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Multiporous and aporous sensilla on the larval antennae of the relict dragonfly *Epiophlebia superstes* (SELYS, 1889) (Odonata: Anisozygoptera: Epiophlebiidae)

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Abstract

The larval antennal sensilla of the relict dragonfly, *Epiophlebia superstes* (Anisozygoptera) have been studied by means of scanning electron microscope. Five types of sensilla are present: curved aporous sensilla chaetica, aporous sensilla filiformia, multiporous sensilla coeloconica, sensilla ampullacea and sensilla basiconica. A tactile function is attributed to the curved sensilla chaetica, a chemoreceptive function to the sensilla ampullacea and sensilla basiconica, a chemoreceptive or hygroreceptive function to the sensilla coeloconica, a vibroreceptive function to the sensilla filiformia. *Epiophlebia*, which lives in the turbulent waters of mountain streams, differs from the other larvae of Zygoptera and Anisoptera, whose habitat is calm water, by the reduced number of sensilla filiformia. *Libellula depressa*, a previously studied anisopteran species, and *Epiophlebia* (Anisozygoptera) both possess sensilla coeloconica. The presence of sensilla coeloconica is common both to the antennae of the final-stadium larva of *Epiophlebia* and of adult Odonats.

Key words: Odonata, *Epiophlebia*, antenna, sensilla, ampullacea, basiconica, coeloconica, curved chaetica, filiformia, aporous, multiporous.

Résumé

Les sensilles antennaires de la larve d'*Epiophlebia superstes* ont été étudiées à l'aide du microscope électronique à balayage. Cinq types de sensilles sont présents : des sensilles chétiformes sans pore incurvées, des sensilles filiformes sans pore, des sensilles coeloconiques multipores, des sensilles ampulliformes et des sensilles basiconiques. Une fonction tactile est attribuée aux sensilles chétiformes, une fonction chimioréceptrice aux sensilles ampulliformes et basiconiques, une fonction chimioréceptrice ou hygroréceptrice aux sensilles coeloconiques, une fonction réceptrice des vibrations aux sensilles filiformes. *Epiophlebia,* qui vit dans les eaux turbulentes des courants de montagnes, diffère des autres larves de Zygoptères et d'Anisoptères qui habitent les eaux calmes, par la réduction du nombre des sensilles filiformes. *Libellula depressa*, un anisoptère précédemment étudié et *Epiophlebia* (Anisozygoptera) possèdent en commun les sensilles coeloconiques. La présence des sensilles coeloconiques est commune aux antennes de la larve du dernier stade d'*Epiophlebia* et des Odonates adultes.

Mots-clés : Odonates, *Epiophlebia*, antenne, sensilles, ampulliformes, basiconiques, coeloconiques, chétiformes incurvées, filiformes, sans pore, multipore.

Introduction

In the insect order Odonata, three extant suborders, namely Zygoptera (damselflies), Anisoptera (dragonflies) and Anisozygoptera, are recognized (HASEGAWA & KASUYA, 2006). In the last half century, structure, diversity and function of mechanoreceptors in odonat 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 odonat neurobiology. None of the previous studies concerns the external sensilla of the antennae and caudal lamellae. We have recently undertaken a study of the cephalic and caudal appendages in three zygopteran (*Erythromma lindenii*, *Chalcolestes viridis* and *Lestes sponsa*) and of an anisopteran (*Aeshna cyanea*). The larval antenna of the four species bear at most four sensillum types: aporous spatula-shaped sensilla chaetica with a tactile function; aporous sensilla filiformia which act as vibroreceptors; aporous sensilla campaniformia on the pedicel or on the flagellum, whose function is proprioceptive or osmoreceptive; aporous curved sensilla chaetica which act as proprioceptors for positioning the flagellomeres in relation to one another (FAUCHEUX, 2006, submitted; FAUCHEUX & MEURGEY, 2006, 2007; MEURGEY & FAUCHEUX, 2006). On the caudal lamellae of three Zygoptera, aporous sensilla filiformia and sensilla campaniformia are present (FAUCHEUX, 2005, submitted). In these species, no chemoreceptive sensillum has been found on the antennae or the caudal appendages except multiporous sensilla ampulliformia on the caudal lamellae of *E. lindenii* (SÉLYS, 1840) (FAUCHEUX, submitted). However, sensilla coeloconica, with a putative chemoreceptive or hygroreceptive function, are described on the terminal flagellomere of the anisopteran *Libellula depressa* (GAINO & REBORA, 1999, 2001; REBORA *et al.*, 2006).

