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VIBRORECEPTORS AND PROPRIOCEPTORS ON THE LARVAL ANTENNAE OF *ERYTHROMMA LINDENII* (SÉLYS) (ZYGOPTERA: COENAGRIONIDAE)

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The larval antennae of *E. lindenii* are short and made up of a scape, a pedicel and a fourth-segmented flagellum. They bear four types of aporous and exclusively mechanoreceptive sensilla: spatula-shaped sensilla chaetica, curved sensilla chaetica, sensilla filiformia and sensilla campaniformia. The curved sensilla chaetica are proprioceptors which monitor the relative position of the 3rd and 4th flagellomeres. Sensilla filiformia are vibration receptors which play the major role in prey detection. The unique sensillum campaniformium on the pedicel is a proprioceptor which informs the larva of the position of the flagellum relative to the pedicel. Spatula-shaped sensilla chaetica are tactile receptors distributed on the scape and the pedicel. No chemoreceptive sensilla has been observed on the antennae.

INTRODUCTION

Structure, diversity, and function of mechanoreceptors in dragonfly larvae has been studied by several authors (PILL & MILL, 1979, 1981; MILL & PILL, 1981; LAVERACK, 1976; IVANOV, 1978a, 1978b; FINLAYSON & LOWENSTEIN, 1958) and two synthesis by MILL (1976, 1982) gave an overview of dragonfly neurobiology. Concerning prey capture there are studies on *Calopteryx splendens* by VASSEROT (1957) and CAILLERE (1968), *Cordula shurtleffi* by PRITCHARD (1965) and of *Xanthocnemis zealandica* by ROWE (1994). When resting, the antennal segments of a larva of *C. splendens* are not quite in line. When a prey is detected, the antennae, now parallel, point to the prey and the larva moves towards it. When the larva reaches the prey, the antennae bend, apparently examining the prey's size and orientation. During prey capture, which includes protraction of the labrum, this protraction is preceded by the antennae being raised and spread to the greatest extent. After prey ingestion and cleaning of the mouthparts, the antennae are aligned sagitally and the scapes diverge slightly. Thus, in the predatory sequence, the antennae take up various positions, their segments being either in line, or curved towards the prey. Mechanoreceptors controlling the position of the antennae are therefore liable to intervene.

The present work on the fine structure of the antennal sensilla of final instar larvae of *Erythromma lindenii* (Sélys) was undertaken to aid our understanding of the sensory basis of odonate larval behaviour.

MATERIAL AND METHODS

The larvae were taken from a pond at l'Île Neuve, Le Cellier, Loire-Atlantique (44), France, on 15 June, 2003.

For study with the scanning electron microscopy (SEM), the antennae of five larvae were dehydrated in absolute ethanol, mounted on specimen holders on either their dorsal or ventral face, and coated with a thin layer of gold and palladium in a JFC 1 100 sputter coater. Preparations were examined with a Jeol JSM 6 400 SEM at different magnifications. The terminology of ZACHARUK (1985) is used in naming the types of sensilla.

RESULTS

The larval antenae of *E. lindenii* are composed of a scape, a pedicel and a four-segmented flagellum (Fig. 1). The lengths of the antennae and their individual parts vary from one individual to another in an identical stage. Furthermore, those of an individual are frequently of different lengths on the two sides. For example, in one particular case, the lengths of the antennal segments for the left antenna (L) and the right antenna (R) were as follows: scape = 300 μm (L), 285 μm (R); pedicel = 433 μm (L), 400 μm (R); 1st flagellomere = 600 μm (L), 500 μm (R); 2nd flagellomere = 166 μm (L), 233 μm (R); 3rd flagellomere = 116 μm (L), 166 μm (R); 4th flagellomere = 120 μm (L), 66 μm (R); total length of antenna = 1735 μm (L), 1640 μm (R).

