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Original article

Flagellar sensilla of bumble bee males (Hymenoptera, Apidae, *Bombus*)

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Summary — The flagellar sensillar distribution in males of 12 species of bumble bees, including five species with large-eyed males, did not show any conspicuous species-specific or behavior-related pattern. The sensillar types were morphologically similar to those of other bee taxa. In contrast to *Apis* drones, the bumble bee antennae lacked ventral wall-pore sensilla.

***Bombus* / antenna / chemoreception / electron microscopy / mechanoreception**

INTRODUCTION

Newman (1851) was the first to describe the characteristic flight of bumble bee males, where they mark objects along a flight path with an odorous secretion from the labial gland (Kullenberg et al, 1973; Ågren et al, 1979), and then patrol this path, probably waiting for receptive females. In a few species, the males do not make such paths, but wait for virgin females outside their nests and 'dart' on them, relying on visual cues (Alcock and Alcock, 1983). These males have larger eyes than path-producing species.

Kullenberg states (1973): "It is clear that the flights are essentially guided by sight". The males are, however, to some part attracted by artificial odor markings (Kullenberg, 1973). In preliminary electroantennogram tests (Ågren, unpublished data), the antennae respond to pheromone compounds.

The set of morphological sensillar types in bumble bees, first described by Leydig (1860), is very similar to that of the familiar honey bee, *Apis mellifera* (Slifer and Sekhon, 1961). Judging from investigations in that species, strong candidates as odor

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receptors are sensilla placodea and sensilla trichodea A (following the typology of Esslen and Kaißling, 1976). The former type responds to pheromones in *A. mellifera* (Lacher and Schneider, 1963; Kaißling and Renner, 1968). Lacher (1964) was unable to find any adequate stimuli for the latter type in *Apis*, but interpreted their function as odor receptors on morphological grounds.

One purpose of this study was to compare the sensilla of bumble bee males of several species, especially to find out whether the two mate-seeking strategies are reflected in a different sensillar setup in the small-eyed and large-eyed species.

MATERIALS AND METHODS

Bees

Antennae from fresh or dried bees of 12 species, one including two subspecies, were examined using SEM and TEM. Except for two pupae, all specimens were adults. The species are listed in table I.

Scanning electron microscopy

Three approaches were used.

1. External cuticular features: antennae were either air-dried, or critical-point dried after being fixed in glutaraldehyde and OsO_4 .
2. Internal cuticular features: antennae were embedded as for TEM (see below), then sectioned in semi-thin sections to the accurate position, and the embedding medium dissolved with sodium methoxide.
3. Internal soft tissues: antennae were fractured following the method of Tokunaga et al (1974).

After being treated by one of the methods above, preparations were either sputtered with gold or coated by evaporation with carbon/gold or pure gold to a thickness of ca 20 nm. Microscopes used were JEOL JSM-U3, JEOL JSM-35, and JEOL JSM T330, working voltages 15-20 kV.

Transmission electron microscopy

Antennae were cut from chilled animals and fixed by two alternative methods: 1) with cool 2% OsO_4 for 2 h and rinsed 6 x 10 min in 0.2 M phosphate buffer; or 2) with 2-3% glutaraldehyde overnight in 0.2 M cacodylate buffer, rinsed in the same buffer, and postfixed for 2 h in 1% OsO_4 . All spec-

Table I. Species with specimen numbers and geographic origin.

<i>Bombus (Alpinobombus) balteatus</i> Dahlbom 1832: 1 SEM, Abisko, Sweden
<i>B (Alpinobombus) hyperboreus</i> Schönherr 1809: 1 SEM, Abisko, Sweden
<i>B (Bombus) nevadensis</i> Cresson 1874: 1 SEM, Portland, OR, USA
<i>B (s s) terrestris</i> (L 1758): 2 SEM, Uppsala, Sweden
<i>B (Crotchibombus) crotchii</i> Cresson 1878: 1 SEM, Fresno County, CA, USA
<i>B (Cullumanobombus) rufocinctus</i> Cresson 1863: 1 SEM, San Mateo County, CA, USA
<i>B (Fraternobombus) fraterus</i> (F Smith 1854): 1 SEM, Richmond County, GA, USA
<i>B (Melanobombus) lapidarius</i> (L 1758): 5 SEM and 6 TEM (including one pupa 5 days before emergence), laboratory-reared in Uppsala, Sweden
<i>B (Pyrobombus) hypnorum</i> (L 1758): 1 TEM pupa 1 day before emergence, Öland, Sweden
<i>B (Pyrobombus) lapponicus lapponicus</i> (Fabricius 1793): 2 SEM, Abisko, Sweden
<i>B (Pyrobombus) lapponicus scandinavicus</i> , Friese 1902: 1 SEM, Abisko, Sweden
<i>B (Separatobombus) griseicollis</i> (De Geer 1773): 1 SEM, Ransom County, ND, USA
<i>B (Separatobombus) morrisoni</i> Cresson 1878: 1 SEM, Inyo County, CA, USA

