2000. The Journal of Arachnology 28:16–22

OPTICAL STRUCTURE OF THE CRAB SPIDER *MISUMENOPS PALLENS* (ARANEAE, THOMISIDAE)

José Antonio Corronca: CRILAR-CONICET-UNLaR. Mendoza esq. Entre Ríos. (5301) Anillaco, La Rioja, Argentina

Héctor R. Terán: Instituto de Morfología Animal, Fundación Miguel Lillo. Miguel Lillo 251. (4000) S.M. de Tucumán, Argentina

ABSTRACT. We describe the histological structure of the eyes of *Misumenops pallens* (Araneae, Thomisidae). We have carried out frontal, sagittal and transverse histological sections of the eyes. All the eyes have cuticular and laminar corneas and lenses. The anterior median eyes have two cellular types in the rhabdom; the remaining eyes have three cellular types. The anterior median eyes have a dark pigmented U-shaped mark in the middle of the retina. The indirect eyes have a dark pigmented band divided by a grate tapetum. The pathway of the optic nerves is also described. Our results suggest that Thomisidae may be a close relative of the superfamily Lycosoidea.

RESUMEN. Se describe la estructura histológica de los ojos de *Misumenops pallens* (Araneae, Thomisidae). Se realizaron cortes de los ojos en sección frontal, sagittal y transversal. Todos los ojos tienen córneas y lentes cuticulares y laminares. Los ojos medios anteriores tienen dos tipos celulares en el rabdoma mientras que los restantes ojos tienen tres tipos celulares. Los ojos medios anteriores poseen, en el centro de la retina, una mancha de pigmento oscuro en forma de U. Los ojos de visión indirecta tienen una banda oscura de pigmento dividida por un tapete de tipo ''grate.'' Se estudia también el recorrido de los nervios ópticos. Nuestros resultados sugieren que Thomisidae puede estar relacionado con la superfamilia Lycosoidea.

Keywords: Eyes, optic nerves, phylogenetic relationship

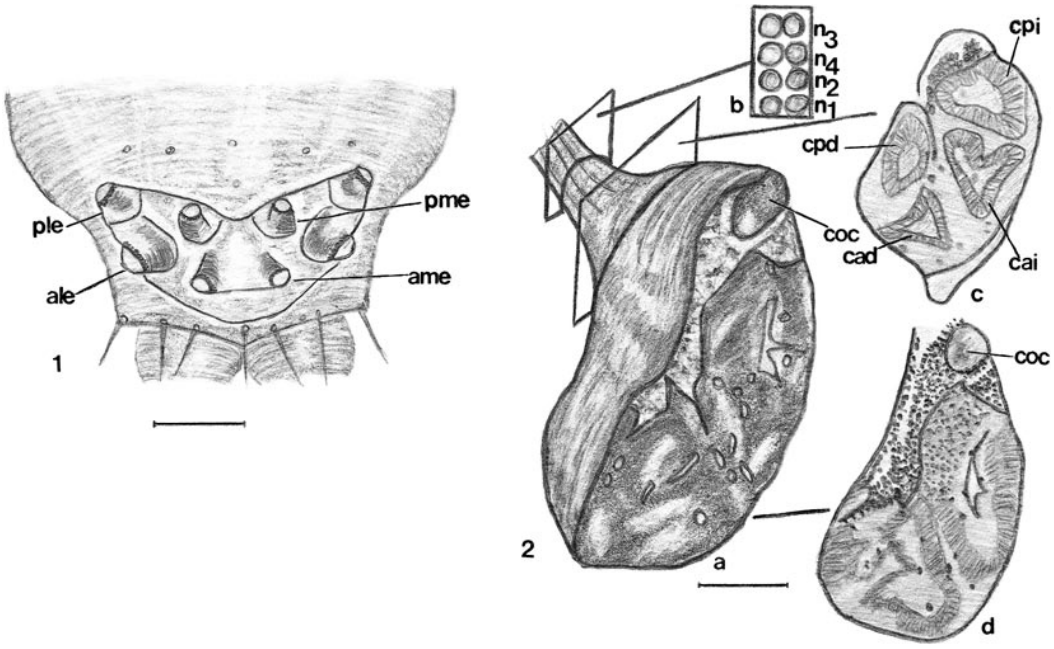
Misumenops *pallens* (Keyserling 1880) (Thomisidae) are spiders that normally inhabit flowers and capture their prey by ambush. Their eyes are arranged in two recurved rows; in the anterior row the anterior median eyes (AME) are next to the bigger anterior lateral eyes (ALE) (Fig. 1). The posterior row eyes are equidistant, the posterior median eyes (PME) being smaller than the posterior lateral eyes (PLE). Lateral eyes are located on prominent tubercles. The dioptical apparatus of all the eyes of *Misumenops pallens* is formed by a cuticular cornea, a laminar lens and the ''vitreous body,'' constituted by cone cells arranged in a unique stratum that rests against a basal membrane. The eyes of *Misumenops* sp. have a dark pigmented ring called the ''pupil,'' a character shared with Lycosidae (Homann 1971). The tapetum of the secondary eyes of Thomisidae is difficult to observe (see Levi 1982). In this study, the optic structure of *Misumenops pallens* is described in order to provide new morphological characters that can be used in phylogenetic studies.