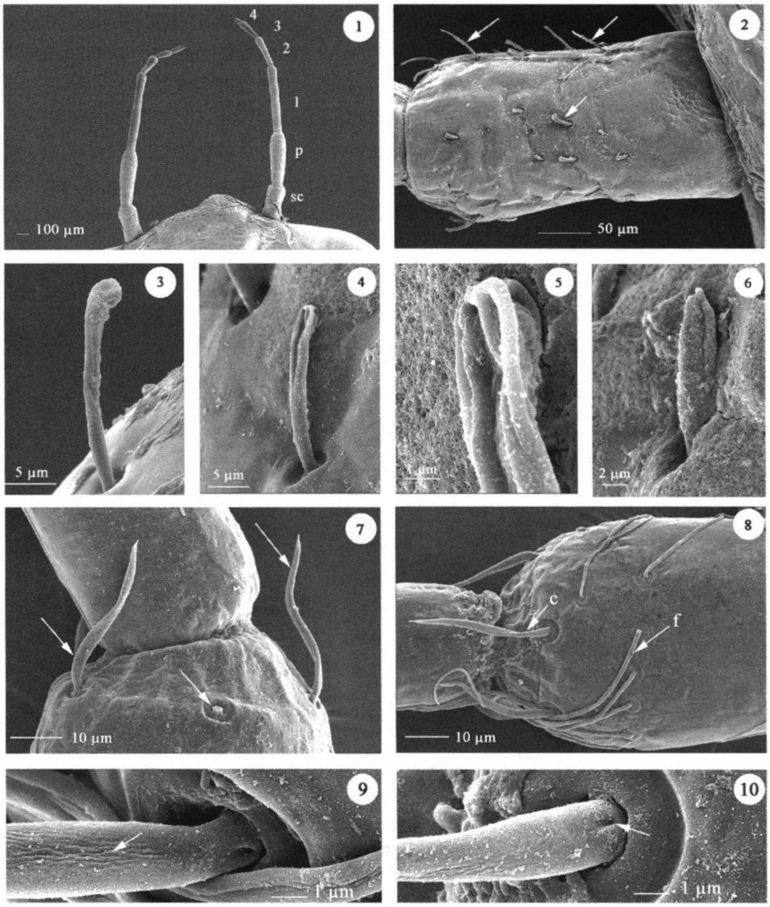
Four types of sensilla were found on the larval antenna of *E. lindenii*: aporous spatula-shaped sensilla chaetica, aporous curved sensilla chaetica, aporous sensilla filiformia, and sensilla campaniformia. The lengths and numbers

Table I
Length, basal width and average numbers of sensilla on a larval antenna of *Erythromma lindenii* (mean ± standard error)

Sensilla (s.)	Length (μm)	Basal width (μm)	Numbers
Spatula shaped s. chaetica	19.2±2.7	1.4±0.2	52
Curved s. chaetica	30.8±4.9	1.5±0.3	12
Short s. filiformia	12.5±1.4	0.6±0.1	38
Median s. filiformia	66.7±3.5	0.7±0.1	44
Long s. filiformia	152.3±6.3	0.8±0.2	62
S. campaniformium		6.6±0.4	1

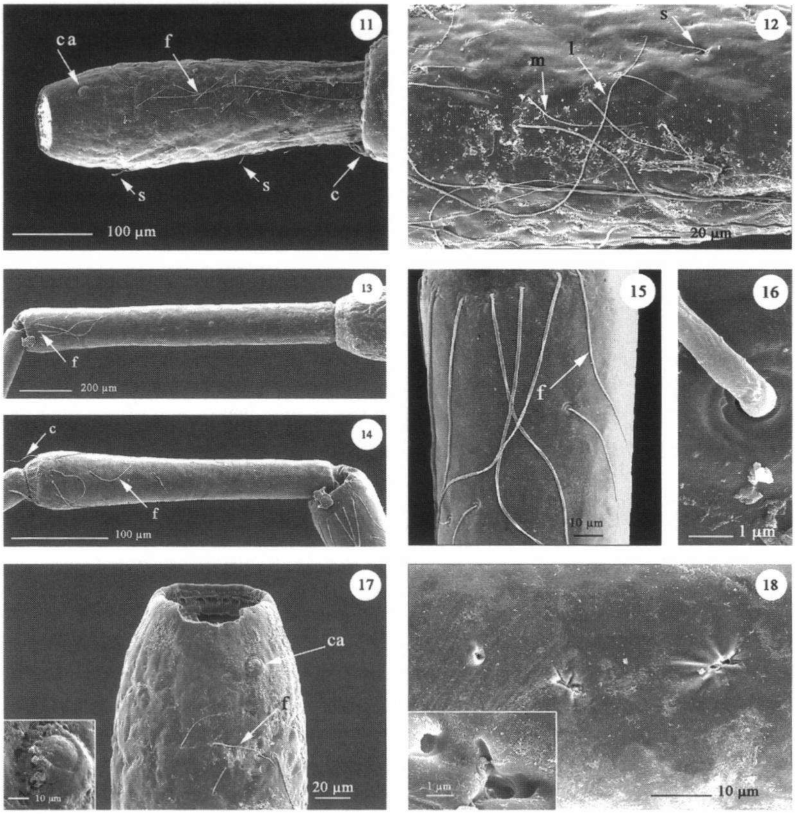
of the sensilla are indicated in Table I.

