A COMPARATIVE INVESTIGATION OF THE ANTENNAL
SENSILLA IN ADULT ANISOPTERA

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A fine structural overview of the flagellar sensilla of *Onychogomphus forcipatus* (Gomphidae), *Aeshna cyanea* (Aeshnidae), *Somatochlora metallica* (Cordulidae) and *Cordulegaster boltonii* (Cordulegastridae) revealed the presence of pits containing sensilla typically located on the latero-ventral side of the first flagellar segments in all four species. These sensilla are represented by coeloconic single-walled olfactory sensilla and deeply sunken sensilla styloconica (type-1 and type-2) sharing common features typical of thermo-hygroreceptors. Sensilla styloconica are located inside deep convoluted cavities. It is suggested that olfactory and thermo-hygrosensory sensilla are the main sensilla on the antennae of all anisopteran families. The attribution of the coeloconic sensilla of dragonflies to single-walled olfactory sensilla (confirmed by the finding of pore tubules in *O. forcipatus*), together with their common occurrence in the suborder Anisoptera, are relevant for phylogenetic studies.

INTRODUCTION

"The face of a dragonfly is practically nothing but eyes!", as a Japanese haiku states. Indeed, dragonflies are remarkable in their powers of vision (CORBET, 1999). In this regard, the sensilla located on the antennae of Odonata have been poorly investigated. An early overview on the antennal flagellum of some Anisoptera and Zygoptera species (SLIFER & SEKHON, 1972) reports the presence of coeloconic sensilla located in simple and compound cavities. Some behavioural studies on *Orthetrum cancellatum* (GEWECKE et al., 1974; GEWECKE & ODENDAHL, 2004) consider the scape and pedicel as important sites for air speed perception and flight control.

Recently, a fine structural investigation of the adults of the dragonfly *Libellula*

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depressa (Libellulidae) performed by REBORA et al. (2008) revealed the presence of sensilla located in pits on the latero-ventral side of the antennal flagellum. These sensilla are represented by sensilla coeloconica and by deeply sunken sensilla styloconica. The structure of the sensilla coeloconica is coherent with that reported for single-walled insect chemoreceptors. The deeply sunken sensilla are represented by two kinds of sensilla styloconica sharing common features typical of thermo-hygroreceptors.

The present paper aims to investigate whether the putative olfactory sensilla and the two kinds of putative thermo-hygrosensory sensilla described in *L. depressa* are widespread in Anisoptera. Thus, the sensilla located on the antennal flagellum of adults belonging to *Onychogomphus forcipatus* (Gomphidae), *Aeshna cyanea* (Aeshnidae), *Somatochlora metallica* (Cordulidae) and *Cordulegaster boltonii* (Cordulegastridae) are analyzed using scanning electron microscopy (SEM). These four species, together with *L. depressa* (Libellulidae) (REBORA et al., 2008), represent the five Anisoptera families found in Italy.

In order to add information on the internal structure of the above reported sensilla, already described in *L. depressa* (REBORA et al., 2008), transmission electron microscopy (TEM) has been carried out on the antennae of *O. forcipatus*, a common species in southern Europe (DIJKSTRA & LEWINGTON, 2006) belonging to the superfamily Aeshnoidea.

The results presented here are part of a programme on the fine structure of antennal sensilla in zygopterans as well as anisopterans. Studies on the sensory biology of Odonata, in consideration of their belonging to Paleoptera, are also useful for phylogenetic studies.

MATERIAL AND METHODS

Adult *Onychogomphus forcipatus* and *Aeshna cyanea* were collected in Umbria (central Italy) during summer 2007. Dry *Somatochlora metallica* and *Cordulegaster boltonii* specimens were investigated after a procedure of rehydration (ALBA-TERCEDOR, 1987).

In the laboratory, antennal flagella were dissected from anaesthetised specimens and fixed for 12 hours in 2.5% glutaraldehyde in cacodylate buffer, pH 7.2.

For scanning electron microscopy (SEM) analysis, the fixed material was rinsed for three times in the same buffer, dehydrated using a graded ethanol series and critical-point dryed in a CPD 030 Bal-Tec critical-point dryer (Bal-Tec Union Ltd, Balzers, Liechtenstein). Specimens were mounted on stubs with silver conducting paint, sputter-coated with gold-palladium in an Emitech K550X sputterer (Emitech, Ashford, England), and observed with a Philips XL30 SEM (Philips, Eindhoven, The Netherlands), at an accelerating voltage of 18kV. For observations of the inner cuticular wall of the antenna, the flagella were sectioned longitudinally with a razor blade and cleaned with KOH-solution. These flagella were then dehydrated in a graded ethanol series, dried in an oven and glued onto the SEM specimen supports in order to allow the observation of the inner side of the antenna.

