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Sensilla and cuticular structures on the larval caudal appendages of *Erythromma lindenii* (SÉLYS, 1840) (Odonata: Zygoptera: Coenagrionidae)

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Abstract

The cuticular structures and the sensilla on the larval caudal appendages (caudal lamellae) of *Erythromma lindenii* have been studied using scanning electron microscope. Four types of sensilla are visible on the external face of the two lateral lamellae and both faces of median lamella. The aporous sensilla filiformia are vibroreceptors which detect a predatory or hostile presence. The aporous sensilla campaniformia are proprioceptors which may play the role of osmoreceptors here. An olfactive function is presumed for the multiporous sensilla coeloconica and a tactile function for the aporous spatula-shaped sensilla chaetica. The sensilla filiformia and the sensilla campaniformia have already been described on the caudal lamellae of Odonata. The sensilla coeloconica and the spatula-shaped sensilla chaetica are observed for the first time on these appendages.

Key words: Odonata, *Erythromma*, caudal appendage, sensilla, campanoformium, filiformium, coeloconicum, spatula-shaped chaeticum.

Résumé

Les structure cuticulaires et les sensilles situées sur les appendices caudaux, ou lamelles caudales, d'*Erythromma lindenii* sont étudiées à l'aide de la microscopie électronique à balayage. Quatre types de sensilles sont présents à la face externe des lamelles latérales et sur les deux faces de la lamelle médiane. Les sensilles filiformes sans pore sont des vibrorécepteurs qui détectent la présence d'un prédateur ou d'un ennemi. Les sensilles campaniformes sont des propriocepteurs qui peuvent jouer ici le rôle d'osmorécepteurs. Une fonction olfactive est présumée pour les sensilles coeloconiques multipores et une fonction tactile pour les sensilles chétiformes sans pore en forme spatule. Les sensilles filiformes et campaniformes ont déjà été décrites sur les lamelles caudales des odonates. Les sensilles coeloconiques et les sensilles chétiformes en forme de spatule sont observées pour la première fois sur les appendices.

Mots-clés: Odonates, *Erythromma*, appendice caudal, sensilles, campaniforme, filiforme, coeloconique, chétiforme en forme de spatule.

Introduction

Little is known about the structure, diversity and function of mechanoreceptors in dragonfly larvae (CORBET, 1999). The larval antennal of Zygoptera are only now beginning to be studied. In *Erythromma lindenii*, they possess mechanoreceptors of various types: sensilla filiformia, sensilla campaniformia, spatula-shaped sensilla chaetica and curved sensille chaetica (FAUCHEUX, 2006; MEURGEY & FAUCHEUX, 2006). As regards the caudal appendages, seceral functions have attributed to them. They may be used for swimming, some of them are important respiratory organs. They also have the facility to be autotomized, enhancing the survival of larvae in the presence of predators or aggressive conspecifics. In certain species, the caudal appendages perform an adhesive function, or they can be used to detect vibrations (CORBET, 1999). Indeed, a recent study carried out on the lamellous caudal appendages of *Lestes sponsa* reveals the presence of aporous sensilla filiformia, acting as vibration receptors, and aporous sensilla campaniformia which are proprioceptors with a presumed osmoreceptive function (FAUCHEUX, 2005). The aim of the present study is to discover the existence of the above mentioned sensilla in another zygopteran odonatan, *Erythromma lindenii* (SÉLYS, 1840) whose antennal sensory equipment is known (FAUCHEUX, 2006; MEURGEY & FAUCHEUX, 2006).

Material and methods

The larvae of *E. lindenii* were taken from a pond at "l'Île Neuve, Le Cellier, Loire-Atlantique (44), France" on 15-VI-2003. For the study with scanning electron microscope (S.E.M.), the caudal appendages of three larvae were separated from the abdomen, dehydrated

in absolute ethanol, mounted both on the external and internal face, on specimen holders and coated with a thin layer of gold and palladium in a JFC 1100 sputter coater. Preparations were examined in a Jeol JSM 6400 SEM at different magnifications. The terminology of SCHNEIDER (1964) and ZACHARUK (1985) is used in naming the types of sensilla.

Results

A — Gross morphology and cuticular structures of caudal appendages.

