

UDC 595.7—14:595.7—11

Enno MERIVEE*

ANTENNAL SENSILLAE OF THE FEMALE AND MALE ELATERID BEETLE *AGRIOTES OBSCURUS* L. (COLEOPTERA: ELATERIDAE)

Abstract. Sensillae of the antennae of *Agriotes obscurus* L. (Coleoptera: Elateridae) were studied with the scanning electron microscope (SEM) to determine their morphological types, relative abundance, distribution, location and possible functions. 12 types and subtypes of hairlike structures can be distinguished from the SEM micrographs of the antennae of both male and female beetle: sensillae trichodea (subtypes T1 and T2), sensillae chaetica (subtypes C1 and C2), sensillae basiconica (subtypes B1, B2, B3, B4, B5, B6, B7), dome-shaped sensillae (D). Last ones are obviously sensillae coeloconica. All types and subtypes of sensillae have characteristic distribution and location pattern that is similar in both sexes. Only the number of sensillae T2 in the male beetle is many times larger than that in the female beetle (716 on one antenna in the male beetle and 150 on one antenna in the female beetle). Comparison of T2 sensillae with pheromone receptors of other insect species shows that obviously T2 sensillae are the pheromone receptors in the male *Agriotes obscurus*.

Introduction

The elaterid beetle *Agriotes obscurus* L. is a serious pest whose larvae, living in the soil, attack a wide range of different crops in Central and North Europe and Siberia (Долин, 1978; Гурьева, 1979). The use of synthetic sex pheromones in the estimation of the population density of the adult beetles and larvae (Гук, 1987), in the determination of the flight dynamics (Ивашенко, 1981), and in the control with the male-female pheromone communication disruption methods (Олещенко et al., 1986; Олой, 1987) seems to be promising in elaterid beetles. The two main components in the sex pheromone of the female *A. obscurus*, geranyl-hexanoate and geranyl-octanoate, have been identified (Borg-Karlson et al., 1988; Олещенко et al., 1986). The sex pheromone of *A. obscurus* synthesized at the Institute of Chemistry of the Estonian Academy of Sciences has a high biological activity, but lacks the species-specific effect, since the male beetles of the related species *A. lineatus* also fall into pheromone traps (Мяхар, 1985). It has been shown that the secretion of the pheromone gland of the female *A. obscurus* contains, besides the two main components, also a number of minor components (Яцынин et al., 1988); however, data about their biological effect are lacking. In order to use synthetic pheromone preparations more effectively in the control of the elaterid beetles, further work is required, including electrophysiological and ethological studies on male receptivity to the female sex pheromone. A prerequisite for such studies is an understanding of the morphology of the antennal sensilla.

* Eesti Teaduste Akadeemia Zooloogia ja Botaanika Instituut (Institute of Zoology and Botany, Estonian Academy of Sciences). Vanemuise 21, EE2400 Tartu, Estonia,

Several reviews deal with the structure and function of the receptors found on insect antennae (Schneider, 1964; Slifer, 1970; McIver, 1975; Keil and Steinbrecht, 1984; Елизаров, 1978), and a small body of literature is devoted to the receptors of various beetles. To date, no work is known to have been done on antennal receptors in elaterid beetles.

Material and methods

The newly emerged adults of the males and females of *A. obscurus*, used in the present study, were collected from fields in South Estonia. For examination with the scanning electron microscope (SEM) the antennae of freshly killed specimens were isolated from the head, cleaned by gentle sonification in distilled water and 70% ethanol for 1 minute, attached vertically to aluminium stubs and dried in the air before being coated with gold in a vacuum evaporator. Observations and microphotographs were performed using a "BS-301" (Tesla) SEM at 16–18 kV.

The antennae of ten male and ten female beetles were observed and photographed with a small magnification, more important sections also with a larger magnification (up to 6000 \times). The outer surface of one male and one female antenna was photographed all over, from four to six sides, with the magnification 2500–3200 \times . Additional microphotos were taken of a single sensilla with the magnification up to 16000 \times . Altogether about 900 microphotos were taken. Sensillar measurements, numbers, distribution and location were determined from SEM montage microphotographs of one male and one female antenna.

Results and discussion

Structure of male and female antennae

The serrate flagellar antennae of *A. obscurus* have a length of 2.7–3.9 mm and consist proximally of two basal segments, the scape and pedicel, and distally of the flagellum composed of nine segments (Figs. 1, 16, 17, 18, 19, 20, 21). Of these antennal segments the first is the longest and the third is the shortest (Fig. 2). No morphological differences were noted between the male and female antennae in terms of their general structure and form.

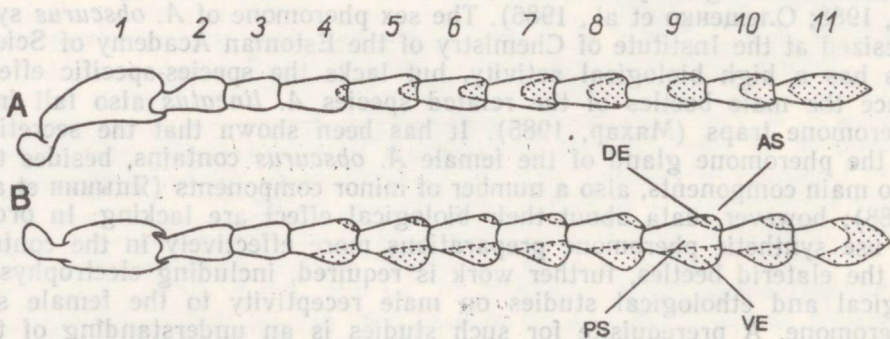


Fig. 1. Right antenna of the elaterid beetle *A. obscurus* from above (A) and from behind (B). Dotted line denotes the dorsal (DE) and ventral (VE) extensions of segments. AS — anterior side of the segment; PS — posterior side of the segment.

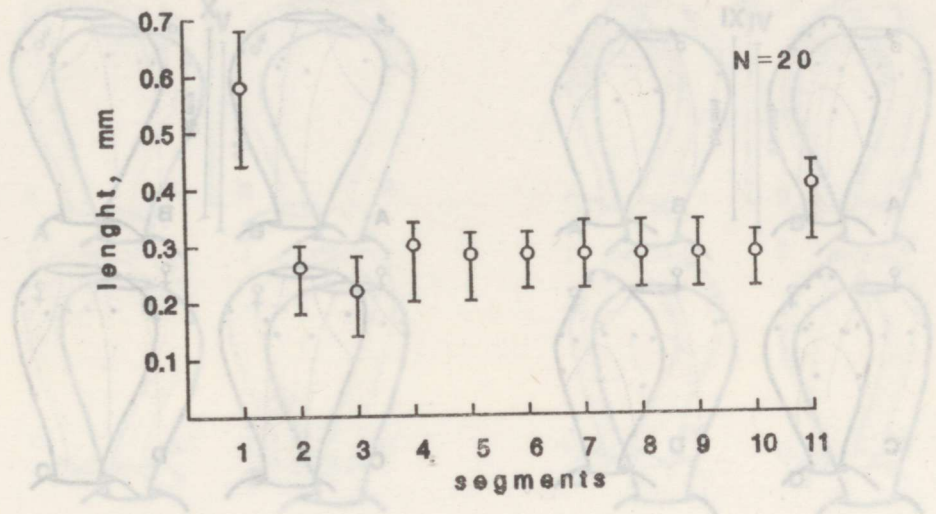


Fig. 2. Average lengths of the segments of the male antenna of *A. obscurus*. Vertical bars denote the range.

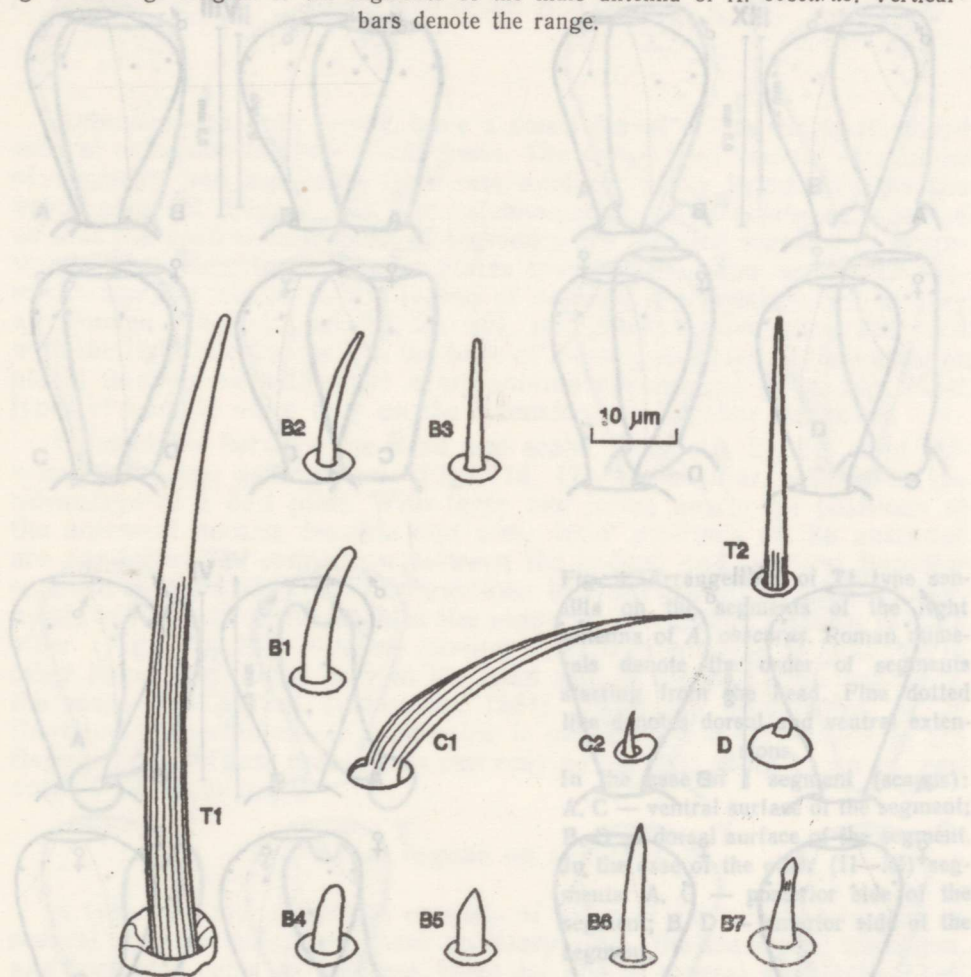


Fig. 3. Morphological types of the sensilla located on the antennae of *A. obscurus*. For explanations see the text.

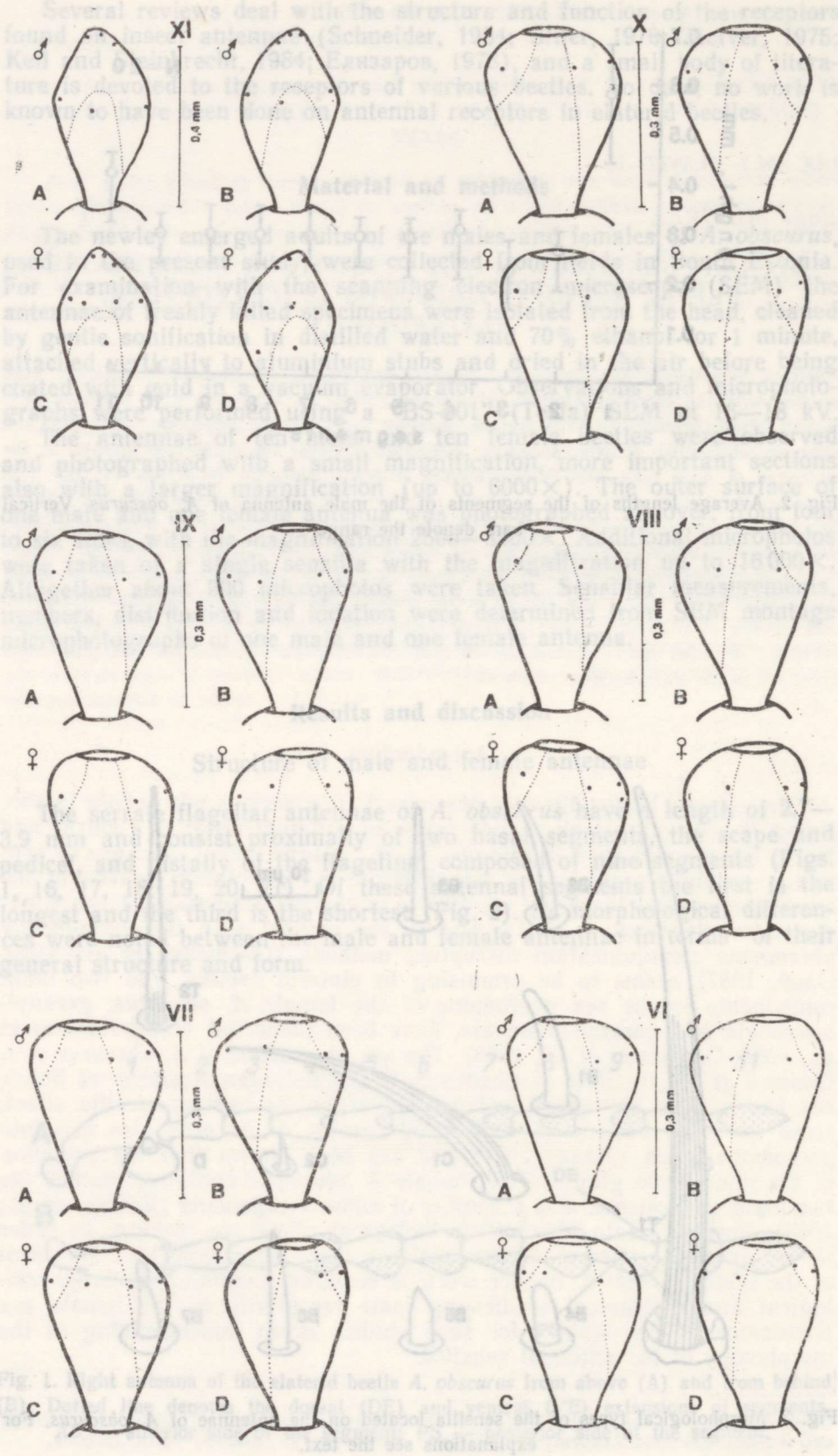


Fig. 1. Right antenna of the water beetle *A. obscurus* from above (A) and from behind (B) and left antenna of the same beetle from above (C) and from behind (D). The structures of the sensilla located in the segments of the antenna are indicated by dots. For explanations see the text.

