

Antennal sensilla in ground beetles (Coleoptera, Carabidae)

A. Ploomi¹, E. Merivee¹, M. Rahi², J. Bresciani³, H. P. Ravn⁴,
A. Luik¹ and V. Sammelselg⁵

¹ Institute of Plant Protection, Estonian Agricultural University, Kreutzwaldi 64, 51014, Tartu, Estonia; e-mail: angela@eau.ee

² Institute of Zoology and Botany, Estonian Agricultural University, Riia 181, 51014 Tartu, Estonia

³ Veterinary and Agricultural University, Bülowsvej 13, DK 1870, Frederiksberg C, Denmark

⁴ Danish Forest and Landscape Research Institute, Hoersholm Kongevej 11, DK 2970, Hoersholm, Denmark

⁵ Institute of Physics, University of Tartu, Riia 142, 51014 Tartu, Estonia

Abstract. The antennal sensilla of male and female ground beetle species *Bembidion lampros* Hbst., *Bembidion properans* Steph. and *Platynus dorsalis* Pont. (Coleoptera, Carabidae) were investigated by using a scanning electron microscope. The filiform antennae of ground beetles consist of the scape, pedicel and 9 flagellomeres. Thirteen different sensillar types were distinguished. These were: four types of *sensilla chaetica*, two types of *sensilla trichodea*, six types of *sensilla basiconica*, pit-organs *sensilla coeloconica*, and small domes *sensilla campaniformia*. *Sensilla chaetica* 4 occur only on the antennae of *P. dorsalis*, and *sensilla trichodea* 1 only on the antennae of *Bembidion* species. No sexual differences in the types of sensilla were found on the antennae of these three species. The possible functions are discussed and three types of sensilla were considered as olfactory, *sensilla trichodea* 2 and *sensilla basiconica* 1 and 2. Olfactory *sensilla trichodea* 2 and *sensilla basiconica* 1 form clear dorsal and ventral sensillar fields on the flagellomeres, which seems to be common in ground beetles.

Key words: ground beetles, Coleoptera, Carabidae, *Bembidion lampros* Hbst., *Bembidion properans* Steph., *Platynus dorsalis* Pont., antenna, sensilla, morphology, typology, number

INTRODUCTION

Ground beetles (Coleoptera, Carabidae) are one of the most common families of surface-active arthropods in agricultural ecosystems, where their habitat distribution has been studied extensively (Lövei & Sunderland, 1996; Kromp, 1999). Habitat selection in ground beetles depends on a complex process involving a multitude of biotic and abiotic parameters. Vegetation, temperature, humidity, light, soil pH, compactness and salt content of the soil, cover of leaf litter, herbs, prey density and pesticides are the most important factors shown to contribute to the composition of carabid assemblages (Lövei & Sunderland, 1996; Kromp, 1999; Magura et al., 2002). Carabid beetles are polyphagous, mainly carnivorous (Lövei & Sunderland, 1996) that prey on a wide range of agricultural pests from aphids (Losey & Denno, 1998) to slugs (Symondson et al., 1996). The ground beetle species *Bembidion lampros* (Hbst.), *B.*

properans (Steph.) and *Platynus dorsalis* (Pont.) are particularly frequent and characteristic in European fields, and also in Estonia (Haberman, 1968; Kromp, 1999).

Insect antennae are mobile, segmented, paired appendages. The entire antenna typically has three main divisions: the first segment, or scape, is generally larger than the other segments and is the basal stalk; the second segment, or pedicel, responds to movement of the distal part of the antenna; the remainder of the antenna, called the flagellum, is often filamentous and multisegmented (with many flagellomeres), but may be reduced or variously modified (Gullan & Granston, 2003). Numerous sensory organs, or sensilla (singular: sensillum), in the form of hairs, pegs, pits or cones, occur on the antennae and function as chemoreceptors (the senses of smell - olfaction and taste - gustation), mechanoreceptors, thermoreceptors and hygroreceptors and bearing sometimes sensors for CO₂ (Gullan & Granston, 2003; Hansson, 1999). A comparison of the differentiation of sense organs in ground beetles with different ecology may give information on their adaptation to serve that kind of life and the knowledge of how certain structures of the sense organs due to their different functional demands. Morphological studies are a prerequisite for electrophysiological experiments. Future experiments using single-cell electrophysiological methods will be necessary to clarify the functions of sensilla in ground beetle antennae.

