

# Scanning Electron Microscopy of the Palp Sense Organs of the Harvestman *Leiobunum townsendi* (Arachnida: Opiliones)<sup>1,2</sup>

GREG S. SPICER

Committee on Evolutionary Biology, University of Chicago,  
1103 East 57th Street, Chicago, Illinois 60637, U.S.A.

*Abstract.* The sense organs on the palp of the harvestman *Leiobunum townsendi* are surveyed using scanning electron microscopy. A total of approximately 1,100 mechanoreceptive sensilla are present on each palp and these are strikingly similar to sensilla reported from spiders and other arachnids. They are differentiated into two forms: sensilla trichodea, averaging 76  $\mu\text{m}$  in length, and sensilla chaetica consisting of two types; type I is 57  $\mu\text{m}$  long and type II is 35  $\mu\text{m}$  long. Sensilla chaetica, especially type I, may be chemoreceptive in function, because they are similar to contact chemoreceptive hair sensilla in spiders. Structures that resemble the chemoreceptive tarsal organs of spiders are located on the tarsus, although dye penetration experiments seem to indicate that they are not innervated. Sensory structures are more abundant on the distal than on the proximal segments, as is the case in many other arachnids and insects.

There have been few studies of the mechanoreceptors and chemoreceptors of arachnids. Most of these studies were based on spiders and mites (Altner & Prillinger, 1980; Barth, 1982, 1985; Foelix, 1982; McIver, 1975; Slifer, 1970). Berland (1949), Kaestner (1935), and Martens (1978) review the sparse information available for harvestman receptors. Only three physiological studies exist concerning the sense organs of the arachnid order Opiliones. These are the works of Curtis (1970) on the structure of the eyes, and Edgar (1963) and Barth & Stagl (1976) on lyriform organs. Such a paucity of information makes useful comparisons of the sensory structures between the arachnid groups and other arthropods difficult. This is unfortunate, because arachnids have been shown to possess some structures that are unique among the arthropods (Foelix & Axtell, 1971; Foelix & Chu-Wang, 1973a; Heimer et al., 1982; Hill, 1977). Moreover, this lack of comparative data greatly limits the use of sense organ structure in taxonomy and systematics.

The palps of opilionids are six-segmented and are dorsal to the mouth and chelicerae (Savory, 1977). The palps are often a useful character in opilionid systematics, having many diagnostic spines and processes. The palp is used primarily as a tactile sense organ to find and manipulate its food (Savory, 1962,

---

<sup>1</sup> I am most grateful to Dr. Howard J. Arnott and the Electron Microscopy Laboratory, University of Texas at Arlington, for supplying some of the materials and facilities used in this investigation. I am further indebted to Dr. H. Bernard Hartman, Texas Tech University, for his help with the cobalt backfilling technique. I thank Mr. James C. Cokendolpher, Ms. Sharon M. Swartz, Dr. Carol S. Giometti, Dr. H. Bernard Hartman, and Dr. Howard J. Arnott for their assistance and useful comments on the manuscript.

<sup>2</sup> Publication costs, in part, are being met by a grant from the Spencer-Tolles Fund of the American Microscopical Society.

1977), but it is also used by the males of some species to clasp the female during copulation (Edgar, 1971). For this purpose, the male has a row of spines on the palp tarsus (Davis, 1934) which is used to restrain the first pair of legs on the female (Figs. 1, 5).

This investigation was undertaken to examine the structures present on the palp of the harvestman *Leiobunum townsendi* using scanning electron microscopy. Although the purpose of this research is not to determine the function of these structures, it represents a starting point for future physiological studies. I also hope that a study of the structure and distribution of sense organs will be of some use in systematics.

#### MATERIALS AND METHODS

Adult male and female specimens of *Leiobunum townsendi* Weed, 1893 were collected in Crosby and Llano Counties, Texas and Eddy County, New Mexico. They were preserved and stored in 70% ethanol and identified according to Davis (1934). In addition, specimens of *Eumesosoma roeweri* (Goodnight & Goodnight, 1943), collected from Tarrant County, Texas and identified according to Cokendolpher (1980), were examined for comparative purposes.

