

On the ultrastructure and identity of the eyes of *Cyphophthalmi* based on a study of *Stylocellus* sp. (Opiliones, Stylocellidae)

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Abstract. The laterally positioned eyes of stylocellid mite harvestmen are simple ocelli composed of a uniconvex cuticular lens, a lentigen layer, a retina, and a layer of pigment cells. Basal laminae separate the lentigen layer (preretinal membrane) and the pigment layer (postretinal membrane) from the retina. The retina is composed of reticular cells and glial cells. The optic nerve comprises mostly afferent axons formed by the reticular cells, which are accompanied by glial cells. Likely there are also few efferent axons. The reticular cells are characterized by their peculiar nuclei, numerous granules and indications of high membrane turnover. A prominent central region of the eye shows numerous, but poorly ordered interdigitations of long microvilli-like processes presenting a poorly developed closed rhabdom. A smaller region with microvilli forming a rather disordered, open rhabdom is located opposite to the lens. The retina is proximally and laterally surrounded by pigment cells containing, in addition to the usual dense granules, some crystalline inclusions, which may act as a tapetum. Hence, the retina seems to be composed of a proximal part and a distal part with two differently organized simple rhabdoms. The eyes of *Stylocellus* thus show basically the same organization as the median (primary) eyes of other Opiliones and are likely laterally displaced median (primary) eyes. The occurrence of these primary eyes in Stylocellidae (and Pettalidae) strengthens the idea that the presence of median eyes is thus a plesiomorphic character of these cyphophthalmid harvestmen.

Keywords: Arachnida, median eyes, mite harvestmen, primary eyes

Opiliones or harvestmen are generally characterized by a pair of dorso-medially positioned eyes often located on a distinct tubercle (e.g., Purcell 1894; Scheuring 1914; Kaestner 1935; Pinto-da-Rocha et al. 2007). However, the members of the suborder *Cyphophthalmi* (mite harvestmen) were thought to be eyeless with the remarkable exception of most Stylocellidae, possessing a pair of laterally positioned eyes in front of the ozophores bearing the opening of the defense glands (Juberthie 1964; Martens 1978; Shear 1993a,b; Giribet & Boyer 2002; Giribet et al. 2002). Earlier descriptions of eyes located on the ozophores of *Cyphophthalmus duricorius* Joseph 1868 (Sironidae) by Joseph (1868) and Janczyk (1956) turned out to be based on misinterpretations caused probably by the lid-like structure covering the opening of the defense glands which might have been mistaken as a lens or cornea (e.g., Juberthie 1964; Gutjahr et al. 2006). Most members of the cyphophthalmid Pettalidae also bear a pair of eyes but incorporated into the base of the ozophore, or even inside, i.e., located under the integument of the ozophore without a lens (Sharma & Giribet 2006; Boyer & Giribet 2007).

The exceptional position of these eyes in some *Cyphophthalmi* is enigmatic and raises the question of homology with respect to other eyes in Opiliones. Clarifying the homology of the stylocellid eyes is not a trivial task (see also Sharma & Giribet 2006). Embryology evidently shows that the medially positioned eyes of most Opiliones are true median (primary) eyes (Moritz 1957; Muñoz-Cuevas 1981). Since *Cyphophthalmi* is now regarded as the sister group to all other Opiliones (Shultz 1998; Giribet et al. 1999, 2002), it may be questioned whether these stylocellid (and pettalidid) eyes are displaced median eyes or whether they are true lateral eyes

retained only in these groups (Stylocellidae and Pettalidae) as a plesiomorphy (Shear 1993b; Giribet et al. 2002). As a contribution towards solving this fundamental problem, the eyes of a stylocellid species were investigated here for the first time using light and electron microscopy.

