



HYMENOPTERAN ORBICULAR SENSILLA

Hasan H. Basibuyuk^{1,2,3}, Alexandr P. Rasnitsyn⁴, Mike G. Fitton² and Donald L. J. Quicke^{1,2}

¹Unit of Parasitoid Systematics, CABI Bioscience UK Centre (Ascot), Department of Biology, Imperial College at Silwood Park, Ascot, SL5 7PY United Kingdom (email: d.quicke@ic.ac.uk)

²Department of Entomology, The Natural History Museum, London SW7 5BD United Kingdom

³Department of Biology, Cumhuriyet University, 58140 Sivas, Turkey

⁴Palaeontological Institute Russian Academy of Sciences, Profsoyuznaya Str. 123, 117647 Moscow, Russia

Introduction

The sensory systems of insects have evolved numerous specialisations that allow them to detect important features of the external environment, monitor their own internal states and provide information on position of their appendages. Considering the vast numbers of insect species and variety of habitats they successfully occupy, it is not surprising that they possess equally diverse sensory systems (Frazier 1985). However, most studies have only covered antennal sensilla, while sensilla located in other body parts have not been thoroughly investigated. Studies on the sensory systems of the Hymenoptera show this general pattern and, apart from several studies on the ovipositor sensilla, there have only been a few papers reporting sensilla from other body parts (Schmidt & Smith 1987; Navasero & Elzen 1991; Meyhöfner *et al.* 1997). Sensilla from other body parts may also be useful potentially for phylogenetic reconstruction.

Although there has been increasing effort to reconstruct the evolutionary history of the Hymenoptera (e.g. Rasnitsyn 1988; Brothers & Carpenter 1993; Dowton & Austin 1994; Vilhelmsen 1997; Ronquist *et al.* 1999), there is still no one robust higher level phylogenetic hypothesis for the order (Ronquist *et al.* 1999). Rasnitsyn's (1988) most comprehensive and fully resolved higher level phylogeny has recently been shown (Ronquist *et al.* 1999) to have no convincing support for any of its major groupings. The relationships among symphytan (Vilhelmsen 1997) and aculeate families (Brothers & Carpenter 1993) have been analysed independently and are relatively robust in comparison with the parasitoid groups. Exploration of novel character systems is essential if we are to test existing hypotheses and obtain a more stable phylogeny.

In this paper, we present some preliminary findings from one novel character system, orbicular sensilla and some associated structures. The orbicula is a dorsal cuticular sclerite at the base of the membranous arolium in the distal most tarsal segment of insect legs (Figs 1–4). Phylogenetic and functional implications, especially for non-aculeate apocritans, are discussed.

Material and Methods

A total of 137 species belonging to 121 genera, representing all superfamilies and most families of non-aculeate apocritans, were studied. Only one species was examined for some relatively rare taxa, but in most cases the number of species examined was three or more. Standard SEM

Table 1 Explanation of characters and character states.

Code	Character	States
A	Sensilla trichodea A (STA) on orbicula	0 = absent; 1 = present
B	Number of STA (when present)	0 = one; 1 = two; 2 = three or more
C	Sensilla trichodea B (STB)	0 = absent; 1 = present
D	Number of STB (when present)	0 = one; 1 = two; 2 = three or more
E	STB (if two or more)	0 = scattered; 1 = forming a single row
F	STB	0 = simple; 1 = basally widened
G	STB	0 = without a basal spur; 1 = with a basal spur
H	Sensilla campaniformia (SC)	0 = none; 1 = with encircling ridge (type A); 2 = without an encircling ridge (type B)
I	Number of SC (when present)	0 = one; 1 = two; 2 = three or more
J	Position of SC relative to STA	0 = anterior (distal); 1 = posterior (basal)

techniques were employed on dry or ethanol preserved specimens. The identifications of orbicular sensilla are based on Frazier (1985).

Results

Four types of morphologically discernible sensilla are found. Of these two are setiform, termed here sensilla trichodea A (STA) and sensilla trichodea B (STB), and the other two are dome-like sensilla, sensilla campaniformia A (SCA) and sensilla campaniformia B (SCB). Variations in these and associated structures are summarised in Tables 1 and 2. We have not specifically investigated intraspecific variation but there appears to be no major variation in several cases we have examined.

