

Ocular Changes Accompanying Eye Loss in the Spider Family Uloboridae

BRENT D. OPELL

Department of Biology, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061

ABSTRACT In uloborid spiders, eye loss is accompanied by increased visual angles, optical material investment, and potential visual acuity of the retained eyes. Relative to carapace volume, the six-eyed *Hyptiotes cavatus* and two four-eyed *Miagrammopes* species have greater retinal hemisphere areas and lens volumes than do the eight-eyed uloborids *Waitkera waitkerensis*, *Uloborus glomosus*, and *Octonoba sinensis*. In *Waitkera*, in which the eyes have little visual overlap, and in *Miagrammopes*, in which eye loss simplifies the spiders' patterns of visual overlap, increased retinal cell density enhances potential visual acuity. However, this occurs at the expense of potential retinal cell sensitivity.

Most members of the spider family Uloboridae construct horizontal orb-webs. However, one lineage is characterized by web simplification, typified by the vertical triangle-webs spun by members of the temperate genus *Hyptiotes* (Opell, '82; Peters, '38) and the irregular, few-stranded webs spun by members of the tropical genus *Miagrammopes* (Lubin, '86; Lubin et al., '78). These changes in web form necessitate changes in web-monitoring tactics. Whereas orb-weavers hang beneath the hubs of their webs and run to wrap prey that become ensnared, reduced-web uloborids more actively monitor and manipulate their webs during prey capture (Opell, '85, '87).

These behavioral changes are facilitated by leg reorientation made possible by reorganization of the prosomal muscles that insert on the leg bases (Opell, '84a). In reduced-web uloborids, the more paraxial orientation of these muscles requires lateral shifts in their origins on the carapace and endosternite. In turn, lateral expansion of the endosternite necessitates lateral shifts in the origins of its suspensor muscles. In reduced-web uloborids, both sets of muscles insert in carapace regions that in orb-weavers are occupied by the anterior eyes. Thus, this muscle reorganization appears to contribute to the altered carapace shape, eye relocation, and eye loss characteristic of *Hyptiotes* and *Miagrammopes* (Fig. 1).

Changes in anatomy and orientation of the remaining eyes of these reduced-web uloborids help conserve their total visual surveillance and maintain their patterns of visual overlap (Opell and Cushing, '86; Opell and Ware, '87). This is achieved principally by expanding and ventrally shifting the eyes' visual angles. An eye's visual angle can be increased by changing its lens parameters (increasing lens thickness, front and rear radii of curvature, and refractive index), by reducing the distance between its rear lens surface and retinal hemisphere, and by perimetrically expanding its retinal hemisphere. Because they involve material expenditure, lens volume (which accounts for both lens thickness and curvature) and retinal surface area lend themselves to comparative studies.

Two qualitative aspects of vision, acuity and sensitivity, can also be estimated from eye anatomy. The greater the number of retinal cells relative to an eye's visual angle, the finer-grain image it receives. However, even if the light-gathering ability (f -number) of the eye's lens remains unchanged, the reduction in retinal cell diameters that enhances its acuity also diminishes retinal sensitivity to a degree not easily compensated for by increased retinal cell length (Blest and Lang, '77). Thus, greater resolution can only be gained at the expense of light sensitivity.