The aporous spatula-shaped sensilla chaetica are located on the two faces of the scape and the pedicel (Figs 2, 11). They generally take the form of a semicircular spatula on one of the faces (Fig. 3) or on both faces (Figs 4, 5) and they are articulated at their base. Some sensilla offer a different aspect (Fig. 6). Their average length is close to 20 µm but varies from 12 µm (Fig. 6) to 35 µm (Fig. 2). The largest are disposed laterally on the scape. There are 44 on the scape and 8 on the pedicel.



Figs 1-10. Dorsal view of the larval antennae of *Erythromma lindenii*: (1) scape (sc), pedicel (p) and 1-4 flagellomeres; – (2) spatula-shaped sensilla chaetica (arrows) on scape; – (3)-(6) different views of spatula-shaped sensilla chaetica; – (7) distal end of 2nd flagellomere showing three curved sensilla chaetica (arrows) of which the middle one is broken at its base; – (8) distal end of 3rd flagellomere with curved sensilla chaetica (c) and sensilla filiformia (f); – (9)-(10) two details of the base of curved sensilla chaetica showing striae (s) and pore (p).

The aporous curved sensilla chaetica are bent twice: in their proximal half, they are bent towards the interior of the segment; in the distal half, towards the exterior. They are flat over their entire length and narrow at their distal end (Fig. 7). All of them are longitudinally aligned on both faces (Fig. 9). They are each inserted in a cupola and an ecdysial pore can be seen at the base of the hair (Fig. 10). They are arranged in a circle comprising 5 sensilla at the distal edge of the 2nd and 3rd flagellomeres (Figs 7, 8, 19). Two smaller sensilla situated at the apex of the scape (Fig. 11c) can also be classified as this sensillum type.



Figs 11-18. Details of antennal larva of *Erythromma lindenii*: (11) dorsal face of pedicel showing location of spatula-shaped sensilla chaetica (s), sensilla filiformia (f), curved sensilla chaetica (c), and sensillum campaniformium (ca); – (12) short (s), median (m) and long (l) sensilla filiformia on pedicel; – (13) ventral face of 1st flagellomere with sensilla filiformia (f); – (14) ventral face of 2nd flagellomere with sensilla filiformia (f) and curved sensilla chaetica (c); – (15) distal end of 1st flagellomere showing long sensilla filiformia arranged in a circle and scattered median sensilla filiformia (f); – (16) base of sensillum filiformium; – (17) distal end of pedicel showing location of sensillum campaniformium (ca) and sensilla filiformia (f); (inset 17) sensillum campaniformium; – (18) lined glandular pores on the ventral face of 1st flagellomere; (inset 18) detail of pores.

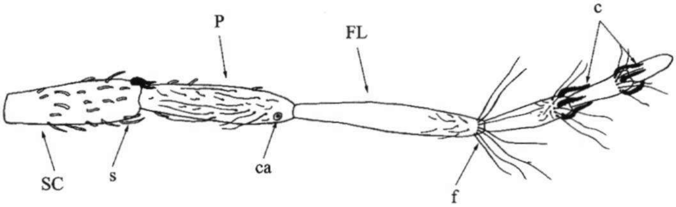


Fig. 19. Diagrammatic representation of distribution of sensilla on dorsal face of scape (sc), pedicel (p) and flagellum (f) of larval *E. lidenii*. [c: curved sensilla chaetica; – ca: sensillum campaniformium; – f: sensilla filiformia; – s: spatula-shaped sensilla chaetica].

The aporous sensilla filiformia are the longest and the most slender on the antenna (Fig. 11f). Their length is variable and they may be classified according to length as: short, median or long sensilla (Tab. I, Fig. 12). They are smooth and fairly flexible and are always flattened against the integument when out of the water (Figs 12-15). Like the above sensilla, the sensilla filiformia are inserted into a cupola (Fig. 16). They are present on both faces of the pedicel (Fig. 11), of the 1st flagellomere (Fig. 13), the 2nd flagellomere (Fig. 14), the 3rd flagellomere (Fig. 8) and the 4th flagellomere (Fig. 19). On the pedicel, the three types (lengths) are scattered over the proximal 2/3 of the segment (Figs 11, 12). On the first three flagellomeres, they colonise the distal 1/3 of the segments; the short and median sensilla are scattered whereas the long sensilla filiformia are inserted in the form of an apical circle which is particularly visible on the 1st flagellomere (Fig. 15). On the 4th flagellomere, they are scattered over the segment (Fig. 19). When the curved sensilla chaetica and the long sensilla filiformia are found together on the same segment, the curved sensilla are always the most distal.

