

Changes in Visual Fields Associated With Web Reduction in the Spider Family Uloboridae

BRENT D. OPELL AND AMY D. WARE

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

ABSTRACT When visual fields of the primitive orb-weaver, *Waitkera waitkerensis*, are reconstructed using measurements taken from intact lenses and cross and longitudinal sections of the prosoma, they show that this species has complete visual surveillance, but that none of the visual fields of its eight eyes overlap. The more advanced orb-weaver, *Uloborus glomosus*, also has eight eyes, but each eye has a greater visual angle, giving this species a complex pattern of overlapping visual fields. Uloborids that spin reduced webs are characterized by reduction or loss of the four anterior eyes and other carapace modifications necessary for them to effectively monitor and manipulate their reduced webs. The eyes of these uloborids have greater visual angles than those of orb-weavers, resulting primarily from perimetric expansion of their retinal hemispheres. Additionally, the axes of their visual fields are more ventrally directed due to greater dorsal than ventral retinal expansion and to ventral redirection of the entire eye. Consequently, even though the anterior lateral eyes of the triangle-weaver *Hyptiotes cavatus* lack retinæ, the species' six functional eyes permit complete visual surveillance and exhibit visual overlap. The single-line-weaver, *Miagrammopes animotus*, has lost its four anterior eyes, and with them much of the anterior vision and all of the visual overlap found in the other species. However, changes similar to those of *H. cavatus* permit this species to retain most of its dorsal and ventral visual surveillance. Thus, ocular changes act in consort to maintain relatively complete visual surveillance in the face of eye loss and other major carapace modifications necessary for the operation of reduced webs.

Carapace shape, eye placement, and eye number are the most conspicuous anatomical differences in the family Uloboridae. For this reason, it is not surprising that they played a major role in early attempts to delineate subgroups within the family (Simon, 1892) and have remained prominent in analysis of uloborid phylogeny. However, the inclusion of additional characters has made it clear that, instead of dividing the family into three major subgroups, these prosomal modifications characterize a single lineage (Opell, '79, '84a,b).

This lineage is also distinguished by progressive reduction of the family's primitive and typical web form, the horizontal orb-web (Opell, '79). The Mediterranean species *Pole-necia producta* constructs a vertical web with radii, but without the sticky (cribellar) spiral component (Wiehle, '31). Instead, this sticky

silk is deposited on the radii. Members of the temperate genus *Hyptiotes* construct vertical, triangular webs consisting of four radii between which sticky (cribellar) threads are spun (Opell, '82; Peters, '38). A spider monitors its taut web from a thread extending from the point where the radii converge. Members of the tropical genus *Miagrammopes* construct an extremely reduced, irregular web that has no stereotypic form. It consists either of a single horizontal thread with sticky silk along most of its length or a nonsticky horizontal or diagonal monitoring thread from which one or several vertical or diagonal prey capture threads extend to surrounding vegetation (Akerman, '32; Lubin et al., '78; Opell, '79).

Address reprint requests to Brent D. Opell, Department of Biology, Virginia Tech, Blacksburg, VA 24061.

Polonecia has a typical pear-shaped carapace with eight (the primitive number) similarly sized eyes. *Hyptiotes* has a short, broad carapace with four small anterior eyes and four large posterior eyes, the posterior lateral eyes being borne on prominent lateral tubercles (Fig. 4). The carapace of *Miagrammopes* is rectangular and bears only the four large posterior eyes (Fig. 4). As in *Hyptiotes*, the posterior lateral eyes are borne on prominent tubercles. This association of progressive carapace modification with successive web reduction is more than coincidental. Opell ('84a) found a statistical association between web form and indexes of carapace shape and eye placement.

This linkage between carapace features and web form results from differences in web-monitoring tactics. Most orb-weaving uloborids simply hang from the hubs of their webs as they wait for prey to become ensnared (Opell and Eberhard, '83), whereas *Hyptiotes* and *Miagrammopes* actively monitor and manipulate their webs via a single thread (Lubin, '86; Lubin et al., '78; Opell, '82). This latter tactic requires spiders to extend their first legs directly forward and exert force parallel to their midsagittal body planes. Proximal muscles that insert on the proximal leg segments originate from both the carapace and an internal, cartilaginous plate, the endosternite, that is suspended from the carapace. In reduced-web uloborids, reorientation of leg muscles and changes in endosternite shape facilitate effective paraxial leg movement and are reflected externally by the carapace differences noted above (Opell, '84a). These changes also contribute to differences in the forces exerted by orb-web and reduced-web uloborids (Opell, '85, '87). In *Miagrammopes*, dorsal shifts of the chelicerae bring their muscle insertions into the region of the carapace where the anterior eyes of orb-weavers are found, a change that probably explains eye loss in this genus. The prominent posterior lateral eye tubercles of this genus also contribute to leg reorientation by providing a strengthened apodeme where first leg muscles insert. Additionally, these tubercles laterally displace the eyes' retinal hemispheres and, thereby, provide space for more direct anterior passage of the first leg muscles (Opell, '84a).

The large relative size of the posterior eyes and the presence of prominent posterior lateral eye tubercles in *Hyptiotes* and *Miagrammopes* (Fig. 4) suggest that, in the face of these cephalothoracic changes, concomitant

selection favored ocular changes that would conserve the visual surveillance of reduced-web uloborids despite the reduction and loss of their anterior eyes. A comparison of the visual fields of the orb-weaver *Octonoba octonaria* and an undescribed *Miagrammopes* species (Opell and Cushing, '86) supports this hypothesis. Despite the loss of its anterior four eyes, this *Miagrammopes* species lost little of its total visual coverage. Consequently, the potential to visually detect predators is not sacrificed for carapace modifications that permit the spider to more effectively monitor and operate its reduced web.

The purpose of this study is to analyze the visual fields of additional uloborids in order to more thoroughly investigate the consequences of carapace changes. For this, we selected two additional orb-weaving uloborids: *Waitkera waitkerensis* (Chamberlain), one of the most primitive living uloborids (Opell, '79), and *Uloborus glomus* (Walckenaer), a species more closely related to the reduced-web uloborids than is *Octonoba octonaria* (Opell, '79). We also studied the triangle-web uloborid, *Hyptiotes cavatus* (Hentz), and the "single-line-web" species *Miagrammopes animotus* Chickering. We chose the latter species because it has a less highly modified carapace than previously studied Costa Rican species. Thus, this study not only compares the visual fields of orb-weavers, triangle-weavers, and single-line-weavers, but also permits analysis of the visual consequences of subsequent carapace changes within the genus *Miagrammopes*.

