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The median eye of freshwater mites (Acari: Parasitengonae, Hydrachnidia) and its fate in the stem lineage of the Euhydrachnidia, Witte & Olomski 1991

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Abstract

The stem species of freshwater mites (Acari: Hydrachnidia) is generally regarded to be provided with a single median eye which is located below the dorsal cuticle of the prosoma. This character state has been reported from members of the superfamilies Hydrachnoidea, 'Hydryphantoidea' and 'Lebertioidea'. There have been no reports of a median eye from the other five superfamilies until now. In this study, it is shown by histological methods and observations on living specimens:

1. the presence of a single median eye in two other superfamilies, in Stygothrombioidea (*Stygothrombium chappuisi*) and Eylaoidea (*Limnochares aquatica*),
2. the presence of a pair of ocelli situated anteromedially between the lateral eyes in those species of the euhydrachnidian superfamilies that lack an unpaired median eye, in 'Hydryphantoidea' (*Hydrodroma despiciens*), 'Lebertioidea' (*Lebertia inaequalis*), 'Hygrobatoidea' (*Limnesia maculata*, *Hygrobates longipalpis*, *Unionicola crassipes*, *Piona carnea*) and 'Arrenuroidea' (*Arrenurus globator*, *A. cuspidator*).

The detection of the median eye in the early derived *Stygothrombium* and *Limnochares* confirms the hypothesis that the stem species of the Hydrachnidia was provided with a single unpaired median eye situated dorsally on its prosoma. Additionally, it is assumed that the pair of ocelli in later derived species of the Euhydrachnidia evolved from the median eye by division and separation.

Keywords: evolution, frontal eye, frontal organ, histology, water mites

1. Introduction

In the course of reconstructing the phylogenetic relationships within freshwater mites (Acari: Hydrachnidia), Harald Witte who unfortunately died in 2003, and I proved the presence and formation of the median eye in order to substantiate sistergroup relationships (Witte & Olomski 1991 and in preparation, see also Witte 1991b).

According to Grandjean (1958), actinotrichid mites originally possess two pairs of lateral eyes and an unpaired single median eye (Alberti & Coons 1999). The latter is located on the ventral side of the so-called naso, a hemispherical frontal protuberance of the prosoma. This character state is still present in members of the Pachygnathoidea and Brachychthonoidea (Grandjean 1958), Bdelloidea (Alberti 1975), Caeculoidea (Coineau 1979), Anystoidea (Witte

1991a) and Trombidioidea (Mischke 1981, Witte 1995). The median eye is frequently bilobed and is considered to be evolved by the fusion of the middle anterior eye pair of Arachnida (e.g. Foelix 1992, Alberti & Coons 1999).

Among the Hydrachnidia, the median eye – also known as a frontal organ or frontal eye – has only been reported from members of more primitive superfamilies Hydrachnoidea, 'Hydryphantoidea' and 'Lebertioidea' (e.g. Cook 1974). In all these specimens, it is situated anterodorsally on the prosoma below the prodorsal shield or below the more or less unsclerotized cuticle of this area. In his ultrastructural study of eyes of the hydryphantoid mite *Hydryphantes ruber* (de Geer, 1778), Mischke (1981) has pointed out that the median eye demonstrates typical characteristics of a photosensitive ocellus. The location of the median eye in the prodorsal region has been regarded by Witte & Olomski (1991) as a synapomorphy of Hydrachnidia, because the closely related terrestrial trombidioid mite *Johnstoniana* and anystoid mite *Anystis* demonstrate the primitive character state as mentioned above.

In the last years, the thesis of a monophyletic origin of the Hydrachnidia has been become more certainty, but the phylogenetic relationships within the Hydrachnidia have remained controversial (e.g. Harvey 1998, Witte & Olomski 1999, Gerecke 2007, Alberti et al. 2008, Krantz & Walter 2009). Cook (1974) established a system in which the Hydrachnidia are subdivided in eight superfamilies. Although some of these superfamilies have been regarded to be paraphyletic or polyphyletic, the system has been used up to now, because it works well in separating the enormous diversity of water mites (Gerecke 2007, 2010; Krantz & Walter 2009). Accordingly Witte & Olomski 1991, the superfamilies Eylaoidea, Hydrovolzioidea, Hydrachnoidea and additionally the Stygothombioidea are regarded to be monophyletic taxa, and the superfamilies 'Hydryphantoidea', 'Lebertioidea', 'Hygrobatoidea' and 'Arrenuroidea' are regarded to be not monophyletic taxa. (Latter taxa are put into quotation marks).

The absence of the median eye in the Stygothrombioidea, Hydrovolzioidea, Eylaoidea, 'Hygrobatoidea' and 'Arrenurroidea', and in many specimens of other three hydrachnidian superfamilies was treated as the result of the reduction (Alberti & Coons 1999). These reductions probably occurred several times independently, because the degree of the development of this organ varies within different taxonomic taxa, e.g. within genera.

Claparède (1868) and Schaub (1888) described a paired 'limpid bladder' in adult 'Hygrobatoidea' which was situated anteromedially to lateral eyes, and which the latter author considers eye rudiments. Lang (1905) and Schmidt (1936) did not agree with this hypothesis.

