

Ultrastructure of antennal sensory organs of horse nasal-myiasis fly, *Rhinoestrus purpureus* (Diptera: Oestridae)

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Abstract *Rhinoestrus purpureus* (Brauer, 1858) (Diptera: Oestridae) is an economically important parasite that can cause severe nasal myiasis in equids or even attacking humans. The antennae of *R. purpureus* were examined using stereoscopic microscopy and scanning electron microscopy. The general morphology was provided detailedly, together with distribution, type, size, and ultrastructure of antennal sensilla. All the three antennal segments, antennal scape, pedicel, and funiculus, are interspersed by microtrichiae. Only mechanoreceptors are detected on antennal scape and pedicel. On antennal funiculus, three types of sensilla were observed, including basiconic sensilla, coeloconic sensilla and clavate sensilla. Two features are characterized of this host-specific bot fly: (1) numerous sensory pits with branched basiconic sensilla on antennal funiculus and (2) the absence of trichoid sensilla. The function of these distinctive traits are discussed in association with the life history. We suggest that more sensory pits with branched sensilla could increase the sensitivity of olfactory system for host orientation, while the capability of pheromone identification might be reduced due to the absence of trichoid sensilla. Besides, we support both thermo- and chemo-functions of coeloconic sensilla.

Keywords Oestridae · *Rhinoestrus* · Sensilla · Scanning electron microscopy

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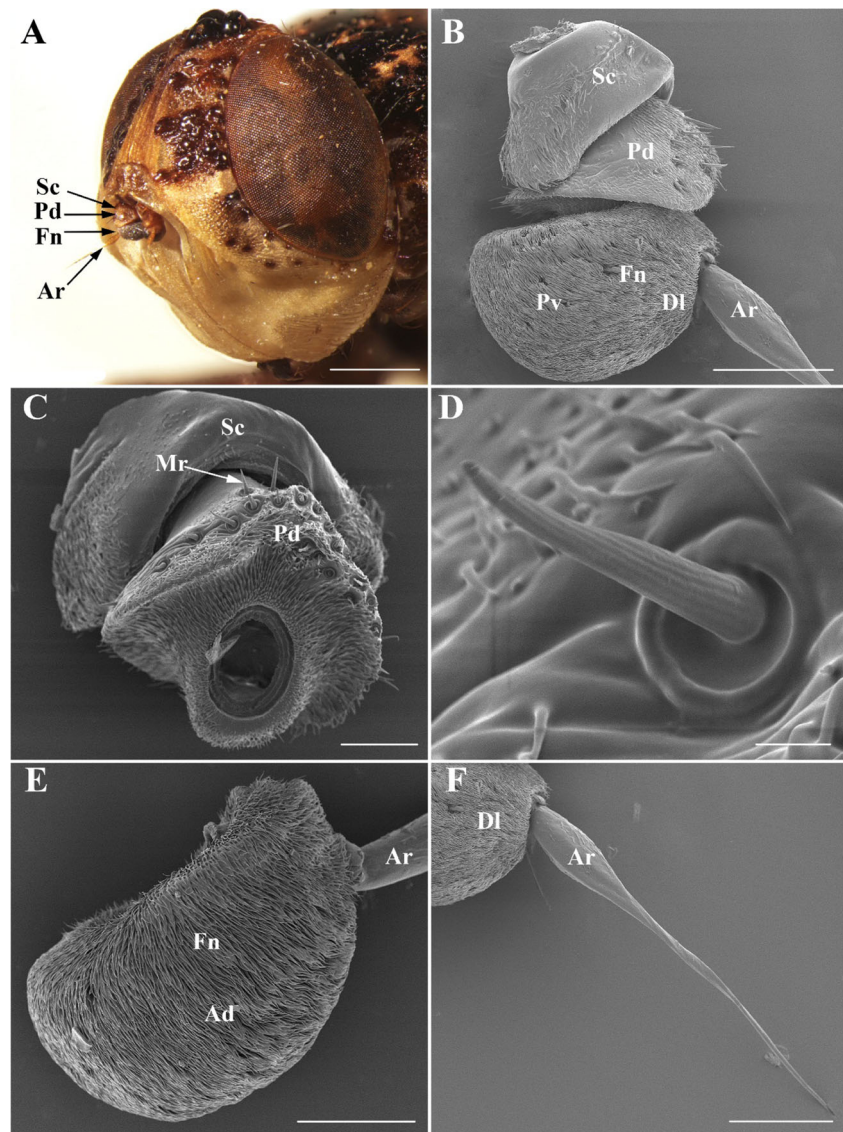
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Introduction