Spiders have simple eyes, each consisting of a single lens and a multicellular retinal hemisphere (Fig. 1). In most eyes, the lens makes available a greater visual field than the retina can capture (Fig. 3). The physical (optical) axis of a lens does not always bisect its retinal hemisphere and, consequently, often does not correspond with a line bisecting the eye's visual angle (here termed its visual axis). For example, in many eyes (Fig. 3) the retinal hemisphere extends further dorsal than ventral to the eye's (lens') physical axis, causing the eye's visual axis to be situated ventral to its physical axis. Thus, an eye's visual field can be enlarged by retinal expansion and reoriented both by shifts in the lens' position and the retinal hemisphere's position relative to the lens. The techniques we employed permitted us to evaluate these ocular changes as well as their consequences for a spider's patterns of visual overlap and surveillance.

MATERIALS AND METHODS

Specimen fixation and sectioning

Mature females were used in all phases of this study. *Waikera waikereensis* were collected in Waiorangomai Valley, Te Aroha, New Zealand (by David Court); *Uloborus glosus* in Blacksburg, Virginia; *Hyptiotes cavatus* near Newport, Virginia; and *Miagrammopes animotus* near El Verde, Puerto Rico. Specimens were relaxed with carbon dioxide, fixed at 20–26°C for 12–18 hours in 3% formaldehyde/3% glutaraldehyde buffered in 0.1 M sodium cacodylate buffer (pH 7.3), and rinsed and stored in 0.1 M sodium cacodylate buffer. Those used for histological study were dehydrated through a graded series of acetone and embedded in Spurr's

epoxy resin. We used a Sorvall JB-4 microtome to make 1 μm -thick cross and sagittal sections and stained these with 1% toluidine blue in 1% borate buffer prior to examining and photographing them.

Focal length

To determine the optical properties of each eye, we used both intact lenses and cross and longitudinal sections of the ocular region and employed modifications of methods described by Meyer-Arendt ('72), Homann ('50, '71), and Land ('69). Table 1 lists the formulas used to compute these values and Table 2 the data used in their computation. Focal length was measured from an eye suspended with its cornea in air from a hanging drop of saline,

TABLE 1. Formulas used in determining optical properties of eyes¹

Focal length (F):

$$F = \frac{i}{o} u$$

i = image length;
o = object length;
u = object and eye separation

Refractive index (n):

$$\frac{1}{n} = (n-1) \left[\frac{1}{r_1} + \frac{1}{r_2} - \frac{d(n-1)}{nr_1 r_2} \right]$$

F = focal length;
n = refractive index;
r₁ = radius of outer curvature;
r₂ = radius of inner curvature;
d = lens thickness

Power of lens surface (P):

$$\text{Front: } P_1 = \frac{\Delta n}{r_1}$$

Δn = difference in refractive index of front lens
and air or of rear lens and body fluids;

$$\text{Rear: } P_2 = \frac{\Delta n}{r_2}$$

r₁ = radius of outer curvature;
r₂ = radius of inner curvature

Equivalent power (P_E):

$$P_E = P_1 + P_2 - \frac{d}{n} P_1 P_2$$

P₁ = front surface power;
P₂ = rear surface power;
d = lens thickness;
n = refractive index

Principal planes (VH):

$$\text{Front: } V_1 H_1 = \frac{d}{n} \times \frac{P_2}{P_E}$$

d = lens thickness;
n = refractive index;
P₁ = power of front lens surface;
P₂ = power of rear lens surface
P_E = equivalent power

$$\text{Back: } V_2 H_2 = \frac{d}{n} \times \frac{P_1}{P_E}$$

Nodal points (N):

Determined by plotting

N₁ = front nodal point;
N₂ = rear nodal point

f-number:

$$\text{f-number} = F/D$$

f = focal length;
D = pigment ring diameter

¹All measurements except refractive indexes are in micrometers.

TABLE 2. Mean eye parameters (number/standard deviation)¹

Species	Eye	Lens thickness	Front radius of curvature	Rear radius of curvature	Refractive index	Focal length	Pigment ring diameter	f-number
<i>Waitkera waitkerensis</i>	AME	77.63 (2/11.3)	57.07 (2/2.8)	37.31 (2/6.3)	1.33 (2/0.05)	88.49 (6/7.02)	76.29 (2/10.3)	1.17 (2/0.16)
	ALE	54.00 (1/—)	45.00 (1/—)	34.00 (1/—)	1.28 (1/—)	80.45 (5/15.04)	66.50 (1/—)	1.21 (1/—)
	PME	92.96 (1/—)	66.40 (1/—)	43.16 (1/—)	1.29 (1/—)	111.05 (6/9.86)	87.98 (1/—)	1.26 (1/—)
	PLE	81.28 (1/—)	69.12 (1/—)	46.72 (1/—)	1.33 (1/—)	101.97 (6/10.05)	80.00 (1/—)	1.27 (1/—)
<i>Uloborus glomosus</i>	AME	77.23 (2/3.15)	59.52 (2/1.08)	36.93 (2/0.81)	1.41 (2/0.002)	73.08 (7/11.09)	78.48	0.93 (2/0.02)
	ALE	46.34 (3/2.79)	37.30 (3/1.23)	26.32 (3/0.84)	1.39 (3/0.01)	49.82 (7/2.89)	49.41	1.01 (3/0.04)
	PME	56.44 (3/6.64)	48.88 (3/2.53)	35.12 (3/1.27)	1.41 (3/0.02)	61.37 (7/4.16)	58.51	1.05 (3/0.01)
	PLE	51.58 (2/2.01)	47.67 (2/4.54)	40.74 (2/3.65)	1.40 (2/0.001)	65.24 (7/7.35)	54.29	1.20 (2/0.08)
<i>Hyptiotes cavatus</i>	AME	48.83 (2/1.65)	40.53 (2/0.04)	39.31 (2/6.79)	1.49 (2/0.03)	51.06 (6/3.84)	57.92 (2/4.13)	0.88 (2/0.06)
	ALE	22.43 (2/4.69)	20.88 (2/8.74)	13.23 (2/4.16)	1.25 (2/0.09)	38.01 (6/7.24)	24.00 (2/9.00)	1.70 (2/0.64)
	PME	83.10 (3/14.48)	61.10 (3/9.26)	44.12 (3/7.19)	1.46 (3/0.09)	74.59 (6/7.20)	79.42 (3/10.48)	0.95 (3/0.13)
	PLE	74.41 (3/3.48)	58.16 (3/5.13)	37.71 (3/3.18)	1.44 (3/0.04)	68.46 (5/5.36)	78.14 (3/5.00)	0.88 (3/0.06)
<i>Miagrammopes animotus</i>	PME	82.12 (2/1.82)	67.63 (2/2.64)	43.82 (2/0.04)	1.38 (2/0.01)	86.91 (7/5.87)	85.55 (2/1.07)	1.02 (2/0.01)
	PLE	79.41 (2/1.57)	67.08 (2/1.52)	49.24 (2/5.23)	1.37 (2/0.02)	94.85 (12/25.7)	83.93 (2/0.78)	1.13 (2/0.01)