One sensillum campaniformium is located on the dorsal face of the pedicel, towards the distal end, close to the joint membrane between the pedicel and the flagellum (Fig. 17). It has a round cap measuring ca. 6.5 µm in diameter, which is surrounded by a concentric 3.5 µm broad cuticular bulge (Fig. 17, inset).

As well as the sensilla, glandular pores are located longitudinally in the middle of the ventral face of the 1st flagellomere (Fig. 18). Three groups are visible: one consisting of an isolated pore, the second comprising four pores arranged in pairs in a furrow, and the third made up of five pores implanted separately or in pairs in furrows (Fig. 18, inset).

DISCUSSION

SENSILLA FILIFORMIA

Sensilla filiformia (also termed thread-hairs, trichobothria) are found on the cerci of crickets (GNATZY & SCHMIDT, 1971), cockroaches (GNATZY, 1976), lepismatids (BERG, 1994), earwigs (FAUCHEUX, 1999) and embiids (FAUCHEUX, 2002) and also on the male genitalia of certain Lepidoptera (FAUCHEUX, 2005a), the antennae of bugs (McIVER & SIEMICKI, 1984) and the pedipalps of spiders (CHRISTIAN, 1971). In all insects, they are deflected by faint air currents and low-frequency sounds or medium vibrations (GNATZY & TAUTZ, 1980). On the cerci of cockroaches, their suspension is constructed in a way which allows deflection of each hair in only one precisely defined plane. They are arranged on the cercus in a stereotyped pattern in rows; in each row, all hairs can be deflected either parallel, or normal to the cercus axis (KEIL, 1997). The circular location of sensilla filiformia on the antennae of *E. lindenii*, particularly on the 2^{nd} and 3^{rd} flagellomeres can allow a similar function.

Considering the different ranges in lengths of the sensilla filiformia, larval *E. lindenii* should be capable of responding to a wide spectrum of frequencies. Presumably, the principle that the length of the sensilla is related to the frequencies perceived (DRASLAR, 1973; FLETCHER, 1978; McIVER & BEECH, 1986) is true when water rather than air is the medium of conductance. SHIMOZAWA & KANOU (1984a, b) distinguished two physiologically different types of sensilla filiformia on the cricket cercus: 1°, the « long » (> 500 µm) hairs are spontaneously active, sensitive to low-frequence stimuli and are considered to be velocity--sensitive; 2°, the « short » (< 500 µm) are not spontaneously active, insensitive to low-frequency stimuli, and are considered to be acceleration-sensitive.

The sensilla filiformia on the cerci of cockroaches allow stimulus localization of a predator approaching from behind, and trigger the escape response whereas the trichobothria of spiders are air current receptors involved in prey detection. The discovery of sensilla filiformia in *E. lindenii* may confirm earlier results. Indeed, according to CAILLERE (1964, 1965), in the case of *Calopteryx splendens*, vision plays no detectable role in prey detection, which is accomplished by mechanoreceptors on the antennae, mainly on the pedicel, and on the tarsi. In the same species, these receptors detect vibrations in the water, the optimal stimulus being a sequence of saccadic, small-amplitude pressure waves resembling those produced by swimming *Daphnia* (VASSEROT, 1957). Later, CAILLERE (1974) showed that the latency of the capture response of *C. splendens* diminishes with increasing frequence and amplitude of stimulations and with their decreasing duration. And, according to CORBET (1999), the mechanoreceptors on tarsi of *C. splendens* may indeed sometimes be spinelike setae resembling the spines of PILL & MILL (1979). If this is the case, it is difficult to imagine how they function. In only stadium 2 larvae of the Zygoptera *Xanthocnemis zealandica*, very long, fine setae are described on the dorsal surfaces of the antennae, tibiae and tarsi (ROWE, 1994). Now, the eyes play a negligible role in prey detection in stadium 2. The fine setae are apparently mechanoreceptors that mediate prey detection within a space around each of these appendages (CORBET, 1999). These setae of *X. zealandica* are probably similar to the sensilla filiformia of *E. lindenii*. In the latter, the distal sensilla filiformia of the 1st, 2nd and 3rd flagellomeres, as well as those of the pedicel, appear to intervene in prey detection. Thus, it would appear that the whole antenna of *E. lindenii*, and not just the pedicel, in fact plays a part.

In addition to prey-generated vibrations, the sensilla filiformia in *E. lindenii* probably respond to changes in water pressure brought about by body, and/or antennal movements, as demonstrated in the mosquito larva (McIVER & BEECH, 1986). Consequently, sensilla filiformia may be part of a feedback mechanism for control of body and/or antennal position, as suggested for larval *Aedes aegypti* (McIVER & SIEMICKI, 1981).