In our studies on living hydrachnids and their histology, I had performed some observations reflecting the fate of median eye, especially in the stem lineage of the Euhydrachnidia.

2. Materials and methods

The following species of eight superfamilies of Hydrachnidia were examined:

1. Stygothrombioidea: *Stygothrombium chappuisi* Walter, 1947
2. Hydrovolzioidea: *Hydrovolzia placophora* (Monti 1905)
3. Hydrachnoidea: *Hydrachna cruenta* Müller, 1776
4. Eylaoidea: *Piersigia intermedia* Williamson, 1912; *Limnochares aquatica* (L., 1758); *Eylais extendens* (Müller, 1776)
5. 'Hydryphantoidea': *Hydryphantes ruber* (de Geer, 1778); *Parathyas barbigera* (Viets, 1908); *Euthyas truncata* (Neuman, 1875); *Hydrodroma despiciens* (Müller, 1776)

6. ‘Lebertioidea’: *Sperchon setiger* Thor, 1898; *Lebertia inaequalis* (Koch, 1837)
7. ‘Hygrobatoidea’: *Limnesia maculata* (Müller, 1776); *Hygrobates longipalpis* (Hermann, 1804); *Unionicola crassipes* (Müller, 1776); *Piona carnea* (Koch, 1836)
8. ‘Arrenuroidea’: *Arrenurus globator* (Müller, 1776); *Arrenurus cuspidator* (Müller, 1776); *Arrenurus compactus* Piersig, 1894

The taxonomic nomenclature used in this paper accords to Gerecke (2007 and 2010); taxa are put into quotation marks if they probably are not monophyletic.

Structural investigations were carried out on living adults and larvae by examination of cleared and mounted specimens and also by histological techniques.

Living specimens were screened for possessing visible pigmented eye spots. Specimens were cleared by lactic acid and mounted in polyvinyl lactic phenol (Chroma). In order to perform histological investigations, animals were fixed in the Bouin’s fixative, dehydrated in alcoholic series and embedded either via three butanol-rinses into Paraplast plus (Lancer) or into glycolmethacrylate (Technovit 7100 by Kulzer). Transverse, sagittal, and horizontal sections were cut with Jung 1140 and Mikrom HM350 microtomes and stained with the Azan method, ferro-hematoxyline, or hematoxylin-eosin according to Romeis (1968).

Additionally, histological section series of *Hydrodroma despiciens* from the collection of Dr. Rodger D. Mitchell (Ohio State University), and of *Limnochares aquatica* from the collection of Dr. Jörg Pahnke (formerly University of Kiel) were studied.

3. Results and Discussion

3.1. Stygothrombioidea

In living adults of *Stygothrombium chappuisi*, I found a small third red spot between the pair of bright red lateral eyes (Fig. 1). As far as it possessed the same conspicuous colour as lateral eyes and because of its arrangement on the prodorsal sclerite, I interpret this structure as the median eye. It is the first record of the existence of the median eye in the superfamily Stygothrombioidea.

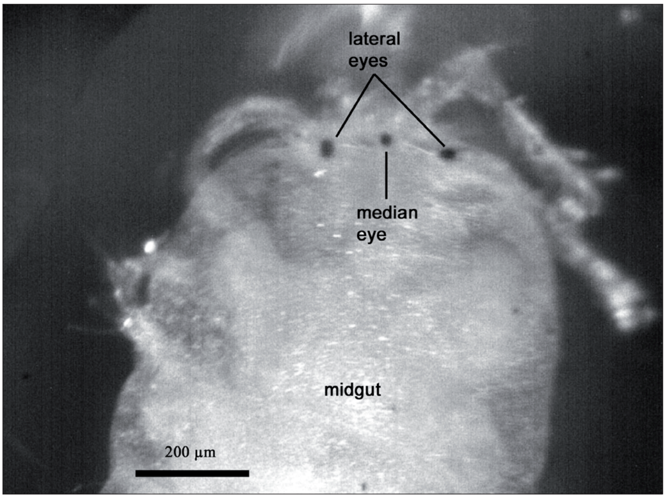

Fig. 1 Lateral eyes and median eye on the prosoma of a living adult of *Stygothrombium chappuisi* (Stygothrombioidea) from dorsal view.

Verification of this hypothesis by means of histological sections needs further studies. The mentioned structure is very small and the conspicuous red colour of the eye spot rapidly vanishes during clearing or conservation of mites with lactic acid or alcohol.

3.2. Hydrovolzioidea

Neither in cleared adults nor in histological sections of *Hydrovolzia placophora*, I have found any trace of a median eye. No living animals were available for the present study.

3.3. Eylaoidea

In *Piersigia intermedia* and *Eylais extendens*, I have not identified a median eye or rudiments of it. Despite of it, I found a small globe of intensively stained cells in a cavity of the frontal tip of the prodorsal sclerite of *Limnochares aquatica*. I believe that these structures detect the unpaired median eye or its derivate (Fig. 2 and 3). The globe is about 14–15 µm in diameter. The cells show no eye pigments but their basal parts continue as a nerve which I could trace for a short distance in ventral direction.

