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Source: Florida Entomologist, 98(2) : 593-605

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.098.0232

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# Types and functions of mole cricket (Orthoptera: Gryllotalpidae) antennal and palpal sensilla

*Olga Kostromytska[1], Michael E. Scharf[2], and Eileen A. Buss[3*]*

**Abstract**

Invasive mole crickets (Orthoptera: Gryllotalpidae: *Scapteriscus* spp.) are destructive subterranean pests that cause significant economic losses for the turfgrass, sod and pasture industries. Their behavior suggests that they may sense insecticides applied to the soil, so we sought to examine and describe the antennal and palpal structures of *S. vicinis* Scudder, *S. borellii* Giglio-Tos, *S. abbreviatus* Scudder, and the native mole cricket, *Neocurtilla hexadactyla* Perty, by scanning and transmission electron micrography. The most abundant sensilla were antennal *sensilla chaetica* with mechanoreceptory and contact chemoreceptory functions. Each segment had olfactory *sensilla basioconica* and *sensilla trichodea*, *sensilla coeloconica* (with olfactory and thermo-hydroreceptory functions), and *sensilla campaniformia* (proprioreceptor). Sensilla on the mole cricket palps were non-pore or tip-pore, which suggests mechanoreceptory and contact chemoreceptory functions. Similar to other hemimetaboulous insects, mole cricket nymphs and adults have the same sensilla types. However, the number and size of antennomeres increased with each molt, allowing the antennae to accommodate more sensory sensilla as insects matured.

Key Words: *Scapteriscus*; chemoreception; sensilla; palp; SEM; TEM

**Resumen**

Los grillotopos invasivos (Orthoptera: Gryllotalpidae: *Scapteriscus* spp.) son plagas subterráneas destructivas que causan pérdidas económicas importantes para las industrias de césped, césped para transplantar y pasto. Su comportamiento sugiere que pueden sentir los insecticidas aplicados al suelo, por lo que quisimos examinar y describir las estructuras de las antenas y palpos *de S. vicinis* Scudder, *S. borellii* Giglio-Tos, *S. abbreviatus* Scudder, y el grillotopo nativo, *Neocurtilla hexadactyla* Perty, por medio de la micrografía electrónica de barrido y de transmisión. Las sensillas antenales más abundantes fueron de *sensilla chaetica* con funciones de recepción mecánica y de recepción química de contacto. Cada segmento tenía sensilas olfativas *sensilla basioconica* y *sensilla trichodea*, *sensilla coeloconica* (con funciones olfativas y receptorias hidrotermales) y *sensilla campaniformes* (proprioreceptor). Las sensillas en los palpos de los grillotopos fueron de tipo sin poro o de poros en la punta, lo que sugiere funciones de recepción mecánica y de recepción química de contacto. Al igual que otros insectos hemimetábulos, las ninfas y adultos de los grillotopos tienen los mismos tipos de sensillas. Sin embargo, el número y tamaño de los antenómeros aumentaron con cada muda, permitiendo que las antenas pueden acomodar más sensillas sensoriales mientras que los insectos van madurando.

Palabras Clave: *Scapteriscus*; quimiorrecepción; sensilla; palpo; SEM; TEM

Invasive mole crickets (Orthoptera: Gryllotalpidae: *Scapteriscus* spp.) are destructive insect pests on managed turfgrasses, sod farms, and pastures in the southern United States (Hudson 1995; Hudson et al. 2008). Their subsurface tunneling disrupts turfgrass uniformity, prevents sod pieces from holding together, reduces forage quality, and kills large patches of grass. Mole cricket preventive control depends on monitoring egg hatch and accurately timing insecticide applications for peak emergence. However, treatments may be ineffective if nymphs can sense treated soil and move into untreated areas where populations can continue to build (E. Buss, Entomology and Nematology Department, University of Florida, personal observations). For example, mole crickets can detect insect pathogens, the insecticides bifenthrin and fipronil, and avoid areas treated with them (Thompson & Brandenburg 2005; Cummings et al. 2006).

Mole cricket mechanoreception, particularly sound perception and phonotaxis, have been described (Ulagaraj & Walker 1975; Ulagaraj 1976; Walker & Forrest 1989; Mason et al. 1998), but little is known about their chemoreception, olfactory and gustatory morphology and how their peripheral chemosensory organs may change during postembryonic development. Morphological descriptions of antennal, palpal and tarsal sensilla provide the basis for understanding mole cricket chemosensory input. Chemosensory structures may exist anywhere on an insect's body, but antennae are the main olfactory organs (Keil 1999) and the mouthparts and tarsi are the primary contact chemoreceptors (Ishikawa et al. 1969; Bland et al. 1998; Glendinning et al. 1998, 2000; Mitchell et al. 1999). In addition to their olfactory role, antennae may also have gustatory, thermo-, hydro-, and mechanoreceptors (exterioreceptors and proprioreceptors) (Rani & Nakamuta 2001). Similarly, the maxillary and labial palps may also have olfactory, mechanoreceptory and other receptor types in addition to gustatory sensilla (Ishikawa et al. 1969; Schoonhoven 1972, 1978; Zacharuk 1985; Ignell et al. 2000).

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Studies on hemimetabolous insects indicate that antennal length increases after each nymphal molt, which increases antennal surface area and accommodates more sensilla (Chinta et al. 1996; Keil 1999). Hemimetabolous nymphs and adults typically share a similar habitat and host range, so any quantitative or qualitative changes in chemosensory structures on the antennae may be due to increasing intraspecific needs in mate finding, mate recognition, and oviposition (Brèzot et al. 1997).

Sensilla function can be deduced from their morphological structure (Altner 1977), which is supported by many studies where morphological examination was combined with electrophysiology (Boeckh 1967; Zacharuk 1980; Klein et al. 1988; Keil 1999; Blaney et al. 2005). Thus, our goal was to describe the external morphology, abundance, and distribution of antennal, labial and maxillary palpal sensilla of 4 mole cricket species (*S. vicinis* Scudder, *S. borellii* Giglio-Tos, *S. abbreviatus* Scudder and *Neocurtilla hexadactyla* Perty). Additionally, we sought to correlate nymphal antennal length, number of flagellomeres and pronotal length, and determine the type and number of sensilla on neonatal nymphal antennae to determine any postembryonic developmental changes in antennal morphology of *S. borellii* or *S. vicinus*.

## Materials and Methods

### INSECTS

*Scapteriscus vicinus, S. borellii*, and *N. hexadactyla* were collected from sound and pitfall traps in horse pastures (Hampton, FL, and the University of Florida Horse Teaching Unit, Gainesville, FL). Laboratory-reared *S. abbreviatus* were obtained from Dr. J. H. Frank (University of Florida).

### ANTENNAL MORPHOLOGY OF ADULTS AND NYMPHS

The antennae of 20 adult *S. vicinus* and *S. borellii* (ten males and ten females for each species), 185 *S. vicinus* nymphs (approx. 7 instars) and 115 *S. borellii* nymphs (approx. 6 instars) were detached from heads and slide-mounted. Antennal and pronotal lengths were measured using an ocular micrometer under a stereomicroscope. The number of flagellomeres per antenna was determined from images taken with Auto-Montage Pro software (version 5.02, Syncroscopy, Frederick, MD) and a stereomicroscope. Because we only had 3 adult *N. hexadactyla* specimens, the number of flagellomeres was determined from SEM micrographs (JSM 5510 LW, JEOL Ltd., Tokyo, Japan).

### SCANNING ELECTRON MICROSCOPY (SEM)

Whole live insects were placed in 70% ethanol (EtOH, Acros® Geel, Belgium) and stored before further processing. The head and thorax of *S. vicinus* and *S. borellii* (10 males, 10 females, and ten 1-d old nymphs of both species), *S. abbreviatus* (5 males, 5 females), and *N. hexadactyla* (one female, 2 large nymphs) were removed and placed into 75% EtOH. Specimens were cleaned in an ultrasound bath for 20 min, dehydrated in an alcohol series [kept approx. 24 h h at each of the following EtOH concentrations: 80, 85, 90, 95, and 100% for each grade (repeated 3 times at 100%)], and further dehydrated by critical point drying (Samdri-780A, Tousimis Research Corporation, Rockville, MD). Next, antennae were removed from each specimen and placed on carbon coated aluminum stubs (Ted Pella Inc., Redding, CA) so the dorsal and ventral sides were exposed. Maxillary and labial palps were placed with lateral proximal and distal sides relative to the insect head and photographed. Specimens were immediately sputter coated with a gold/palladium (50/50) in Denton Vacuum Desc III® (Denton Vacuum LLC, Moorestown, NJ) sputter coater and examined in a tungsten low vacuum scanning electron microscope at either the Florida Department of Agriculture Division of Plant Industry (DPI) (JSM 5510LW) or University of Florida's ICBR Electron Microscopy Core Lab in Gainesville, FL. Micrographs of the ten most proximal, ten most distal and ten midsection flagellomeres were obtained for adults, and all flagellomeres of the nymphal antennae were examined. Sensilla length and basal diameter were measured on ten sensilla of each type on each specimen. The number of each sensilla type per flagellomere for adults and nymphs was compared among *Scapteriscus* spp. using analysis of variance (GLM procedure, SAS Institute, 2008) with species and sex (only for adults) as factors and the number of sensilla per flagellomere as the dependent variable. Counts per unit usually follow a Poisson distribution, but at a large sample size (>20) it approximates a Gaussian distribution, which allows the use of parametric statistics.