To prepare specimens for scanning electron microscopy, the palps were dissected and affixed to a brass stub using double-stick tape. These were air-dried for several hours and sputter-coated with gold using a Technics Hummer Jr. The specimens were examined at 15 kV using a JEOL-35C scanning electron microscope. Some specimens also were cleared in xylene and examined by light microscopy to aid in determining the numbers and distribution of mechanoreceptive structures on the palp.

To determine the presence of chemoreceptive structures, dye penetration experiments, using the crystal violet method of Slifer (1960) and the cobalt backfilling technique modified from Quicke & Brace (1979), were carried out. With the crystal violet method, the specimens were fixed in 3% formaldehyde for several days. The palp was then dissected and placed in a 0.5% crystal violet solution for periods of 1 h to 1 day, following which it was rinsed three times in distilled water, dried under a lamp until all of the surface water was removed, transferred to a dish of xylene for clearing, and examined by light microscopy. In the cobalt backfilling technique, a 0.06 M cobalt acetate solution was applied to the severed nerve endings of the palp. This preparation was refrigerated for one day. The following day, the cobalt acetate solution was removed and replaced with an ammonium sulfide solution. This solution precipitates the cobalt so that the nerves can be discerned. The developing preparation was observed over a period of several hours by light microscopy.

#### RESULTS

A total of about 1,100 mechanoreceptive structures were found on each palp of *Leiobunum townsendi*. These structures are strikingly similar to sensilla that have been reported from spiders (Foelix, 1970a, 1982, 1985; Foelix & Chu-Wang 1973a; Harris & Mill, 1977a; Hill, 1977). They are not evenly distributed, being more numerous on the distal segments (Figs. 1-5). This can best be