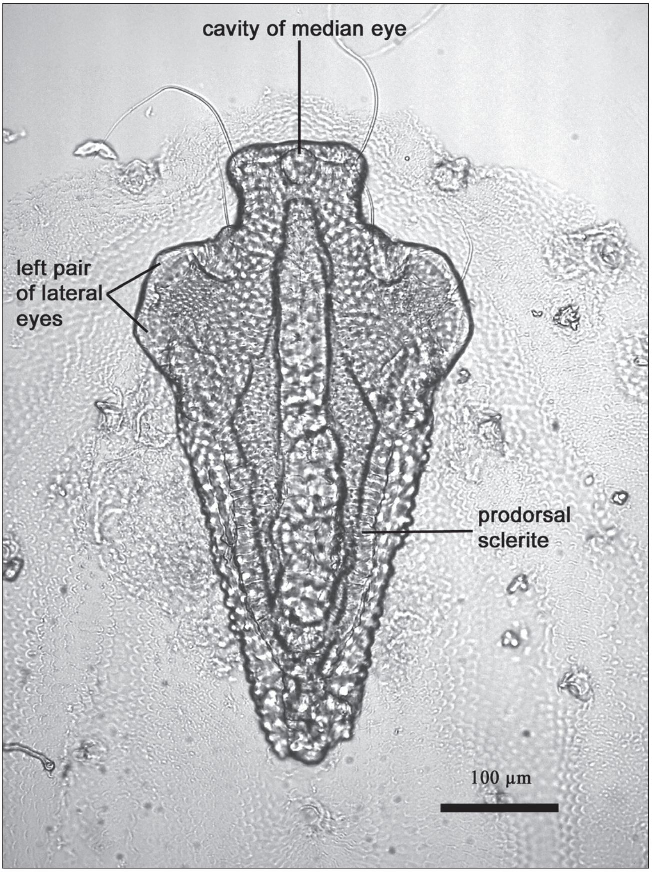

Fig. 2 Prodorsal sclerite with the cavity of the median eye of a cleared and mounted adult of *Limnochares aquatica* (Eylaoidea) from dorsal view.

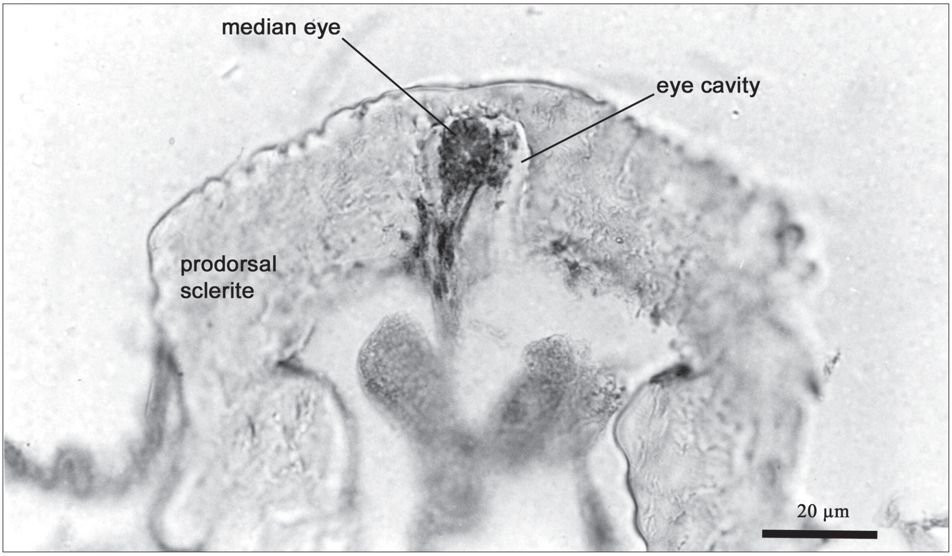

Fig. 3 Median eye of an adult *Limnochares aquatica* (Eylaoidea) in horizontal section.

3.4. 'Hydryphantoidea', Hydrachnoidea and 'Lebertioidea'

In these three superfamilies, the existence of a single median eye is well documented. I have proved it in adults and larvae of *Hydryphantes ruber*, *Parathyas barbigera* and *Euthyas truncata*, and in adult *Hydrachna cruenta* and *Sperchon setiger*. The pigmentation of the median eye of *Euthyas* indicates that the eye of this species is bilobed (Fig. 4).