For transmission electron microscopy (TEM), the fixed antennal flagella were rinsed three times in cacodylate buffer and post-fixed for 1 hour at 4°C in 1% osmium tetroxide in cacodylate buffer. Afterward the material was washed three times in the same buffer, dehydrated using a graded ethanol series and embedded in an Epon-Araldite resin mixture. Ultrathin sections, cut on a Leica EM

UC6 ultracut (Leica Microsystem GmbH, Wien, Austria), were collected on formvar-coated copper grids, stained with uranyl acetate and lead citrate, and examined with a Philips EM 208 (Philips, Eindhoven, The Netherlands).

RESULTS
OBSERVATIONS UNDER SEM

Onychogomphus forcipatus (Gomphidae). − The antenna consists of a scape, a pedicel and a two-segmented flagellum. The proximal flagellar segment is well developed (in terms of its sensory structures) in comparison with the distal one and bears numerous sensilla located in pits on its latero-ventral side (Fig. 1a). Most of these pits (about 40) host sensilla coeloconica while a few of them (about 2) are wider and represent the openings of large cavities inside the antenna (Figs 1a-c). The sensilla coeloconica are visible on the antennal surface as pegs located in pits (Figs 1a, c, d). The cuticle of the peg bears pore-like structures clearly evident under the SEM (Fig. 1d). The large cavities each measure about 40 μm in width and about 20 μm in depth. The cavity is very convoluted and hosts numerous type-1 and type-2 deeply sunken sensilla styloconica (Fig. 1c), both characterized by a wide stylus bearing an apical cone (Fig. 1e). Type-1 sensilla have a cone with cuticular 'fingers' in its distal portion (Fig. 1e). Type-2 sensilla have a cone with a rugged cuticular surface (Fig. 1e). No pore is visible on the cuticle of either type-1 or type-2 sensilla (Fig. 1e).

Aeshna cyanea (Aeshnidae). − The antenna consists of a scape, a pedicel and an antennal flagellum of four segments. The first (proximal) and the second flagellar segments show wide pits on their latero-ventral sides (Fig. 1f), with about 6 on the first segment and 3 on the second. Images of the inner cuticular wall reveal that these wide pits are the openings of convoluted cavities, which measure about 20 μm in width and 30-50 μm in depth (Fig. 1g). Longitudinally fractured cavities show coeloconic pegs located on the edge of the pits (Figs 1h, i) and type-1 and type-2 deeply sunken sensilla styloconica located inside the cavities (Fig. 1j). The sensilla coeloconica bear pore-like structures on their surface (Fig. 1i). Type-1 sensilla have a cone with cuticular 'fingers' in their distal portion (Fig. 1j). Type-2 sensilla have a cone with a rugged cuticular surface (Fig. 1j). No pore is visible on the cuticle of either type-1 or type-2 sensilla (Fig. 1j).