### TRANSMISSION ELECTRON MICROSCOPY (TEM)

*Scapteriscus vicinus* antennae were immersed in Trump's Fixative (Electron Microscopy Sciences, Hatfield, PA). Fixed tissues were processed with the aid of a Pelco BioWave laboratory microwave (Ted Pella, Redding, CA, USA). The samples were washed in 0.1M sodium cacodylate pH 7.24, post-fixed with 2% $OsO_4$, water-washed and dehydrated in a graded ethanol series (25, 50, 75, 95, and 100%) followed by 100% acetone. Dehydrated antennae were infiltrated in graded acetone/Spurrs epoxy resin (Ellis 2006; 30, 50, 70, and 100%) and cured at 60 °C. Cured resin blocks were trimmed, thin sectioned and collected on formvar copper slot grids, post-stained with 2% aq. uranyl acetate and Reynold's lead citrate. Sections were examined with a Hitachi H-7000 TEM (Hitachi High Technologies America, Inc., Schaumburg, IL) and digital images acquired with a Veleta 2k×2k camera and iTEM software (Olympus Soft-Imaging Solutions Corp, Lakewood, CO).

## Results

### ANTENNAL MORPHOLOGY

All 4 mole cricket species had typical antennae: a scape, a pedicel (true segments, capable of active movement), and a multisegmental filiform flagellum that tapered distally. The flagellum consisted of approx. 70 and 32 flagellomeres for adults and neonates, respectively. When alive, they positioned their antennae in front of them, parallel to the body axis with an approx. 90° angle between antennae. If individuals were alert or an odor was introduced, the antennae were lifted perpendicular to the body axis with the angle preserved. Mole crickets vigorously examined the environment with their antennae and palps while tunneling or moving forward in a tunnel. When grooming, antennae were bent into the mouth with the forelegs.

Slight cuticular constrictions were considered as segmental boundaries for the basal segments of the flagellum, but the midsection and distal antennal regions had distinct sutures (Fig. 1). The number of adult flagellomeres and antennal length differed among the mole cricket species and sexes (Table 1). *Neocurtilla hexadactyla* numerically had the most flagellomeres (85.3 ± 2.8), but this species was excluded from the statistical analysis due to the small sample size. *Scapteriscus borellii* (82.1 ± 1.2) had the most flagellomeres among the other species examined, followed by *S. abbreviatus* (76.8 ± 1.4), and *S. vicinus* (73.1 ± 0.9) had the fewest flagellomeres ($F = 19.0$; df = 2, 59; $P < 0.01$). No structural dimorphism was observed in any of the 3 *Scapteriscus* species, but female *S. borellii* and *S. vicinus* had significantly more flagellomeres compared to their males ($F = 19.2$; df = 1, 59; $P < 0.01$) (Table 1). Flagellomere dimensions changed with the proximity to the pedicel. The most proximal flagellomeres were short and wide (length

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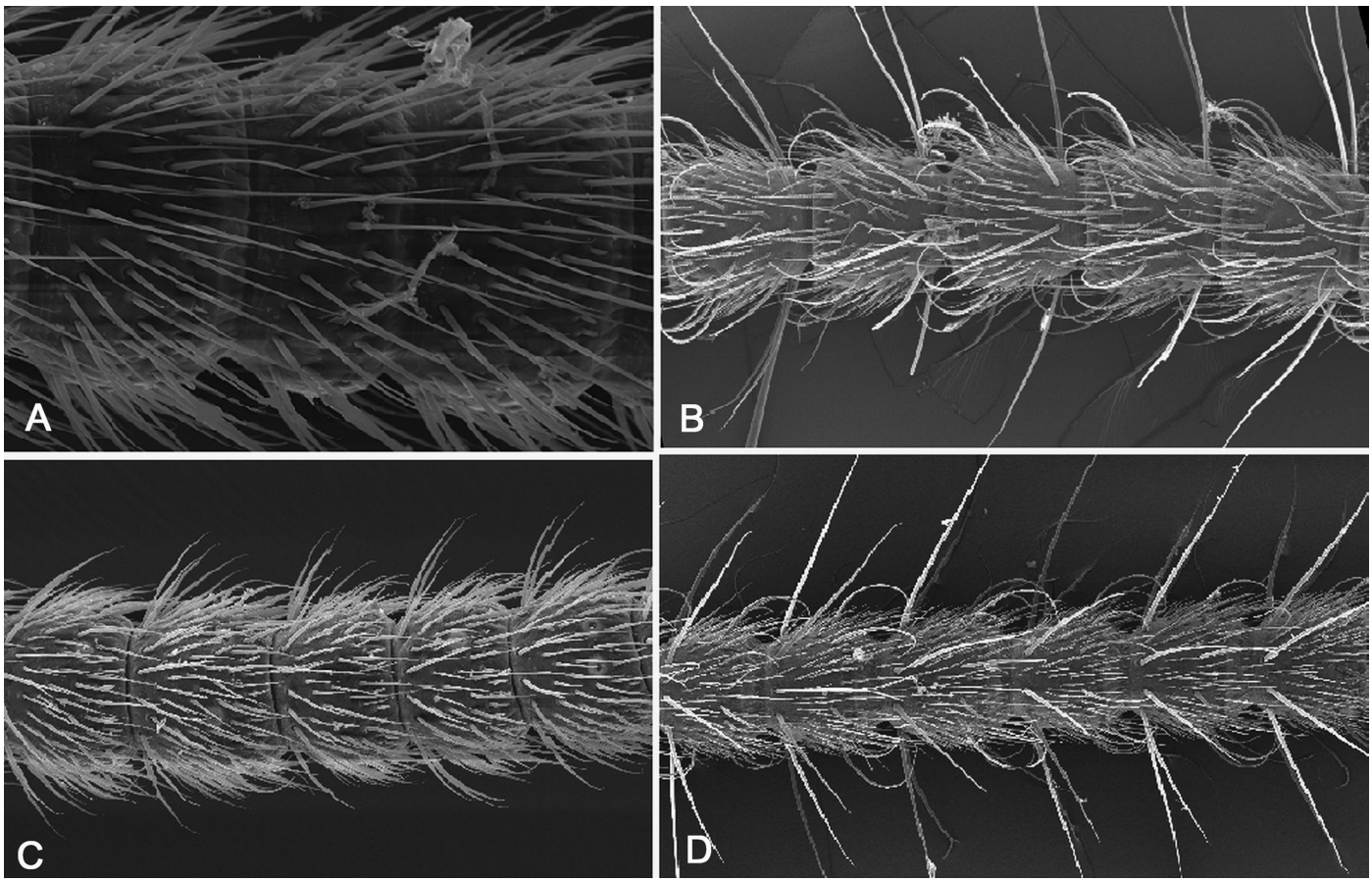



**Fig. 1.** SEM photos of the flagellum mid-section of *N. hexadactyla* (A), *S. abbreviatus* (B), *S. vicinus* (C) and *S. borellii* (×140) (D).

to width ratio = 0.5), in the mid-section flagellomeres were slightly longer (length to width ratio = 0.6), and distal segments were longer than wide (length to width ratio = 1.2).

## ANTENNAL GROWTH DURING POST-EMBRYONIC DEVELOPMENT

The pronotum lengths of *S. vicinus* and *S. borellii* nymphs were strongly associated with the number of their flagellomeres ($R^2$ = 0.82, $P$ < 0.01 and $R^2$ = 0.80, $P$ < 0.01, respectively) and antennal length ($R^2$ = 0.91, $P$ < 0.01 and $R^2$ = 0.90, $P$ < 0.01, respectively). Our prediction model suggested that 6-8 flagellomeres were added to an antenna with each molt. Moreover, the total number of sensilla per antennal segment in adults was significantly greater (up to 120), compared to nymphs (≤ 60) (Tables 2 and 3). The flagellum of neonate *Scapteriscus* spp. had an average of 32 segments, which is less than half of the number of flagellomeres on adult antennae (Table 1). However, *S. abbreviatus* nymphs, on average, had longer antennae (3.3 mm) than the other 2 species (2.7 mm). For all species, flagellum length tripled during nymphal development (Table 1). Nymphal and adult antennae had the same types of sensilla; only quantitative changes were observed.

