Volume 1 Issue 2

Online Available at www.entomoljournal.com

Journal of Entomology and Zoology Studies

Eye Ultrastructure Investigation of *Scaphidium japonum* Reitter (Coleoptera: Staphylinidae: Scaphidiidae)

Monalisa Mishra [1*]

1. Department of Biological Sciences, Birla Institute of Technology & Science Pilani, Pilani 333 031, Rajasthan, India.
[E-mail: mmishra@pilani.bits-pilani.ac.in]

The compound eye of the fungus beetle *Scaphidium japonum* Reitter was investigated using both light and electron microscopy techniques. The external appearance of the eye is found to be oval in shape and compromising 1400-1500 ommatidia. Each ommatida has dioptric apparatus and a layer of retinula cells. Dioptric apparatus include the cornea, corneal processes, and a crystalline cone. The retinula cells form the photoreceptor organ which is known as the rhabdom. The rhabdom is long, and wide at the distal region, which then becomes narrow at the most proximal region. Banded arrangement is observed in the rhabdom. The microvilli are parallel to each other in a rhabdomere. Seven retinular cells reach upto the cone level to form the fused rhabdom. The eighth retinular cell joins to the rhabdom at the proximal region of the ommatidia. Only one retinula cell nucleus appears at the most proximal regions of the ommatidia while the rest appear at the distal one third of the ommatidia. The eye ultrastructure of the Scaphidiidae depicts the adaptation towards a fungus habitat.

Keyword: Compound Eye, Vision, Closed Rhabdom, Banded Arrangement, Staphylinidae, Scaphidiidae, Fungus Beetles.

1. Introduction

Scaphidiidae, a subfamily of rove beetles (Staphylinidae), which while seldom observed [22], are abundant inhabitants of many forest floor ecosystems. Most species are associated with a variety of decomposing materials, classifying them as mycophagus (feeding on fungi) and myxomycophagus (feeding on slime moulds)[23]. Scaphidiidae is a member of the Staphylinidae of oxyteline group [21] . Like most members of the Oxyteline group, Scaphidiidae are box-like and highly convex, with the elytra covering the abdomen. However they are lacking of flexible staphylinoid body form, which is present in most members of the Oxyteline group, and the majority of Staphylinidae. Because of this variation, the Scaphidiidae were regarded as a separate family for many years. Based on larval characters, Kasule first recognized the Scaphidiidae as a subfamily of Staphylinidae [16,41]. More recent studies regarding the larval structures, male genitalia and other characters recommended Scaphidiidae to be within the Staphylinidae [40].

Eye ultrastructure plays an important role in determining the essential and familial characters [36,37] that has been neglected for many years for Scaphididae. The current study deals with the eye ultrastructure of a member of this subfamily *Scaphidium japonum*. The genus *Scaphidium* is plesiomorphic for Scaphidiidae and is associated with saprophagy and general mycophagy [42]. The present study of the eye will not only help the phylogenetist but the functional anatomist will

also get an idea about the mycophagus adaptation of Scaphidiidae.

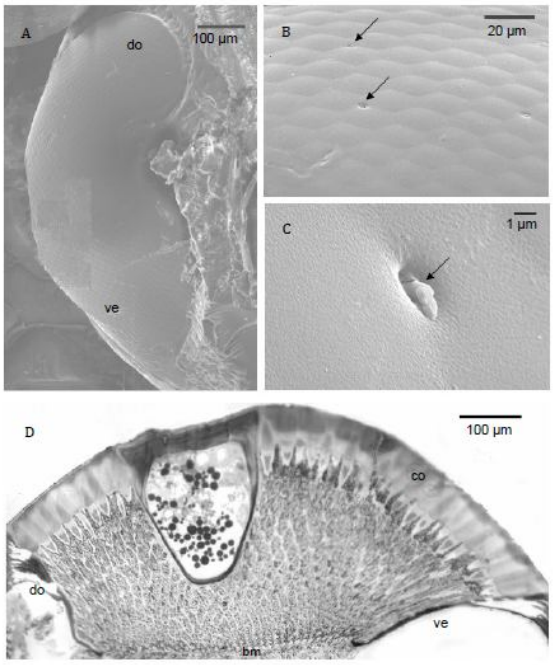

Fig. 1. General appearance of the compound eye of *S. japonum*. A. Scanning electron micrograph of the whole eye showing a low relief of facets that are not aligned in well defined rows. B. Scanning electron micrograph of facets in the central region of the eye showing more or less hexagonal shape. Interommatidial hairs (ioh) are found randomly between facets which are indicated by the arrow. C. Scanning electron micrograph of an ommatidium showing the inter ommatidial hair (ioh) and rough cornea. D. Light micrograph of the whole eye showing retinal structures between the distal cornea (co) and the proximal basement membrane (bm).