Somatochlora metallica (Corduliidae). − The antenna consists of a scape, a pedicel and an antennal flagellum of four segments. The first (proximal) and the second flagellar segments show, on their latero-ventral sides, a number of pits (Fig. 2a), with about 40 on the first segment and 3 on the second. The pits are isolated or in groups of two or three (Figs 2a, b) and most of them host sensilla coeloconica (Figs 2a, b, d), while some represent the openings of deep cavities (Figs 2a-c). The sensilla coeloconica are evident on the antennal surface as pegs with pore-like structures on the cuticle (Fig. 2d). Each deep cavity is parallel to
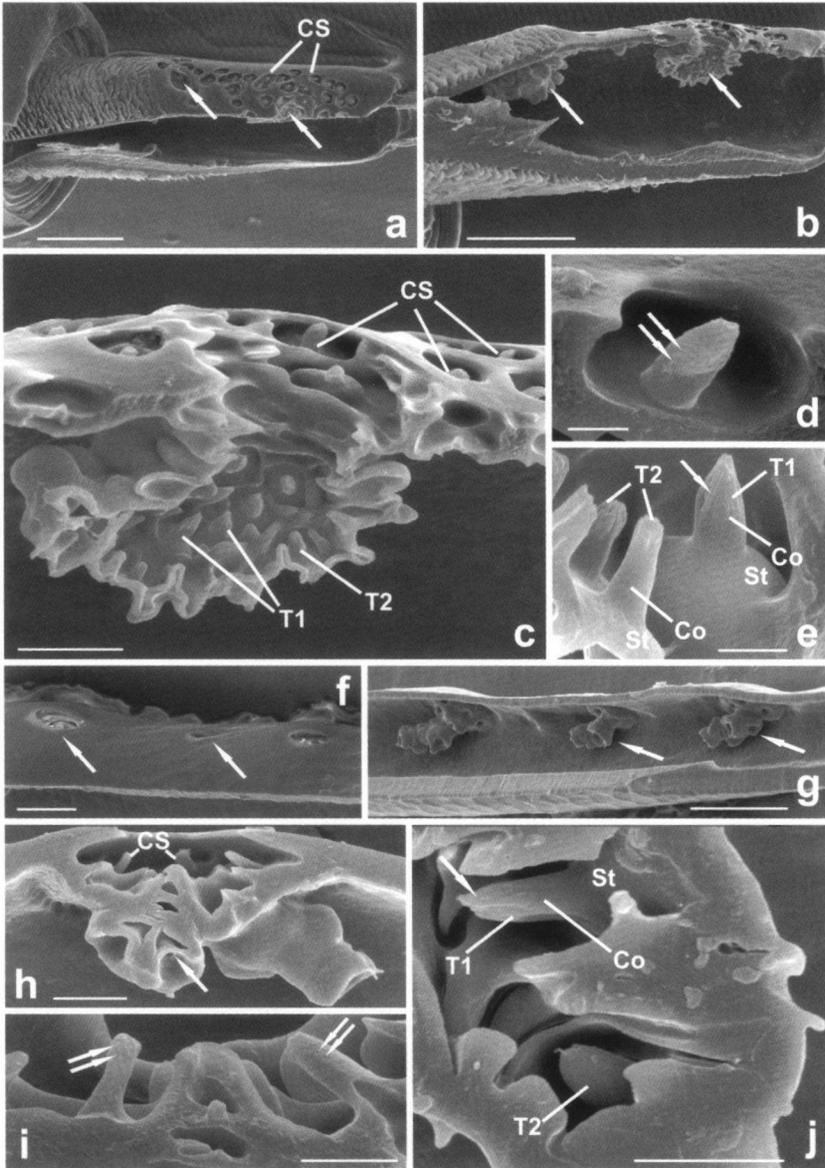
Fig. 1. Longitudinally fractured antennal flagella of *Onychogomphus forcipatus* (a-e) and *Aeshna cyanea* (f-j) under SEM; (a) outer cuticular wall of the first flagellar segment showing pits, on its latero-ventral side, containing sensilla coeloconica; arrows point to the openings of large cavities bearing deeply sunken sensilla styloconica. Scale bar 50 µm; — (b) inner cuticular wall showing the shape of the large cavities (arrows). Scale bar 50 µm; — (c) enlarged view of a fractured cavity showing type-1 and type-2 deeply sunken sensilla styloconica. Scale bar 10 µm; — (d) detail of a sensillum coelo-

the longitudinal axis of the antenna and measures about 15 μm in width and 70 μm in depth. It is very convoluted and hosts numerous type-1 and type-2 deeply sunken sensilla styloconica (Fig. 2c). Type-1 sensilla have a cone with cuticular 'fingers' in its distal portion (Fig. 2e). Type-2 sensilla have a cone with a fairly rugged cuticular surface (Fig. 2f). No pore is visible on the cuticle of either type-1 or type-2 sensilla (Figs 2e, f).

Cordulegaster boltonii (Cordulegastridae). — The antenna consists of a scape, a pedicel and an antennal flagellum of four segments. The first and the second flagellar segments show wide pits on their latero-ventral sides (Fig. 2g), with about 9 on the first segment and 3 on the second. Images of the inner cuticular wall reveal that the wide pits are the openings of convoluted cavities measuring about 20 μm in width and 20-30 μm in depth (Fig. 2h). Longitudinally fractured cavities show sensilla coeloconica located on the edge of the pits (Fig. 2h, i), and type-1 and type-2 deeply sunken sensilla styloconica inside the cavities (Figs 2j-k). The sensilla coeloconica bear pore-like structures on their surface (Fig. 2i). Type-1 sensilla have a cone with cuticular 'fingers' in its distal portion (Fig. 2j). Type-2 sensilla have a cone with a rugged cuticular surface (Fig. 2k). No pore is visible on the cuticle of either type-1 or type-2 sensilla (Figs 2j, k).