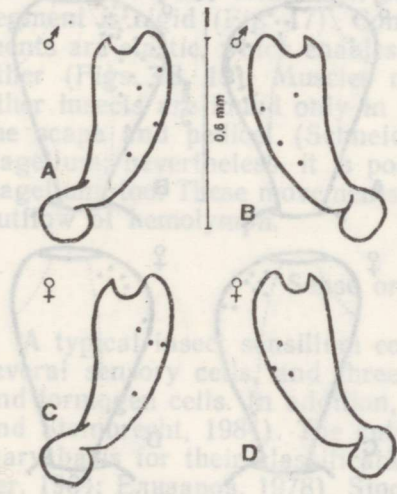
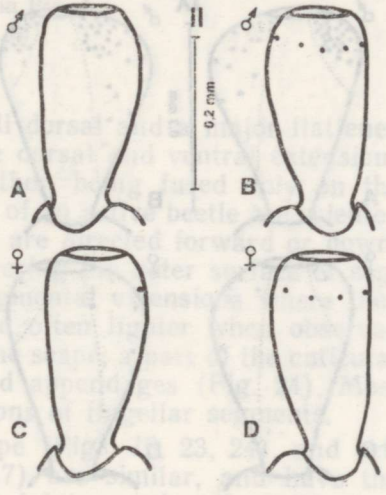
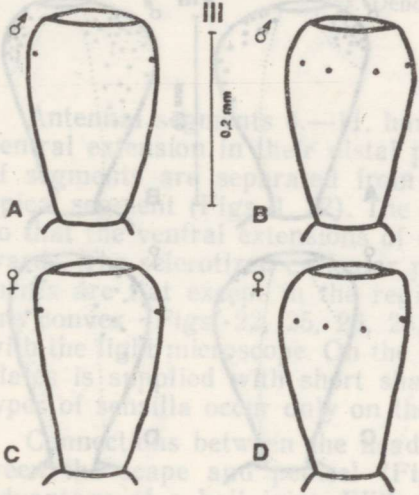
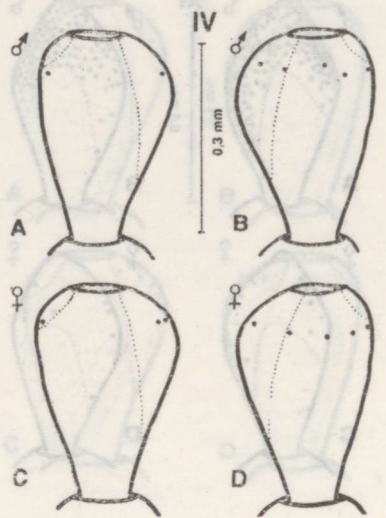
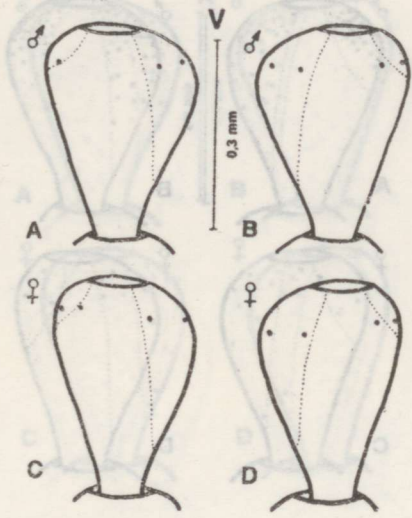
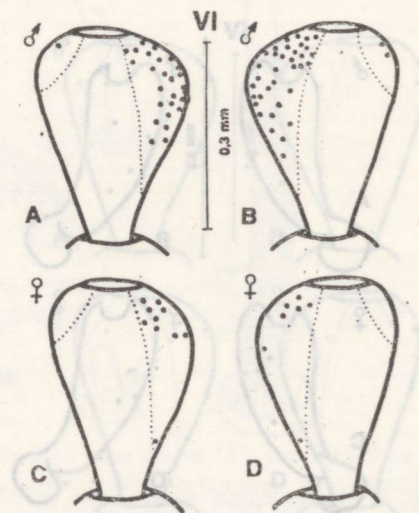
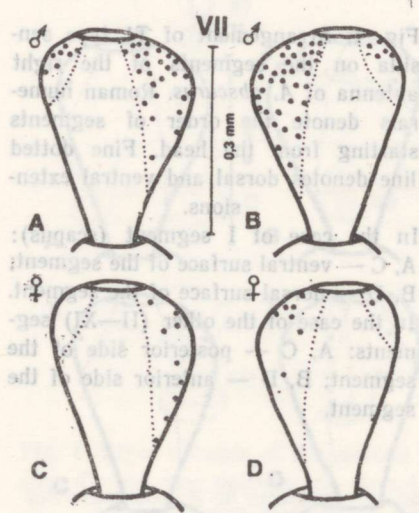
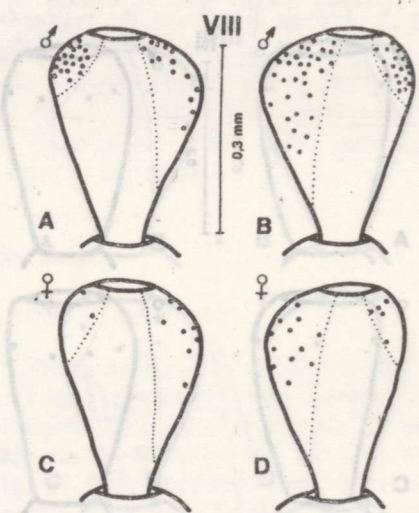
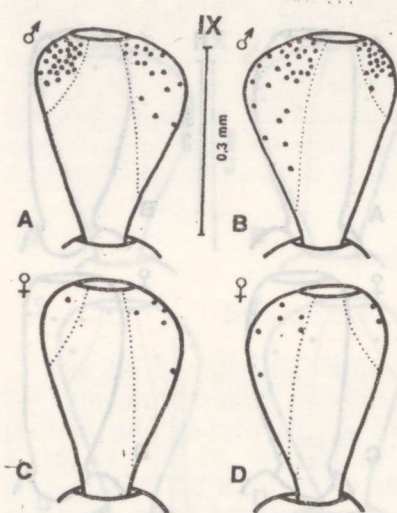
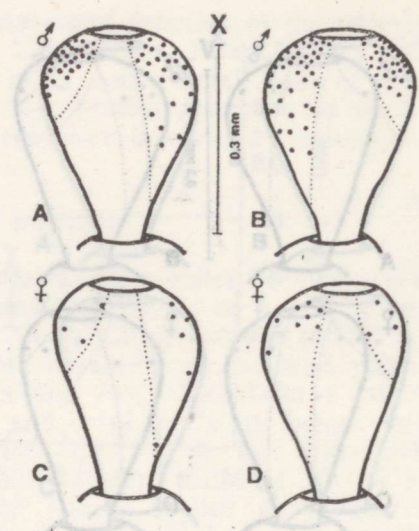
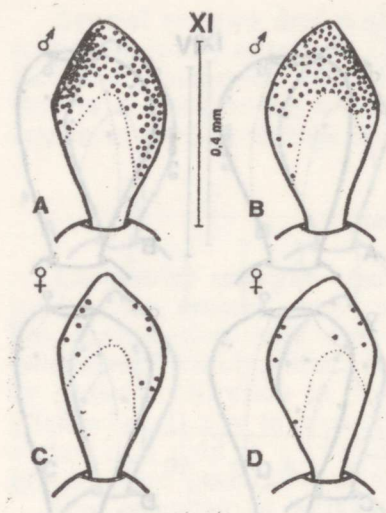


Fig. 4. Arrangement of T1 type sensilla on the segments of the right antenna of *A. obscurus*. Roman numerals denote the order of segments starting from the head. Fine dotted line denotes dorsal and ventral extensions.

In the case of I segment (scapus): A, C — ventral surface of the segment; B, D — dorsal surface of the segment. In the case of the other (II—XI) segments: A, C — posterior side of the segment; B, D — anterior side of the segment.



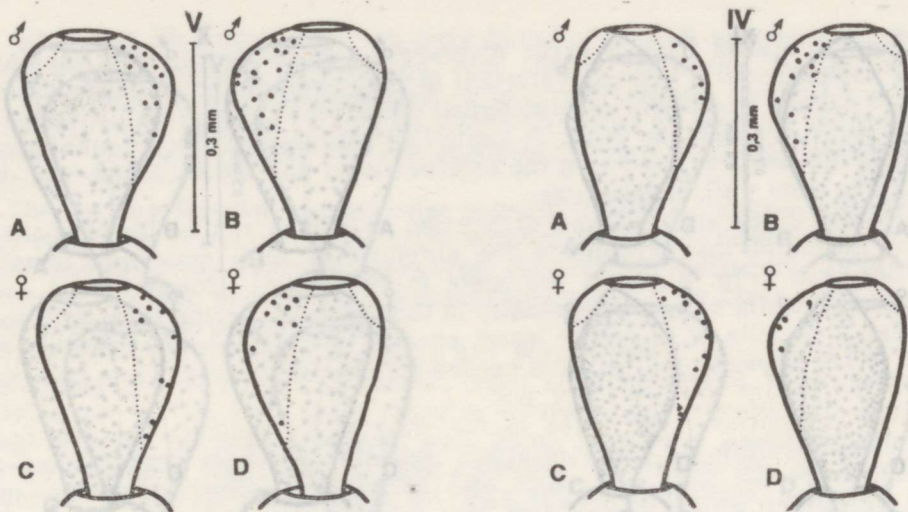


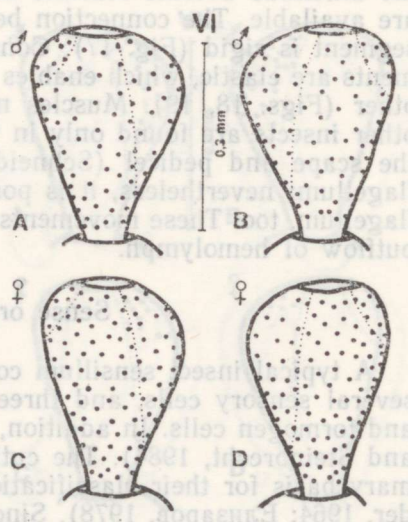
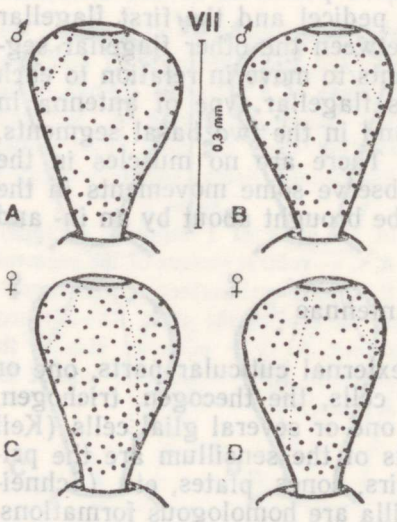
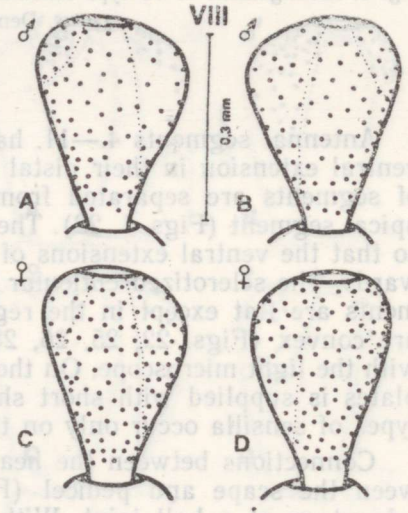
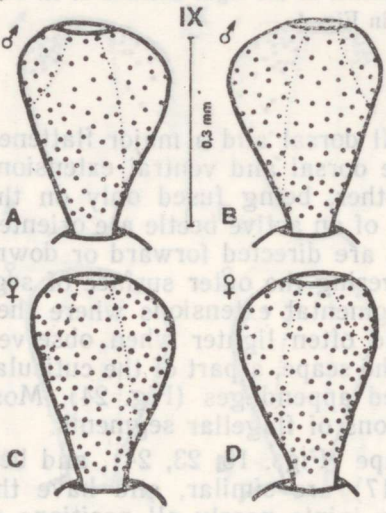
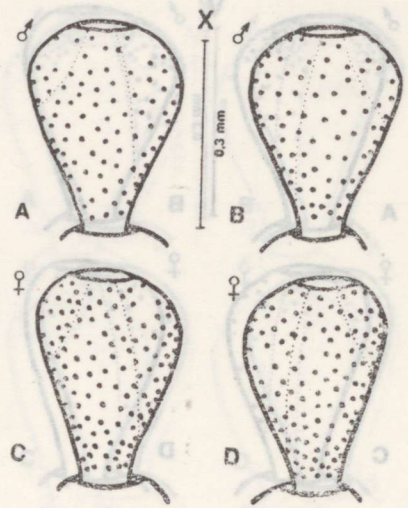
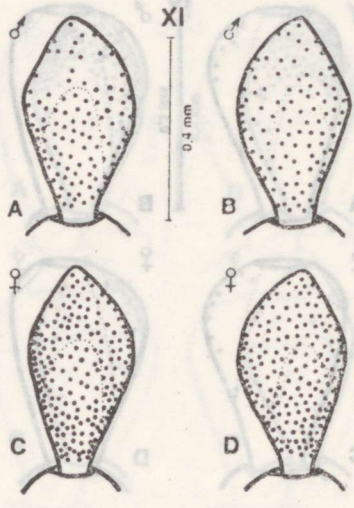
Fig. 5. Arrangement of T2 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

Antennal segments 4.—11. have a small dorsal and a major flattened ventral extension in their distal parts. The dorsal and ventral extensions of segments are separated from one another, being fused only on the apical segment (Figs. 1, 22). The antennae of an active beetle are oriented so that the ventral extensions of segments are directed forward or downwards. The sclerotized cuticular plates covering the outer surface of segments are flat except in the region of segmental extensions where they are convex (Figs. 22, 25, 26, 28, 32), and often lighter when observed with the light microscope. On the base of the scape, a part of the cuticular plates is supplied with short sharp-pointed appendages (Fig. 24). Most types of sensilla occur only on the extensions of flagellar segments.

Connections between the head and scape (Figs. 16, 23, 24), and between the scape and pedicel (Figs. 16, 17) are similar, and have the advantage of a ball joint. With these two joints nearly all positions of the antennae become feasible and some fixed positions of the antennae are available. The connection between the pedicel and the first flagellar segment is rigid (Fig. 17). Connections between the other flagellar segments are elastic, which enables the segments to move in relation to each other (Figs. 18, 19). Muscles moving this flagellar type of antenna in other insects are found only in the head and in the two basal segments, the scape and pedicel (Schneider, 1964). There are no muscles in the flagellum; nevertheless, it is possible to observe some movements in the flagellum, too. These movements can only be brought about by an in- and outflow of hemolymph.

Sense organs on antennae

A typical insect sensillum consists of external cuticular parts, one or several sensory cells, and three auxiliary cells, the thecogen, trichogen, and tormogen cells. In addition, there are one or several glial cells (Keil and Steinbrecht, 1984). The cuticular parts of the sensillum are the primary basis for their classification into hairs, cones, plates, etc. (Schneider, 1964; Елизаров, 1978). Since all sensilla are homologous formations,



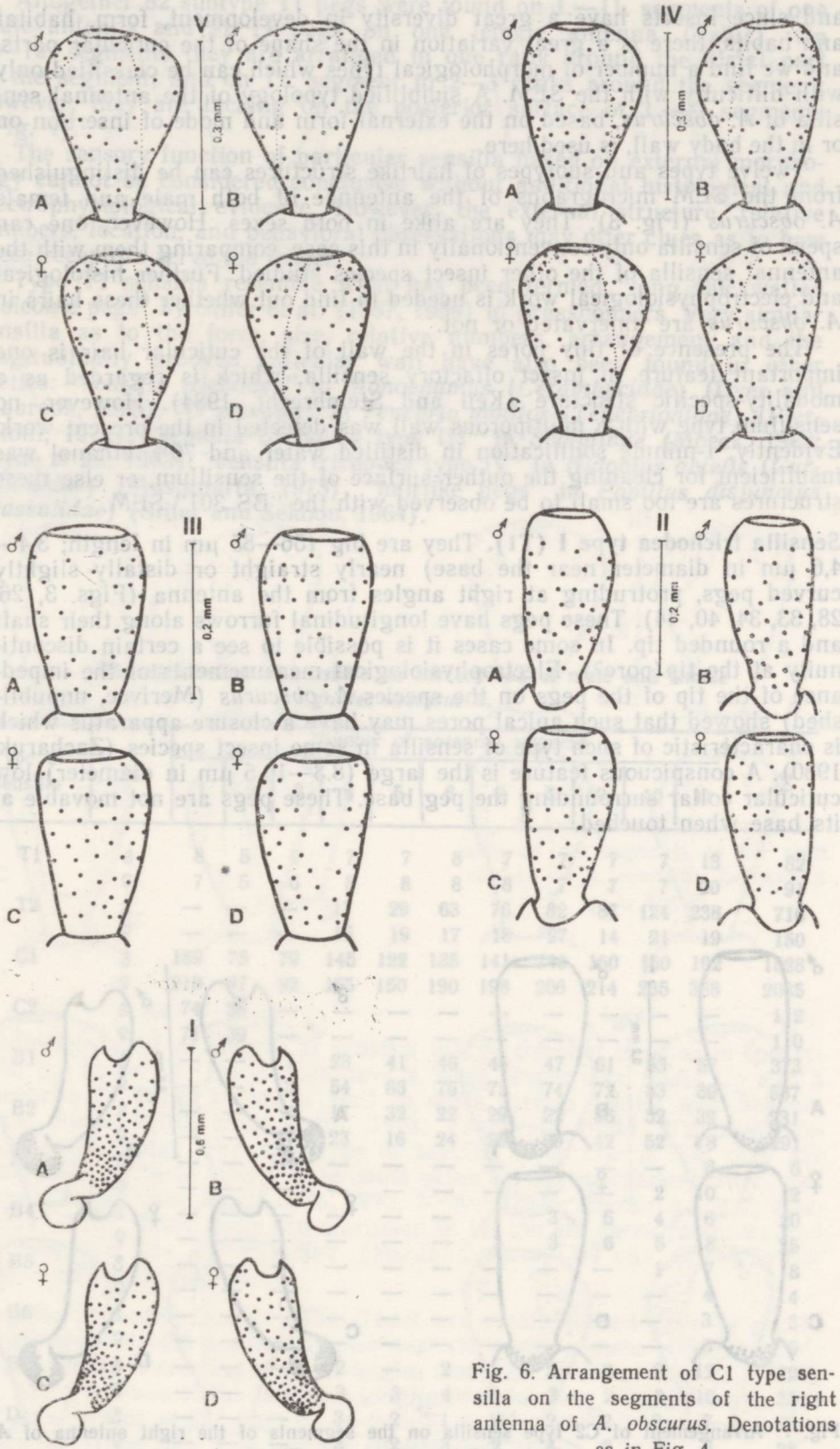


Fig. 6. Arrangement of C1 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

and since insects have a great diversity in development, form, habitat and habits, there is a great variation in the shape of the cuticular parts, and we find a number of morphological types which can be classified only with difficulty with the SEM. A simplified typology of the antennal sensilla of *A. obscurus*, based on the external form and mode of insertion on or in the body wall, is used here.