STA arise from a flexible socket with the hair trunk gradually tapering towards the tip (Figs 1–4). STB can be differentiated from the STA in usually being shorter and more slender, positioned posterior to the STA and usually with a less pronounced socket (Figs 1–3). STB are usually simple cylindrical hairs with an irregular distribution but, in some cases, they are arranged into a single transverse row (Figs 2–3) and may be basally compressed and widened (Fig. 2). Some taxa additionally possess a spur on the sensilla socket (Fig. 2).

Of the two types of sensilla campaniformia, SCA are usually in the shape of a rounded dome encircled by a pronounced cuticular ridge (Fig. 1); their number and placement are variable. SCB, however, usually have no distinct encircling ridge but consistent in number and are always located laterally (Fig. 2).

Discussion

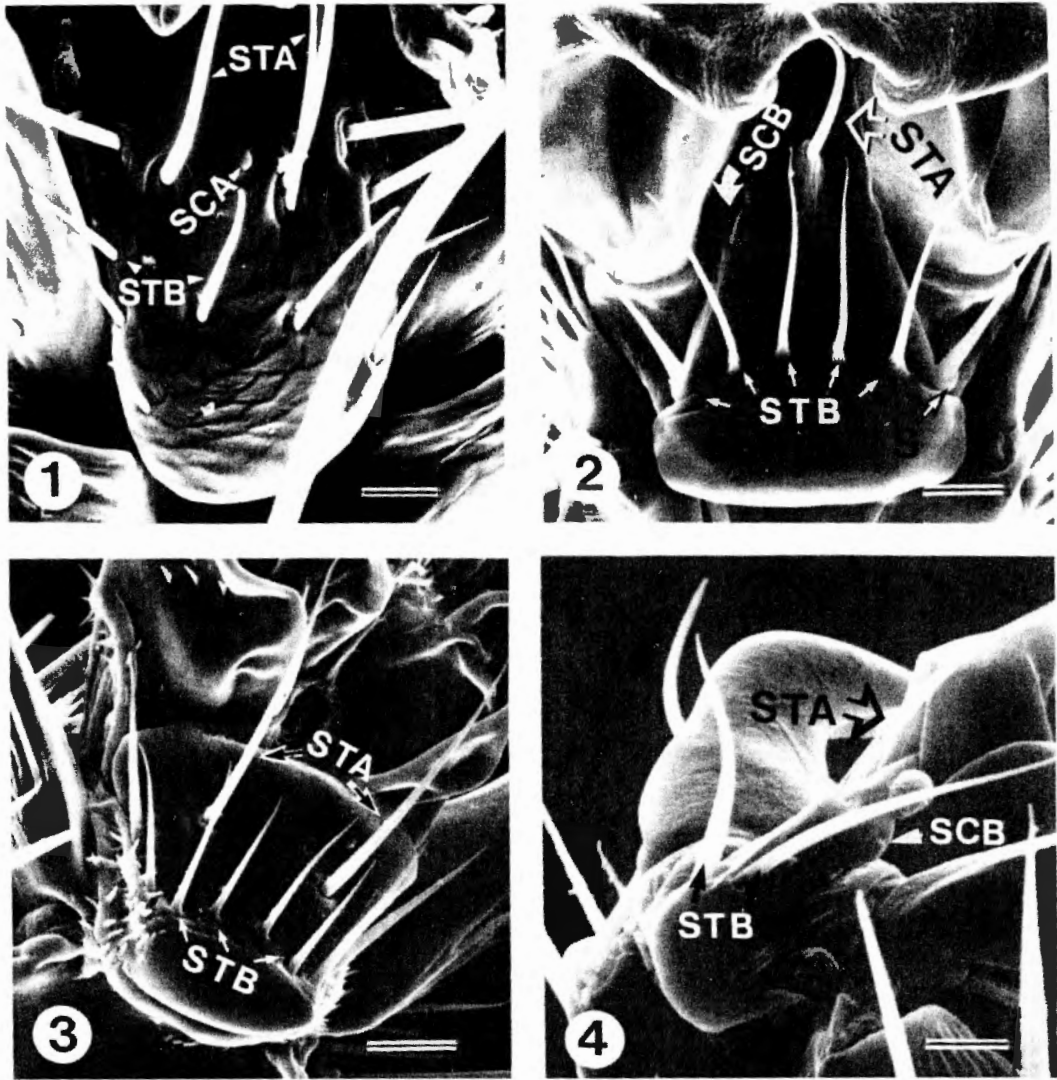
The orbicular sensilla are arguably all mechanoreceptors (McIver 1985). In one eulophid, they have been suggested as having a role in detecting vibration produced by its leaf miner host (Meyhöfer *et al.* 1997). However, the presence of orbicular sensilla in early phytophagous lineages (Basibuyuk *et al.* 2000), as well as in males, suggest that they must have other roles. It is most likely that they evolved primarily to monitor the state of stress caused by locomotive behaviour. Host detection, in this context, can be seen as a secondary role assumed after the evolution of parasitism.

