



The mechanoreceptors on the endophytic ovipositor of the dragonfly *Aeshna cyanea* (Odonata, Aeshnidae)



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ABSTRACT

This study investigates the mechanoreceptors located on the cutting valvulae of the ovipositor of the dragonfly *Aeshna cyanea* (Aeshnidae), using both SEM and TEM, with the aim of providing an overview of the sensory equipment of an odonatan endophytic ovipositor. Four kinds of sensilla have been described. Notwithstanding their different external and internal morphology, they show features typical of mechanoreceptors. Three of them are evident along the external surface of the two cutting valvulae in the form of sub-spherical pegs, pit organs type 1 (holes) and pit organs type 2 (depressions), these last are similar to amphinematic scolopidia, while the fourth type is represented by subintegumental mononematic scolopidia having no direct relationship with the cuticle. In spite of their structural differences, the morphology of the described mechanoreceptors is consistent with performing a main role in allowing the perception of compression/stretching of the thick cuticle of the valvulae and their bending due to the pressure acting on the distal end of the ovipositor during substrate penetration. Such an organization is coherent with the need of endophytic Odonata to be able to evaluate the stiffness of the plant where to lay eggs.

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1. Introduction

In Odonata a cutting ovipositor is present in all the members belonging to the suborder Zygoptera, in the genus *Epiophlebia* (Anisozygoptera) and in the family Aeshnidae (Anisoptera), whereas this structure is strongly modified or reduced in the remaining Anisoptera. Species with a cutting ovipositor lay their eggs endophytically (endophytic ovipositor) while exophytic oviposition is inherent to the anisopterans with modified or reduced ovipositor, designed to drop the eggs in water or to attach them superficially onto water plants or other periaquatic objects (Corbet, 1999). The endophytic oviposition is assumed to be a plesiomorphic feature of Odonata (Bechly et al., 2001), as proved by traces on the deposits of fossil plants documented in Eocene (Sarzett et al., 2009), Oligocene (Petrulevičius et al., 2011) and recently also from early Mesozoic (Moisan et al., 2012).

The endophytic ovipositor of Odonata is formed by three paired valvulae, leaf-like appendages of abdominal segments, two of which are used as cutting instruments (V1 = lower, V2 = upper), whereas the third pair (V3) forms a sheath protecting the first two pairs and bears a mobile process, called the stylus, at its posterior

edge. The two cutting valvulae on each body side are interconnected by a sliding joint (Matushkina and Gorb, 1997, 2007).

Matushkina and Gorb markedly contributed to an improvement of the knowledge on female genitalia in Odonata. These authors have mainly explored the function and major muscular connections as well as the morphology, the function and the development of the odonatan ovipositor (Matushkina, 2008, 2011; Matushkina and Gorb, 1997, 2002a, 2002b, 2007). A detailed study of the exoskeleton and musculature of the middle and posterior abdomen of ovipositor-bearing Odonata has been published by Klass (2008).

As far as the sensory equipment of the odonatan ovipositor is concerned, light and scanning electron microscopy and behavioral investigations demonstrated the presence of campaniform sensilla (mechanoreceptors), located on the base of the stylus, the mobile process of V3, that are involved in controlling egg positioning in clutches in two damselflies, *Lestes sponsa* and *Lestes barbarus* (Lestidae) (Matushkina and Gorb, 2002a). Likewise, campaniform sensilla have been mentioned on the cutting valvulae (V1 and V2) of *Lestes macrostigma* (Matushkina and Lambret, 2011) and *Epiophlebia superstes* (Matushkina, 2008). In these two papers, the presence of mechanoreceptors and chemoreceptors on the ovipositor has been only hypothesized on the basis of their external morphology (Matushkina and Lambret, 2011).

A recent investigation under SEM and TEM (Reborá et al., 2013) revealed the fine structure of coeloconic sensilla located on the

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cutting valvulae of the endophytic ovipositor of two Odonata species, the anisopteran *Aeshna cyanea* (Aeshnidae) and the zygopteran *Ischnura elegans* (Coenagrionidae). In both species these coeloconic sensilla are innervated by four unbranched neurons forming four outer dendritic segments enveloped by dendrite sheath. One dendrite terminates at the base of the peg forming a well developed tubular body, while the other three enter the peg after interruption of the dendrite sheath. The cuticle of the peg shows an apical pore and a joint membrane. The ultrastructural organization of these coeloconic sensilla is in agreement with their belonging to gustatory sensilla.

The present study investigates the other sensory structures located on the cutting valvulae of the ovipositor of the dragonfly *A. cyanea* (Aeshnidae), using both SEM and TEM, with the aim of providing an overview of the sensory equipment of an odonatan endophytic ovipositor.

2. Material and methods

Adults of *A. cyanea* (Aeshnidae) were collected along a natural pond in Lisciano Niccone (Perugia, Central Italy) in June–July 2011. In the laboratory, 10 ovipositors (V1 and V2 valvulae) were dissected from anesthetized specimens and fixed for 12 h in 2.5% glutaraldehyde in cacodylate buffer, pH 7.2.

For scanning electron microscopy (SEM) analysis, the fixed material was repeatedly rinsed in the same buffer, and then dehydrated by using ethanol gradients, followed by critical-point drying in a critical-point dryer CPD 030 Bal-Tec (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 (Philips, Eindhoven, The Netherlands), at an accelerating voltage of 18 kV.