OBSERVATIONS UNDER TEM

Onichogomphus forcipatus (Gomphidae). — Longitudinal sections of one of the large cavities reveal the presence of type-1 and type-2 deeply sunken sensilla styloconica inside the cavity and sensilla coeloconica on its edge (Fig. 3a).

SENSILLA COELOCONICA. The sensilla coeloconica are innervated by three unbranched neurons (Figs 3c-e), whose outer dendritic segments enter the peg (Fig. 3e). The three dendrites are enveloped by the tormogen, the trichogen and the thecogen cell, this last secreting the dendrite sheath and containing a scolopale-like structure (Fig. 3c). The dendrite sheath ends at the base of the peg (Fig. 3b), and the dendrites are in contact with the sensillum lymph of medium electron-density (Fig. 3f). The cuticle of the peg shows wide pore-like structures,

conicum with pore-like structures (arrows) on the peg surface. Scale bar 2 μm; — (e) detail of type-1 and type-2 deeply sunken sensilla styloconica showing the stylus and the cone; arrow points to the cuticular fingers of the type-1 cone. Scale bar 2.5 μm; — (f) outer cuticular wall of the first (proximal) flagellar segment showing wide pits (arrows) on its latero-ventral side. Scale bar 20 μm; — (g) inner cuticular wall showing the shape of the cavities (arrows) corresponding to the pits. Scale bar 50 μm; — (h) fractured cavity showing deeply sunken sensilla styloconica (arrow); sensilla coeloconica are located on the edge of the pit. Scale bar 10 μm; — (i) enlarged view showing the pore-like structures (arrows) visible on the cuticle of sensilla coeloconica. Scale bar 5 μm; — (j) fractured cavity showing type-1 and type-2 deeply sunken sensilla styloconica; arrow points to the cuticular fingers of type-1. Scale bar 5 μm. — [Co: cone; — CS: coeloconic sensillum; — St: stylus; — T1: type-1 deeply sunken sensillum styloconicum; — T2: type-2 deeply sunken sensillum styloconicum]
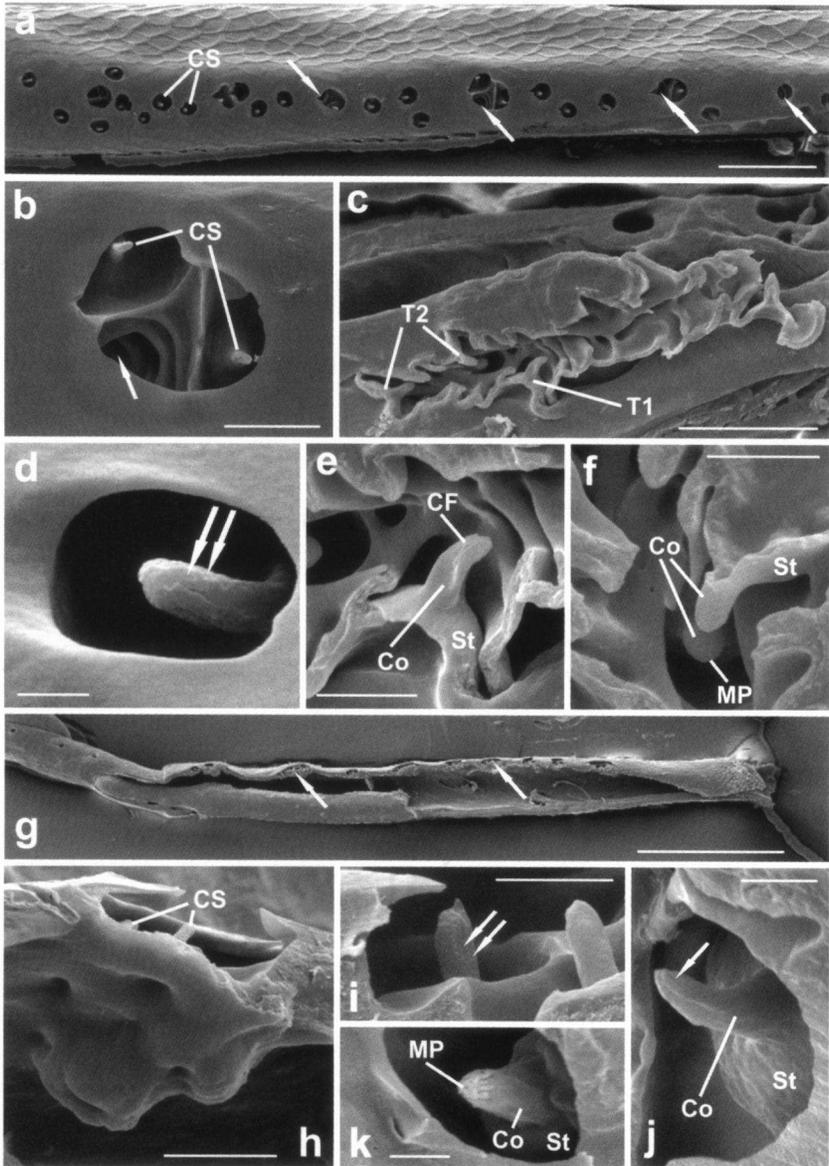
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Fig. 2. Antennal flagella of *Somatochlora metallica* (a-f) and *Cordulegaster boltonii* (g-k) under SEM: (a) outer cuticular wall of the first flagellar segment showing pits on its latero-ventral side containing sensilla coeloconica; some pits are the openings (arrows) of deep cavities hosting deeply sunken sensilla styloconica. Scale bar 50 μm; − (b) enlarged view showing sensilla coeloconica and the opening (arrow) of a deep cavity. Scale bar 10 μm; − (c) longitudinally fractured cavity showing type-1 and type-2 deeply sunken sensilla styloconica. Scale bar 20 μm; − (d) detail of a sensillum coeloconicum