Table 2 Orbicular sensilla and associated structures in the non-aculeate apocritan Hymenoptera. Symbols: (—) not applicable; (?) state is unknown due to unavailability of data; (x?) a specified state with question mark shows our best judgement but not absolutely certain (see Table 1 and text for explanation of characters).

	A	B	C	D	E	F	G	H	I	J
Stephanidae	0/1	1	0/1	2	0	0	0	0/1	1	0
Trigonalidae	1	1/2	1	2	0	0	0	1	1	0
Megalyridae	0/1	2	1	2	0	0	0	1	0	0
Evanioidea	1	1	1	2	0	0	0	0	—	—
Ibaliidae	1	1	1	2	0	0	0	0	—	—
other Cynipoidea	1	1	0/1	1/2	1	1	0?	0	—	—
Megaspilidae	1	2?	0/1	2?	0	0	0	0	—	—
Ceraphronidae	1	0	0/1	2?	0/1	?	0	0	—	—
Diapriidae	1	0	1	1	1	1	0	2	1	0
Heloridae	1	1	1	2	0	0	0	0	—	—
Vanhorniidae	1	1	1	2	1	?	0	0	—	—
Pelecniidae	1	1	1	2	0	0	0	0	—	—
Proctotrupidae	0/1	1?	1?	1/2	0	?	0	0	—	—
Roproniidae	1	1	1	2	0	0	0	0	—	—
Monomachidae	1	1	1	2	0	0	0	0?	—	—
New Zealand fam n.	1	0	1	1	1	1	1	2?	?	?
Scelionidae	1	1	0/1	0/2	0	?	0	0/2	1	0
Platygastridae	0?	—	1?	1	1	1	0	0	—	—
Chalcididae	1	0	1	2	0	1	0	2	1	1
other Chalcidoidea	1	0	1	1/2	1	1	1	2	1	1
Mymarommatidae	1	0	1	1	1	?	?	?	?	?
Braconidae	1	1/2	1	2	0	0	0	1	1	1
Ichneumonidae	1	1/2	0/1	0/1/2	0	0	0	1	1/2	0/1

Variation in the number, shape, position and arrangement of orbicular sensilla and associated structures are found to be particularly informative for relationships of several microhymenoptera. Most basal lineages of Apocrita have two STA and a change in number is considered to be derived. Presence of a single STA with a well-developed socket and collar is a putative synapomorphy for the Chalcidoidea, Diapriidae, Mymarommatidae, the undescribed New Zealand family of Proctotrupoidea and possibly the Ceraphronidae (Figs 2, 4).

Arrangement of the STB into a single transverse row (Figs 2–4) supports a larger putative clade comprising the Chalcidoidea (except Chalcididae), Mymarommatidae, Ceraphronidae,



Figures 1-4 Orbicular sensilla in various Hymenoptera: 1) *Megalyra fasciipennis* (Megalyridae), scale bar = 10 mm; 2) *Gastracanthus pulcherrimus* (Pteromalidae), scale bar = 8 mm; 3) *Callaspidia defonscolombeii* (Figitidae), scale bar = 7 mm; 4) *Coptera occidentalis* (Diapriidae), scale bar = 3 mm. B = basal spur; SCA = sensilla campaniformia A; SCB = sensilla campaniformia B; STA = sensilla trichodea A; STB = sensilla trichodea B.

Cynipoidea, Diapriidae, Platygasteridae, Vanhorniidae and the undescribed New Zealand family of Proctotrupoidea. STB are laterally compressed and widened basally (Fig. 2-4) in the Chalcidoidea, Cynipoidea, Diapriidae, Platygasteridae and the undescribed New Zealand family of Proctotrupoidea, suggesting another clade within the above larger grouping. A spur is present at the base of each STB in the Chalcidoidea (except Chalcididae) and in the undescribed New Zealand family of Proctotrupoidea (Fig. 2), and a similar structure, but situated far from the sensillum, is also present in some Cynipoidea.