The purpose of this study is to evaluate two

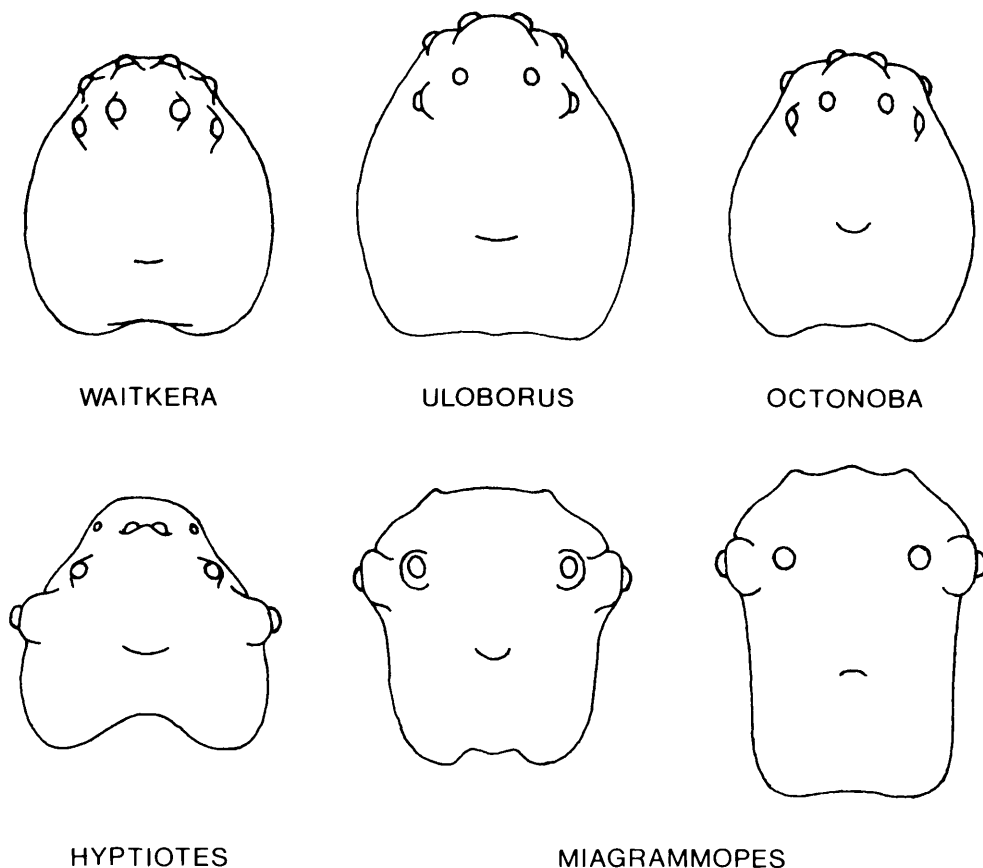


Fig. 1. Carapaces of species studied, showing differences in eye placement and number. *Miagrammopes* sp. is at the center, and *M. animotus* is at the right.

additional changes that should characterize the eyes of reduced-web uloborids. First, to compensate for eye loss, the material invested in their remaining eyes should exceed that found in the homologous eyes of orb-weavers and, consequently, their total ocular investments should more closely approximate those of orb-weavers than their eye numbers alone predict. Second, because eye loss reduces the complex patterns of visual overlap found in advanced orb-weavers and, thereby, the spiders' potential for detecting motion and evaluating distances (Forster, '82; Opell and Cushing, '86; Opell and Ware, '87), the eyes of reduced-web uloborids and those of primitive orb-weavers with little visual overlap should compensate for this by having

greater visual acuity than those of orb-weavers.

MATERIALS AND METHODS

Specimen fixation and sectioning

Adult females of six species were used in this study: the primitive New Zealand orb-weaver *Waitkera waitkerensis*, the Asian orb-weaver *Octonoba sinensis* (which, as a United States introduction was known as *O. octonaria* until synonymized by Yoshida '80), the eastern North American orb-weaver *Uloborus glomosus*, the eastern North American triangle-weaver *Hyptiotes cavatus*, the Puerto Rican "single-line-weaver," *Miagrammopes animotus*, and an undescribed Costa Rican *Miagrammopes* species, belonging to the

Miagrammopes aspinatus species group (Opell, '84b). Represented genera are related as follows: (*Waitkera* ((*Hyptiotes* *Miagrammopes*) (*Uloborus* *Octonoba*))) [Opell, '79, '84b]. Specimens were anesthetized with carbon dioxide (only *W. waitkerensis* was not so treated, as it was collected, fixed, transferred to buffer, and mailed to me), fixed at 20–26°C for 12–18 hours in 3% glutaraldehyde/3% formaldehyde in 0.1 M sodium cacodylate buffer (pH 7.3), rinsed in 0.1 M sodium cacodylate buffer, dehydrated through a graded series of acetone, and embedded in Spurr's epoxy resin. One-micron-thick serial cross sections were made with a Sorvall JB-4 microtome and stained with toluidine blue.