2. Methods

Scaphidium japonum Reitter (1877), a shiny black with orange pattern beetle of 5-7 mm long species were obtained from Japan. All of the specimens studied were light adapted. The heads were fixed in a mixture of 2% paraformaldehyde and 2.5% glutaraldehyde, in 0.1M cacodylate buffer (pH 7.4) for one day, and postfixed in 2% OsO_4 solution in 0.1M cacodylate buffer (pH 7.4) for one hour. After the fixation was completed, the samples were rinsed three times in the same buffer and twice in distilled water. The eyes were passed through a graded series of ethanol followed by acetone/Epon mixture for one day. The specimens were finally embedded in Epon-812 resin and hardened at 60 ^{0}C for three days. For light microscopy experiments, semithin sections were cut with a glass knife on an Ultramicrotome (RMC) and stained with a 0.5% aqueous solution of toluidine blue on a hotplate. Ultrathin sections were prepared either with a glass or diamond knife and picked up with an uncoated copper grid. The ultrathin sections were stained with Reynold's lead citrate for twenty minutes and 2% aqueous uranyl acetate for fifteen minutes and finally observed under a Zeiss EM 10 transmission electron microscope (TEM), operated at 60KV.

For observation by scanning electron microscopy (SEM), the eyes were dehydrated in a graded series of acetone, coated with gold by sputter coater (EMI Tech, K550X) and observed under a JSM-5900 scanning electron microscope (Jeol), operated at 20 KV.

3. Results

3.1 General Organization

The compound eye is present on the dorsal side of the head and widely separated, kidney shaped, (Fig, 1A) with a diameter of approximately 750 µm. Each eye has about 1400-1500 ommatidia/facets. Ommatidia are typically hexagonal in shape (Fig, 1B) and measures about 20-30 µm throughout the eye. The surface of the cornea appears to be rough at higher magnification images (Fig. 1C). Interommatidial hairs are present over the eye and the shape is similar to other Staphylinidae (Meyer-Rochow, 1972). Dorso-ventral variation is not observed for *S. japonum* (Fig. 1D). Length and diameter of an ommatidium near the center of the eye are ca. 390 µm and 25µm respectively. Each ommatidium posses a corneal lens, an eucone assembly of four cone cells surrounded by two primary pigment cells, eight retinula (i.e. photosensitive) cells, and six secondary pigment cells (Fig. 2). The retinula cells reunite to form the axon and exit through holes in the basement membrane.

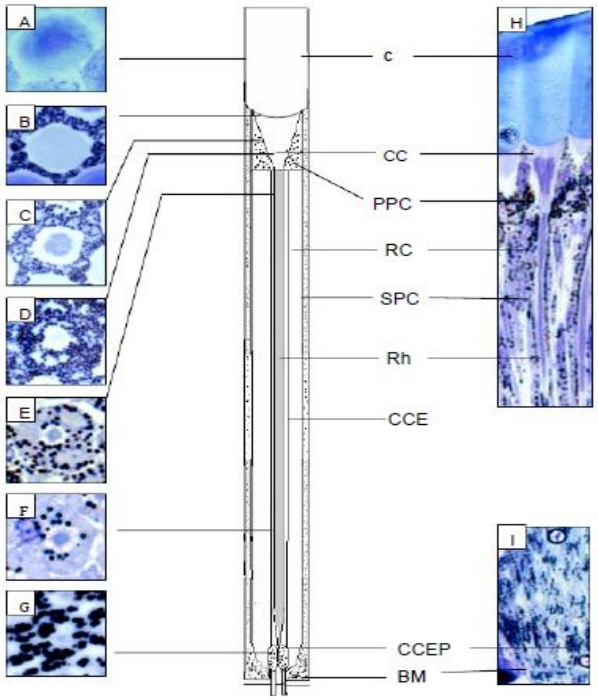

Fig. 2. Fine structures of the retina in *S. japonum*. Schematic drawing of an ommatidium (centre) with photographs of transverse (A-G) and longitudinal (H,I) sections at representative levels. The dioptric apparatus of the ommatidium consists of the prominent corneal facet (C) crystalline cone (CC) (A-D). The crystalline cone is surrounded by two primary pigment cells (PPC) and twelve secondary pigment cells (SPC). Eight retinular cells (RC) build up the fused rhabdom (Rh). Four crystalline cone extensions (CCE) reach from the crystalline cone to the proximal retina. At the proximal level CCE reunite to form crystalline cone extension processes (CCEP) which surround the proximal rhabdom before the retinula cells pass the basement membrane (BM) in the form of an axon.