Rhinoestrus purpureus is an obligatory parasite of nasal-pharyngeal cavities in horses, donkeys, and zebras (Zumpt, 1965), which irritates the mucous membrane of nasopharyngeal cavity and injures both olfactory nerves and cerebral membrane, inducing encephalomyelitis and high mortality of the hosts (Zumpt 1965; Zayed 1992; Kaboret et al. 1997; Otranto et al. 2004, 2005; Colwell et al. 2006, 2007). Attacks on humans causing ophthalmomyiasis and conjunctivitis by this species are also reported (Peyresblanques 1964). Myiasis caused by *R. purpureus* is considered to be confined to Asiatic and African countries (Zumpt 1965; Zayed et al. 1993; Deconinck et al. 1996; Kaboret et al. 1997; Tibayrenc et al. 1999); however, infestations has extended to Europe, specifically in southern Italy (Otranto et al. 2004, 2005).

As the crucial sensory organs involved in feeding, mating, and spawning (Fernandes et al. 2005; Amer and Mehlhorn 2006; Smallegange et al. 2008; Guha et al. 2012; Wang et al. 2012), antennal sensilla of flies have managed to evolve various features to enhance their sensitivity and adaptability to the ever-changing environment (Ross 1992; Sukontason et al. 2004; Zhang et al. 2012a, b, 2013a, b, c; Wang et al. 2014). Little is known about the antennal sensilla of adult *R. purpureus*. Thus, the antennal investigation of this mouthparts atrophied and host-specific species (Catts and Garcia 1963; Papavero 1977; Colwell et al. 2006) can provide more valid information that might further our understanding of parasitic adaptation, especially host-parasite interaction and co-evolution (Hall 1995; Colwell et al. 2007; Zhang et al. 2012a, b). In this study, we characterize the antennal structures and distribution, type, size, and ultrastructure of antennal sensory organs of *R. purpureus*, evaluate distinctive antennal characters by comparing with the previous findings, and discuss their potential function in the life history of this parasite.

Fig. 1 Features on the head of adult *Rhinoestrus purpureus*. **a** Antennae are located centrally between compound eyes. **b** Magnification of whole antenna. **c** Magnification of antennal scape and pedicel. **d** Magnification of the mechanoreceptor on antennal pedicel. **e** Anterodorsal surface of antennal funiculus. **f** Antennal arista. *Scale bars: a*=1.00 mm, *b*=150 μ m, *c*=60 μ m, *d*=5 μ m, *e*=100 μ m, *f*=150 μ m. *Ad*, anterodorsal surface, *Ar* arista, *Mr* mechanoreceptor, *Dl* dorsolateral margin, *Fn* funiculus, *Pd* pedicel, *Pv* posteroventral surface, *Sc* scape



Materials and methods

Both male and female *R. purpureus* were obtained from Siziwang Banner, Ulanqap, Inner Mongolia, North China, 1971, identified and pinned as museum samples, and air-dried on site.