The presence of sensilla filiformia is only significant in a calm, aquatic environment. Larvae occupying a stream, which is an acoustically chaotic milieu, will find it difficult to distinguish vibrations generated by the water current from those coming from potential prey. But, larvae of *Epiophlebia superstes*, which live in streams, do not possess any sensilla filiformia on the antennae of different stadia (unpublished observations). Furthermore, sensilla filiformia are present on the caudal appendages of *Lestes sponsa* which lives in a calm environment (FAUCHEUX, 2005b).

CURVED SENSILLA CHAETICA

This type of sensilla does not appear so far to have been described in other insects. The particular localization at the distal end of the 2nd and 3rd flagellomeres and the curved shape of the aporous curved sensilla chaetica of *E. lindenii* suggest that they act as proprioceptors for positioning the 3rd flagellomere in relation to the 2nd, and the 4th flagellomere in relation to the 3rd. Figure 7 is interesting because it explains the function of these sensilla. When the 3rd flagellomere of the right antenna bends towards the interior of the head, the left sensillum of 2nd flagellomere in contact with the 3rd flagellomere is stimulated, whereas the right sensillum loses contact with the 3rd flagellomere. When a displacement of the 3rd flagellomere takes place from left to right, i.e. from the interior towards the exterior, the right sensillum comes in contact with the 3rd flagellomere and is stimulated in its turn. The broken median sensillum and the corresponding ventral sensillum, which is invisible on Figure 7, are each stimulated in turn during the dorsal (or ventral) displacement of the 3rd flagellomere. The positioning of the 4th flagellomere in relation to the 3rd flagellomere may be explained in the same way. The longitudinal striae of curved sensilla enables them to adhere to the flagellomere with which they are in contact.

This positioning has been observed in the Zygoptera and the Anisoptera. According to MATSUKI & YOSHITANI (1984), the positioning of the antennae of certain Anisoptera (*Planaeschna milnei* and *Stylogomphus suzukii*) during the predatory sequence suggests that these antennae are serving as mechanoreceptors. It would be interesting to look for the existence of curved or of similar sensilla in these two Anisoptera. In positioning the flagellomeres, the curved sensilla would seem to act in relation with the sensilla filiformia in order to increase the effectiveness of the latter in the spaces around the antennae within which larvae detect prey.

SPATULA-SHAPED SENSILLA CHAETICA

These are similar to bristles which seem to be the most common type of mechanoreceptor, and usually respond to direct touch. They do not appear to be directly involved in the search for prey.

SENSILLA CAMPANIFORMIA

Sensilla campaniformia in insects are found wherever passive mechanical deformations of the cuticle might occur (GNATZY et al., 1987; MORAN *et al.*, 1971). On the larval antennae of *E. lindenii*, they perceive the movements of the flagella with respect to the pedicels and are stimulated each time the flagella change direction.

The function of the integumental glands opening onto the first flagellomere is not known. Epidermal glands almost anywhere on an insect's body are common (NOIROT & QUENNEDEY, 1974). In the diving water beetle *Graphoderus occidentalis*, LEUNG & ZACHARUK (1986) suggest that the primary role of the gland cell secretions is to provide a surface mucoid coating that would facilitate movements under water, and prevent excessive water loss when out of the water. A similar function is possible for the antennal glands of *Erythromma* larvae.

In summary, the most efficient sensilla on the antennae of *E. lindenii* are the sensilla filiformia which detect vibrations in the water. The other sensilla (curved sensilla chaetica, campaniformia) serve to optimize the action of sensilla filiformia. Sensilla filiformia have recently been described on the caudal appendages of *Lestes sponsa* (FAUCHEUX, 2005); they are absent from the caudal appendages of *E. lindenii* (unpublished observations). Moreover, the sensilla filiformia which are located in other insect orders on the caudal appendages (cerci of Blattodea, Orthoptera, Dermaptera, and caudal lamellae of *L. sponsa*), are here described for the first time on the larval antennae of Odonata. The study of the juvenile stadium of *E. lindenii* would be worthwhile because in *X. zealandica*, ROWE (1994) has shown that the relative importance of visual and mechanoreceptors of antennae, tibiae and tarsi, may change greatly during ontogeny. The absence of chemoreceptors on the antennae provides evidence that *E. lindenii* does not use chemoreception to locate prey.

To confirm these results, further work is required, including ultrastructural and electrophysiological studies.

Our studies concern only antennal sensilla, but other sensilla located on other organs: legs (PILL & MILL, 1979; MILL & PILL, 1981), abdomen (PILL & MILL, 1981), Johnston organ (IVANOV, 1978a, 1978b) can also take part in prey detection.

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