Twelve types and subtypes of hairlike structures can be distinguished from the SEM micrographs of the antennae of both male and female *A. obscurus* (Fig. 3). They are alike in both sexes. However, one can speak of sensilla only conventionally in this case, comparing them with the antennal sensilla of the other insect species studied. Further histological and electrophysiological work is needed to find out whether these hairs in *A. obscurus* are innervated or not.

The presence of tiny pores in the wall of the cuticular hair is one important feature in insect olfactory sensilla, which is regarded as a modality-specific structure (Keil and Steinbrecht, 1984). However, no sensillum type with a multiporous wall was detected in the present work. Evidently, 1-minute sonification in distilled water and 70% ethanol was insufficient for cleaning the outer surface of the sensillum, or else these structures are too small to be observed with the "BS 301" SEM.

Sensilla trichodea type I (T1). They are big (56–85 μm in length; 3,4–4,6 μm in diameter near the base) nearly straight or distally slightly curved pegs, protruding at right angles from the antenna (Figs. 3, 26, 28, 33, 34, 40, 44). These pegs have longitudinal furrows along their shaft and a rounded tip. In some cases it is possible to see a certain discontinuity at the tip (pore?). Electrophysiological measurements of the impedance of the tip of the pegs on the species *A. obscurus* (Merivee, unpublished) showed that such apical pores may have a closure apparatus which is characteristic of such type of sensilla in some insect species (Zacharuk, 1980). A conspicuous feature is the large (8.3–10.5 μm in diameter) low cuticular collar surrounding the peg base. These pegs are not movable at its base when touched.

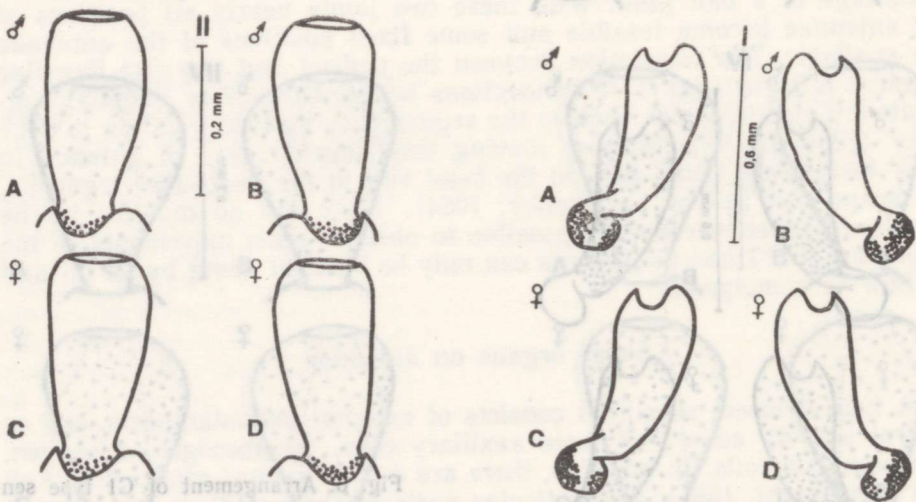


Fig. 7. Arrangement of C2 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

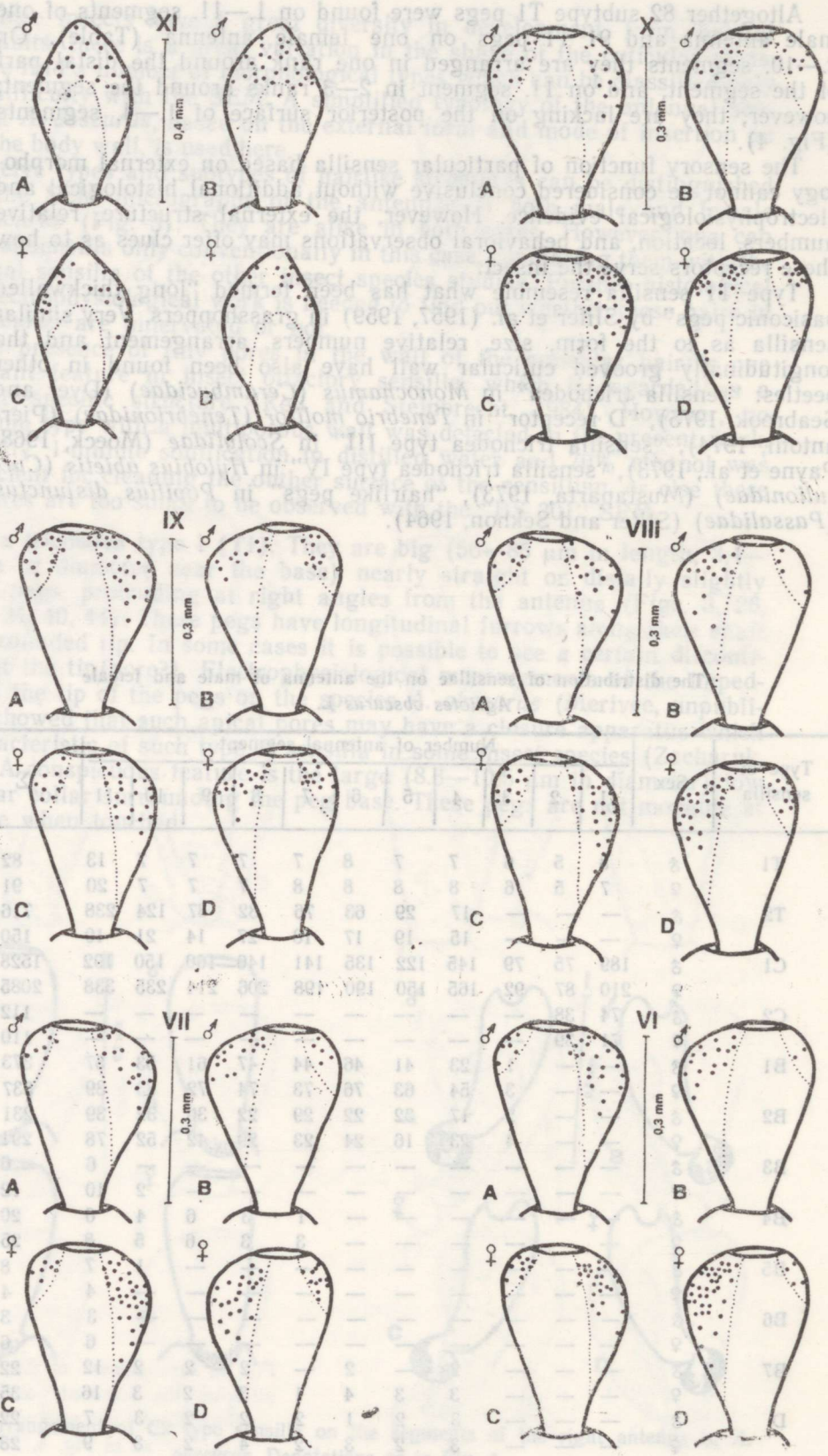
Altogether 82 subtype T1 pegs were found on 1.—11. segments of one male antenna and 91 T1 pegs on one female antenna (Table). On 2.—10. segments they are arranged in one rank around the distal part of the segment, and on 11. segment in 2—3 ranks around the segment; however, they are lacking on the posterior surface of 1.—4. segments (Fig. 4).

The sensory function of particular sensilla based on external morphology cannot be considered conclusive without additional histological and electrophysiological evidence. However, the external structure, relative numbers, location, and behavioral observations may offer clues as to how these receptors serve the insect.

Type T1 sensilla resemble what has been termed "long thickwalled basiconic pegs" by Slifer et al. (1957, 1959) in grasshoppers. Very similar sensilla as to the form, size, relative numbers, arrangement and the longitudinally grooved cuticular wall have also been found in other beetles: "sensilla trichodea" in *Monochamus* (*Cerambycidae*) (Dyer and Seabrook, 1975), "D receptor" in *Tenebrio molitor* (*Tenebrionidae*) (Pierantoni, 1974), "sensilla trichodea type III" in *Scolytidae* (Moeck, 1968; Payne et al., 1973), "sensilla trichodea type IV" in *Hylobius abietis* (*Curculionidae*) (Mustaparta, 1973), "hairlike pegs" in *Popilius disjunctus* (*Passalidae*) (Slifer and Sekhon, 1964).

The distribution of sensillae on the antenna of male and female
Agriotes obscurus L.

| Type of sensilla | Sex | Number of antennal segment | | | | | | | | | | Σ | |
|------------------|-----|----------------------------|----|----|-----|-----|-----|-----|-----|-----|-----|-----|------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | 11 |
| T1 | ♂ | 8 | 5 | 6 | 7 | 7 | 8 | 7 | 7 | 7 | 7 | 13 | 82 |
| | ♀ | 7 | 5 | 6 | 8 | 8 | 8 | 8 | 7 | 7 | 7 | 20 | 91 |
| T2 | ♂ | — | — | — | 17 | 29 | 63 | 76 | 82 | 87 | 124 | 238 | 716 |
| | ♀ | — | — | — | 15 | 19 | 17 | 18 | 27 | 14 | 21 | 19 | 150 |
| C1 | ♂ | 189 | 75 | 79 | 145 | 122 | 135 | 141 | 140 | 160 | 150 | 192 | 1528 |
| | ♀ | 210 | 87 | 92 | 165 | 150 | 190 | 198 | 206 | 214 | 235 | 338 | 2085 |
| C2 | ♂ | 74 | 38 | — | — | — | — | — | — | — | — | — | 112 |
| | ♀ | 71 | 39 | — | — | — | — | — | — | — | — | — | 110 |
| B1 | ♂ | — | — | 1 | 23 | 41 | 46 | 44 | 47 | 61 | 53 | 57 | 373 |
| | ♀ | — | — | 3 | 54 | 63 | 76 | 73 | 74 | 72 | 83 | 39 | 537 |
| B2 | ♂ | — | — | 2 | 17 | 32 | 22 | 29 | 22 | 36 | 32 | 39 | 231 |
| | ♀ | — | — | 4 | 23 | 16 | 24 | 23 | 29 | 42 | 52 | 78 | 291 |
| B3 | ♂ | — | — | — | — | — | — | — | — | — | — | 6 | 6 |
| | ♀ | — | — | — | — | — | — | — | — | — | 2 | 10 | 12 |
| B4 | ♂ | — | — | — | — | — | — | 1 | 3 | 6 | 4 | 6 | 20 |
| | ♀ | — | — | — | — | — | — | 3 | 3 | 6 | 5 | 8 | 25 |
| B5 | ♂ | — | — | — | — | — | — | — | — | — | 1 | 7 | 8 |
| | ♀ | — | — | — | — | — | — | — | — | — | — | 4 | 4 |
| B6 | ♂ | — | — | — | — | — | — | — | — | — | — | 3 | 3 |
| | ♀ | — | — | — | — | — | — | — | — | — | — | 6 | 6 |
| B7 | ♂ | — | — | — | 2 | — | 2 | — | 2 | 2 | 2 | 12 | 22 |
| | ♀ | — | — | — | 3 | 3 | 4 | 1 | 3 | 2 | 3 | 16 | 35 |
| D | ♂ | — | — | — | 3 | 2 | 1 | 2 | 2 | 2 | 3 | 7 | 22 |
| | ♀ | — | — | — | 3 | 2 | 3 | 2 | 4 | 2 | 3 | 9 | 28 |



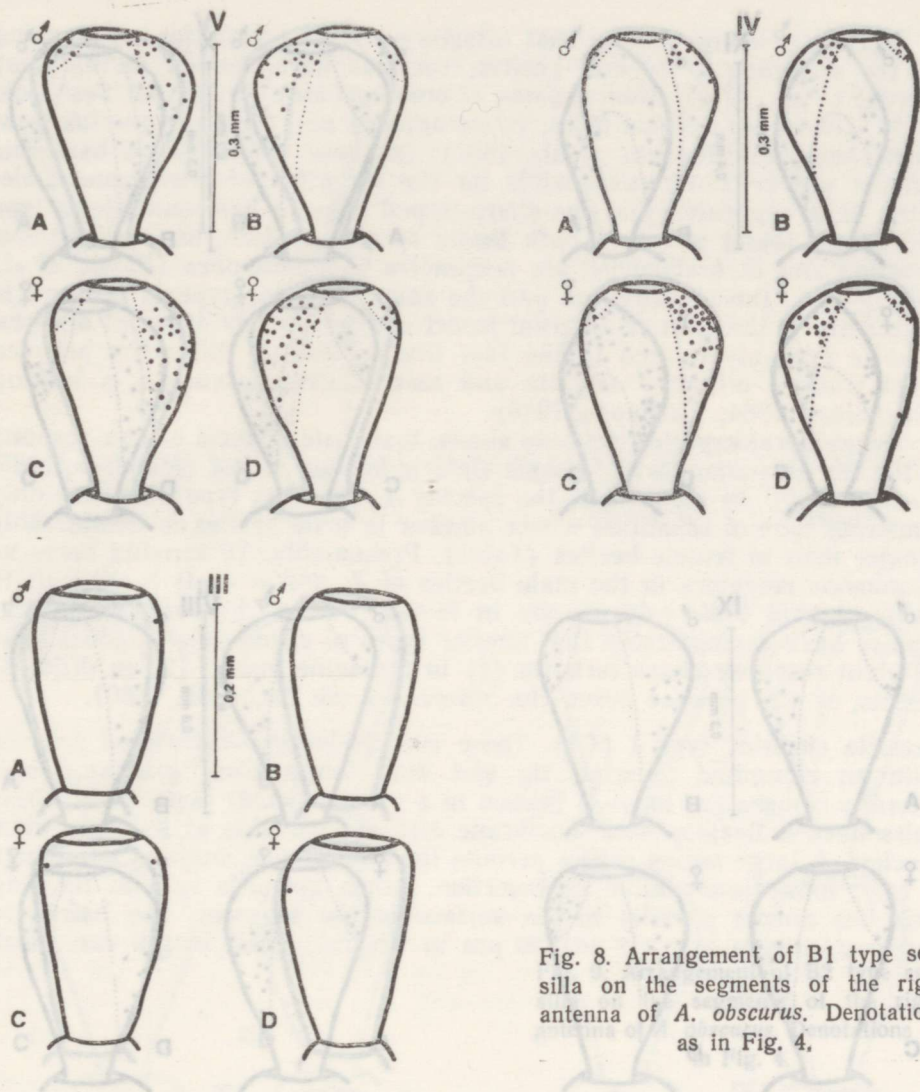
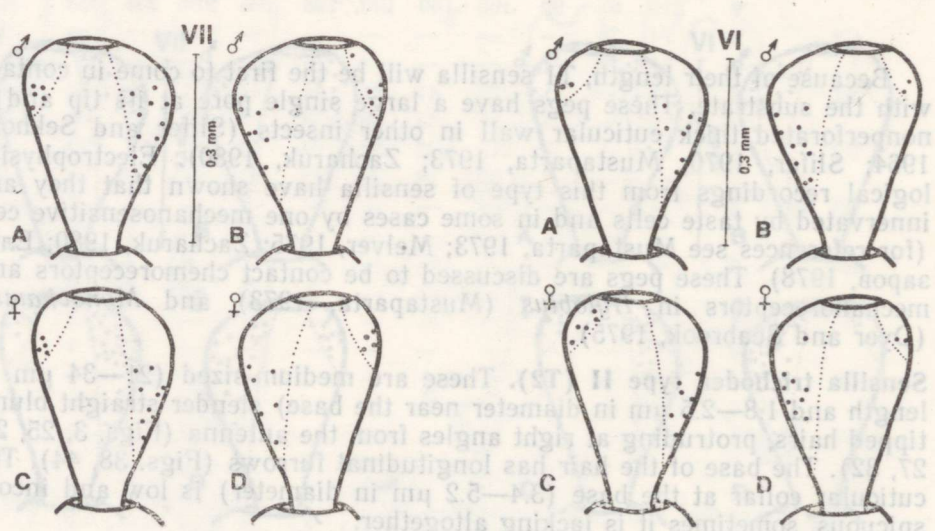
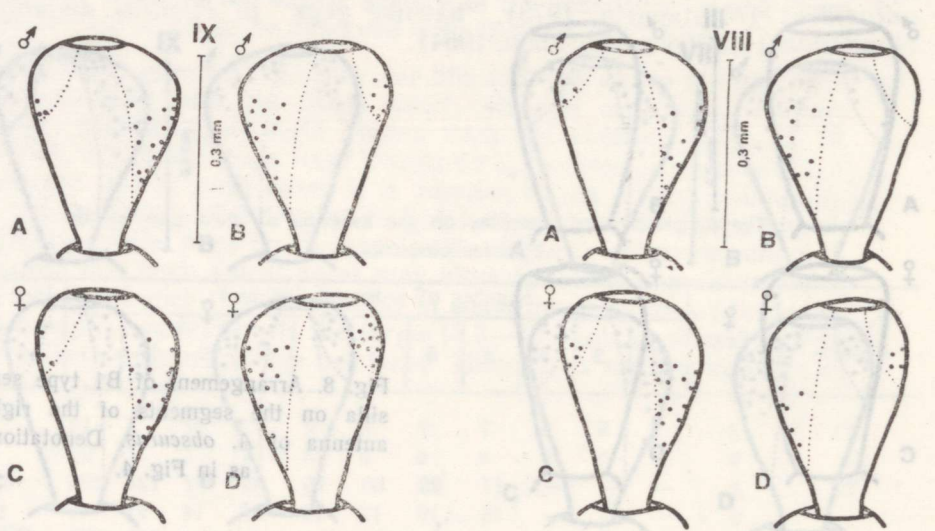
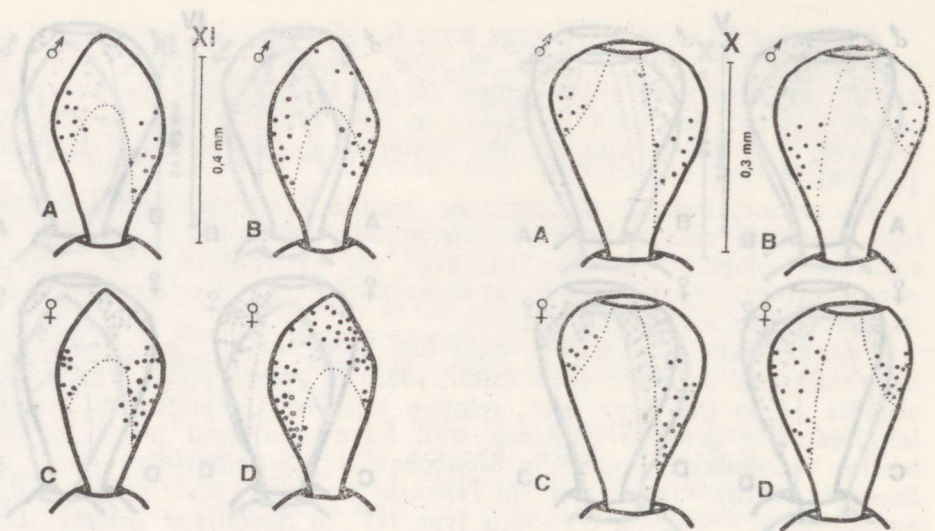