According to the classification of caudal appendages of larval Zygoptera in relation with shape and posture, and habitat (TILLYARD, 1917; DAVIES & TOBIN, 1984), the appendages of *E. lindenii* are of type D: lamellate and are held in the vertical plane (GARDNER, 1954). The shape and posture of caudal lamellae correlate within the larval habitat which is lentic permanent in *E. lindenii.*

There are three caudal lamellae: two lateral and one median. An axial trunk divides each lamella into an upper and a lower one (Figs 1, 3, 4). When the lamellae are held vertically, it is possible to distinguish both a dorsal and a ventral edge. Each lateral lamella possesses an external and internal face; the axial trunk resembles a kind of ridge which is convex on the external face and flattened on the internal one (Figs 1, 4).

Strong spines, from 45 to 55 µm long, articulated on a cylindrical base of 30 µm, are located on the ventral margin of each lamella, except for the distal third, and totality of axial trunk (Fig. 1). They overlap and two longitudinal rows of spines can be observed side by side (Figs 1, 2). In the median region of the lamellae, they are more widely spaced (Fig. 3). The dorsal margin is without spines (Fig. 4). The axial trunk is smooth on the internal face of lamellae (Fig. 5). The external surface of lamellae also possesses spines, but only in the proximal region; the spines are much thinner and of variable length, although most of them do not exceed that of half of the previous spines (Fig. 1). Apart from the region with spines, the cuticle shows alveolar structures which are visible both in the lower part and in the upper part of lamellae (Figs 3, 5). When enlarged, the cuticle reveals a reticulous pattern (Fig. 7).

B — The different types of sensilla

Four types of sensilla are present on both faces of lamellae

Aporous spatula-shaped sensilla chaetica

The aporous spatula-shaped sensilla chaetica have the shape of a hair 20µm long, cylindrical at the base, then widening to form a hollowed spatula on the external face, terminating in an excrescence (Fig. 6). The base with a diameter of 2.3 µm is located in a narrow internal cavity of 3 µm in diameter, surrounded by a semi-circular depression of 4.5 µm which limits the movement of the hair. No pore was observed at the apex or on the wall. All the sensilla are oriented towards the distal extremity of the lamellae.

Aporous sensilla filiformia

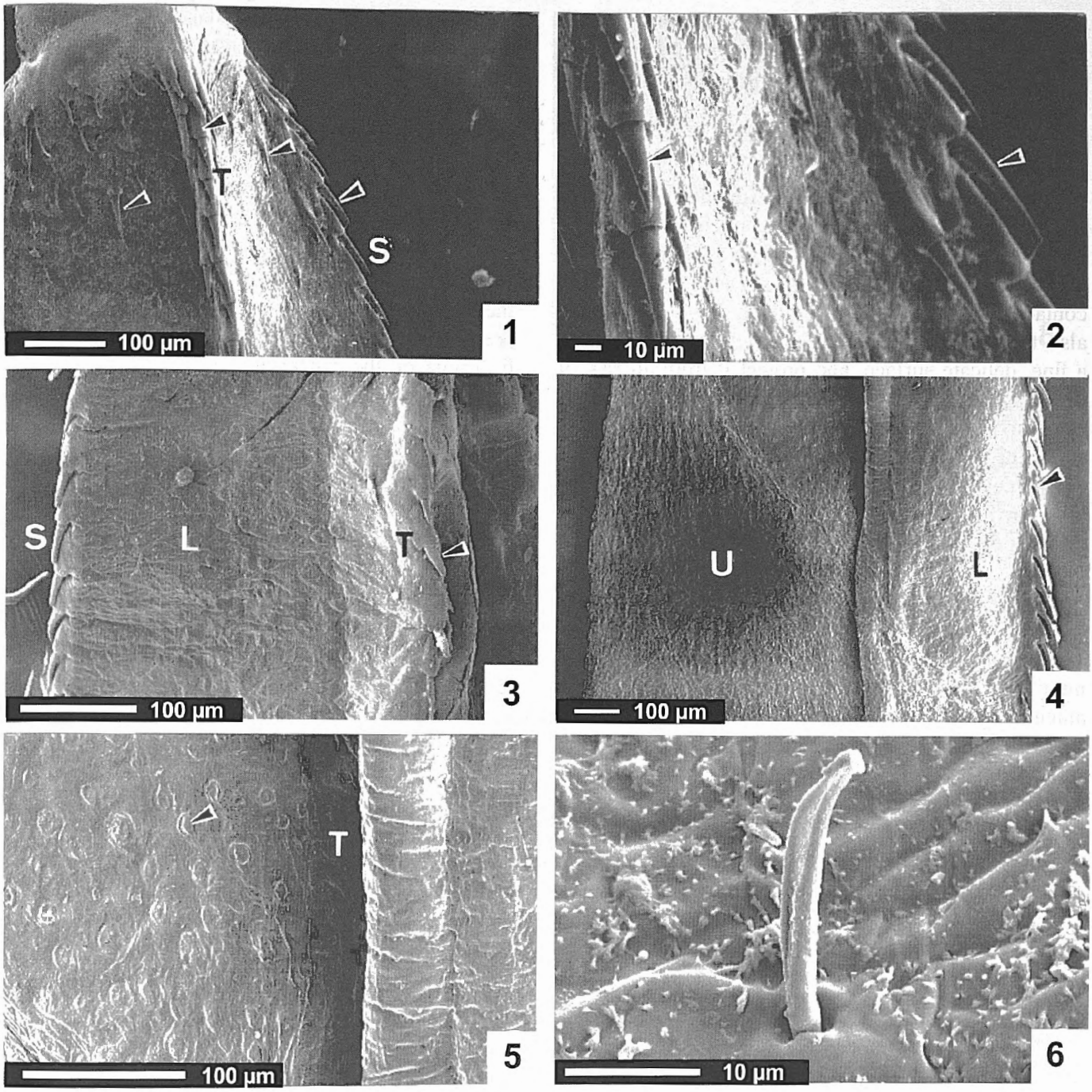
The aporous sensilla filiformia are very long, slender sensilla, measuring from 45 µm to 90 µm in length (Figs 7, 8) and retain a diameter of 1 µm over the whole of their length apart from the apex and the base (Fig. 9). Unlike the sensilla filiformia of terrestrial insects, they are not very rigid and adhere to the cuticle of lamellae when out of water or when being prepared for the study in SEM. Their base is located in a narrow aperture of roughly the same diameter of the sensillum, pierced in a flat bottomed membrane of flexible aspect, which is itself bordered by a circular fold, the whole is surrounded by a thick cuticular ring (Fig. 9). The sensillum wall is without pores.