MATERIALS AND METHODS

Samples of the ground beetle *Bembidion properans* were collected in Denmark (Lyngby) in 1996, and in Estonia 1998. The ground beetle *B. lampros* were collected in the fields in South Estonia in October 1998 and the ground beetle *Platynus dorsalis* were collected from a hibernating aggregation of the beetles at a field margin in Southern Estonia in September 2000. Three antennae of both sexes were examined and micrographed from all sides, using a scanning electron microscopy. In classifying sensilla, the terminology of Schneider (1964) and Zacharuk (1985) was used.

RESULTS AND DISCUSSION

The filiform antennae of both sexes of the ground beetles *B. lampros*, *B. properans* and *P. dorsalis* are composed of 11 distinct segments: the scape, the pedicel and the nine segments (flagellomeres) of the flagellum. Based on external morphology of sense organs, *sensilla chaetica*, *sensilla trichodea*, *sensilla basiconica*, *sensilla coeloconica* and *sensilla campaniformia* were distinguished. The mean numbers and probable functions of sensilla have been summarised in Table 1. No sexual differences in the types of sensilla were found on the antennae of these three species. *Sensilla trichodea* 1 were not found on the *P. dorsalis* antennae and *sensilla chaetica* 4 occur only on the antennae of *P. dorsalis* (Merivee et al., 2000, 2001, 2002).

Three types of sensilla were considered as olfactory, *sensilla trichodea* 2 (Fig. 1A,B) and *sensilla basiconica* 1 and 2. In male moths, trichoid sensilla respond to female sex pheromone related compounds (Keil & Steinbrecht, 1984; Zacharuk, 1985; Hansson et al., 1986; Hallberg et al., 1994). Striking differences in the number of these trichoid sensilla, for example, in click beetles (Merivee, 1992; Merivee et al., 1999) suggest that they probably function as sex pheromone receptors in males of some beetles. In contrast, no considerable sexual differences in the number of the immovable

blunt-tipped trichoid sensilla were found on the ground beetles *B. lampros*, *B. properans* and *P. dorsalis*, indicating that these sensilla respond to aggregation pheromone produced by some ground beetles (Moore & Wallbank, 1968; Wautier, 1970, 1971). Non-articulated blunt-tipped basiconic sensilla, which resemble *sensilla basiconica* 1 and 2 of *B. lampros*, *B. properans* and *P. dorsalis*, are common on the antennal flagellum of most insects. In the cigarette beetle *Lasioderma serricorne* (Fab.) (Okada et al., 1992) and the ground beetle *Nebria brevicollis* (Fab.) (Daly & Ryan, 1979), it was demonstrated that the wall of these sensilla is perforated by numerous tiny pores. The numerous pores and branched dendrites are considered to be evidence that these basiconic sensilla function as olfactory receptors (Altner & Prillinger, 1980; Zacharuk, 1985). The total number of olfactory trichoid and basiconic sensilla on the antennae of *P. dorsalis* is many times higher than on the antennae of the ground beetles *B. lampros* and *B. properans*, suggesting that nocturnally active *P. dorsalis* is much more sensitive to odours perceived by these sensilla than *Bembion* species with diurnal activity and hunting predominantly by sight (Merivee et al., 2000, 2001, 2002).

Olfactory *sensilla trichodea* 2 and *sensilla basiconica* 1 form clear dorsal and ventral sensillar fields on the flagellomeres, which seems to be common in ground beetles. Their numbers on the flagellomeres, growing towards the tip of the antenna, are unevenly distributed between the two fields of sensilla. The number of *sensilla trichodea* 2 per flagellomere is increasing towards the tip of the antenna more rapidly in the dorsal sensillar fields than in the ventral ones. Most of basiconic sensilla are located on the ventral side of the antenna. Similar asymmetry in the distribution of antennal olfactory sensilla has also been observed in click beetles *Agriotes obscurus* (L.) and *Melanotus villosus* (Geof.) (Merivee et al., 1997, 1999). It has been suggested (Merivee et al., 1997) that asymmetries in the distribution pattern of olfactory sensilla on insects' antennae may be due to the peculiarities of their search behaviour (waiting, walking, flying, antennal movements), which causes certain areas of the antennal surface to catch the wind-borne odour molecules more effectively than the others.