**Table 1.** Flagellum measurements of four mole cricket species.

| Species | Life stage | No. antennal pairs | Flagellum length, Mean ± SEM (mm) | No. flagellomeres, Mean ± SEM[1] |
|---|---|---|---|---|
| *S. vicinus* | Adult ♂ | 10 | 9.6 ± 0.1 | 70.0 ± 0.9 a |
| | Adult ♀ | 10 | 8.9 ± 0.2 | 75.8 ± 0.9 b |
| | Neonate | 10 | 2.7 ± 0.1 | 32.5 ± 0.2 |
| *S. borellii* | Adult ♂ | 10 | 11.6 ± 0.2 | 78.0 ± 0.9 a |
| | Adult ♀ | 10 | 10.2 ± 0.2 | 86.2 ± 1.3 b |
| | Neonate | 10 | 2.7 ± 0.1 | 32.5 ± 0.6 |
| *S. abbreviatus* | Adult ♂ | 10 | 10.9 ± 0.2 | 75.6 ± 1.8 a |
| | Adult ♀ | 10 | 10.9 ± 0.1 | 78.1 ± 2.3 a |
| | Neonate | 10 | 3.3 ± 0.04 | 32.3 ± 0.7 |
| *N. hexadactyla* | 1♀, 2 late nymphs | 3 | — | 85.3 ± 2.8 |

[1]Mean number of flagellomeres were compared between males and females of each species; means marked with the same letters are not statistically different at $\alpha$ = 0.05 ($F$ = 19.2; df = 1, 59; $P$ < 0.01)

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**Table 2.** Sensilla types and abundance on adult *S. abbreviatus, S. borellii* and *S. vicinus* antennae.

| | | No. sensilla per flagellomere (Mean ± SEM) | | |
|---|---|---|---|---|
| Species | Type of sensilla | Distal | Middle | Proximal |
| *S. vicinus,* ♂ | *s. chaetica* | 88.7 ± 1.9 | 107.9 ± 2.3 | 82.7 ± 2.9 |
| | *s. basioconica* | 6.1 ± 0.9 | 13.4 ± 0.7 | 5.5 ± 0.7 |
| | *s. trichodea* | 1.7 ± 0.3 | 2.5 ± 0.2 | 2.1 ± 0.4 |
| | *s. coeloconica (I)* | 0.7 ± 0.1 | 1.2 ± 0.1 | 1.3 ± 0.3 |
| | *s. coeloconica (II)* | 0.9 ± 0.1 | 1.0 ± 0.1 | 0.5 ± 0.1 |
| | *s. campaniform* | 0.9 ± 0.1 | 0.5 ± 0.1 | 0.2 ± 0.1 |
| *S. vicinus,* ♀ | *s. chaetica* | 102.8 ± 1.1 | 120.7 ± 1.4 | 85.2 ± 2.0 |
| | *s. basioconica* | 11.2 ± 0.6 | 15.1 ± 0.9 | 6.3 ± 0.5 |
| | *s. trichodea* | 1.9 ± 0.1 | 2.5 ± 0.2 | 1.9 ± 0.1 |
| | *s. coeloconica (I)* | 0.7 ± 0.1 | 0.7 ± 0.1 | 1.0 ± 0.1 |
| | *s. coeloconica (II)* | 0.5 ± 0.1 | 0.8 ± 0.1 | 0.2 ± 0.1 |
| | *s. campaniform* | 0.8 ± 0.1 | 0.3 ± 0.1 | 0.3 ± 0.1 |
| *S. borellii,* ♂ | *s. chaetica* | 112.3 ± 2.4 | 118.8 ± 2.4 | 90.4 ± 2.5 |
| | *s. basioconica* | 9.6 ± 0.6 | 6.8 ± 0.4 | 3.0 ± 0.4 |
| | *s. trichodea* | 2.2 ± 0.3 | 2.1 ± 0.3 | 2.0 ± 0.2 |
| | *s. coeloconica (I)* | 0.9 ± 0.1 | 0.8 ± 0.1 | 0.8 ± 0.2 |
| | *s. coeloconica (II)* | 0.7 ± 0.1 | 0.7 ± 0.1 | 0.3 ± 0.1 |
| | *s. campaniform* | 0.7 ± 0.1 | 0.6 ± 0.1 | 0.5 ± 0.1 |
| *S. borellii,* ♀ | *s. chaetica* | 100.4 ± 1.7 | 120.0 ± 2.4 | 104.2 ± 3.1 |
| | *s. basioconica* | 10.8 ± 0.6 | 15.2 ± 0.8 | 3.9 ± 0.2 |
| | *s. trichodea* | 2.4 ± 0.4 | 2.2 ± 0.3 | 1.8 ± 0.2 |
| | *s. coeloconica (I)* | 1.0 ± 0.1 | 0.7 ± 0.1 | 1.0 ± 0.2 |
| | *s. coeloconica (II)* | 0.6 ± 0.1 | 0.8 ± 0.1 | 0.2 ± 0.1 |
| | *s. campaniform* | 0.9 ± 0.1 | 0.9 ± 0.1 | 0.6 ± 0.1 |
| *S. abbreviatus,* ♂ | *s. chaetica* | 118.5 ± 2.4 | 127.2 ± 2.6 | 81.4 ± 2.4 |
| | *s. basioconica* | 7.9 ± 1.4 | 6.3 ± 1.0 | 3.8 ± 2.2 |
| | *s. trichodea* | 2.1 ± 0.4 | 2.8 ± 0.5 | 1.9 ± 0.4 |
| | *s. coeloconica (I)* | 0.7 ± 0.1 | 0.3 ± 0.1 | 0.2 ± 0.1 |
| | *s. coeloconica (II)* | 1.3 ± 0.3 | 1.4 ± 0.3 | 0.3 ± 0.1 |
| | *s. campaniform* | 0.9 ± 0.1 | 0.5 ± 0.2 | 0.1 ± 0.1 |
| *S. abbreviatus,* ♀ | *s. chaetica* | 126.5 ± 2.4 | 135.1 ± 3.4 | 81.4 ± 3.4 |
| | *s. basioconica* | 10.7 ± 2.4 | 11.3 ± 2.1 | 9.8 ± 3.2 |
| | *s. trichodea* | 2.5 ± 0.4 | 2.9 ± 0.4 | 1.6 ± 0.4 |
| | *s. coeloconica (I)* | 0.6 ± 0.1 | 0.5 ± 0.1 | 0.3 ± 0.1 |
| | *s. coeloconica (II)* | 1.5 ± 0.3 | 1.2 ± 0.3 | 0.5 ± 0.1 |
| | *s. campaniform* | 0.9 ± 0.1 | 0.5 ± 0.2 | 0.1 ± 0.1 |

## TYPES, ABUNDANCE AND DISTRIBUTION OF SENSILLA ON MOLE CRICKET ANTENNAE

Mostly *sensilla chaetica, s. campaniformia* and Böhm sensilla were on the pedicel and scape (Fig. 2). *Sensilla chaetica* and *s. campaniformia* were also present on the flagellum. However Böhm sensilla were located specifically at articulations of 2 segments in 2 parallel rows (20 total sensilla) on the scape and 2 angled rows (10 total sensilla) on the pedicel (Fig. 2). At least 5 types of sensilla were observed on antennae flagellum, including *s. basioconica*, *s. chaetica* (3 types), *s. coeloconica* (2 types), *s. campaniform*, and *s. trichodea*. For all species examined, the midsection of the antennae had the most sensilla.

### *S. chaetica*

These sensilla were the most abundant on mole cricket antennae (up to 120 per segment) (Table 2). The surface of these sensilla had transverse ridges with no evidence of wall pores (Fig. 3 A, B). Three types of *s. chaetica* were observed based on their size and distribution pattern on the antennae. Type I were relatively large *s. chaetica* (~100 µm long and 5 µm wide) and they created ring–like transverse patterns (relative to the antennal axis) at the base of an antennal segment (Fig. 1 B, D and Fig. 3 C). They were relatively straight, in contrast to other types of sensilla which were medium (type II) in size and curved toward the following antennal segment. Medium *s. chaetica* (~60 µm long and 3 µm base diameter) usually were observed in the rows at the distal part of the segment. The smallest *s. chaetica* (type III) were distributed evenly on the antennal segment (40 µm long and 2 µm base diameter). Wall pores were not observed on the *s. chaetica* and TEMs showed that the larger *s. chaetica* (types I and II) were filled with dense material with no evidence of dendritic processes in the lumen (Fig. 4 A, B). However small (type III) *s. chaetica* were innervated (Fig. 4 C, D).