3.2 Dioptric and other supporting structures

3.2.1Cornea

The diameter of a cornea varies between 20 and 30 µm. The outer radius of curvature of the cornea is almost equal to the radius of curvature of the eye while the inner radius of curvature varies from 19-24µm. Corneal thickness varies from 60 to 70 µm. The cornea appears laminated (Fig.2a and 3A) due to the well-documented orientation of cucticular micelles [3]. In the longitudinal sections, the lamination between parabolas (Fig. 3A) varies ca. 8 µm at the distal region and 2 µm at the proximal region. In transverse sections, the laminations form a spiral with progressively tighter spacing towards the outer side (Fig. 2A). Laminations are also found in the interommatidial space of the cornea with a distance measure in the range of 3-4µm (Fig. 3A). The dark staining material of the interommatidial space as found in *N. leiwisi* [34] is absent for this fungus beetle.

3.2.2 Cone cells

The cone cells contain crystalline materials with eucone characteristics [10], which can be divided into: (a) a strongly widened distal part, (b) a median zone of insertion of the distal cone cell processes and (c) a proximal region. The cone is in physical contact with the corneal cuticle and thus, shows obvious cytoplasmic difference from the cornea (Fig. 3A). The length of the cone measures from 42-45 µm. From cross-sectional view, the cone is made up of four cone cells and is not circular in cross section (Fig. 3B). The cone cell has a diameter of 10 µm distally and 8 µm proximally (Fig. 3C). The crystalline material appears at the proximal level and are recognised as β-glycogen [43], with the conclusion that the cone glycogen is non-metabolic with only an optical function, contributing to the refractive index.

The cone cells are enclosed by two primary pigment cells. At the most distal region, primary pigment cell do not contain pigment granules (Fig.3A and B), however, pigments appear at the proximal level (Fig.3D). The nuclei of the primary pigment cell appear at the level of pigment granule. The size of the pigment granules varies from 0.5 to 1.2 µm. Surrounding the primary pigments, twelve units of secondary pigment cells are found (Fig. 3C). Structurally, the secondary pigment is smaller than the primary pigments and their size varies between 0.31 and 0.75 µm. But, under an electron microscope, both primary and secondary pigments look equally electron dense.

3.2.3 Retinula cells and Rhabdom

The rhabdom stretches from the proximal tip of the crystalline cone to basement membrane. Rhabdom is surrounded by the cytoplasm of the retinula cell bodies and the four cone cell

processes. The positions of the four cone cell extensions among the retinula cells do not vary as in *Panulirus longiceps* eye [30].

Distally the group of seven retinula cells measures ca.17 µm in diameter. All the seven cells contribute their rhabdomeres for the formation of fused rhabdom column that measures about 155-175 µm in length. The overall shape of the rhabdom appears more or less circular in the transverse section. The distal rhabdom measures around 2.5 µm in diameter. The rhabdom is surrounded by a less electron dense cytoplasm in the retinula cell, which measures ca. 0.95 µm (Fig.4A). This less electron dense structure is present throughout the length of the rhabdom. In the distal rhabdom, the microvilli are arranged in two directions. Microvilli of each rhabdomere are parallel to each other within the rhabdomere and perpendicular to the adjacent rhabdomere (Fig. 4B). The longest microvilli measures 0.8 µm and have a diameter of 60nm.

The eighth retinula cell contributes its rhabdomere at the proximal part of the retina near the basement membrane (Figs. 4C, D). The diameter of the retinula cell and rhabdom measures ca. 10.5 µm and 2.5 µm respectively. In an oblique section, rhabdom shows banded arrangement of microvilli (Fig. 5A). Both horizontal and vertical bands have an average thickness of 0.8 µm. Although banded arrangement can be identifiable under light microscope due to the small microvilli and small alternate banded arrangement, it is not identifiable in the case of *S. japonum*. The nuclei of the seven retinula cells found within the distal half of the ommatidium. However, the eighth (basal) retinular cell and it's nucleus appear at the proximal one third of the ommatidium (Fig. 4C).

Just above the basement membrane, the extensions of the four cone cells reunite (Fig.5B). At this level some trachea and numerous amounts of other cell organelles are found (Fig.5C). Retinular cells are arranged in the form of axon and penetrate the basement membrane (Fig.5D). The axon contains mitochondria of 0.3-0.7 µm, apart from usual microtubules.