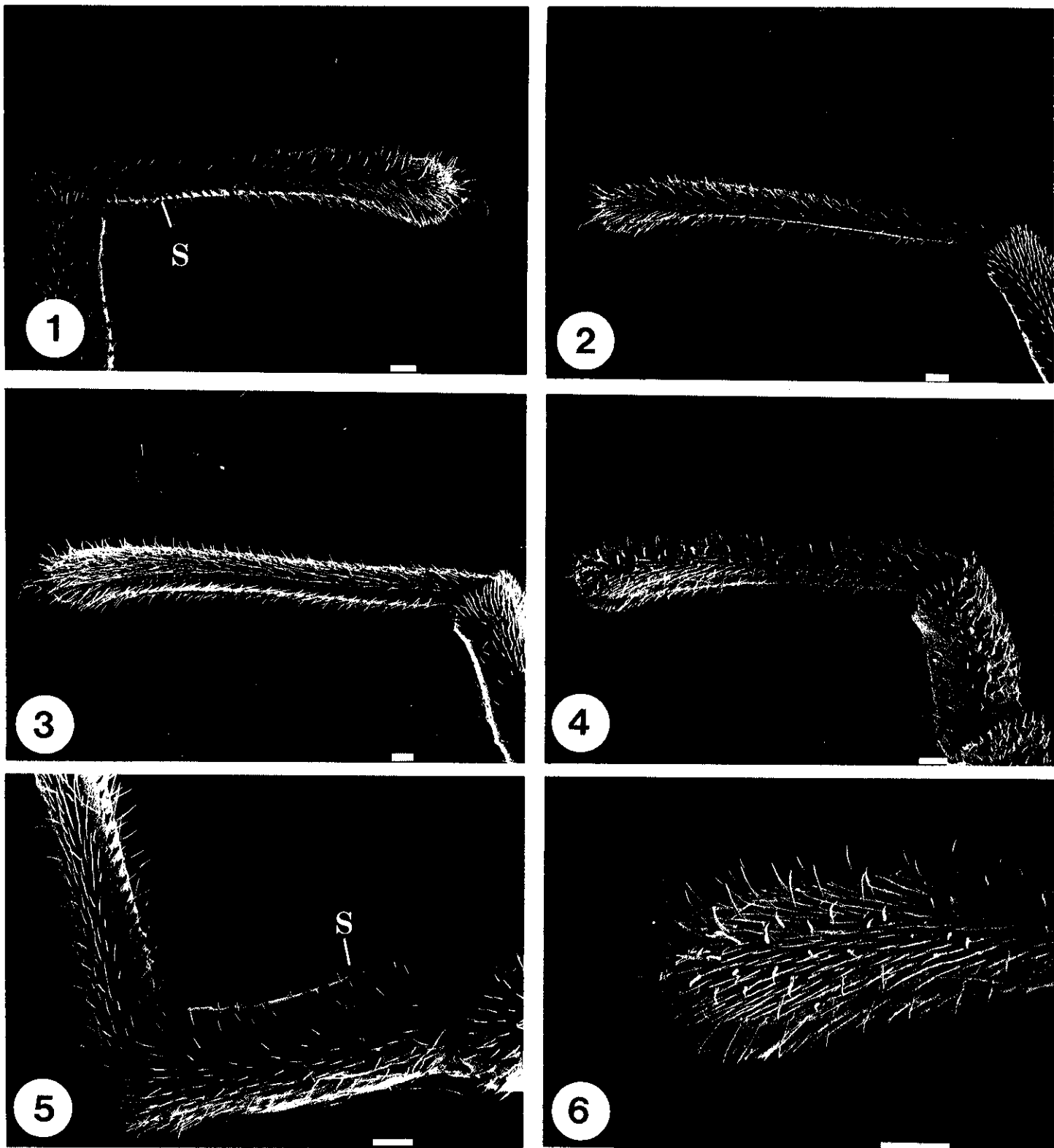
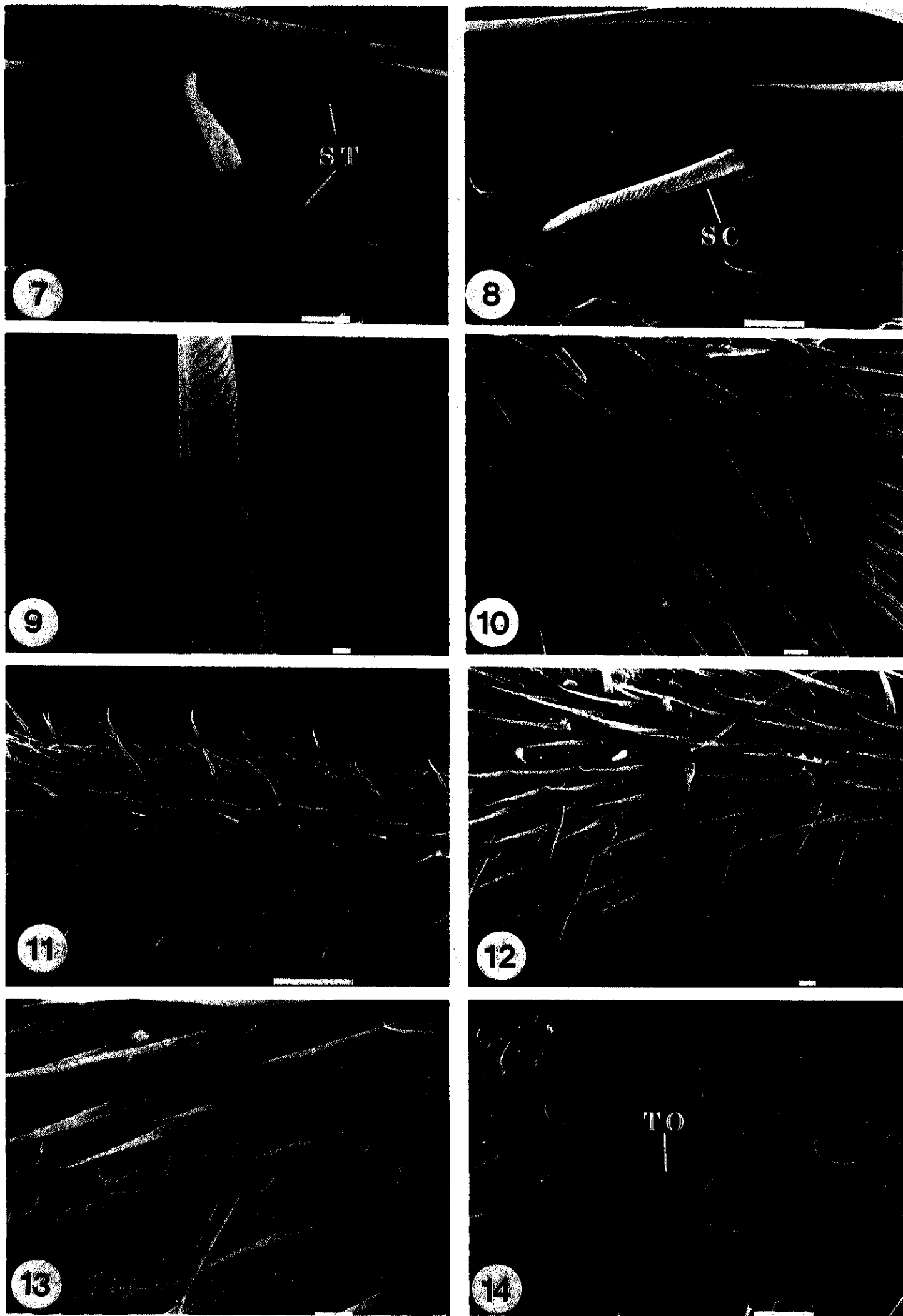