¹All measurements are in micrometers.

as described by Blest and Land ('77). This drop hung from the underside of a No. 1 cover glass that was sealed with a thin film of silicone vacuum grease to the rim of the 3 mm-high glass cylinder of a microscope culture slide. A piece of moist cotton placed along the cylinder's inside edge retarded evaporation of the saline. We placed this preparation on the stage of a compound microscope whose condenser apparatus had been removed. This permitted us to focus the 20 or 40 power objective on the lens' rear surface in order to measure the image size of a 2 cm-long scale bar placed atop the microscope's light source. When the image was in sharp focus, the lens-to-object (scale) distance was measured with a caliper mounted on the microscope stage. We then used these measurements to compute focal length of the lens. All eyes used for this purpose were removed from fixed specimens that had been stored in buffer. However, an earlier comparison of the measured focal lengths of fixed and fresh *Uloborus glomus* eyes showed that the effect of fixation was within the accuracy limits of this measuring technique (Opell and Cushing, '86).

Size of visual angle

Measured focal length was used in conjunction with lens measurements taken from eye cross sections (Fig. 1) to compute the refrac-

tive index of each lens. This value permitted us to compute the position of each lens' front and rear principal planes (Table 1). We then reconstructed each lens and its retinal hemisphere using mean measured values (Table 2) and to this drawing added the front and rear principal planes. Using measured focal length, we next plotted the lens' front and rear nodal points. To determine the visual angle of each eye, we measured the angle formed by lines drawn from the most peripheral retinal cells to the rear nodal point. An inverted projection of this angle from the front nodal point yielded the eye's visual cone (Fig. 3). As the lens' physical axis had been established when the eye was reconstructed, the relationship of the visual axis to this axis could be measured.

Orientation of visual angle

In order to determine the anatomical orientation of these visual angles for purposes of evaluating their shifts (Tables 3 and 4) and using them to reconstruct visual surveillance (Fig. 4), a method was needed to accurately transpose visual angles from reconstructed eyes to eyes as seen in cross and longitudinal sections of a spider's complete carapace. To accomplish this, we drew a line through the pigment cell clusters at each edge of a reconstructed eye and measured the angle this formed with the eye's physical axis. As these

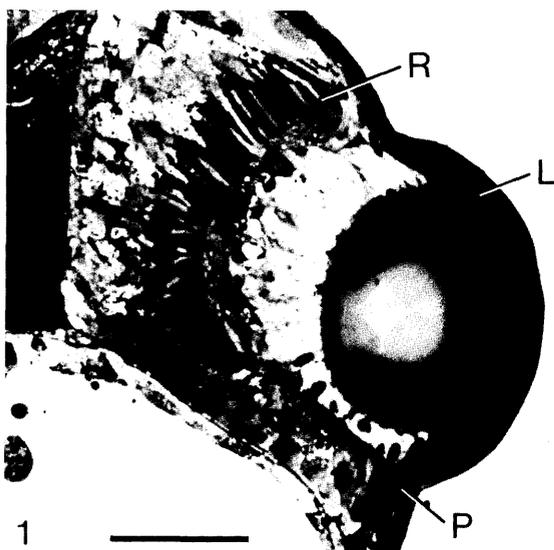


Fig. 1. Cross section of the posterior lateral eye of *Miagrammopes animotus*. L, lens; P, pigment ring; R, retinal hemisphere. Scale bar 50 μ m.



Fig. 2. Cross section of the anterior lateral eye of *Hyptiotes cavatus*, demonstrating the absence of retinal cells. L, lens. Scale bar, 50 μ m.

TABLE 3. Mean visual angles and their orientation relative to their physical angles and to the spider's frontal and sagittal planes.¹

Species	Eye	Total visual angle	Visual axis from physical axis	Visual axis from frontal plane (0 = lateral)	Visual axis from sagittal plane (0 = lateral)
<i>Waitkera waitkerensis</i>	AME	48	1 v	3 d	60 a
	ALE	29	22 v	20 v	40 a
	PME	59	3 v	62 d	0
	PLE	37	9 v	25 d	0
<i>Uloborus glomus</i>	AME	57 (+9)	12 v (11 v)	3 d (0)	66 a (6 a)
	ALE	67 (+38)	52 v (30 v)	51 v (31 v)	41 a (1 a)
	PME	71 (+12)	5 v (2 v)	60 d (2 v)	0 (0)
	PLE	47 (+10)	29 v (20 v)	9 d (16 v)	0 (0)
<i>Hyptiotes cavatus</i>	AME	70 (+22)	15 v (14 v)	41 d (38 d)	61 a (1 a)
	PME	107 (+48)	1 v (2 d)	41 d (21 v)	0 (0)
	PLE	94 (+57)	20 v (11 v)	2 d (23 v)	0 (0)
<i>Miagrammopes animotus</i>	PME	83 (+24)	14 v (11 v)	52 d (10 v)	0 (0)
	PLE	70 (+33)	26 v (17 v)	16 v (41 v)	0 (0)

¹All values are in degrees; d = dorsal, v = ventral, a = anterior, p = posterior. Values in parentheses are differences from *Waitkera waitkerensis*.