Fig. 8. Arrangement of B1 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

Because of their length, T1 sensilla will be the first to come in contact with the substrate. These pegs have a large single pore at its tip and a nonperforated thick cuticular wall in other insects (Slifer and Sekhon, 1964; Slifer, 1970; Mustaparta, 1973; Zacharuk, 1980). Electrophysiological recordings from this type of sensilla have shown that they are innervated by taste cells and in some cases by one mechanosensitive cell (for references see Mustaparta, 1973; Melder, 1975; Zacharuk, 1980; Елизаров, 1978). These pegs are discussed to be contact chemoreceptors and mechanoreceptors in *Hylobius* (Mustaparta, 1973) and *Monochamus* (Dyer and Seabrook, 1975).

Sensilla trichodea type II (T2). These are medium-sized (21–34 μm in length and 1.8–2.5 μm in diameter near the base) slender straight blunt-tipped hairs, protruding at right angles from the antenna (Figs. 3, 25, 26, 27, 32). The base of the hair has longitudinal furrows (Figs. 38, 44). The cuticular collar at the base (3.4–5.2 μm in diameter) is low and inconspicuous, sometimes it is lacking altogether.



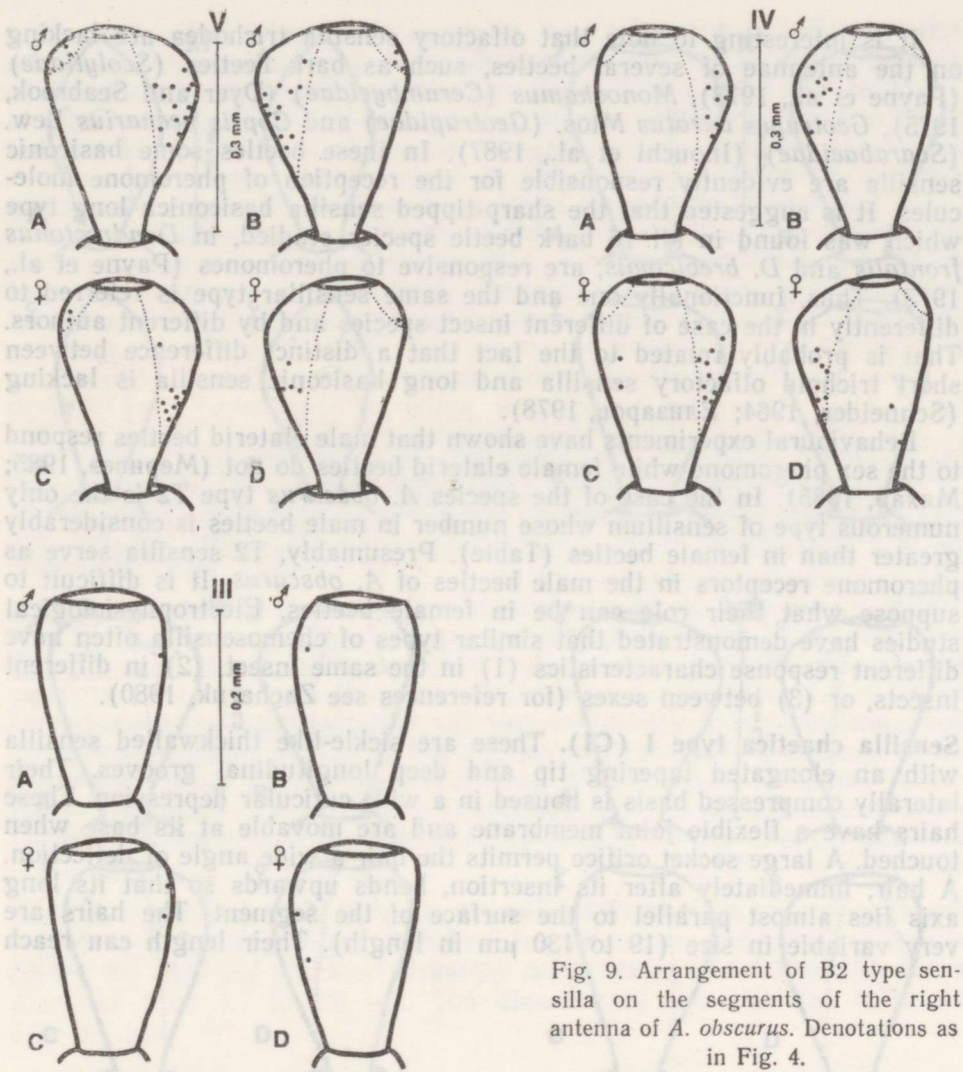


Fig. 9. Arrangement of B2 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

On 4.—11. segments of one female antenna altogether 150 T2 sensilla have been found, on one male antenna 716. In the female beetle their number on all segments is nearly the same, in the male beetle it increases towards distal segments (Table). On proximal flagellar segments T2 sensilla occurred only on the ventral extension, on medial and distal flagellar segments both on the ventral and dorsal extensions while their number was slightly larger on the ventral extension. The number of T2 sensilla was nearly the same on the anterior and posterior surface of the antenna (Fig. 5).

Subtype T2 sensilla resemble "sensilla trichodea type II" in *H. abietis* (Mustaparta, 1973). The olfactory function of these sensilla in *H. abietis* has been demonstrated by electrophysiological recordings. Moreover, the sensory cells innervating sensilla trichodea are highly specialized cells responding to pheromone-related compounds (Mustaparta, 1975). Likewise, electrophysiological recordings in male moths such as *Bombyx mori* or *Antheraea pernyi*, have shown that long sensilla trichodea are innervated by highly specialized pheromone receptor cells (Schneider et al., 1964; Kaissling and Priesner, 1970; Kaissling, 1974).

It is interesting to note that olfactory sensilla trichodea are lacking on the antennae of several beetles, such as bark beetles (*Scolytidae*) (Payne et al., 1973), *Monochamus* (*Cerambycidae*) (Dyer and Seabrook, 1975), *Geotrupes auratus* Mtos. (*Geotrupidae*) and *Copris pecuarius* Lew. (*Scarabaeidae*) (Inouchi et al., 1987). In these beetles some basiconic sensilla are evidently responsible for the reception of pheromone molecules. It is suggested that the sharp-tipped sensilla basiconica long type which was found in all 16 bark beetle species studied, in *Dendroctonus frontalis* and *D. brevicomis*, are responsive to pheromones (Payne et al., 1973). Thus, functionally one and the same sensillar type is referred to differently in the case of different insect species and by different authors. That is probably related to the fact that a distinct difference between short trichoid olfactory sensilla and long basiconic sensilla is lacking (Schneider, 1964; Елизаров, 1978).

Behavioural experiments have shown that male elaterid beetles respond to the sex pheromone while female elaterid beetles do not (Меривеэ, 1985; Мяхар, 1985). In the case of the species *A. obscurus* type T2 is the only numerous type of sensillum whose number in male beetles is considerably greater than in female beetles (Table). Presumably, T2 sensilla serve as pheromone receptors in the male beetles of *A. obscurus*. It is difficult to suppose what their role can be in female beetles. Electrophysiological studies have demonstrated that similar types of chemosensilla often have different response characteristics (1) in the same insect, (2) in different insects, or (3) between sexes (for references see Zacharuk, 1980).

Sensilla chaetica type I (C1). These are sickle-like thickwalled sensilla with an elongated tapering tip and deep longitudinal grooves. Their laterally compressed basis is housed in a wide cuticular depression. These hairs have a flexible joint membrane and are movable at its base when touched. A large socket orifice permits the hair a wide angle of deflection. A hair, immediately after its insertion, bends upwards so that its long axis lies almost parallel to the surface of the segment. The hairs are very variable in size (19 to 130 μm in length). Their length can reach

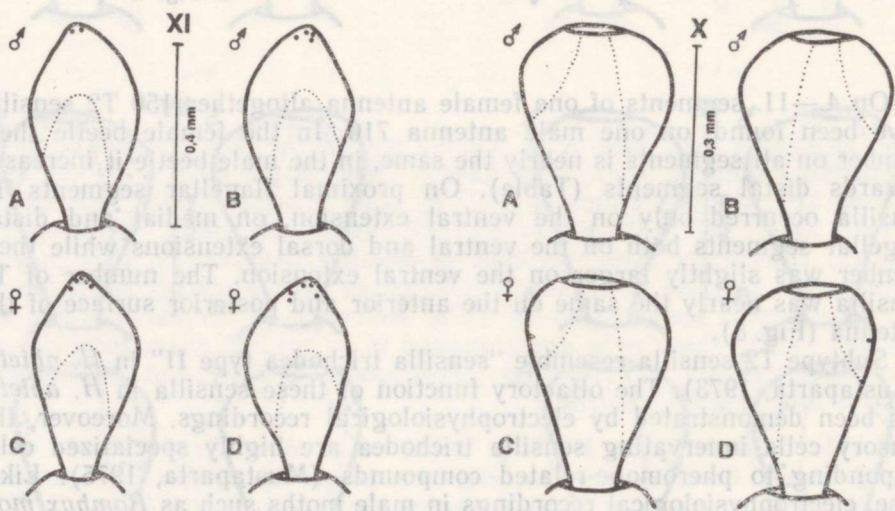


Fig. 10. Arrangement of B3 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

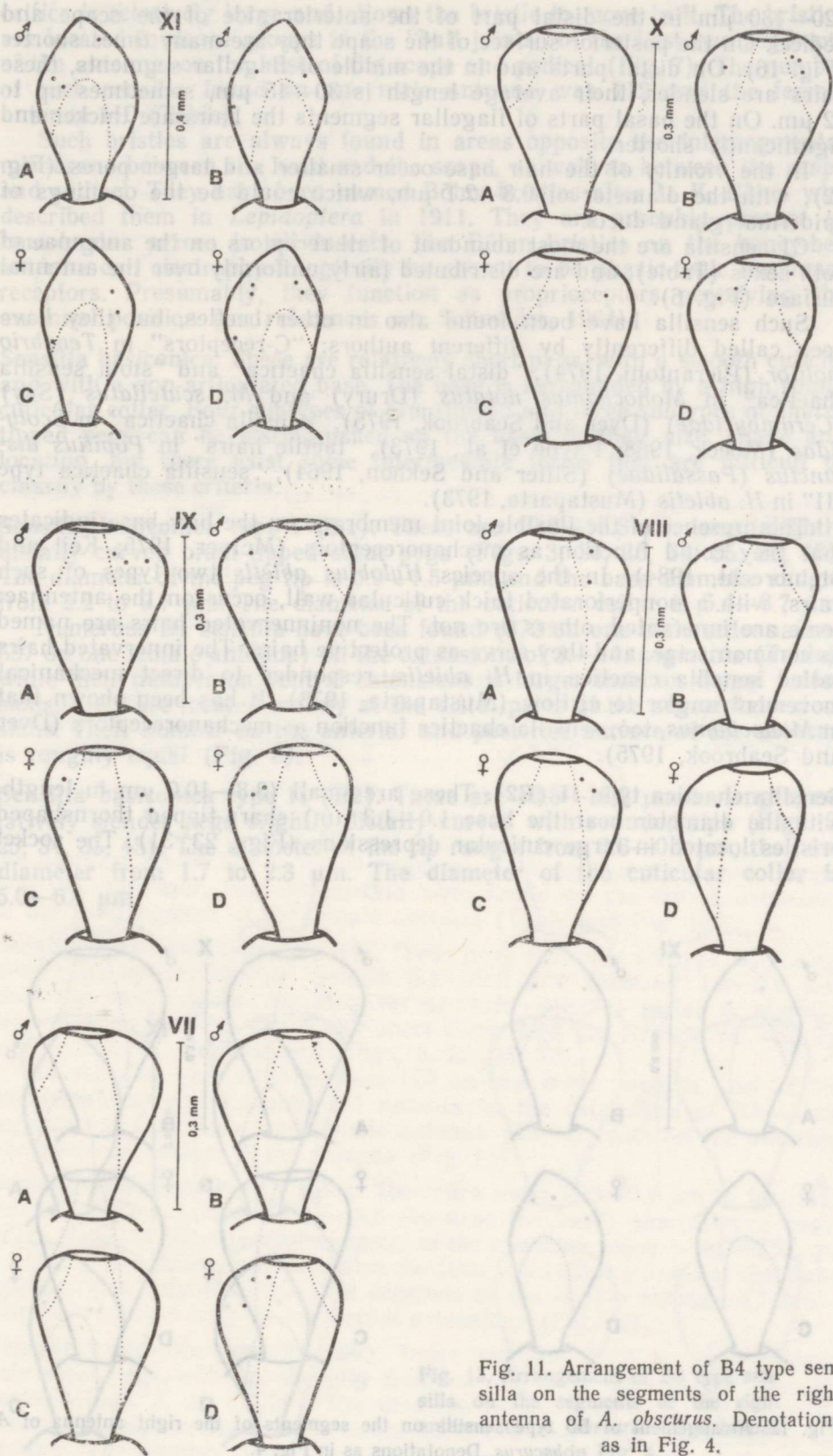


Fig. 11. Arrangement of B4 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

120—130 μm in the distal part of the anterior side of the scape and pedicel. On the posterior surface of the scape they are many times shorter (Fig. 16). On distal parts and in the middle of flagellar segments, these hairs are slender, their average length is 30—45 μm , sometimes up to 62 μm . On the basal parts of flagellar segments the hairs are thicker and significantly shorter.

In the vicinity of the hair base occur smaller and larger pores (Fig. 32), with the diameter of 0.8—2.1 μm , which could be the openings of epidermal gland ducts.

C1 sensilla are the most abundant of all receptors on the antennae of both sexes (Table), and are distributed fairly uniformly over the antennal surface (Fig. 6).

Such sensilla have been found also in other beetles, but they have been called differently by different authors: "C-receptors" in *Tenebrio molitor* (Pierantoni, 1974), "distal sensilla chaetica" and "stout sensilla chaetica" in *Monochamus notatus* (Drury) and *M. scutellatus* (Say) (*Cerambycidae*) (Dyer and Seabrook, 1975), "sensilla chaetica" in *Scolytidae* (Moeck, 1968; Payne et al., 1973), "tactile hairs" in *Popilius disjunctus* (*Passalidae*) (Slifer and Sekhon, 1964), "sensilla chaetica type III" in *H. abietis* (Mustaparta, 1973).

The presence of the flexible joint membrane on the hair base indicates that they could function as mechanoreceptors (McIver, 1975; Keil and Steinbrecht, 1984). In the species *Hylobius abietis* two types of such hairs, with a nonperforated thick cuticular wall, occur on the antennae: some are innervated, others are not. The noninnervated hairs are named as common setae, and they serve as protective hairs. The innervated hairs called sensilla chaetica in *H. abietis*, responded to direct mechanical movement and/or to airflow (Mustaparta, 1973). It has been shown that in *Monochamus*, too, sensilla chaetica function as mechanoreceptors (Dyer and Seabrook, 1975).

