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Ultrastructural characterization of sensilla and microtrichia on the antenna of female *Haematopota pandazisi* (Diptera: Tabanidae)

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Abstract

The haematophagous females of the cleg fly *Haematopota pandazisi* (Kröber) (Diptera: Tabanidae) are a common pest in areas inhabited by wild and domestic ungulates in southern Europe, North Africa and Anatolia. A morphological investigation by scanning electron microscopy (SEM) was carried out for the first time on the antennae of females of *H. pandazisi*, with special attention to the type and distribution of sensilla and microtrichia. The typical brachyceran antenna is divided into three regions: the scape, the pedicel and the flagellum, which is the longest of the three and is composed of four flagellomeres. The scape and pedicel are characterized by only one type of microtrichium and chaetic sensillum, whereas five types of microtrichia and sensilla were identified on the flagellum and classified according to shape and distribution. The sensilla are of the chaetic, clavate, basiconic, trichoid and coeloconic types; the latter with either a basiconic or grooved peg inside. The results obtained in this study were compared to those found in other species in the family Tabanidae and other Diptera, with special attention to haematophagous species.

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Introduction

The family Tabanidae includes about 4406 species and sub-species belonging to 137 genera worldwide (Roskov et al. 2013), some of which are of medical and veterinary importance (Mullens 2009). The family is divided into three sub-families: Pangoniinae, Chrysopsinae and Tabaninae. The species of the subfamily Pangoniinae are also called "long-tongued horse flies" because of their elongated and thin proboscis, and have a relevant role as pollinators. Those of the subfamily Chrysopsinae, known as "deer flies", have brilliantly coloured eyes and long antennae. The subfamily Tabaninae, known as "horse flies", has the highest species diversity within the family. The species of the genus *Haematopota*, commonly known as "clegs", belong to the subfamily Tabaninae (Chainey 1993; Morita et al. 2016).

Feeding habits in adult Tabanidae differ according to sex: females feed on blood and males on nectar. Female tabanids are therefore relevant vectors of many diseases due to the accumulation of microorganisms in their mouthparts, salivary

glands and/or on their tarsi, which they transfer to their hosts during feeding (Lessard et al. 2013). Their piercing proboscis allows them to feed on vertebrates, including cattle and humans (Krenn and Aspöck 2012). The genera *Haematopota*, *Tabanus*, and *Hybomitra* are important pests in the Old World (Mullens 2009). All species of *Haematopota* are terrestrial, with edaphic larvae able to develop on humus and colonize habitats distant from water bodies (Di Luca 2012). The genus contains 28 species in Europe (Chvála 2004). *Haematopota pandazisi* (Kröber) is distributed in southern Europe, North Africa and Anatolia (Chvála et al. 1972; Chvála 2004), and has been reported from the Italian mainland and Sicily (Di Girolamo et al. 1995; Chvála 2004). It is a common pest in areas inhabited by wild and domestic ungulates, including cattle farms and stables (Rivosecchi et al. 1986; Trentini 2001), and may also bite humans (Krčmar and Marić 2006).

Ultrastructural studies on the antennae of species of Tabanidae are few and include descriptions of chaetic, basiconic, coeloconic and trichoid sensilla (Elizarov and Chaika 1977; Faucheux 1981; Parashar et al. 1994; Ivanov 2007), whose functions range from mechanotactile to olfactory (Elizarov and Chaika 1977; Parashar et al. 1994; Ivanov 2007). Previous ultrastructural studies on the antennae of species of the genus *Haematopota* were limited and scarcely detailed (Elizarov and Chaika 1977; Parashar et al. 1994).

This paper provides the first scanning electron microscopy investigation of the morphology of the antenna of the female of *H. pandazisi*, including information on the type and distribution of its sensilla and microtrichia. This detailed study on antennal morphology and distribution of sensilla and microtrichia could be relevant for further investigations on sensorial activities related to the search for suitable hosts, mates, and larviposition sites in the Tabanidae family. These data could also be useful for taxonomic and phylogenetic studies.

Materials and methods

The specimens used in this study were collected from July to September 2016 in the rural areas around "Podere Nappo", "Oasi Dynamo Società Agricola", Limestre (Pistoia province, Italy) (44° 2′ 2.33″ N; 10° 47′ 42.86″ E), at elevations of about 1000–1100 m. They were captured with an insect net in an area densely populated by wild and domestic ungulates, placed in plastic boxes and brought live to the Laboratory of Urban Ecology, Medical and Veterinary Entomology of the University of Ferrara. The insects were then anaesthetized with CO_2, individually placed in 1.5-ml plastic tubes and, while still anaesthetized, killed in a freezer at -20 °C, where they were stored. The specimens were morphologically identified as females of *H. pandazisi* under a Nikon SMZ 800

stereomicroscope (Nikon Instruments Europe, Amsterdam, The Netherlands) and using the identification keys of Chvála et al. (1972) and Krčmar et al. (2011).

Given the morphological similarity of this species to *Haematopota italica* Meigen, a molecular analysis through COI gene-based DNA barcoding (Hebert et al. 2003) was carried out through the "DNA Analysis Service" of FEM2-Ambiente s.r.l., University of Milan-Bicocca (Milan, Italy). The results of DNA barcoding excluded the specimens from belonging to *H. italica*, due to high genetic distances with reference barcode sequences of this species. These analyses also excluded possible similarity with nine other *Haematopota* species with sequences deposited in the international genetic repository (https://www.ncbi.nlm.nih.gov/). The DNA barcoding data therefore supported the morphological identification of the species as *H. pandazisi*.