The number of blunt-tipped contact chemoreceptors *sensilla chaetica* 2 (Fig. 1C) on all flagellomeres is extremely stable, in *B. lampros* and *B. properans* 66 bristles per antenna and in *P. dorsalis* 71 bristles per antenna. The number of contact chemoreceptors (70–90), their placement and distribution pattern is also very stable and similar on the antennae of click beetles *Melanotus villosus* (Merivee et al., 1999), *Agriotes obscurus* (Merivee, 1992; Merivee et al., 1997) and *Limoniuss aeruginosus* (Oliv.) (Merivee et al., 1998). Contact chemoreceptors are of primary importance in relation to feeding (Chapman, 1998).

Sensilla basiconica 3 on the antennae of *P. dorsalis* (approximately 150) is almost 30 times more numerous than in *Bembidion*. Their function on the antennae of *Platynus* and *Bembidion* is not clear. A small groove or depression, not characteristic for mechanoreceptive pegs, at the tip of tiny *sensilla basiconica* 3 indicate that they probably function as chemoreceptors. These sensilla are absent in the ground beetles *Nebria brevicollis* and *Carabus fiduciarius saishutoicus* beetles (Csiki) (Daly & Ryan, 1979; Kim & Yamasaki, 1996), and also in Elateridae (Merivee, 1992; Merivee et al., 1998, 1999), Scolytidae (Faucheux, 1989, 1994), Curculionidae (Alm & Hall, 1986), and other Coleoptera.

Table 1. Total numbers of sensilla on the antenna of male and female *Bembidion lampros*, *Bembidion properans* and *Platynus dorsalis*. N = 3, r.– reception.

Type of sensilla	Probable functions	<i>B. lampros</i>		<i>B. properans</i>		<i>P. dorsalis</i>	
		Male	Female	Male	Female	Male	Female
<i>chaetica</i> 1	mechanor.	610	695	814	838	1,843	1,733
<i>chaetica</i> 2	mechanor. or contact chemor.	66	66	66	66	71	71
<i>chaetica</i> 3	mechanor.	5	5	5	5	1	1
<i>chaetica</i> 4	mechanor.	-	-	-	-	20	17
<i>trichodea</i> 1	mechanor.	118	118	118	118	-	-
<i>trichodea</i> 2	olfactory r.	166	146	220	206	1,044	978
<i>basiconica</i> 1	olfactory r.	389	339	413	406	1,813	1,708
<i>basiconica</i> 2	olfactory r.	44	54	51	42	101	120
<i>basiconica</i> 3	chemor.	4	5	4	9	152	143
<i>basiconica</i> 4	(?)	4	3	3	3	3	3
<i>basiconica</i> 5	mechanor.	10	9	8	15	9	12
<i>basiconica</i> 6	mechanor.	*	*	56	56	131	117
<i>coeloconica</i>	thermo- and hygror. or chemor.	21	20	17	21	62	61
<i>campani- formia</i>	thermor.	19	19	18	20	25	25

* The number of *basiconica* 6 sensilla was not counted in the *Bembidion lampros*.

Sensilla trichodea 1 (Fig. 1C) was found only on the antennae of *Bembidion* species. These bristles are innervated by a single sensory neurone, ending with the typical tubular body, attached to the base of the hair shaft. This indicates a mechanosensory function (Zacharuk, 1985). *Sensilla trichodea* 1 may have a tactile function. However, it is possible that not all sensilla *trichodea* 1 are innervated. Mustaparta (1973) found that similar sensillar types on the weevil *Hylobius abietis* (L.) had either a mechanoreceptive function, or no receptor function, possibly acting as protective hairs (Bartlet et al., 1999).