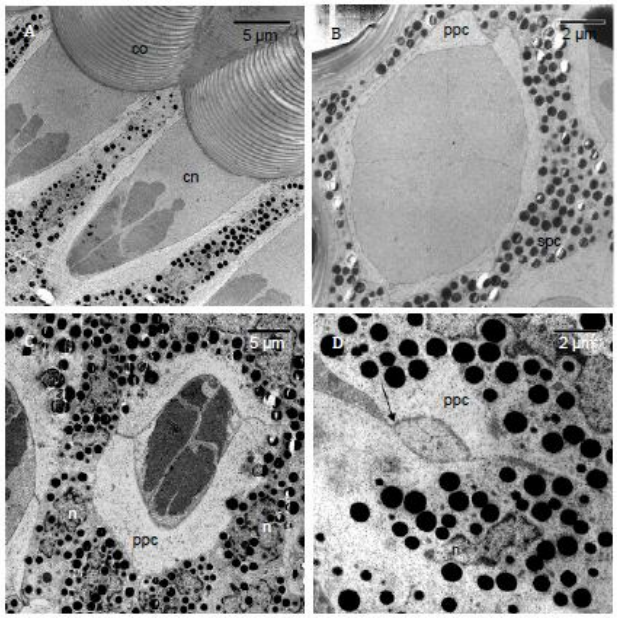

Fig. 3. Transmission electron micrographs through the dioptric apparatus of the eye in *S. japonum*. A. Longitudinal section of an ommatidium showing the cornea (co) and cone (cn). The cornea shows the lamellar arrangement which differs in the interommatidial region. The cone is surrounded by primary pigment cells (PPC).Between two ommatidia secondary pigments are found. B. Transverse section through the distal region of the cone showing irregular contribution of the cone cells surrounded by primary pigment cells (PPC) and secondary pigment cells (SPCs). The primary pigment cells are less electron dense and lack pigment. C. Transverse section through the proximal region of the cone showing crystalline material. Nuclei of the secondary pigment cells appear at this level. D. Transverse section of the cone at the level of retinular cell. Pigment granules appear in the primary pigment cells at the level of nuclei (n). Attachment to the retinular cell (indicated by arrow) can be seen at this level.

4. Discussion

The eye of *S. japonum* is a eucone and, apposition type with closed rhabdom. Closed rhabdom has been reported among various beetle families [6]. Structurally the rhabdom is cylindrical and contains photosensitive microvilli with banded arrangement. The banded arrangement is found in most of the family members of Staphylinoidea [6]. The present study, however, provides a description of the compound eye of a member of a subfamily, the Scaphidiidae, not presented in the earlier studies.

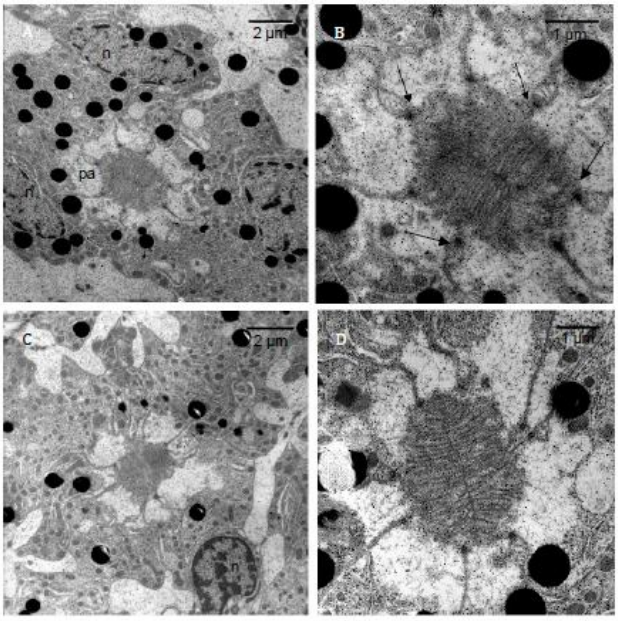

Fig. 4: Transmission electron micrographs through retinula cells and rhabdom in *S. japonum*. A. Transverse section through the distal region of the rhabdom. Rhabdom is surrounded by a less electron dense structure like palisade (pa). Numerous mitochondria, endoplasmic reticulum, and pigment granules found in the cytoplasm of the retinula cell. Retinula cell nuclei (n) are kidney shaped and can be seen at this level. B. Higher magnification of the distal rhabdom showing the arrangement of the microvilli. Four cone cell attachments (indicated by arrow) can be seen. The retinula cell is attached by means of adherent junctions. C. Transverse section through the proximal region of the retinula cells showing eight retinular cells. The nuclei (n) of the eighth retinula cell can be seen. The nucleus is more circular. D. Higher magnification of the proximal rhabdom showing the arrangement of the microvilli, cone, and retinular cell attachment by means of adherent junctions.

4.1 Dioptric apparatus and supporting structures

As in other insect species, the cornea is an array of colorless and transparent facets, with hexagonal shape. *S. japonum* does not show any facet irregularities, besides eariler report in other Staphylinidae [31]. The cornea is laminated due to the alternative arrangement of chitin and protein [9]. However, it is known that insect cuticle is relatively homogenous, being composed of oriented chitin microfibrils embedded in a protein matrix [39]. When this arrangement is warped into helicoids, as in the cornea, the 180° repeat pattern of the microfibrils in the helicoids appears as one lamella [38].