TABLE 4. Positions of the margins of visual angles and visual overlap of eyes.¹

Species	Eye	Margin of visual angle from frontal plane (0 = lateral)		Margin of visual angle from sagittal plane (0 = lateral)		Eye overlap
		Dorsal margin	Ventral margin	Anterior margin	Posterior margin	
<i>Waitkera waitkerensis</i>	AME	27 d	20 v	85 a	38 a	—
	ALE	5 v	34 v	54 a	26 a	—
	PME	92 d	33 d	30 a	30 p	4
	PLE	44 d	7 d	18 a	18 p	3
<i>Uloborus glomus</i>	AME	31 d (4 d)	26 v (6v)	96 a (11 a)	39 a (1 a)	2
	ALE	18 v (13 v)	85 v (51 v)	76 a (22 a)	9 a (17 p)	1, 4
	PME	95 d (3 d)	24 d (9 v)	35 a (5 a)	35 p (5 p)	4
	PLE	31 d (13 v)	15 v (22 v)	24 a (6 a)	24 p (6p)	2, 3
<i>Hyptiotes cavatus</i>	AME	75 d (48 d)	5 d (25 d)	94 a (9 a)	24 a (14 p)	3, 4
	PME	94 d (2 d)	13v (46 v)	53 a (23 a)	53 p (23 p)	1, 4
	PLE	49 d (5 d)	45 v (52 v)	47 a (29 a)	47 p (29 p)	1, 3
<i>Miagrammopes animotus</i>	PME	93 d (1 d)	10 d (23 v)	41 a (11 a)	41 p (11 p)	—
	PLE	19 d (25 v)	51 v (58 v)	35 a (17 a)	35 p (17 p)	—

¹All values are in degrees; d = dorsal, v = ventral, a = anterior, p = posterior, 1 = AME, 2 = ALE, 3 = PME, 4 = PLE. Values in parentheses are differences from *Waitkera waitkerensis*.

pigment cells are easily seen in sections (Fig. 1), a line can be drawn through them on tracings of enlarged carapace cross sections. From this reference line, we determined the orientation of each eye's physical axis and then drew the angles of its visual field relative to this axis. We refer to the line that bisects an eye's visual angle as its visual axis and use this as a reference for reporting the eye's visual orientation relative to the spider's carapace (Table 3).

A complete description of an eye's visual orientation requires the position of its visual axis to be determined relative to both its sagittal and frontal planes. To determine the former, we positioned preserved specimens under a dissecting microscope equipped with a camera lucida and drew a line corresponding to each specimen's midline. A second line was drawn through the points where each lens merged with the carapace. In the case of posterior median eyes, this second line was drawn through the widest part of the eye's ellipse. The center of each lens was marked and a reference line drawn through this point perpendicular to the line through the eye. The angle formed by this reference line and the spider's midline described the eye's sagittal orientation.

For those eyes, such as the posterior median eyes (PME) and posterior lateral eyes (PLE) that are directed laterally (sagittal orientation of 50–90°), frontal angles (Table 3) were determined from cross sections; for those such as the anterior median eyes (AME) and anterior lateral eyes (ALE) that are directed anteriorly (sagittal orientation 24–30°), frontal angles were determined from sagittal sections. In each case, the visual axis was extended to a line representing the frontal plane, and the angle (dorsal or ventral) it formed with this plane was measured.

In order to document the consequences of changes in eye angles and orientations, it was useful to know how closely the dorsal and ventral extremes of each eye's visual angle approached a sagittal plane. We determined this by drawing a sagittal line through the front nodal point of each eye and measuring the angles separating the dorsal and ventral extremes of an eye's visual angle from this line. These measurements are presented in Table 4, along with their difference from the eyes of *Waitkera*.

Overlap of visual fields

We determined the visual overlap of each eye by positioning visual angle cut-outs on

carapace models according to the frontal and sagittal orientation presented in Table 3. Rotating these planar cut-outs on their axes permitted us to evaluate the intersections reported in Table 4.

To produce accurate frontal diagrams of each species (Fig. 4), we superimposed tracings made from projected photographic slides of cephalothorax cross sections through the center of each eye. To these reconstructions we added the visual angle of each eye (Fig. 3). We constructed the dorsal views shown in Figure 4 using the sagittal and frontal angular measurements described above and presented in Table 3. Visual cones so described were added to enlarged camera lucida drawings of preserved specimens. Figure 4 describes in detail the convention used to depict visual angles in these composite views.

Uniformity of refractive index

The methods used in this study require that at least two specimens be used to evaluate each eye's visual field; one to determine the eye's focal length and one to determine its physical properties and orientation. To minimize errors that might result from this dichotomy, we used the means of measurements taken from both eyes of several specimens. The optical formulas used in this and most previous studies of spider vision (Honnann, '50, '71; Land, '69; Opell and Cushing, '86) assume that each lens has a uniform refractive index. However, as a lens is composed of concentric layers (Fig. 1), the refractive indexes of these layers may differ. Land ('79) found that the lens layers of *Limulus* ommatidia have different refractive indexes and that this alters their optical properties. To evaluate refractive index uniformity of uloborid lenses, we studied 6 μm -thick cross sections of uloborid specimens that were fixed as described above, stored in buffer, frozen, and sectioned with a cryostat. When these sections are covered by aqueous buffer and examined under a compound microscope equipped with differential interference contrast optics, lens layers with different refractive indexes have different colors (Land, '79). Due to section damage, we were unable to study the ALE of *W. waitkerensis*. However, at 500 power, we found that the remaining eyes of this species, as well as those of the other three species used in this study, had lenses of uniform color. From this we conclude that the refractive index of each lens is, likewise, uniform and that the assump-

tions of the optical formulas we employed are satisfied.

RESULTS

Table 2 lists primary data obtained from intact lenses and eye cross sections. Unlike other values in this table, f-number does not influence visual angle. Instead, it is an index of an eye's ability to admit light: eyes with lower values admit more light to the retina. For this reason, the effect of this value is, unlike visual angle, absolute rather than additive. When the f-number of an eye is altered by the square root of 2, its light-gathering properties show a two-fold change. Therefore, when two eyes have f-numbers that differ by a factor of 0.7071, the one with the larger f-number will admit only half the light of the other.