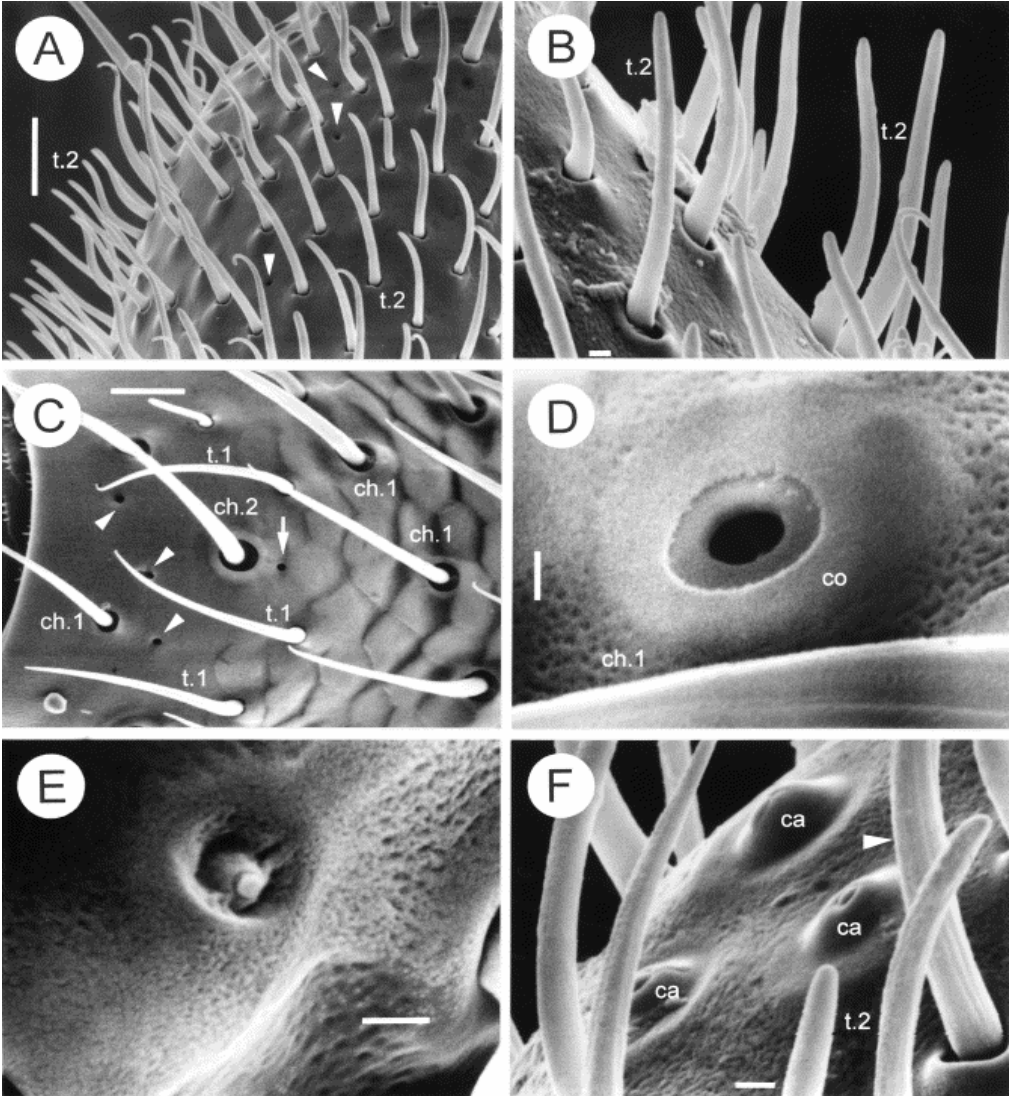


Fig. 1. Antennal sensilla in *B. properans*. Bar = 10 μm (A and C) or 1 μm (B and D–F). (A) Distal part of the ninth flagellomere. T.2, *sensilla trichodea* type 2; arrowheads show tiny cuticular pores. (B) *Sensilla trichodea* type 2 (t.2). (C) Distal part of the third flagellomere. Ch.1 and ch.2, *sensilla chaetica* types 1 and 2, respectively; t.1, *sensilla trichodea* type 1; arrow shows a pore associated with *sensilla chaetica* type 2; arrowheads show tiny cuticular pores at the distal margin of the flagellomere. (D) *Sensillum coeloconicum* (co). Ch.1, middle part of the *sensillum chaeticum* type 1. (E) *Sensillum campaniformium*. (F) A group of *sensilla campaniformia* at the tip of the ninth flagellomere. T.2 show the tips of *sensilla trichodea* type 2; arrowhead shows the base of *sensillum chaeticum* type 1.

