

The visual system of the Australian wolf spider *Lycosa leuckartii* (Araneae: Lycosidae): visual acuity and the functional role of the eyes

Christofer J. Clemente¹, Kellie A. McMaster², Elizabeth Fox³, Lisa Meldrum⁴, Tom Stewart⁴ and Barbara York

Main⁴: ¹The Rowland Institute at Harvard, Harvard University, Cambridge, MA 02142, USA. E-mail: clemente@rowland.harvard.edu; ²Outback Ecology, 1/71 Troy Terrace Jollimont, Western Australia 6014, Australia; ³Ecologia Environment, 1025 Wellington Street, West Perth, Western Australia 6005, Australia; ⁴School of Animal Biology M092, University of Western Australia, 35 Stirling Highway, Crawley, Western Australia, 6009, Australia

Abstract. Ocular arrangement and visual acuity were examined in *Lycosa leuckartii* Thorell 1870 (Araneae: Lycosidae), using histological techniques. Major structural and functional features of the visual system, including external and internal ocular organizations, resolution, sensitivity, focal lengths and the field of view, were characterized for each eye. *Lycosa leuckartii* had a large developmental investment in a specialized visual system with high visual acuity. The field of view extended 360° and displayed the potential for good depth perception. Anterior eyes showed average focal lengths (AL eyes 230.88 µm, AM eyes 276.84 µm), while the posterior eyes far exceeded them (PL eyes 499.26 µm, PM eyes 675.35 µm). Resolution of the anterior eyes was comparable to records in the literature for other lycosids (inter-receptor angle AL eyes 2.45°, AM eyes 1.85°), while the resolution of the posterior eyes was higher (PL eyes 0.78°, PM eyes 0.67°). Sensitivity of the lens (*f*-numbers) was highest in the secondary eyes and was close to some of the highest reported for Araneae (*f*-numbers PM eyes 0.58), but when receptor diameters were included in estimates, S-numbers were similar or lower than closely related species (PL eyes 17.5 µm², PM eyes 17.6 µm²). There is a clear distinction in organization and function between the posterior and anterior eyes of *L. leuckartii*. The posterior eyes suit long-range predator and prey detection, while the anterior eyes are best for distance judgment and prey capture.

Keywords: Field of view, focal length, resolution, sensitivity

The modern arachnids are the only group of arthropods in which the eyes are camera-type, similar to our own, rather than compound eyes (Land 1985). Despite this, the structure and function of the visual system of spiders has been inadequately studied in many families of spiders when compared to chemo- and mechanoreception. This is likely based on the assumption that most spiders are nocturnal and vision may be of limited use (Foelix 1982). However, for some species, vision can be very important. Members from at least one family, the Salticidae, have been shown to hunt exclusively using vision (Jackson 1977), and members of five other families of spiders, Lycosidae, Pisauridae, Thomisidae, Oxyopidae and Deinopidae, show visually guided behaviors during locomotion, homing, prey capture, and courtship (Bristowe & Locket 1926; Kaston 1936; Whitcomb & Eason 1965; Robinson & Robinson 1971; Forster 1982; Uetz & Stratton 1982; Rovner 1996).

The visual acuity of a species is determined by characteristics of the eyes such as field of view, focal length, resolution, and sensitivity. The external placement and internal arrangement determine the field of view of each eye (Land 1985). The ancestral eye arrangement, as hypothesized by Homann (1971), consists of two transverse rows, each containing four eyes. The first row consists of the anterior median (AM) eyes in the middle and the anterior lateral (AL) eyes on the periphery. Similarly, the posterior eyes are grouped into posterior median (PM) eyes and posterior lateral (PL) eyes. The visual angle of the field of view for each eye can vary greatly, from relatively narrow pinpoint views of only 24° in the PL eyes of *Badumna insignis* Koch 1872 (Clemente et al. 2005) to 182° wide-angle views in the AM eyes of *Octonoba sinensis* Simon 1880 (Opell 1988). Forward-facing binocular

vision is a product of overlapping visual fields, and is necessary for good distance judgment.

The distance over which an eye can focus upon an object is determined by the focal length of its lens (Homann 1971). This ranges from 38 µm in the AL eyes of the uloborid *Hyptiotes cavatus* Hentz 1847 (Opell & Ware 1987), to 448 µm in the PM eyes of *Cupiennius salei* Keyserling 1877 (Land & Barth 1992), up to 1980 µm in the AM eyes of the jumping spider *Portia* (Williams & McIntyre 1980).

The ability of the eye to resolve detail depends on the fineness of the retinal mosaic, usually expressed as the inter-receptor angle. The finer this angle, the better the resolution of the eye. The finest inter-receptor angles reported in the literature are for members of Salticidae, the diurnal jumping spiders, for which the inter-receptor angle in the AM eyes can be less than 1°. The largest angle reported for hunting spiders is 7° in the AL eyes of a lycosid species (Homann 1931; Land 1969, 1985).

Sensitivity, or the ability to see in low light levels, is a combination of the physical properties of an optical system and the physiological sensitivity of photoreceptors. The physical ability of the lens to admit light is often expressed in the literature as an *f*-number, which decreases with increasing sensitivity (Opell & Ware 1987). This ranges from 2.68–5.90 in diurnally active jumping spiders (Land 1969; Foelix 1982) to 0.58 in the PM eyes of the wholly nocturnal ogre-faced spider *Deinopis subrufa*, Koch 1879 (Blest & Land 1977). However, a more complete estimate of sensitivity is given by an S-number (Land 1981), which is a product of the relative aperture of the eye, determining the light flux passing through to the retina, the cross sectional area of the receptor, and the proportion of light entering a receptor that is actually