METHODS

Six adult females of *Misumenops pallens*, collected in March 1995 on soybean flowers in Burruyacu department (Tucumán, Argentina), were studied. Voucher specimens and histological slides are deposited in the arachnid collection of Fundación Miguel Lillo, Tucumán, Argentina (lot FML N^0 2203). The spiders were anesthetized with chloroform. The cephalic regions of these spiders were dissected and were fixed in Bouin. The material was kept in n-Butyl alcohol during the time required to soften the cuticle, prior to embedding in Paraplast.

Serial sections of 6 μm thickness were cut, following the frontal, transverse and sagittal planes. Preparations were stained with Mallory-(Azan) Heidenhain and Haematoxylin-Eosin.

Diagrams of optic nerves were prepared to



Figures 1, 2.—*Misumenops pallens.* 1. Ocular disposition; 2. Diagram showing the union of the ocular nerves in the cerebral ganglion –a. General view of the cerebral ganglion showing optic center, b. Transverse section showing the distribution of the optic nerves before their union with the cerebral ganglion, c. Transverse section showing the four optic centers, d. Transverse section of the optic center formed by the fusion of the four centers. *Abbreviations:* ale = anterior lateral eyes; ame = anterior median eyes; cad = anterior right optic center; cai = anterior left optic center; co = optic center; coc = optic center of cerebral ganglion; cpd = posterior right optic center; cpi = posterior left optic center; n_1 = optic nerve of anterior median eye; n_2 = optic nerve of anterior lateral eye; n_3 = optic nerve of posterior median eye; n_4 = optic nerve of posterior lateral eye. *Scale bars:* Fig. 1 = 0.42 mm; Fig. 2 = 66 μm.

