

## Surface structures of the antenna of Mantophasmatodea (Insecta)

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### Abstract

The cuticular fine structure of the antenna in Mantophasmatodea (Austrophasmatidae: *Hemilobophasma montaguense*, *Austrophasma gansbaaiense*) is described based on SEM images. The armature of sensilla (=s.) on the basiflagellum (14 basal flagellomeres, the distal ones of which are subdivided) and distiflagellum (7 distal flagellomeres) differs strongly. A basiflagellomere has a sporadic vestiture of prominent s. chaetica B as well as distal s. scolopidia and scattered s. coeloconica. The distiflagellum also bears scattered s. chaetica B and s. coeloconica but is also densely covered with sensilla of various other types: numerous s. trichodea and s. basiconica, sporadic s. coelocapitula, and a probably new type of branched sensilla; the distiflagellum is probably the main sensory region, including gustatory and olfactory chemoreception, mechanoreception, and hygroreception. The scape and pedicel also bear s. chaetica B, and s. chaetica A arranged in 4 (scape) or 2 (pedicel) hair-plates. Terminal s. campaniformia are only found on the pedicel. A ‘dark spot’ is present apically on distiflagellomeres 6 (as reported previously) and 1. The two spots are of similar structure and are possibly associated with glands; each comprises a complicated external aperture and a larger internal pouch enclosing a cavity; projections protrude from the pouch walls into the cavity. The surface structure of the basiflagellomeres shows differences that are possibly species specific. An overview is given on antennal apomorphies in Mantophasmatodea.

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### 1. Introduction

The insect order Mantophasmatodea (heelwalkers, gladiators) was introduced by Klass et al. (2002). Meanwhile 16 extant species of these wingless insectivorous predators are formally described (list in Damgaard et al., 2008). Their classification into genera and families is mainly based on genital morphology and phylogenetic analyses of molecular data (Klass et al., 2003; Damgaard et al., 2008). Extant representatives are restricted to Africa south of the equator, with

strong species-level endemism in South Africa and Namibia. However, the presence of fossil species in Eocene Baltic amber (Zompro, 2001, 2005, 2008; Engel and Grimaldi, 2004; Arillo and Engel, 2006; Damgaard et al., 2008) and in the Jurassic of China (Huang et al., 2008) demonstrates that Mantophasmatodea also occurred in the northern hemisphere in their earlier evolutionary history.

Mantophasmatodea is clearly a subgroup of Neoptera (Klass et al., 2002, 2003; Klass, 2007; Beutel and Gorb, 2006) but its relationships to other principal neopteran lineages have remained unclear. Results of molecular studies suggested a sistergroup relationship either to Notoptera (=Grylloblattodea; Terry and Whiting, 2005; Kjer et al., 2006) or to Phasmatodea (Cameron et al., 2006). Morphological characters are inconsistent (Klass et al., 2003; Klass, 2007, 2009).

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Some features suggest a clade including Mantophasmatodea, Dictyoptera, Orthoptera, and Notoptera (presence of connecting bands in the sperm flagellum, Dallai et al., 2003, 2005), and within this lineage a closer relationship between Mantophasmatodea and Dictyoptera (similar right part of male genitalia; Klass et al., 2003; double-walled antennal vessels with inner transport epithelium; Pass et al., 2006). Other characters suggest a sistergroup relationship between Mantophasmatodea and Phasmatodea (sclerotised appendage above male genitalia: vomer or vomeroid; euplantulae with microtrichia; Beutel and Gorb, 2008). Due to this conjectural evidence we do not agree with Arillo and Engel's (2006) proposal of downranking Mantophasmatodea and Grylloblattodea to suborders of Notoptera (in a wider sense; see Damgaard et al., 2008).