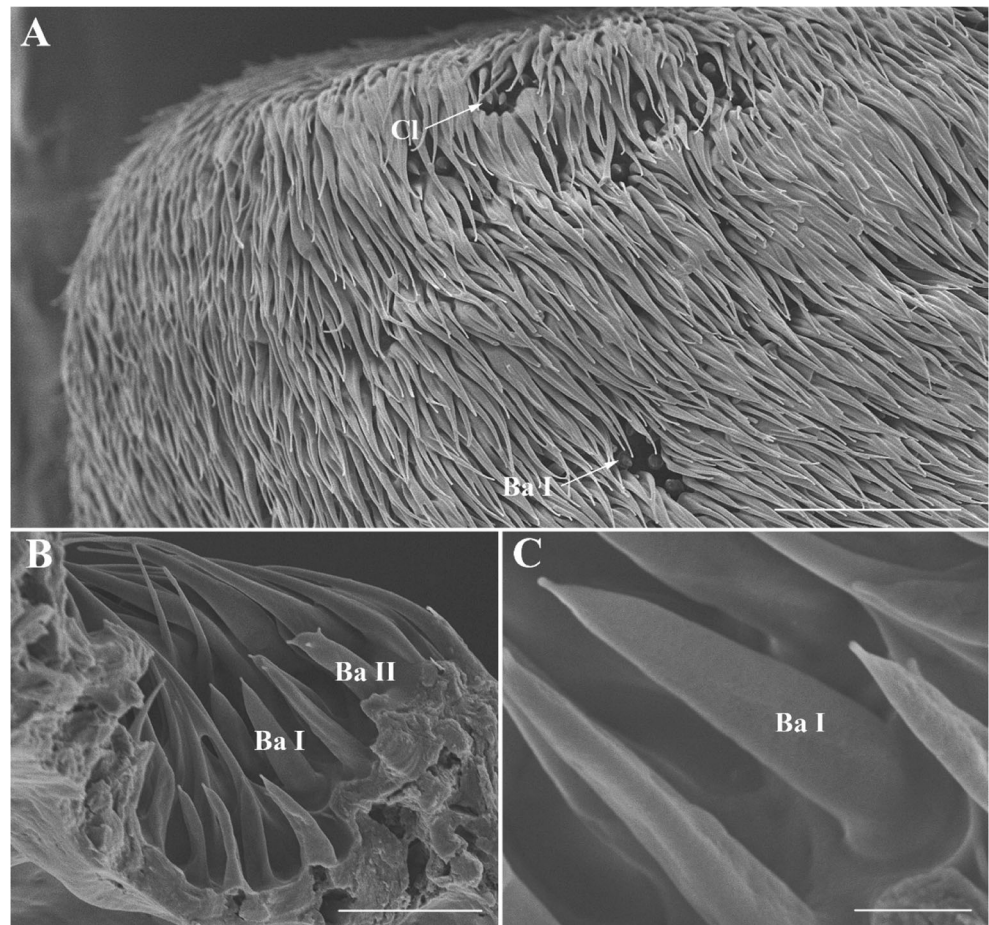
The morphology of antenna was studied using an Olympus SZX16 stereoscopic microscope (Olympus Corp., Tokyo, Japan). A series of photographs of continuous sequences taken by a Canon 500D digital camera (Canon, Inc., Tokyo, Japan) were superimposed on a standard Windows 7 platform by Adobe Photoshop CS4 (Adobe Systems, Inc., San Jose, CA, USA).

To prepare for observation through the scanning electron microscope (SEM), the heads of flies were first excised and rinsed in phosphate-buffered saline (PBS) buffer (pH 7.4) to remove surface debris. For further

processing, the antennae were dissected from the head and dehydrated in a graded ethanol series (two times 15 min each with 60, 70, 80, 90, 95, and 100 % ethanol), mounted on stubs with double-sided adhesive tape, left in a desiccator overnight to dry completely, and then covered with gold and observed by HITACHI S3400 SEM (Hitachi Corp., Tokyo, Japan) at the Microscopy Core Facility, Biological Technology Center, Beijing Forestry University (Beijing, China). The length, basal diameter, and distal dilatation diameter of antennal sensilla were measured, combined with comparison of their dimension and distribution between males and females.

The terminology and nomenclatures used to identify antennal sensilla types and describe antennal morphology in this study follow the ones used by Zhang et al. (2012a, b, 2013a, b, c, 2015).