imens were then dehydrated in ethanol, transferred via propylene oxide to Epon (polymerized at 60 °C), sectioned, and contrasted with lead citrate and uranyl acetate. Microscopes used were Siemens Elmiskop II at 60-80 kV, or JEOL 1 200 EX at 60 kV.

Counts

Sensilla were counted from micrographs that showed the cuticular surface as level as possible. A dorsal area not far from the proximal border of the annulus was chosen, if possible. As the counted areas varied between 2 500 and 8 600 μm^2 , the values were recalculated to numbers per mm^2 . One to four counts were made per individual.

Terminology

The flagellar annuli were designated fl¹-fl¹¹ in a proximal to distal direction. Terminology of surface sculpturing followed Harris (1979), designation of sensilla followed Esslen and Kaißling (1976) and Altner (1977), and the nomenclature of the bumble bees followed Löken (1973) for European and Krombein et al (1979) for north American taxa. For positional descriptions, the antenna was considered to be positioned straightforward and not rotated.

RESULTS

Distribution of cuticular structures

The entire fl¹ and half fl² were provided almost exclusively with non-innervated setae, but on mid fl² and outwards two main zones as regards the distribution of cuticular structures were found: one dorsal characterized by the presence of s placodea (placodea zone) (fig 1), and one ventrolateral dominated by non-innervated setae (setal zone) (fig 2), but also possessing s trichodea B and C/D.

The placodea zone reached to just proximal to the apex of the antenna. In this zone,

thousands of s placodea were intermingled with s trichodea A (figs 1, 5). Sensilla trichodea B and C/D were present but more sparse. Non-innervated setae bordered the distal end of every annulus in a double row. Compared to s trichodea A, s placodea occurred further laterally in all annuli and further proximally on fl². Sensilla ampullacea and coeloconica were clustered laterally (s coeloconica sometimes proximally) on the dorsal side (fig 4), occasionally together with some coelocapitular sensilla; s ampullacea were only found on one lateral side. The apex was conflated (crowded) with hairs, mostly s trichodea B and C/D. Sensilla basiconica did not occur in males.

There was no ventral mutic (unarmed) area in the terminal annulus, as in some other bees (Ågren, 1977, 1978; Ågren and Svensson, 1982) (fig 2). Around 50 s trichodea B and 15 s trichodea C/D were counted among the non-innervated setae in the ventral part of fl¹¹ in one *B lapidarius* male.