The antennae of Mantophasmatodea have so far mainly been studied using a light microscope (Klass et al., 2003); this includes the antennal development in nymphs (Hockman et al., 2009). A few details based on SEM micrographs were presented in a study of the head of *Karoophasma* (Baum et al., 2007). As in other ectognathous insects, the mantophasmatodean antennae are composed of a scape, a pedicel, and a long multi-jointed flagellum. As shown in Klass et al. (2003: section 4.3, fig. 4A), however, the flagellum shows a unique structure: it is sharply divided into a basal (basiflagellum) and a distal part (distiflagellum). The number of antennomeres is consistently 14 in the basi- and 7 in the distiflagellum; however, distal basiflagellomeres are bipartite (Klass et al., 2003: fig. 4A; Hockman et al., 2009), and the number of subdivided basiflagellomeres varies between and within species. The basiflagellomeres are cylindrical and bear only widely scattered long setae. The distiflagellomeres are slightly wider, spindle-shaped, and separated from each other by distinct constrictions; in all species the first distiflagellomere is very long, the second is very short, and the remaining ones are of intermediate length. The distiflagellomeres also bear scattered long setae, but in addition they show a dense vestiture of numerous smaller setae. A tiny dark spot is visible at the distal end of the sixth distiflagellomere (Klass et al., 2003: 'ds' in fig. 4A); its structure and function have remained unknown.

The antennae of insects bear a variety of sensilla that are mechano- and/or chemosensitive (olfactory or gustatory), hygro-sensitive, or thermosensitive (Table 1). All are structurally derived from a basic type of sensory unit that is composed of a seta as the externally visible cuticular structure and one or more sensory cells beneath and/or inside it. There is a rich literature on the cuticular fine structure of the antennae in various insects, especially on the antennal sensilla (e.g. Altner, 1977; Zacharuk, 1980; Keil and Steinbrecht, 1984; Keil, 1998; Steinbrecht, 1999; Kaib et al., 1999; Hallberg and Hansson, 1999). Detailed information on the sensillar equipment and other aspects of the fine structure of the antennae of Mantophasmatodea was not available so far.

To fill this gap, the present contribution provides information on structural details of the antenna, mainly based

on SEM micrographs. Focal issues are the equipment of scape, pedicel, basiflagellum, and distiflagellum with sensilla, the basal articulations of the antenna, the structure of the 'dark spots' on the distiflagellum, and the surface sculpture of the basiflagellomeres. For the sensilla, preliminary comparisons with other insects are included based on the literature.

## 2. Materials and methods

### 2.1. Taxa and specimens examined

Two species of Mantophasmatodea (Austrophasmatidae) were examined. We used 4 ♂♂ and 2 ♀♀ of *Hemilobophasma montaguense* Klass et al., 2003 (Montagu, South Africa, 33,769°S 20,129°E) and 2 ♂♂ and 2 ♀♀ of *Austrophasma gansbaaiense* Klass et al., 2003 (2.7 km S of Stanford, South Africa, 34,497°S 19,430°E). All specimens were fixed and stored in 95% ethanol.

### 2.2. Scanning electron microscopy

Antennae were removed by cutting the cuticle of the head capsule around the antennal foramen. They were treated with ultrasonic sound for 2 min and then critical point dried (Balzers Union CPD 020) using CO<sub>2</sub> as transfer fluid; all dried preparations were mounted on holders, sputter-coated with gold (2 min with an Edwards S150B) and examined in a scanning electron microscope Zeiss EVO 50.

For examining the inner surface and internal structure of the 'dark spots' of the distiflagellomeres, the relevant parts of the antenna were cut either obliquely (internal view) or perpendicular to the antennal axis (cross-section view) using a piece of a breakable razor blade. These preparations were macerated carefully (2 h in 5% KOH) and then rinsed, critical point dried, and examined as described above.

### 2.3. Terminology and identification of sensilla types

We adopt the traditional classification and terminology of sensilla of Schafer and Sanchez (1973) and Keil (1998), which distinguishes the sensilla types listed in Table 1. In contrast, Altner (1977) uses the presence and structure of pores on the surface as a major criterion for sensilla classification into three groups (see also Altner et al., 1981, 1983): (1) poreless sensilla (PL), (2) sensilla with a terminal pore or field of pores (TP), and (3) sensilla with wallpores; the latter group is further divided into (3a) single-walled (SW) and (3b) double-walled sensilla (DW) based on differences in the construction of the pore system: pores are distributed over the entire surface of the shaft in single-walled sensilla, whereas only narrow pores in longitudinal grooves of the shaft are present in double-walled sensilla. Altner's (1977)

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