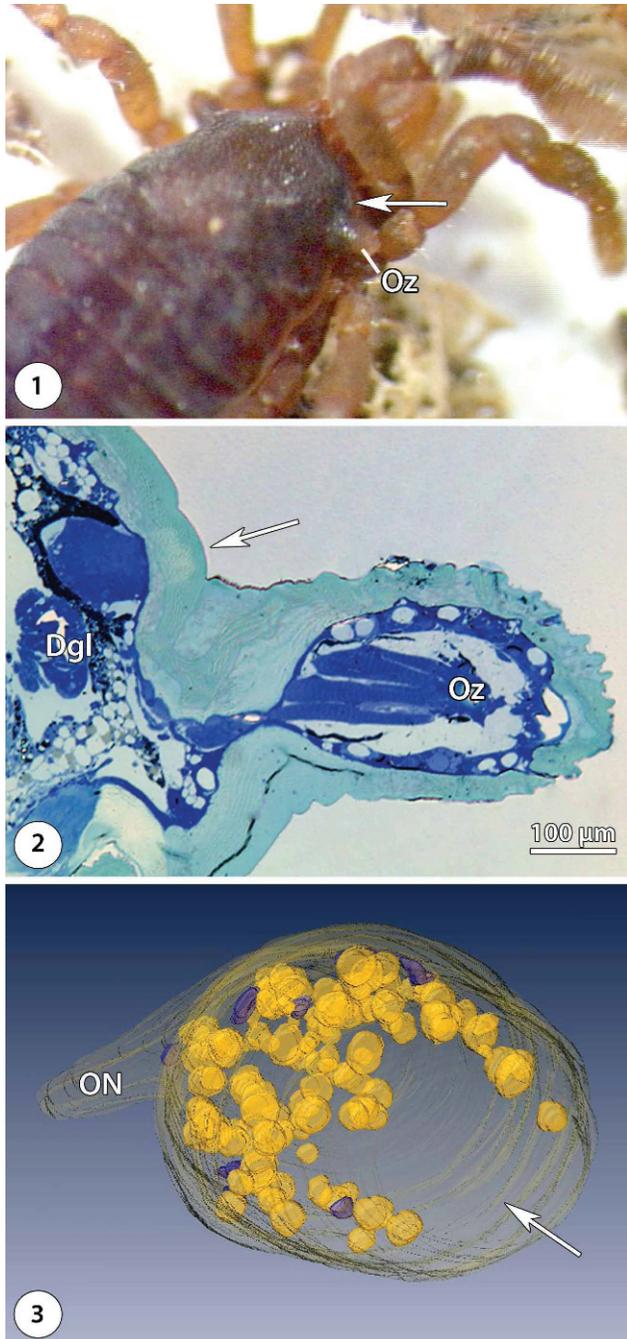
METHODS

Two males of *Stylocellus* sp. collected in Thailand (Krabi Province, Khao Phanom Bencha National Park, rain forest, 22.VII.2005, 8°14'19.9"N, 98°55'11.0"E) by P. Schwendinger were, after videotaping, cut into pieces with a razor blade and fixed in cold 3.5% buffered glutaraldehyde (phosphate buffer pH 7.4; 0.1M) for about 2 h. A 2%, buffered OsO₄-solution for another 2 h was used for post-fixation. The specimens were then dehydrated in graded ethanol series and embedded in Araldite. Ultrathin sections (70 nm) were obtained with a Leica-Ultracut using a diamond knife. Sections were stained with uranylacetate and lead citrate. Semithin sections (400 nm) stained according to Richardson et al. (1960) were used for general orientation with a light microscope Olympus BX60 with digital camera DP 10 (LM). A JEOL JEM-1011 transmission electron microscope (TEM) was used for examining the sections. For 3-D reconstruction Amira software (Mercury Computer Systems GmbH) was used. One specimen, fixed in the same way as the one used for TEM, was studied after critical point drying with a Zeiss DSM 940A scanning electron microscope (SEM).

RESULTS

In the living animals, the eyes are distinct and shiny due to their almost smooth lenses, which slightly project (Figs. 1, 4). Sections through the eyes reveal that they are prominent, nearly spherical structures comprising a uniconvex cuticular