Fig. 2 Scanning electron micrographs of basiconic sensilla on the antennal funiculus in *Rhinoestrus purpureus*. **a** Overview of basiconic sensilla I and clavate sensilla in sensory pits. **b** Basiconic sensilla I and basiconic sensilla II in sensory pits. **c** Magnification of basiconic sensilla I. Scale bars: **a**=30 μm , **b**=10 μm , **c**=2.5 μm . *Ba I* basiconic sensilla I, *Ba II* basiconic sensilla II, *Cl* clavate sensilla



Results

General description of antenna

Adult *R. purpureus* bears a pair of aristate antennae that locate on the frontal region of the head between the compound eyes (Fig. 1a). The antenna is composed of three segments, a proximal scape (Sc), a pedicel (Pd), and a distal flagellum, which consists of funiculus (Fn) and arista (Ar) (Fig. 1a–c, e, f).

Scape and pedicel

Scape is the most proximal and shortest segment (Fig. 1a–c), whose surface is interspersed by hair-like and acuminate microtrichiae (Fig. 1b, c).

Pedicel is the second segment of antenna, on which the only sensilla are morphologically similar mechanoreceptors (Mrs). Mr is a long and relatively straight bristle with longitudinal grooved wall, inserting into a socket (Fig. 1c, d). Microtrichiae are also spread around the cuticular surface of antennal pedicel.