The cornea is thick, which can be explained with multiple explanations. If the resolving power is poor, details concerning its behavior in the environment cannot be discerned and the insect may crash into obstacles. Under such conditions, a thicker cornea provides greater protection than a thin one. A thicker cornea can also attenuate the intensity of the light reaching the receptive elements inside the eye and, thus less probability for the visual membranes to damage. However, in *S. japonum,* the surface of the eye is strongly curved; making it less likely that one part of the eye experiences a prolonged exposure to sunlight.

The ultrastructural arrangement of the interfacetal region of the cornea is quite different from the fungus beetle *N. lewisi* [34]. The lamellar arrangement, present in the interfacetal region of *S. japonum* helps in filtering out off-axis and stray light. Numerous minor irregularities are found on the cornea. Although they are not as efficient as corneal nipple, this may help to decrease reflections from the cornea, effectively camouflaging the animal. The small corneal processes further act as an impedance converter, by reducing the amount of reflection from the corneal surface and increasing the transmission of light through the cornea [2].

Hair like structure, projecting from some corners between the facets, termed ommatrichia [50] are observed for this beetle. They are often useful taxonomic features for the identification of species [25,7]. The size of the interommatidial hair is found to be similar as reported in other Staphylinidae [31]. Although they are commonly known for mechanosensory function, there is evidence for protection from strong light by forming shadow [18]. Due to the small size of interommatidial hair the protection from strong light is customarily ruled out for *S. japonum*.

S. japonum has eucone type of crystalline cone; a feature shared by some of the Staphylinoidea members [6]. In Staphylinoidea, the eucone type of crystalline cone is associated with the primitive families. The crystalline cone is of much lower protein content (based on histological

staining properties) and irregular in shape. The distal level of the cone is smaller than the proximal cornea. The smaller cone size indicates that the light focused by the cornea is not fully absorbed.

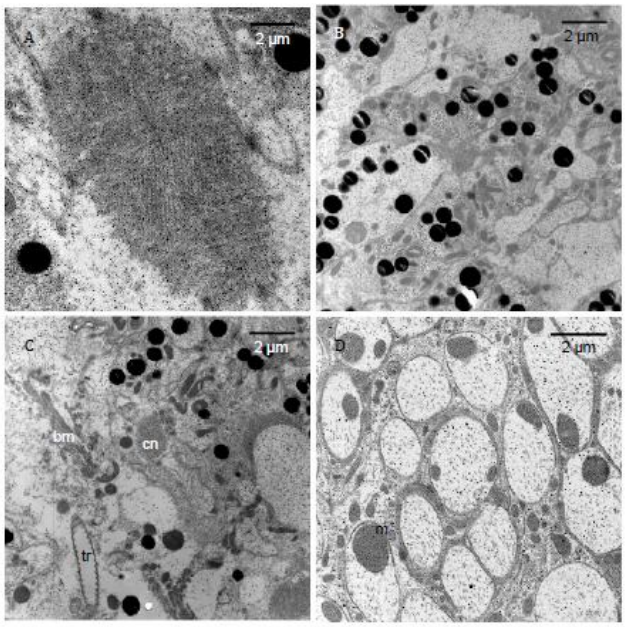

Fig. 5. Transmission electron micrographs through the rhabdom of *S. japonum*. A. Oblique section of the rhabdom showing the banded arrangement. B. Proximal region of the rhabdom showing the various organelles and the point rhabdom. C. Just above the basement membrane the cone cells (cn) reunite and form a cap like structure to the rhabdom. Some tracheoles (tr) found at the level of the basement membrane (bm) D. Transverse section through axon bundles. Axon contains mitochondria (mt) and neurotubule.

4.2 Primary pigment cell

Two primary pigment cells surround the cone cell. Primary pigment cells are involved in secreting the cornea and contain large pigment granules, often participate in adaptational phenomena. In *S. japonum*, the distal most areas are pigment free; however, pigments appear at the proximal most regions. A similar type of primary pigment is also reported in Neuroptera [1] and Blattodea. Absence of the pigment granule at the distal region of *S. japonum* may allow the beetle to collect more amount of light. The primary pigment granules are larger than other pigment granules, and remain stationary or move slower than the other smaller granules [26,17].

4.3 Photoreceptive elements

Closed rhabdom is observed in *S. japonum*. A rather similar type of rhabdom is reported earlier from Staphylinidae family [31,6]. After the cone level, the rhabdom is circular in cross section. The arrangement of the microvilli of the distal rhabdom is as found in honey bee [43] and the distal rhabdom of cockroach [4, 33]. According to the theoretical calculation by Snyder [47], such arrangement of rhabdomere allows a better fit between polarization sensitivity and dichroic ratio than others.