at the base of which the continuity of the dense cuticulin layer is interrupted by actual pores (Fig. 3f). In the sensillum lymph, between the pores and the dendrites, pore tubules measuring about 20 nm in diameter, are clearly evident (Fig. 3f).

SENSILLA STYLOCONICA. – Type-1 sensilla styloconica are innervated by four unbranched neurons enveloped by the accessory cells (Figs 3g, h). The outer dendritic segments are enveloped by the dendrite sheath (Figs 3g-i), which disappears in the apical portion of the cone (Figs 3j, k). Three dendrites enter the cone of the sensillum while the fourth one ends before (Figs 3h-j). The accessory cells enter the stylus and produce an enormous number of electron-lucid vesicles strictly adhering to the dendrite sheath surrounding the outer dendritic segments (Figs 3g-i). At the apex of the cone, the cuticle forms cuticular fingers (Figs 3g, i-k). A cap-like structure, consisting of amorphous material, covers the apex of the dendrites (Figs 3g, j, k). The cuticular fingers surround the cap-like structure at the tip of the cone (Figs 3g, k). No socket and no pores connecting the dendrites with the outside are visible.

Type-2 sensilla styloconica are innervated by three unbranched neurons enveloped by the accessory cells (Figs 3l, m), the latter producing an electron-dense secretion interspersed among the microvilli of the labyrinth (Figs 3l, m). One (in some sensilla two) of the three dendrites stops before entering the cone. Thus two dendrites (Fig. 3p), (but in some sensilla only a single one, Figs 3n, o), enter the cone, where they are enveloped by a tightly adherent dendrite sheath in close contact with the surrounding cuticle. The cuticle of the cone is solid in its proximal portion (Fig. 3n) while it shows round holes in its distal portion (Figs 3o-p). The apex of the cone shows a rough cuticular surface and a central, plugged molting pore (Fig. 3q). No socket and no connection of the dendrites with the outside are visible.