FIG. 1. Medial view of male palp tarsus (*Leiobunum townsendi*). FIG. 2. Lateral view of male palp tarsus (*L. townsendi*). FIG. 3. Medial view of female palp tarsus (*L. townsendi*). FIG. 4. Medial view of male palp tarsus (*Eumesosoma roeweri*). FIG. 5. Medial view of male palp tibia and tarsus (*L. townsendi*). FIG. 6. Medial view of male palp tarsus claw region (*E. roeweri*). Scale bars each represent 100  $\mu$ m. S, spine.

→

FIG. 7. Sensilla chaetica, type II, and sensilla trichodea on a male palp tarsus (*Leiobunum townsendi*). FIG. 8. Sensilla chaetica, type II, on a male palp tarsus (*L. townsendi*). FIG. 9. Sensilla chaetica showing the characteristic whorls. FIG. 10. Near distal end of male palp tarsus (*L. townsendi*). FIG. 11. Female palp tarsus showing band of presumed chemoreceptors (*L. townsendi*). FIG. 12. Male palp tarsus showing band of presumed chemoreceptors (*Eumesosoma roeweri*). FIG. 13. Sensilla chaetica, sensilla trichodea, and presumed chemoreceptors on a male palp tarsus (*E. roeweri*). FIG. 14. Presumed chemoreceptors on a male palp tarsus (*L. townsendi*). In Fig. 11, the



scale bar represents 100  $\mu\text{m}$ , in Figs. 7, 8, 10 and 12, 13, 14, the scale bars each represent 10  $\mu\text{m}$ , and in Fig. 9, the scale bar represents 1  $\mu\text{m}$ . SC, sensilla chaetica; ST, sensilla trichodea; TO, tarsal organ.

demonstrated in terms of density. The tarsus has one sensillum per  $1,200 \mu\text{m}^2$ , the tibia one per  $2,700 \mu\text{m}^2$ , the patella one per  $6,000 \mu\text{m}^2$ , and the femur only one per  $9,700 \mu\text{m}^2$ . Such density distributions commonly occur in many insect groups (Schneider, 1964). The sensilla also are not distributed uniformly over a single segment (Fig. 2). The dorsal part of the palp tarsus has one sensillum per  $790 \mu\text{m}^2$ , but the ventral part has only one per  $6,300 \mu\text{m}^2$ . This is probably because the dorsal surface is directed away from the organism and toward the environment for more effective reception of sensory information. Two different forms of structures were observed. These are classified according to Schneider (1964). No differences attributable to sexual dimorphism were recognizable in these structures (Figs. 1–3), although such differences have been reported for some insects (Alm & Kurczewski, 1982; Cook et al., 1980; Schneider & Steinbrecht, 1968; Wibel et al., 1984).

*Sensilla trichodea.* This form of mechanoreceptor is recognizable by its greater length, sharp-pointed end, low angle to the palp, and lack of a specialized basal membrane (Figs. 7, 10, 11). They possess distinctive whorled striae that also are found in the hair sensilla of spiders (Foelix, 1970a). They average  $76 \mu\text{m}$  in length with a range of  $74\text{--}82 \mu\text{m}$ . Sensilla trichodea are common sensory structures on the palp tibia and tarsus, but they are not found on the femur or patella.