For transmission electron microscopy (TEM), the fixed ovipositors were repeatedly rinsed in cacodylate buffer and post-fixed for 1 h at 4 °C in 1% osmium tetroxide in cacodylate buffer. The samples were then repeatedly washed in the same buffer, dehydrated by using ethanol gradients and finally embedded in an Epon–Araldite mixture resin. Afterward, ultrathin sections were cut on a Leica EM UC6 ultracut (Leica Microsystems GmbH, Wetzlar, Germany), collected on collodium-coated copper grids, stained with uranyl acetate and lead citrate, and examined with a Philips EM 208 (Philips, Eindhoven, The Netherlands).

Transversal semithin sections stained with methylene blue were observed and photographed under light microscope in order to have an idea of the shape of the valvulae and of the thickness of their cuticle.

3. Results

Adult females of *A. cyanea* show a very developed ovipositor, with the cutting valvulae V1 and V2 showing a total length of about 5–6 mm (Figs. 1 and 6) and a total width of about 1 mm in their proximal portion. The cuticle of the valvulae tends to be thicker along their outer side (about 10–15 µm) and thinner along their inner side (about 5 µm) but in some areas it reaches a thickness of about 30 µm (Fig. 1d). A longitudinal groove (aulax) on V1 provides a sliding articulation with V2 (Fig. 1d).

The outer surface of V1 is fairly smooth along all its length with a longitudinal ridge in its distal portion (Fig. 1a); the cuticle of V2 is smooth in its proximal portion whereas in its distal portion a sequence of ridges gives it a rough appearance (Fig. 1b).

Under SEM both valvulae show numerous cuticular decorations along their outer surfaces (Fig. 1a,b). These structures are represented by sensilla coeloconica (Fig. 1c) whose internal structure is

in agreement with a gustatory function (see Rebora et al., 2013); they are mainly located on the distal third of the ovipositor, they show a reduced number in comparison with mechanoreceptors and are more numerous on V1 than on V2 (Fig. 6). Other cuticular sensilla are visible on the outer surfaces of V1 and V2 as pegs, pit organs type 1 (holes) and pit organs type 2 (depressions) (Figs. 1c and 6).

The pegs are sub-spherical structures set in circular pits, with a wide pore-like depression in their center (Figs. 1c and 2a). They have a diameter of about 2.5 µm, are located along the whole length of the valvulae and represent the most numerous kind of sensillum on both valvulae (Fig. 6). In longitudinal section, the pegs reveal their internal structure, consisting of a long structure (about 8 µm) inserted deeply in the thick cuticle of the ovipositor (Fig. 2b–d). The sensory cuticle of the peg (the modified cuticle allowing the transduction of the signal) is well distinguishable from the cuticle of the ovipositor because of a different electron density and texture that shows scattered crevices (Fig. 2b–e). The pore-like depression in the center of the peg is not an actual pore (inset of Fig. 2b), but a slight depression due to the infolding of the outermost cuticular border. No joint membrane is clearly visible (Fig. 2b–d). At the insertion of the peg, a neuron, the outer dendritic segment of which shows a tubular body enveloped by a well developed dendrite sheath, is visible (Fig. 2b–e). The neuron is connected to the sensory cuticle by the intermediate of well developed suspension fibers (Fig. 2b–e). At a lower level, the neuron is surrounded by the accessory cell and the sensory cuticle (Fig. 2f). Proceeding downward, the sensory cuticle disappears and the neuron equipped with the dendrite sheath and the accessory cells reaches the epidermal layer (Fig. 2g). In Fig. 2h a schematic reconstruction of the internal structure of the peg is reported.

The pit organs type 1 (holes) measure about 1.5 µm in diameter (Figs. 1c and 3a) and are randomly distributed along the whole length of the valvulae (Fig. 6). They are less numerous than the pegs but more numerous than the other kinds of sensilla (Fig. 6). In longitudinal section it becomes evident that the holes represent the openings of cavities (length of about 6.5 µm) in the thick cuticle of the ovipositor (Fig. 3b). At the base of each cavity, a sensory cuticle with a loose texture (well distinguishable from the cuticle of the ovipositor because of its different electron density) is visible, together with the anchoring of an outer dendritic segment (Fig. 3b–d). At a lower level, the outer dendritic segment shows a tubular body enveloped by a dendrite sheath (Fig. 3e). The neuron is connected to the sensory cuticle by the suspension fibers (Fig. 3f). The dendrite sheath is very pleated and penetrates deeply inside the outer dendritic segments (Fig. 3g). The outer dendritic segment, surrounded by the dendrite sheath and the outer and inner accessory cells, is enveloped by the sensory cuticle that extends for a long tract inside the cuticle of the ovipositor (Fig. 3g). In Fig. 3h a schematic reconstruction of the internal structure of the pit organ type 1 is reported.

The pit organs type 2 are visible along the two cutting valvulae in the form of small depressions, measuring about 1.5, 2 µm in diameter (Figs. 1c and 4a). Their number and distribution are difficult to assess because they are not always well distinguishable on the external surface of the valvulae (Fig. 6). Under SEM we could distinguish a low number of these sensilla especially located in the distal portion of the valvulae but it is possible that they are much more numerous (indeed under TEM we observed many sensilla with similar features) (Fig. 6). In section, they show morphological details similar to those of amphinematic scolopidia. Indeed they have a neuron whose outer dendritic segment shows a type 2 cilium with a $9 \times 2 + 0$ arrangement of microtubules in the axoneme (Fig. 4b). The scolopale cell surrounds the cilium and joins upon itself to form a mesaxon (Fig. 4b). Scolopale rods are visible

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