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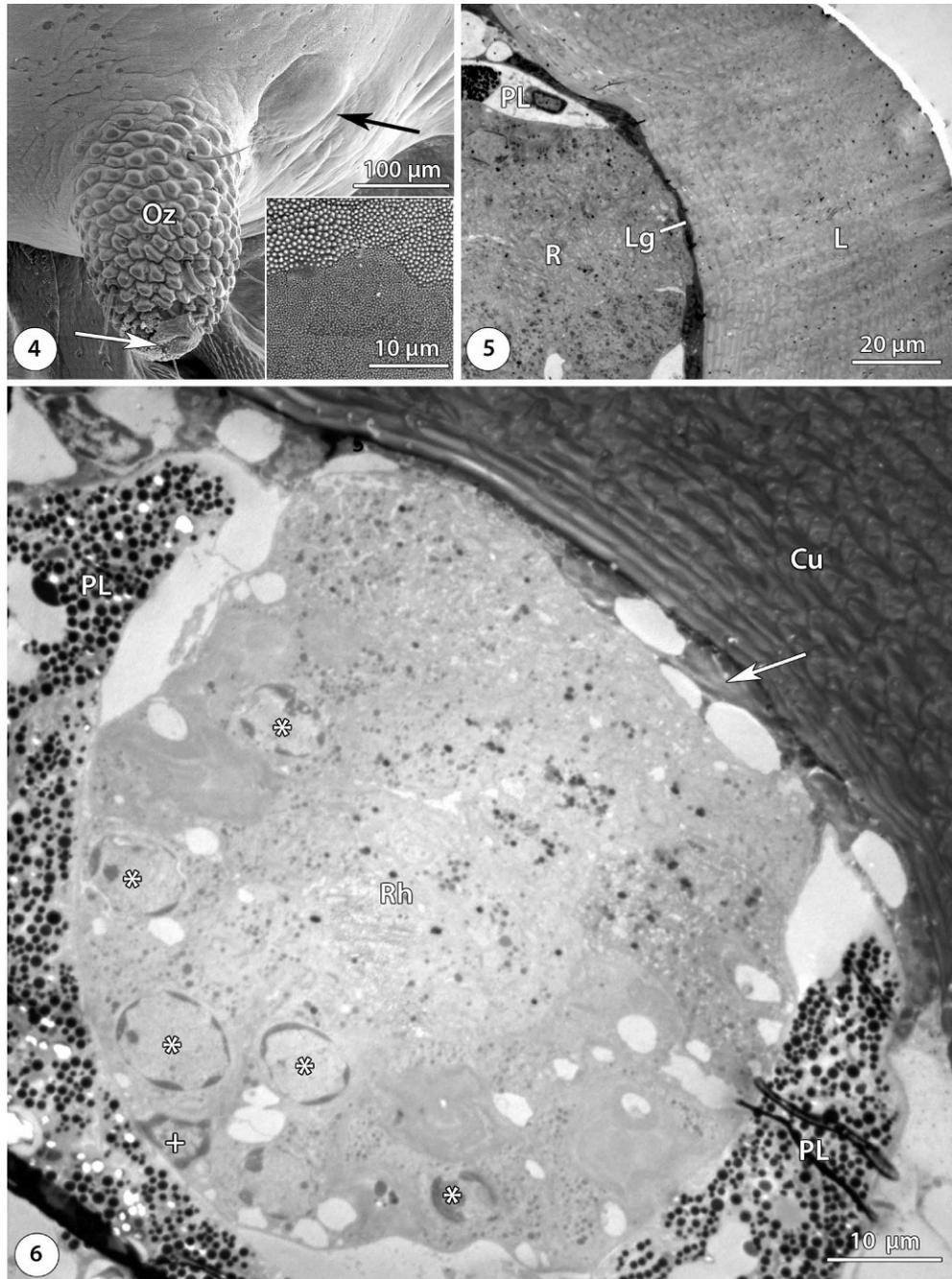
Figures 1–3.—*Stylocellus* sp.: 1. In the living specimen, the eyes are distinct and shiny due to their prominent lens (arrow) in front of the ozophore; 2. LM of a section through ozophore and eye (arrow). The eye is a prominent, nearly spherical structure comprising a uniconvex cuticular lens, a group of cells forming the sensory part, i.e., the retina. The latter is partly surrounded by a layer of pigment cells containing numerous mostly densely staining granules. Note that these granules also occur distant from the eye, though less abundantly; 3. 3-D-reconstruction of retina showing arrangement of nuclei of reticular cells (yellow) and glial cells (blue). Arrow indicates direction of incidence of light. The center of the retina is mainly occupied by the distal rhabdom (compare Figs. 6, 13, 14). The location of the proximal rhabdom is close to the origin of the optic nerve. Dgl = defense gland; ON = optic nerve; Oz = ozophore.

lens, a thin electron-dense lentigen layer and a group of cells arranged spherically forming the sensory part, i.e., the retina. The latter is partly surrounded by a thick layer of pigment cells containing numerous mostly densely staining granules. The optic nerve leaves the structure penetrating this latter layer (Figs. 2, 3, 19).

Lens.—The slightly projecting lens is composed of multi-layered cuticle (thickness: about $50\mu\text{m}$) which appears hardly modified when compared to the adjacent cuticle (Figs. 5, 6). The cuticle seems to be strongly sclerotized. A very thin epicuticle is found (Fig. 5). The outer surface of the lens is covered with protuberances, which are slightly smaller than those found in adjacent parts (Fig. 4, inset).

Lentigen layer.—The lentigen layer is composed of flat, densely staining cells containing densely staining nuclei. A thin basal lamina is present (Figs. 5, 7). The lentigen layer is continuous with the epidermal layer (Figs. 2, 6).

Retina.—The nearly hemispherical retina is composed of a layer of epithelial reticular cells containing basally (or peripherally) located nuclei with a distinctive arrangement of heterochromatin (Fig. 6). The patches of heterochromatin are attached to the nuclear envelope, which here does not show nuclear pores, and they are regularly interrupted by heterochromatin-free regions (Figs. 8, 9, 19). In these latter regions many nuclear pores are located (Fig. 9). These nuclei are not found in the region of the retina directed toward the lens (Figs. 3, 5). Adjacent to the nuclei, conspicuous and quite large whorls of membranes occur. In the center of these whorls, dense granules are frequently located (Figs. 8, 10). In this nuclear region and slightly towards the center of the retina, the cells contain many moderate-densely staining granules, which originate from small Golgi bodies (Fig. 11). Further centrally, the cytoplasm of these cells is dominated by numerous cisterns or lamellae arranged (in the sections) in circles, which frequently contain more of such circles. It seems that some of the dense granules come into contact with these cisterns and may discharge their contents in the space between the membranes (Figs. 7, 12). There are also cytoplasmic processes interdigitating with similar structures of a neighboring cell (Figs. 13, 14). Though a regular arrangement of rhabdomeric microvilli was not found, we postulate that this area represents a simple closed rhabdom. Furthermore, a small area of irregularly arranged microvilli which are provided by cells similar to those just described was found rather close to the origin of the optic nerve (Figs. 15, 16). In this region, representing a rather disordered open rhabdom, centrioles were found (Fig. 17 inset). The reticular cells are connected by small zonulae adhaerentes (Fig. 16). The optic nerve is composed of processes of the reticular cells which are found at the periphery of the structure converging upon the origin of the nerve (Figs. 17, 19, 21). In addition to these reticular cells which are easily recognized because, e.g., of the very peculiar nuclei, we found a few nuclei which were distinctly smaller and more dense (Figs. 3, 6, 19). These nuclei likely belong to glial cells which extend with flat processes between the reticular cells. Similar nuclei were also found in the optic nerve. Rarely small cell processes were observed containing small vesicles. These processes likely represent nerve endings (Fig. 18). The reticular cells may differ with regard to electron-density of their cytoplasm. They are also partly shrunk with distinct intercel-