The sensory organs of the 3rd suborder, Anisozygoptera, have never bee studied. This suborder consists of a single extant family, Epiophlebiidae TILLYARD, 1917 with a single genus *Epiophlebia* CALVERT, 1903 and only two species, *Epiophlebia superstes* (SÉLYS, 1889) and *E. laidlawi* (TILLYARD, 1921). The two species have characteristics that are intermediate between those of Zygoptera and Anisoptera in terms of morphology and behavior (RUEPPELL & HILFERT, 1993). The phylogenetic position of the Anisozygoptera is an ambiguous point in the phylogeny of the Odonata. All the methods resulted in similar branching patterns that suggested a basal and paraphyletic relationship in the Zygoptera and the position of *Epiophlebia* as the sister taxon of the monophyletic Anisoptera (HASEGAWA & KASUYA, 2006). These authors suggested an intermediate position of *Epiophlebia* (Anisozygoptera) between the Zygoptera and Anisoptera. Our aim is to discover whether *E. superstes* possesses antennal sensilla types analogous to those present in Zygoptera and Anisoptera. Furthermore, the odonat species previously studied (*E. lindenii*, *Chalcolestes viridis* VAN DER LINDEN, 1825; *Aeshna cyanea* (MÜLLER, 1764)) all live in calm water. Thus, their sensilla filiformia respond to changes in water pressure and to prey-generated vibrations. However, the larvae of *E. superstes* live on the contrary in streams which are an acoustically chaotic milieu and will find it difficult to distinguish vibrations generated by the water current from those coming from potential prey; in this case, the presence of sensilla filiformia seems unlikely. Moreover, the larva remains out of water for several months before its emergence. During this period, it is exposed to dehydratation and predators. Consequently, hygroreceptors would probably be useful for it.

Material and methods

Live larvae and specimens preserved in alcohol of *E. superstes* were kindly provided for us by Takashi Aoki (Rokko Island High School, Kobe, Japan). They were found by Dr Kozo Tani, on May 5, 2002, in the upper reaches of the Akadani, Kurotaki village, Yoshino-gun, Nara Pref., Japan. The larvae live on the gravel beds of Japanese torrents. For SEM observation, only the final-stadium larva has been studied extensively; younger larvae have been observed to confirm the presence of sensilla. After dehydrating in an alcohol series to 100%, the antennae were mounted on specimen holders using double face sticky paper. They were coated with a thin layer of 60% gold/40% palladium and were examined in a Jeol J.S.M. 6400 scanning electron microscope (SEM) at 7 kV. The terminologies of SNODGRASS (1926) and ZACHARUK (1985) are used in naming the types of sensilla.

Results

The antenna of final instar larva of *E. superstes* is five-segmented, the scape is short and thick, the pedicel is almost three times as long as wide, the distal three flagellomeres are narrow, the ratio of their length is ca. 4: 2: 2 (Fig. 2). The number of flagellomeres sometimes differs from one antenna to another in the same individual; for example, there are three on the left antenna, two on the right antenna (Fig. 1). The total length of the antenna with three flagellomeres is 1 mm. An ornamentation consisting of conical non-innervated protuberances is present on the whole of the antenna (Figs 3, 4, 7).