Aporous sensilla campaniformia

The aporous sensilla campaniformia of lamellae are recognisable thanks to the star-shape of the cuticular reticulum around their dome (Fig. 7). This dome, 5 µm in diameter, is slightly convex and delicately granulous (Fig. 10). It also possesses a central hollow closed by a globulous papilla of 200 µm in diameter (Fig. 11). The sensillum appears to be embedded in the cuticle of the lamellae. The characteristic ring of the sensilla campaniformia has an outer diameter of 7 µm and is difficult ro distinguish from the surrounding cuticular furrows (Fig. 10).

Multiporous sensilla coeloconica

The multiporous sensilla coeloconica can at first sight be confused with pores (Fig. 7), but they differ by their convex cupula shape, 1.8 µm in diameter, and their internal aperture measuring 0.8 µm. The structure inside the cavity is difficult to identify. Their general form makes us classify them with the coeloconicum type (ZACHARUK, 1985).



Figs 1-6 — 1-6: structures and sensilla on the caudal appendages of *Erythromma lindenii*. **1.** base of lateral lamella showing noninnervated spines (s. arrows) on the external surface, the axial trunk (T) and the ventral margin. **2.** detail of Fig. 1. **3.** median region of lamella seen on the external face with spines (S) on the margin and axial trunk, and the lower part without spines. **4.** internal face of lamella in the median region showing the upper part (U), the lower part (L) and the trunk without spines. **5.** detail of Fig. 4 showing the alveola pattern of the upper part (arrow). **6.** spatula-shaped sensillum chaeticum on the external face of lamella.

Distribution and numbers of sensilla

The four types of sensilla are present on the three lamellae, they are slightly more numerous on the external face of lateral lamellae and exist in equivalent numbers on the two faces of median lamella. The sensilla are distributed without clear pattern and always in limited numbers; for example, Fig. 7 presents only three sensilla which belong to different types. If the spatula-shaped sensilla chaetica are oriented towards the distal end of lamellae, the sensilla filiformia adopt very varied orientations. Counting the sensilla on the external

face of a lateral lamella produced the following results: 3 spatula-shaped sensilla chaetica, 5 sensilla filiformia, 3 sensilla campaniformia and 4 sensilla coeloconica.