### *S. basioconica*

Each antennal segment had on average 5-6 (range, 3 to 12) *s. basioconica* (18.1 µm long, 2.25 µm base diameter) near the tip of each segment (Fig. 5). These sensilla had non-flexible sockets and a thin wall pierced with numerous pores, and most likely had an olfactory

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**Table 3.** Sensilla types and abundance on *S. abbreviatus, S. borellii* and *S. vicinus* neonate antennae.

| Species | Sensilla type | No. sensilla per flagellomere (Mean ± SEM) |
|---|---|---|
| *S. vicinus* | *s. chaetica* | 52.3 ± 0.7 |
| | *s. basioconica* | 6.0 ± 0.2 |
| | *s. trichodea* | 1.6 ± 0.1 |
| | *s. coeloconica (I)* | 0.7 ± 0.1 |
| | *s. coeloconica (II)* | 0.6 ± 0.0 |
| | *s. campaniform* | 0.6 ± 0.1 |
| *S. borellii* | *s. chaetica* | 51.0 ± 0.6 |
| | *s. basioconica* | 3.5 ± 0.2 |
| | *s. trichodea* | 1.8 ± 0.3 |
| | *s. coeloconica (I)* | 0.3 ± 0.0 |
| | *s. coeloconica (II)* | 0.5 ± 0.1 |
| | *s. campaniform* | 0.7 ± 0.1 |
| *S. abbreviatus* | *s. chaetica* | 63.4 ± 0.7 |
| | *s. basioconica* | 4.7 ± 0.7 |
| | *s. trichodea* | 2.1 ± 0.9 |
| | *s. coeloconica (I)* | 0.5 ± 0.1 |
| | *s. coeloconica (II)* | 0.6 ± 0.2 |
| | *s. campaniform* | 0.5 ± 0.1 |

function. For all of the mole cricket species, all the sensilla types were about the same size, although the *s. basiconica* of *N. hexadactyla* were shorter (7.5 µm long, 1.85 µm wide) than in the other species (Fig. 6).

### *S. trichodea*

These hair-like structures were on the distal (top) part of each segment (Fig. 7 A). One to 2 *s. trichodea* were on each flagellomere. Each sensillum was ~40 µm long with a basal diameter of 2 µm. External morphology of these sensilla was similar to *s. basioconica*; sensilla had smooth surfaces pitted with pores, but were more slender and longer than *s. basioconica. S. trichodea* could be confused with *s. chaetica*, although the former lacks a flexible pocket and their surface was pitted, not ridged. TEM examination of *s. trichodea* revealed the presence of dendrites in the sensilla lumen and wall pore (Fig. 7 B).

### *S. coeloconica*

Two main types of *s. coeloconica* (0 to 6 per antennal segment) occurred on mole cricket antennae. Type I *s. coeloconica* were located in the cuticular pits (Fig. 8 A). An external diameter of bulging cuticle surrounded its round opening. Type II *s. coeloconica* were located on the cuticle surface (Fig. 8 B). These sensilla varied in size, but as with *s.*

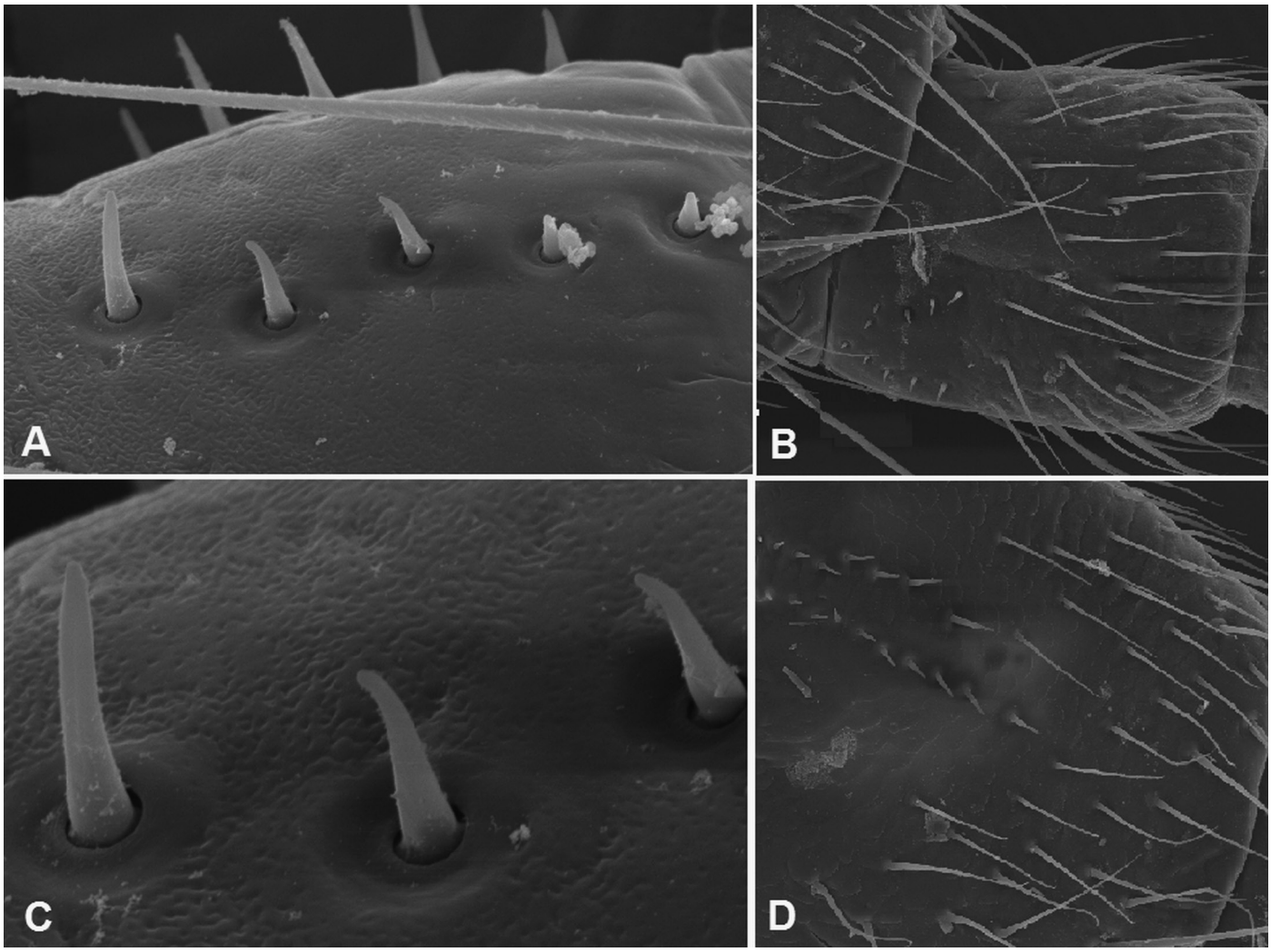



**Fig. 2.** Böhm sensilla (*Bs*) (SEM, ×1.1k and ×2K) (A, B) on the *S. abbreviatus* pedicel (×500) (C) and scape (×650) (D).