Measurements used to determine retinal hemisphere area, lens volume, and effective retinal cell length were taken from cross sections through the center of each eye (Fig. 2A). Those used to compute retinal cell diameter and density were taken from cross and sagittal sections through the posterior and lateral regions of an eye's retinal hemisphere (2B).

Retinal hemisphere area and retinal cell number

To compute retinal hemisphere area, I first determined (by plotting) the center and radius of curvature of the reconstructed retinae (presented in Opell and Cushing, '86; and Opell and Ware, '87) and the angle from the center that included the dorsal- and ventral-most retinal cells. Using these measurements, I computed the retinal area as if it were a sphere, multiplied this area by the measured angle just cited, and then divided the product by 360 degrees to determine the actual retinal area.

I determined retinal cell density from enlarged micrographs of retinal regions sectioned perpendicular to the retinal cell axes (Fig. 2B). The surface area of a region of well-defined cells and their intervening pigment was measured with a Numonics® electromagnetic digitizing tablet interfaced with an IBM pc running Sigma-Scan® software. Using scale marks inscribed on each photographic negative prior to printing enlargements, I converted this measurement to μm^2 and divided it by the number of retinal cells included in the region whose surface area was measured. This calculation yields the average surface area of a retinal cell and its associated pigment. The inverse of this value gives retinal cell density, and dividing

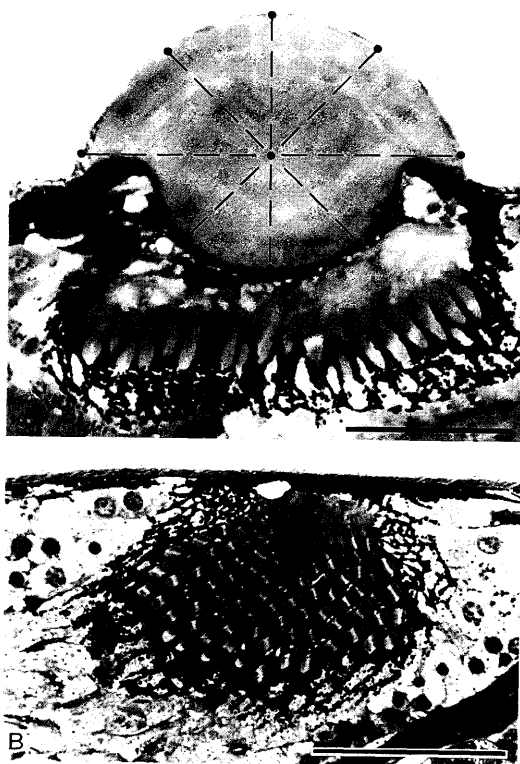


Fig. 2. Cross sections through the center of the retinal hemisphere and lens (A) and through the periphery of the retinal hemisphere (B) of a *Miagrammopes animotus* posterior median eye. The radiating lines in A are the eight measurements used to compute the lens' mean radius. Scale bar = 50 μm .

this value into a retinal hemisphere's total surface area estimates an eye's total retinal cell number.

Lens volume

Lens volume was also determined from enlarged photographs of cross or sagittal sections through the center of each lens (Fig. 2A). Sagittal sections were used for the anteriorly directed anterior median eyes (AME), and cross sections were used for the remaining eyes. The cross-sectional surface area of each lens was measured with a digitizing tablet. Lens volume was then computed as if the lens were a sphere by multiplying its cross-sectional area by $4/3$ the lens' mean radius (as determined from the eight measurements shown in Fig. 2A).