Discussion

The spines are too numerous, too regularly distributed and too close to one another to be confused with sensory organs. When the larva is placed on a pond bed or on a plant, the spines on the margin of lamella come into contact with the substrate to which they adhere; they also thicken and rigidify the lamella, which presents a fine, delicate surface, and protect it from all risk of deterioration. The spines located on the external face of the axial trunk of the two lateral lamellae probably also have a protective function. It is significant that the axial trunk is spineless on its internal side, indeed, if this were not the case, two adjacent lamellae could be in danger of intertwining.

Spatula-shaped aporous sensilla chaetica

The spatula-shaped sensilla are present in great numbers on both faces of the scape and pedicel of the antenna of *E. lindenii* (Faucheux, 2006). According to their morphological characteristics, they are mechanoreceptors which are stimulated by direct contact. Since they exist on the three caudal lamellae, the lamella's sensilla are stimulated by contact with a neighbouring lamella that happens to be too close. Thus, these sensilla seem to allow the larva to keep its lamellae well separate, and therefore more efficient. In the present case, the spatula-shaped sensilla appear to possess a proprioceptive function.

Aporous sensilla filiformia

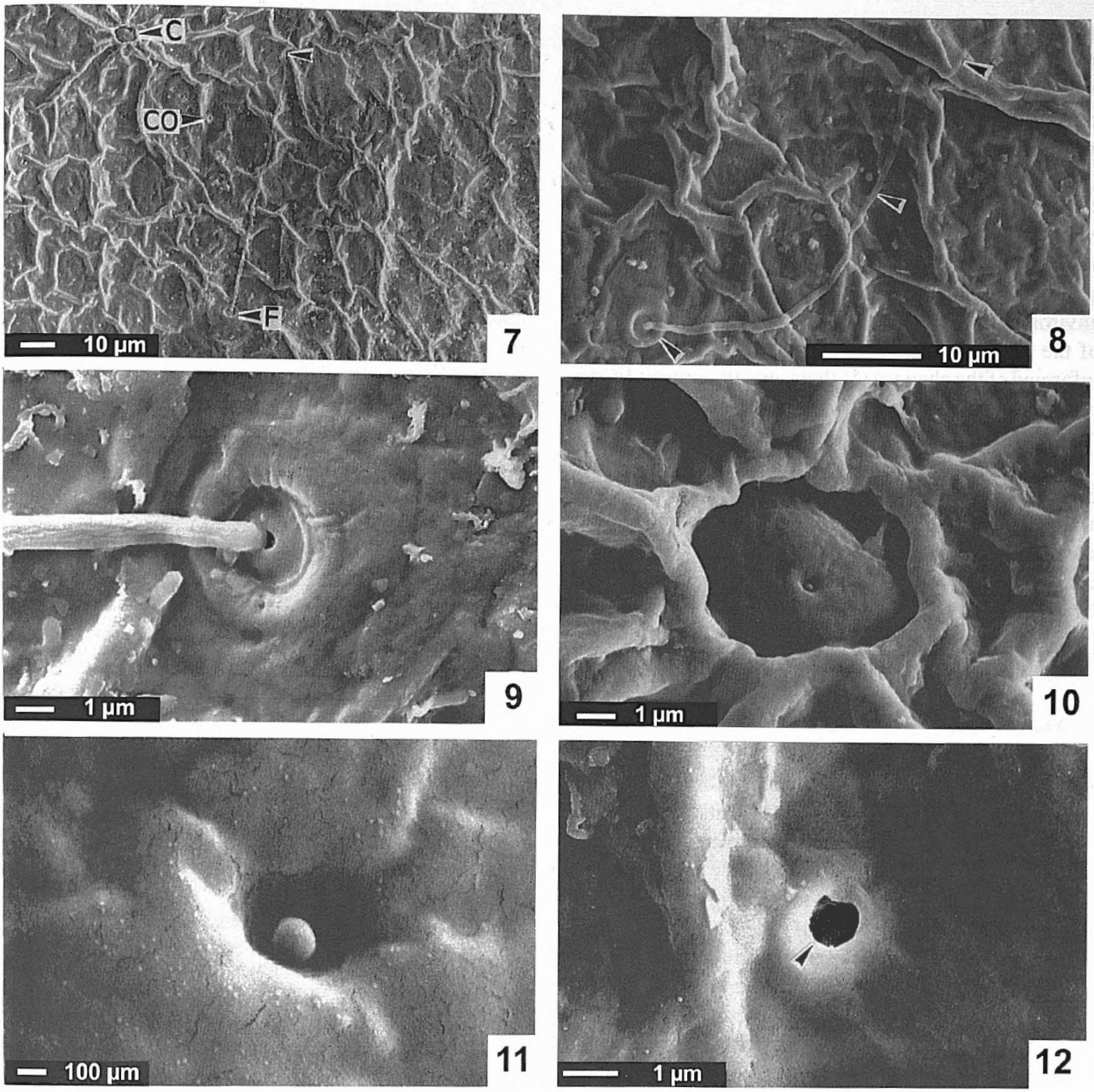