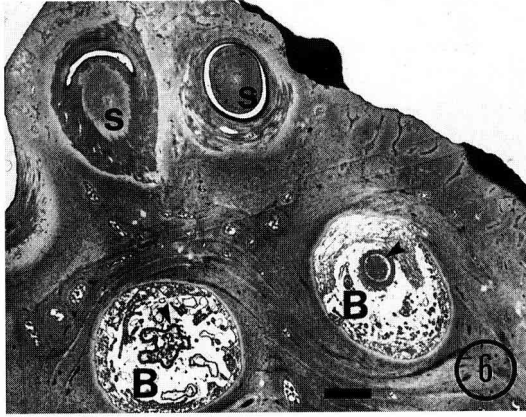
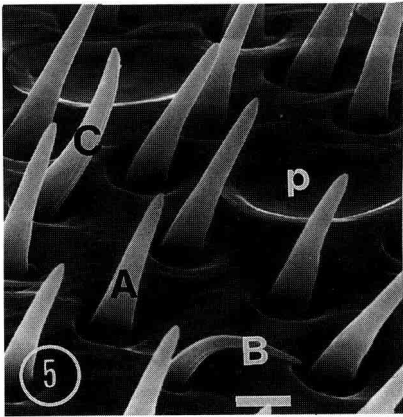
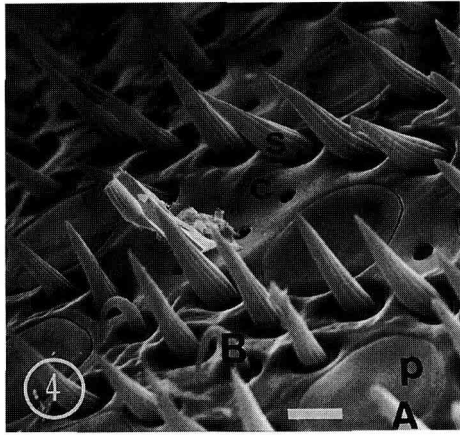
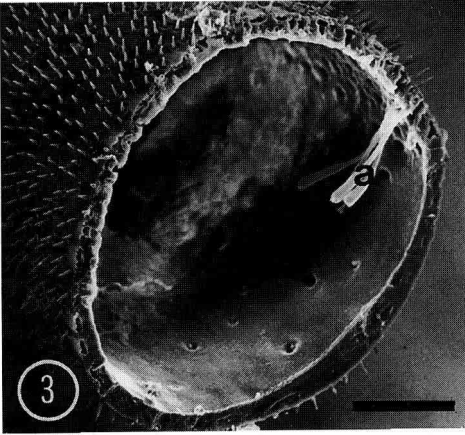
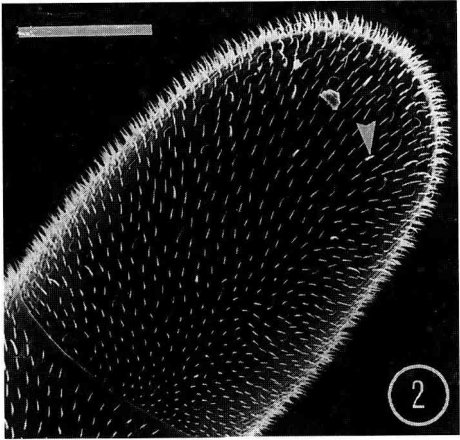
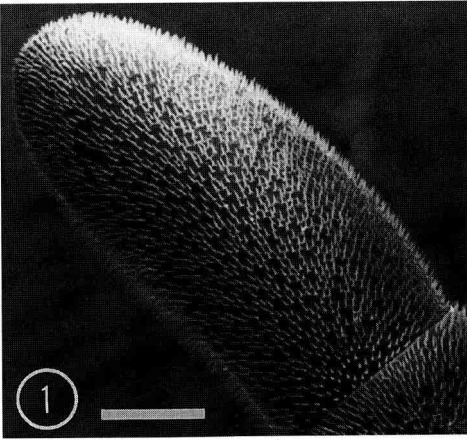
An ocular inspection of the micrographs did not reveal any obvious differences in the sensillar densities or distributional patterns between the species. The densities (table II, figs 14, 15) did not show any statistical grouping of any sensillum type between large-eyed and small-eyed species (unbalanced ANOVA at 5% significance level).

Morphology of sensilla and other hairs

The sensillar morphology was indistinguishable in all investigated specimens, and the observations below thus refer to all species.

Non-innervated setae

These appeared to form a diverse class of hairs that shared at least some common



features (figs 2, 4, 6). They did not penetrate through the cuticle and were thus uninervated (figs 3, 6), ranged 15-20 μm in length, with a basal width of 1.6-4 μm . The most proximal setae of fl¹ and fl² were longer and sometimes branched.

Sensilla trichodea A

These sensilla were typical thin- and single-walled hairs with wall pores (WP of Altner, 1977), 1.4-3.1 μm thick and about 11 μm long, slightly S-shaped, and with blunter tips than setae (figs 1, 3, 4, 5, 7, 11).

Each sensillum was innervated by two to six receptor cells (fig 11) and had three types of accessory cells, apparently thecogen, trichogen, and tormogen cells, wrapped around each other respectively. The dendritic outer segments had no surrounding dendrite sheath.

Sensilla trichodea B

The thin (1.3 x 11 μm) lineate to lineolate (finely lineate) hairs were curved about 90° (figs 2, 4, 5, 6). Under the hair was one receptor cell with a tubular body (fig 6).

Sensilla trichodea C/D

The two types C and D, as identified in *Apis* light-microscopically by Esslen and Kaißling (1976), were not distinguishable by SEM, and only one type was identified by TEM in

B. balteatus, one thinner and one thicker type could be discriminated by SEM, the thicker having a more distinct socket (figs 2, 5, 8, 9). Considered here together, they could be recognized as slightly curved long (13-18 x 1.7-2.4 μm), sparsely lineate or lineolate hairs, with a terminal pore at the blunt tip. The sensilla were innervated by 4 + 1 cells. The single cell had a tubular body between hair and socket, whereas the other four reached into the hair (fig 8).