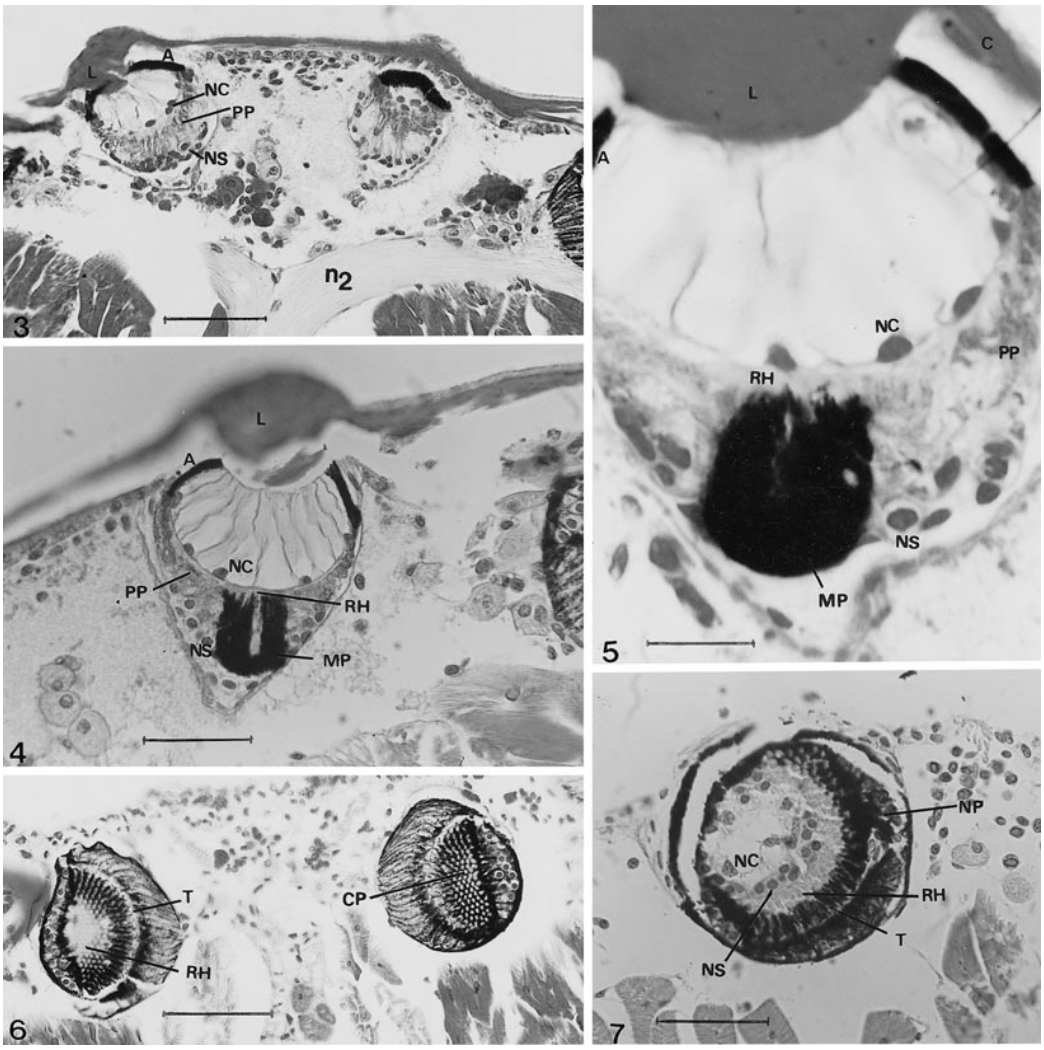
trace their course as they leave each eye and enter the optic center of the cerebral ganglion; the nerves of each eye are designated as follows: n_1 (AME), n_2 (ALE), n_3 (PME) and n_4 (PLE).

RESULTS

Anterior median eyes (AME).—(Figs. 3–5). These eyes are pyriform, with their vertex towards the inner part. They have a cuticular and laminar cornea, with the outer surface formed by overlapping plates, separated by complete transverse grooves. The lens, located beneath the cornea, is laminar, ogival, with the greater convexity towards the inner part of the eye (Figs. 3, 5). It has few transverse grooves. Cone cells (Eakin & Brandenburger 1971) lie below the lens and contain a few irregular basal nuclei with homogeneous granular chromatin (Figs. 4, 5). Cone cells are arranged in only one stratum and send out projections towards the lens. Cone cells rest against a thin basal membrane that separates them from the retina (Fig. 4). There is a wide dark pigmented ring (the ''pupil'') in the anterior portion of the vitreous body (Figs. 4, 5).

The retina is sub-conical and is formed by two cellular types, pigmented supporting cells and sensitive cells. Pigmented supporting cells are distributed in the central region of the rhabdom forming a U-shaped spot of dark pigment. There is a calyx-shaped layer of brown pigment between this spot and the pigmented ring of the dioptical apparatus (Figs. 4, 5). The pigmented layer is constituted by granules of brown and black pigment. Brown pigment disposition is similar to the location of the dark pigment in the secondary eyes, while black pigment is located only in the central pigmented zone of the retina. The function of each type of pigment has yet to be established.