Size-specific indexes

Several relative indexes were used to compare the eyes of the six species studied. To obtain relative retinal hemisphere areas and lens volumes, I divided absolute values by the volume of each species' prosoma. To determine prosomal volume, I drew each species' carapace with the aid of a camera lucida, measured separately the surface areas of cephalic (ocular) and thoracic regions with a digitizing tablet, measured the dorsal-ventral thickness of cross sections through each region, multiplied each area by its respective thickness, and summed the resulting volumes. To determine relative retinal cell density I divided an eye's total visual angle by its total number of retinal cells. The greater this value the more potential an eye has for resolving detail.

Relative light absorbance

Although f-number (focal length/lens aperture) is a useful index of a lens' ability to admit light, it does not account for retinal cell sensitivity. The following index of the relative amount of light absorbed per receptor (R) was used by Blest and Land ('77) and incorporates both an eye's light-gathering ability and potential retinal cell sensitivity. The greater this value, the more sensitive are an eye's retinal cells.

$$R = (A/F)^2 d^2 (1 - e^{-kx})$$

In this equation A = the lens' entrance pupil diameter, F = the lens' focal length, d = retinal cell diameter, k = light absorption coefficient of the retinal cell, and x = length of the absorbing segment of the retinal cell. All measurements but k are in μm . As the light absorption coefficient for spider eyes has never been experimentally determined, I follow Blest and Land's ('77) approach of letting $k = 0.01$ per μm , a value similar to that reported for other arthropods (Hays and Goldschmith, '69; Kirschfeld, '69). Focal lengths and entrance pupil diameters used in this equation were taken from Opell and Cushing ('86) and Opell and Ware ('87). Retinal cell diameters and lengths were measured from cross- and sagittal-section photographs.

Comparisons of total ocular investments

If reduced-web uloborids compensate for eye loss by investing more material in their

remaining eyes, then their total relative retinal hemisphere areas and total relative lens volumes should be greater than their eye numbers alone predict. That is, in *H. cavatus* these values should be more than 3/4 those of orb-weavers, and in *Miagrammopes* species they should be more than 1/2 those of orb-weavers.

However, the small anterior lateral eyes (ALE) of orb-weavers lower these predicted values by basing their ocular investments largely on the values of three rather than four eyes. To overcome this problem and to provide a more conservative test, I based predicted values on the three largest eyes of each orb-weaving species. This I achieved by multiplying the sum of each orb-weaving species' three greatest relative retinal hemisphere areas and three greatest relative lens volumes by 1.333. The means of these adjusted total relative values for the three orb-weaving species were used to predict values against which those of reduced-web species were compared.

RESULTS

In most cases, the relative retinal hemisphere areas (Table 1) and relative lens volumes (Table 2) of the posterior eyes of reduced-web uloborids exceed those of the homologous eyes of orb-weavers, the only exception being that the posterior median eyes (PME) of *Waitkera waitkerensis* have 10% greater relative retinal hemisphere areas and 18% greater relative lens volumes than those of *Miagrammopes animotus*. The AMEs of *H. cavatus* have smaller values than those of orb-weavers. Compared with mean values for the three orb-weavers, the PME of *H. cavatus*, *M. animotus*, and *Miagrammopes* sp. have relative retinal hemisphere areas and relative lens volumes that are, respectively, 2.0 and 1.8, 1.6 and 1.5, and 2.2 and 2.0 times greater. The posterior lateral eyes (PLE) of these reduced-web species have values that are, respectively, 4.0 and 1.9, 3.7 and 1.9, and 2.4 and 2.9 times greater than those of the orb-weavers.

As a consequence of these changes, the total ocular investment by reduced-web uloborids is, relative to carapace volume, greater than eye number alone predicts. In *H. cavatus* total relative retinal hemisphere area is 1.9 times greater, and total relative lens volume is 1.3 times greater than expected. In *M. animotus* they are, respectively, 2.0 and 1.5 times greater than expected and in *Mia-*

TABLE 1. Absolute and relative retinal cell numbers and measurements used in their determination