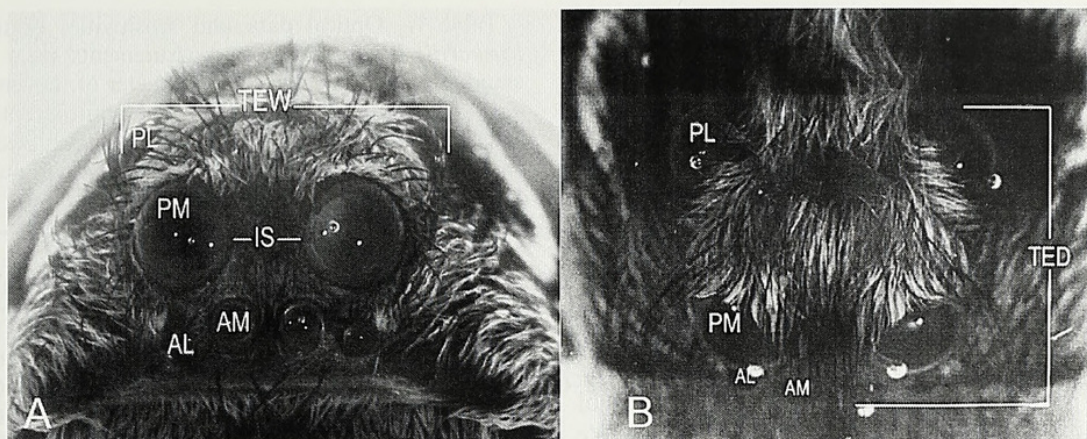


Figure 1.—External measurements taken on *L. leuckartii*. A = anterior view, B = dorsal view. AM, anterior median eyes; AL, anterior lateral eyes; PM, posterior median eyes; PL, posterior lateral eyes; TED, total eye depth; TEW, total eye width; IS, interocular space.

absorbed by it. This has the advantage of increasing as sensitivity increases, and can range from $0.09 \mu\text{m}^2$ in the AM eyes of jumping spiders to $387 \mu\text{m}^2$ in the PM eyes of *Deinopis* (Land 1985).

Both resolution and sensitivity vary in relation to the light conditions under which species operate (Opell & Ware 1987). While resolution improves as the ratio of receptor diameter to focal length decreases, sensitivity improves as the same ratio increases. Therefore, in the structure of the eyes, there is a trade-off between resolution and sensitivity. The only solution to the trade-off is to increase the total size of the eye; therefore, total eye size can be an indicator of the relative importance of vision.

Many studies link various eyes to their probable role or relative use in prey acquisition (Uehara et al. 1978; Forster 1979; Kovoor et al. 1992; Rovner 1993; Schmid 1998; Ortega-Escobar & Munoz-Cuevas 1999). There are two important components of prey acquisition. The first is prey detection, which incorporates initial detection of an item, specifically distinguishing the item as prey, predator or conspecific, and some orientation and movement toward the prey item. Therefore, prey detection requires long-distance detection and image clarity. The second component is prey capture. This may involve some identification of prey or non-prey items and orientation toward the prey, but mainly comprises judgment of distance for accurate lunging and striking (Lizotte & Rovner 1988).

Previous studies have demonstrated that the visual system of lycosid spiders is particularly complex. The eyes of lycosids have intricate visual fields (Homann 1931), high resolution and sensitivity (Lizotte & Rovner 1988; Kovoor et al. 1992; Rovner 1993; Ortega-Escobar & Munoz-Cuevas 1999) and the ability to detect polarized light (Kovoor et al. 1993; Dacke et al. 2001; Ortega-Escobar 2006). However, much of this work has been performed on relatively few species of lycosids, and it is unclear how much variation exists within the family. A recent molecular phylogeny of lycosids has suggested that the family consists of several clades (Murphy et al. 2006). While much of the work on vision in lycosids has focused on Palearctic and Nearctic species, the Australian species form a separate distinct clade. Almost no information is available on variation among clades. As a taxonomic aside, it is noted that

the generic position of *Lycosa leuckartii* is currently under review by V.W. Framenau with a proposed reallocation of the species pending. We present details of the visual acuity of *Lycosa leuckartii* and compare them to other lycosids and other families of spiders.

METHODS

External ocular organization.—Twenty individual *Lycosa leuckartii* were used to record external measurements. These included total eye width (TEW), total eye depth (TED) and eye diameters (Figs. 1A & B). We took measurements under a binocular dissecting microscope with an eyepiece micrometer. The values were then standardized for the animals' size by dividing each measurement by the carapace length. A repeated-measures ANOVA with one within-subject factor and no between-subject factors, and Student-Newman-Keuls post-hoc test, were used to determine significant differences in the relative eye diameters.

Internal ocular organization.—Two specimens of *L. leuckartii* were killed, using CO_2 gas, trimmed to a small block of tissue and fixed in Karnovsky's fixative for at least 72 h. We then washed and further trimmed down specimens in spider saline (scorpion saline excluding the CaCl_2 ; Zwicky 1968) and placed them in phosphate buffer prior to their being embedded in araldite/procure. Longitudinal and transverse (frontal plane) sections ($1 \mu\text{m}$ thin) were cut using an LKB ultratome and a diamond knife. We mounted sections on slides and stained them with toluidine blue. As well as determining the internal ocular organization, we also used these sections in measurements of resolution and sensitivity.

Focal length.—The focal length (f) of each lens was determined using the 'hanging drop' method described in Homann (1928) and Land (1985). The lens, along with a small proportion of the surrounding cuticle, was dissected from the head and stored in spider saline. After being cleared of excess tissue in warm, dilute, sodium hydroxide, the lens was suspended in a drop of spider saline from the underside of a cover slip. Using a microscope, we then viewed the image through the lens, targeting an object of known size (o). The distance between the slide and the object was then measured using calipers (u). The size of the image (i) was ascertained, using calibrated digital images, and the focal length was

calculated, using the formula (1) described by Opell & Ware (1987):

$$f = (i/o) (u) \quad (1)$$

For each lens type, we determined an average of the values measured. Repeated-measures ANOVA, with one within-subject factor (eye) and no between-subject factors, with a Tukey-Kramer post-hoc test, were used to determine differences between the focal lengths of the different eyes.