The sensilla filiformia in terrestrial insects are known to be vibroreceptive, they are deflected by faint air currents and low-frequency sounds or medium vibrations (GNATZY & TAUTZ, 1980). They occur on the cerci of cockroaches (GNATZY, 1976), crickets (GNATZY & SCHMIDT, 1971), earwigs (FAUCHEUX, 1999a) and embiids (FAUCHEUX, 2002), and the antennae of bugs (MCIVER & SIEMICKI, 1984). The have recently been discovered in aquatic insects, on the larval caudal appendages of *Lestes sponsa* (FAUCHEUX, 2005), the larval antennae of *Chalcolestes viridis* (FAUCHEUX & MEURGEY, 2006) and of *E. lindenii* (FAUCHEUX, 2006) Their distribution on the surface of caudal lamellae varies according to species, they are located on the external face of lamellae held vertically, like those of *E. lindenii* whereas they are regularly laid out on the edge of horizontal lamellae as in *L. sponsa* (FAUCHEUX, 2005). According to VASSEROT (1957), mechanoreceptors on the antennae of *Calopteryx splendens* detect vibrations in the water, but the sensilla were not figured. Later, fine setae have been described on the dorsal surfaces of the antennae, tibiae and tarsi of *Xanthocnemis zealandica* (ROWE, 1994); they are apparently mechanoreceptors which mediate prey detection within a space around each of these appendages (CORBET, 1999). In *E. lindenii*, the antennal sensilla filiformia probably function during prey detection (FAUCHEUX, 2006) whereas the sensilla filiformia on the caudal appendages would appear to warn larvae of the rearward approach of a predator. Indeed, it is the latter role which is carried out by the caudal appendages of terrestrial insects such as the cerci of cockroaches (FÜLLER & ERNST, 1977) or crickets (GNATZY & TAUTZ, 1980) in which the stimulation of cercal filiform hairs provokes the behaviour of excape.