In *S. Japonum*, all microvilli (within a rhabdomere) are parallel so that each rhabdomere is sensitive to the plane of incident polarization light [47]. The microvilli are of 60 nm in size as reported for *P. ramburi* [28]. According to Laughlin *et al*., [20] a narrow microvillus facilitate e-vector detection [15]. Moreover, cells with parallel microvilli of small diameters not only seem to display the highest polarization sensitivity but also are most sensitive to UV part of the spectrum. The microvilli are arranged in more than one direction. According to Shaw [44], a unit length of rhabdom is more efficient as a light capturer if it contains microvilli orientated in more than one direction. It seems that, as in the case of acuity and sensitivity, polarization and high absolute sensitivity are incompatible.

Banded arrangement of rhabdom is present in *S. japonum*. Although banded arrangement is a unique phenomena in decapod crustaceans [52, 29, 32] it is still reported in some other insect orders like thysanura, coleoptera, lepidoptera [29] and is well suited to analyze polarized light [47]. Banded arrangement helps in enhancing the contrast and helps in E-vector discrimination, which is involved in orientation task [51]. Surrounding the entire length of the rhabdom, a less electron dense structure is found which can be compared with palisade (Palisades are known to improve the light guiding properties of the rhabdoms) [14]. Presence of palisade does not allow the pigment granule to reach the rhabdom and thus, increases the sensitivity at the cost of resolution. As fungus

beetles are living inside bark (in a less lighted area), presence of palisade-like structure probably helps the beetle to capture more amount of light.

4.4 Functional considerations

A growing body of evidence suggests that a fused rhabdom is, in general, formed by rhabdomeres with different spectral absorption characteristics. Examples include the worker bee [12, 11], the cockroach *Periplaneta* [5, 35] the ant *Formica polyctena* [26] the butterfly *Deilephila* [13] and the crayfish *Procambus* [8]. One of the advantages of such a functional unit is the potential for fine gain in colour vision, i.e., for discrimination in a small field of view [47]. Since all the retinula cells and their associated rhabdomers are jointed together in a cylindrical structure, the possibility of interaction between the components of the fused rhabdom is enhanced [45].

The rhabdom is long and, wide at the distal end, and becomes very narrow at the most proximal end. The wide distal rhabdom presumably helps in matching the angular diameter of the rhabdom with the inter ommatidial angle to provide the best compromise between spatial acuity and photon capture [46]. Long rhabdom allows the receptor to collect more light [14, 19], whereas wide distal rhabdom allows more light to be trapped within it [49] and thus, corresponds for higher sensitivity. On the other hand, narrow rhabdom at the proximal end fails to act as "perfect point detector" and allows the light to form interference patterns within narrow light-guiding structures as these patterns are known as wave guide modes [48].

4.5 Adaptational Conclusions

Visual task of the compound eye depends on the life style of insects. The ultrastructure of the eye of fungus beetle Erotylidae (*N. lewisi*) has been studied [32]. The comparison of the ultrastructure of *S. Japonum* and *N. lewisi* will give an idea towards the adaptation of mycophagy. Like *N. lewisi,* one part of the eye in *S. japonum* is more curved than the other, which does not allow the beetle to be a good flier. In both species the cornea is thick, which is probably to provide better protection to the eye. Both the beetles seem to be adaptive towards polarized light. In *N. lewisi*, the polarization is due to parallel arrangement of the microvilli in an open rhabdom [32] whereas, in *S. japonum,* the polarization sensitivity is achieved due to the banded arrangement. Numerous corneal irregularities and eucone type of cone makes *S. japonum* a better light absorber than *N. lewisi*. Interommatidial hairs are found in both the fungus beetles. Although both beetles found in the similar habitat, eye ultrastructure still reflects more familial characters.

4.6 Phylogenetic Conclusions

The subfamily Scaphidiidae contains approximately 1300 described species worldwide [24] and is unequivocally monophyletic [23], although its direct sister relationships are uncertain within the Oxyteline Group. Leschen and Löbl [23] studied the phylogenetic relationships among the Scaphidiidae tribes, and the genera contained in Cyparíini, Scaphiini, and Scaphidiini demonstrating the monophyly of Scaphisomatini. Scaphisomatini includes five subtribes. The eye of Scaphidiidae has many similarities with other Staphylinidae. Not only has the external appearance of the eye but the ultrastructure also reflected similar character. The arrangement of the cone shows its lower placement within Staphylinidae. The ultrastructure of the eye is in agreement of the Scaphidiidae under the subfamily of Staphilinydae.

5. Acknowledgements

I would like to thank Prof. V. B Meyer-Rochow and Prof. N Gokan for providing the specimens; the staff of the Electron microscope facility at Jacobs University Bremen (Germany) for their invaluable help; and finally, the Dean at Jacobs University Bremen for financial support.

6. References

1. Autrum H. Light and dark adaptation in invertebrates. In Comparative Physiology and Evolution of Vision in Invertebrates C, Invertebrate Visual Centers and Behavior II. chapter 1, Ed. Autrum H, Springer-Verlag, Berlin, 1981, 1–91.