Sensitivity.—Sensitivity (*f*-number), or the eye's ability to admit light, was calculated using values for focal length (*f*) and the diameter of the retina (*d*), measured from the extremities of the rhabdomeres in each species (Opell & Ware 1987). We determined focal lengths by the above methods and ascertained retinal diameters by taking measurements from slides obtained using methods described for internal ocular organization. These values were then entered into the sensitivity equation (2) outlined in Opell & Ware (1987):

$$f\text{-number} = f/d \quad (2)$$

The sensitivity of the eye can also be given in terms of an S-number, as described by Land (1985). Here sensitivity is defined, not only by the relative aperture of the eye, but also by the cross sectional area of the receptor and the amount of light absorbed by the receptor, as shown in equation (3):

$$S = \left(\frac{\pi}{4}\right)^2 \left(\frac{D}{f}\right)^2 (d_r^2) (1 - e^{-kl}) \quad (3)$$

where *D* is the diameter of the lens, *f* is the focal length, *d_r* is the receptor diameter (assumed to equal the center-to-center spacing of the receptors), *l* is the length of the receptor and *k* is the extinction coefficient of the photopigment in the receptors. Following Land (1981, 1985) *k* was approximated to be 0.0067 for rhabdomeric photoreceptors, and *l* was multiplied by 2 in the secondary eyes as the reflective tectum may allow photons to bounce back past the receptor, effectively lengthening it.

Resolution.—We counted the numbers of axons exiting each eye from sections cut using the same methods as for internal ocular organization. Resolution is dependent upon the number of photoreceptors, or rhabdomeric cells per eye. The higher the density of cells, the finer the resolution of an image (Land 1985). The number of nerve axons exiting a spider's eye is in a 1:1 ratio with the number of photoreceptors (Uehara & Uehara 1996). To compare the density of visual cells per eye, we figured the inter-receptor angle ($\Delta\phi$) based upon Land (1985) as given by equation (4):

$$\Delta\phi = \frac{d_{cc}}{f} \quad (4)$$

where *d_{cc}* is the center-to-center spacing of retinal receptors and *f* is the focal length. The inter-receptor angle was calculated by measuring the pigment ring diameter of the retinal mosaic from histological sections and using the average maximum visual angle from the field of view (see below) to calculate the total area of the retinal mosaic. This was divided by the total numbers of photoreceptors per eye to give an estimate of receptor area, and hence diameter. Retinal diameter was assumed to equal *d_{cc}* based on Land (1985).

Table 1.—Optical data and sensitivities of the eyes of *Lycosa leuckartii*. Where multiple measurements were taken, mean plus standard error is shown. *D* = diameter of the lens, *f* = focal length, *d_{cc}* = center to center spacing of the photoreceptors, *f* = number as calculated in Equation 3. S-numbers, as calculated in Equation 3, are shown based upon the length of the tapetum. S-numbers based on 2× length of the tapetum are shown in parentheses.

Eyes	<i>D</i> μm	<i>f</i> μm	<i>d_{cc}</i> μm	<i>f</i> -number	S-number μm ²
AM	292 ± 10.4	276.84 ± 16.89	8.93	1.08	-
AL	230 ± 8.4	230.88 ± 5.74	9.87	0.69	-
PM	752 ± 21.9	675.35 ± 56.19	7.96	0.56	9.82 (17.6)
PL	647 ± 18.7	499.26 ± 13.40	6.81	0.75	9.72 (17.5)

Field of view.—We used a Welch Allyn medical ophthalmoscope, along with an Aimark perimeter arc (153 mm diameter) constructed for use on spiders, to determine the extent of visual fields for *L. leuckartii*. A freshly killed *L. leuckartii* was utilized, and measurements were taken in a darkened room, using the light reflecting from the tapetum to determine limits of the fields of view of each eye. We moved the ophthalmoscope around the perimeter arc, viewing the bright green reflection from the tapetum of the secondary eyes, or the dull red reflection from the rhabdomeres of the primary eyes. Readings were taken on the perimeter arc at every 10° from horizontal, and were plotted directly onto a Geological Stereonet by rotating the stereonet 10° between each point. A stereonet is typically used to plot three-dimensional angles in two dimensions and, similar to the Aitoff equal area projection (utilized by Land & Barth 1992), the resultant plot represents 180° of a globe at infinity with the spider at the center. Average maximal visual angle (AMVA) was calculated by averaging the maximum horizontal and vertical arcs.

Representative specimens from the study population along with slide preparations are held in the Zoology Building, School of Animal Biology, University of Western Australia.

RESULTS

External ocular organization.—The average carapace length of *L. leuckartii* was 826 μm. *Lycosa leuckartii*'s eyes appear to form three rows. The first of these is similar to the ancestral arrangement, a single row consisting of the AL and AM eyes. With subtle evolutionary modifications, the PL eyes have moved around and back to form a row separate from the central row of the PM eyes. These modifications result in the total eye width being similar to total eye depth (TEW = 247 ± 4.8 μm; TED = 221 ± 4.4 μm).

For the *Lycosa leuckartii* specimen, all pairs of eyes showed significant differences in diameters from one another ($F_{19,3} = 406.9$, $P < 0.001$), the forward facing PM eyes had the largest diameter, closely followed by the obliquely oriented PL eyes, and then the AM and AL eyes (Table 1).

Internal ocular organization.—The AM eyes display a typical bi-convex lens formed by a visible thickening of the cuticular layer. The lens is separated from the retina by a layer of columnar vitreous cells. The retina is composed of visual cells and pigment cells. The most anterior portion of the visual cell, which contains the rhabdomeres, borders the vitreous