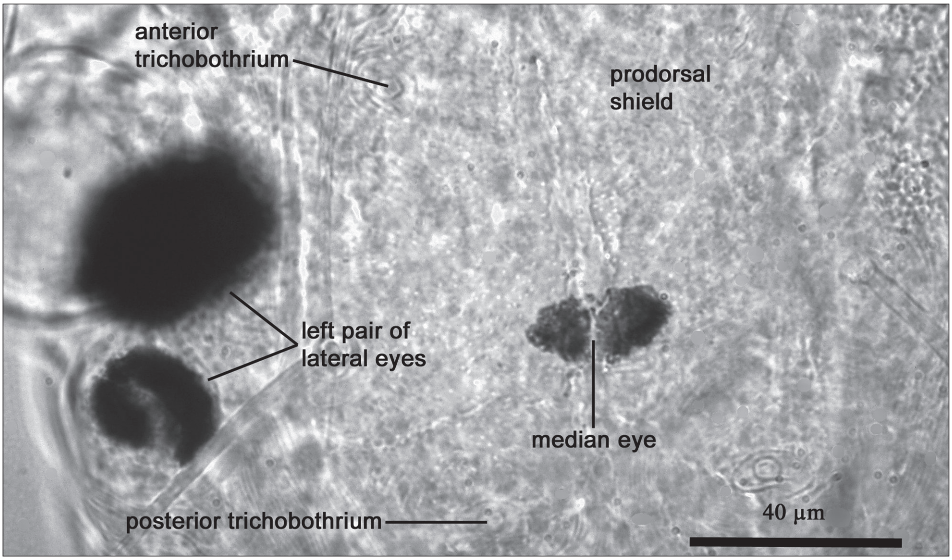

Fig. 4 Bilobed pigment spot of the median eye of a cleared and mounted larva of *Euthyas truncata* ('Hydryphantoidea') from dorsal view.

In *Hydrodroma despiciens* and *Lebertia inaequalis*, I found a small paired globular structure I consider as the result of the evolution of a single median eye by its subdivision and separation (Fig. 5 and 6).

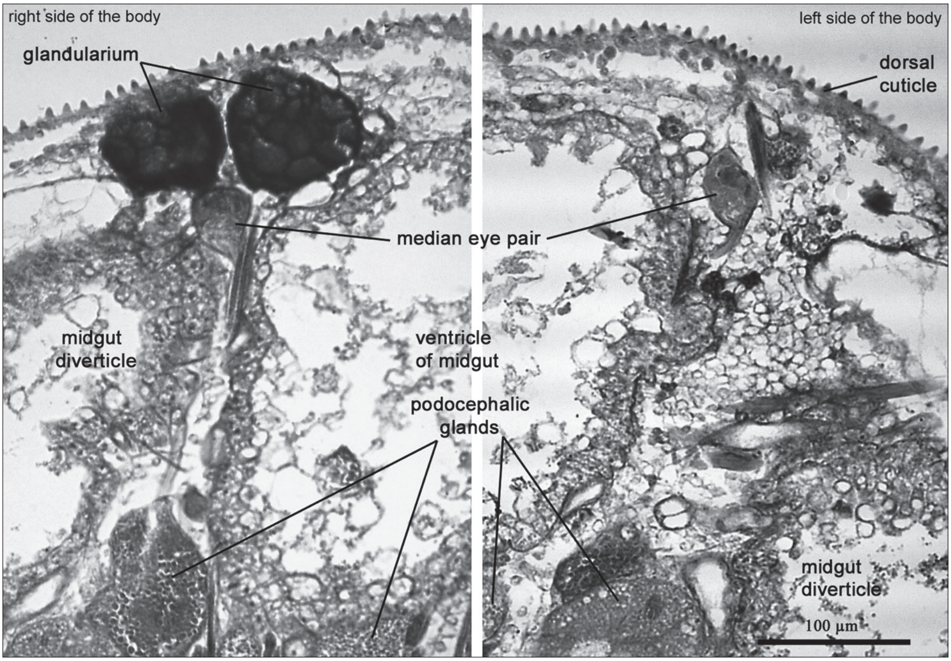

Fig. 5 Paired median eye of an adult of *Hydrodroma despiciens* ('Hydryphantoidea') in transverse sections of the prosoma.

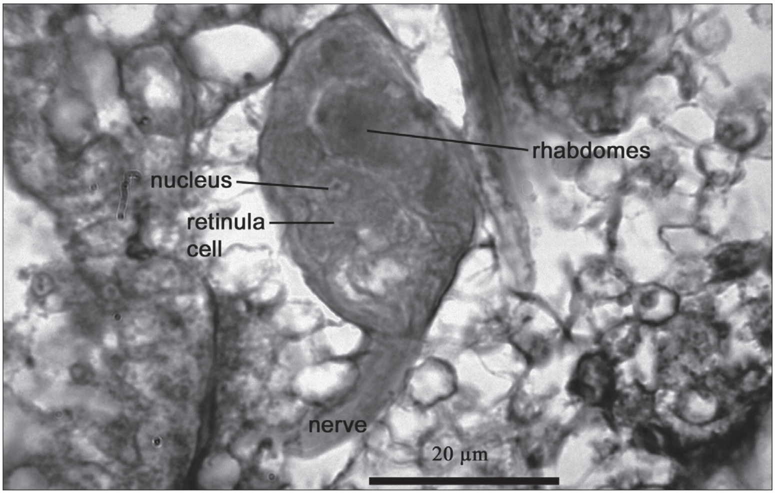

Fig. 6 Left median eye of an adult *Hydrodroma despiciens* ('Hydryphantoidea') in transverse section of the prosoma.