Sensilla campaniformia (Fig. 1E,F) described in *B. lampros*, *B. properans* and *P. dorsalis* (Merivee et al., 2000, 2001, 2002) are similar to some other beetles, for instance click beetles (Merivee, 1992; Merivee et al., 1998, 1999). In another ground beetle, *C. fiduciaris saishutoicus*, two types of campaniform sensilla occur only on two apical flagellomeres (Kim & Yamasaki, 1996). The electrophysiological recordings of campaniformia sensilla on the antennae of the ground beetle *Pterostichus aethiops* (Pz.) were distinguished as cold receptors (Merivee et al., 2003). Thermoreceptors are probably involved in habitat selection of carabid beetles and enable to avoid hyperthermia of insects.

CONCLUSIONS

The typology, number and distribution pattern of antennal sensilla of three ground beetle species – *Bembidion lampros*, *Bembidion properans* and *Platynus dorsalis*, was elucidated by using scanning electron microscopy techniques.

- * Based on morphological features, there were distinguished thirteen types of sensilla.
- * *Sensilla trichodea* 1 was found only on the *Bembidion* antennae and *sensilla chaetica* 4 occur only on the antennae of *P. dorsalis*.
- * No sexual dimorphism was found in the structure, or distribution of the antennal sensilla.
- * Some (but not significant) differences were found in the number of antennal sensilla.
- * Three types of sensilla were considered as olfactory – *sensilla trichodea* 2, *sensilla basiconica* 1 and 2.
- * Olfactory sensilla form two separate, dorsal and ventral, fields of sensilla on the flagellomeres. Probably these asymmetries are involved in insects' behaviour to catch the wind-borne odour molecules.

ACKNOWLEDGEMENTS. The study was supported by the Estonian Science Foundation (grant no. 5423).

REFERENCES

- Alm, S.R. & Hall, F.R. 1986. Antennal sensory structures of *Conotrachelus nenuphar* (Coleoptera, Curculionidae). *Ann. Entomol. Soc. Am.*, **79**, 324–333.
- Altner, H. & Prillinger, L. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *International Review of Cytology*, **67**, 69–139.
- Bartlet, E., Romani, R., Williams, I.H. & Isidoro, N. 1999. Functional anatomy of sensory structures on the antennae of *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae). *Int. J. of Insect Morphol. and Embryol.*, **28**, 291–300.
- Chapman, R.F. 1998. *The Insects. Structure and Function*. Cambridge University Press.
- Daly, P.J. & Ryan M.F. 1979. Ultrastructure of antennal sensilla of *Nebria brevicollis* (Fab.) (Coleoptera: Carabidae). *Int. J. Insect Morphol. Embryol.* **8**, 169–181.
- Faucheux, M.J. 1989. Morphology of the antennal club in the male and female bark beetles *Ips sexdentatus* Boern. and *I. typographus* (L.) (Coleoptera, Scolytidae). *Ann. Sci. Nat. Zool.*, **10**, 231–243.