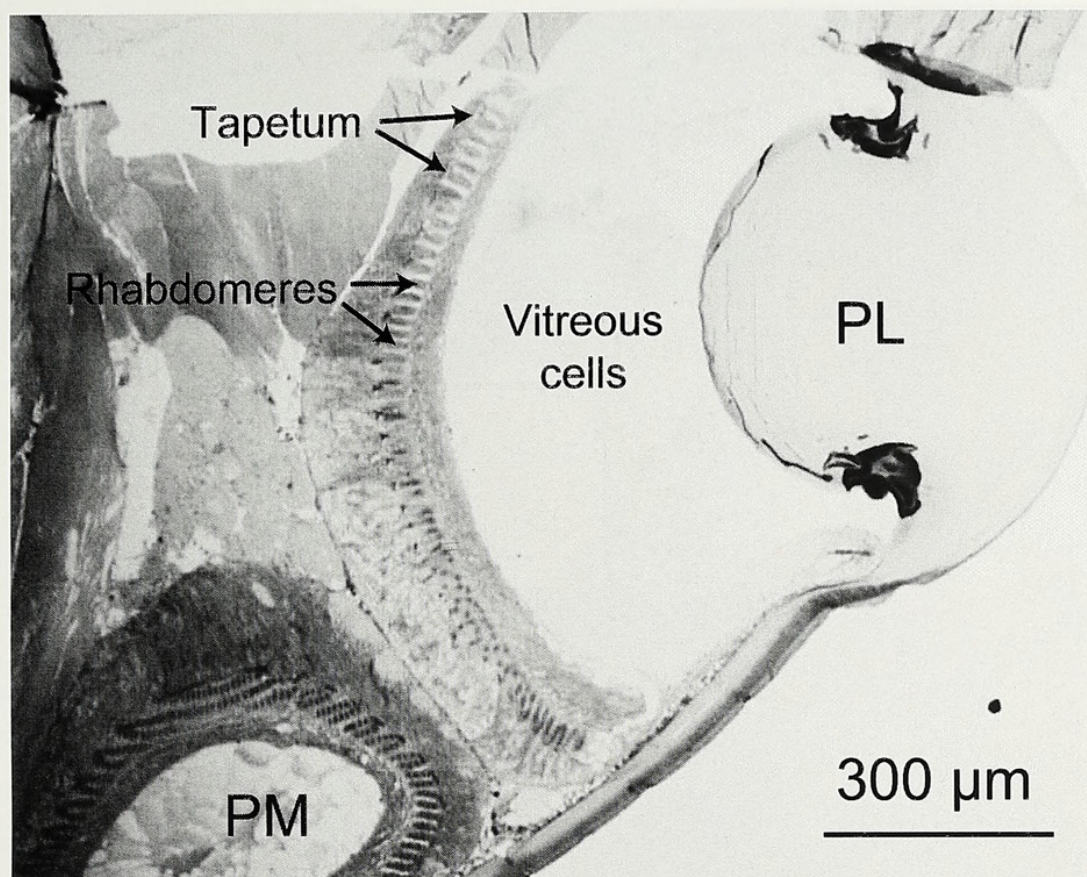


Figure 2.—Structure of the posterior lateral eye (PL) and the posterior medial eye (PM) of *L. leuckartii*, in a transverse section of the prosoma.

layer, and the nuclei lie below. The secondary eyes of *L. leuckartii* have a distinct 'grid-shaped' tapetum (Fig. 2). A thin dark layer of visual cells containing the rhabdomeres separates the vitreous cells and the tapetum. The length of the tapetum measured directly from cross-sections averaged 31.75 and 32.22 μm long for the PL eyes and the PM eyes, respectively.

In the anterior eyes of *L. leuckartii*, one discrete nerve bundle was found to emerge from each eye, but the posterior eyes produced multiple bundles of nerve axons. These emerged from various points around the perimeter of the eyecups and moved through the middle of the prosoma toward the supraesophageal ganglion (Fig. 3). The PL eyes together gave rise to 18 bundles of axons. Each contained from 92 to 987 nerve axons per bundle. The PM eyes together generated 35 bundles. Each of these contained from 30 to 728 nerve axons per bundle.

Focal length.—There were significant differences in the focal lengths of the four pairs of eyes in *L. leuckartii* ($F_{1,3} = 42.4$, $P = 0.006$; Table 1). A Tukey-Kramer post-hoc test revealed that there were significant differences between the anterior and posterior pairs of eyes. Both pairs of anterior eyes had similar focal lengths (average = 253.86 μm). The posterior eyes were similar to each other, but showed much longer focal lengths than the anterior eyes (average = 587.30 μm). Direct inspection of the image produced by the lens showed that it was of good quality and therefore not subject to spherical aberration (Fig. 4).

Sensitivity.—Based upon f -numbers, the highest sensitivity for *L. leuckartii* was found in the PM eyes. The other secondary eyes of *L. leuckartii* (PL and AL) also displayed

similarly low f -numbers, indicating high sensitivity (Table 1). The highest f -number in *L. leuckartii* was found in the AM eyes, suggesting it has lower light sensitivity than the secondary eyes. S-numbers calculated for the PL eyes were similar to estimates for S-number of the PM eyes (Table 1).

Resolution.—The optic nerves from all four pairs of eyes of *L. leuckartii* were found grouped together, surrounded by muscle along the midline of the prosoma. Identification of which nerve bundles originated from the left and right anterior eyes was possible by observing the arrival sequence (within the slides) of each nerve bundle and the direction from which it originated. The multiple nerve bundles originating from the posterior eyes of *L. leuckartii* could be distinguished as belonging to the PM or PL eyes, but could not be further separated into left and right eye nerve bundles; thus, total counts were made and half of this attributed to each eye.

The posterior eyes of *L. leuckartii* gave rise to approximately 12 times the number of nerve axons seen in the anterior eyes (Table 2). Receptor diameters were larger for the anterior eyes (average = 9.4 μm) when compared to the posterior eyes (average = 7.4 μm ; Table 1). Accounting for eye size and visual fields, we concluded that this translated into greater resolution, the inter-receptor angle for the posterior eyes being less than a third that of the anterior eyes (Table 2). This appears to be below the potential resolution of the eyes. Following Land & Barth (1992), we discovered that the ultimate limit to resolution is determined by the blur resulting from diffraction at the aperture, given by $57.3w/D$ deg, where w is the wavelength of light (assumed to be 0.5 μm) and D is the diameter of the lens. This results in potential grating