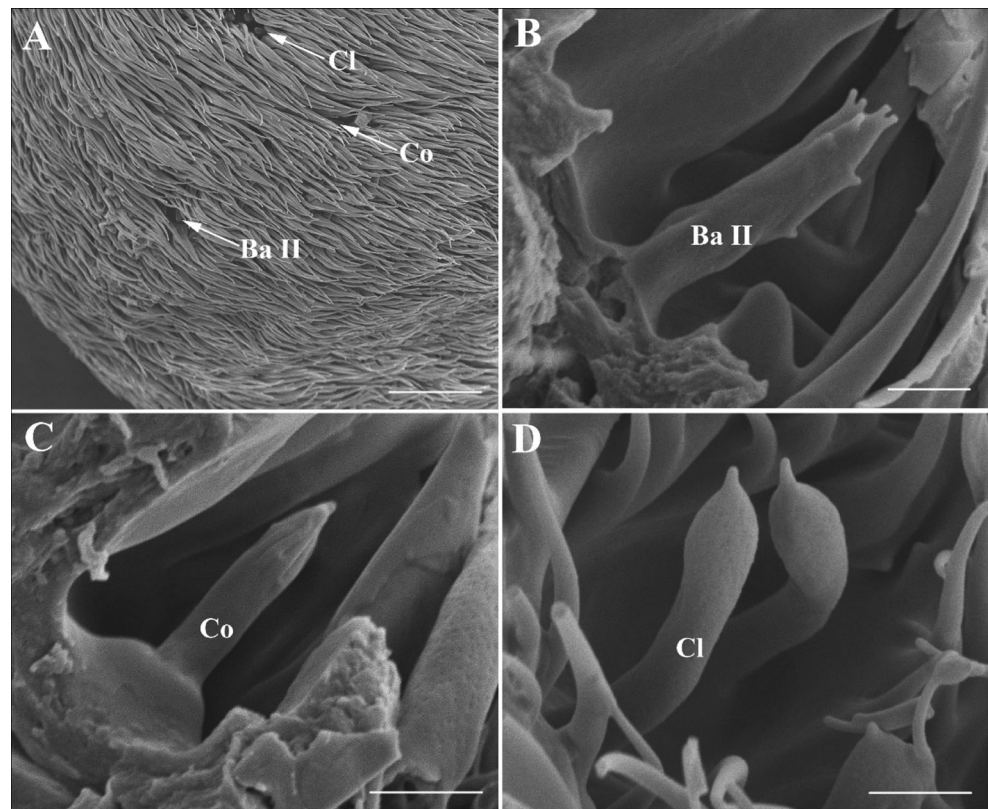
Funiculus

The antennal funiculus is the most important segment of the antenna (Fig. 1a, b, e) to which has numerous sensilla attached. For orientation, antennal funiculus has been divided into three regions: the anterodorsal surface (Ad), the dorsolateral margin (Dl), and the posteroventral surface (Pv) (Fig. 1b, c, e, f). A total of three types of antennal sensilla are distributed on it, including basiconic sensilla (Figs. 2a–c and 3a, b), coeloconic sensilla (Fig. 3a, c), and clavate sensilla (Fig. 3a, d). The length, basal diameter, and distal dilatation diameter of these antennal sensilla for both male and female species are summarized in Table 1, and their distribution is also examined, displayed in Fig. 4. The arista consists of one short basal segments and one long distal segment, with sparse microtrichiae on basal part (Fig. 1a, b, e, f).

Sensilla on antennal funiculus

A majority of the antennal sensilla are seated in sensory pits, which resemble the antennal sensilla on surface of the funiculus morphologically.

Fig. 3 Scanning electron micrographs of basiconic sensilla, coeloconic sensilla, and clavate sensilla on the antennal funiculus in *Rhinoestrus purpureus*. **a** Overview of basiconic sensilla II, coeloconic sensilla, and clavate sensilla in sensory pits. **b** Magnification of basiconic sensilla II in sensory pits. **c** Magnification of coeloconic sensilla. **d** Magnification of clavate sensilla. Scale bars: **a**=25 μm ; **b**, **c**, **d**=2.5 μm . *Ba II* basiconic sensilla II, *Cl* clavate sensilla, *Co* coeloconic sensilla



Basiconic sensilla

In adult *R. purpureus* examined, two subtypes of basiconic sensilla (*Ba*) can be distinguished by their shape and size. Basiconic sensilla I (*Ba I*) are sharp tipped (Fig. 2a–c) and distributed widely, especially middle and distal part on antennal funiculus (Fig. 4a–d), while basiconic sensilla II (*Ba II*) are only observed in sensory pits, with short branches at their apical part (Figs. 2b and 3a, b), and longer and wider than *Ba I* in general (Table 1).

Table 1 Antennal sensilla length, basal diameter and distal dilatation diameter of *Rhinoestrus purpureus* on antennal funiculus (mean \pm SD)

Sensilla	Sex	Length (μm)	Basal diameter (μm)	Distal dilatation diameter (μm)
<i>Ba I</i>	M	8.12 \pm 1.32	2.15 \pm 0.47	–
	F	9.09 \pm 1.82	1.63 \pm 0.53	–
<i>Ba II</i>	M	7.35 \pm 0.50	2.53 \pm 0.17	–
	F	9.56 \pm 0.71	2.01 \pm 0.38	–
<i>Co</i>	M	4.24 \pm 0.54	1.31 \pm 0.09	–
	F	4.77 \pm 0.51	1.35 \pm 0.95	–
<i>Cl</i>	M	9.76 \pm 1.82	1.62 \pm 0.19	1.95 \pm 0.38
	F	10.83 \pm 1.29	2.56 \pm 0.37	2.99 \pm 0.16

Ba I basiconic sensilla I, *Ba II* basiconic sensilla II, *Cl* clavate sensilla, *Co* coeloconic sensilla, *F* female, *M* male, – absent

Coeloconic sensilla

Coeloconic sensilla (*Co*), which are located in slightly sunken depressions of antennal funiculus, are relatively short sensilla characterized by distinct longitudinal ridges on their cuticular walls (Fig. 3a, c), with lower density than *Ba* (Fig. 4a–d).