Sensilla placodea

By SEM, the s placodea (figs 1, 4, 5, 10) were characterized by a radially striate oval plate (12-14 x 8 μm , *B. lapidarius*), encircled by a fissure (figs 4, 5).

The arrangement of enveloping cells was similar to that in s trichodeum A (fig 10). There was no visible dendrite sheath.

The number of receptor cells per sensillum ranged from 13-20, with 14-15 being (fig 10) most common.

Sensilla coeloconica

This sensillum type (figs 4, 12) was recognized as a 1.5-2 μm wide pore in the cuticle. Below the pore was a 1-1.5 μm deep, 2-3 μm wide cavity with a central short peg, encircled by folds. The sensillum was innervated by three cells, and was of DW type (Altner, 1977) (fig 12).

Fig 1. Apex of flagellum, *Bombus rufocinctus*, dorsal side. Dark patches are s placodea and most hairs are s trichodea A. Magnification x 140. Bar is 100 μm .

Fig 2. Apex of flagellum, *B. lapidarius*, ventral side. Hairs are mostly non-innervated setae and s trichodea B, the latter bent. Arrow points at s trichodeum C/D. Magnification x 180. Bar is 100 μm .

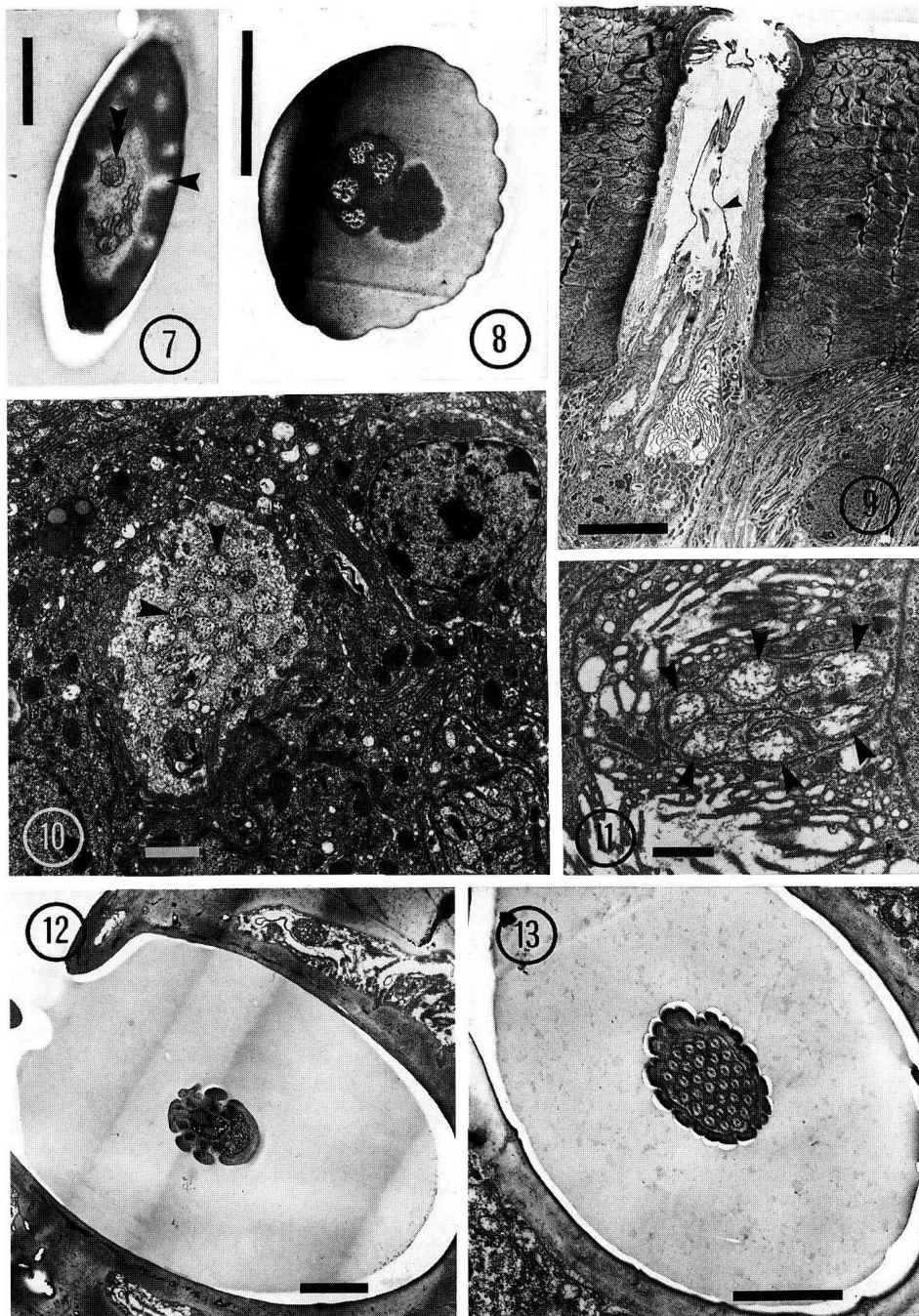
Fig 3. Cut flagellum of *B. lapidarius* with soft tissue dissolved, fl¹⁰. On the inside a few crevices of sensilla (setal zone) are seen, the non-innervated setae do not penetrate through the cuticle. Magnification x 270. Bar is 50 μm .

