziganow S. 1976. Cardiac amplitude rhthmicity in the scorpion and in Limulus. A preliminary study. Journal of Interdiscipilinary Research, 7: 39-46

Zwicky KT. 1968. A light response in the tail of *Urodacus*, a scorpion. Life Sciences, 7: 257-262

Zwicky KT. 1970a. Behavioural aspects of the extraocular light sense of *Urodacus* scorpion. Experientia, 26 (7): 247-248

Zwicky KT .1970b. The spectral sensitivity of the tail of *Urodacus*, a scorpion. Experientia, 26(3): 317