In *Hydrodroma despiciens*, the globes are situated anteromedially to lateral eyes. There, they lie under the soft dorsal cuticle between glandularia and gut diverticula. They are about 55 µm high and 42 µm in diameter, but they are frequently pressed and vary in shape. The globes are composed of several cells which proximally continue into a nerve and apically form a common intensively stained inhomogeneous area. This area resembles rhabdomes of lateral eyes in a disordered arrangement. The cells do not possess any pigment.

The paired globes of *Lebertia* are similar to those of *Hydrodroma*, but they are smaller, constituting about 10–16 µm in diameter and in height.

3.5. 'Arrenuroidea'

In histological sections of adult *Arrenurus globator,* I also found paired structures. These structures are cup-shaped and provided with dark pigments in males (Fig. 7). These cups constitute about 14–15 µm in diameter. They demonstrate typical histological character of ocelli. The ocelli are composed of about 8 retinula cells whose rhabdomeres are arranged in the centre of the globe. The cells continue proximally in the optical nerve. The striation of the intensively stained rhabdomes indicates a regular arrangement. The cup seems to be covered by a thin membranous envelope. In *A. globator* males, I found an assemblage of fine dark eye pigments, shielding the rhabdomes at one side of the cup (Fig. 7). The investigated females lacked eye pigments.

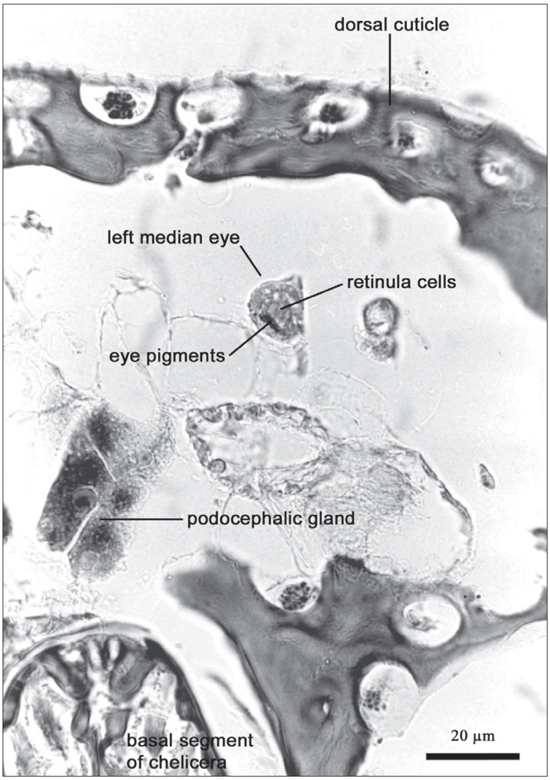

Fig. 7 Left median eye of a male of *Arrenurus globator* ('Arrenuroidea') in transverse section.

In living larvae of *A. globator* (Fig. 8) and in cleared larvae of *A. cuspidator* (Fig. 9), I found a pair of cup-shaped agglomerations of dark pigments below the prodorsal shield in the same places where the paired ocelli were situated in adults. Cup dimensions constituted about 6 and 7 µm in height and 7 and 10 µm in diameter, respectively. By contrast to these species, I have not found this structure in larvae of *A. compactus*.

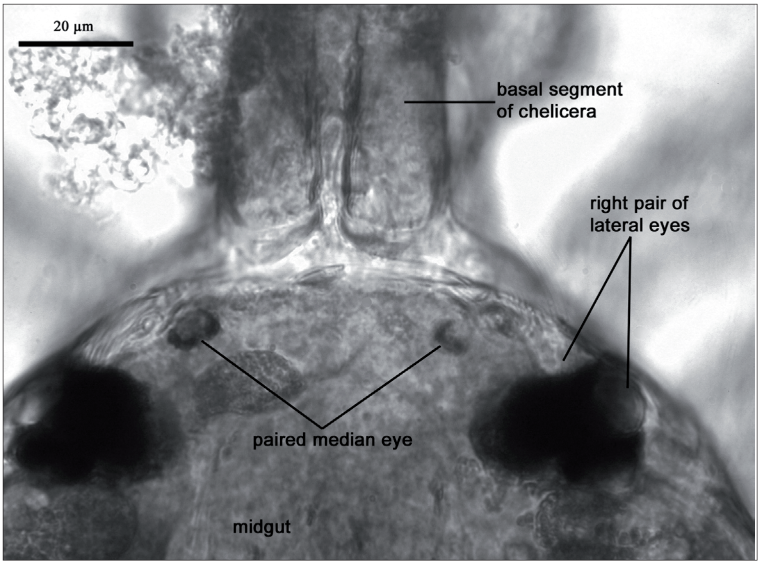

Fig. 8 Pigmented cups of the paired median eye of a living larva of *Arrenurus globator* (‘Arrenuroidea’) from dorsal view.