Species & carapace volume ($\times 10^6 \mu\text{m}^3$)	Eye	Retinal hemisphere			Retinal hemisphere area/ carapace volume ($\mu\text{m}^2/\mu\text{m}^3 \times 10^{-8}$)	Retinal cell area			Total retinal cells	Visual angle ¹ (°)	Retinal cells per degree of visual angle
		Radius (μm)	Angle (°)	Area (μm^2)		$\bar{X}$ (μm^2)	SD	Sections/ specimens			
<i>Waitkera waitkerensis</i> (1,173)	AME	44	95	6,257	534	42.0	12.1	3/2	149	48	3.1
	ALE	18	214	2,420	206	52.4	23.7	3/2	46	29	1.6
	PME	105	57	21,537	1,837	51.8	5.4	4/3	416	59	7.1
	PLE	54	78	7,939	677	64.7	12.7	5/3	123	37	3.3
Total				38,153	3,254				734	173	(3.8)
<i>Uloborus glomus</i> (1,222)	AME	61	65	8,305	679	38.5	11.5	4/3	216	57	3.8
	ALE	32	129	4,593	376	45.9	12.2	2/2	100	67	1.5
	PME	65	64	9,294	760	75.5	6.2	5/3	123	71	1.7
	PLE	31	98	3,182	260	86.4	11.6	3/2	37	47	0.8
Total				25,374	2,075				476	242	(2.0)
<i>Octonoba sinensis</i> (1,711)	AME	56	182	20,066	1,173	40.8	2.3	2/1	492	182	2.7
	ALE	20	53	722	42	46.7	1.8	2/1	16	53	0.3
	PME	50	101	8,639	505	76.7	16.3	3/1	113	101	1.1
	PLE	31	62	2,080	122	77.6	7.7	2/1	27	62	0.4
Total				31,507	1,842				648	398	(1.1)
<i>Hyptiotes cavatus</i> (818)	AME	57	64	7,132	872	67.5	18.7	2/2	106	70	1.5
	ALE	—	—	—	—	—	—	—	—	—	—
	PME	60	132	16,525	2,020	77.1	11.3	3/2	214	107	2.0
	PLE	59	95	11,543	1,411	74.6	6.6	4/2	155	94	1.7
Total				35,200	4,304				475	271	(1.7)
<i>Miagrammopes animotus</i> (1,055)	PME	73	94	17,486	1,657	28.4	5.5	3/1	616	83	7.4
	PLE	63	99	13,716	1,300	38.2	8.2	3/1	359	70	5.1
Total					2,956				975	153	(6.3)
<i>Miagrammopes</i> sp. (964)	PME	71	123	21,796	2,260	33.2	1.9	4/1	657	123	5.3
	PLE	52	84	8,012	831	28.6	—	1/1	280	84	3.3
Total			31,202	29,808	3,091				937	207	(4.3)

¹From Opell and Cushing ('86) and Opell and Ware ('87).

TABLE 2. Absolute and relative lens volumes and measurements used in their determination (standard deviation is given in parentheses)

Species	Eye	Lens area (μm^2)	Radius (μm)	Lens volume ($\mu\text{m}^3 \times 10^3$)	No.	Lens volume/ carapace volume ($\mu\text{m}^3/\mu\text{m}^3 \times 10^6$)
<i>Waitkera waitkerensis</i>	AME	7,574 (728)	47 (2)	479 (67)	2	408
	ALE	3,516	32	150	1	128
	PME	9,315	53	655	1	558
	PLE	6,992	47	437	1	373
Total				1,721		1,467
<i>Uloborus glomosus</i>	AME	6,213 (570)	42 (3)	345 (52)	4	282
	ALE	2,388 (202)	27 (1)	85 (11)	3	69
	PME	4,158 (187)	36 (1)	198 (15)	2	162
	PLE	2,951 (740)	30 (3)	119 (40)	3	98
Total				747		611
<i>Octonoba sinensis</i>	AME	8,769	51	594	1	347
	ALE	3,812	34	173	1	101
	PME	6,581	43	375	1	219
	PLE	5,469	41	295	1	173
Total				1,437		840
<i>Hyptiotes cavatus</i>	AME	3,094 (284)	29 (3)	121 (22)	2	148
	ALE	789	14	15	1	18
	PME	7,306 (2,991)	46 (10)	465 (282)	2	569
	PLE	5,945 (797)	32 (3)	337 (66)	3	412
Total				938		1,147
<i>Miagrammopes animotus</i>	PME	7,819 (273)	48 (92)	499 (34)	2	472
	PLE	7,024 (53)	46 (1)	428 (1)	2	406
	Total			927		878
<i>Miagrammopes</i> sp.	PME	8,879	51	607	1	630
	PLE	8,910	51	609	1	632
Total				1,216		1,262