One particular difference distinguishes the sensilla filiformia of antennae from the same sensilla on the caudal appendages of *E. lindenii*. On the antennae, they constitute three types (short, median or long sensilla) and they should be capable of responding to a wide spectrum of frequencies as has in particular been shown in the cricket *Gryllus bimaculatus* (SHIMOZAWA & KANOU, 1984). The existence of a single type of sensilla filiformia on the caudal appendages of the odonatan larva is probably related to a situation of urgency (flight) which appears not to require various types of sensilla. The slightest unusual stimulation of sensilla filiformia no doubt provokes the reflex of flight.

In the rare larvae of odonatans whose sensilla have so far been studied, the sensilla filiformia exist both on the antennae and the caudal appendages: *E. lindenii* (FAUCHEUX, 2006; this paper), *Chalcolestes viridis* (FAUCHEUX & MEURGEY, 2006; personal observations). Their presence is fully justified only in larvae living in a calm aquatic environment in which the slightest perturbation will be detected; this is the case of the two zygopteran species previously mentioned. To confirm this hypothesis, we propose to enquire subsequently into their possible presence in the anisozygopteran insect, *Epiophlebia superstes*, which lives in streams in Japan.

Aporous sensilla campaniformia

The sensilla campaniformia on the caudal appendages of *E. lindenii* are morphologically different both from those located on the antennae of the same species (FAUCHEUX, 2006), and from those situated on the



Figs 7-12 — Sensilla on the caudal appendages of *Erythromma lindenii*, located on the external face. **7.** reticulated aspect of cuticle with sensilla campaniformium (C)., coeloconicum (CO), filiformium (F, arrow). **8.** sensillum filiformium. **9.** base of sensillum filiformium. **10.** sensillum campaniformium. **11.** globulous papilla closing the molting channel of sensillum campaniformium. **12.** sensillum coeloconicum.

caudal appendages of *L. sponsa* (Faucheux, 2005). In these two examples, they are typical and possess a concentric broad cuticular bulge. Now, this annular structure is barely visible (Fig. 10) no doubt because of the reticulated and wrinkled aspect of the integument of the caudal lamellae. Furthermore, in hemimetabolan insects, such as the Odonata, the dendrite sheath of sensilla campaniformia is inserted in the cuticle of the dome, often running through a special channel in the cuticle, called the "molting channel" (Keil, 1997). The closing molting channel usually is visible in the center of the cap of sensilla. It so happens that the molting channel is absent in the caudal sensilla of *L. sponsa* and the antennal sensilla of *E. lindenii*. It is visible, in the form of a cavity, on the pedicellar sensillum of adult odonat *Brachythemis leucosticta* (Faucheux, unpublished). The presence of a globulous papilla closing the molting channel of sensilla campaniformia

on the caudal lamellae of *E. lindenii* has so far not been reported.

As concerns their function, the sensilla campaniformia are proprioceptors which are found whenever mechanical deformations of the cuticle occur (GNATZY *et al.*, 1987; GRÜNERT & GNATZY, 1987). The register all degrees of compression or extension which occur on the body's surface. The caudal appendages, which represent a relatively large lamellar surface, are exposed to the osmotic pressure of the aquatic environment, probably to a greater degree than the rest of the body. When this pressure varies, the larvae are informed of the changes via their sensilla campaniformia which perform the function of osmoreceptors and, as a result, they can adapt their behaviour to these variations in the environment. This possible fucntion of sensilla campaniformia is important for an aquatic animal and justified their permanent presence in the studied species (*L. sponsa* and *E. lindenii*). If the sensilla campaniformia of the caudal appendages in zygopteran larvae are really osmoreceptive, it is only to be expected that their number should differ between species living in streams with different levels of osmotic pressure.

Multiporous sensilla coeloconica

The sensilla coeloconica are observed for the first time on the caudal lamellae of larval Odonata. They do not resemble typical sensilla coeloconica in insects, for their internal cuticular structure is not very characteristic. In this sense, they are close to the cupuliform organs present on the antennae of the sunflower moth (FAUCHEUX, 1992), neopseustid moths (FAUCHEUX *et al.*, 2006) and of a carabid beetle, *Ceroglossus buqueti* (JAFFREZIC & FAUCHEUX, 2006). The sensilla coeloconica of insects are usually olfactive chemoreceptors (ZACHARUK, 1985).

To attribute an olfactive function to caudal sensilla coeloconica of *E. lindenii* is curious but not surprising. Indeed, several cases of olfactive or gustative sensilla have recently been described on the ovipositors of lepidopteran insects (FAUCHEUX, 1988, 1999b; BANGA *et al.*, 2003).

Comparison with the antennal sensilla of E. lindenii

The antennae and the caudal lamellae of *E. lindenii* possess in common the sensilla filiformia, sensilla campaniformia and spatula-shaped sensilla chaetica. On the two types of appendages, the sensilla filiformia are vibration receptors. The sensilla campaniformia belong to two different subtypes and do not have the same function. On the antennal pedicel, as on that of most adult insects, the single sensillum campaniformium is a proprioceptor which assures the correct disposition of the flagellum as regards the pedicel. On the caudal lamellae, the sensilla campaniformia perform rather the function of osmoreceptors. The function of the spatula-shaped sensilla chaetica is probably proprioceptive in the two types of appendages. However, two sensillum types are specific to one or other of the appendages. The antennal curved sensilla chaetica act as proprioceptors for positioning the flagellomeres in relation to one another (FAUCHEUX, 2006). The sensilla coeloconica of caudal lamellae seem to possess an olfactive function.

Conclusion

A study in transmission electron microscopy is necessary to examine more closely and confirm the results obtained with the scanning electron microscope. As it is, two particular types of mechanoreceptors are common to the small number of species described, these are the sensilla filiformia and campaniformia. The presence of sensilla coeloconica in *E. lindenii* supposes a possible olfactive function carried out by the caudal appendages.

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