Sensilla chaetica type II (C2). These are small (3.8—10.0 μm in length, with the diameter near the base 1.0—1.3 μm) sharp-tipped thornshaped bristles located in large cuticular depressions (Figs. 23, 31). The socket

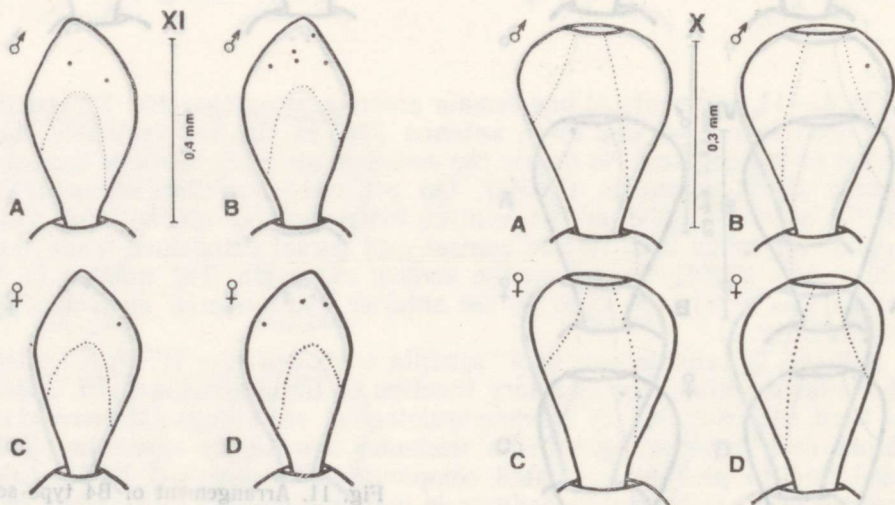


Fig. 12. Arrangement of B5 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

orifice is relatively large and allows the bristle to move in it. The bristles are located in dense groups in the "ball joints" of the first two segments of the antenna, on the base of the scape and pedicel (Fig. 7). The number of such sensilla found on one male antenna was 112 and the female antenna 110 (Table).

Such bristles are always found in areas opposite the intersegmental membrane between the head and the scape, as well as between the scape and pedicel. They have been named Böhm bristles after L. K. Böhm who described them in *Lepidoptera* in 1911. They are probably present in homologous places in all insects. The Böhm bristles on the honey-bee antenna can electrophysiologically be shown to be phasic-tonic mechanoreceptors. Presumably, they function as proprioceptors perceiving the antennal position (for references see Schneider, 1964).

Sensilla basiconica. These are relatively short pegs, with a smooth cuticle, and with a non-articulated base. The base is surrounded by a high round cuticular collar. Four subtypes of bluntheaded and three subtypes of sharp-tipped pegs can be distinguished on the basis of their size, shape and location, but there exist some intermediate forms that are difficult to classify by these criteria.

Sensilla basiconica type I (B1). These are 10.8—15.8 μm long, slightly distally curved blunt-tipped stout pegs (Figs. 3, 25, 26, 34, 35, 36, 45). The diameter of the peg tip is 0.9—1.5 μm , and the base diameter ranges from 2.2 to 2.7 μm . The diameter of the cuticular collar is 5.4—6.7 μm .

Numerous B1 sensilla have been found (373 on one male antenna and 537 on one female antenna) on the extensions of 3.—11. segments (Table), while their number on ventral extensions is larger than on dorsal extensions. They are located mainly at the distal parts of the segmental extensions. Their number on the anterior and posterior surface of the antenna is roughly equal (Fig. 8).

Sensilla basiconica type II (B2). These are 10.8—18.8 μm in length, relatively slender pegs slightly distally curved with rounded tips (Figs. 3, 25, 34, 35, 45). The diameter of the tip ranges from 0.6—0.9 μm , the base diameter from 1.7 to 2.3 μm . The diameter of the cuticular collar is 5.0—6.4 μm .

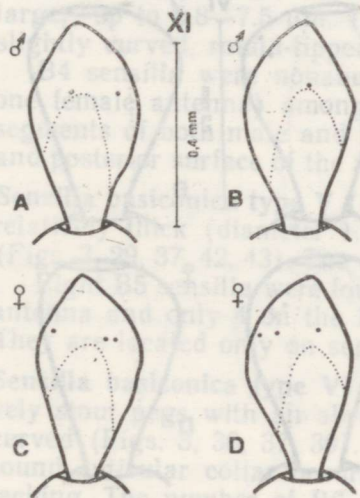
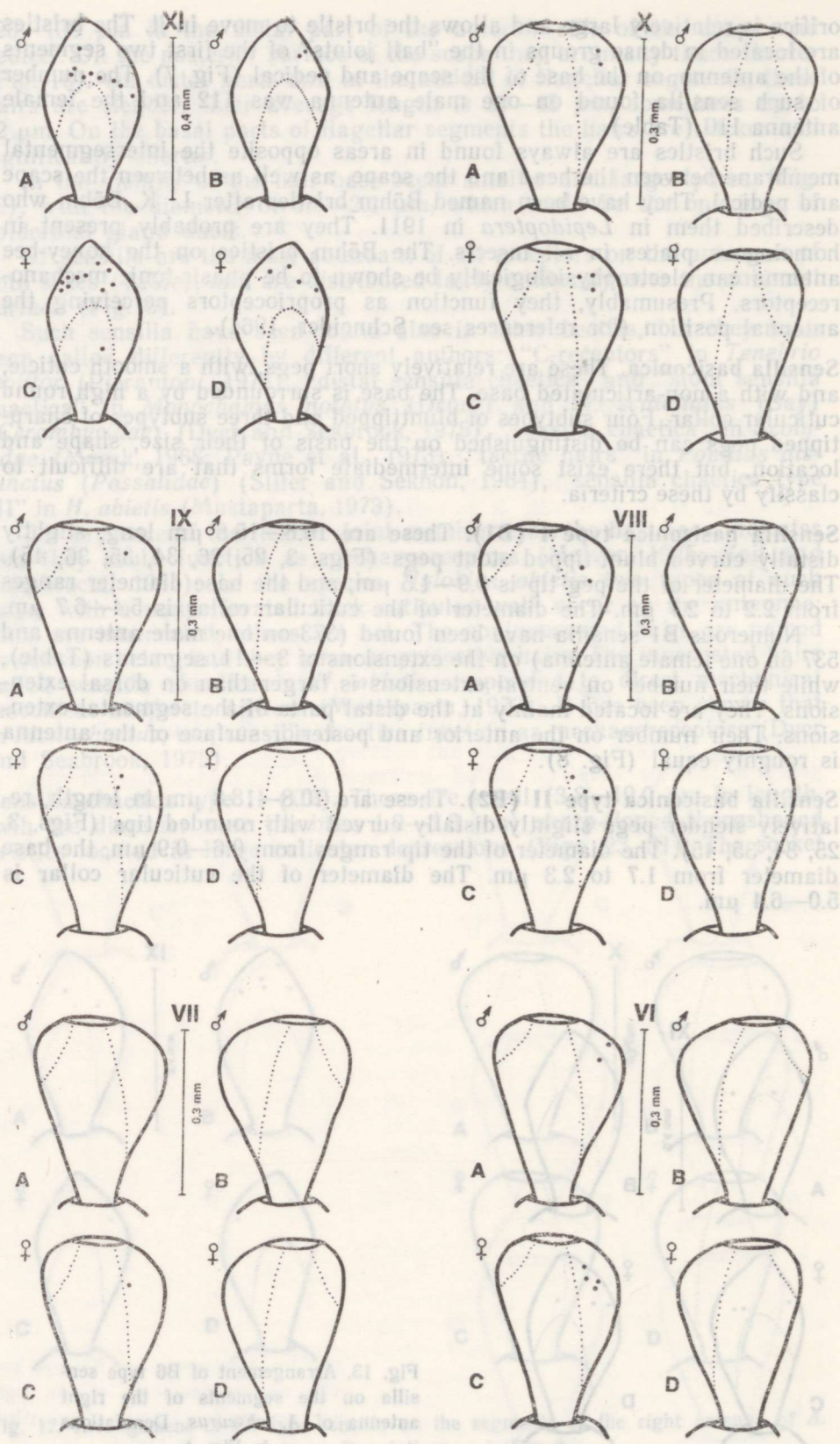


Fig. 13. Arrangement of B6 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.



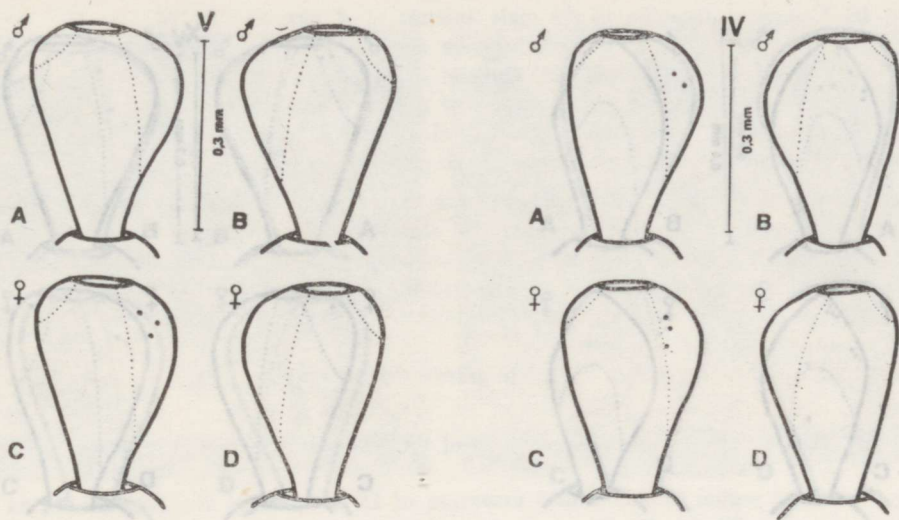


Fig. 14. Arrangement of B7 type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

B2 sensilla were found in large numbers (231 on one male antenna and 291 on one female antenna) on the extensions of 3.—11. segments (Table). Their number on ventral extensions is larger than on dorsal extensions. They are mainly located at the proximal parts of the segmental extensions and occur nearly equally on the anterior and posterior surface of the antenna (Fig. 9).

Sensilla basiconica type III (B3). These pegs resemble subtype B2, differing from it only by the fact that they are nearly straight or slightly proximally curved (Figs. 3, 33, 40) and are located as a small group at the extreme tip of the terminal segment, both on the male and female antenna. However, two B3 sensilla were found on the dorsal extension of the 10th segment of the female antenna (Table and Fig. 10).

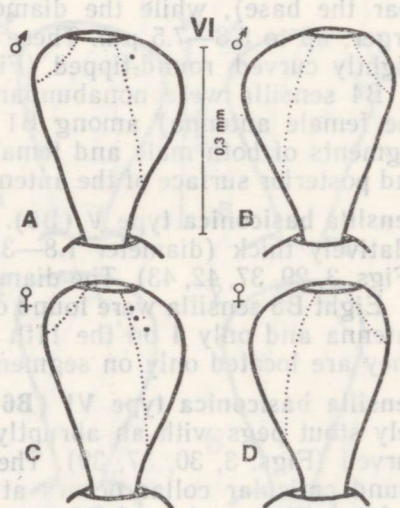
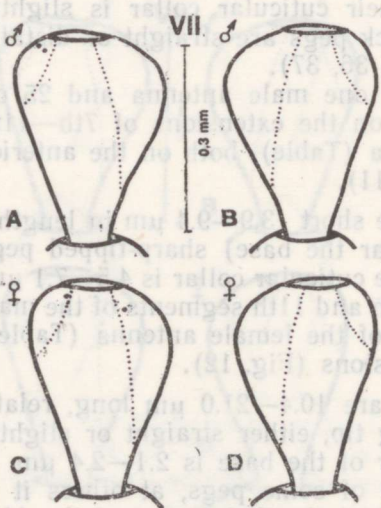
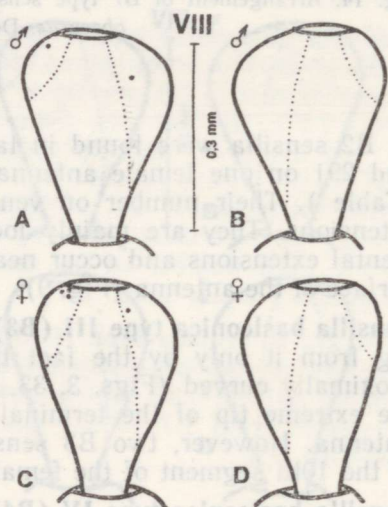
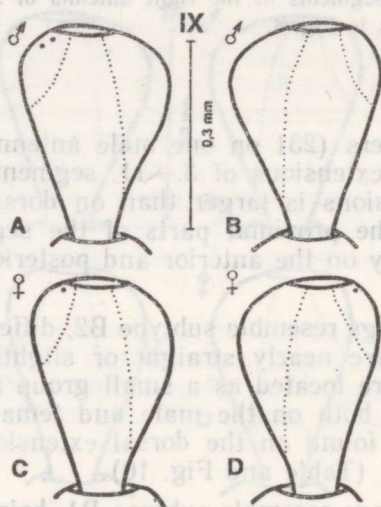
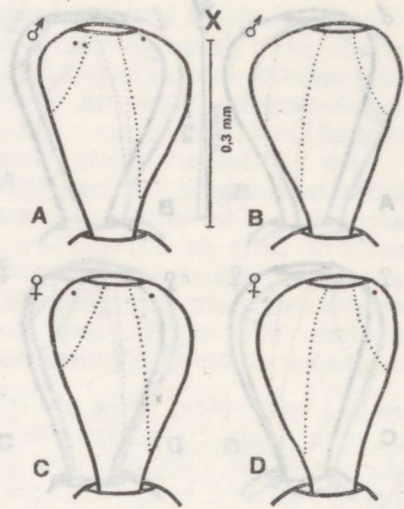
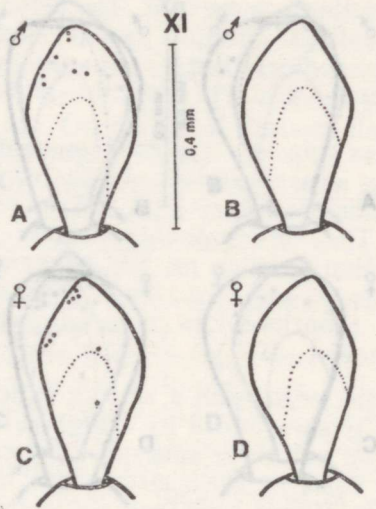
Sensilla basiconica type IV (B4). These pegs resemble subtype B1, being only considerably shorter (length 5.1—10.2 μm , diameter 1.9—2.9 μm near the base), while the diameter of their cuticular collar is slightly larger, up to 5.8—7.5 μm . These short thick pegs are straight or distally slightly curved, round-tipped (Figs. 3, 26, 36, 37).

B4 sensilla were nonabundant (20 on one male antenna and 25 on one female antenna) among B1 sensilla on the extensions of 7th—11th segments of both male and female antenna (Table), both on the anterior and posterior surface of the antenna (Fig. 11).

Sensilla basiconica type V (B5). These are short (3.9—9.4 μm in length), relatively thick (diameter 1.8—3.0 μm near the base) sharp-tipped pegs (Figs. 3, 29, 37, 42, 43). The diameter of the cuticular collar is 4.5—7.1 μm .

Eight B5 sensilla were found on the 10th and 11th segments of the male antenna and only 4 on the 11th segment of the female antenna (Table). They are located only on segmental extensions (Fig. 12).

Sensilla basiconica type VI (B6). These are 10.4—21.0 μm long, relatively stout pegs with an abruptly tapering tip, either straight or slightly curved (Figs. 3, 30, 37, 39). The diameter of the base is 2.1—2.4 μm . A round cuticular collar occurs at the base of some pegs, at others it is lacking. The number of B6 sensilla found at the distal part of the 11th



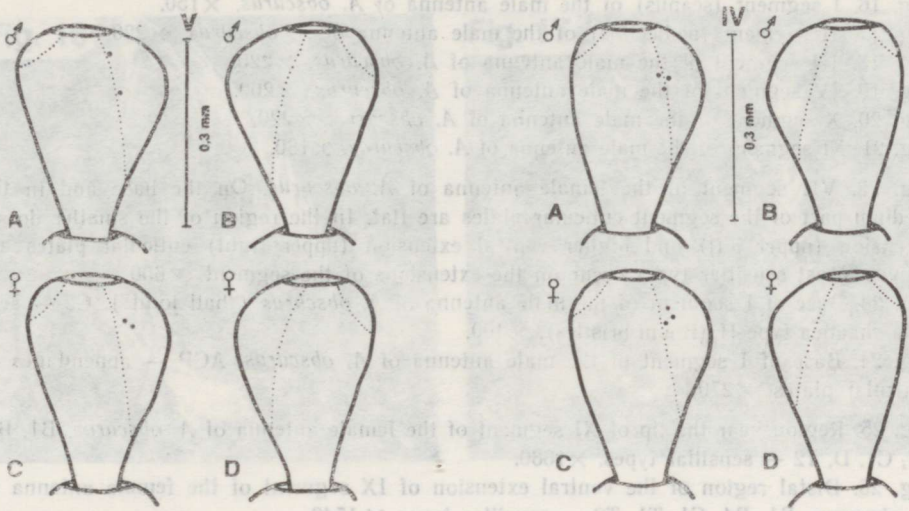


Fig. 15. Arrangement of D type sensilla on the segments of the right antenna of *A. obscurus*. Denotations as in Fig. 4.

segment of the male antenna was 3, the corresponding number in the case of the female antenna was 6 (Table), (Fig. 13).