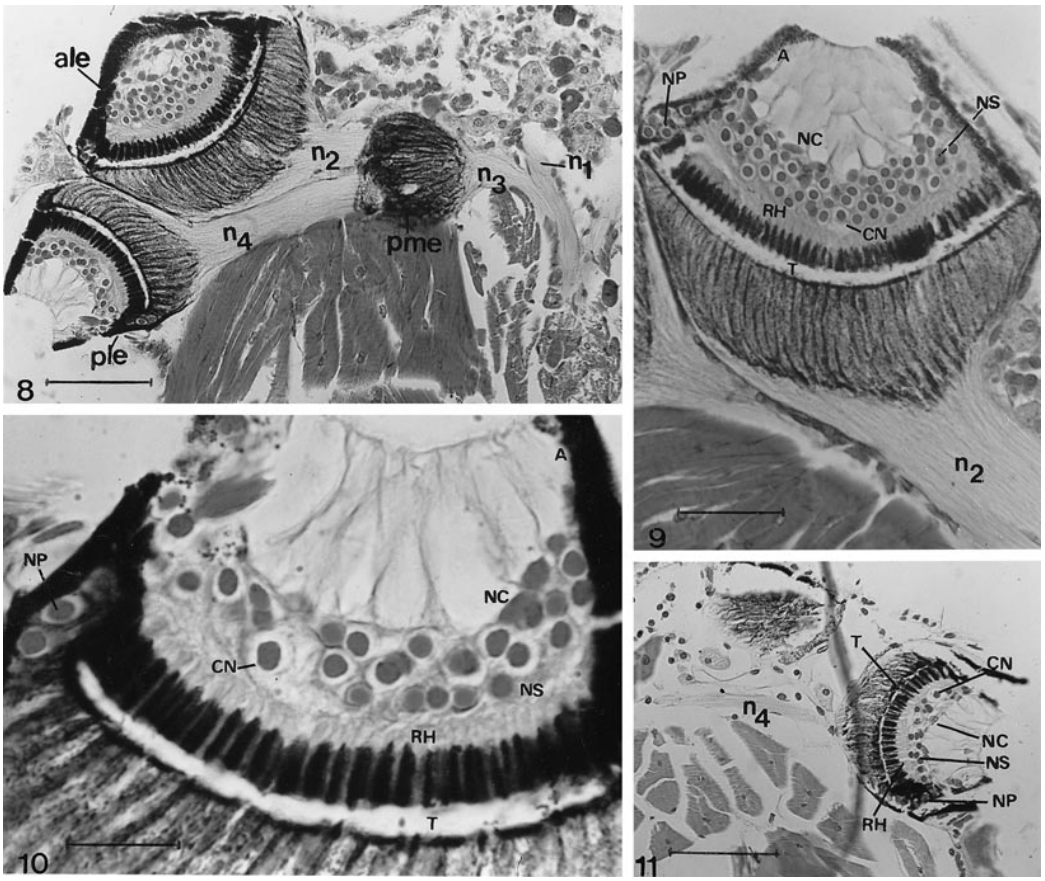
Each sensitive cell consists of a distal portion below the basal membrane, that forms a thin rhabdom located only in the central por-



Figures 3–7.—*Misumenops pallens*. 3–5. Anterior median eyes (AME); 3. Frontal section showing arrangement (250×); 4. Frontal section showing structural elements (400×); 5. Frontal section showing details of rhabdomeres and nuclei of sensitive cells (1000×). 6–7. Posterior median eyes; 6. Frontal section showning tapetum (250×); 7. Frontal sections showning structural elements (400×). *Abbreviations:* A = pigmented ring; C = cornea; CP = pigmented supporting cell; L = lens; MP = pigmented spot; NC = nucleus of cone cell; NS = nucleus of sensitive cell; n_2 = optic nerve of lateral anterior eyes; NP = nucleus of pigmented supporting cell; PP = brown pigment; RH = rhabdomeres; T = tapetum. *Scale bars:* Fig. 3 = 60 μm, Fig. 4 = 4 μm, Fig. 5 = 1.6 μm, Fig. 6 = 66 μm and Fig. 7 = 42.6 μm.

tion in front of the central pigmented spot (Fig. 5). The intermediate segment of the sensitive cells crosses the pigmented layer and ends in the nuclear portion, where the cell increases its volume (Fig. 5). The nuclei of sensitive cells are irregular, with homogeneous granular chromatin. They are located in a peripheral basal stratum (Fig. 4).

Anterior lateral eyes (ALE).—(Fig. 9). These eyes are conical and situated in a anterio-lateral position. Cornea, lens and cone cells are similar to those of the AME. The retina is formed by three cellular types, sensitive cells, pigmented supporting cells, and non-pigmented supporting cells (Fig. 9). Sensitive cells are arranged in at least two or three strata. They contain rounded nuclei, with granular chromatin homogeneously distribut-