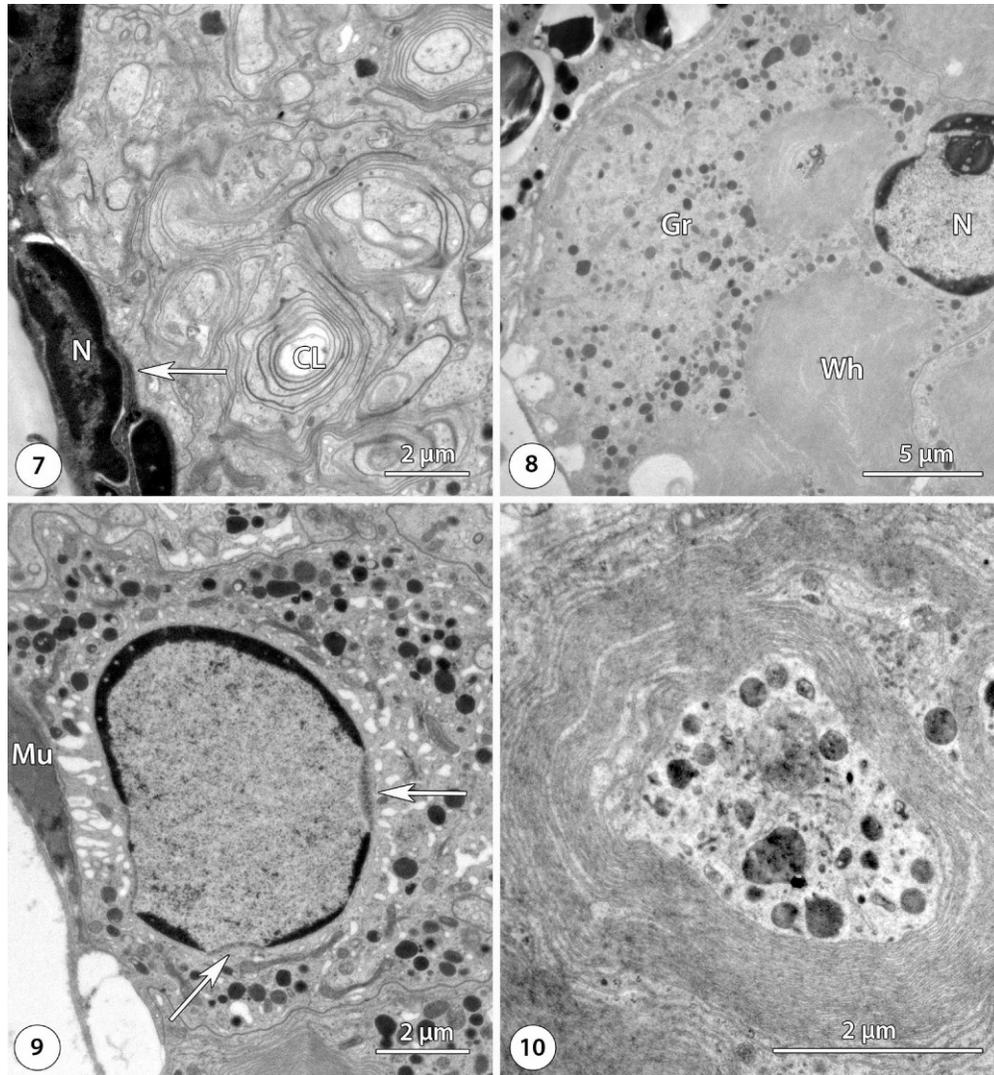


Figures 4-6.—*Stylocellus* sp.: 4. SEM of ozophore with opening of defense gland (white arrow) and lens (black arrow). Inset: border between lens and adjacent cuticle. Note distinctly smaller tubercles on the cuticular lens; 5, 6. TEM: 5. The lens slightly projects and is composed of about 20 layers of endocuticle and an almost homogeneous exocuticle which appears hardly modified when compared with the adjacent cuticle (see Fig. 6). The thin epicuticle is provided with small tubercles (compare Fig. 4). The lenticular layer is continuous with the epidermal layer; 6. Overview showing cuticle adjacent to the lens, epidermal layer (arrow), retina and pigment layer. * nuclei of reticular cells; + nucleus of glial cell. Cu = cuticle; L = lens; Lg = lenticular layer; Oz = ozophore; PL = pigment layer; R = retina; Rh = region of distal rhabdom.

lular spaces running between each other. Such differences may reflect different physiological phases. The retina is surrounded by a thin basal lamina. In one of the eyes we observed a thin cross-striated muscle fiber (Figs. 9, 20) between the basal lamina and the layer of reticular cells.