Sensilla basiconica type VII (B7). These are small (7.0–9.1 μm in length and 2.0–2.9 μm in diameter near the base) sharp-tipped conical pegs with a subapical annular groove (Figs. 3, 25, 29, 39, 42, 43, 45). The diameter of the high round cuticular collar ranges from 5.3–7.4 μm .

A few B7 sensilla (22 on one male antenna and 35 on one female antenna) were found on the 4th–11th segments of the antenna of both sexes (Table). On the 4th–10th segments they are located on the posterior surface of the ventral extension, only on the 11th segment they were found both on the posterior and anterior surfaces (Fig. 14).

Basiconic pegs are found in most insect species investigated. Mostly they have a multiporous cuticular wall and are very variable in shape (Schneider, 1964; Schneider and Steinbrecht, 1968; Slifer, 1970; Payne et al., 1973; Keil and Steinbrecht, 1984).

Using both electron microscopy and electrophysiology, it was determined in all cases that basiconic pegs with a multiporous wall have an olfactory function (for review see Slifer, 1970; Altner and Prillinger, 1980; Zacharuk, 1980; Keil and Steinbrecht, 1984). The receptors innervating sensilla basiconica in *H. abietis* and in male moths such as *Bombyx mori* or *Antheraea pernyi*, were lowly specialized cells responding to a variety of odours (Mustaparta, 1975; Schneider et al., 1964; Kaissling and Priesner, 1970; Kaissling, 1974).

Dome-shaped sensilla (D). The cuticular collar of these sensilla forms a high rounded dome (height 4.5–5.8 μm , diameter 6.7–7.5 μm) from which the round tip of the peg protrudes only 1–2 μm (Figs. 3, 25, 33, 40, 41, 44).

Twenty two D sensilla were found on one male antenna and 28 on one female antenna (Table). On the 4th–6th segments they are located on the posterior surface of the ventral extension, on the 7th–10th segments on the posterior surface of the ventral and dorsal extensions, and on the 11th segment dorsally and posteriorly (Fig. 15).

- Fig. 16. I segment (scapus) of the male antenna of *A. obscurus*. $\times 150$.
- Fig. 17. II segment (pedicellus) of the male antenna of *A. obscurus*. $\times 220$.
- Fig. 18. III segment of the male antenna of *A. obscurus*. $\times 220$.
- Fig. 19. IV segment of the male antenna of *A. obscurus*. $\times 200$.
- Fig. 20. X segment of the male antenna of *A. obscurus*. $\times 220$.
- Fig. 21. XI segment of the male antenna of *A. obscurus*. $\times 180$.
- Fig. 22. VII segment of the female antenna of *A. obscurus*. On the base and in the medium part of the segment cuticular plates are flat. In the region of the smaller dorsal extension (upper left) and bigger ventral extension (upper right) cuticular plates are convex. Most sensillar types occur on the extensions of the segment. $\times 650$.
- Fig. 23. Base of I segment of the male antenna of *A. obscurus* ("ball joint"). C2 — sensilla chaetica type II (Böhm bristles). $\times 400$.
- Fig. 24. Base of I segment of the male antenna of *A. obscurus*. ACP — appendages of cuticular plates. $\times 270$.
- Fig. 25. Region near the tip of XI segment of the female antenna of *A. obscurus*. B1, B2, B7, C1, D, T2 — sensillar types. $\times 1680$.
- Fig. 26. Distal region of the ventral extension of IX segment of the female antenna of *A. obscurus*. B1, B4, C1, T1, T2 — sensillar types $\times 1540$.
- Fig. 27. Ventral extension of X segment of the male antenna of *A. obscurus*. T2 sensilla with the longitudinally grooved base are shown. $\times 2150$.
- Fig. 28. Distal region of the dorsal extension of VII segment of the female antenna of *A. obscurus*. C1, T1 — sensillar types; CP — cuticular plates (convex). $\times 1600$.
- Fig. 29. XI segment of the female antenna of *A. obscurus*. B5, B7 — sensillar types. $\times 1970$.
- Fig. 30. XI segment of the male antenna of *A. obscurus*. B6 type sensilla. $\times 1920$.
- Fig. 31. Base of I segment of the male antenna of *A. obscurus* ("ball joint"). C2 — sensilla chaetica type II (Böhm bristles). $\times 1700$.
- Fig. 32. Ventral extension of IV segment of the female antenna of *A. obscurus*. B1, C1, T2 — sensillar types; CP — flat cuticular plates; P — pores. $\times 1200$.
- Fig. 33. Region near the tip of XI segment of the female antenna of *A. obscurus*. B3, C1, D, T1 — sensillar types. $\times 2000$.
- Fig. 34. Ventral extension of IX segment of the female antenna of *A. obscurus*. B1, B2, C1, T1 — sensillar types. $\times 1680$.
- Fig. 35. Dorsal extension of X segment of the female antenna of *A. obscurus*. B1, B2, C1 — sensillar types. $\times 1800$.
- Fig. 36. IX segment of the female antenna of *A. obscurus*. B1, B4 — sensillar types. $\times 2500$.
- Fig. 37. XI segment of the female antenna of *A. obscurus*. B4, B5, B6 — sensillar types. P — pores. $\times 2400$.
- Fig. 38. XI segment of the male antenna of *A. obscurus*. The longitudinally grooved base of type T2 sensilla, with a small cuticular collar. $\times 10500$.
- Fig. 39. XI segment of the male antenna of *A. obscurus*. B6, B7 — sensillar types. $\times 4000$.
- Fig. 40. Tip of XI segment of the male antenna of *A. obscurus*. B3, D, T1 — sensillar types. The longitudinally grooved base of type T1 sensilla is seen. $\times 6000$.
- Fig. 41. Tip of XI segment of the female antenna of *A. obscurus*. D — dome-shaped sensilla. $\times 4020$.
- Fig. 42. XI segment of the male antenna of *A. obscurus*. B5, B7 — sensillar types. $\times 4000$.
- Fig. 43. XI segment of the female antenna of *A. obscurus*. B5, B7 — sensillar types. $\times 3600$.
- Fig. 44. Tip of XI segment of the male antenna of *A. obscurus*. D, T1, T2 — sensillar types. $\times 5900$.
- Fig. 45. XI segment of the male antenna of *A. obscurus*. B1, B2, B7, C1 — sensillar types. $\times 4800$.