No difference in the number and morphology of the described sensilla has been found in males and females of the four observed species.

with pore-like structures (arrows). Scale bar 2 μm; – (e) detail of a type-1 deeply sunken sensillum styloconicum with stylus, cone and apical cuticular fingers. Scale bar 5 μm; – (f) detail of two type-2 deeply sunken sensilla styloconica with stylus, cone and apical molting pore. Scale bar 5 μm; – (g) longitudinally fractured first flagellar article showing wide pits (arrows) on its latero-ventral side. Scale bar 200 μm; – (h) enlarged view showing the shape of a cavity located in correspondence of one of the wide pits; sensilla coeloconica are located on the edge of the pit. Scale bar 10 μm; – (i) detail of a sensillum coeloconicum with pore-like structures (arrows). Scale bar 5 μm; – (j) detail of a type-1 deeply sunken sensillum styloconicum with stylus, cone and apical cuticular fingers (arrow). Scale bar 2 μm; – (k) detail of a type-2 deeply sunken sensillum styloconicum with stylus, cone and the molting pore. Scale bar 2 μm. – [CF: cuticular fingers; – Co: cone; – CS: coeloconic sensillum; – MP: molting pore; – St: stylus; – T1: type-1 deeply sunken sensillum styloconicum; – T2: type-2 deeply sunken sensillum styloconicum]
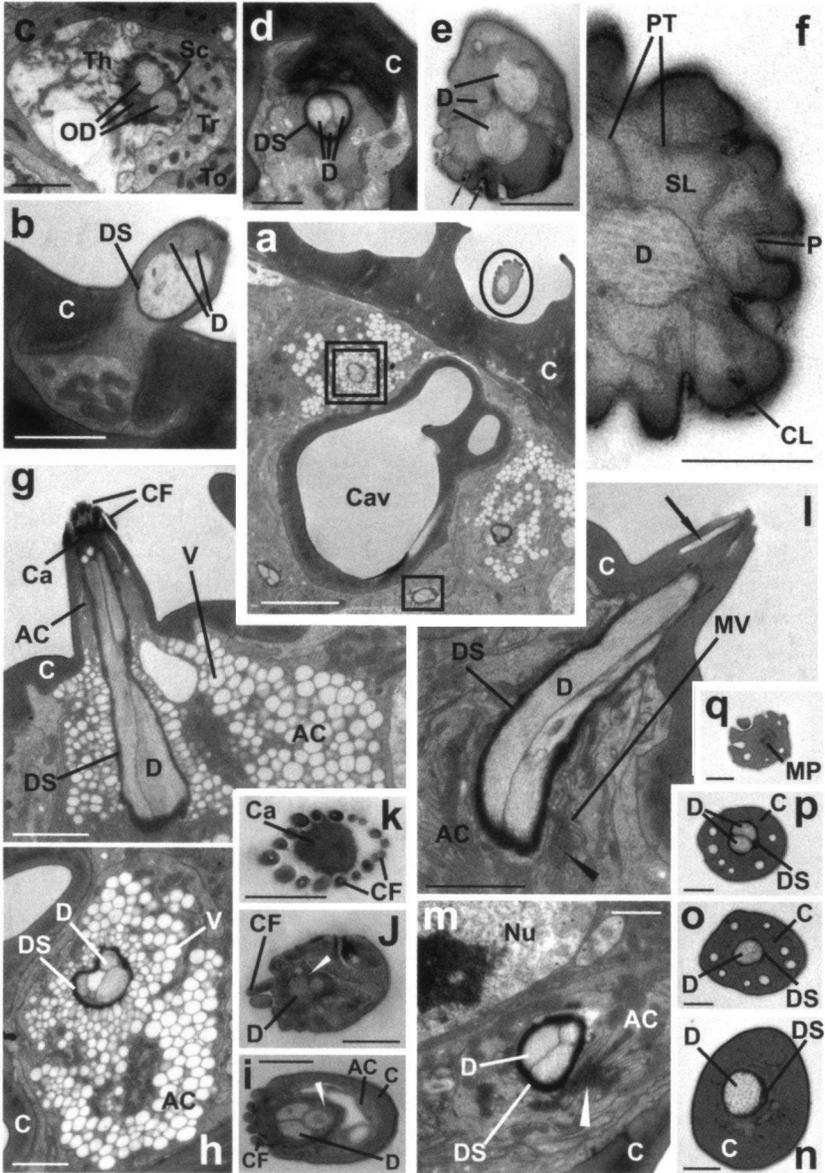
Fig. 3. Antennal flagellum of *Onychogomphus forcipatus* under TEM [a: cross section of the antennal flagellum at the level of a large cavity, − b-f: sensilla coeloconica, − g-k: type-1 deeply sunken styloconic sensillum, l-q: type-2 deeply sunken styloconic sensillum]: (a) note the coeloconic sensillum (circle) in longitudinal section on the antennal surface and the deeply sunken sensilla styloconica, type-1 (double square) and type-2 (square) in cross section. Scale bar 5 μm; − (b) sensillum coeloconicum