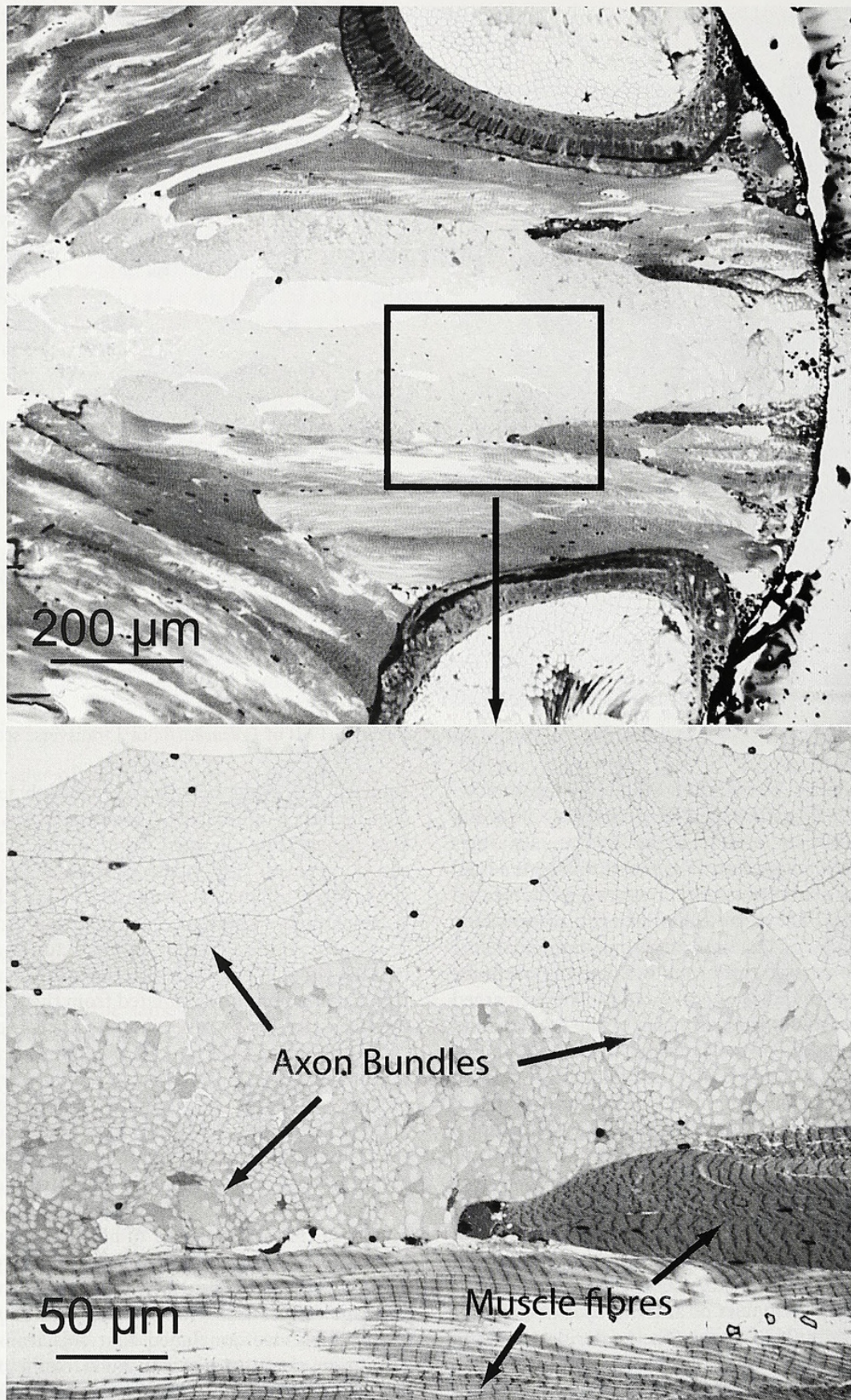


Figure 3.—Multiple nerve bundles of the posterior eyes of *L. leuckartii*. Upper panel = 10× magnification in transverse section; Lower panel = magnified (100×) view of the enclosed area above showing the discrete nerve bundles.