Clavate sensilla

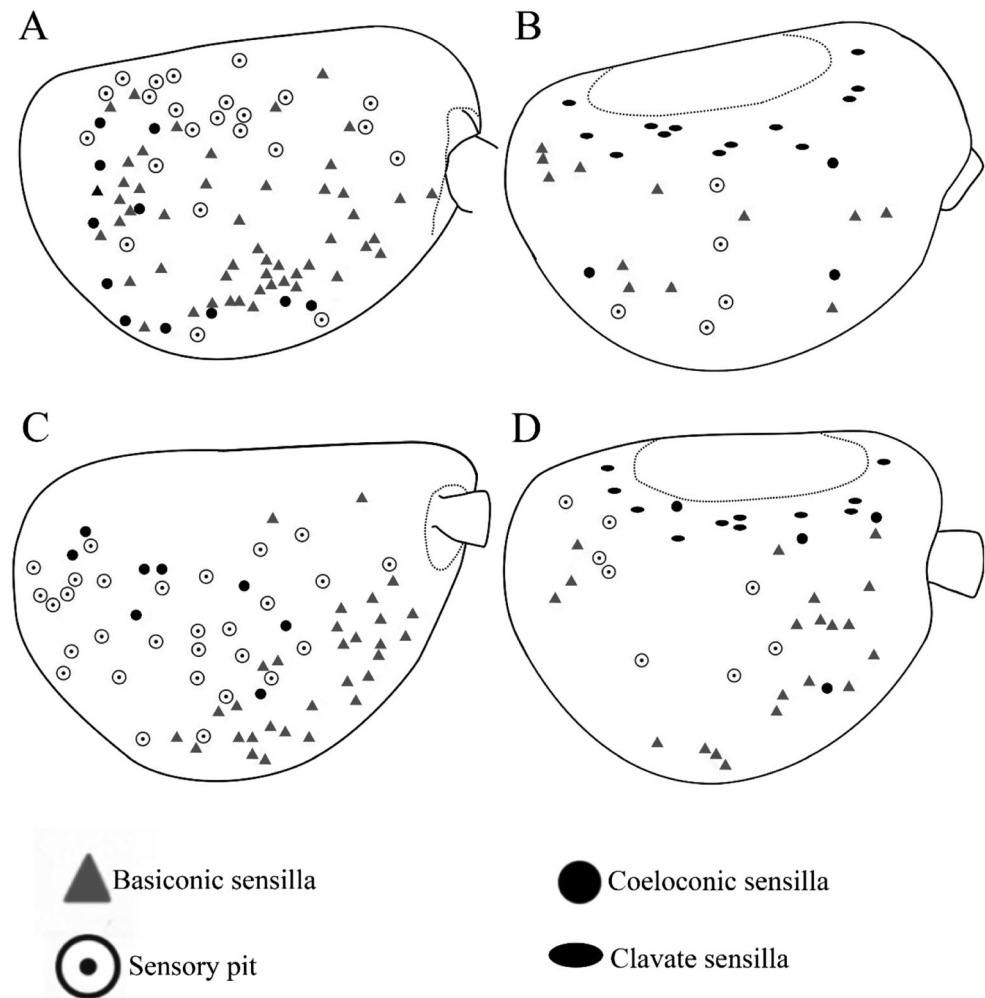
Clavate sensilla (*Cl*) are club like and featured by distal dilatations, which are seated in a superficial cavity with wall pierced by numerous pores (Fig. 3a, d) and observed only on the most proximal regions of antennal funiculus (Fig. 4a–d).

Discussion

As an obligatory parasite with rather short life span, typically about 1 week (Zumpt 1965; Papavero 1977; Zayed 1992; Zayed et al. 1993; Deconinck et al. 1996; Kaboret et al. 1997; Tibayrenc et al. 1999; Otranto et al. 2004, 2005; Colwell et al. 2006), the antennal sensilla in *R. purpureus* are distinctive in many respects compared with other species in Calypttratae.

An unusual aspect of *R. purpureus* antenna is the decreasing number of surface sensilla but numerous sensory pits and

Fig. 4 Distribution of antennal sensilla and sensory pits on each side of the antennal funiculus in *Rhinoestrus purpureus*. **a** Anterodorsal surface and dorsolateral margin of male *R. purpureus*. **b** Posteroventral surface of male *R. purpureus*. **c** Anterodorsal surface and dorsolateral margin of female *R. purpureus*. **d** Posteroventral surface of female *R. purpureus*