Pigment layer.—Pigment cells are not only found surrounding the reticular cells, but also distant from the eye. These cells

are evidently derived from connective tissue or fat bodies. However, they are distinctly concentrated around the reticular cells leaving free only the part of the retina under the lens. The pigment cells are dominated by very densely staining granules, which surround a moderate to densely staining ovoid cytoplasm and nucleus (Figs. 2, 6, 19). However, there are also larger electron-lucent inclusions or small vacuoles containing irregu-



Figures 7–10.—*Stylocellus* sp. TEM: 7. The lentigen layer is composed of flat densely staining cells containing densely staining nuclei. A thin basal lamina is present (arrow). Note circles of membranous lamellae in reticular cell; 8. Overview of peripheral part of retina showing nucleus with peculiar chromatin pattern and whorls of membranes; 9. Close up of peripheral region of retina with nucleus. Note nuclear pores (arrows) and granules. Between postretinal membrane (basal lamina) and retinula cell, a small muscle cell is found; 10. Conspicuous whorl of membranes with dense granules. Cl = circles of membranous lamellae; Gr = granules in reticular cells; Mu = muscle cell; N = nucleus; Wh = whorl of membranes.

larly shaped components. Furthermore, some of the inclusions seem to contain crystalline material. These latter inclusions are found only opposite to the lens (Fig. 20). The layer of pigment cells is bordered by a thin basal lamina.

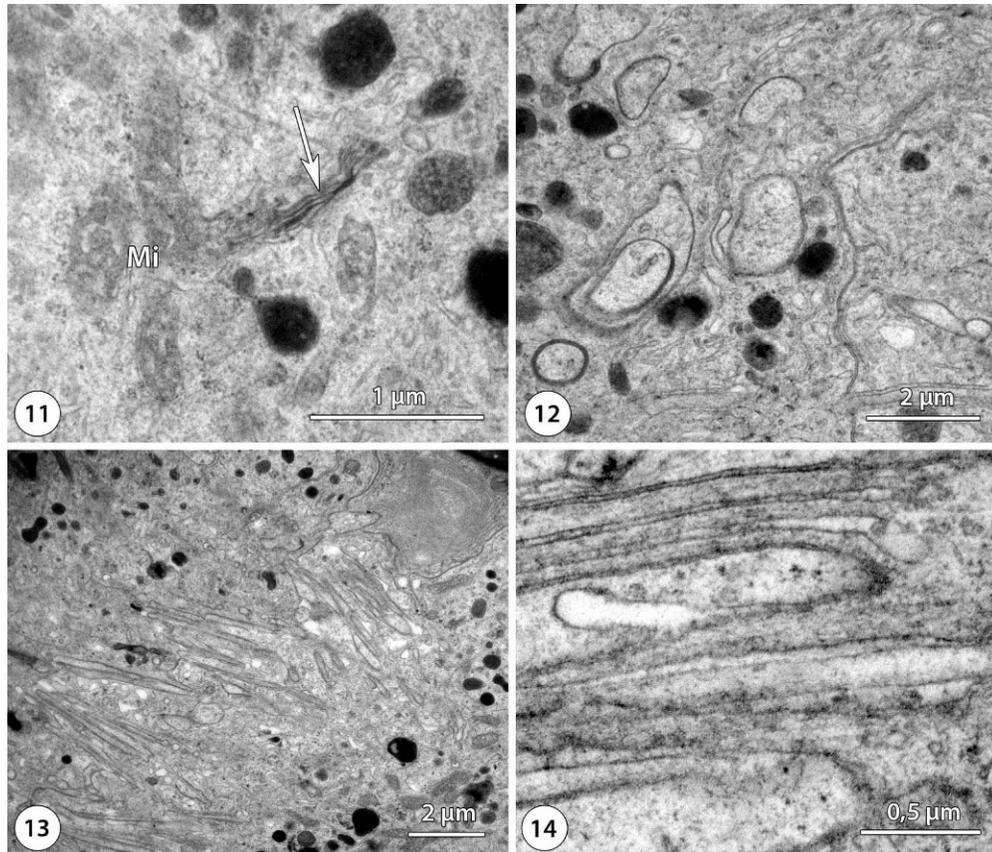
A few cells of unknown function are found between the basal lamina of the pigment cells and the basal lamina surrounding the retina. A small trachea enters the pigment layer.

Optic nerve.—The optic nerve leaves the retina at the posterior inner border of the eye (Figs. 3, 19). It penetrates the layer of pigment cells and is composed of more than 40 axons (Figs. 19, 21). The axons are moderately densely stained and contain numerous microtubules, some mitochondria and occasionally also some of the granules described from the reticular cells (see above). The axons are accompanied and surrounded by extensions of glial cells, which are more electron-lucent than the axons themselves. A thin basal lamina

surrounds the nerve. A small trachea runs along with the nerve but outside its basal lamina (Fig. 21).