Figures 8–11.—*Misumenops pallens*. 8. Arrangement of posterior eyes and lateral anterior eyes, frontal section, showing disposition of optic nerves (250×); 9. Lateral anterior eyes showing principal structures (400×); 10–11. Lateral posterior eye; 10. Posterior lateral eye showing non-pigmented supporting cells (1000×); 11. Posterior lateral eyes showing optic nerve and structural elements (250×). *Abbreviations:* ale = anterior lateral eye; pme = posterior median eye; ple = posterior lateral eye; A = ring (''pupil''); CN = non-pigmented supporting cell; NC = nucleus of cone cell; NP = nucleus of pigmented supporting cell; NS = nucleus of sensitive cell; n_1 = optic nerve of anterior median eye; n_2 = optic nerve of anterior lateral eye; n_3 = optic nerve of posterior median eye; n_4 = optic nerve of posterior lateral eye; RT = rhabdomeres; T = tapetum. *Scale bars:* Figs. 8 and 11 = 66 μm; Fig. 9 = 42.6 μm; Fig. 10 = 15 μm.

ed, and clear cytoplasm around the nucleus. The intermediate segment extends from the soma of sensitive cells and continues in the parallel rhabdomeres (Fig. 9), whose projections cross the ''RT'' type tapetum (according to Homann 1971) (Fig. 9). The few non-pigmented supporting cells are large and have ovoid nuclei with homogeneous granular chromatin. They have abundant clear cytoplasm with projections that can cross the rhabdomere layer (Fig. 9). Pigmented supporting cells contain cytoplasm with a great number of granules of concentrated pigment arranged in a dark layer. They are located between the rhabdomeres and the tapetum, and extend forward enclosing the vitreous body up to the lens base. There is a less pigmented wide layer below the tapetum. It is difficult to observe the nuclei of these cells due to the great amount of pigment, except in the peripheral lateral zone, where groups of nuclei of these cells can be observed (Fig. 9).

Posterior median eyes (PME).—(Figs. 6, 7). These rounded eyes are located in a dorsolateral position. Cornea, lens and cone cells are similar to those of the AME. Retina cells are similar to those of the ALE, except that the nuclei of sensitive cells are arranged in

two strata. Non-pigmented supporting cells are rare; they possess pyriform nuclei with homogeneous granular chromatin and small cytoplasm projections between the rhabdomeres. There are two layers of pigmented supporting cells, as in the ALE. These cell are separated by a well-developed ''RT'' type tapetum (Fig. 6). In a transverse section, rounded nuclei are visible, with homogeneous granular chromatin and some peripheral clear cytoplasm (Fig. 7).

Posterior lateral eyes (PLE).—(Figs. 10, 11). These eyes are conical eyes and have cornea, lens and cone cells that are similar to those of the AME. The retina is similar to the retina of the ALE, except the nuclei of the sensitive cells are arranged in at least three strata. Pigmented cells, non-pigmented cells and shape of the tapetum are similar to those of the ALE (Figs. 10, 11).

Trajectory of optic nerves.—Optic nerves from the AME run independently and parallel as they leave each eye, following the prosomal median line (Fig. 12). The rest of the nerves emerge from the corresponding eyes, curve and run paired along the body median line (Fig. 13), between the poison glands.

At the median region of the prosoma optic nerves remain paired. Their arrangement from the ventral to the dorsal part of the body is: n_1, n_2, n_4 and n_3 (Figs. 2b, 8). Posteriorly, optic nerves fuse to form four optic centers (Figs. 2c, 14). The two ventral optic centers correspond to the fusion of n_1 and n_2 of their respective sides, while the dorsal optic centers, right and left, are formed by the fusion of the corresponding n_4 and n_3. The four optic centers fuse in the posterior region of the prosoma in a dorsal optic center located in the cerebral ganglion (Figs. 2d, 15).