For scanning electron microscopy (SEM), 15 females were fixed, postfixed and dehydrated using the methods described in Pezzi et al. (2017). The method proposed by Khedre (1997) was employed to visualize the inner parts of the antenna under SEM. After dehydration, the samples were critical point dried in a Balzers CPD 030 dryer (Leica Microsystems, Wetzlar, Germany), mounted on stubs and coated with gold-palladium using an Edwards S-150 sputter coater (HHV Ltd., Crawley, UK). The SEM observations were conducted at the Electron Microscopy Centre, University of Ferrara, with a Zeiss EVO 40 SEM (Zeiss, Milan, Italy). Morphometric measurements were performed during SEM observations, using the software ZEISS SmartSEm v.5.09.SP10 (Carl Zeiss Ltd., Oberkochen, Germany). Measurements were expressed as an average with standard deviation.

The terminology of the antennal segments follows Keil (1999), who divides the antenna into the scape, the pedicel and the flagellum, composed of several flagellomeres. The terminology of sensilla and microtrichia follows McIver (1982) and Khedre (1997).

Results

The antenna of the female of *H. pandazisi* (total length $2.30 \pm 0.05 \times 10^3$ μm) is composed of three segments, the scape, the pedicel and the flagellum (Fig. 1a and inlay). The scape (964.38 ± 31.71 μm long) is cylindrical with a thinner proximal region (Fig. 1b). Its surface is covered by short and thin microtrichia with longitudinal grooves and a blunt tip (Fig. 1b, c), and by numerous chaetic sensilla (83.13 ± 17.34 μm long), each composed of a long articulated bristle with longitudinal grooves and a sharp tip (Fig. 1b, d). The pedicel (154.68 ± 10.89 μm long) is of a truncated conical shape with two distal triangular processes, the first in a dorsal position (101.40 ± 7.53 μm long) and the second, much shorter, in a ventral position (33.60 ± 4.82 μm long) (Fig. 1a, e). The surface of
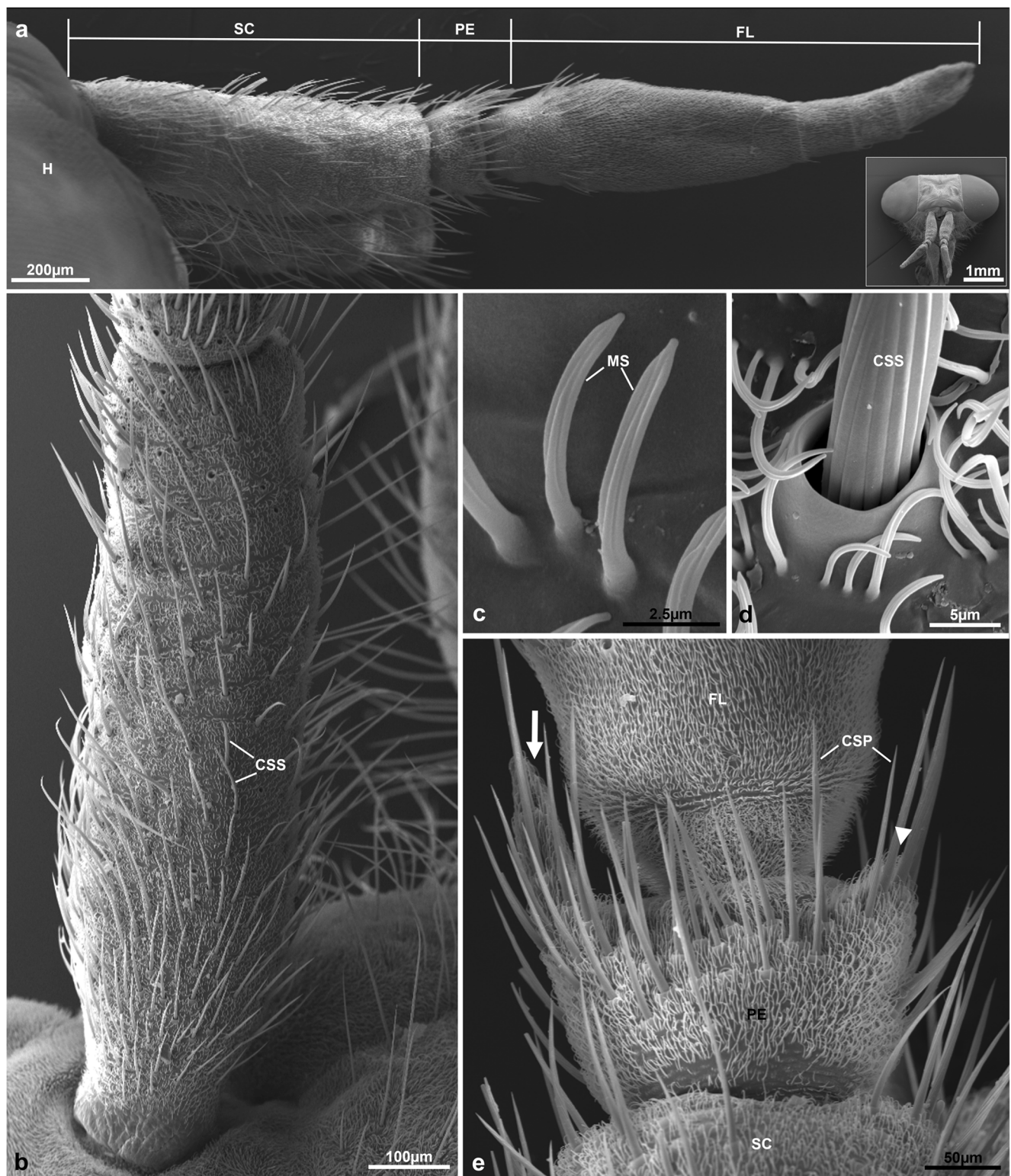
Fig. 1 Scanning electron micrographs of head of female of *Haematopota pandazisi*. **a** Lateral view of right antenna. Inlay: female head capsule. **b** Scape. **c** Detail of surface of scape, showing microtrichia. **d** Detail of base of chaetic sensillum. **e** Lateral view of pedicel, showing dorsal (arrow) and ventral (arrowhead) processes. CSP, chaetic sensilla of pedicel; CSS, chaetic sensilla of scape; FL, flagellum; H, head; MS, microtrichia of scape; PE, pedicel; SC, scape