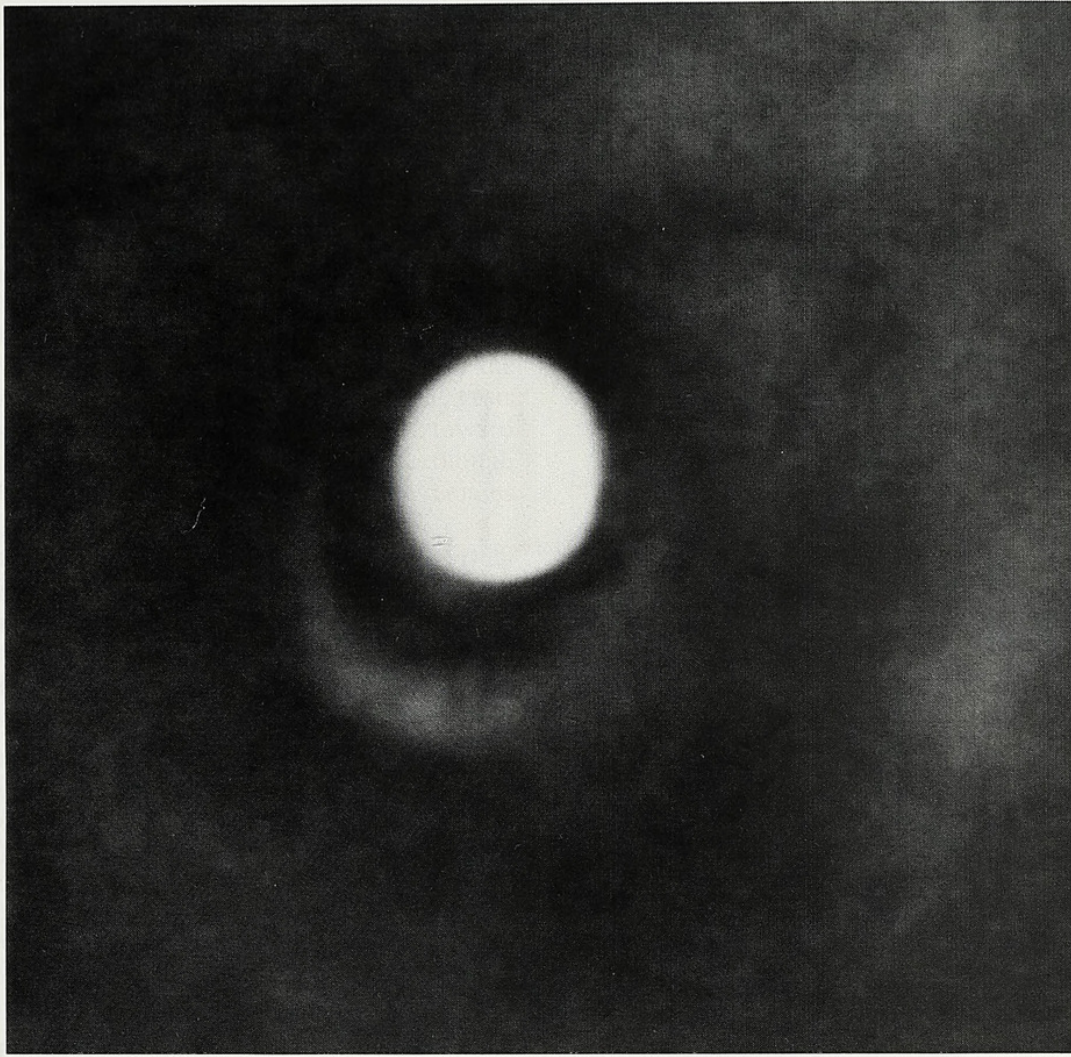


Figure 4.—View through the lens of *L. leuckartii*, suspended from a drop of saline underneath a glass cover-slip. The image is focused on two parallel lines.

periods between 0.12° (AL eyes) and 0.04° (PM eyes), which are an order of magnitude smaller than the inter-receptor angles measured, suggesting diffraction does not limit resolution.

Field of view.—Visual fields for *L. leuckartii* (Figs. 5A & B) were found to extend 360° around the animal, with a large overlap within 70° of the center. The PL eyes provided 220° of peripheral vision along the horizontal meridian, extending around the animal's sides and overlapping behind the animal. AMVA of each individual eye was greater than 80° (Table 1) and up to 107.8° in the PL eyes. The other three pairs of eyes

(AM, AL and PM) all had some degree of forward facing overlap, indicating the potential for good overall binocular vision. The PM eyes, while covering 120° vertical maximum and 140° along the horizontal meridian, did not greatly overlap (maximum overlap 7° between 0 to 10° above the horizontal). The AL eyes provided a large degree of overlap (maximum 57°), but their visual axis was directed well below the horizontal (maximum overlap at 42° below horizontal). The AM eyes had a potentially large amount of binocular vision, with a maximum overlap of 42° at 24 to 30° above the horizontal, and with overlap extending from 20° below to 60° above horizontal.

DISCUSSION

The greatest differentiation of the eyes of *L. leuckartii* occurs between the posterior eyes and the anterior eyes, suggesting that these eyes play different roles in the visual system. This is most evident in the overlapping visual fields of not only the AL eyes with the PM eyes, as was shown by Homann (1931), but also of the AM and PM eyes (Fig. 5). The visual fields of the posterior eyes have large visual angles and cover an almost 360° view, while the anterior eyes appear to be focused forward.

Table 2.—Optical data and resolution of the eyes of *Lycosa leuckartii*. d = diameter of the pigment ring, AMVA = average maximal visual angle, A_r = calculated area of the retina based upon AMVA, $\Delta\theta$ = inter-receptor angle based upon Equation 4.

Eyes	d (μm)	AMVA $^\circ$	Nerve no. axons	A_r μm^2	$\Delta\theta$ $^\circ$
AM	255.7	82.4	476	29,797	1.85
AL	335.8	80.2	257	19,670	2.45
PM	1194.7	96.9	4848	241,208	0.68
PL	662.5	107.8	4423	160,871	0.78

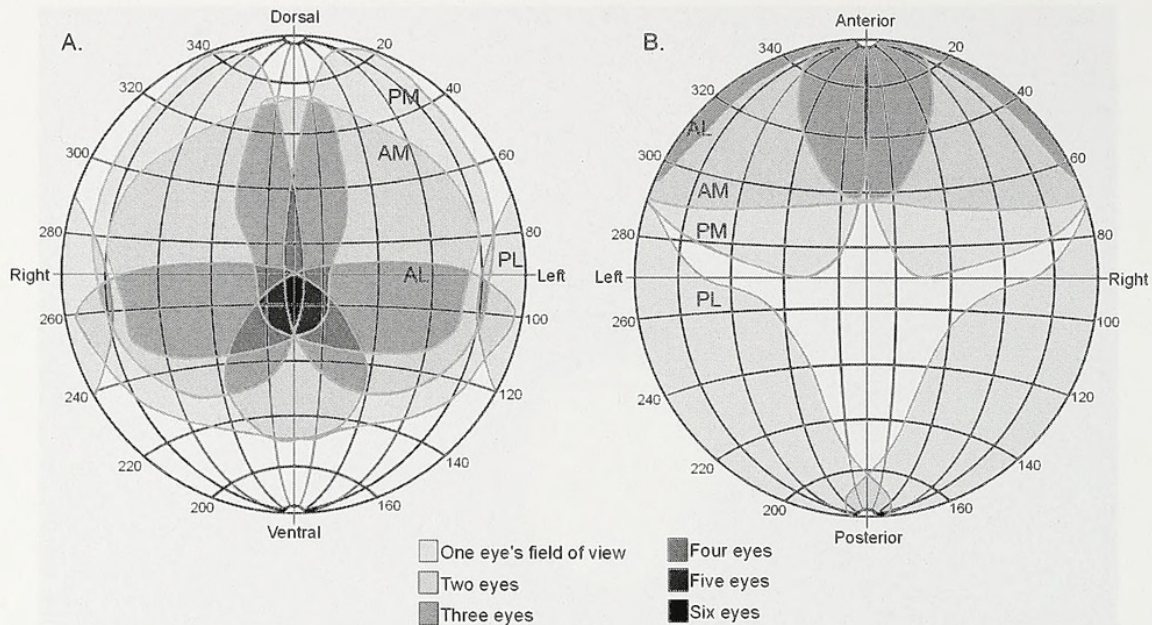


Figure 5.—Fields of view for *L. leuckartii*: A = frontal view; B = overhead view.

Differentiation in focal length is also evident between anterior and posterior eyes. These estimates of focal length can also be used to calculate the eye's depth of focus, which is the animal's nearest distance of clear vision. Following Land (1981), we determined that the nearest distance of clear vision (U) is given by $U = fD/2d_{cc}$, where f is the focal length, D is the diameter of the lens, and d_{cc} is the center-to-center spacing of the photoreceptors. This results in values for U of 4.5 mm for the AM eyes and 2.7 mm for the AL eyes. This is much less than the length of the legs, which suggests even the closest objects appear in focus. The posterior eyes, in contrast, have much larger U values of 32 mm (PM eyes) and 24 mm (PL eyes) and may therefore be of limited use at close range.