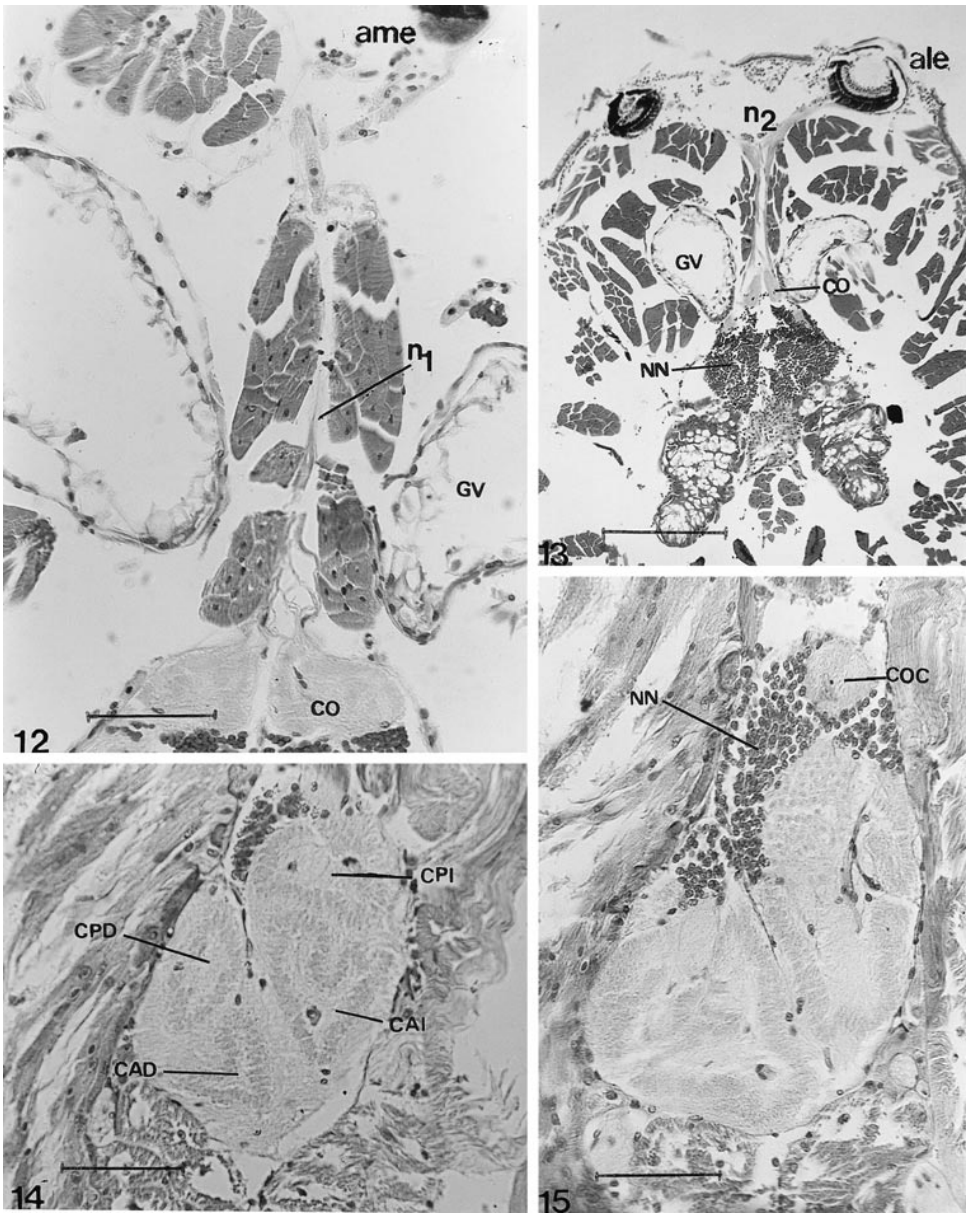
DISCUSSION

Different cellular types were observed in the ocular structure of *Misumenops pallens*. This agrees with Eakin & Brandenburger's (1971) description for Salticidae, Melamed & Trujillo Cenóz's (1966) for Lycosidae and Corronca & Terán's (1997) for *Selenops* Latreille (Selenopidae). However, the similarities found in the cellular types of the eyes of these families of spiders do not imply that there are no differences in their general structure.