2. Bernhard CG, Miller WH, Møller AR. The insect corneal nipple array. Acta Physiologica Scandinavica 1965; 243:1-25.
3. Bouligand Y. Twisted fibrous arrangement in biological materials and cholesteric mesophases. Tissue Cell 1972; 4:189-217.
4. Butler R. The anatomy of the compound eye of Periplaneta americana L. 2. Fine structure. Journal of Comparative Physioogy 1973; 83: 239-262.
5. Butler R. The Identification and mapping of Spectral Cell type in the Retina of Periplaneta americana. Zeitschrift Fur Vergleichende Physiologie 1971; 72:67-80.
6. Caveney S. The phylogenetic significance of ommatidium structure in the compound eyes of polyphagan beetles. Cannadian Journal of Zooogy 1986; 64:1787-1819.
7. Cumming JM, Brooks SE. Electrophorella, a new genus of parathalassiine flies from Baltic amber, with a cladistic analysis of the Microphorinae + Dolichopodidae lineage (Diptera: Empidoidea). Studia dipterologica 2002; 9:41-54.
8. Eguchi E, Waterman TH, Akiyama J. Cellular basis of wavelength discrimination in crayfish Procambarus. American Zoologist 1972; 12: 252.
9. Gordon H, Winfree AT. A single spiral artifact in arthropod cuticle. Tissue Cell 1978; 10:39-50.
10. Grenacher H. Untersuchungen über das Sehorgan der Arthropoden, insbesondere der spinnen, Insekten und Crustaceen. Vandenhoek and rupprecht, Göttingen, 1879.
11. Gribakin FG. The distribution of the long wave photoreceptors in the compound eye of the honey bee as revealed by selective osmic staining. Vision Research 1972; 12:1225-1230.
12. Gribakin FG. Types of photoreceptor cells in the compound eye of the worker honey bee relative to their spectral sensitivity. Cytologia 1969; 11: 309-314.
13. Hamdorf K, Höglund G, Langer H. Mikrophotometrische Untersuchungen an der Retinula des Nachtschmetterlings Deilephila elpenor. Verh dtsch Zool Ges 1972; 65:276-280.
14. Horridge GA, Bernard PBT. Movement of palisade in locust retinula cells when illuminated. The Quarterly journal of microscopical science Royal Microscopical Society 1965; 106:131-135.
15. Israelachvilli JN, Sammut RA, Snyder AW. Birefringence and dichroism of photoreceptors. Vision Research 1976; 16:47-52.
16. Kasule FK. The subfamilies of the larvae of Staphylinidae (Coleoptera) with keys to larvae of British genera of Steninae and Proteininae. Transactions of the Entomological Society of London 1966; 115-138.
17. Kolb G, Autrum H. Die Feinstruktur im Auge der Biene bei Hell-und Dunkeladaptation. Journal of Comparative Physiology 1972; 77:113-125.
18. Kolb G. Ultrastructure and adaptation in the retina of Aglais urtcae (Lepidoptera). Zoomorphology 1985; 105:90-98.
19. Land MF. Optics and vision in invertebrates. In: Handbook of Sensory Physiology. Ed. H. Autrum, Vol. VII/6B, springer Verlag, Berlin, Heidelberg, New York, 1981, 471-592.
20. Laughlin SB, Menzel R, Snyder AW. In: Photoreceptor optics. ed. Snyder, A.W and Menzel R, Springer-Verlag, Berlin, 1975, 523.
21. Lawrence JF, Newton AF. Evolution and classification of beetles. Annual Review of Ecology and Systematics 1982; 261-290.
22. Leschen RAB, Löbl I, Stephan K. Review of the ozark highland Scaphisoma (Coleoptera: scaphididae). Coleopterists Bulletin 1990; 274-294.
23. Leschen RAB, Löbl I. Phylogeny of Scaphidinae with redefinition of tribal and generic limits (Coleoptera: Staphylinidae). Revue Suisse de Zoologie1995; 425-474.
24. Löbl I. The Scaphidiidae (Coleoptera) of the Nepal Himalaya. Revue suisse Zool 1992; 99: 471-627.
25. McAlpine DK. Review of the Australian kelp flies (Diptera: Coelopidae). Syst. Entomol 1991; 16: 29–84.
26. Menzel R, Lange G. Anderungen der Feinstruktur im Komplexauge von Formica polyctena bei Helladaptation. Z Naturforsch 1971; 26(b):357-359.
27. Menzel R. Feinstruktur des komplexauges der Roten Waldameise, Formica polyctena (Hymnoptera, Formicidae). Z Zellforsch Mikrosk Anat 1972; 127:356-373.
28. Meyer-Rochow VB, Mishra M. Structure and putative function of dark- and light-adapted as well as UV-exposed eyes of the food store pest Psyllipsocus ramburi Sélys-Longchamps (Insecta: Psocoptera: Psyllipsocidae). Journal of Insect Physiology 2007; 53:157-169.
29. Meyer-Rochow VB. A crustacean-like organization of insect-rhabdoms. Cytobiologie 1971; 4:241-249.
30. Meyer-Rochow VB. Larval and adult eye of the Western rock lobster Panulirus longipes. Cell and Tissue Research 1975; 162:439-457.
31. Meyer-Rochow VB. The eyes of Creophilus erythrocephalus F. and Sartallus signatus sharp (Staphylinidae: Coeloptera). Z Zellforsch 1972; 133:59-86.