the pedicel is covered by microtrichia and chaetic sensilla (107.63 ± 24.92 μm long), both morphologically similar to those of the scape (Fig. 1e). The flagellum, the longest region of the antenna ($1.10 \pm 0.03 \times 10^3$ μm), is composed of four
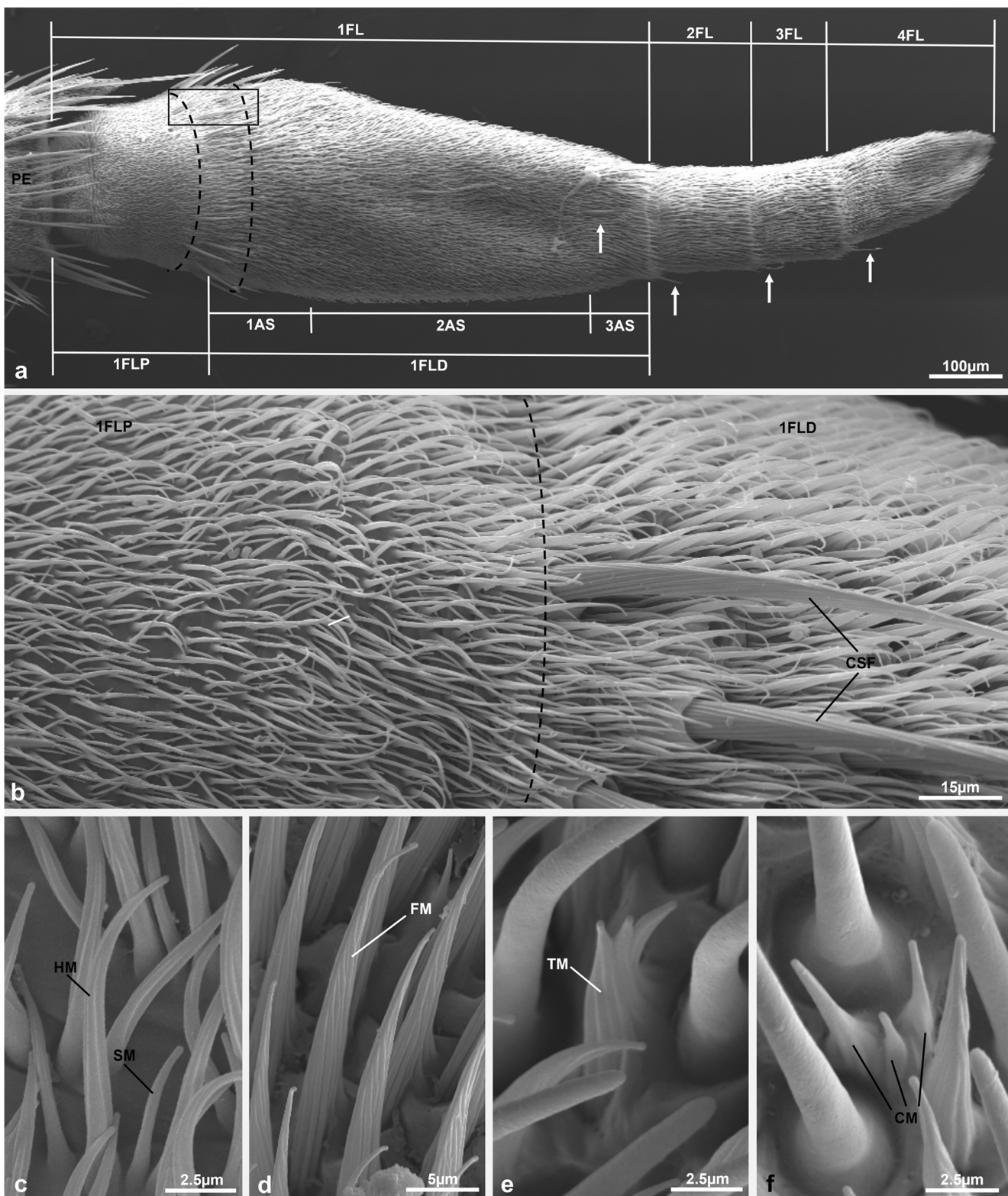
flagellomeres, of which the first is the longest (Figs. 1a and 2a). The first flagellomere (768.98 ± 29.98 μm long) can be divided into two regions according to microtrichia and sensilla types (Fig. 2a). The proximal region (193.65 ± 15.31 μm

long) (Fig. 2b) has only two types of microtrichia: the first type hair-like with longitudinal grooves, the second shorter and smooth (Fig. 2c). The proximal and distal regions of the flagellomere are separated by a "crown" of chaetic sensilla

Fig. 2 Scanning electron micrographs of flagellum of female of *H. pandazisi*. **a** Lateral view of flagellum. Dashed lines highlight crown of chaetic sensilla between proximal and distal regions of first flagellomere. Rectangle outlines region enlarged in (**b**). Arrows indicate chaetic sensilla on flagellomeres. **b** Detail of (**a**) showing boundary between proximal and distal regions of first flagellomere, indicated by dashed line. **c** Hair-like grooved microtrichia and short smooth ones in proximal region of first flagellomere. **d** Flat triangular microtrichia, found on all flagellomeres except in proximal region of first. **e** Microtrichia with three tips, found on all flagellomeres except in proximal region of first. **f** Conical microtrichia, found on all flagellomeres except in proximal region of first. 1AS–3AS, parts of distal region of first flagellomere, characterized by different associations of sensilla; 1FL–4FL, flagellomeres; 1FLD, distal region of first flagellomere; 1FLP, proximal region of first flagellomere; CM, conical microtrichia; CSF, chaetic sensilla of flagellomeres; FM, flat triangular microtrichium; HM, hair-like microtrichium; SM, short, smooth microtrichium; TM, microtrichium with three tips. Other abbreviations as in Fig. 1