pit sensilla on antennal funiculus. The semblable examples were found in *Hypoderma bovis* (Hypodermatinae) (Hunter and Adserballe 1996), *Oestrus ovis* (Oestrinae) (Poddighe et al. 2010), and *Gasterophilus nigricornis* (Gasterophilinae) (Zhang et al. 2012a). Meanwhile, the branched antennal sensilla, Ba II, are detected in these sensory pits, which show a resemblance among some other dipterans, such as branched trichoid sensilla in *Portschinskia magnifica* (Zhang et al. 2012b) and *Delia radicum* (Ross and Anderson 1987), and mosquito larvae from later developmental stages (McIver and Beech 1986; Green and Hartenstein 1997). Based on previous studies, sensory pits could support a more efficient way to capture odor molecules in vicinity, and branched sensilla enlarge the surface area of antennal sensilla (Ross 1992; Hunter and Adserballe 1996; Bruyne et al. 2001; Sukontason et al. 2004; Poddighe et al. 2010; Zhang et al. 2012a, b, 2013a, b, c); thus, the capacity of odor detection is highly facilitated in combination of these two features. Considering *R. purpureus* are known to aggregate and mate at specified landmarks on mountain tops (Ullrich 1939; Grunin 1959; Catts 1964; Papavero 1977; Hall 1995;

Colwell et al. 2006), large number of sensory pits and branched antennal sensilla might contribute significantly to finding the vital station (Ross 1992; Hunter and Adserballe 1996; Bruyne et al. 2001; Sukontason et al. 2004; Poddighe et al. 2010; Zhang et al. 2012a, b, 2013a, b). In *R. purpureus*, more sensory pits in females were observed than in males. Since the high specialization of *R. purpureus* larvae to equid hosts (Colwell et al. 2006), more sensory pits on female antennae could provide a more sensitive olfactory system for host orientation (Hall 1995; Ross 1992; Hunter and Adserballe 1996; Bruyne et al. 2001; Sukontason et al. 2004; Poddighe et al. 2010; Zhang et al. 2012a, b, 2013a, b).

Trichoid sensilla, as one of the basic type of antennal sensilla in many other flies (Ross 1992; Shanbhag et al. 1995; Hunter and Adserballe 1996; Shanbhag et al. 2000; Sukontason et al. 2004, 2007; Smallegange et al. 2008; Liu et al. 2013; Zhang et al. 2013a, b), are undiscovered in *R. purpureus*. In some hippoboscids (*Hippobosca equina*, *Hippobosca longipennis*, *Melophagus ovinus*) (Zhang et al. 2015) and phorids (*Megaselia scalaris*) (Loew) (Sukontason et al. 2005), trichoid sensilla are also absent. Clyne et al.

(1999) confirm the pheromone sensitivity of trichoid sensilla by electrophysiological studies. In consideration of the fact that male bot flies try to chase any flies about their own size passing in front of them when waited at mating sites (Grunin 1959; Catts 1964; Papavero 1977; Colwell et al. 2006), this relatively violent mating strategy might be the consequence of reduced pheromone identification capability due to the absence of trichoid sensilla.

The function of grooved coeloconic sensilla is usually a controversy, which is involved in thermo- or hygromoreception (McIver 1969; Altner et al. 1983; Zacharuk 1985; Ochieng et al. 2000) or possibly chemo- (CO₂) reception (Olson and Andow 1993; Renthall et al. 2003). As temperature can greatly impact the behavior of this nasal botfly and the carbon dioxide direct the females to hunt healthy hosts (Papavero 1977; Hall 1995; Colwell et al. 2006), the coeloconic sensilla on antennal funiculus of *R. purpureus* appear to have both thermo- and chemo-functions.

Myiasis caused by oestrid flies is a global health hazard for ungulates, especially for those endangered (Zumpt 1965; Papavero 1977; Hunter and Adserballe 1996; Otranto et al. 2004, 2005; Colwell et al. 2006; Poddighe et al. 2010). Clearly, great potentials for further investigations of antennal sensilla based on more oestrid samples are demonstrated, which would contribute to the development of synthetic attractants for the monitoring studies and ultimately in fly populations control (Hall 1995; Colwell et al., 2006; Poddighe et al. 2010; Zhang et al. 2012a, b, 2015).

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