The tapetum and the anatomical structure of eyes are characters that can be used to reconstruct the phylogenetic relationships of spiders. Homann (1971) mentioned the presence of the ''pupil'' and the tapetum type as among the characters shared by both the Thomisidae and Lycosidae. Homann (1975) considered Thomisidae as sister group of the monophyletic group Lycosoidea (Lycosidae, Senoculidae and Oxyopidae). Levi (1982) placed Thomisidae in their own superfamily together with Aphantochilidae, while Coddington & Levi (1991) considered Thomisidae in the Dionycha, even when its placement is not very clearly established. Philodromidae, Heteropodidae and Selenopidae could be considered as groups related with Thomisidae, because of the presence of laterigrad legs and the locomotion type (Coddington & Levi 1991). Griswold (1993) studied the phylogenetic relationships of Lycosoidea and considered the copious and diverse anatomical and morphological characters, and established that the presence of an RT type of tapetum in at least one of the eyes is one of the two synapomorphies that supports the monophyly of this superfamily. The same author considered that the possible homology of the tapetum shape is the only evidence to include this family within Lycosoidea. Corronca & Terán (1997) suggested the probable relationship of Selenopidae with Lycosoidea. Results obtained from the study of the ocular structure of *Misumenops pallens,* and extrapolated to the rest of Thomisidae, show the existence of certain anatomical characters (presence of a well developed RT type tapetum in all secondary eyes, except in PME where is reduced, and the ''pupil'') shared with Lycosidae and of others (RT tapetum and sensitive cells in the secondary eyes arranged in al least two strata) with Selenopidae. These affinities suggest the probable relationship of both families (Thomisidae and Selenopidae) with Lycosoidea.

The U-shaped spot of dark pigment, located in the central portion of AME retina in Thomisidae, could be homologous with the V-shaped pigmented spot, typical of AME of Salticidae. Both structures present the same topology, but the four layers of receptive segments that have been described by Eakin & Brandenburger (1971) for Salticidae are not present in Thomisidae.

Recent observations by De la Serna & Spinelli (1995) for *Latrodectus* species (Theridiidae) show that the four optic centers fuse to-



Figures 12–15.—*Misumenops pallens*. 12. Connection between anterior median eyes into the cerebral ganglion (250×); 13. Pathway of optic nerves of the anterior lateral eyes until fusion with the optic center, frontal section (160×); 14. Four optic centers, transverse section in the middle portion of the prosoma (250×); 15. Optic center formed by the fusion of the four centers, transverse section to the posterior portion of the prosoma (250×). *Abbreviations:* ame = anterior median eyes; ale = anterior lateral eye; CAD = anterior right optic center; CAI = anterior left optic center; CO = optic center; COC = optic center of cerebral ganglion; CPD = posterior right optic center; CPI = posterior left optic center; GV = venom gland; NN = neuronal nucleus; n_1, optic nerve of anterior median eye; n_2 = optic nerve of anterior lateral eye. *Scale bars:* Figs. 12, 14 and 15 = 66 μm, Fig. 13 = 94.2 μm.

gether in an unique optic center in the cerebral ganglion. Our study of the trajectory of the optic nerves in *Misumenops pallens* agrees with these authors; however, the nerves do not fuse in their trajectory until they form the first optic centers. The presence of this character in Lycosidae and Salticidae should be studied.

ACKNOWLEDGMENTS

To Fundación Miguel Lillo, INSUE and CRILAR-CONICET-UNLaR, for their support and María Eugenia Morales for her help with the English version.

LITERATURE CITED

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Annu. Rev. Ecol. Syst., 22:565–592.

Corronca, J.A. & H.R. Terán. 1997. Estructura ocular de *Selenops cocheleti* Simon (Araneae, Selenopidae). J. Arachnol., 25:42–48.

De la Serna de Esteban, C. & C.M. Spinelli. 1995. Los nervios ópticos en cuatro especies de *Latrodectus* (Araneae, Theridiidae). J. Arachnol., 23:31–36.

Eakin, R.M. & J.L. Brandenburger. 1971. Fine structure of the eyes of jumping spiders. J. Ultrastr. Res., 37:618–663.

Griswold, C.E. 1993. Investigations into the phylogeny of the lycosid spiders and their kin (Arachnida, Araneae, Lycosoidea). Smithsonian Contrib. Zool., 539:1–39.

Homann, H. 1971. Die Augen der Araneae. Anatomie, Ontogenie und Bedeutung für die Systematik (Chelicerata, Arachnida). Z. Morph. Tiere, 69:201–272.

Homann, H. 1975. Die Stellung der Thomisidae und der Philodromidae im System der Araneae. Z. Morphol. Tiere, 80:181–202.

Levi, H.W. 1982. Araneae. Pp. 77–95, *In* Synopsis and Classification of Living Organisms, 2. (S.P. Parker, ed.).

Melamed, J. & O. Trujillo-Cenóz. 1966. The fine structure of the visual system of *Lycosa* (Araneae, Lycosidae). Z. für Zellfor., 74:12–31.

Manuscript received 30 November 1996, revised 4 June 1999.