Fig 4. Sensilla at the border between setal and placodea zones. Magnification x 7 300. Bar is 1 μm .

Fig 5. View from placodea zone, *B. lapidarius*. Magnification x 7 600. Bar is 1 μm .

Fig 6. *B. lapidarius* flagellum, transversal section. Note lack of nervous tissue in non-innervated setae. S trichodea B, sectioned at different levels, have pronounced dendrite sheaths (arrows). Magnification x 6 200. Bar is 1 μm .

Abbreviations used in the micrographs: a = Sensillum ampullaceum; A = Sensillum trichodeum A; B = Sensillum trichodeum B; c = Sensillum coeloconicum; C = Sensillum trichodeum C/D; p = Sensillum placodeum; s = Non-innervated seta.



Sensilla ampullacea

These pit organs (figs 3, 13) had a pore only 0.7–0.9 μm wide and a peg situated at the bottom of a 50–80 μm long tube (fig 3). The tube had a diameter of 6 μm for the basal third of its length and 3 μm for the rest. It terminated distally in a cavity 1 μm below the cuticular surface, surrounded by a rim of lamellar or finger-like protuberances. The peg seemed to be a 'poreless sensillum with inflexible socket' according to Altner (1977), with one receptor cell. The dendrite sheath accompanied the dendrites distally. At its peg base was a tubular body.

Sensilla coelocapitula

These sensilla were characterized by a conflatedly acinose (granulated like a blackberry) small protuberance (2 μm across) with a circumferential fissure, centered in an immaculate (destitute of sculpturing), slightly depressed field 8–11 μm across. The appearance of the central protuberance was sensitive to fixation artifacts and was flat and porous in some preparations, in others smaller and more bulbous. This sensillum was not investigated by TEM.

DISCUSSION

Comparisons between species of bumble bees

The five large-eyed species (*Bombus crotchii*, *B. fraternus*, *B. griseicollis*, *B. mor-*

risoni, and *B. nevadensis*), did not seemingly differ from the other species investigated, neither in terms of the density of the wall-pore (probably olfactory) sensilla, nor in sensillar morphology. By comparing the sensillar densities instead of totals, we assumed that the total flagellar area was about equal in all species. It must be taken into account that these numbers were achieved from very few individuals and from areas of various sizes, which of course affected the bias. The error bars in figs 14 and 15 were thus influenced both on variations in densities and in measured areas. Our interpretation is that differences in the sensillar setup between the two groups of bumble bee males cannot be excluded, but are not very obvious.

Classification of sensilla

The trichoid sensilla type A (Esslen and Kaißling, 1976), and the s placodea belong to the wall-pore sensilla, among which only olfactory receptors have been identified. An olfactory function has also been assigned to coeloconic sensilla (Boeckh, 1967), which have radial slit-like pores (double-walled sensilla).

Sensilla trichodea C/D have the characteristics of being combined taste and tactile sensilla, with one mechanosensory unit and four gustatory receptor cells. Altner (1977) named this type 'terminal pore sensillum'.

Fig 7. *B. lapidarius*, transverse section of s trichodeum A hair. Note pore kettles (single arrow) and sections of dendrite distal parts (double arrow). Magnification $\times 12\,000$. Bar is 1 μm .