grammopes sp. they are 2.1 and 2.2 times greater than expected.

The retinal cells of each eye are indistinguishable on the basis of size or structure. Relative retinal cell density (Table 1) is greatest in the eyes of uloborids that have the least visual overlap. The anterior eyes of *W. waitkerensis* exhibit no visual overlap, and the posterior eyes overlap only one another's visual fields (Opell and Ware, '87). This species has a mean retinal cell density that is 1.9 times that of *Uloborus glomosus* and 3.5 times that of *Octonoba sinensis*. Despite loss of its ALE, *H. cavatus* loses little of its total visual overlap (Opell and Ware, '87) and has a mean retinal cell density intermediate between *U. glomosus* and *O. sinensis*. With only one-half the number of eyes of the orb-weavers, the two *Miagrammopes* species have a mean retinal cell density that is 2.3 times greater than that of the three orb-weavers and 3.3 times as large as the mean for *U. glomosus* and *O. sinensis*.

The similarity of f-numbers between the *Miagrammopes-Hyptiotes* lineage and the most closely related uloborid studied, *U. glomosus* (Table 3), shows that the light-gathering abilities of reduced-web uloborid eyes (lenses) are conserved as their visual angles increase. When compared with *M. animotus*, the more highly derived species *Miagrammopes* sp. (Opell, '84b) shows a 0.35 reduction in PLE's f-number, a change that permits 25% more light to strike its retinal cells. Despite this light-gathering ability, the smaller retinal cell diameters of *Miagrammopes* result in their having relative light absorbance values that average 0.67 those of the homologous eyes of orb-weavers.

DISCUSSION

Previous studies quantify the mechanisms and visual consequences of ocular changes associated with eye loss in reduced-web uloborids (Opell and Cushing, '86; Opell and Ware, '87). This investigation shows that

TABLE 3. Relative light absorbance and visual benefit cost indexes and measurements used in their determination

Species	Eye	f.No. ¹	Retinal cell diameter			Retinal cell effective length			Relative light absorbance
			$\bar{X}$	SD	No.	$\bar{X}$	SD	No.	
<i>Waitkera waitkerensis</i>	AME	1.2	5.7	0.4	14	17.5	0.0	3	3.9
	ALE	1.2	5.9	0.7	12	13.1	2.4	4	2.8
	PME	1.3	5.6	0.3	14	18.4	1.2	5	3.4
	PLE	1.3	6.1	0.8	13	16.2	1.9	3	3.5
	Mean	1.3							3.4
<i>Uloborus glomosus</i>	AME	0.9	6.1	1.0	14	16.3	2.5	4	6.4
	ALE	1.0	4.9	1.1	12	15.5	1.1	5	3.3
	PME	1.1	6.0	0.5	14	18.0	0.0	3	5.6
	PLE	1.2	7.0	1.5	12	15.8	1.3	7	5.1
	Mean	1.1							5.1
<i>Octonoba sinensis</i>	AME	0.8	5.3	0.7	12	17.5	0.0	5	6.7
	ALE	0.6	4.9	0.5	10	16.7	1.4	3	8.8
	PME	0.8	5.2	0.8	10	16.5	2.2	5	6.6
	PLE	0.8	5.0	0.7	14	17.5	—	1	6.5
	Mean	0.8							7.2
<i>Hyptiotes cavatus</i>	AME	0.9	5.2	0.4	12	15.0	0.0	3	4.8
	ALE	1.7	—	—	11	—	—	—	—
	PME	1.0	5.7	0.5	14	23.6	3.2	7	7.7
	PLE	0.9	6.1	0.5	14	22.7	1.9	7	9.7
	Mean	1.1							7.4
<i>Miagrammopes animotus</i>	PME	1.0	4.9	0.4	14	18.6	1.6	7	4.0
	PLE	1.1	4.3	0.3	14	17.9	1.5	7	2.3
	Mean	1.0							3.2
<i>Miagrammopes sp.</i>	PME	1.0	4.1	0.2	14	18.7	1.3	7	2.9
	PLE	0.8	4.1	0.3	14	14.2	2.0	6	3.6
	Mean	0.9							3.3