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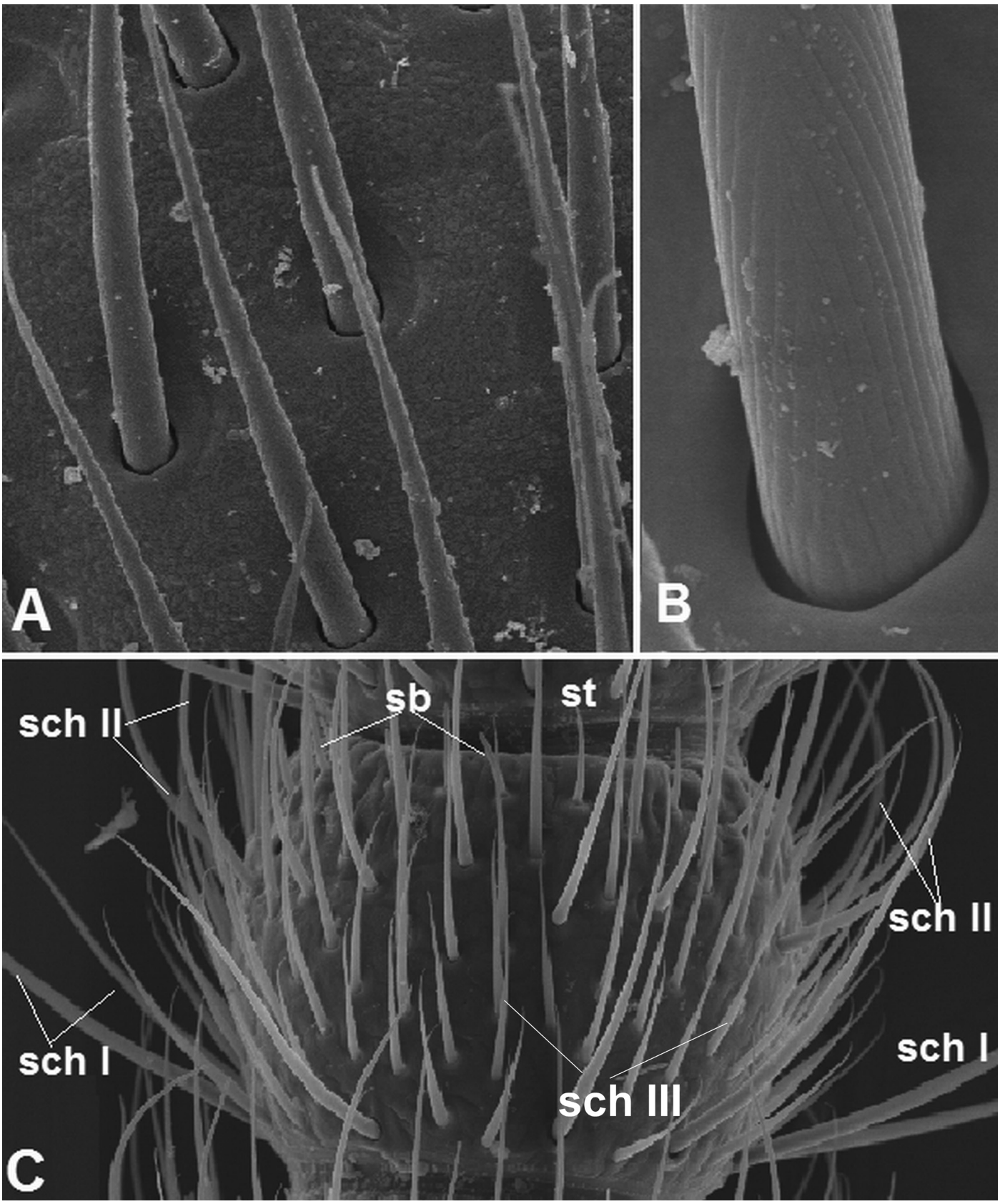



**Fig. 3.** *Sensilla chaetica*, the most abundant sensilla on *S. vicinus* antennae. Antennal surface of *S. vicinus* with *s. chaetica* positioned in the flexible sockets (maginifaication ×9k) (A), aporous ridged surface of the sensillum (magnification ×6k) (B), antennal segment and different types of sensilla, *s. chaetica* types I and II (schI and II), arranged into transverse patterns, type III *s. chaetica* (sch III) are small and evenly distributed on the flagellomere (×600) (C). Row of *s. basioconica* (sb) and *s. trichodea* (si) (C) usually observed on the apical portion of the flagellomere.

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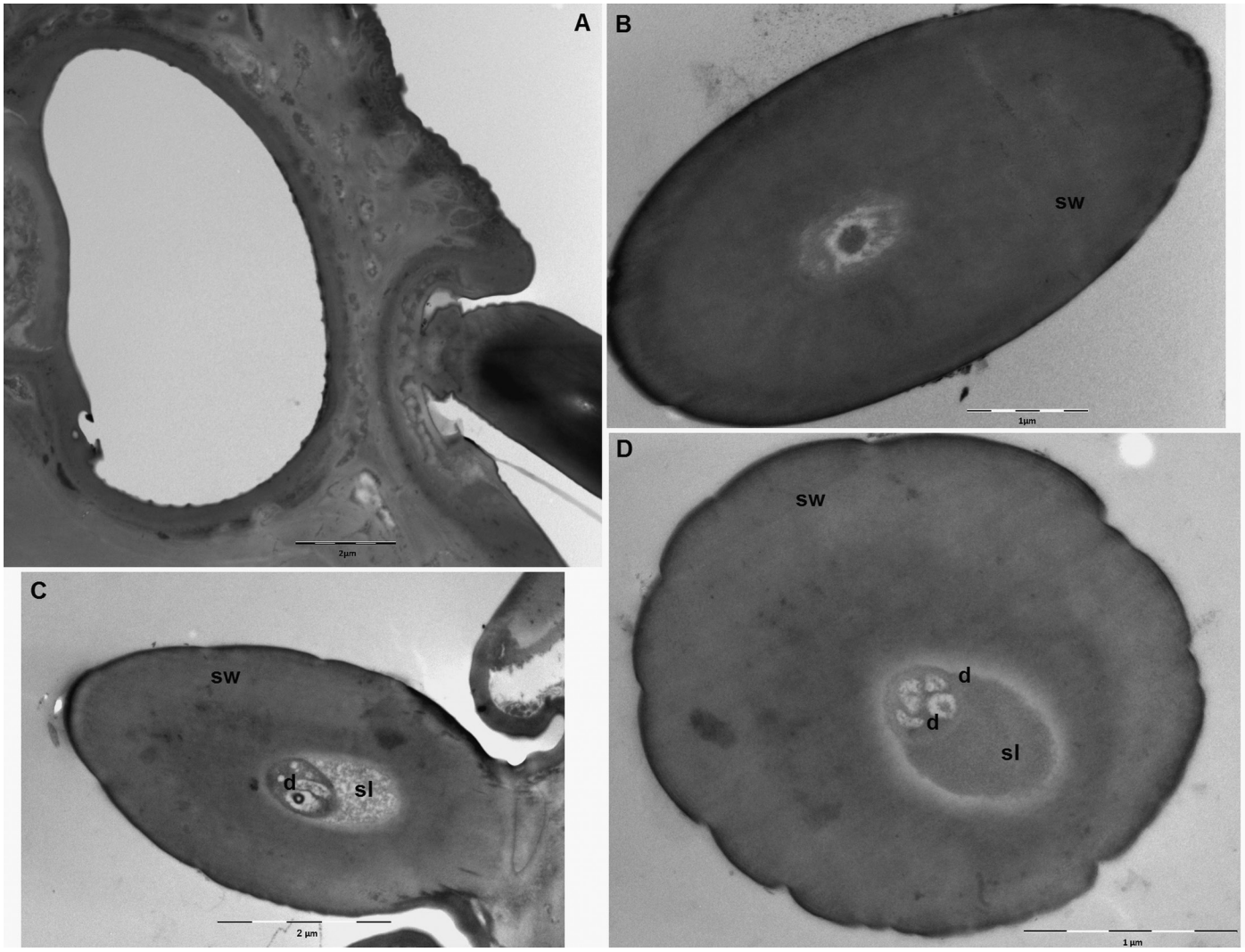



**Fig. 4.** Transmission electron micrographs of *s. chaetica* type I and II (A, B) which are not innervated and are dense inside with thick sensillum wall (sw), type III *s. chaetica* have less dense sensillar lumen (sl) and are innervated with 4 dendrites (d) (C, D).

*basioconica* and *s. trichodea*, were almost always located on the apical part of each segment.

### *S. campaniformia*

These sensilla were on the palps and nearly every flagellomere. They had a round or ovoid central area (cap of the sensilla) encircled by a cuticular ring. The dimensions of *s. campaniformia* of the antennae were on average 3 and 6 µm for the inner and outer circles, respectively (Fig. 8 C, D). Their dimensions ranged from 9 × 16 µm to 5 × 65 µm. This type of sensilla was present on various parts of the insect body and occurred on each mole cricket species examined.

## TYPES, ABUNDANCE AND DISTRIBUTION OF SENSILLA ON MOLE CRICKET MAXILLARY AND LABIAL PALPS

The tips of the maxillary and labial palps were weakly sclerotized, with a distinct sensillar field of about 0.35 mm², which was densely covered with sensilla of different types and functions (Fig. 9A). About 0.2 sensilla were found per µm² on the palps. Most of the observed sensilla on maxillary and labial palps matched the description of *s. chaetica* (Keil 1999), which are usually associated with mechanoreception and contact chemoreception (Fig. 9 B). SEM inspection indicated that they had slits/grooves at least on one side, which suggested they might be multifunctional. Other sensilla on the maxillary and labial palps were *s. coeloconica* with tip pores (Fig. 9 C, D), tip-pore sensilla (Fig. 9 E), and club-like *s. basioconica* (Fig. 9 F).

## DIFFERENCES IN SENSILLA TYPES, SIZES, ABUNDANCE AND DISTRIBUTION AMONG MOLE CRICKET SPECIES, SEXES AND LIFE STAGES

The numbers of *s. chaetica* (I, II and III types combined) and *s. basioconica* varied depending on mole cricket species, sex and location on the antennae. On average, *S. borellii* and *S. abbreviatus* had more *s. chaetica* compared to *S. vicinus* ($F = 17.5$; df = 1, 567; $P < 0.001$). The middle part of the antennae had more *s. chaetica* ($F = 95$; df = 3, 567; $P < 0.001$) and *s. basioconica* ($F = 60.4$; df = 3, 567; $P < 0.001$) than the distal and basal parts. Sensilla were more abundant on female antennae ($F = 51.2$; df = 1, 567; $P < 0.001$) than on male antennae for all species.