Fig. 16

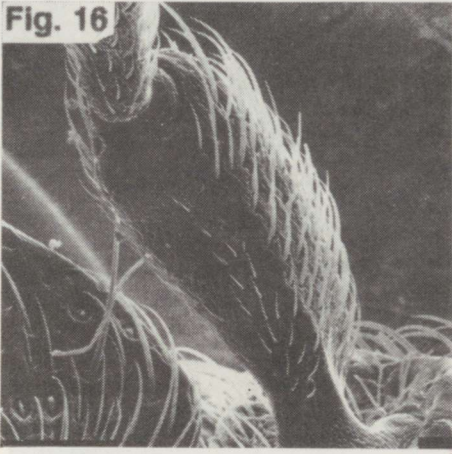


Fig. 17

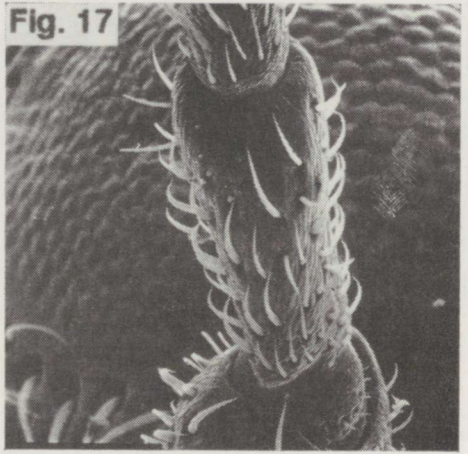


Fig. 18

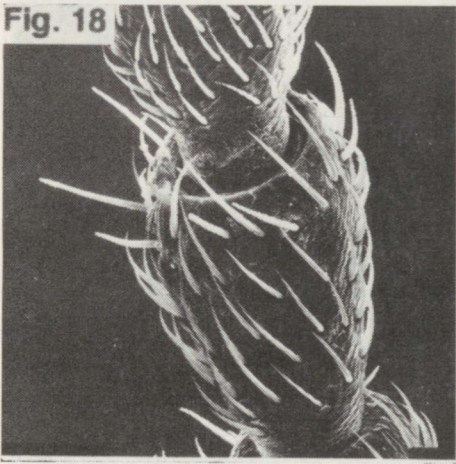


Fig. 19

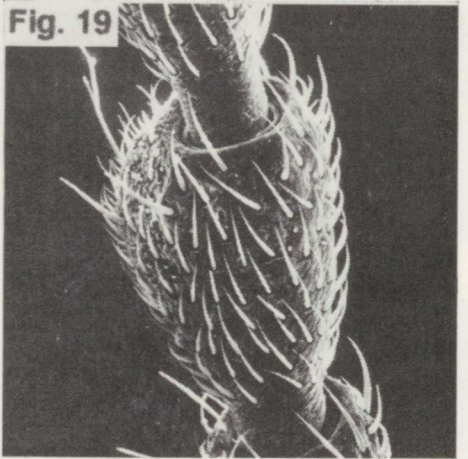


Fig. 20

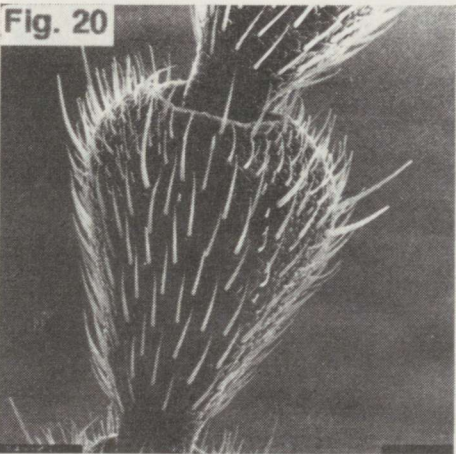


Fig. 21

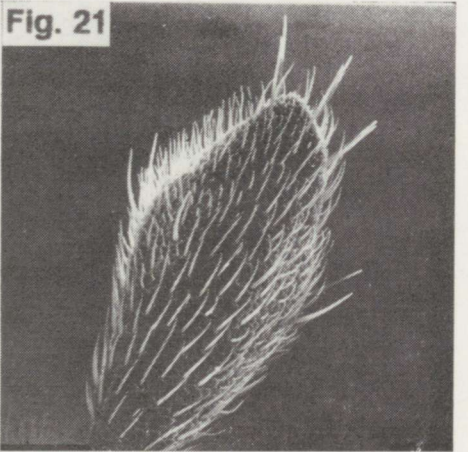


Fig. 22



Fig. 23

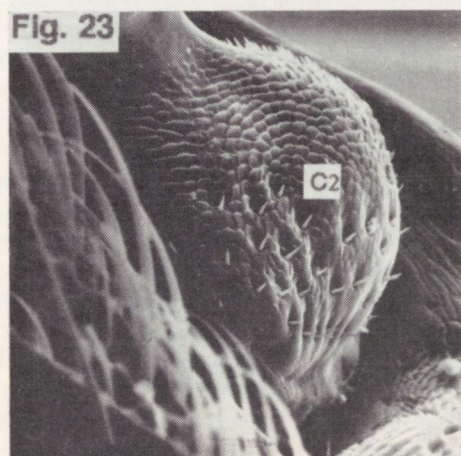


Fig. 24

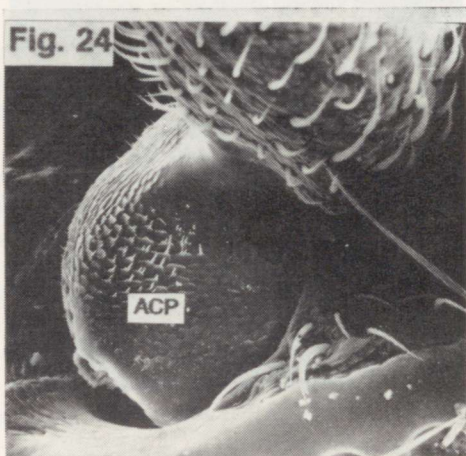


Fig. 25

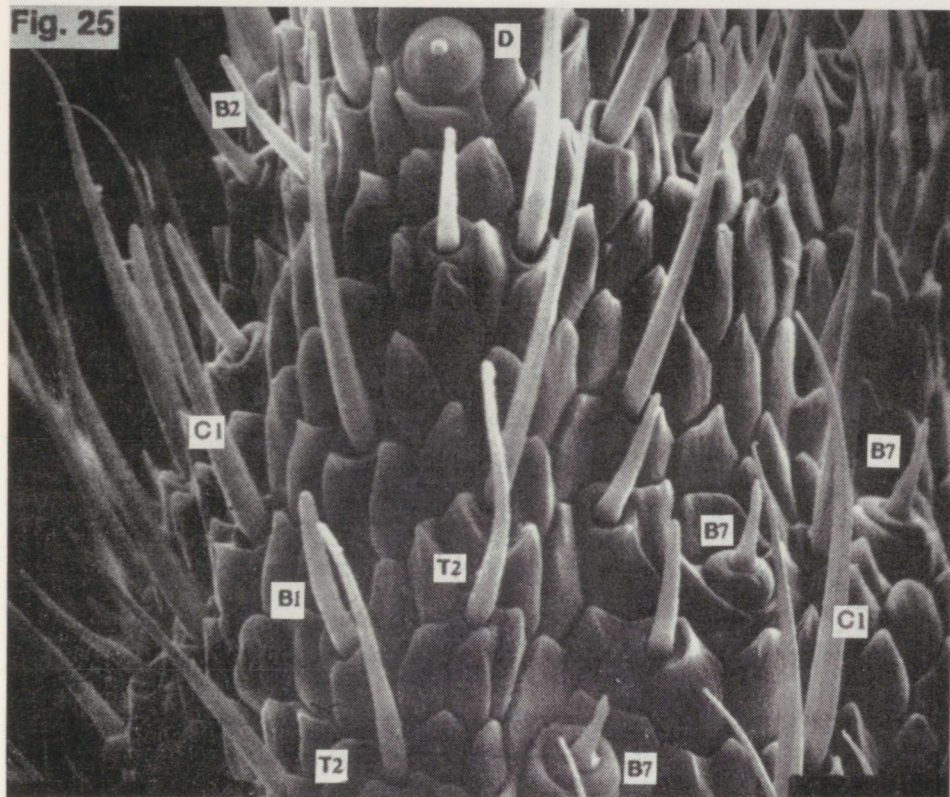


Fig. 26

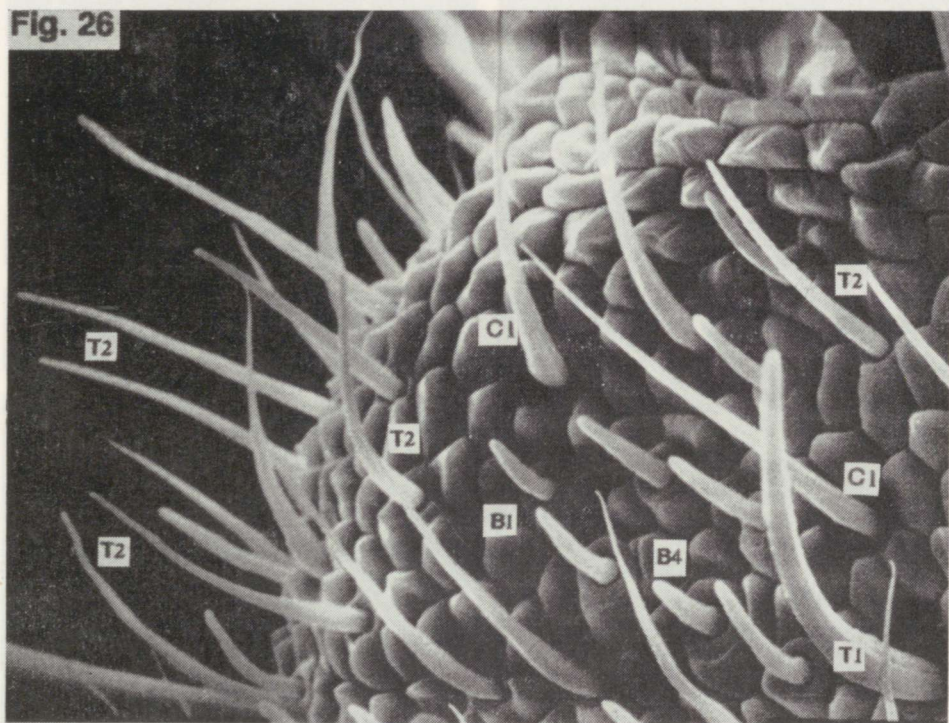


Fig. 27



Fig. 28

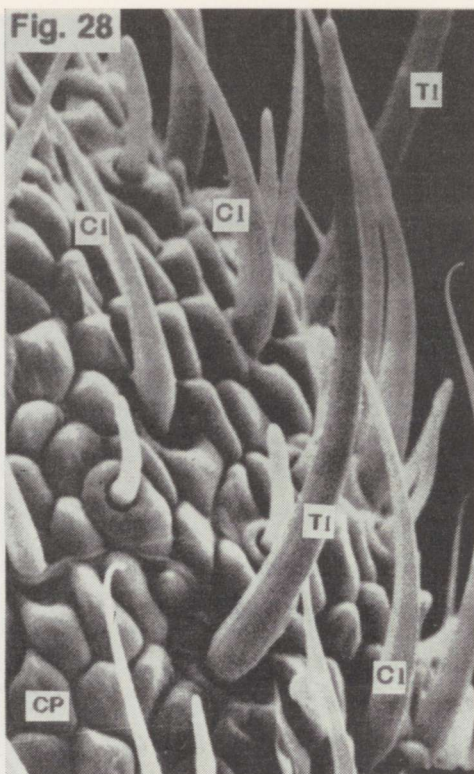


Fig. 29

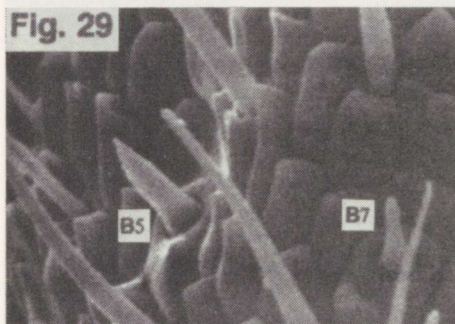


Fig. 30

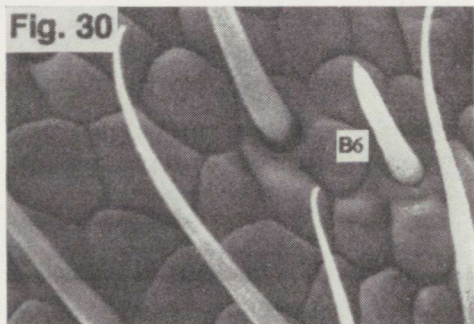


Fig. 31

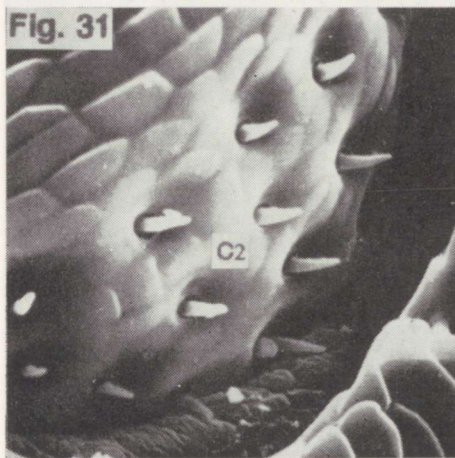


Fig. 32

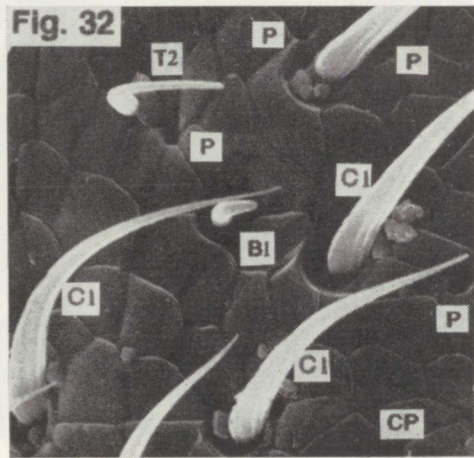


Fig. 33

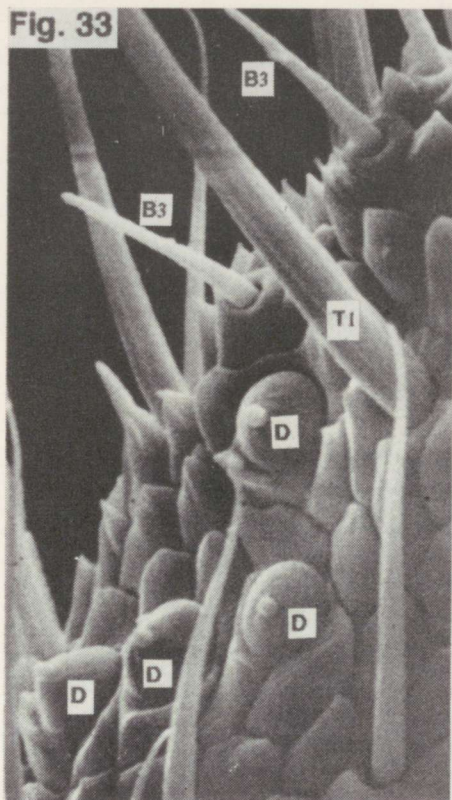


Fig. 34

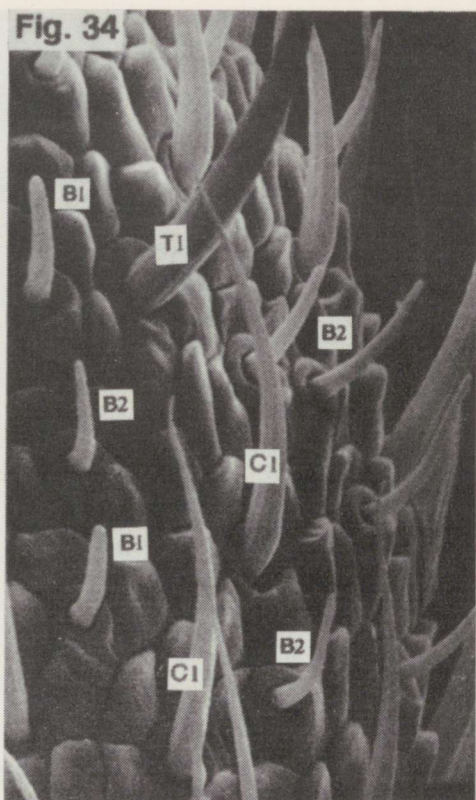


Fig. 35

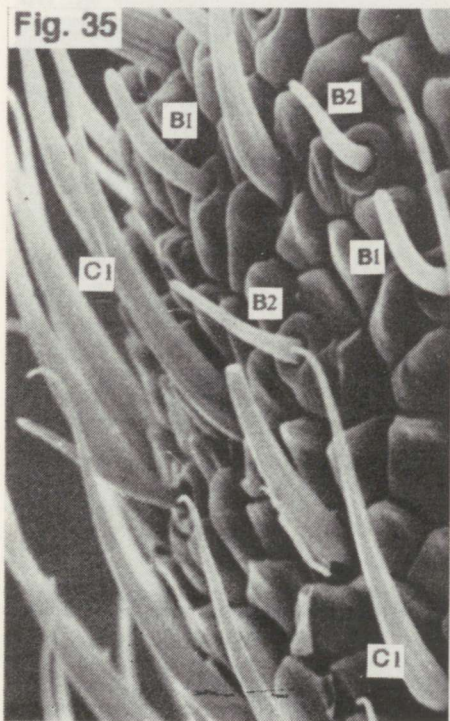


Fig. 36

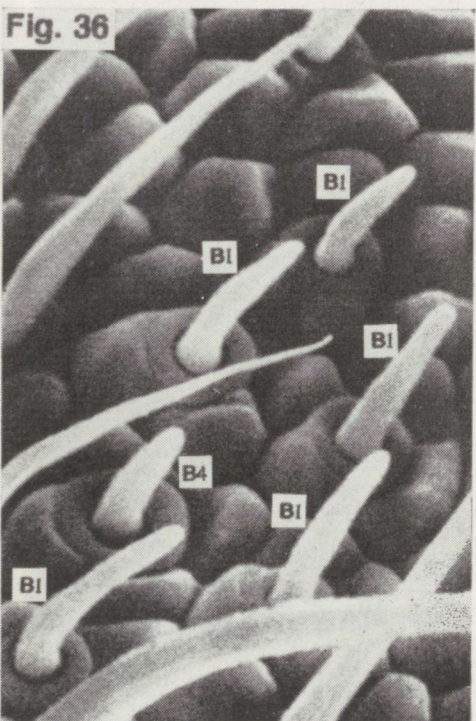


Fig. 37

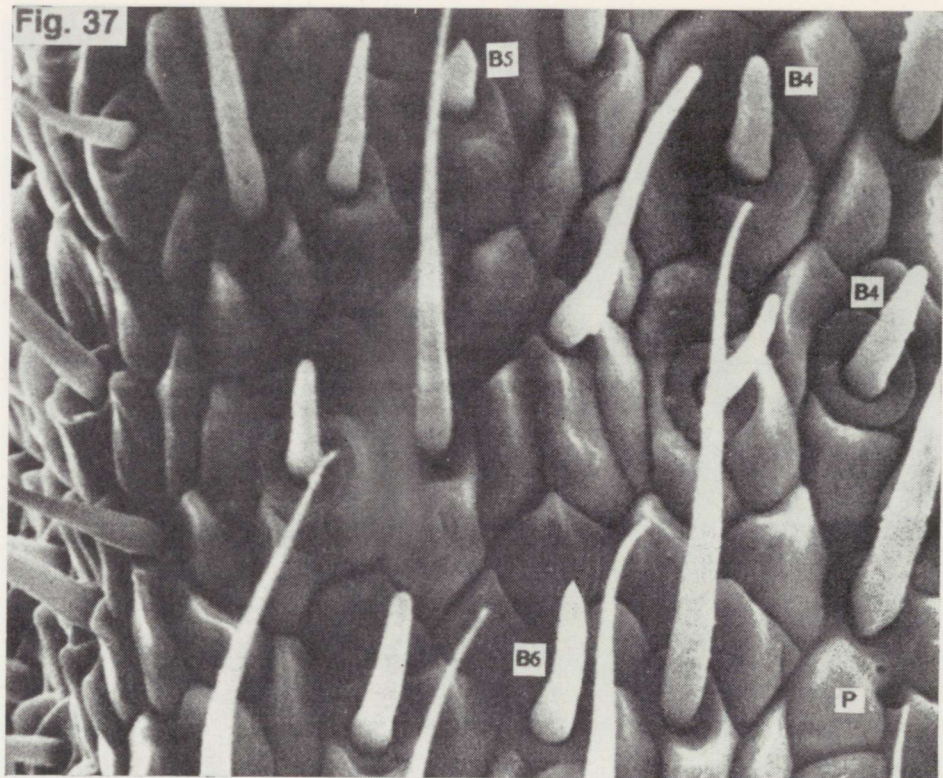


Fig. 38

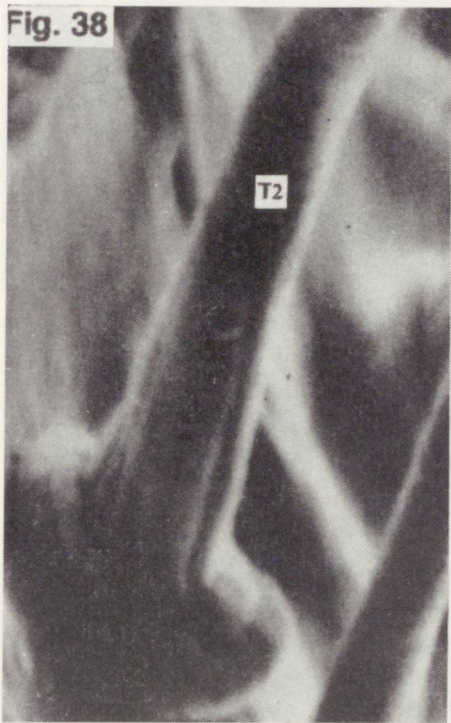


Fig. 39

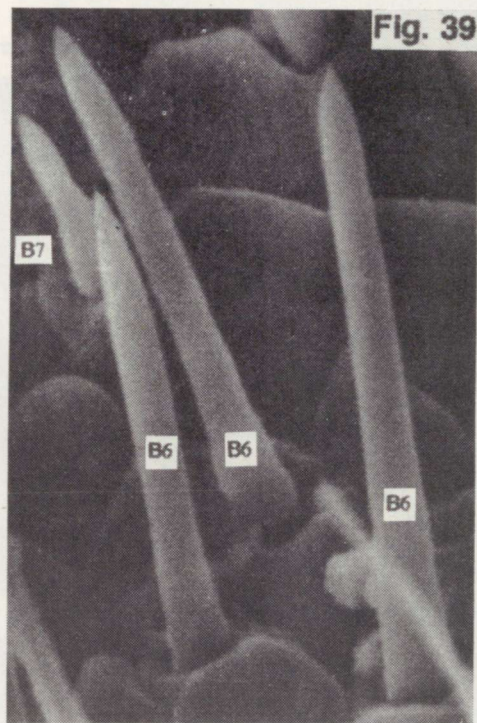


Fig. 40

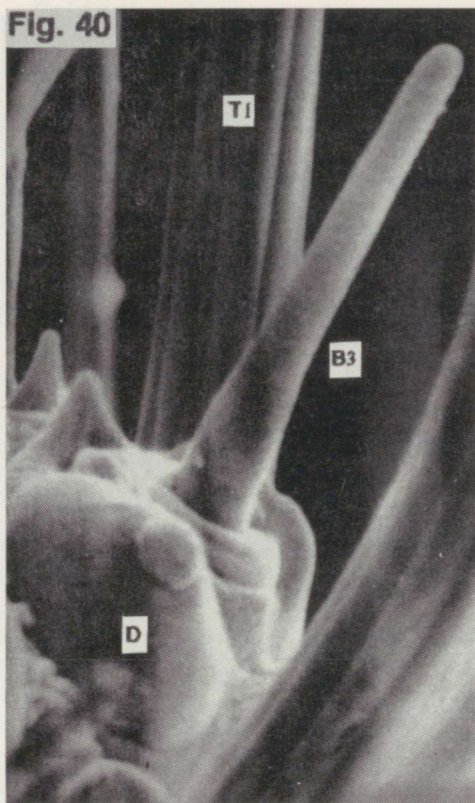


Fig. 41

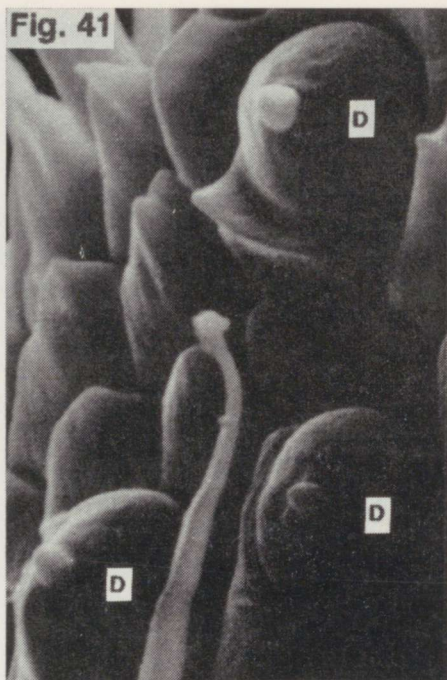


Fig. 43

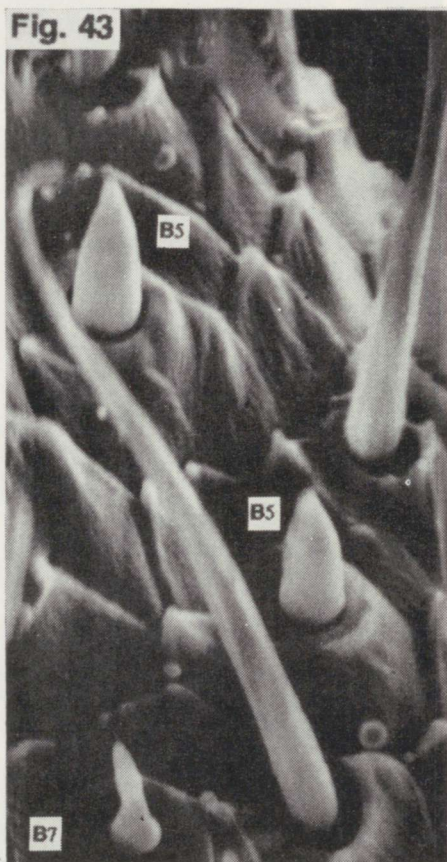


Fig. 42

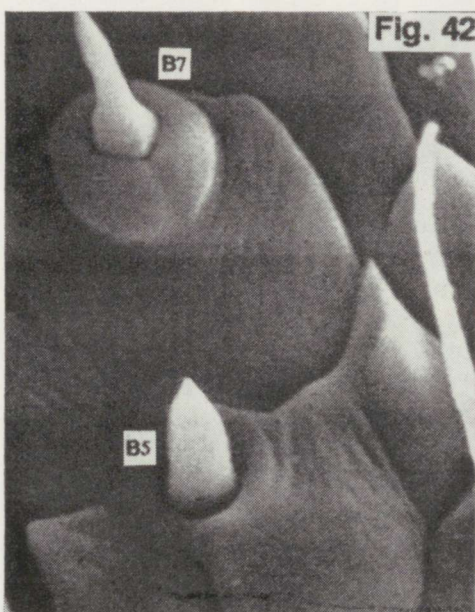


Fig. 44

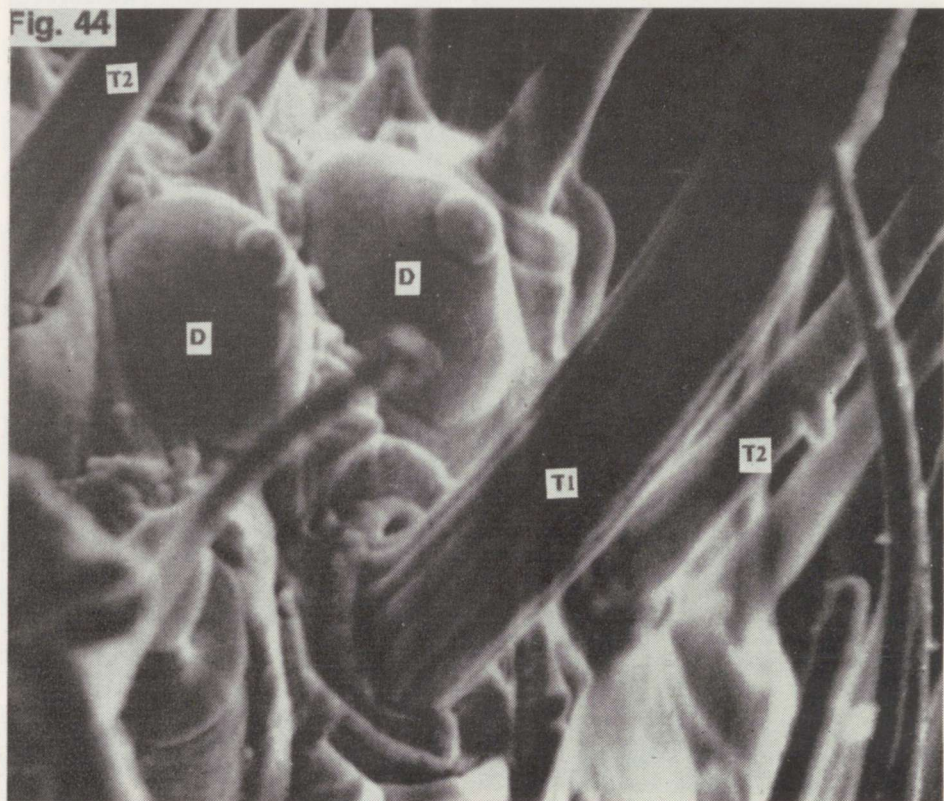
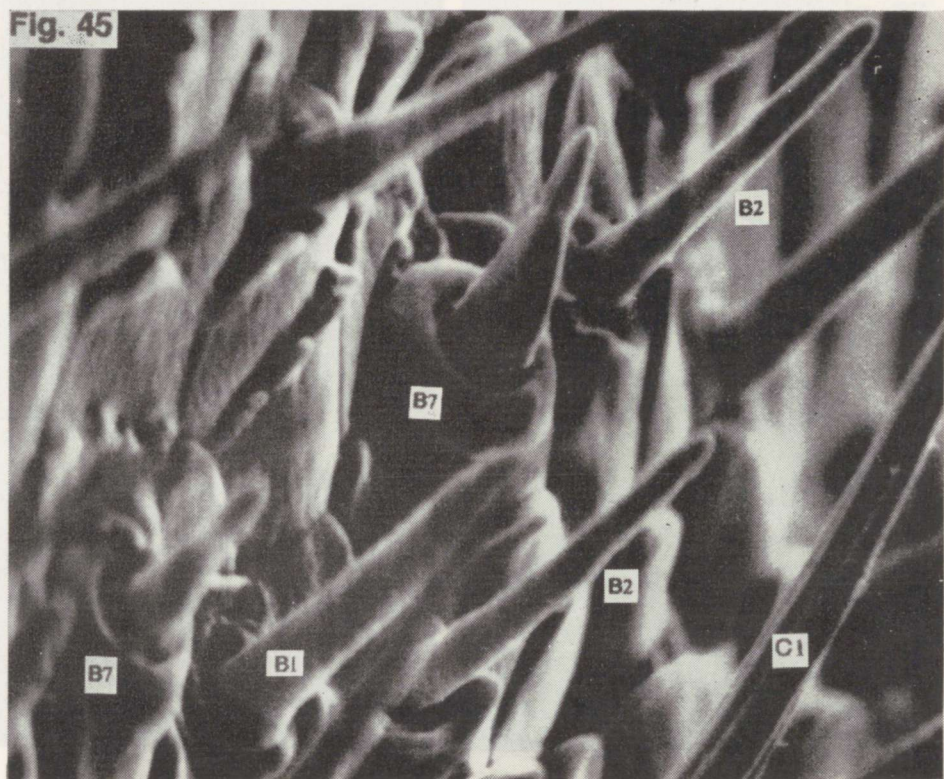


Fig. 45



Evidently, these structures represent coeloconic sensilla (Schneider, 1964; Елизаров, 1978). Further analysis of the fine structure with the transmission electron microscope is, however, necessary in order to describe these sensilla in more detail. Antennal sensilla coeloconica are lacking in some other beetles studied, such as *Hylobius*, *Monochamus* and *Scolytidae* (Mustaparta, 1973; Dyer and Seabrook, 1975; Payne et al., 1973; Moeck, 1968). However, they are present in *Dytiscus marginalis* L. (*Dytiscidae*) (Hochreuther, 1912). Coeloconic sensilla have been found in the specimens of a number of other insect orders (*Orthoptera*, *Lepidoptera*, *Diptera Hymenoptera*), and they presumably comprise several morphological subtypes. Electrophysiological measurements have proved that they can function as olfactory, CO₂, hygro- or thermoreceptors (Lacher, 1964; Boeckh et al., 1965; Davis and Sokolove, 1975; Altner and Prillinger, 1980).

Acknowledgements

I would like to thank Urve Kallavus (Tallinn Technical University), Jevgeni Klimov (Institute of Geology of the Estonian Academy of Sciences) and Mart Rahi (Institute of Zoology and Botany of the Estonian Academy of Sciences) whose skill in operating the scanning electron microscope made this work possible.

REFERENCES

- Altner, H., Prillinger, L. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygro-receptors and its functional significance. — *Int. Rev. Cytol.*, **67**, 69—139.
- Boeckh, J., Kaissling, K. E., Schneider, D. 1965. Insect olfactory receptors. — *Cold Spring Harbor Symp. Quant. Biol.*, **30**, 263—280.
- Borg-Karlson, A.-K., Agren, L., Dobson, H., Bergström, G. 1988. Identification and electroantennographic activity of sexspecific geranyl esters in an abdominal gland of female *Agriotes obscurus* (L.) and *A. lineatus* (L.) (*Coleoptera*, *Elateridae*). — *Experientia*, **44**, **6**, 531—534.
- Davis, E. E., Sokolove, P. G. 1975. Temperature responses of antennal receptors of the mosquito, *Aedes aegypti*. — *J. Comp. Physiol.*, **96**, 223—236.
- Dyer, L. J., Seabrook, W. D. 1975. Sensilla on the antennal flagellum of the Sawyer Beetles *Monochamus notatus* (Drury) and *Monochamus scutellatus* (Say) (*Coleoptera*: *Cerambycidae*). — *J. Morph.*, **146**, 513—532.
- Hochreuther, R. 1912. Die Hautsinnesorgane von *Dytiscus marginalis* L., ihr Bau und ihre Verbreitung am Körper. — *Z. wiss. Zool.*, **103**, 1—114.
- Inouchi, J., Shibuya, T., Matsuzaki, O., Hatanaka, T. 1987. Distribution and fine structure of antennal olfactory sensilla in Japanese dung beetles, *Geotrupes auratus* Mts. (*Coleoptera*: *Geotrupidae*) and *Copris pecuarius* Lew. (*Coleoptera*: *Scarabaeidae*). — *Int. J. Insect Morphol. & Embryol.*, **16**, **2**, 177—187.
- Kaissling, K.-E. 1974. Sensory transduction in insect olfactory receptors. — In: Jaenicke, L. (ed.). *Biochemistry of Sensory Functions*. Berlin, Heidelberg, New York, 243—269.
- Kaissling, K.-E., Priesner, E. 1970. Die Riechschwelle der Seidenspinner. — *Naturwissenschaften*, **57**, 23—28.
- Keil, T. A., Steinbrecht, R. A. 1984. Mechanosensitive and olfactory sensilla of insects. — *Insect Ultrastructure*, **2**, 477—516.
- Lacher, V. 1964. Elektrophysiologische Untersuchungen an einzelnen Rezeptoren für Geruch, Kohlendioxyd, Luftfeuchtigkeit und Temperatur auf Antennen der Arbeitsbiene und der Dohne. — *Z. vergl. Physiol.*, **48**, 587—623.
- McIver, S. B. 1975. Structure of cuticular mechanoreceptors of arthropods. — *Ann. Rev. Entomol.*, **20**, 381—399.
- Moeck, H. A. 1968. Electron microscopic studies of the antennal sensilla in the ambrosia

- beetle, *Trypodendron lineatum* (Oliver) (Scolytidae). — Can. J. Zool., 46, 521—556.
- Mustaparta, H. 1973. Olfactory sensilla on the antennae of the pine weevil, *Hylobius abietis*. — Z. Zellforsch., 144, 559—571.