¹f.Nos. and the entrance pupil diameters and focal lengths from which they were calculated are taken from Opell and Cushing ('86) and Opell and Ware ('87).

these adaptations also entail a number of congruent qualitative changes with the potential to compensate for eye loss by enhancing the visual acuity of the remaining eyes. As eye number decreases, more retinal and lens material is invested in the remaining eyes.

The size reduction of *Miagrammopes* retinal cells that enhances their eyes' potential visual acuity (Table 1) does so at the expense of their retinal cells' relative light absorbance (Table 3). However, even the lowest value of 2.3 is 11 times greater than Blest and Land ('77) report for the large primary eyes of jumping spiders. Thus, the eyes of *Miagrammopes* probably function effectively at daytime light levels present in the tropical forest understory where these spiders are typically found.

However, unlike members of the family Deinopidae, whose PME relative light absorbance values of 495 (Blest and Land, '77) permit them to hunt at night (Baum, '38; Coddington and Sobrevila, '87; Roberts, '55; Robinson and Robinson, '71), the eyes of *Miagrammopes* probably afford little night vi-

sion. If the vision of reduced-web uloborids serves principally to detect diurnal, visually hunting predators, then enhanced visual acuity would be of greater value to them than would visual sensitivity that extended farther into the early morning and late evening hours when the threat of predation is slight. The increased retinal cell density and reduced retinal cell diameter that characterized *Miagrammopes* is consistent with Blest and Land's ('77) contention that spider retinal cells do not pool their signals. Pooled units of retinal cells would function as enlarged retinal cells and would have no selective advantage in situations where visual acuity was favored. However, it is possible that, just as in vertebrate eyes (Levine, '85), pooling occurs at low light levels, permitting the eyes to function but reducing their resolution.

Relative retinal cell number and lens volume and relative retinal cell density (Tables 1, 2) show the PME of *Waitkera waitkerensis* to be surprisingly well developed, both relative to the other eyes of this species and to the eyes of other orb-weavers and of *Hyp-*

tiotes cavatus. Coddington ('86a,b) concludes that Deinopidae is the sister group of Uloboridae. These "ogre-faced" spiders take their common name from the extremely large and well developed PME (Blest and Land, '77) used by members of the family's most common genus, *Deinopis*, to detect prey and direct their forward prey-capture strike (Baum, '38; Coddington and Sobrevila, '87; Roberts, '55; Robinson and Robinson, '71). Although members of the less highly derived genus *Menneus* use similar prey-capture tactics (Mascord, '70), their eyes are more nearly the same size and the ratio of their diameters suggests a grade of development similar to that of *W. waitkerensis*. The mean ratios for eight *Menneus* species are AME: 0.8, ALE: 0.7, PME: 1.0, PLE: 0.9. (Coddington and Opell, unpublished observations). This similarity suggest that the well-developed PME of uloborids is a plesiomorphic character of the two sister families that favored the increase in size of these eyes in the genus *Deinopis*.

ACKNOWLEDGMENTS

Elizabeth M. Reinoehl assisted with measurements. Jonathan A. Coddington and an anonymous reviewer made suggestions that improved earlier versions of this paper. National Science Foundation grants DEB-8011713 and BSR-8407979 awarded to the author supported this study.