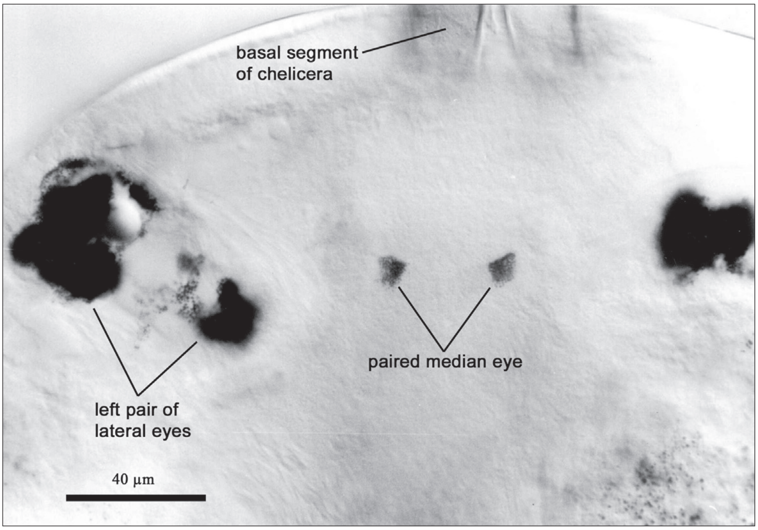

Fig. 9 Pigmented cups of the paired median eye of a cleared and mounted larva of *Arrenurus cuspidator* (‘Arrenuroidea’) from dorsal view.

3.6. 'Hygrobatoidea'

At a location comparable to that of the paired ocelli in *A. globator* adults, I found in adults of *Piona carnea* a paired structure which was treated by earlier authors in case of several 'Hygrobatoidea' as a 'sensory organ with unknown function' (Figs 10–12). Claparède (1868) and Schaub (1888) described this organ as a 'limpid bladder' in the dorsal view in representatives of the genus *Atax* (synonym to *Unionicola*). Lang (1905) described this organ more precisely in *Curvipes carneus* (Koch, 1836) (synonym to *Piona carnea*). His description corresponds to my observations of the same species.

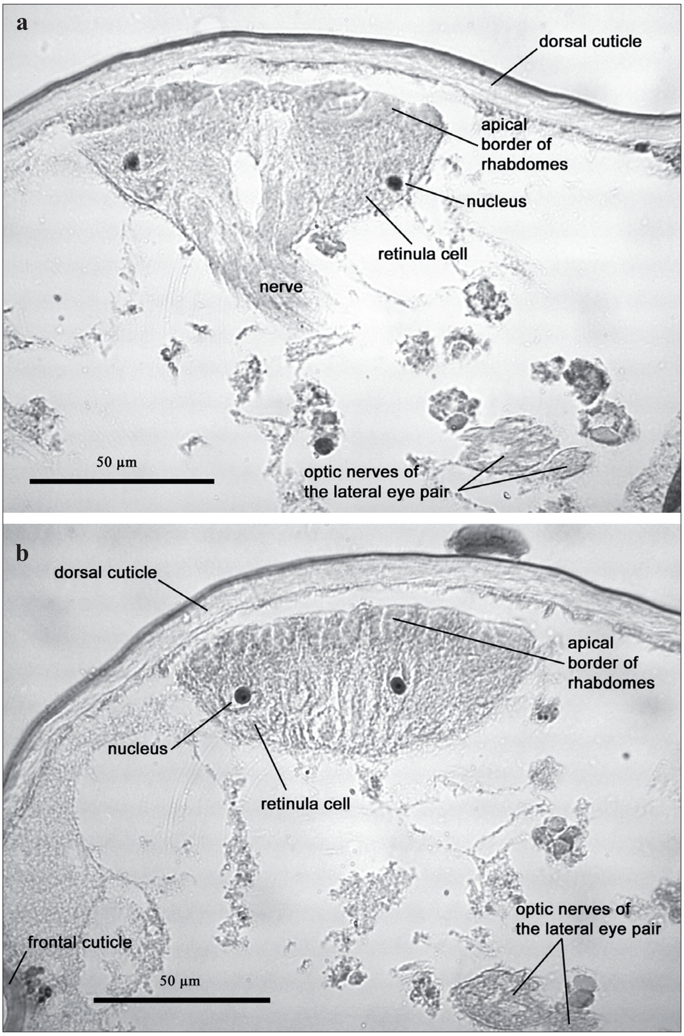

Fig. 10 Left median eye of an adult of *Piona carnea* ('Hygrobatoidea') in sagittal sections. **a**: Section through the central region, **b**: Section more peripheral.