The posterior eyes also show potential for superior performance in both resolution and sensitivity, when compared to the anterior eyes. This implies that the posterior eyes may be best suited for long-range, wide-angle recognition of objects in low light conditions and would therefore be ideal for tasks such as prey detection. Similar predictions were reported based upon behavioral experiments on the lycosid spider *Rabidosa rabida* Walckenaer 1837 (Rovner 1993). When different combinations of eyes were occluded in *R. rabida*, spiders with usable PL eyes were able to perform sizable orientations (up to 160°) toward a stimulus, while the PM eyes were found essential for mediating long-range approaches toward the stimulus (Rovner 1993). This suggests the PL and PM eyes could determine the outer limits of the spider's visual perception and foraging patch.

In contrast, the short focal length and considerable binocular vision of the anterior eyes indicate good potential depth perception at short range, which may be an important component for short-range orientation and approaches during activities such as prey capture or courtship. This has been supported behaviorally for the AL eyes by Rovner (1993), but not for the AM eyes. However, a comparison of the roles of anterior eyes between *L. leuckartii* and *R. rabida* may be difficult, since the AM eyes are smaller than the AL eyes in *R. rabida*, while the opposite is true for *L. leuckartii* (AM eyes

larger than AL eyes). This may signify a greater role in orientation, or more likely, approach, toward stimuli, for the AM eyes in *L. leuckartii*. Alternatively, the AM eyes have also been shown to play a role in orientation via polarized light (Magni et al. 1964, 1965; Magni 1966; Ortega-Escobar & Munoz-Cuevas 1999). Further, the AM eyes of *L. tarantula* Linnaeus 1758 also differ from the other eyes in having muscle attachments, and therefore better mobility (Ortega-Escobar & Munoz-Cuevas 1999). This led Land & Barth (1992) to conclude that one function of the AM eyes may be to analyze stationary objects, since small movements prevent the neural image from adapting, as occurs in the secondary eyes.

We observed a further distinction between the posterior and anterior eyes of *L. leuckartii* in the organization of the optic nerves. While each of the anterior eyes of *L. leuckartii* connects to one discrete nerve bundle, the posterior eyes exhibit multiple bundles (up to 35) exiting each eye. Multiple nerve bundles have previously been reported in another lycosid species. Researchers have found *Lycosa tarentula fasciventris* to have 20 nerve bundles exiting the PL eyes and 30 from the PM eyes (Kovoor et al. 1992). The function of multiple nerve bundles in the posterior eyes of *L. leuckartii* is not known. The presence of these discrete nerve bundles may be the result of developmental or functional differences and remains to be investigated.

The posterior eyes appear to have partially overcome the trade-off between resolution and sensitivity by increasing in size relative to the carapace. A comparison of the inter-receptor angle of the PL with other species of lycosid suggests that *L. leuckartii* has a much better resolution than *L. horrida* Keyserling 1877 (1.5–2.5°; Homann 1931), *L. singoriensis* Laxmann 1770 (= *Trochosa singoriensis*) (1.7–2.6°; Homann 1931) and two other species of *Lycosa* published in Homann (1931) (both 1.8°). Further, it appears that resolution for each eye of *L. leuckartii* is better than the corresponding eyes of that found in the closely related, nocturnal ctenid spider *Cupiennius salei* (Land & Barth 1992).

The sensitivity of the lens was also high for *L. leuckartii* when compared with other species. The least sensitive of the

eyes of *L. leuckartii*, the AM eyes, are comparable in *f*-numbers to nocturnally active web-building uloborids, whose *f*-number's range from 0.88–1.70 (Opell & Ware 1987). The sensitivity of the secondary eyes of *L. leuckartii* even closely approximates that of the PM eyes of the nocturnal ogre-faced spider *Deinopis subrufa* (*f*-number of AM eyes = 0.58: Blest & Land 1977).

When estimates of receptor size are included (S-numbers), the sensitivity for the PL eyes of *L. leuckartii* appeared twice as good as that of the PL eyes of a lycosid species reported in Homann (1931) and Land (1985); however, the S-number for the PL eyes of *L. leuckartii* was about ten times less than the PL eyes of *Cupiennius salei* (S-number 147 μm^2). This suggests that the visual system of *L. leuckartii* may be biased toward providing better resolution rather than sensitivity, though whether this translates into differences in performance remains to be investigated.

There appear to be important differences in the visual systems between Australian lycosids and Palaeartic lycosids. One possible source of this variation may be prey capture strategies. While most of the Australian lycosid species studied appear to be burrowing, the Palaeartic species are vagrant, or build temporary webs (Murphy et al. 2006). The quality of vision in one particular genus, *Pardosa*, should be examined, since this group appears to be predominately vagrant and may therefore show more reliance on vision. Nevertheless, there are a number of vagrant and web-weaving lycosids in Australia. Also a distinctive granite-rock-inhabiting genus in southern Western Australia, which shelters under exfoliated slabs on the rock surface and hunts in a vagrant fashion, is currently being described by Framenau et al. (in press) as a new genus. It certainly invites further research regarding its ocular capability.