DISCUSSION

Extant Arachnida typically have one pair of median (primary) eyes and up to five pairs of lateral (secondary) eyes (Paulus 1979, 2004; Weygoldt & Paulus 1979; Giribet et al. 2002) classified as ocelli. Exceptions are, besides Opiliones (see below), Pseudoscorpiones (Weygoldt 1969), and anactinotrichid mites (Anactinotrichida = Parasitiformes s.l.) (Alberti 2006; Dunlop & Alberti 2007), which have no median eyes, and the eyeless Palpigradi. The extant Ricinulei are usually considered to lack eyes although they bear more or less distinct light spots on the cuticle that may be associated with light reception. A similar situation is found in Schizomida (e.g., Moritz 1993).



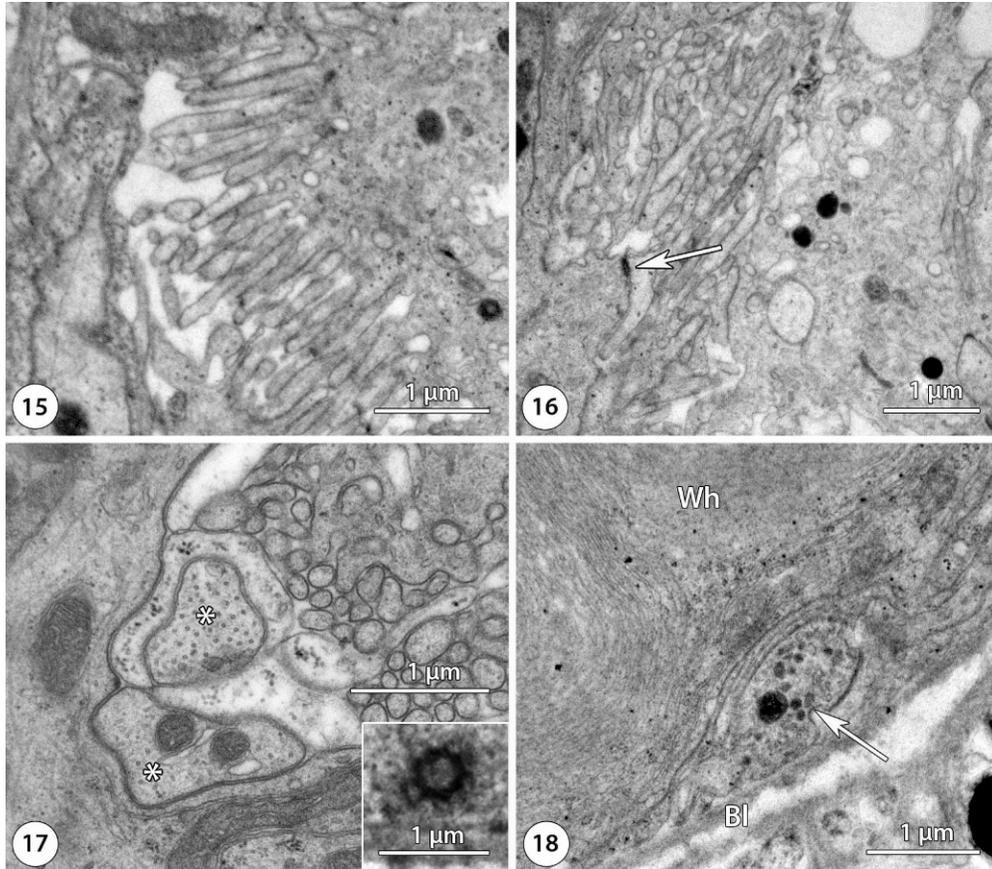
Figures 11–14.—*Stylocellus* sp. TEM: 11. Dense granules in the reticular cells are produced by small Golgi bodies (arrow); 12. Close to the center of the retina (compare Figs. 3, 5, 6) circles of membranous lamellae are frequent; 13. Overview showing the interdigitations of the poorly developed distal, closed rhabdom; 14. Close up of the distal rhabdom with interdigitating rhabdomeric microvilli-like projections of reticular cells. Mi = mitochondria.

The presence of laterally positioned eyes in Cyphophthalmi is remarkable for two reasons. First, presence of eyes in this group was, until recently, regarded as exceptional, being restricted to some species of Stylocellidae (the detection of eyes in Pettalidae as reported above makes this less peculiar). Second, the lateral position of these eyes is remarkable since eyes of Opiliones are usually located medially and are frequently referred to as median eyes (e.g., Kaestner 1935; Paulus 2004), although several cases of a lateral migration of the median eyes are known in Laniatores. Hence the question with regard to Stylocellidae (and Pettalidae) is whether these eyes represent lateral eyes homologous to those occurring in most of the other Arachnida or whether these eyes are displaced median eyes, as is the case in the abovementioned derived Laniatores, as already discussed by Juberthie (1964). However, Shear (1993a, b) homologized stylocellid eyes with arachnid lateral eyes because of the presence of a tapetum indicative of many lateral eyes; a tapetum is always lacking in median eyes. This interpretation of the stylocellid eyes was accepted by Giribet et al. (2002). Another possibility could be that these eyes are secondarily evolved, as those detected in oribatid mites (Alberti & Fernandez 1988). The evidence presented here refutes this latter hypothesis.