An eye's sensitivity is determined both by the ability of its lens to admit light and by the sensitivity of its retinal cells that receive this light. Neurophysiological techniques are required to measure the actual sensitivity of an eye, although f-number is an index of potential sensitivity that can be determined from data gathered in this study. In *Waitkera*, the AME have the smallest f-number. In *Miagrammopes*, the PME have the smallest f-number and admit 1.6 times more light than those of *Waitkera*. The AME of *Uloborus* have the smallest f-numbers and admit 1.8 times more light than the AME of *Waitkera*. The AME and PLE of *Hyptiotes* have the lowest f-numbers of the spiders studied, each admitting 1.9 times more light than the AME of *Waitkera*. When the mean f-numbers of these species are compared, the same relationship holds: *Waitkera* has a mean value of 1.23, *Miagrammopes*, a mean value of 1.08 (1.6 increase in mean light admittance); *Uloborus*, a mean value of 1.05 (1.7 increase in mean light admittance); *Hyptiotes*, a mean value of 0.90 (1.9 increase in mean light admittance).

As Figure 2 shows, the ALE of *Hyptiotes* have lost their retinal cells and are, therefore, functionless. In this specimen the ALE areas showed evidence of a hemispherical organization with some peripheral pigment granules. In another, even these vestiges were not present, and only the eyes' small lenses were visible.

An eye's visual angle is increased by changes in the physical properties of its lens and by perimetric expansion of its retinal hemisphere. Increases in lens thickness, front and/or rear radius of curvature, and refrac-

tive index increase an eye's visual angle. Visual angle is also increased by a decrease in focal length, although this is a secondary value determined by those physical properties listed above. A comparison of visual angles (Table 3) shows that the PME of each species has the largest angle and that when species are ranked in order of increasing maximum (PME) angle (*Waitkera*, *Uloborus*, *Miagrammopes*, and *Hyptiotes*) the angles of each of the other eyes are also arranged in increasing order. The largest angular increases in this sequence are a 131% increase in the ALE of *Uloborus* and a 154% increase in the PLE of *Hyptiotes*.

The orientation of an eye's visual angle can be altered by shifts in both its visual axis relative to its physical axis and its physical axis relative to its carapace. The former result from asymmetrical changes in the retinal hemisphere, as would occur when an eye's visual axis is ventrally shifted by the addition of more retinal cells dorsal to rather than ventral to its physical axis (cf. PLE of *Waitkera* and *Uloborus*, Fig. 3). Shifts in the orientation of an eye's physical axis occur with such changes as the development of eye tubercles (cf. PLE of *Waitkera* and *Miagrammopes*, Fig. 3).

As Figure 2 and Table 3 demonstrate, relative to *Waitkera*, all eyes except the PME of *Hyptiotes* (whose 2° dorsal shift is probably within the limits of resolution of our techniques) show a ventral shift in the position of their visual axes relative to their physical axes. In many eyes, this trend is also reflected in the orientation of the visual axis relative to the frontal plane (Table 3). Only the AME of *Hyptiotes* shows a notable dorsal shift. The AME and PME of *Uloborus* and PLE of *Hyptiotes* show a negligible change of 3° or less; all other eyes are directed 16–41° more ventrally than are those of *Waitkera*.

Such ventral shifts in eye orientation do not necessarily mean that dorsal visual coverage is lost. This trend is at least partly compensated for by an increase in visual angle. The net result is either no reduction in the dorsal extent of an eye's visual angle or a loss that is much less than the ventral gain (Table 4, Fig. 3). For example, relative to *Waitkera*, the visual axis of the ALE of *Uloborus* is ventrally shifted by 31° (Table 3), but its dorsal margin is ventrally shifted by only 13° (Table 4). Likewise, in *Hyptiotes*, the PLE visual axis is ventrally shifted by 23°, but its dorsal visual margin is dorsally shifted by 5°. In both species, these relatively

small changes in each eye's dorsal vision are accompanied by an impressive 51° ventral shift in their visual axis (Table 4, Fig. 3). Similar trends are seen in the PLE of *Uloborus*, the PME of *Hyptiotes*, and the PME and PLE of *Miagrammopes*. The AME and PME of *Uloborus* show changes in their visual margins of less than 10° . The AME of *Hyptiotes* is the only eye where concerted change favors a major increase in the dorsal vision (52°) at a significant loss (25°) in ventral coverage. Even here, the ventral loss is only half as great as the dorsal gain.

Thus far, attention has been devoted to dorsal and ventral changes in visual coverage. As Tables 3 and 4 show, there are also sagittal changes in the eyes' axes and visual margins. These changes occur only in the anterior eyes, whose visual axes shift $1-6^\circ$ anteriorly. Coupled with increased visual angles, these small changes expand the front and rear visual margins of most eyes by $5-29^\circ$. The only exception to this is found in the AME of *Uloborus*, where a 6° anterior shift in visual axis eliminates the posterior gains that result from a 9° increase in total visual angle.

When these spiders' visual fields are reconstructed (Fig. 4), their visual surveillance remains surprisingly similar. Although *Hyptiotes* has lost the function of its ALE, its visual coverage differs little from that of *Waitkera* and *Uloborus*. *Miagrammopes*, with only four eyes, retains its dorsal-ventral coverage and loses only its direct anterior visual coverage. Figure 4 also presents a picture of the changing roles of the eyes and changing patterns of visual overlap. In *Waitkera* and *Uloborus*, the AME is responsible for most of the spider's anterior vision, the ALE for most of its ventral vision, the PLE for most of its lateral vision, and the PME for most of its dorsal vision. In *Hyptiotes* visual fields of the remaining eyes shift to compensate for loss of the ALE and the anterior and ventral vision they provide. The AME provide anterior visual coverage and also some median dorsal coverage. The PME provide both dorsal and lateral coverage, and the PLE both lateral and ventral vision. In *Miagrammopes*, the PME are responsible for the dorsal and lateral vision provided by the posterior eye row of orb-weavers and the PLE for some of the lateral and ventral vision of an orb-weaver's anterior row.

The relatively narrow visual fields of *Waitkera* eyes result in each eye playing a distinct visual role and only the PME and PLE having overlapping visual fields (Fig. 4 and Ta-

ble 4). In *Uloborus*, the visual field of each eye overlaps that of at least one other eye, and the ALE and PLE each overlap the fields of two other eyes. This double overlap is also found in the three functional eyes of *Hyptiotes*. Only in *Miagrammopes* is there no visual overlap.