*Sensilla chaetica.* This form of mechanoreceptor is characterized by a specialized basal articulating membrane, a rounder tip, and it projects from the palp at an almost perpendicular angle (Figs. 7, 8). Two types can be distinguished based on their lengths, and both possess whorled striae (Fig. 9). Type I is about  $57 \mu\text{m}$  long with a range between  $52\text{--}60 \mu\text{m}$ . This type is restricted to the palp tarsus, being found on both the dorsal and ventral surfaces, and also is abundant around the palp claw. Type II averages  $35 \mu\text{m}$  in length (range,  $30\text{--}39 \mu\text{m}$ ). This is the only type found on the femur, patella, and tibia, but also is present on the lateral surfaces of the tarsus.

*Chemoreceptors (?)*. In addition to possible chemoreceptive sensilla, structures that resemble chemoreceptive tarsal organs of spiders (Blumenthal, 1935; Dumpert, 1978; Foelix, 1970b; Foelix & Chu-Wang, 1973b) are present on the underside of the palp tarsus (Figs. 11, 14). Approximately 150 are located in a band extending for the length of the tarsus (Fig. 3). The cuticular capsule is  $22\text{--}25 \mu\text{m}$  in diameter, with a pore opening of about  $2 \mu\text{m}$ .

Dye penetration experiments, using the crystal violet method of Slifer (1960) and a modified cobalt backfilling technique from Quicke & Brace (1979), were performed to determine whether or not the pores are innervated. Although the experiments were inconclusive, they suggested that the pores lack innervation. If they are not innervated, the pores cannot be considered chemoreceptive in function, but may be secretory in nature.

*Sensilla ultrastructure and systematics.* Palpal sensilla of *L. townsendi* were compared to another harvestman, *Eumesosoma roeweri*, which is in the same subfamily (Gagrellidae: Leiobuninae). Although *E. roeweri* was not examined extensively, this species seems to possess the same basic sensory structures as *L. townsendi*. The size and proportions of the palps are different, but the general

arrangement and ultrastructure are extremely similar (cf. Figs. 3, 4 with 5, 6 and Figs. 11, 14 with 12, 13). Homologizing sensory structures, such as sensilla is difficult (Altner & Prillinger, 1980), but Haupt (1979) has shown that proposed phylogenetic relationships based on sense organ structures are reasonable. However, the systematic value of such characters within the Opiliones at large cannot be determined until ultrastructural comparisons of palpal sensilla include additional species.

#### DISCUSSION

Although experimentation to test the function of these sensilla was not conducted, they are structurally similar to chemo- and mechanoreceptors of other arachnids (Dumpert, 1978; Foelix 1970a,b, 1982, 1985; Foelix & Chu-Wang 1973a,b; Harris & Mill, 1977a,b; Hill, 1977). Harvestmen, like other arachnids, use their palps extensively in ways that seem entirely tactile (Savory, 1962, 1977), and use of their palp during mating has been demonstrated (Edgar, 1971). Presumably, then, the abundant palpal sensory receptors of opilionids play an important role in both feeding and mating.

The absence of a basal membrane in sensilla trichodea is a highly unusual condition for an arachnid, because one of the main characteristics of a tactile hair in this group is the possession of an articulating membrane (Foelix, 1985). Consequently, because the sensilla trichodea have no specialized basal membrane, they are probably restricted in their movement (McIver, 1975). Although each sensillum is usually characterized by having only one neuron in insects, they have been shown to have 2 neurons in ticks (Foelix & Axtell, 1971), 3 neurons in spiders (Foelix & Chu-Wang, 1973a), and 7 neurons in scorpions (Foelix & Schabronath, 1983). This condition would seem to be advantageous; that multi-innervated trichobothria are better able to respond to direction has been demonstrated (Görner, 1965). However, this directional sensitivity is not the case for arachnid tactile hairs, which seem only to respond to downward deflections (Foelix, 1985; Harris & Mill, 1977a).