Fig 8. *B. lapidarius*, transverse section of s trichodeum C/D hair. Four taste cells. Magnification $\times 20\,000$. Bar is 1 μm .

Fig 9. *B. lapidarius*, longitudinal section of s trichodeum C/D. Arrow shows dendrite sheath. Magnification $\times 2\,500$. Bar is 5 μm .

Fig 10. *B. lapidarius*, transverse section of s placodeum below the cuticle. Arrows point at two of the 16 receptor cells. Magnification $\times 7\,500$. Bar is 1 μm .

Fig 11. *B. lapidarius*, transverse section of s trichodeum A below the cuticle. Six receptor cells (arrows). Magnification $\times 8\,200$. Bar is 1 μm .

Fig 12. *B. lapidarius*, oblique section of s coeloconicum. Magnification $\times 9\,400$. Bar is 1 μm .

Fig 13. *B. lapidarius*, transverse section of s ampullaceum. Magnification $\times 15\,000$. Bar is 1 μm .

Sensilla trichodea B are mechanoreceptors (McIver, 1975) with one sensory cell provided with a tubular body.

Sensilla ampullacea have previously been thoroughly described in ants (Walther, 1979; Hashimoto, 1990, 1991). The poreless (NP) sensilla usually possess a triad of sensory cells (Altner et al, 1983). One of these has a lamellated outer segment, and is a thermoreceptor, while the other two respond to high and low humidity, respectively (Steinbrecht, 1989). Deviations from this pattern are found, and there might be one or four sensory cells connected to this sensillar type (Altner et al, 1983). The functional interpretation of s ampullacea is thus

far from clear-cut. Similar types of sensilla have been described in Coleoptera (Guse and Honomichl, 1980; Honomichl and Guse, 1981), where the sensillum (called digitiform sensillum) has a more superficial position and a thicker cuticular wall, but is innervated by a single sensory cell with branches within the hair. The function of these has been suggested to be either thermo- or hygrometry (Guse and Honomichl, 1980), mechanoreception (Zacharuk et al, 1977), or perception of CO₂ (Honomichl and Guse, 1981). These functions seem plausible for the s ampullacea, except for mechanoreception. In *Apis*, Lacher (1964) could not differ morphologically between s

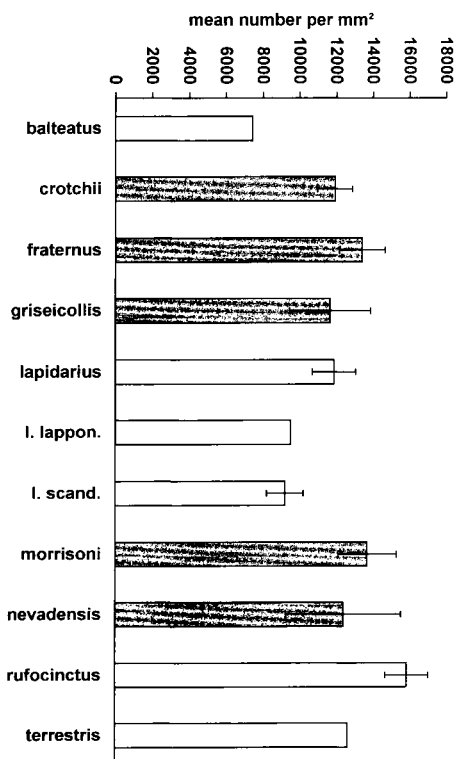


Fig 14. Numbers per mm² of s trichodea A in different species (placodea zone). Large-eyed species indicated by darker pattern. Error bars indicate standard deviation of sensillar number.

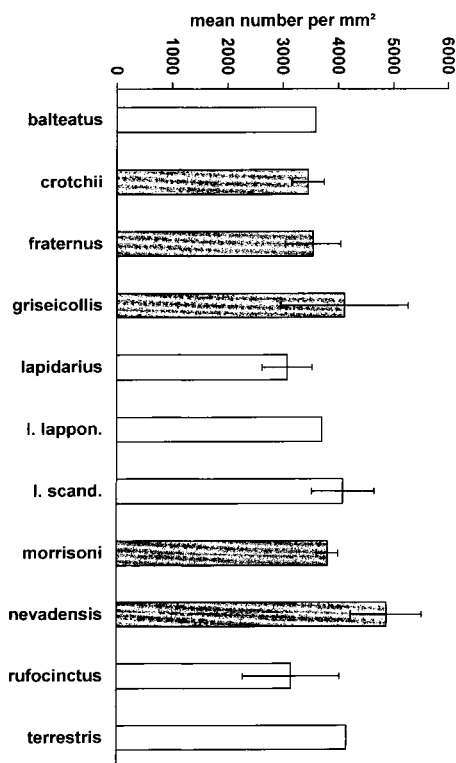


Fig 15. Numbers per mm² of s placodea in different species (same areas as in fig 14). Large-eyed species indicated by darker pattern. Error bars indicate standard deviation of sensillar number.