DISCUSSION

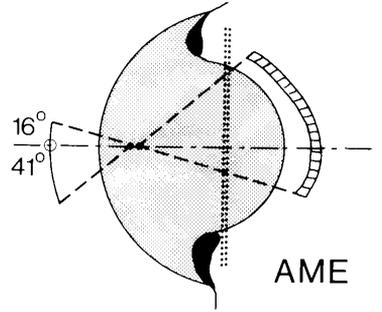
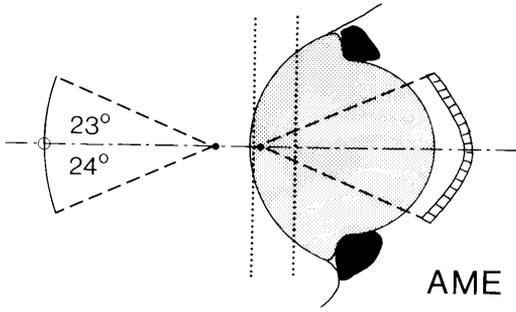
This study shows that significant changes have occurred in the eyes and visual fields of both orb-web and reduced-web uloborids. Although the primitive orb-weaver *Waitkera waitkerensis* has complete visual surveillance (Fig. 4), none of its eyes' visual fields overlap. In contrast, the advanced orb-weavers, *Uloborus glomosus* and *Octonoba octonaria* (Opell and Cushing, '86), both show extensive visual overlap that increases their potential to evaluate distance and detect movement. These changes result from an expansion and ventral shift of each eye's visual field. This is accomplished principally by perimetric expansion of the retinal hemisphere, with the dorsal region being more greatly expanded than the ventral.

The eye loss and carapace modification that characterize *Hyptiotes* and *Miagrammopes* are accompanied by positional shifts and structural changes of the remaining eyes. These changes act in consort to conserve a surprising amount of a spider's visual surveillance. The visual fields of most eyes show even greater expansion and ventral shifts than those of advanced orb-weavers. Only the AME of *Hyptiotes* do not follow this trend. Instead, their expanded visual fields have shifted dorsally to provide more anterior dorsal visual coverage and greater visual overlap than is present in *Miagrammopes*. The prominent posterior lateral eye tubercles of both *Hyptiotes* and *Miagrammopes* play a crucial role in the extreme ventral shifts of the PLE. When coupled with their expanded visual fields, these shifts give the PLE lateral and ventral coverage similar to that of the entire anterior eye row of an orb-weaver (Fig. 4). Changes in the PME give them dorsal and lateral visual coverage similar to that of the posterior row of an orb-weaver. In *M. animotus*, this compensation occurs at the expense of visual overlap, although subsequent carapace and ocular changes in *M. sp.* (Opell and Cushing, '86) restore visual overlap of the PME.

Using techniques similar to those de-

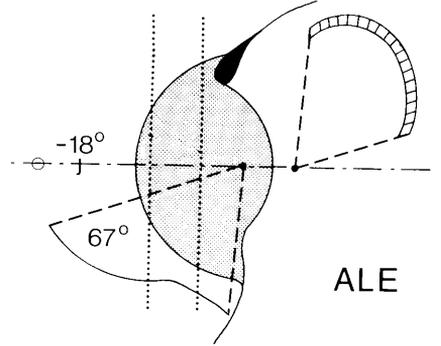
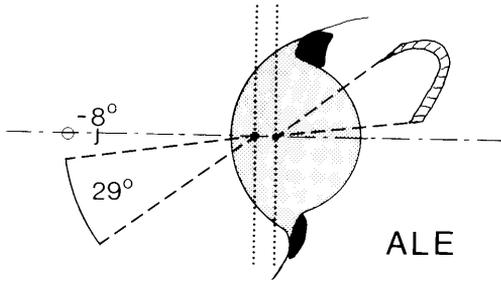
WAITKERA

ULOBORUS



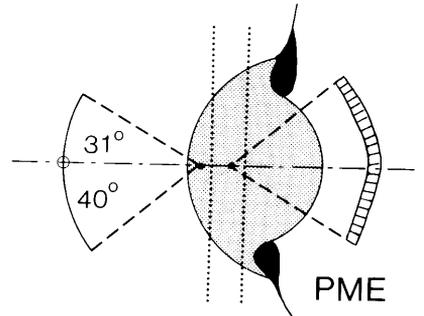
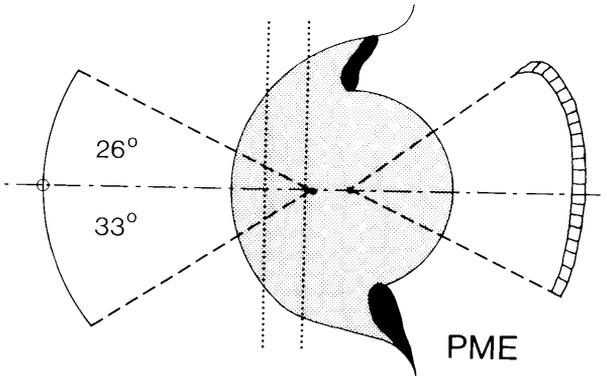
AME

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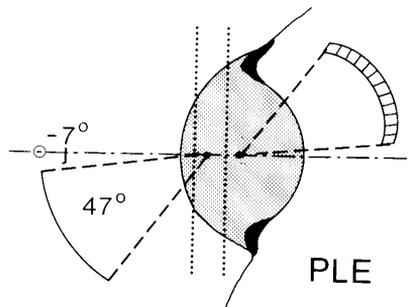
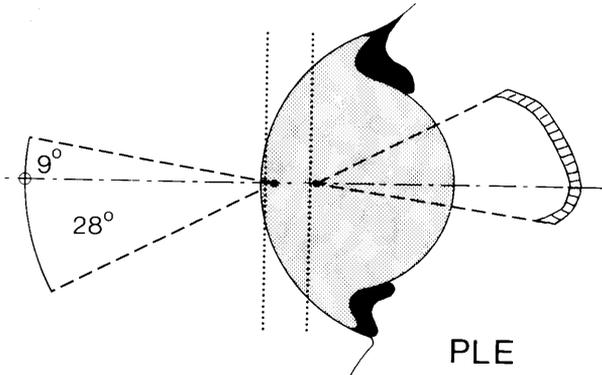
ALE