All described types of sensilla were found on the nymphal antennae, and the 3 *Scapteriscus* species doubled the number of segments and sensilla per segment during their development. On average, *S. abbreviatus* had more *s. chaetica* per flagellomere than *S. vicinus* (*F* =

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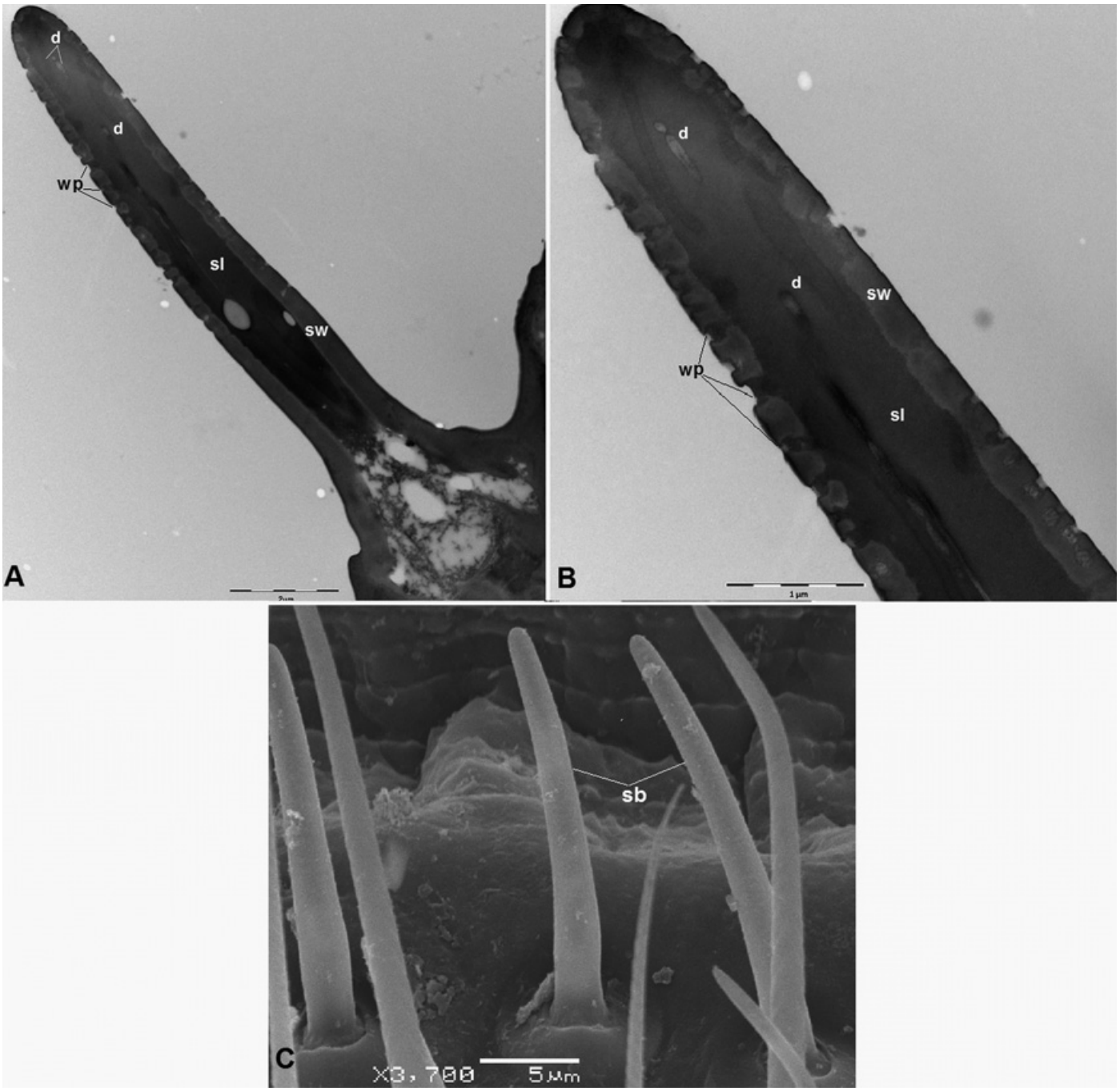



**Fig. 5.** Transmission electron micrographs (A, B) and the longitudinal section of *s. basioconicum* (sb), located on the tip of the each segment (C), indicate presence of the wall pore (wp), sensilla lumen (sl) and dendrites (d).

97.9; df = 1, 559; $P < 0.001$). *Scapteriscus abbreviatus* had the most *s. basioconica* and *S. borellii* had the fewest of these sensilla among the 3 species ($F = 92.7$; df = 1, 559; $P < 0.001$).

## Discussion

### PUTATIVE FUNCTION OF SENSILLA ON MOLE CRICKET ANTENNAE AND PALPS

Sensilla function can be deduced from their morphological structure (Altner 1977), which is supported by many studies where morphological examination was combined with electrophysiology (Boeckh 1967; Zacharuk 1980; Klein et al. 1988; Keil 1999; Blaney et al. 2005). The presence of pores suggests a chemosensory function for sensilla because they are the entry gate for odorant molecules into the sensillum lumen (Steinbrecht 1997). Single and double wall sensilla are 2 morphologically distinct types of olfactory sensilla (Steinbrecht 1969; Altner 1977; Altner & Peillinger 1980). Single wall olfactory sensilla are usually multiporous (Keil 1999), such as *s. basioconica* and *s. trichodea* on mole cricket antennae. Sensilla with tip pores can function in both gustation and mechanoreception, and occur on mole cricket maxillary and labial palps. The presence of the wall-pores and dendritic endings suggests an olfactory function for these sensilla.

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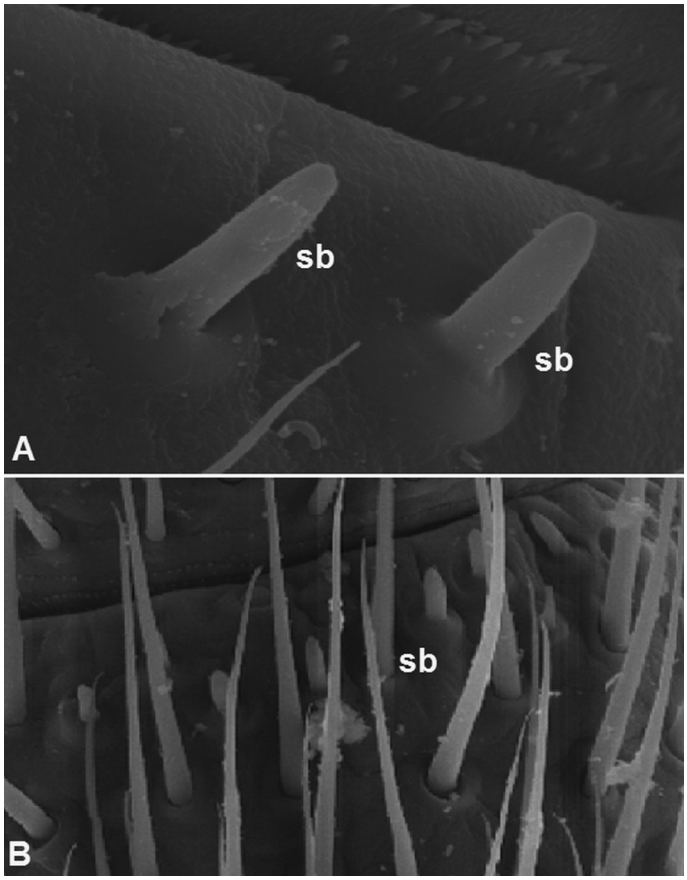



**Fig. 6.** Short *s. basioconica* (×22k and 15k) (sb) (A), arranged in transverse row on the apical part of antennal segment of *N. hexadactyla* (×900) (B).