Table II. Counts of the sensillar densities per mm² on the flagellum of male bumble bees.

Species	Sensilla trichodea C/D	SD	Sensilla trichodea B	SD	Sensilla placodea	SD	Sensilla trichodea A	SD	Area (μm^2)	SD	Number of individuals	Number of measurements
<i>B balteatus</i>	0		696		3 594		7 420		8 625		1	1
<i>B crotchii</i>	195	159	924	531	3 456	289	11 925	952	5 136	36	1	4
<i>B fraternus</i>	147	187	737	802	3 546	504	13 392	1 232	5 080	74	1	4
<i>B griseicollis</i>	0	0	1 076	126	4 117	1 156	11 658	2 213	5 110	60	1	2
<i>B lapidarius</i>	0	0	706	150	3 080	453	11 869	1 176	8 081	2 715	2	2
<i>B lapponicus</i>	1 626		3 717		3 708		9 502		4 315		1	1
<i>B l. scandinavicus</i>	185	185	4 168	319	4 092	563	9 209	995	2 511	205	1	3
<i>B morrisoni</i>	97	137	389	271	3 810	194	13 683	1 581	5 120	75	1	2
<i>B nevadensis</i>	99	140	678	400	4 873	644	12 392	3 128	5 137	98	1	2
<i>B rufocinctus</i>	97	138	1 180	16	3 153	876	15 840	1 183	5 085	67	1	2
<i>B terrestris</i>	462		308		4 156		12 621		6 497		1	1

ampullacea and s coeloconica, but found receptors for CO₂, temperature, and humidity in the pit organs in single cell recordings.

The s coelocapitulum is a hygro- and thermoreceptor in *Apis* (Yokohari, 1983). With a similar function for the same sensillum in *Bombus*, the s ampullacea most likely respond to carbon dioxide, since several sensillar types responding to temperature and humidity usually do not exist on the same antenna.

Comparison with *Apis*

The sensillar equipment of the investigated bumble bee males was principally similar to that of the closely related honey bee *Apis mellifera* drones. A main difference was the shorter flagellar annuli and the lack of ventral s placodea in bumble bees. For a bumble bee male (*B hypnorum*), the literature gives a number of around 1 900 (Fonta and Masson, 1987) s placodea per antenna, for a honey bee drone between 18 000 and 19 000 (Esslen and Kaißling, 1976). Although male bumble bees, in opposite to honey bee drones, have s placodea on fl², they have thus only a tenth as many s placodea as the latter. The areas of the antenna covered by s placodea are, however, quite similar: 2.25 mm² in *Bombus* (Fonta and Masson, 1987), 2.37 mm² in *Apis* (Esslen and Kaißling, 1976). Densities of bumble bee s placodea were 3 100–4 900/mm² in this investigation, which well agrees with the counts by Fonta and Masson (1987) (3 800–4 130/mm²). In *Apis*, Esslen and Kaißling's (1976) estimation of 1 300 s placodea/mm² must be a mistake, as a count from their illustrations (pore plate-rich area) gives about 9 600/mm².

The number of receptor cells under the s placodea differ between the males of the two genera. In bumble bees, they were counted to around 14 in this investigation in *B lapidarius* and *B hypnorum*, compared

to 15–30 (mean 18) in *Apis*. This makes 26 600 in *Bombus* (1 900 x 14) and 334 700 in *Apis* (Esslen and Kaißling, 1976) per antenna. It means that drones possess more than 12 times as many odor receptor cells, as *Bombus* males.