32. Mishra M, Jeffs A, Meyer-Rochow VB. Eye structure of the phyllosoma larva of the rock lobster Jasus edwardsii (Hutton, 1875): How does it differ from that of the adult?. Invertebrate Reproductive Development 2006; 49:213-222.
33. Mishra M, Meyer-Rochow VB. Fine structural description of the compound eye of the Madagascar 'hissing cockroach' Gromphadorhina portentosa (Dictyoptera: Blaberidae). Insect Science 2008; 197:197-210.
34. Mishra M, Meyer-Rochow VB. Fine structure of the compound eye of fungus beetle Neotriplax lewisi (Coleoptera: Cucujiformia: Erotylidae). Invertebrate Biology 2006; 125:265-278.
35. Mote MI, Goldsmith TH. Compound eyes: Localisation of two color receptors in the same ommatidium. Science 1971; 17:1254-1255.
36. Müller CHG, Meyer-Rochow VB. Fine structural description of the lateral ocellus of Craterostigmus tasmanianus Pocock, 1902 (Chilopoda: Craterostigmomorpha) and phylogenetic considerations. Journal of Morphoogy 2006; 267:850-865.
37. Müller CHG, Rosenberg J, Richter S, Meyer-Rochow VB. The compound eye of Scutigera coleoptrata (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural reinvestigation that adds support to the mandibulata concept. Zoomorphology 2003; 122:191-209.
38. Neville AC, Luke BM. A biological system producing a self assembling cholesterin protein liquid crystal. Journal of Cell Science 1971; 8: 93-109.
39. Neville AC. Cuticle ultrastructure in relation to the whole insect. Symposia of the Royal Entomological Society of London 1970; 5:17-39.
40. Newton AF, Thayer MK, Ashe JS, Chandler DS. Staphylinidae Latreille. 1802. In: American Beetles, Volume 1: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. 2001 ed. Arnett, R. H. Jr. & Thomas, M. C., CRC Press, Boca Raton, USA, 272-418.
41. Newton AF, Thayer MK. Current classification and family-group names in Staphyliniformia (Coleoptera). Fieldiana 1992; 1-92.
42. Newton AF. Mycophagy in Staphylinoidea (Coleoptera). In: Fungus –Insect Relationships: Perspectives in Ecology and Evolution, 1984. eds. Wheeler. Q and Blackwell. M. Columbia University Press.
43. Perrelet A. The fine structure of the retina of the honey bee drone. An electron microscopic study. Z Zellforsch 1970; 108:530-562.
44. Shaw SR. Optics of arthropod compound eye. Science 1969; 165:88–90.
45. Snyder AW, Pask C. Spectral sensitivity of dipetran retinula cells. Journal of Comparative Physiology 1973; 84:59-76.
46. Snyder AW, Stavenga DG, Laughlin SB. Spatial information capacity of compound eyes. Journal of Comparative Physiology 1977; 116:183-207.
47. Snyder AW. Polarization sensitivity of individual retinula cells. Journal of Comparative Physiology 1973; 83:331-360.
48. Snyder AW. The physics of vision in compound eyes. In: Comparative physiology and evolution of vision in invertebrates.. A: Invertebrate photoreceptors (Handbook of sensory physiology. ed. Autrum H, vol VII/6A, Springer, Berlin Heidelberg, New York, 1979, 225–314.
49. Stavenga DG. Angular and spectral sensitivity of fly photoreceptors. I. Integrated facet lens and rhabdomere optics. Journal of Comparative Physiology 2003; 189:1-17.
50. Sukontason K, Sukontason KL, Piangjai S, Choochote W, Vogtsberger RC. Ultrastructure of the ommatidia in Megaselia scalaris (Loew) (Diptera: Phoridae). Micron 2005; 36:191-194.
51. Wehner R. Spatial vision in arthropods. In: Handbook of sensory physiology. ed. Autrum, H., Vol VII, Springer Verlag, Berlin, Heidelberg, New York, 1981, 287-616.
52. Wolken JJ. Invertebrate photoreceptors a comparative analysis. Academic Press, New York and London, 1971.