- Faucheux, M.J. 1994. Distribution and abundance of antennal sensilla from two populations of the pine engraver beetle, *Ips pini* (Say) (Coleoptera, Scolytidae). *Ann. Sci. Nat. Zool.*, **15**, 15–31.
- Gullan, P.J. & Cranston, P.S. 2003. *The Insects. An Outline of Entomology*. Blackwell Publishing.
- Haberman, H. 1968. *Eesti jooksiklased*. Valgus, Tallinn (in Estonian).
- Hallberg, E., Hansson, B.S. & Steinbrecht, R.A. 1994. Morphological characteristics of antennal sensilla in the european cornborer *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Tissue and Cell*, **26**, 489–502.
- Hansson, B.S. (Ed.). 1999. *Insect olfaction*. Springer Verlag, 6.
- Hansson, B.S., Löfstedt, C. & Löfqvist, J. 1986. Spatial arrangement of different types of pheromone-sensitive sensilla in a male moth. *Naturwissenschaften*, **73**, 269–270.
- Keil, T.A. & Steinbrecht, R.A. 1984. Mechanosensitive and olfactory sensilla of insects. In *Insect Ultrastructure* (King, R.C & Akai, H., eds), vol. **2**, pp. 477–516. Plenum, New York.
- Kim, J.L. & Yamasaki, T. 1996. Sensilla of *Carabus (Isiocarabus) fiduciaris saishutoicus* Csiki (Coleoptera: Carabidae). *Int. J. Insect Morphol. Embryol.*, **25**, 153–172.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.*, **74**, 187–228.
- Losey, J.E. & Denno, R.F. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, **79**, 6, 2143–2152.
- Lövey, G.L. & Sunderland, K.D. 1996. Ecology and behaviour of ground beetles (Coleoptera, Carabidae). *Annu. Rev. Entomol.*, **41**, 231–256.
- Magura, T., Elek, Z. & Tóthmérész, B. 2002. Impacts of non-native spruce reforestation on ground beetles. *European Journal of Soil Biology*, **38**, 291–195.
- Merivee, E. 1992. Antennal sensilla of the female and male elaterid beetle *Agriotes obscurus* L. (Coleoptera, Elateridae). *Proc. of the Estonian Academy of Sciences, Biology*, **41**, 189–215.
- Merivee, E., Ploomi, A., Luik, A. & Sammelseg, V. 2001. Antennal sensilla of the ground beetle *Platynus dorsalis* (Pontoppidan, 1763) (Coleoptera, Carabidae). *Microscopy Research and Technique*, **55**, 339–349.
- Merivee, E., Ploomi, A., Rahi, M., Bresciani, J., Ravn, H.P., Luik, A. & Sammelseg, V. 2002. Antennal sensilla of the ground beetle *Bembidion properans* Steph. (Coleoptera, Carabidae). *Micron*, **33**, 429–440.
- Merivee, E., Ploomi, A., Rahi, M., Luik, A. & Sammelseg, V. 2000. Antennal sensilla of the ground beetle *Bembidion lampros* Hbst. (Coleoptera, Carabidae). *Acta Zoologica (Stockholm)*, **81**, 339–350.
- Merivee, E., Rahi, M. & Luik, A. 1999. Antennal sensilla of the click beetle, *Melanotus villosus* (Geoffroy) (Coleoptera, Elateridae). *Int. J. Insect Morphol. Embryol.*, **28**, 41–51.
- Merivee, E., Rahi, M., Bresciani, J., Ravn, H.P. & Luik, A. 1997. Distribution of olfactory and some other antennal sensilla in the male click beetle *Agriotes obscurus* L. (Coleoptera, Elateridae). *Int. J. Insect Morphol.*, **26**, 75–83.
- Merivee, E., Rahi, M., Bresciani, J., Ravn, H.P. & Luik, A. 1998. Antennal sensilla of the click beetle, *Limonius aeruginosus* (Olivier) (Coleoptera, Elateridae). *Int. J. Insect Morphol. Embryol.*, **27**, 311–318.
- Merivee, E., Vanatoa, A., Luik, A., Rahi, M., Sammelseg, V. & Ploomi, A. 2003. Electrophysiological identification of cold receptors on the antennae of the ground beetle *Pterostichus aethiops*. *Physiological Entomology*, **28**, 1–9.
- Moore, B.P. & Wallbank, B.E. 1968. Chemical composition of the defensive secretion in carabid beetles and its importance as a taxonomic character. *Proc. of the Royal Entomological Society (London)*, **B 37**, 62–72.

- Mustaparta, H. 1973. Olfactory sensilla on the antennae of the pine weevil. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **144**, 559–571.
- Okada, K., Mori, M., Shimazaki, K. & Chuman, T. 1992. Morphological studies on the antennal sensilla of the cigarette beetle, *Lasioderma serricornis* (F.) (Coleoptera, Anobiidae). *Appl. Entomol. Zool.*, **27**, 269–276.
- Schneider, D. 1964. Insect antennae. *Annu. Rev. Entomol.*, **9**, 103–122.
- Symondson, W.O.C., Glen, D.M., Wiltshire, C.W., Langdon, C.J. & Liddell, J.E. 1996. Effects of cultivation techniques and methods of straw disposal on predation by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable field. *J. Appl. Ecol.*, **33**, 741–753.
- Zacharuk, R.Y. 1985. Antennae and sensilla. *Comparative Insect Physiology, Chemistry and Pharmacology* (Kerkut, G.A. & Gilbert, L.I., eds.), vol. **6**, pp. 1–69. Pergamon Press, Oxford.
- Wautier, V. 1970. Existence d'une interattraction olfactive chez les Brachinides (Col. Carabidae). *Annales de la Société entomologique de France (N. S.)*, **6**, 433–436.
- Wautier, V. 1971. Un phénomène social chez les Coleoptères: le gregarisme des *Brachinus* (Caraboidea Brachinidae). *Insectes Sociaux (Paris)*, **18**, 1–84.