Aporous sensilla (*s. chaetica*, type I and II) were predominant for the 4 mole cricket species examined. Their morphology and distribution suggest mechanoreceptory functions. Their arrangement in rows perpendicular to the antennal axis suggests their sensitivity to very fine air movements, media flow and/or low frequency sound and vibrations (Keil 1999; Barth 2004; Humphrey & Barth 2008). The lack of wall pores and the presence of dendritic endings in the lumen suggest a gustatory function of *s. chaetica* type III. Our findings are similar to the previous description of *s. chaetica* of other insect taxa (Hallberg 1981; Jorgensen et al. 2007; Crook et al. 2008). Although similar in appearance, 2 different functional types were reported: aporous (usually large) with mechanoreceptory function and tip-pores that are innervated with additional chemosensory (mostly gustatory) neurons. The prevalence of antennal *s. chaetica* was also previously documented for other species. Particularly, antennae of American (*Periplaneta americana* (L.)) and Australian (*Paratemnopteryx* spp.) cockroaches are covered with similar sensilla, arranged in transverse rows. Electrophysiological recordings have shown that these types of sensilla respond to chemical and mechanical stimulation, especially to a conspecific tergal secretion, which is a component of the mating process (Hansen-Delkeskamp 1992; Bland et al. 1998). Having gustatory sensilla on the antennae corresponds with the antennating behaviors of mole crickets in the presence of odorants. The role of chemoreception in mole cricket mate recognition has not been studied, but many cricket species use cuticular pheromones in close range intraspecific recognition (Otte & Cade 1976; Rence & Loher 1977; Hardy & Shaw 1983; Tregenza & Wedell 1997). Interspecific and intersexual differences in mole cricket cuticular lipid composition suggest their involvement in intra- and interspecific recognition (Castner & Nation 1984).

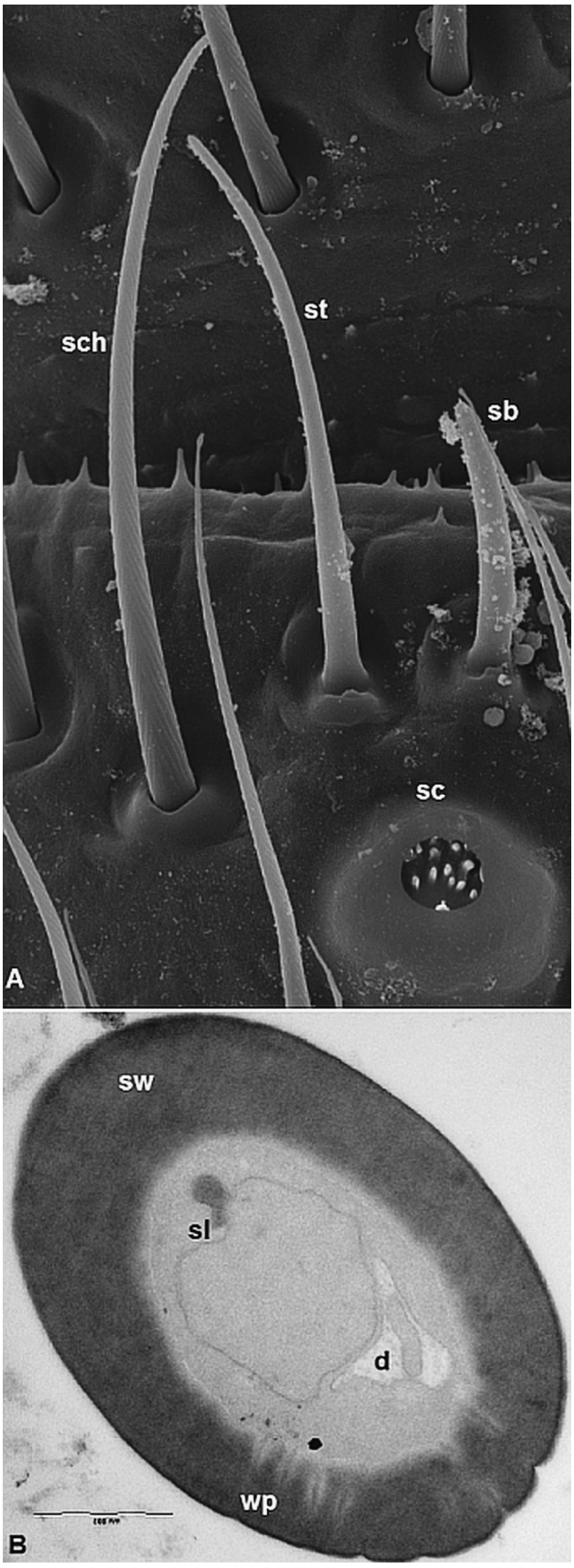



**Fig. 7.** *Sensillum trichodium* (st) located at the distal part of flagllomere together with *s. chaeticum* (sch), *s. basioconicum* (sb) and *s. coeloconicum* (sc) (×9k) (A); cross-section of *s. trichodium* (B) showing presence of the sensillum lumen (sl) with dendrites (d) and thick wall (sw) with pores (wp) (C).

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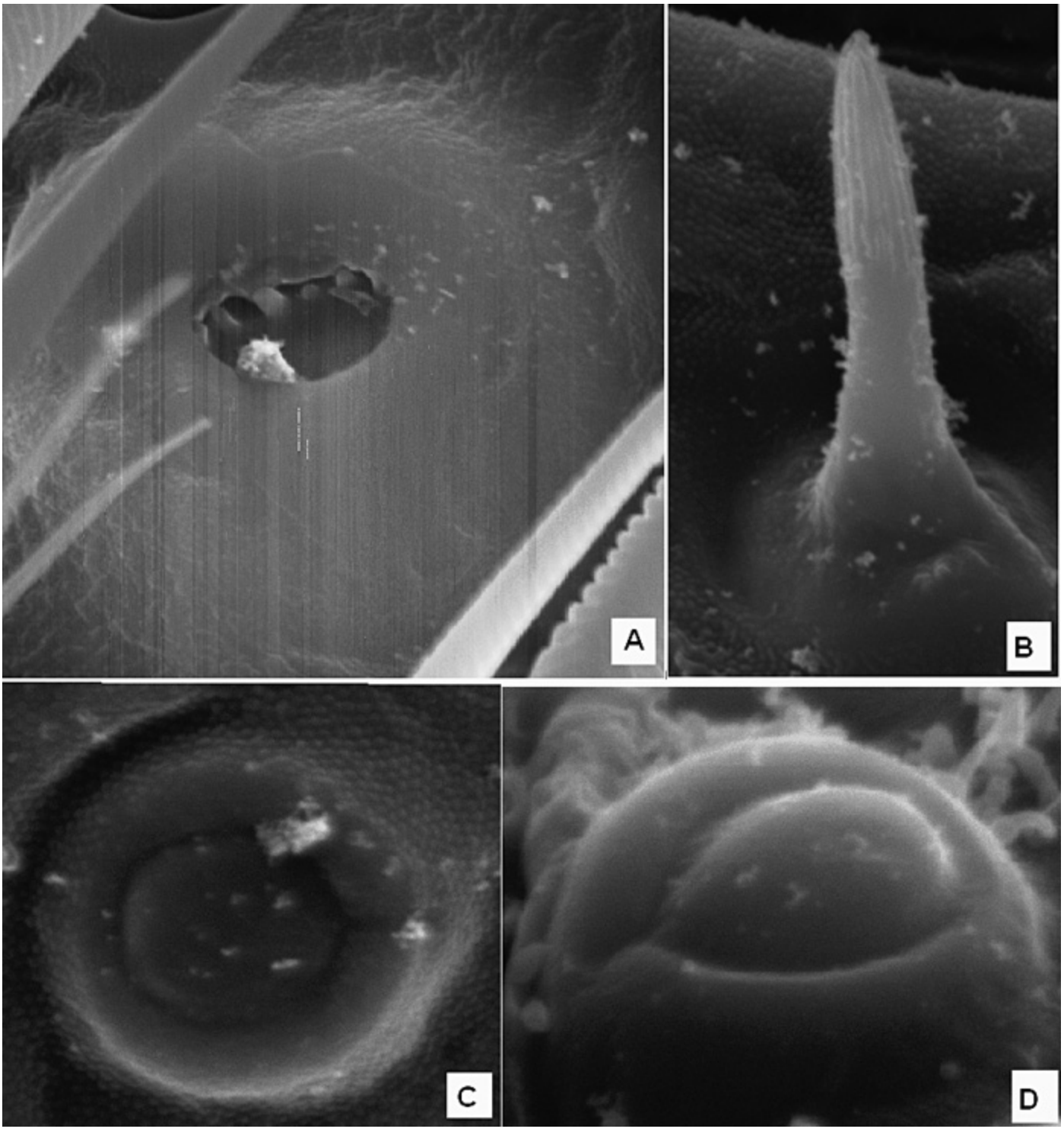



**Fig. 8.** Antennal *s. coeloconicum* (type I), located in the cuticular pit (×28k) (A), in contrast to *s. ceoloconicum* (×25k) (type II) positioned on the antennal surface (B). *S. campaniformia*, proprioreceptor, can be located on the tip of the segment (× 17k ) (C) and at the midsection (× 21k) (D).