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PME

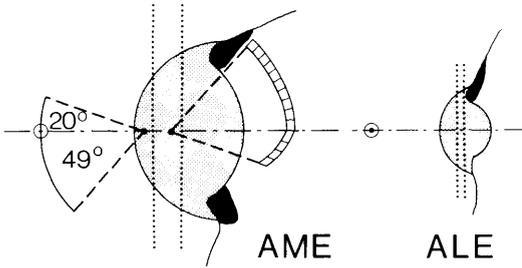
PME



PLE

PLE

HYPTIOTES



MIAGRAMMOPES

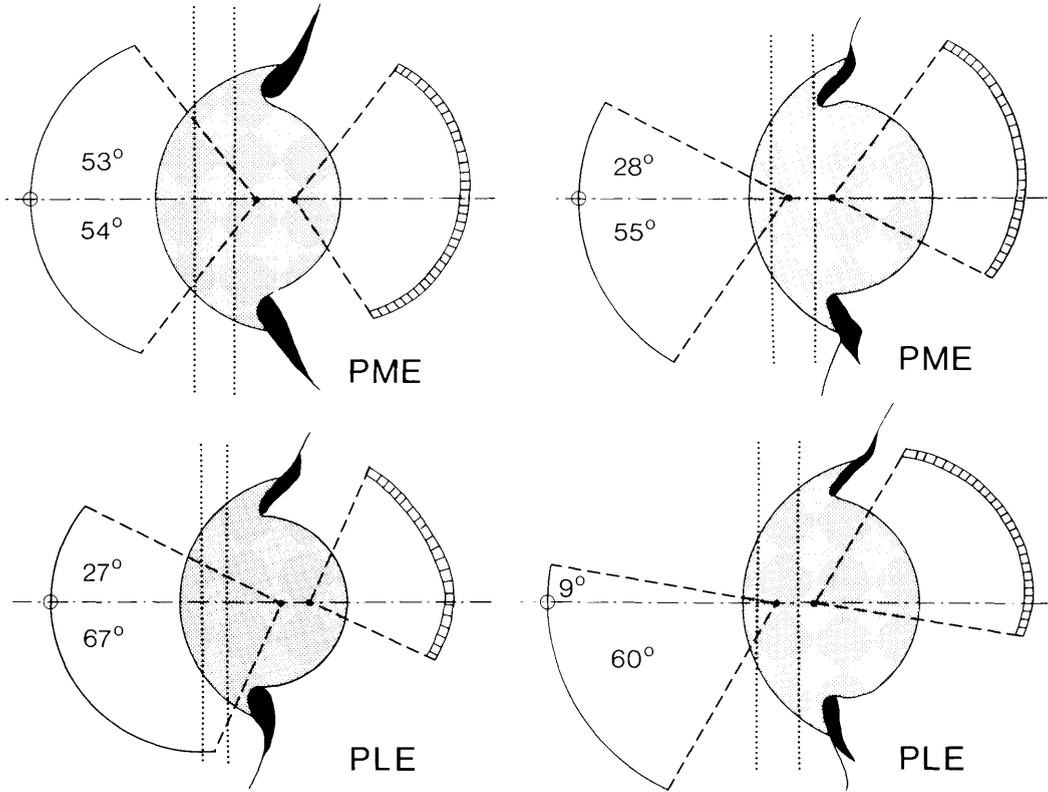


Fig. 3. Reconstruction of the eyes of *Waitkera waitkensis*, *Uloborus glomosus*, *Hyptiotes cavatus*, and *Miagrammopes animotus*, showing the retinal hemisphere to the right of each eye and the visual angle to the left. An alternating short and long dashed line represents an eye's physical axis, the small open circles to the left of

the eye, its focal length; the two vertical dotted lines, an eye's front and rear principal planes; and the two solid dots, the eye's front and rear nodal points. AME, anterior median eye; ALE, anterior lateral eye; PME, posterior median eye; PLE, posterior lateral eye.

scribed above, Opell and Cushing ('86) compared the visual fields of the orb-weaver *Octonoba octonaria* (Muma) and an undescribed Costa Rican *Miagrammopes* species.

Their findings show that all eyes of *Octonoba* except the ALE have greater angles than their *Uloborus* homologs. Although the visual axes of the PLE of *Octonoba* are more