(69.71 ± 5.61 μm long) with the same morphology as those on the scape and pedicel (Fig. 2a, b). These sensilla are also scattered on the surface of the other flagellomeres (Fig. 2a) and near the joints connecting the flagellomeres. The distal region of the first flagellomere (549.86 ± 16.60 μm long) (Fig. 2a) is characterized by three types of microtrichia (Fig. 2d–f), five types of sensilla (Figs. 2b and 3a–i), and cuticle perforations (Fig. 3b–d, g). The microtrichia of the first type cover the entire surface of the region and are of a flat, triangular shape with longitudinal grooves and a sharp tip (Fig. 2d). Those of the second type are characterized by three tips and longitudinal grooves (Fig. 2e). Those of the third type are shorter, conical and with a rounded tip (Fig. 2f). These last two types of microtrichia are scattered along the distal region of the flagellomere. The sensilla of the distal region of the first flagellomere are complex and include clavate, basiconic and trichoid sensilla plus two different types of coeloconic sensilla. The clavate sensilla, each located within a low depression, are club-shaped with a blunt tip (Fig. 3a). The basiconic sensilla, each located within a shallow depression, are all morphologically similar and with rounded tips, but range in length from 6.24 to 15.33 μm (Fig. 3b). The trichoid sensilla, each located within a shallow depression, are conical with a rounded tip (Fig. 3c). The coeloconic sensilla belong to two types based on their general shape and inner peg. Those of the first type are dome-shaped, with an oval opening at the top (Fig. 3d). Some perforations are visible on the dome (Fig. 3d). When the flagellum is longitudinally sectioned, the coeloconic sensillum shows a spherical invagination (Fig. 3e). When opened, the coeloconic sensillum appears divided into two spaces by a thickening. The upper space corresponds to the outside dome and the lower space to the spherical invagination, which in turn contains a basiconic peg, off-centered and with a blunt tip (Fig. 3f). The coeloconic sensillum of the second type appears on the outside as a circular opening surrounded by microtrichia, with the tip of a peg visible in its center (Fig. 3g). When the flagellum is longitudinally

sectioned, this type of sensillum appears as a squat cylinder (Fig. 3h) with a single internal cavity containing a centered peg, deeply grooved, with a large conical base and blunt tip (Fig. 3i).

The distribution of sensilla varies in the distal region of the first flagellomere, with three different associations of sensilla along the major axis of the flagellomere (Fig. 2a): an association of clavate sensilla and both types of coeloconic sensilla, from the base of the distal region to a distance of about 102.60 ± 7.92 μm (Figs. 2a and 4a); an association of basiconic and trichoid sensilla from this limit to about 361.26 ± 16.64 μm (Figs. 2a and 4b); and an association of basiconic sensilla and coeloconic sensilla of the first type, with rare trichoid sensilla, in the most apical part of the region (80.13 ± 3.79 μm long) (Figs. 2a and 4c).

The second, third and fourth flagellomeres are shorter than the first (Figs. 1a and 2a), respectively 129.53 ± 14.31 μm, 110.13 ± 4.74 μm and 171.90 ± 8.14 μm. The second and third flagellomeres are cylindrical while the fourth is conical (Fig. 2a), and their entire surface is covered by microtrichia similar to those found in the distal region of the first flagellomere (Fig. 4d). Basiconic and trichoid sensilla as well as coeloconic sensilla of both types are scattered throughout their surface, whereas clavate sensilla are rare and restricted to the base of each flagellomere (Fig. 4d).