The eyes of *Stylocellus* sp. are largely composed of the same components as the median eyes of other Opiliones (e.g., Purcell 1894; Scheuring 1914; Juberthie 1964; Curtis 1970;

Schliwa 1979; Meyer-Rochow & Liddle 1988). These authors observed cuticular lenses, which are often biconvex, contrasting with the simple uniconvex lens of *Stylocellus*. A vitreous (glassy) body is located under the lens, which is comprised of a modified epidermal layer and hence corresponds to the less modified lentigen layer in *Stylocellus*. A pronounced vitreous body is evidently not developed in *Stylocellus*. The preretinal and postretinal membranes correspond to the basal laminae of the lentigen layer, retina and pigment cell layer. The retina of *Stylocellus* evidently is comparable to the more complex retina of other harvestmen. As in other Opiliones there is a conspicuous layer of pigment cells.

Peculiarities of the *Stylocellus* eyes are mainly found in the retina, which unfortunately is yet not completely understood based solely on the studied material. The reason for this is the peculiar arrangement and shape of reticular cells, which do not show an evident regular organization of the retina, and the limited material available for this study. At present we can distinguish two cell types, reticular cells (receptor cells) and glial cells (corresponding probably to the sheath cells of Schliwa 1979). We could furthermore recognize distinct regions in the retina: a nuclear region with conspicuous whorls of membranes and numerous dense granules, a region characterized by many membranes or lamellae and interdigitations between neighboring cells. These interdigitations may



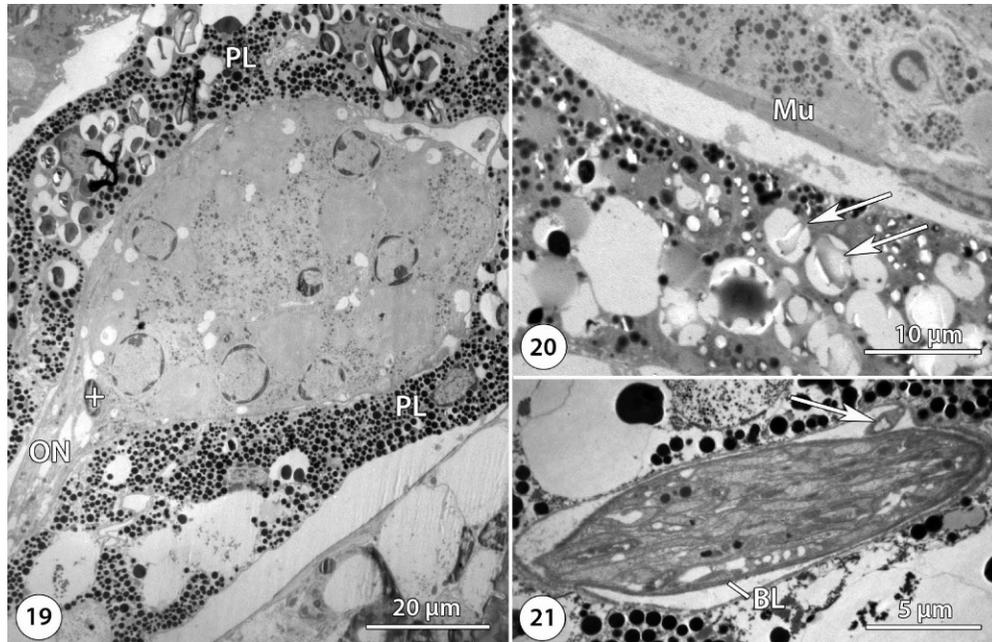
Figures 15–18.—*Stylocellus* sp. TEM: 15. The proximal, open rhabdom; 16. Another detail of the proximal rhabdom with irregularly arranged microvilli. Arrow points to small zonula adhaerens. 17. Axons (*) close to the proximal rhabdom. Inset: Centriole observed in reticular cell; 18. Putative efferent nerve ending (arrow) at the base of a reticular cell. Bl = basal lamina (postretinal membrane); Wh = whorl of membranes.