LITERATURE CITED

- Baum, J. (1938) On the habits of the Australian spider *Dinopis subrufus* L. Koch. Mem. Soc. Zool. Tcheosl. Prague 5:28-32.
- Blest, A.D., and M.F. Land (1977) The physiological optics of *Dinopis subrufus* L. Koch: A fish lens in a spider. Proc. R. Soc. Lond. [Biol.] 196:197-222.
- Coddington, J.A. (1986a) The monophyletic origin of the orb-web. In W.A. Shear (ed): Spiders: Webs, Behavior and Evolution. Stanford: Stanford University Press, pp. 319-363.
- Coddington, J.A. (1986b) Orb-webs in "non-orb weaving" ogre-faced spiders (Araneae: Dinopidae): A question of genealogy. Cladistics 2:53-67.
- Coddington, J.A., and C. Sobrevila (1987) Web manipulation and two stereotypic attack behaviors in the ogre-faced spider, *Dinopis spinosus* Marx (Araneae, Dinopidae). J. Arachnol. 15:213-225.
- Forster, L.M. (1982) Vision and prey-catching strategies in jumping spiders. Am. Sci. 70:167-175.
- Hays, D., and T.H. Goldsmith (1969) Microspectrophotometry of the visual pigment of the spider crab, *Libinia emarginata*. Z. Vergl. Physiol. 65:218-232.
- Kirschfeld, K. (1969) Absorption properties of photopigments in single rods, cones, and rhabdomeres. In W. Reichardt (ed): Processing of Optical Data by Organisms and Machines. New York: Academic Press, pp. 116-143.
- Levine, J.S. (1985) The vertebrate eye. In M. Hildebrand, D.M. Branble, K.F. Liem, and D.B. Wake (eds): Functional Vertebrate Morphology. Cambridge: Belknap Press, pp. 317-337.
- Lubin, Y.D. (1986) Web function and prey capture behavior in Uloboridae. In W.A. Shear (ed): Spiders: Webs, Behavior, and Evolution. Stanford: Stanford Univ. Press, pp. 132-171.
- Lubin, Y.D., W.G. Eberhard, and G.G. Montgomery (1978) Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche (Stuttg.) 85:1-23.
- Mascord, R.M. (1970) Australian Spiders. Rutland, VT: Charles E. Tuttle Co.
- Opell, B.D. (1979) Revision of the genera and tropical American species of the spider family Uloboridae. Bull. Mus. Comp. Zool. 148:433-549.
- Opell, B.D. (1982) Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). J. Arachnol. 10:185-191.
- Opell, B.D. (1984a) Comparison of the carapace features in the family Uloboridae (Araneae). J. Arachnol. 12:105-114.
- Opell, B.D. (1984b) Phylogenetic review of the genus *Miagrammopes sensu lato* (Araneae: Uloboridae). J. Arachnol. 12:229-240.
- Opell, B.D. (1985) Force exerted by orb-web and triangle-web spiders of the family Uloboridae. Can. J. Zool. 65:580-583.
- Opell, B.D. (1987) Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae. Can. J. Zool. 65:1028-1034.
- Opell, B.D., and P.E. Cushing (1986) Visual fields of orb-web and single-line-web spiders of the family Uloboridae. Zoomorphology 106:199-204.
- Opell, B.D., and A.L. Ware (1987) Changes in visual fields associated with web reduction in the spider family Uloboridae. J. Morphol. 192:87-100.
- Peters, H.M. (1938) Ueber das Netz der Dreieckspinne, *Hyptiotes paradoxus*. Zool. Anz. 121(3-4):49-59.
- Roberts, N.L. (1955) The Australian netting spider, *Deinopis subrufus*. Roy. Soc. New South Wales 54:24-33.
- Robinson, M.H., and B. Robinson (1971) The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge. Am. Midl. Natur. 85:85-96.
- Yoshida, H. (1980) Six Japanese species of the genera *Otonoba* and *Philoponella* (Araneae: Uloboridae). Acta Arachnol. 29:57-64.