ACKNOWLEDGMENTS

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Résumé — Les sensilles du flagelle des mâles de bourdons (Hymenoptera, Apidae, *Bombus*). Le but de cette étude était de comparer les sensilles du flagelle des mâles de 12 espèces et deux sous-espèces de bourdon pour savoir si l'on retrouve dans l'organisation des différentes sensilles les deux stratégies de recherche du partenaire sexuel (espèces à petits yeux qui patrouillent le long de chemins de vol ou espèces à gros yeux qui «se précipitent» sur les femelles). Des antennes prélevées sur des insectes frais (capturés au champ ou élevés en laboratoire) ou sur des spécimens de musées ont été examinées en microscopie électronique à transmission et à balayage. Les types morphologiques des sensilles du flagelle ressemblent à ceux des autres abeilles et comprennent des sensilla placodea (sensille à pore entouré d'un pli ; figs 1, 4, 5 et 10), des s trichodea A (sensille à pore entouré d'un pli ; fig 1, 3, 4, 5, 7 et 11), des s trichodea B (mécanorécepteurs ; fig 2, 4, 5 et 6), des s trichodea C/D (sensille à pore terminal ; fig 2, 5, 8 et 9), des s coelocapitulata (sensille sans pore), des s ampullacea

(sensille sans pore, fig 3 et 13) et des *s coeloconica* (sensille à double paroi ; fig 4 et 12). Les espèces de bourdons dont les mâles ont de gros yeux (*B crotchii*, *B frater-nus*, *B griseicollis*, *B morrisoni*, *B nevadensis*) et qui utilisent les stimulus visuels plus que les olfactifs pour localiser le partenaire sexuel, ne présentent apparemment pas de différence dans les types de sensilles ni de différence dans la densité des sensilles considérées comme olfactives (figs 14 et 15). Ainsi il est impossible de distinguer les espèces étudiées d'après la répartition de leurs sensilles. Les seules différences que l'on ait trouvées par rapport aux mâles d'abeille domestique sont : i) les antennes de mâles de bourdons n'ont pas de sensilles à pore entouré d'un pli en position ventrale, ii) les sensilla placodea des mâles de bourdons sont moins nombreuses et leur densité est plus faible, iii) les puits des sensilla ampullacea sont plus de quatre fois plus profonds chez *Bombus*.

***Bombus* / antenne / chimioréception / mécanoréception / microscopie électronique**

Zusammenfassung — Sensillen des Flagellums bei Hummelmännchen (Hymenoptera, Apidae, *Bombus*). Die Sensillen des Flagellums bei den Männchen von 12 Arten und 2 Unterarten von Hummeln wurden insbesondere daraufhin untersucht, ob die beiden Suchstrategien nach Paarungspartnern (kleinäugige auf Flugwegen 'patrouillierende' Arten und großäugige 'hervorschießende' Arten) sich in unterschiedlicher Ausstattung mit Sensillen widerspiegeln. Die Antennen von frischen Hummeln (entweder Wildfänge oder Laborzuchten) wurden elektronenmikroskopisch und raster-elektronenmikroskopisch untersucht. Die gefundenen morphologischen Typen der flagellären Sensillen ähnelten denen der Bienen und umfassten *s placodea* (Sensillen mit Wandporen, Abb 1, 4, 5, 10), *s tricho-*

dea A (Sensillen mit Wandporen, Abb 1, 3, 4, 5, 7, 11), *s trichodea B* (Mechanorezeptoren, Abb 2, 4, 5, 6), *s trichodea C/D* (Sensillen mit terminaler Pore, Abb 2, 5, 8, 9), *s coelocapitula* und *s ampullacea* (porenlose Sensillen, Abb 3, 13) und *s coeloconica* (doppelwandige Sensillen, Abb 4, 12). Hummelarten, deren Männchen große Augen besitzen und die bei der Partnersuche mehr visuelle als olfaktorische Reize benutzen (*B crotchii*, *B frater-nus*, *B griseocollis*, *B morrisoni*, *B nevadensis*), zeigten kein deutlich abweichendes Verteilungsmuster der Sensillen oder eine unterschiedliche Dichte von Sensillen, für die eine olfaktorische Funktion angenommen wurde (Abb 14, 15). Die untersuchten Arten waren daher bezüglich ihrer Sensillenverteilung ununterscheidbar. Die einzigen Unterschiede im Vergleich zu Drohnen der Honigbienen waren 1. die Antennen der Hummelmännchen besitzen keine ventralgelegenen Sensillen mit Wandporen; 2. *S placodea* sind in geringerer Anzahl und Dichte vorhanden; 3. Die Gruben der *s ampullacea* sind bei den Hummelmännchen etwa vier mal tiefer.

Antennen, Chemorezeption, Elektronenmikroskopie, Mechanorezeption, *Bombus*

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