be regarded as forming a poorly developed closed rhabdom. Finally we found a region with distinct, but irregularly arranged microvilli forming a rather disordered, open rhabdom. Remarkably, this latter part of the retina is not found close to the lens but, instead, opposite to it, close to the origin of the optic nerve, suggesting an inverse (indirect) orientation. The retina thus shows a differentiation into a distal and a proximal part with a distal, closed and evert rhabdom and a proximal open and inverse rhabdom. However, we could not yet discriminate different types of reticular cells, i.e., (proximal) reticular cells and distal reticular cells, contributing to these rhabdoms (see Schliwa 1979). All the reticular cells show similar ultrastructure, except for varying cytoplasmic densities as mentioned above. We also could not detect the arhabdomeric (or eccentric) cells known from other Opiliones, as well as from other chelicerates including *Limulus* (e.g., Fahrenbach 1975, 1999; Fleissner & Siegler 1979; Schliwa 1979; Kaiser & Alberti 1991; Alberti & Coons 1999). However, the few processes representing putative nerve endings may indicate an efferent innervation known also from other chelicerate eyes, which have been shown to induce the movements of pigment granules according to a circadian clock in scorpions (Fleissner & Schliwa 1977; Fleissner 1986). Displacement of pigments as an adaptation to varying light intensities has long been known

from, e.g., spiders and may also be induced through stimuli by these efferent nerves (e.g., Scheuring 1914; Fahrenbach 1999). Membranous cisterns or lamellae have also been described from other arachnid eyes including Opiliones (e.g., Schliwa 1979). In *Stylocellus* the very conspicuous whorls of membranes in the nuclear region are most remarkable. We suggest that all these membranous structures are signs of a high membrane turnover, probably related to circadian changes of sensitivity as reported from other chelicerates (e.g., Blest 1978; Fleissner 1986; Fahrenbach 1999).

A remarkable feature is the presence of different types of granules in the pigment cells. Besides densely staining pigment granules, there are lucent granules containing irregular inclusions or even crystalline material. These inclusions seem to be concentrated in the background of the eye and may represent a tapetum (corroborating Shear's observation 1993a, b) and thus correspond to the peculiar positioned proximal, open rhabdom of the retina (see above). Presence of a tapetum is interpreted as an adaptation to nocturnal life, but may also be advantageous to species living in cryptic environments, as is the case of *Cyphophthalmi*. It is lacking, e.g., in the diurnal jumping spiders (Eakin & Brandenburger 1971).

It can be concluded that the eyes of *Stylocellus* largely correspond structurally to those known from other Opiliones, though being much simplified. In contrast to other eyes



Figures 19–21.—*Stylocellus* sp. TEM: 19. Overview of eye showing origin of optic nerve; + indicates nucleus of glial cell; other nuclei belong to reticular cells (compare Figs. 6, 8, 9); 20. Part of pigment layer opposite the incident light showing peculiar inclusions that might serve a tapetum function. Arrows point to crystal-like inclusions. However, a distinct tapetum layer is not present; 21. Oblique section through optic nerve composed of about 40 axons. Arrow points to small trachea. BL = basal lamina; Mu = muscle cell; PL = pigment layer.

described from harvestmen, *Stylocellus*' eyes appear to present a partly inverse retina directed towards a tapetum suggesting that these eyes might really represent lateral (secondary) eyes (Shear 1993a, b). However, the tapetum of *Stylocellus* differs strikingly from the tapeta known from spiders, whip scorpions and whip spiders, or the early derivative opilioacarid mite *Neocarus texanus* (Chamberlin & Mulaik 1942). In these taxa, tapeta represent distinct layers of specialized cells containing flat crystalline material (Scheuring 1914; Baccetti & Bedini 1964; Homann 1971; Meyer-Rochow 1987; Kaiser & Alberti 1991; Weygoldt 2000). This is evidently not the case in *Stylocellus*. Here the putative tapetum is simply a modification of certain pigment cells. Tracing the optic nerve into the brain may help to solve this problem of eye homology in *Stylocellus*. Also clarifying embryonic development of the eyes would be helpful. Do they develop by invagination as the typical median eyes of Chelicerata including Opiliones (Moritz 1957; Paulus 1979, 2004)? In any case it is evident that the presence of eyes in most Stylocellidae (and most Pettalidae) is a plesiomorphic character within Cyphophthalmi (Sharma & Giribet 2006; Boyer et al. 2007), and therefore the lack of eyes in all members of the families Neogoveidae, Ogoveidae, Sironidae and Troglisirionidae must be a derived adaptation to a cryptic mode of life pretty much limited to the leaf litter environments, caves, or the soil.

Following our observations, which did not show fundamental differences in the laterally positioned eyes of *Stylocellus* with those of Phalangida, the interpretation that median (primary) eyes moved laterally in the evolution of Cyphophthalmi and later disappeared in most taxa of mite harvestmen seems most likely to us. In accord with the study of Muñoz-Cuevas (1981) on eye regression in *Ischyropsalis* species, the simplified lens and the absent vitreous body

may be regarded as signs of regression in the eyes of *Stylocellus*.

While stylocellid eyes are conspicuous and located in front of the ozophores, pettalid eyes seem to have suffered a process of internalization. Pettalid eyes are, when found, located at the base of the ozophore (e.g., in *Chileogovea*, *Pettalus*, and some *Rakaia*), while species of *Aoraki*, *Austropurcellia*, *Neopurcellia*, and some *Rakaia* have the eyes incorporated into the ozophore (Sharma & Giribet 2006; Boyer & Giribet 2007). This type of eye is only visible in light microscopy, but not appreciated through scanning electron microscopy, as the eye lacks a cuticular lens entirely. Whether this particular pettalid eye is ultrastructurally similar to the stylocellid eye described in this study remains to be determined.

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