The intraspecific behavioral responses of *S. vicinus* to anal gland secretions further support the importance of chemoreception in mole cricket communication. *Scapteriscus vicinus* anal glands (Kidd 1825) secrete an odorous compound which is mixed with feces and excreted when an individual is disturbed, and thus may serve a defensive role. Laboratory Y-tube assays demonstrated that such secretions from one sex of *S. vicinus* adults illicited no response by the opposite sex. But, secretions of the same sex were repellent for both male and female *S. vicinus* (Kostromytska 2010). *Neocurtilla hexadactyla* also secretes a sticky substance when attacked by parasitoids (*Larra* spp.) which facilitates the mole cricket's escape (Walker & Masaki 1989).

*Sensilla coeloconica*, or double-walled sensilla, consist of partially fused cuticular fingers, are multiporous, and are often only olfactory (McIver 1973; Hunger & Steinbrecht 1998). They can be located in pits or stand on the cuticle, and both of these types were observed on mole cricket antennae and palps in our study. Cuticular pits could facilitate

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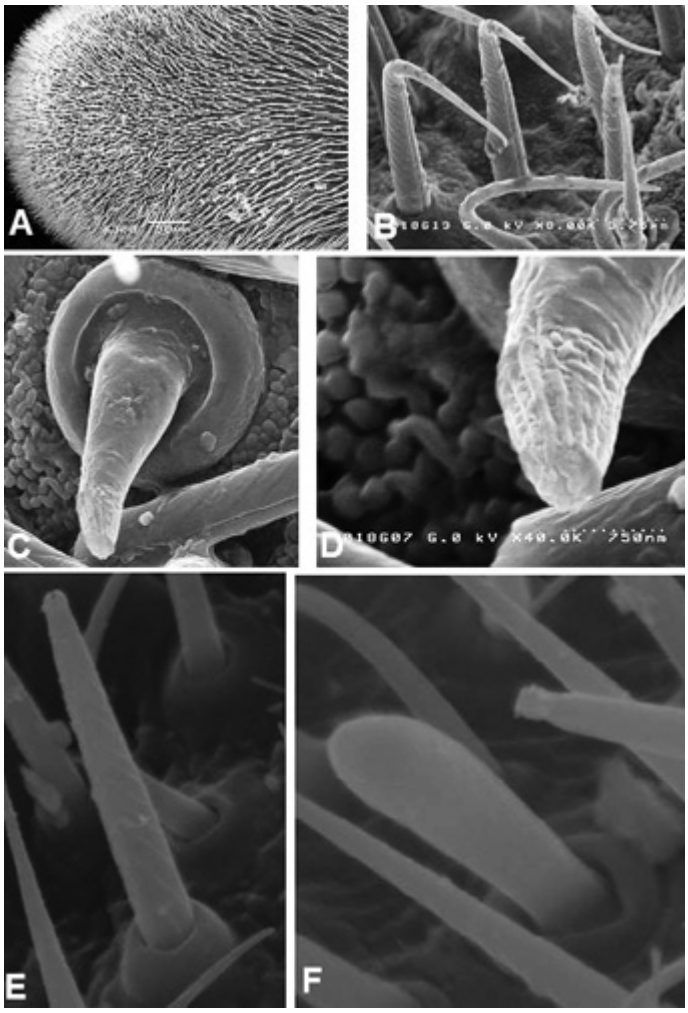



**Fig. 9.** Mole cricket labial and maxillary palps are densely covered with sensilla (× 300) (A). The dominant type is *s. chaetica* (× 8k) (B), other types include *s. coeloconica* (×15k) (C) with tip-pore (× 40k) (D), single-wall tip-pore sensilla (× 9k) (E) and club-like *s. basioconica* (× 11k) (F).

selectivity of sensilla to specific odors or protect against moisture loss (Altner 1977; Hunger & Steinbrecht 1998).

Sensilla on the pedicel and scape (*s. chaetica*, *s. campaniformia* and Böhm sensilla) are more likely to serve mechanoreceptory functions, potentially informing mole crickets about antennal position and movement. These structures are described mostly in beetles (Merivee et al. 1998). *Sensilla campaniformia* alternatively are proprioreceptors that detect cuticle deformation (Moran et al. 1971; Keil 1999).

Only about 10% of mole cricket antennal sensilla have chemosensory functions, whereas many other insect species primarily have olfactory sensilla. The dominance of mechanoreceptor structures could be explained by the subterranean habits of mole crickets and limited air movement. Mechanical stimulation by the soil surrounding them may more directly influence their complex tunneling behavior. Within newly created tunnels, mole crickets are constantly antennating, and repeatedly correct the tunnel shape and width (O. Kostromytska, personal observation). In addition, they use sound for intraspecific communication (e.g., mate location, aggression) (Walker & Masaki 1989). In spite of mechanoreceptor dominance, mole crickets apparently possess complex chemosensory capabilities that are enabled by at least 3 types of antennal sensilla and 3 types of palpal sensilla. The types and abundance of sensilla on mole cricket antennae differ greatly from those found in above-ground orthopterans, such as Tetrigidae and Acrididae (Bland 1989, 1991). The chemosensory structures observed here and, in preceding work, are similar to the structures on cockroach antennae (Hansen-Delkeskamp 1992; Bland et al. 1998).

### POSTEMBRYONIC DEVELOPMENT OF MOLE CRICKET ANTENNAE

The exact number of nymphal instars of *S. vicinus*, *S. borellii* and *S. abbreviatus* is unknown. An estimation made by Matheny & Stackhouse (1980) using pronotum length as a diagnostic character suggested the presence of 7 and 6 instars for *S. vicinus* and *S. borellii*, respectively, which is consistent with our results. Consequently, pronotum measurements were used to estimate the developmental stage of these 2 species; but only *S. abbreviatus* neonates could be examined. Variation in size within each instar may be a source of error in the model, but results show clearly that the number of flagellomeres and antennal length significantly increased with each molt, allowing the accommodation of more sensilla. If the estimated number of sensilla per antenna are compared between neonatal (avg. = 50) and adult mole crickets (avg. = 110), it is clear that the number of sensilla of different modalities on the antennae significantly increased during postembryonic development. Thus mole crickets increased their number of sensilla during development by increasing flagellomere surface area and increasing the number of flagellomeres with each molt. This also occurs for other hemimetabolous insects (Chinta et al. 1996).

### SIMILARITIES OF ANTENNAE, PALPS AND SENSILLA STRUCTURE AMONG SPECIES AND SEXES

Chemosensory structures were morphologically very similar across the 4 mole cricket species. *Neocurtilla hexadactyla* was the most taxonomically distinct species examined (both quantitatively and based on sensilla structure), but the primary structural difference was the size of the *s. basioconica*. Only the number of sensilla differed among the other species. These differences could be related to differences in feeding habits and life style. For instance, *S. borellii* had more antennal sensilla per segment and more flagellomeres, suggesting greater sensitivity to stimuli, which may be necessary for its predatory feeding habits. Although both are herbivores, *S. abbreviatus* had more antennal sensilla and flagellomeres than *S. vicinus*. This may be relevant for mate location, since *S. abbreviatus* cannot fly, whereas the other 3 species can.

Structural sexual dimorphism was not detected among these species, although females had more flagellomeres than males. Male mole crickets were observed clipping the antennae of other males, possibly as an act of aggression. High magnification was needed to detect clipped antennae, and despite all attempts to select adults with seemingly intact antennae, clipping activity may still have contributed to some variation in antennal length among species and sexes. The complexity of sensory structures usually correlates with their function, which directly correlates with fitness, reproductive success, and evolutionary success of a species. For example, mole cricket females might be more sensitive to environmental stimuli because they respond to male auditory signals, which also affects their selection of favorable oviposition sites. Of note is that females of other hemimetabolous species also tend to have longer antennae than males (Chinta et al. 1996).

## Conclusions

This study was the first to describe and compare the antennal and palpal sensory structures of 4 mole cricket species. Mechanoreceptory sensilla were most prevalent on the antennae and palps. Olfactory and gustatory sensilla also occurred on mole cricket antennae, but the palps had predominately gustatory sensilla. Given that mole cricket reproductive and oviposition behaviors, and habitats were similar, it follows that all structural characteristics were highly conserved across

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species, life stages and sexes. Mole cricket detection of chemicals (e.g., insecticides) applied to the soil could be associated with the presence and abundance of chemosensory sensilla on their mouthparts and antennae. Sensitivity to chemical stimuli corresponds with the number of receptors involved (Keil 1999), and sensitivity increased with age (as the number of sensilla per antenna increased with each molt), thus hypothetically, mole cricket females may be more chemically sensitive than males. These findings provide a foundation for behavioral and electrophysiological studies to further investigate and compare sensory functions.

## Acknowledgments

We are grateful for P. Skelley's (Florida Department of Agriculture Division of Plant Industry) assistance with SEMs and the University of Florida's ICBR Electron Microscopy Core Lab. Funding was provided by the U.S. Golf Association.

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