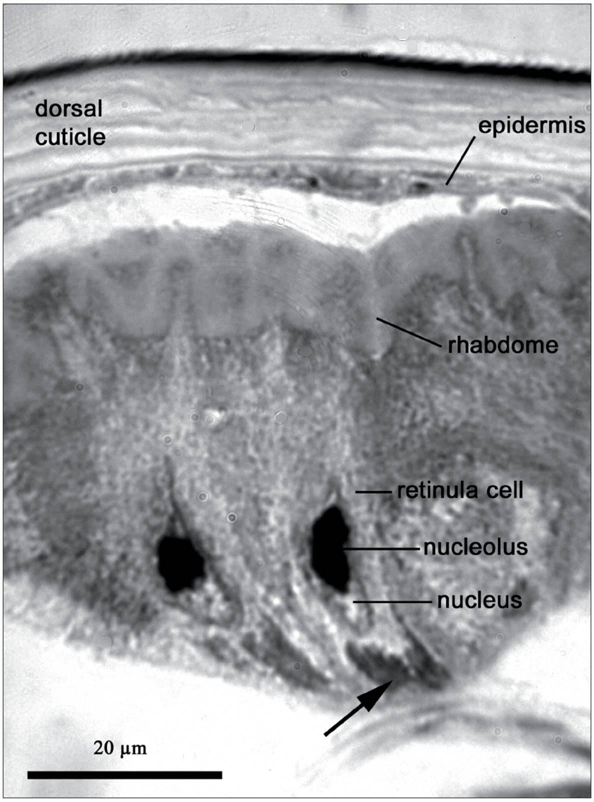

Fig. 11 Details of the left median eye of an adult of *Piona carnea* ('Hygrobatoidea') in sagittal section. The arrow indicates proposed mitochondrial rich infoldings of the basic membrane.

In sagittal cuts, this organ looks like a mushroom which extends its umbrella below the cuticle. The 'umbrella' is maximally 53 µm in height and 105 µm in diameter. It is composed of a single layer of prismatic cells, forming an apical fringe and continuing as a fibre at their proximal ends. Because of the specific histological appearance, I assume that these cells are retinula cells, provided with apical rhabdomeres and the proximal afferent axon. The axons form a nerve running in the posteroventral direction, thus forming a 'mushroom stalk'. At some distance, this nerve joins the optical nerve of the corresponding body side. The nuclei of the proposed retinula cells are large and located basically. Proximally to the nucleus, in the transition zone to the axon, perpendicularly orientated striations of different lengths, provided with fine granules, are observed (Fig. 11, indicated by an arrow). Possibly, they are mitochondrial rich infoldings of the cell membrane. The entire organ is enveloped by a thin layer of epidermal cells. No eye pigments or a cornea were observed.

I also found these paired mushroom-shaped organs in adults of *Limnesia maculata*, *Hygrobates longipalpis* and *Unionicola crassipes*.

4. General Discussion

The results of the present microscopic study on the median eye of freshwater mites are partly preliminary and should be proved by further investigations especially on the ultrastructure of the organ. Nevertheless, the observations performed confirm some previous assumptions and give rise to new hypotheses.

The red 'eye' spot on the prodorsal sclerite of *Stygothrombium chappuisi* (Fig. 1) and the globular cellular structure which is supplied by a nerve and which lies at the top of the prodorsal sclerite of *Limnochares aquatica* (Figs 2, 3) possibly refers to the single median eye known from other primitive Hydrachnidia, e.g. *Hydryphantes*. Thus, it confirms the previous assumption that the stem species of freshwater mites possessed a single unpaired median eye situated dorsally on the prosoma.

Moreover, it supports the hypothesis of Witte & Olomski (1991) that the location of the median eye below the dorsal cuticle of prosoma is a synapomorphy of the Hydrachnidia (Fig. 12). In the terrestrial outgroups of the Hydrachnidia, the Trombidioidea and Anystoidea, the median eye is situated on the ventral side of the so-called naso, the frontal protuberance of the prosoma (Mischke 1981, Witte 1991a and 1995).

The paired globular or cup-shaped organs of *Hydrodroma despiciens* (Figs 5, 6), *Lebertia inaequalis* and *Arrenurus globator* (Figs 7, 8) and the paired mushroom-shaped organs of *Piona carnea* (Figs 10–11), *Limnesia maculata*, *Hygrobates longipalpis* and *Unionicola crassipes* demonstrate typical structural elements of a photosensitive organ (rhabdomes, afferent nerve, and dark pigments in *Arrenurus*). As far as these organs are situated in the same region of the prosoma as the single median eye and because the single median eye is lacking, I can assume that these paired organs had obviously evolved from the unpaired median eye and thus, they are homologous.

Schaub (1888) had already assumed that paired 'limpid bladders' found by him and Claparède (1868) anteromedially to lateral eyes of *Unionicola* were 'rudimentary eyes'. Unfortunately, in his descriptions of *Hydryphantes* and *Eylais*, Schaub was obviously mistaking the cellular part of the prodorsal trichobothria (ocularia) for the 'limpid bladder'. That might be the reason why Lang (1905) and Schmidt (1936) did not agree with the 'eye-hypothesis' of Schaub, and why this hypothesis was not developed in subsequent studies. However, Lang and Schmidt also treated the paired structure as a sensory organ, but of an unknown function.

In Witte & Olomski (1991), I preliminary treated these paired median sense organs as 'akzessorische Augen' (see also Witte 1991b: Tab. 8.1, 'accessory eyes'). Now I am convinced that they are homologous to the single median eye of more primitive Hydrachnidia. Probably, in the course of evolution of the Euhydrachnidia, the single median eye had subdivided into two eyes that later shifted laterally. The single median eye of Acari is frequently bilobed and is treated as a result of the fusion of the middle anterior eye pair of ancient Arachnida in a course of evolution (e.g. Foelix 1992, Alberti & Coons 1999). Thus, the proposed division of the eye in the course of the evolution of the Euhydrachnidia can be regarded as evolutionary 'throwback'.