DISCUSSION

The present fine structural investigation of the flagellar sensilla of *Onychogomphus forcipatus*, *Aeshna cyanea*, *Somatochlora metallica* and *Cordulegaster boltonii*, revealed that sensilla are located in pits on the latero-ventral side of the first flagellar segments in all four species. These sensilla are represented by porous coeloconic sensilla and deeply sunken sensilla styloconica (type-1 and type-2), very similar to those described in *Libellula depressa* (REBORA et al., 2008).

The porous coeloconic sensilla are always visible on the antennal surface but their distribution differs in the different species. In the species belonging to the superfamily Libelluloidea (*S. metallica* and *L. depressa*) most of the pits containing the coeloconic sensilla are isolated. In the superfamily Aeshnoidea, two of the three analysed species (*C. boltonii* and *A. cyanea*) show coeloconic sensilla on the edge of the opening of the convoluted cavities, while in the third species,

in longitudinal section showing the dendrite sheath opening at the base of the peg and the dendrites entering the peg. Scale bar 2 μm; − (c) cross section at the level of the outer dendritic segments surrounded by the thecogen, trichogen and tormogen cells; the thecogen cell contains a scolopale-like structure. Scale bar 2 μm; − (d) cross section at the level of the outer dendritic segments surrounded by the dendrite sheath. Scale bar 1 μm; − (e) cross section at the level of the peg; note the dendrites without a dendrite sheath and the pore-like structures (arrows). Scale bar 1 μm; − (f) cross section at the level of the peg showing that the continuity of the cuticulin layer at the base of the wide pore-like structures is interrupted by actual pores; note the presence of pore tubules in the sensillum lymph. Scale bar 500 nm; − (g) longitudinal section showing the dendrites entering the cone, surrounded by the dendrite sheath. In the sensory cone the dendrites are in contact with a cap-like structure surrounded by cuticular fingers; note the large number of electron-lucid vesicles in the accessory cells. Scale bar 2 μm; − (h) cross section of the four dendrites at the level of the outer dendritic segments. Scale bar 2 μm; − (i) cross section of the proximal portion of the cone showing three dendrites entering the cone, surrounded by the dendrite sheath (arrow head); note the accessory cell. Scale bar 1 μm; − (j) cross section of the cone at a more distal level showing the dendrites, without dendrite sheath, surrounded by amorphous material (arrow head). Scale bar 1 μm; − (k) apical cross section of the cone showing the cap-like structure surrounded by cuticular fingers. Scale bar 1 μm; − (l) longitudinal section showing the dendrites entering the cone surrounded by the dendrite sheath. In the sensory cone the dendrites are in close contact with the cuticle; arrow points to the clefts in the cuticle; arrow head points to the electron-dense secretion in the accessory cells. Scale bar 2 μm; − (m) cross section of the three dendrites at the level of the outer dendritic segments surrounded by the dendrite sheath; arrow head points to the electron dense secretion in the accessory cells. Scale bar 1 μm; − (n) cross section of the cone showing one dendrite with the dendrite sheath strictly adhering to the surrounding cuticle. Scale bar 500 nm; − (o/p) subapical cross sections of the cone of two different sensilla showing one (o) and two (p) dendrites surrounded by the dendrite sheath in the sensory cone; note the round clefts in the cuticle. Scale bar 500 nm; − (q) apical cross section of the cone showing the central plugged molting pore. Scale bar 500 nm. − [AC: accessory cell; − C: cuticle; − Ca: cap; − Cav: cavity; − CF: cuticular fingers; − CL: cuticulin layer; − D: dendrites; − DS: dendrite sheath; − MP: molting pore; − MV: microvilli; − Nu: nucleus of the accessory cell; − OD: outer dendritic segments; − P: pores; − PT: pore tubules; − Sc: scolopale-like structure; − SL: sensillum lymph; − Th: thecogen cell; − To: tormogen cell; − Tr: trichogen cell; − V: vesicles]

O. forcipatus, coeloconic sensilla tend to be isolated, in pairs or associated with the very large cavities. This last species differs from the others also in consideration of the reduced number of the flagellomeres (two instead of four). In this regard, it is worth stressing that a molecular phylogenetic analysis of Anisoptera (MISOF et al., 2001), reports that all the morphologically recognized families are monophyletic and the Gomphidae are well differentiated from the others.