SCB are present in almost all members of the Chalcidoidea (Fig. 2) and Diapriidae (Fig. 4), and in some Scelionidae and possibly in the New Zealand family of Proctotrupoidea. However, its presence in the new family has yet to be confirmed.

Several recent investigations of novel character systems have suggested alternative relationships among parasitic taxa (e.g. Basibuyuk & Quicke 1997, 1999; Quicke *et al.* 1998; Gibson 1999), but no single character system is likely to verify the 'true' relationships. A formal parsimony analysis including all the new findings is needed to evaluate these alternative hypotheses and is currently in preparation.

Acknowledgements

We wish to thank the staff of electron microscopy and photographic units, NHM, London for their assistance. Kees van Achterberg, Nando Bin, Barry Bolton, John LaSalle, Massimo Olmi, Andy Polaszek, Frank van Veen and Annette Walker donated some of the material studied. This work was supported in part by a Leverhulme Trust research grant to DQ and MF and by the NERC Initiative in Taxonomy.

References

- Basibuyuk, H. H. & Quicke, D. L. J. (1997) Hamuli in the Hymenoptera (Insecta) and their phylogenetic implications. *Journal of Natural History* **31**: 1563-1585.
- Basibuyuk, H. H. & Quicke, D. L. J. (1999) Grooming behaviours in the Hymenoptera (Insecta): potential phylogenetic significance. *Zoological Journal of the Linnean Society* **125**: 349-382.
- Basibuyuk, H. H., Quicke, D. L. J., Rasnitsyn, A. P. & Fitton, M. G. (2000) Morphology and sensilla of the orbicula, a sclerite between the tarsal claws in Hymenoptera. *Annals of the Entomological Society of America* **93**: 625-636.
- Brothers, D. J. & Carpenter, J. M. (1993) Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). *Journal of Hymenoptera Research* **2**: 227-304.
- Dowton, M. & Austin, A. D. (1994) Molecular phylogeny of the insect order Hymenoptera: Apocritan relationships. *Proceedings of the National Academy of Sciences, USA* **91**: 9911-9915.
- Frazier, J. L. (1985) Nervous system: sensory system. pp. 287-356. In Blum, M. S. (Ed.), *Fundamentals of Insect Physiology*. John Wiley and Sons, New York.
- Gibson, G. A. P. (1999) Sister-group relationships of the Platygastroidea and Chalcidoidea (Hymenoptera) – an alternate hypothesis to Rasnitsyn (1988). *Zoologica Scripta* **28**: 125-138.
- McIver, S. B. (1985) Mechanoreception. pp. 71-132. In Kerkut, G. A. and Gilbert, L. I. (Eds), *Comprehensive Insect Physiology Biochemistry and Pharmacology*, Volume 6. Pergamon Press, Oxford.
- Meyhöfner, R., Casas, J. & Dorn, S. (1997) Mechano- and chemoreceptors and their possible role in host-location behavior of *Sympiesis sericeicornis* (Hymenoptera: Eulophidae). *Annals of the Entomological Society of America* **90**: 208-219.
- Navasero, R. C. & Elzen, G. W. (1991) Sensilla on the antennae, foretarsi and palpi of *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* **93**: 373-347.
- Quicke, D. L. J., Wyeth, P., Fawke, J. D., Basibuyuk, H. H. & Vincent, J. (1998) Manganese and zinc in the ovipositors and mandibles of hymenopterous insects. *Zoological Journal of the Linnean Society* **124**: 387-396.

- Rasnitsyn, A. P. (1988) An outline of evolution of the hymenopterous insects (Order Vespida). *Oriental Insects* 22: 115-145.
- Ronquist, F., Rasnitsyn, A. P., Roy, A., Eriksson, K. & Lindgren, M. (1999) Phylogeny of the Hymenoptera: A cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta* 28: 13-50.
- Schmidt, J. M. & Smith, J. B. (1987) The external sensory morphology of the legs and hairplate system of female *Trichogramma minutus* Riley (Hymenoptera: Trichogrammatidae). *Proceedings of the Royal Society of London Series B* 232: 323-366.
- Vilhelmsen, L. (1997) The phylogeny of lower Hymenoptera (Insecta), with a summary of the early evolutionary history of the order. *Journal of Zoological Systematics and Evolutionary Research* 35: 49-70.

**Andrew D. Austin &
Mark Downton
(Editors)**

HYMENOPTERA

Evolution, Biodiversity and Biological Control