Discussion

The present study is the first to describe the ultrastructural morphology of the antenna of the female of *H. pandazisi*. Morphological studies on the antennae of Tabanidae are limited and the antennae of only two species of *Haematopota* have been described: *Haematopota pluvialis* L. (Smith 1919; Elizarov and Chaika 1977) and *Haematopota dissimilis* Ricardo (Parashar et al. 1994). Other tabanid genera for which the antennae have been described are *Atylotus*, *Chrysops*, *Hybomitra*, and *Tabanus* (Smith 1919; Lall 1970; Elizarov and Chaika 1977; Faucheux 1981; Parashar et al. 1994; Ivanov 2007). The antennae of *H. pandazisi* are generally similar to those of other species of the genus (Chvála et al. 1972). The antennae of females of this species are characterized by five types of sensilla: chaetic, clavate, coeloconic, basiconic and trichoid. As in other species of Tabanidae, the chaetic sensilla of *H. pandazisi* are articulated, with longitudinal grooves and a sharp tip (Lall 1970; Elizarov and Chaika 1977; Faucheux 1981; Parashar et al. 1994; Ivanov 2007). Similar chaetic sensilla have been described as "sensilla with a thick wall" (Elizarov and Chaika 1977), or more recently as "trichoid sensilla" (Ivanov 2007). The distribution of chaetic sensilla on the scape and pedicel is also similar to that of other Tabanidae (Lall 1970; Elizarov and Chaika 1977; Faucheux 1981; Parashar et al. 1994; Ivanov 2007). As in *H. pandazisi*,
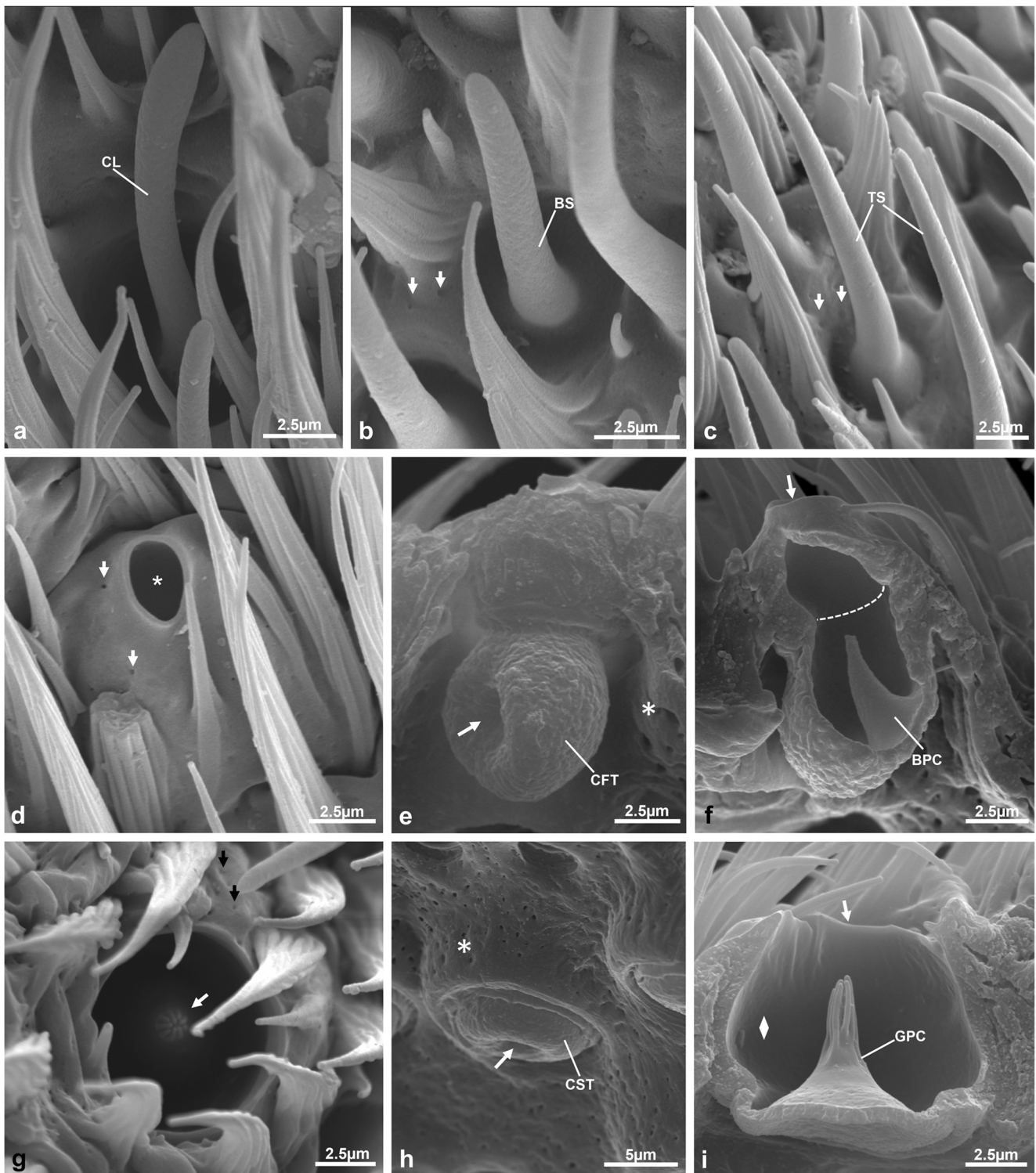
the chaetic sensilla are found in the proximal part of the first flagellomere in *Hybomitra lasiophthalma* (Macquart) and *Tabanus lineola* Fabricius (Lall 1970), *H. pluvialis* and *Tabanus bromius* L. (Elizarov and Chaika 1977). The chaetic sensilla observed on the distal part of each flagellomere in *H. pandazisi* have also been observed in *Chrysops vittatus*

Wiedemann, *H. lasiophthalma*, *T. lineola* (Lall 1970), *Chrysops relictus* Meigen, *H. pluvialis*, *T. bromius* (Elizarov and Chaika 1977), and *Atylotus fulvus* Meigen (Faucheux 1981). The chaetic sensilla form an encircling "crown" around the proximal region of the first flagellomere in *H. pandazisi*; whereas in *H. lasiophthalma*, *T. lineola* (Lall 1970),

◄ Fig. 3 Scanning electron micrographs of flagellum detail of female of *H. pandazisi*. **a** Clavate sensillum. **b** Basiconic sensillum. Arrows indicate cuticle perforations. **c** Trichoid sensilla. Arrows indicate cuticle perforations. **d** Outside surface of coeloconic sensillum of first type, dome-shaped and with oval opening (asterisk). Arrows indicate cuticle perforations. **e** Coeloconic sensillum of first type. Asterisk indicates inner surface of flagellum and arrow indicates cavity of peg connected with antennal cavity. **f** Coeloconic sensillum of first type, opened to show basiconic peg. Dashed line highlights presence of two spaces inside sensillum. Arrow indicates oval opening of sensillum. **g** Outside surface of coeloconic sensillum of second type, with circular opening. White arrow indicates grooved peg and black arrows indicate cuticle perforations. **h** Coeloconic sensillum of second type. Asterisk indicates inner surface of flagellum and arrow indicates cavity of peg connected with antennal cavity. **i** Coeloconic sensillum of second type, opened to show grooved peg. Diamond and arrow respectively indicate inside and opening of sensillum. BPC, basiconic peg of coeloconic sensillum of first type; BS, basiconic sensillum; CFT, coeloconic sensillum of first type; CL, clavate sensillum; CST, coeloconic sensillum of second type; GPC, grooved peg of coeloconic sensillum of second type; TS, trichoid sensilla