In all the analysed species the convoluted cavities always include the two kinds of sensilla styloconica. The cavities are variable in number and shape and are particularly developed in *O. forcipatus* where they host a high number of sensilla styloconica.

The internal structure of the sensilla of *O. forcipatus*, as a representative of Aeshnoidea, confirmed the fine structural characteristics already shown in *L. depressa* (REBORA et al., 2008) and revealed some additional details. Its porous coeloconic pegs are innervated by three unbranched dendrites, which enter the peg, the dendrite sheath ending at the base of the peg. The peg has no socket and its cuticle shows wide pore-like structures at the base of which the cuticulin layer is interrupted giving rise to actual pores. Pore tubules measuring 20 nm in diameter are clearly visible and closely resemble those described in the olfactory receptors of other insects (see review in STEINBRECHT, 1997). This confirms the attribution of the dragonfly coeloconic sensilla to single-walled olfactory sensilla. In no preparation of *L. depressa* was it possible to determine whether pore tubules were actually present in the sensillum lymph (REBORA et al., 2008).

The deeply sunken sensilla styloconica of *O. forcipatus* have no pores, an inflexible socket and unbranched dendrites in close association with the cone wall, showing features typical of thermo/hygroreceptors (reviews in ALTNER & LOFTUS, 1985, TICHY & LOFTUS, 1996, STEINBRECHT, 1998 and YOKOHARI, 1999). Likewise in *L. depressa* (REBORA et al., 2008), the accessory cells show secretory activity and contain electron-lucid vesicles in type-1 sensilla and electron-dense material in type-2 sensilla. In the type-1 sensilla of *O. forcipatus* there is a large number of electron-lucid vesicles tightly adherent to the dendrite sheath. This material, probably lipoid in nature, has been noted in other insect sensilla (ALTNER et al., 1977; BARTLET et al., 1999; BIN et al., 1989; McIVER, 1974). The location of thermo/hygroreceptors inside deep cavities on dragonfly antennae probably guarantees mechanical protection and acts as a buffering system from the outside air, protecting the sensilla against exposure to random changes in humidity and temperature.

The above reported data, together with the observations on the antenna of *L. depressa* (REBORA et al., 2008), allow us to forward the following considerations:

(1) Olfactory and thermo-hygrosensory sensilla are the main sensilla on the antennae of Anisoptera. Thus, the small antennae of dragonflies could play an important role in the biology of these insects. This role needs to be investi-

gated with behavioural and electrophysiological studies.

(2) The presence of thermo-hygroreceptors in a wide range of anisopterans is important, considering that dragonflies are typically heliothermic insects (MAY, 1976). The ability to perceive the microclimate conditions concerning temperature and humidity is probably crucial in regulating basking behavior. The structural differences of type-1 and type-2 deeply sunken sensilla, observed both in *L. depressa* and *O. forcipatus*, probably correspond to functional differences.

(3) The attribution of the coeloconic sensilla of dragonflies to single-walled olfactory sensilla (confirmed by the finding of pore tubules in *O. forcipatus*), together with their common presence in the suborder Anisoptera, is relevant for phylogenetic studies. Neuroanatomical studies on the insect brain have allowed researchers to hypothesize that paleopteran insects, such as Ephemeroptera and Odonata, are probably all anosmic with respect to airborne odors, because they lack glomerular antennal lobes, typically receiving olfactory receptor neurons in Neoptera, and mushroom body calyces, probably important for processing olfactory information (FARRIS, 2005; STRAUSFELD et al, 1998). Recent neuroanatomical studies on the ground plan of the insect mushroom bodies claim that Odonata possess a remnant calyx equipped with microglomeruli receiving inputs from visual neurons that may reflect the great importance of vision in the ecology of this group (SVIDERSKY & PLOTNIKOVA, 2004; STRAUSFELD et al., 2009). On the other hand, the protocerebrum lateral lobe of these insects is connected with the antennal nerve and could play an olfactory function according to PLOTNIKOVA & ISAVNINA (2006). Further physiological, behavioural and anatomical studies are necessary to shed light on this controversial field of research to ascertain the supposed ability of dragonflies to perceive odors.

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