Sensilla chaetica may have chemoreceptive functions in addition to any mechanoreceptive functions. Their perpendicular angle to the palp, blunt tips, and whorled striae are characteristic of chemoreceptive hair sensilla of spiders (Foelix, 1970a,b; Foelix & Chu-Wang, 1973b; Harris & Mill, 1973, 1977b). The position of type I sensilla around the palp claw also is reminiscent of contact chemoreceptors among spiders and other arachnids (Foelix, 1985; Hill, 1977), although no distal opening, as in spiders, or small pores, as in thin-walled pegs (Slifer, 1970), were noted on the opilionid specimens examined. However, this is not unusual, because the pore openings are minute and often clogged, so that the only reliable means of detection are through the use of dyes or transmission electron microscopy (Foelix, 1985). Further study is needed to determine if these receptors are multi-innervated before any conclusive statements relative to function can be made. Some chemoreceptive sensilla have been found on the legs of Opiliones (see Foelix, 1976, 1985); thus, their presence on the palp is not unexpected.

The position of the putative chemoreceptors on the underside of the palp

suggests that they may be used in detecting food and possibly in mating behavior. Frequently, harvestmen have been observed to scrape the ground with the ventral part of their palps in search of food; their use by males during mating is well documented (Edgar, 1971). As noted, the ventral portion of each of the palps are characterized by a paucity of mechanoreceptors. This may indicate that the organism is using these structures in a chemoreceptive capacity as an alternative means of locating its food.

#### LITERATURE CITED

- ALM, S. R. & KURCZEWSKI, F. E. 1982. Antennal sensilla and setae of *Anoplius tenebrosus* (Cresson) (Hymenoptera: Pompilidae). *Proc. Entomol. Soc. Wash.*, 84: 586-593.
- ALTNER, H. & PRILLINGER, L. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *Int. Rev. Cytol.*, 67: 69-139.
- BARTH, F. G. 1982. Spiders and vibratory signals: sensory reception and behavioral significance. In Witt, P. N. & Rovner, J. S., eds., *Spider Communication*, Princeton Univ. Press, Princeton, New Jersey, pp. 67-122.
- BARTH, F. G., ed. 1985. *Neurobiology of Arachnids*. Springer-Verlag, Berlin. 385 pp.
- BARTH, F. G. & STAGL, J. 1976. The slit sense organs of arachnids. *Zoomorphologie*, 86: 1-23.
- BERLAND, L. 1949. Order des Opilions. In Grasse, P.-P., ed., *Traite de Zoologie*, Vol. 6, Masson, Paris, pp. 761-793.
- BLUMENTHAL, H. 1935. Untersuchungen über das "Tarsalorgan" bei Netzspinnen. *Z. Morph. Oekol. Tiere*, 29: 667-719.
- COKENDOLPHER, J. C. 1980. Replacement name for *Mesosoma* Weed, 1892, with a revision of the genus (Opiliones, Phalangiidae, Leiobuninae). *Occas. Papers Mus., Texas Tech Univ.*, 66: 1-19.
- COOK, B. J., SMITH, R. L. & FLINT, H. M. 1980. The antennal sense organs of the pink bollworm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae). *Proc. Entomol. Soc. Wash.*, 82: 117-123.
- CURTIS, D. J. 1970. Comparative aspects of the fine structure of the eyes of Phalangida (Arachnida) and certain correlations with habitat. *J. Zool. (London)*, 160: 231-265.
- DAVIS, N. W. 1934. A revision of the genus *Leiobunum* (Opiliones) of the United States. *Am. Midl. Nat.*, 15: 662-705.
- DUMPERT, K. 1978. Spider odor receptor: electrophysiological proof. *Experientia*, 34: 754-756.
- EDGAR, A. L. 1963. Proprioception in the legs of phalangids. *Biol. Bull. (Woods Hole)*, 124: 262-267.
1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). *Misc. Pub., Univ. Michigan Zool. Mus.*, 144: 1-64.
- FOELIX, R. F. 1970a. Structure and function of tarsal sensilla in the spider *Araneus diadematus*. *J. Exp. Zool.*, 175: 99-124.
- 1970b. Chemosensitive hairs in spiders. *J. Morphol.*, 132: 313-334.
1976. Rezeptoren und periphere synaptische Verschaltungen bei verschiedenen Arachnida. *Entomol. Germ.*, 3: 83-87.
1982. *Biology of Spiders*. Harvard Univ. Press, Cambridge, Massachusetts. 306 pp.
1985. Mechano- and chemoreceptive sensilla. In Barth, F. G., ed., *Neurobiology of Arachnids*, Springer-Verlag, Berlin, pp. 118-137.
- FOELIX, R. F. & AXTELL, R. C. 1971. Fine structure of tarsal sensilla in the tick *Amblyomma americanum* (L.). *Z. Zellforsch. mikrosk. Anat.*, 129: 548-560.
- FOELIX, R. F. & CHU-WANG, W. 1973a. The morphology of spider sensilla. I. Mechanoreceptors. *Tissue & Cell*, 5: 451-460.
- 1973b. The morphology of spider sensilla. II. Chemoreceptors. *Tissue & Cell*, 5: 461-478.
- FOELIX, R. F. & SCHABRONATH, J. 1983. The fine structure of scorpion sensory organs. I. Tarsal sensilla. *Bull. Br. Arachnol. Soc.*, 6: 53-67.