H. pluvialis and *T. bromius* (Elizarov and Chaika 1977) they are grouped together in one or two tufts. In *H. lasiophthalma*, *T. lineola* (Lall 1970) and *T. bromius* they form a single tuft near the dorsal process, while in *H. pluvialis* they form two tufts: one dorsal and one ventral (Elizarov and Chaika 1977). In other species such as *H. dissimilis*, *Tabanus rubidus* Wiedemann, *Tabanus striatus* Fabricius, and *Tabanus subcinerascens* Ricardo, the chaetic sensilla are apparently confined to only the scape and pedicel. In these four species a mechanotactile function of the chaetic sensilla has been suggested (Parashar et al. 1994). The same has been suggested for these sensilla in *Hybomitra bimaculata* (Macquart) and *Tabanus bovinus* L. (Ivanov 2007), as well as in other haematophagous Diptera belonging to the families Ceratopogonidae (Blackwell et al. 1992) and Culicidae (McIver 1982). The single chaetic sensillum located at the tip of the antenna in both sexes of *Culicoides impunctatus* Goetghebuer and *Culicoides nubeculosus* (Meigen) (Diptera: Ceratopogonidae) is thought to have a general tactile function for investigation of substrates and textures (Blackwell et al. 1992). In *Simulium baffinense* Twinn, *Simulium euryadminiculum* Davies, *Simulium rugglesi* Nicholson and Mickel, and *Simulium venustum* Say (Diptera: Simuliidae), the arrangement of chaetic sensilla around the distal boundary of the pedicel and the scape suggests the ability to detect the direction and degree of bending of the pedicel and flagellum (Mercer and McIver 1973). The similar distribution of chaetic sensilla in *H. pandazisi* also suggests a role in detecting the direction and degree of bending of the same structures.

In *Simulium arcticum* Malloch (Diptera: Simuliidae), a chemoreceptive role has been proposed for the chaetic sensilla at the antennal tip. These sensilla would perceive host epidermis during biting site selection, and perhaps flower parts during nectar feeding (Shipp et al. 1988). In *H. pandazisi*, the clavate sensilla are each localized in a circular depression and are club-shaped with

blunt tips, similar to those classified as a type of basiconic sensillum in *H. dissimilis*, *T. rubidus*, *T. striatus* and *T. subcinerascens* by Parashar et al. (1994), and in *H. bimaculata* and *T. bovinus* by Ivanov (2007). Clavate sensilla are rather unusual in haematophagous Diptera. Those of *H. pandazisi* are similar to those described in *S. arcticum* and *Haematobia irritans irritans* (L.) (Diptera: Muscidae) (White and Bay 1980; Shipp et al. 1988), and are classified as basiconic sensilla in *S. arcticum* (Shipp et al. 1988). Clavate sensilla are common in non-haematophagous Diptera and have been previously described in Anthomyiidae (Honda et al. 1983; Ross 1992), Calliphoridae (Fernandes et al. 2004; Zhang et al. 2014), Fanniidae (Wang et al. 2012; Zhang et al. 2013b), Muscidae (Been et al. 1988; Smallegange et al. 2008; Zhang et al. 2013a; Wang et al. 2014), Oestridae (Hunter and Adserballe 1996; Zhang et al. 2012; Liu et al. 2015), Sarcophagidae (Khedre 1997; Pezzi et al. 2016), Scathophagidae (Liu et al. 2016), and Tephritidae (Giannakakis and Fletcher 1985; Levinson et al. 1987; Mayo et al. 1987; Lee et al. 1994; Arzuffi et al. 2008; Castrejón-Gómez and Rojas 2009; Bisotto-de-Oliveira et al. 2011). Sensilla of this type are located in the proximal region of the first flagellomere in *H. pandazisi* and scattered at the base of the other flagellomeres. This condition is in part similar to that found in other Tabanidae, where sensilla with a clavate shape are distributed on the proximal part of the first flagellomere but are missing on the other flagellomeres (Parashar et al. 1994; Ivanov 2007). An olfactory role has been proposed for these sensilla, which are also thought to possess hygrosensitive cells (Lewis 1972), in haematophagous Diptera such as *S. arcticum* (Shipp et al. 1988) and *Stomoxys calcitrans* L. (Muscidae) (Tangtrakulwanich et al. 2011). An olfactory role for clavate sensilla has also been suggested in five non-haematophagous species of the family Anthomyiidae (Honda et al. 1983; Ross 1992).

In *H. pandazisi* there are two types of coeloconic sensilla. The first type is dome-shaped with an oval opening and contains an off-centered basiconic peg, while the second type has a circular opening containing a centered and grooved peg. The presence of two types of coeloconic sensilla and their detailed morphology has never been previously documented for the antennae of Tabanidae.