- Mustaparta, H. 1975. Responses of single olfactory cells in the pine weevil *Hylobius abietis* L. (Col.: Curculionidae). — J. Comp. Physiol., 97, 271—290.
- Payne, T. L., Moeck, H. A., Willson, C. D., Coulson, R. N., Humphreys, W. J. 1973. Bark beetle olfaction-II. Antennal morphology of sixteen species of Scolytidae (Coleoptera). — Int. J. Insect Morphol. & Embryol., 2, 177—192.
- Pierantoni, R. 1974. Electron scanning microscopy of the antennal receptors in *Tenebrio molitor*. A stereoscopic analysis. — Cell Tiss. Res., 148, 127—142.
- Schneider, D. 1964. Insect antennae. — Ann. Rev. Entomol., 9, 103—122.
- Schneider, D., Lacher, V., Kaissling, K.-E. 1964. Die Reaktionsweise und das Reaktionsspektrum von Riechzellen bei *Antheraea pernyi* (Lepidoptera, Saturniidae). — Z. vergl. Physiol., 48, 632—662.
- Schneider, D., Steinbrecht, R. A. 1968. Checklist of insect olfactory sensilla. — Symp. zool. Soc. London, 23, 279—297.
- Slifer, E. H. 1970. The structure of arthropod chemoreceptors. — Ann. Rev. Entomol., 15, 121—142.
- Slifer, E. H., Prestage, J. J., Beams, H. W. 1957. The fine structure of the long basiconic sensory pegs of the grasshopper (Orthoptera, Acrididae) with special reference to those on the antenna. — J. Morphol., 101, 359—397.
- Slifer, E. H., Prestage, J. J., Beams, H. W. 1959. The chemoreceptors and other sense organs on the antennal flagellum of the grasshopper (Orthoptera, Acrididae). — J. Morph., 105, 145—191.
- Slifer, E. H., Sekhon, S. S. 1964. Fine structure of the thin-walled sensory pegs on the antenna of a beetle, *Popilius disjunctus* (Coleoptera; Passalidae). — Ann. Entomol. Soc. Amer., 57, 541—548.
- Zacharuk, R. Y. 1980. Ultrastructure and function of insect chemosensilla. — Ann. Rev. Entomol., 25, 27—47.
- Гук А. М. 1987. К методике оценки численности проволочников с помощью феромонных ловушек. — In: Защита сельскохозяйственных растений в условиях применения интенсивных технологий. Минск, 129—130.
- Гурьева Е. Л. 1979. Фауна СССР, Жесткокрылые. XII, вып. 4. Жуки-щелкуны (Elateridae). Подсемейство Elaterinae. Трибы Megapenthini, Physorhini, Ampedini, Elaterini, Pomachilini. Ленинград.
- Долин В. Г. 1978. Определитель личинок жуков-щелкунов фауны СССР. Киев.
- Елизаров Ю. А. 1978. Хеморецепция насекомых. Москва.
- Иващенко И. И. 1981. Изучение динамики лёта кубанского и степного щелкунов с помощью феромонов. — In: Проблемы почвенной зоологии. Киев, 84.
- Меривез Э. 1985. Явление брачной агрегации у щелкуна черного *A. niger* L. — In: Методика и результаты изучения физиологического состояния насекомых. Тарту, 69—73.
- Мяхар Т. А. 1985. Изучение видоспецифичности и селективности ловушек для щелкунов темного и полосатого в условиях Эстонской ССР. — In: Методика и результаты изучения физиологического состояния насекомых. Тарту, 91—95.
- Олещенко И. И., Исмаилов В. Я., Пасько А. К., Волков Г. И., Козлов Е. И., Шлапак Н. И. 1986. Эффективность авиационного метода рассеивания феромона в борьбе с щелкуном степным. — In: Химическая коммуникация животных. Теория и практика. Москва, 117—122.
- Олой И. Н. 1987. Влияние различных препаративных форм и доз феромона на отлов посевного и западного жуков-щелкунов. — Новые методы в защите растений, 6, 15—18.
- Яцынин В. Г., Орлов В. Н., Рубанова Е. В. 1988. Идентификация феромона и исследование его диалектов у самок *Agriotes obscurus* L. (Coleoptera, Elateridae). — In: Рефераты IV Всес. симп. по хеморецепции насекомых. Вильнюс, 42.

**TUME-VILJANAKSURI *AGRIOTES OBSCURUS* L. (COLEOPTERA:
ELATERIDAE) EMAS- JA ISASMARDIKA ANTENNAALSENSILLID**

Tume-viljanaksuri *Agriotes obscurus* L. (*Coleoptera*, *Elateridae*) isas- ja emasmardika tundlail eristati 12 sensilli morfoloogilist tüüpi ja alatüüpi: trihhoidsed (alatüübid T1 ja T2), hetooidsed (alatüübid C1 ja C2), basikoonilised (alatüübid B1, B2, B3, B4, B5, B6 ja B7) ning kuppeljad (D) sensillid. Viimaste puhul on tõenäoliselt tegu tsölokooniliste sensillidega. Kõigil neil on iseloomulik jaotumise (sensillide hulk tundra segmentidel) ja paiknemise (sensillide asukoht segmentidel) muster, mis on sarnane mõlemal sugupoolel. 716 T2-sensilli leiti isasmardika ühel tundlal, emasmardikal on nende hulk mitu korda väiksem. Viimati nimetatud sensillide võrdlemine teiste putukaliikide feromoonireseptoritega näitab, et tõenäoliselt on T2-sensillid feromoonireseptoriteks tume-viljanaksuri isasmardikail.

ЭНО МЕРИВЕЭ

**АНТЕННАЛЬНЫЕ СЕНСИЛЫ САМКИ И САМЦА ТЕМНОГО ЩЕЛКУНА
AGRIOTES OBSCURUS L. (COLEOPTERA: ELATERIDAE)**

На антеннах самца и самки темного щелкуна *Agriotes obscurus* L. (*Coleoptera*, *Elateridae*) различали 12 морфологических типов и подтипов сенсилл: трихонидные (подтипы T1 и T2), хетоидные (подтипы C1 и C2), базиконические (подтипы B1, B2, B3, B4, B5, B6, B7) и куполообразные (D). Последние, вероятно, являются целокопическими сенсиллами. Сенсиллы расположены на антеннах жука не случайно, а каждый тип имеет характерную картину распределения (количество сенсилл на сегментах) и локализации (месторасположение на сегментах), схожую у обоих полов. 716 трихонидных сенсилл подтипа T2 было найдено на одной антенне самца, их количество у самки в несколько раз меньше. Сенсиллы подтипа T2 на антеннах самца, вероятно, являются ольфакторными рецепторами, воспринимающими половой феромон самки.