- GOODNIGHT, C. J. & GOODNIGHT, M. L. 1943. New and little known phalangids from the United States. *Am. Midl. Nat.*, 29: 643-656.
- GÖRNER, P. 1965. A proposed transducing mechanism for a multiply-innervated mechanoreceptor (trichobothrium) in spiders. *Cold Spring Harb. Symp. Quant. Biol.*, 30: 69-73.
- HARRIS, D. J. & MILL, P. J. 1973. The ultrastructure of chemoreceptor sensilla in *Ctiniflo* (Araneida, Arachnida). *Tissue & Cell*, 5: 679-689.
- 1977a. Observations on the leg receptors of *Ctiniflo* (Araneida: Dictynidae). I. External mechanoreceptors. *J. Comp. Physiol.*, 119: 37-54.
- 1977b. Observations on the leg receptors of *Ctiniflo* (Araneida: Dictynidae). II. Chemoreceptors. *J. Comp. Physiol.*, 119: 55-62.
- HAUPT, J. 1979. Phylogenetic aspects of recent studies on myriapod sense organs. In Camatini, M., ed., *Myriapod Biology*, Academic Press, London, pp. 391-406.
- HEIMER, S., HUNTER, J. M., OEY, T. T. & LEVI, H. W. 1982. New sensory (?) organ on a spider tarsus. *J. Arachnol.*, 10: 278-279.
- HILL, D. E. 1977. The pretarsus of salticid spiders. *Zool. J. Linn. Soc.*, 60: 319-338.
- KAESTNER, A. 1935. Opiliones. In Kukenthal, W. & Krumbach T., eds., *Handbuch der Zoologie*, Bd. 3, Halfte 2, Walter de Gruyter & Co., Berlin, pp. 300-393.
- MARTENS, J. 1978. Spinnentiere, Arachnida. Weberknechte, Opiliones. *Die Tierwelt Deutschlands*, 64: 1-464.
- MCIVER, S. B. 1975. Structure of cuticular mechanoreceptors of arthropods. *Ann. Rev. Entomol.*, 20: 381-397.
- QUICKE, D. L. J. & BRACE, R. C. 1979. Differential staining of cobalt- and nickel-filled neurones using rubeanic acid. *J. Microsc.*, 115: 161-163.
- SAVORY, T. H. 1962. Daddy longlegs. *Sci. Am.*, 207: 119-128.
1977. *Arachnida*, 2nd ed. Academic Press, London. 340 pp.
- SCHNEIDER, D. 1964. Insect antennae. *Ann. Rev. Entomol.*, 9: 103-122.
- SCHNEIDER, D. & STEINBRECHT, R. A. 1968. Checklist of insect olfactory sensilla. In Carthy, J. D. & Newell, G. C., eds., *Invertebrate Receptors*, Symp. Zool. Soc. Lond., Vol. 23, pp. 279-297.
- SLIFER, E. H. 1960. A rapid and sensitive method for identifying permeable areas in the body wall of insects. *Entomol. News*, 71: 179-182.
1970. The structure of arthropod chemoreceptors. *Ann. Rev. Entomol.*, 15: 121-142.
- WIBEL, R. G., CASSIDY, J. D., BUHSE, H. E., CUMMINGS, M. R., BINDOKAS, V. P., CHARLESWORTH, J. & BAUMGARTNER, D. L. 1984. Scanning electron microscopy of antennal sense organs of *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *Trans. Am. Microsc. Soc.*, 103: 329-340.