In *Chrysops caecutiens* (L.), *C. relictus*, *Chrysops rufipes* Meigen, *H. pluvialis*, *Hybomitra montana* (Meigen), *T. bromius* (Smith 1919; Elizarov and Chaika 1977), *A. fulvus* (Faucheux 1981), *H. bimaculata* and *T. bovinus* (Ivanov 2007), coeloconic sensilla have been observed but no description of their outer and inner morphology has been provided. In other documented species of Tabanidae including *H. dissimilis*, *T. rubidus*, *T. striatus* and *T. subcinerascens* (Parashar et al. 1994), no coeloconic sensilla have been reported. The distribution of these sensilla in *H. pandazisi* is similar to that reported for *A. fulvus* (Faucheux 1981) and *H. pluvialis* (Elizarov and Chaika 1977). Two types of
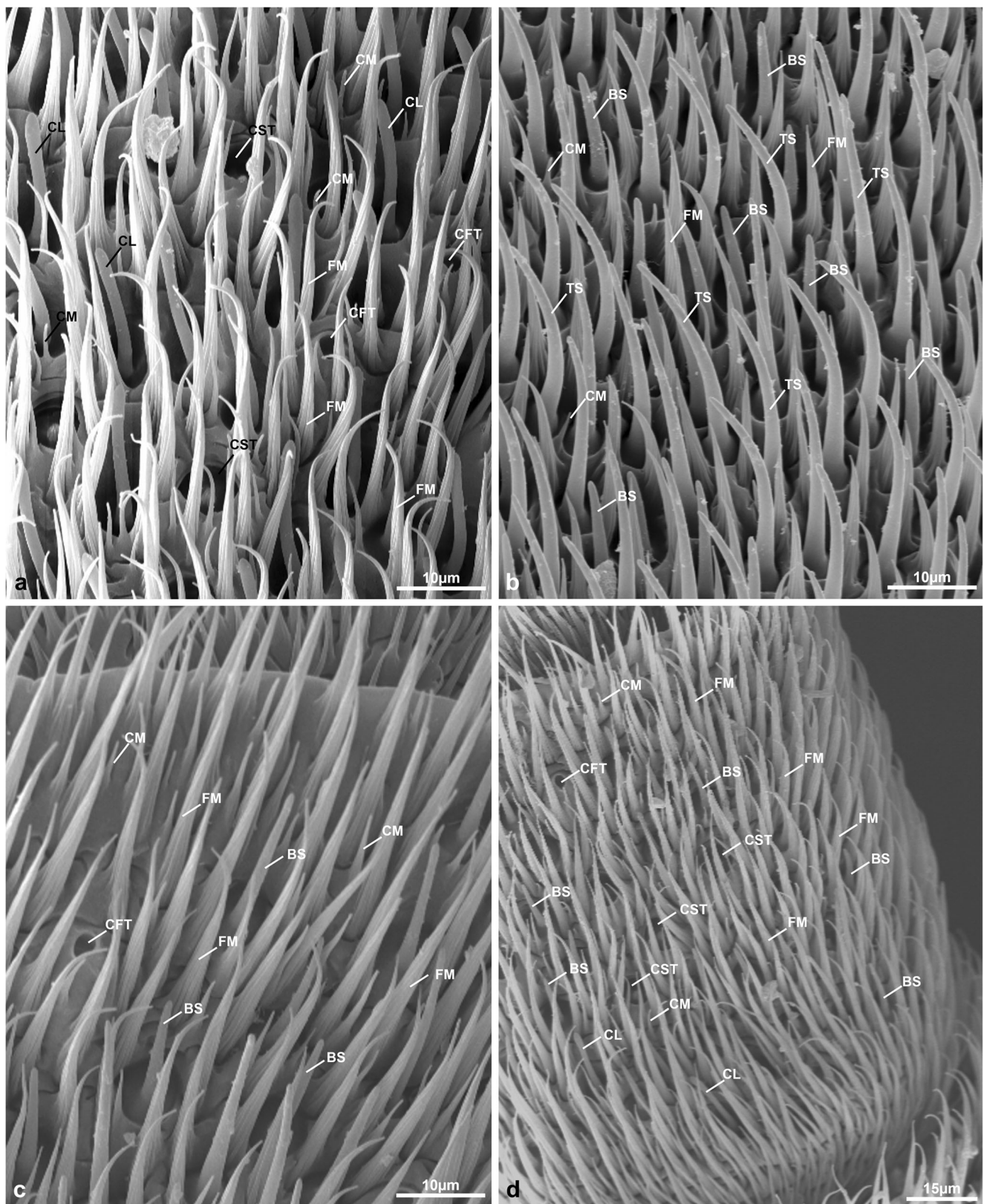
Fig. 4 Scanning electron micrographs of first and second flagellomere details of female of *H. pandazisi*. **a** Detail of distal region of first flagellomere showing first association of sensilla (1AS, Fig. 2a), consisting of clavate sensilla and two types of coeloconic sensilla. **b** Detail of distal region of first flagellomere showing second association of sensilla (2AS, Fig. 2a), consisting of basiconic and trichoid sensilla. **c** Detail of distal region of first flagellomere showing third association of sensilla (3AS, Fig. 2a), consisting of basiconic sensilla and coeloconic sensilla of first type, with rare trichoid sensilla. **d** Variety of microtrichia and sensilla of second flagellomere. Abbreviations as in Figs. 2 and 3

coeloconic sensilla have been described in other haematophagous Diptera belonging to the subfamily Anophelinae (Diptera: Culicidae) (Boo 1980; Pitts and Zwiebel 2006; Hempolchom et al. 2017; Taai et al. 2017), in *Lutzomyia longipalpis* (Lutz and Neiva) (Diptera: Psychodidae) (Fernandes et al. 2008), and in *H. irritans irritans* (White and Bay 1980). Coeloconic sensilla bearing a single peg without longitudinal grooves have also been described in *Anopheles maculipennis* Meigen (Ismail 1964) and *Anopheles stephensi* Liston (Diptera: Culicidae) (Boo and McIver 1975; Boo 1980). Coeloconic sensilla with a single grooved peg are common in families of haematophagous Diptera such as Ceratopogonidae (Chu-Wang et al. 1975; Blackwell et al. 1992; Alexandre-Pires et al. 2010; Isberg et al. 2013; Urbanek et al. 2014), Culicidae (Ismail 1964; Boo and McIver 1976; Boo 1980; Pitts and Zwiebel 2006; Hempolchom et al. 2017; Taai et al. 2017), Psychodidae (Fernandes et al. 2008) and Hippoboscidae (Zhang et al. 2015). Concerning these sensilla, a thermoreception role has been proposed in *Aedes aegypti* L. (Diptera: Culicidae), and a thermoreception (Boo and McIver 1975) and an olfactory one (Boo and McIver 1976) in *A. stephensi*. Olfactory and hygroreceptor roles have also been suggested in *Culicoides furens* (Poey) (Diptera: Ceratopogonidae) by Chu-Wang et al. (1975).