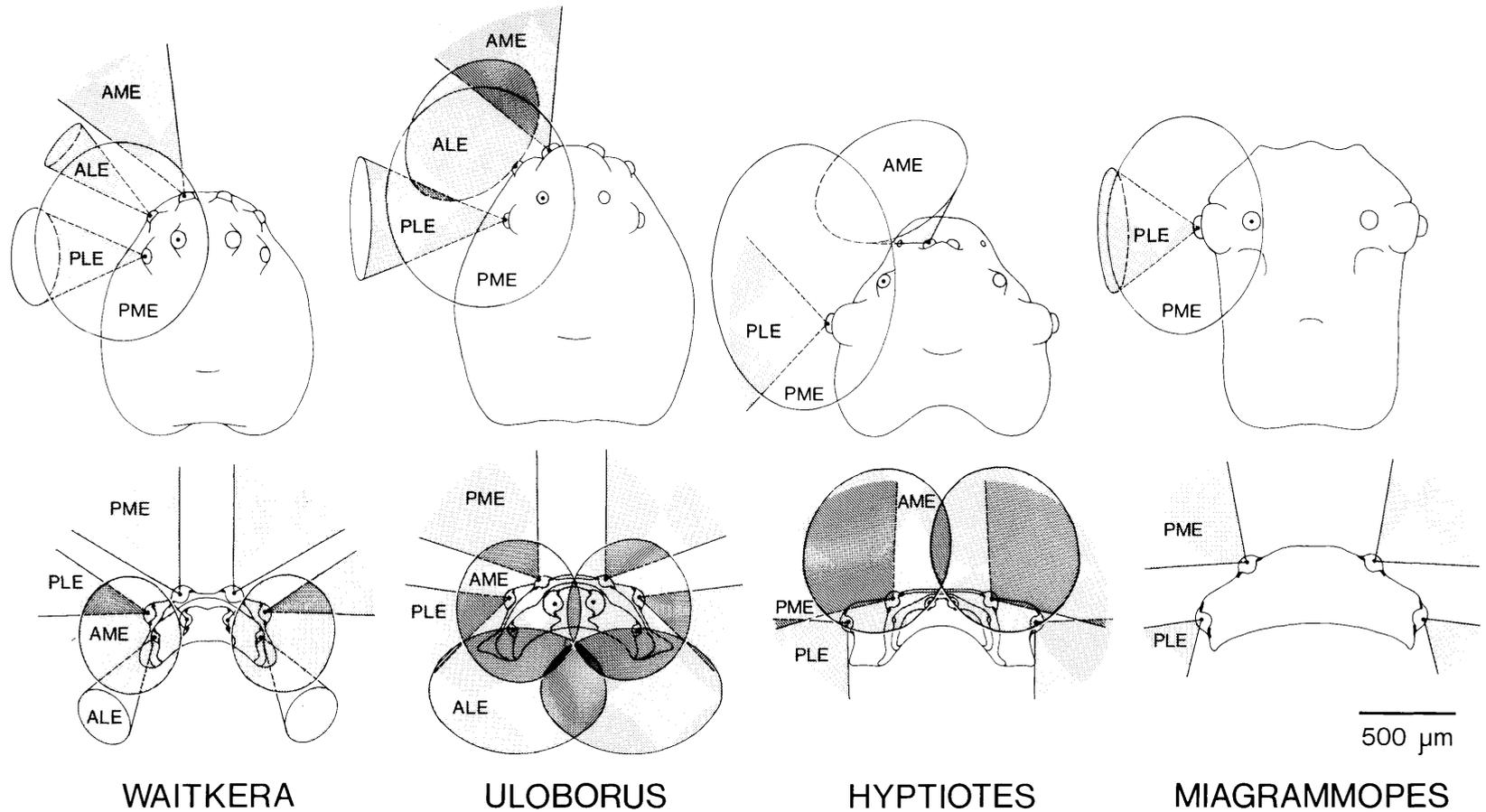


Fig. 4. Dorsal (top) and frontal (bottom) views of the reconstructed visual fields of *Waitkera waitkerensis*, *Uloborus glomus*, *Hyptiotes cavatus*, and *Miagrammopes animotus*. In dorsal view, the openings of visual cones that are directed upward and downward are represented as ellipses. A dashed line denotes the ventral rim of an ellipse, and the width of its opening is directly propor-

tional to its dorsal or ventral orientation. Because the PME are directed dorsally, their visual fields are shown as circles. In frontal views, a similar convention is followed. Eyes that are the most anteriorly directed have ellipses that most closely approach circles. AME, anterior median eye; ALE, anterior lateral eye; PME, posterior median eye; PLE, posterior lateral eye.

ventrally directed than those of *Uloborus*, the visual axes of other eyes are more similar to those of *Waitkera*. These differences result in the posterior eyes of *Octonoba* having visual coverages similar to those of *Uloborus* and the AME having more dorsally directed visual fields than either *Uloborus* or *Waitkera*. A notable consequence of the three-fold increase in visual angle of the AME of *Octonoba* is the overlap of their visual fields with those of all other eyes.

The *Miagrammopes* species studied by Opell and Cushing ('86) has a more highly derived cephalothorax than *M. animotus* (Opell, '84b), two important differences being the former species' more widely spaced PME and more prominent posterior lateral eye tubercles. Compared with *M. animotus*, the former species has PME visual angles that are 14° greater, PLE angles that are 40° greater, PME whose visual coverage extends 12° more dorsally, and PLE whose visual coverage extends 12° more ventrally. These differences result in the Costa Rican species having slightly more anterior and ventral visual coverage than *M. animotus* and, unlike *M. animotus*, PME visual fields that overlap. Therefore, it appears that carapace modifications within the genus *Miagrammopes* have enhanced visual coverage.

The f-numbers of all uloborids studied are much less than those of visually hunting, diurnal jumping spiders, whose values range from 2.68 to 5.90 (Forster, '82; Land, '69). They more closely approximate those of the nocturnal, ogre-faced spider *Dinopis subrufus*, in which the large PME have an f-number of 0.58 (Blest and Land, '77) and are used to locate prey (Baum, '38; Roberts, '55; Robinson and Robinson, '71). Therefore, it seems probable that, like *Dinopis*, uloborid eyes are adapted to low-light conditions encountered in forests and at night. This study and that of Opell and Cushing ('86) show that within uloborids there is reduction of both mean and maximum f-number. Among the orb-weavers, *Waitkera* has the greatest values, *Uloborus* lower values, and *Octonoba* the lowest values. The eyes of *M. animotus* have greater f-numbers than those of a more derived Costa Rican species. The eyes of *Hyptiotes* have a mean f-number similar to that of this latter species.

There are two possible advantages for the maintenance of visual coverage in reduced-web uloborids: it may aid in prey capture, and it may aid in predator avoidance. Vision

plays an important role in the prey capture behavior of *Dinopis*, where it permits the spider to both detect a prey and determine its distance before throwing its web (Roberts, '55; Robinson and Robinson, '71). Although the role of vision in uloborids and other orb-weaving families is poorly studied, it is generally assumed to be of little importance for prey capture, as most of these spiders do not manipulate their webs in the manner of *Dinopis*. Even studies of bolas spiders that actively twirl a sticky droplet on the end of a thread (Eberhard, '77, '80), have not suggested that vision plays a major role in prey capture. It is possible that reduced web uloborids may detect approaching prey and either alter the tension of their webs or prepare to jerk them when a prey strikes. Although neither of us have seen clear evidence of this, we have not conducted the careful observations necessary to disprove this hypothesis. There is no evidence that reduced-web uloborids specialize on particular insects (Lubin, '86; Opell, unpublished observations), such that vision would be useful in allowing these spiders to selectively respond to prey.

In view of the cryptic appearance of reduced-web uloborids, the predator avoidance hypothesis seems more plausible. The short legs and rotund abdomen of *Hyptiotes* makes them resemble a bump on the twig from which they monitor their webs. The elongate legs and abdomen of *Miagrammopes* give them the appearance of thorns or broken twigs as they monitor their webs. The ability to visually detect movement would permit these spiders either to remain in or to assume a cryptic posture (and perhaps even disregard the vibrations of struggling prey caught in their webs) in the presence of a potential predator. This explanation is consistent with one hypothesized advantage of web reduction (Opell, '84b): that reduced webs are less conspicuous to visually hunting predators than are orb-webs.

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