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LITERATURE CITED

- Blest, A.D. & M.F. Land. 1977. The physiological optics of *Dinopis subrufus* L. Koch: a fish-lens in a spider. *Proceedings of the Royal Society of London Series B* 196:197–222.
- Bristowe, W.S. & G.H. Locket. 1926. The courtship of British lycosid spiders, and its probable significance. *Journal of Zoology* 96:317–347.
- Clemente, C.J., K.A. McMaster, L. Fox, L. Meldrum, B.Y. Main & T. Stewart. 2005. Visual acuity of the sheet-web building spider *Badumna insignis* (Araneae, Desidae). *Journal of Arachnology* 33:726–734.
- Dacke, M., T.A. Doan & D.C. O'Carroll. 2001. Polarized light detection in spiders. *Journal of Experimental Biology* 204:2481–2490.
- Foelix, R.F. 1982. *Biology of Spiders*. Harvard University Press, Cambridge, Massachusetts.
- Forster, L.M. 1979. Visual mechanisms of hunting behaviour in *Trite planiceps*, a jumping spider (Araneae: Salticidae). *New Zealand Journal of Zoology* 6:79–93.
- Forster, L.M. 1982. Visual communication in jumping spiders (Salticidae). Pp. 161–212. *In* *Spider Communication: Mechanisms and Ecological Significance* (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.
- Homann, H. 1928. Beiträge zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden. II. Das Sehvermögen der Salticiden. *Zeitschrift für Vergleichende Physiologie* 7:201–269.
- Homann, H. 1931. Beiträge zur Physiologie der Spinnenaugen. III. Das Sehvermögen der Lycosiden. *Zeitschrift für Vergleichende Physiologie* 14:40–67.
- Homann, H. 1971. Die Augen der Araneae, Ontogenie und Bedeutung für die Systematik (Chelicerata, Arachnida). *Zoomorphology* 69:201–272.
- Jackson, R.R. 1977. Prey of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology* 5:145–149.
- Kaston, B.J. 1936. The senses involved in the courtship of some vagabond spiders. *Entomologia Americana* 16:97–167.
- Kovoor, P.J., A. Munoz Cuevas & J. Ortega Escobar. 1992. Le système visuel de *Lycosa tarentula fasciventris* (Araneae, Lycosidae). I: Organisation des nerfs et des premiers ganglions optiques. *Annales des Sciences Naturelles* 13:25–36.
- Kovoor, P.J., A. Munoz Cuevas & J. Ortega Escobar. 1993. Microanatomy of the anterior median eye and its possible relation to polarized light reception in *Lycosa tarentula* (Araneae, Lycosidae). *Bollettino di Zoologia* 60:367–375.
- Land, M.F. 1969. Structure of the retinæ of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology* 51:443–470.
- Land, M.F. 1981. Optics and vision in invertebrates. Pp. 471–592. *In* *Handbook of Sensory Physiology Volume VII/6B. Vision in Invertebrates. B: Invertebrate Visual Centers and Behaviour 1* (H. Antrum, ed.). Springer Verlag, Berlin.
- Land, M.F. 1985. The morphology and optics of spider eyes. Pp. 53–78. *In* *Neurobiology of Arachnids* (F.G. Barth, ed.). Springer-Verlag, Berlin.
- Land, M.F. & F.G. Barth. 1992. The quality of vision in the ctenid spider *Cupiennius salei*. *Journal of Experimental Biology* 164:227–242.
- Lizotte, R.S. & J.S. Rovner. 1988. Nocturnal capture of fireflies by lycosid spiders: visual versus vibratory stimuli. *Animal Behaviour* 36:1809–1815.
- Magni, F. 1966. Analysis of polarized light in wolf-spiders. Pp. 171–186. *In* *The functional organization of the compound eye* (C.G. Bernhard, ed.). Pergamon Press, Oxford, UK.
- Magni, F., F. Papi, H.E. Savely & P. Tongiorgi. 1964. Research on the structure and physiology of the eyes of a lycosid spider. II. The role of different pairs of eyes in astronomical orientation. *Archives Italiennes de Biologie* 102:123–136.
- Magni, F., F. Papi, H.E. Savely & P. Tongiorgi. 1965. Research on the structure and physiology of the eyes of a lycosid spider. 3. Electroretinographic responses to polarised light. *Archives Italiennes de Biologie* 103:146–158.
- Murphy, N.P., V.W. Framenau, S.C. Donnellan, M.S. Harvey, Y.C. Park & A.D. Austin. 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28S rRNA, and NADH1 genes: Implications for classification, biogeography, and the evolution of web building behavior. *Molecular Phylogenetics and Evolution* 38:583–602.
- Opell, B.D. 1988. Ocular changes accompanying eye loss in the spider family Uloboridae. *Journal of Morphology* 196:119–126.
- Opell, B.D. & A.D. Ware. 1987. Changes in visual fields associated with web reduction in the spider family Uloboridae. *Journal of Morphology* 192:87–100.

- Ortega-Escobar, J. 2006. Role of the anterior lateral eyes of the wolf spider *Lycosa tarentula* (Araneae, Lycosidae) during path integration. *Journal of Arachnology* 34:51–61.
- Ortega-Escobar, J. & A. Munoz-Cuevas. 1999. Anterior median eyes of *Lycosa tarentula* (Araneae, Lycosidae) detect polarized light: behavioral experiments and electroretinographic analysis. *Journal of Arachnology* 27:663–671.
- Robinson, M.H. & B. Robinson. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). *American Midland Naturalist* 85:85–96.
- Rovner, J.S. 1993. Visually mediated responses in the lycosid spider *Rabidosia rabida*: the roles of different pairs of eyes. *Memoirs of the Queensland Museum* 33:635–638.
- Rovner, J.S. 1996. Conspecific interactions in the lycosid spider *Rabidosia rabida*: the roles of different senses. *Journal of Arachnology* 24:16–23.
- Schmid, A. 1998. Different functions of different eye types in the spider *Cupiennius salei*. *Journal of Experimental Biology* 201:221–225.
- Uehara, A., Y. Toh & H. Tateda. 1978. Fine structure of the eyes of orb-weavers, *Argiope amoena* L. Koch (Aranea: Argiopidae). *Cell and Tissue Research* 186:435–452.
- Uehara, A. & K. Uehara. 1996. Efferent fibers and the posteromedial eye of the liphistiid spider *Heptathela kimurai* (Araneae: Liphistiomorphae). *Journal of Experimental Zoology* 275:331–338.
- Uetz, G.W. & G.E. Stratton. 1982. Acoustic communication and reproductive isolation in spiders. Pp. 123–158. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.
- Whitcomb, W.H. & R. Eason. 1965. The mating behavior of *Peucetia viridans* (Araneida: Oxyopidae). *Florida Entomologist* 48:163–167.
- Williams, D.S. & P. McIntyre. 1980. The principal eyes of a jumping spider have a telephoto component. *Nature* 288:578–580.
- Zwicky, K.T. 1968. Innervation and pharmacology of the heart of *Urodacus*, a scorpion. *Comparative Biochemistry and Physiology* 24:799–808.

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