The basiconic sensilla of *H. pandazisi*, characterized by having blunt tips and being located within shallow depressions on the flagellum, are similar to those observed in other Tabanidae such as *C. caecutiens*, *C. relictus*, *C. rufipes*, *H. pluvialis*, *H. montana*, *T. bromius* (Elizarov and Chaika 1977), and *A. fulvus* (Faucheux 1981), and to a fourth type of basiconic sensillum seen in *H. dissimilis*, *T. rubidus*, *T. striatus*, and *T. subcinerascens* (Parashar et al. 1994), as well as a fifth type of basiconic sensillum in *H. maculata* and *T. bovinus* (Ivanov 2007). In two other species of *Haematopota*, *H. dissimilis* and *H. pluvialis*, this type of sensillum was apparently found only on the first flagellomere (Elizarov and Chaika 1977; Parashar et al. 1994). However, in other Tabanidae such as *C. relictus* (Elizarov and Chaika 1977), *A. fulvus* (Faucheux 1981), *H. maculata*, and *T. bovinus* (Ivanov 2007), these sensilla were found on all flagellomeres. Basiconic sensilla are thought to play an olfactory role in Tabanidae (Elizarov and Chaika 1977; Parashar et al. 1994). As with clavate sensilla, the basiconic sensilla are thought to play an olfactory role in the haematophagous species *S. arcticum* (Shipp et al. 1988) and *S. calcitrans* (Tangtrakulwanich et al. 2011), whereas a hygrosensitive role has also been reported for *S. calcitrans* (Lewis 1972). An olfactory role of these sensilla has also been proposed in non-haematophagous Diptera, including Anthomyiidae (Honda et al. 1983), Drosophilidae (Clyne et al. 1997), Phoridae (Lu et al. 2012), Stratiomyidae (Faucheux and Mason 2001),

Sarcophagidae (Sukontason et al. 2004), Muscidae (Sukontason et al. 2004, 2007) and Calliphoridae (Sukontason et al. 2004; Hore et al. 2017).

In *H. pandazisi*, the trichoid sensilla are conical with a rounded tip and each located within a shallow depression. Trichoid sensilla with similar morphology have been reported in *H. dissimilis*, *T. rubidus*, *T. striatus*, *T. subcinerascens* (Parashar et al. 1994), *H. bimaculata* and *T. bovinus* (Ivanov 2007), although in these species they were described as basiconic sensilla. Trichoid sensilla that are morphologically similar to those of *H. pandazisi* have never been reported in other haematophagous Diptera besides Tabanidae, but they have been found in non-haematophagous species such as *Bactrocera tryoni* (Froggatt) (Tephritidae) (Giannakakis and Fletcher 1985), *Hydrotaea irritans* (Fallén) (Muscidae) (Been et al. 1988), *Bactrocera dorsalis* (Hendel) (Tephritidae) (Lee et al. 1994), *Pselaphomyia nigripennis* (Bigot) (Stratiomyidae) (Faucheux and Mason 2000) and *Pseudacteon* sp. (Phoridae) (Lu et al. 2012). In *H. irritans*, these sensilla have been described as basiconic (Been et al. 1988). In Tabanidae, an olfactory role has been proposed for trichoid sensilla (Parashar et al. 1994). Investigations on the role of these sensilla in haematophagous Diptera have been conducted mainly in Culicidae and an olfactory role was clearly demonstrated, especially in relation to detection of hosts and oviposition sites (Qiu et al. 2006; Hill et al. 2009; Siju et al. 2010). An olfactory role for trichoid sensilla has also been proposed in other haematophagous species such as *Boophthora erythrocephala* (De Geer) (Diptera: Simuliidae) (Elizarov and Chaika 1975), but in *S. calcitrans* (Lewis 1972) they have been reported as chemoreceptors. The same role has been proposed in non-haematophagous families such as Anthomyiidae (Ross 1992), Oestridae (Hunter and Adserballe 1996), Psilidae (Ross 1992) and Tephritidae, where a role in the perception of sexual pheromone and host plant volatiles has also been suggested (Levinson et al. 1987; Arzuffi et al. 2008).

Other common structures observed on the antennae of *H. pandazisi* are the microtrichia. The present study includes the first detailed description of their morphology and distribution in a species of Tabanidae.

In Tabanidae, microtrichia are generally distributed on all regions of the antenna (Elizarov and Chaika 1977; Parashar et al. 1994; Ivanov 2007), but in *H. dissimilis*, *T. rubidus*, *T. striatus* and *T. subcinerascens* they have been indicated as "sensilla stellate" (Parashar et al. 1994). A total of six different types of microtrichia have been found in *H. pandazisi* according to their location and morphology. Those of the first type, distributed on the scape and pedicel, are short and characterized by longitudinal grooves and a blunt tip, and are similar to those described in *H. bimaculata* and *T. bovinus* (Ivanov 2007). Those of the second and third types, distributed on the proximal region of the first flagellomere in *H. pandazisi*, are hair-like with longitudinal grooves and short and smooth, respectively. Microtrichia of a similar shape had never been

previously described in Tabanidae and their distribution in the proximal region of the first flagellomere is also unusual since this region is devoid of sensilla. A similar distribution has been apparently observed only in *C. vittatus* (Lall 1970), *C. relictus*, and *H. pluvialis* (Elizarov and Chaika 1977), and could be related to the mechanoreceptive role of the chaetic sensilla of the pedicel and of the crown on the first flagellomere.

The last three types of microtrichia found on the antennae of females of *H. pandazisi* are distributed on the distal part of the first flagellomere and on all other flagellomeres. The first of these additional types has a flat triangular shape with longitudinal grooves and a sharp tip, and is similar to microtrichia reported in *H. bimaculata* and *T. bovinus* (Ivanov 2007). The remaining two types of microtrichia are of a tricuspid and a conical shape, respectively, and had never been previously described in any species of Tabanidae.

The high morphological diversity of sensilla and microtrichia on the antennae of females of *H. pandazisi* shows the relevance of these structures in the sensorial perception of this haematophagous species as well as in other Diptera. Investigations of the sensorial structures in Tabanidae may establish a base for electrophysiological and molecular studies on sensorial activities involved in the search for hosts, mates, and larviposition sites, as well as for applications in the control of infesting populations, such as developing attractants for traps or repellents for animal and human protection. Finally, the ultrastructural details of these antennal structures may contribute key data to taxonomic and phylogenetic studies on this important group of Diptera.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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