In accordance to Witte & Olomski (1991) concept concerning phylogenetic relationships within the Hydrachnidia, the apomorphic transformation had occurred before *Hydrodroma* derived from the euhydrachnidian stem lineage (Fig. 12). Because the later derived *Hydrachna* and *Sperchon* show the plesiomorphic state of an unpaired median eye, the transformation to the paired eye seems to be stabilized later, in the evolution of the 'Hygrobatoidea' and 'Arrenuroidea'.

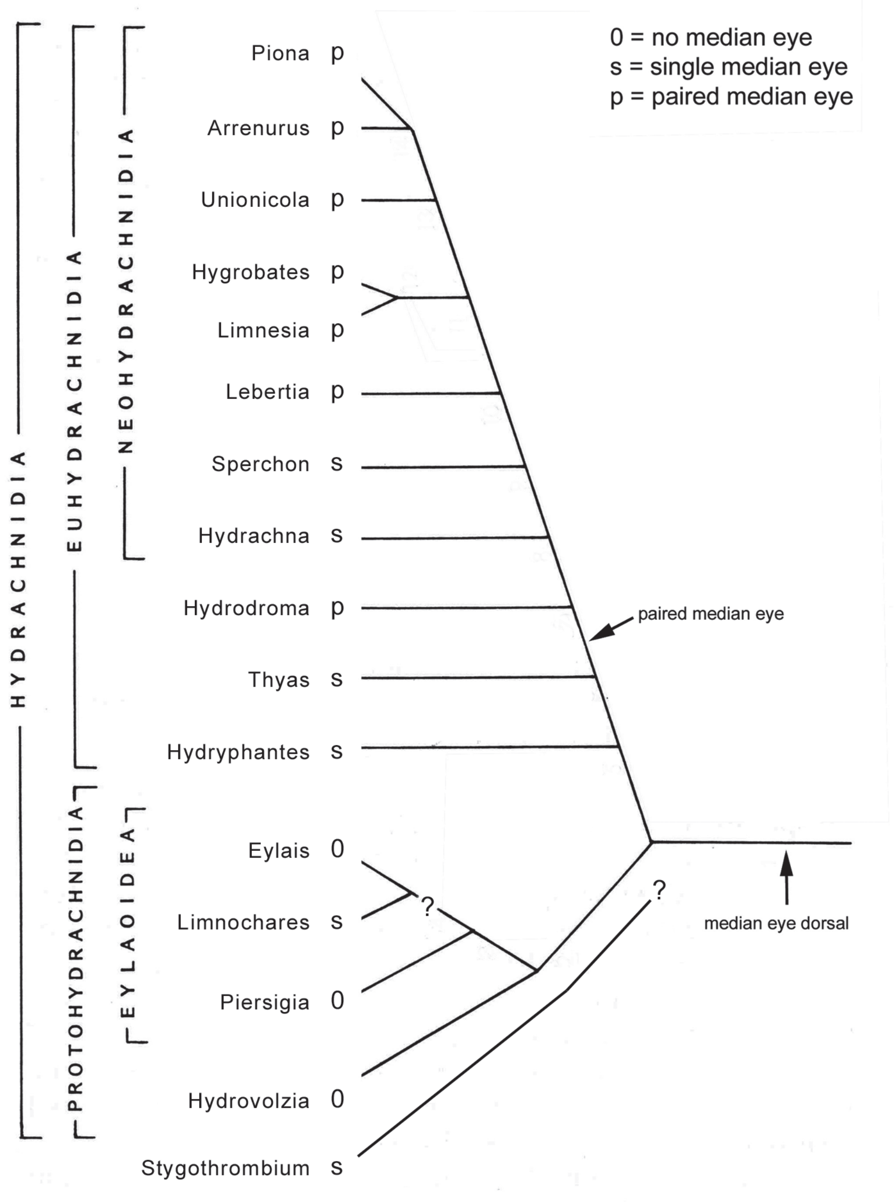

Fig. 12 The appearance of median eyes in the phylogeny of the freshwater mites (Acari: Hydrachnidia); diagram of the phylogenetic relationships after Witte (1991b: Fig. 8.1), modified.

Mischke (1981) has pointed out in his ultrastructural study of the unpaired median eye of the 'primitive' freshwater mite *Hydryphantes* that this organ probably functions as a light receptor. The optical capabilities of the eye must be very limited, because the eye is very small and composed only of few cells; arrangement of rhabdomes shows no regular orientation. From the histological appearance of the paired ocelli of *Arrenurus globator,* it is evident that the median eye has maintained its functional ability as a photoreceptor organ even after its subdivision into a paired structure. However, the tendency of reduction dominates in the majority of taxa of the freshwater mites, including the loss of a cornea, the loss of pigments, or the total loss of the organ. In contrast to this tendency, in the 'Hygrobatoidea', the paired median eye evolved into a conspicuous mushroom-shaped sensory organ which is about 5–10 times larger in diameter than the single median eye of the more primitive freshwater mites, e.g. of *Hydryphantes* or *Limnochares*, or the paired ocelli of *Hydrodroma, Lebertia* or *Arrenurus*. It is of great interest, to reveal the detailed structure and special function of these transformed mushroom-shaped organs by further investigations.

5. Acknowledgements

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