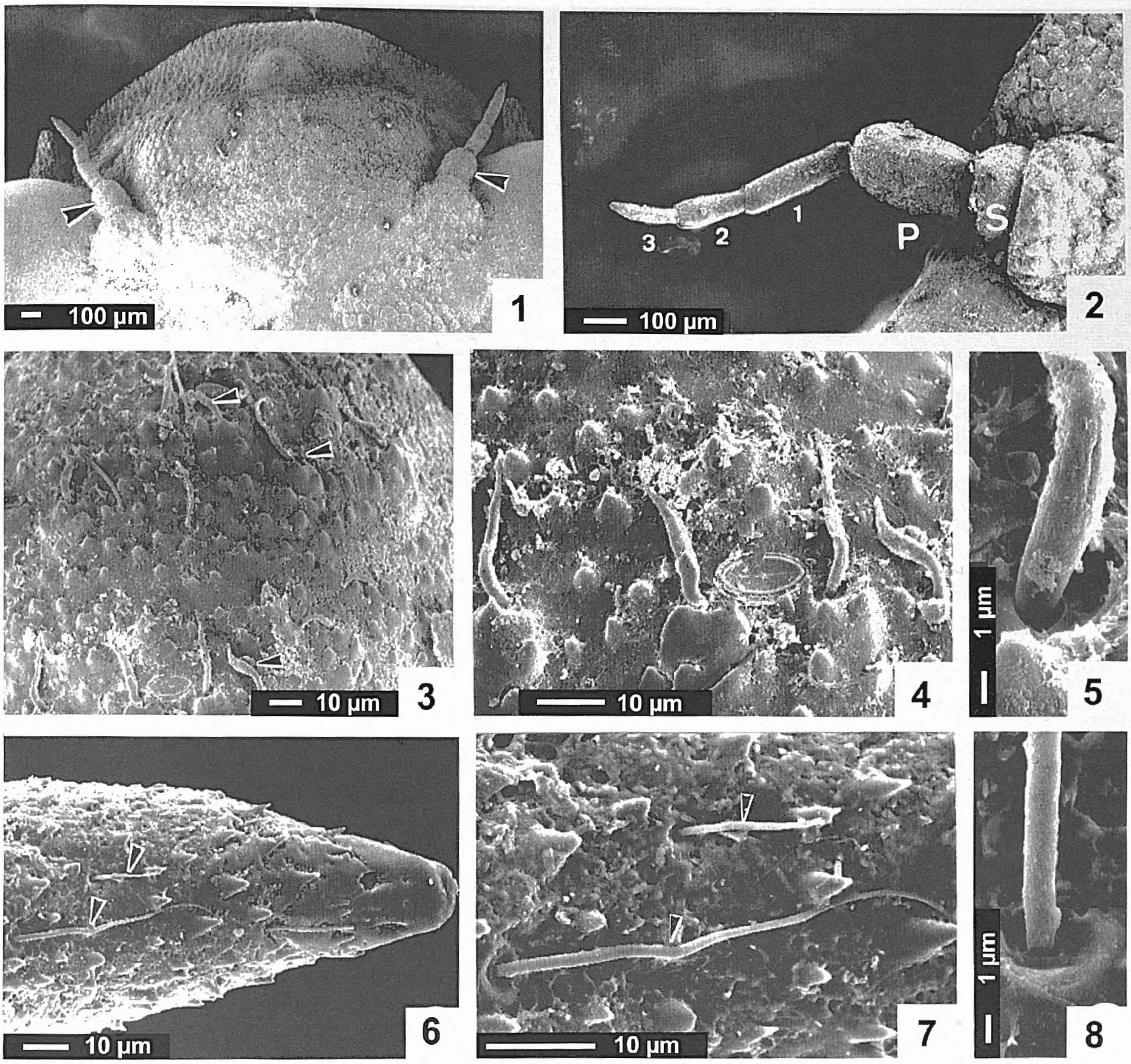
A – Antennal sensilla

Five types of sensilla have been observed: sensilla chaetica, sensilla filiformia, sensilla coeloconica, sensilla ampullacea and sensilla basiconica. Their distribution is shown diagrammatically in Fig. 21.

1 – Aporous curved sensilla chaetica, 20 µm long, are spread out over the scape, the distal half of the pedicel where they are often lined up transversally (Figs 3, 4). They are rare on the first and the second flagellomeres and are present on both faces of the segments. The sensilla are bent twice: in their proximal half, they are bent towards the interior of the pedicel; in the distal half, towards the exterior. They are flat over their entire length and narrow at their distal end; they are inserted into a cupola (Fig. 5).

2 – Aporous sensilla filiformia are only present on both faces of the second and third flagellomeres. Their number does not exceed seven sensilla on the terminal flagellomere (Fig. 6). They are of variable length, the longest measuring 40 µm (Fig. 7). They are inserted into a cupola (Fig. 8).

3 – Three multiporous sensilla coeloconica are grouped in the distal part of the first flagellomere on the dorsal surface (Fig. 9, 10). They appear externally as more or less circular openings in the antennal cuticle. They consist of a single pit with a peg, 3 µm long, plunging into the pit and marked by a dozen deep ridges (Fig. 11). This pedicel possesses a globular head with some 50 pores. The pores have a diameter varying



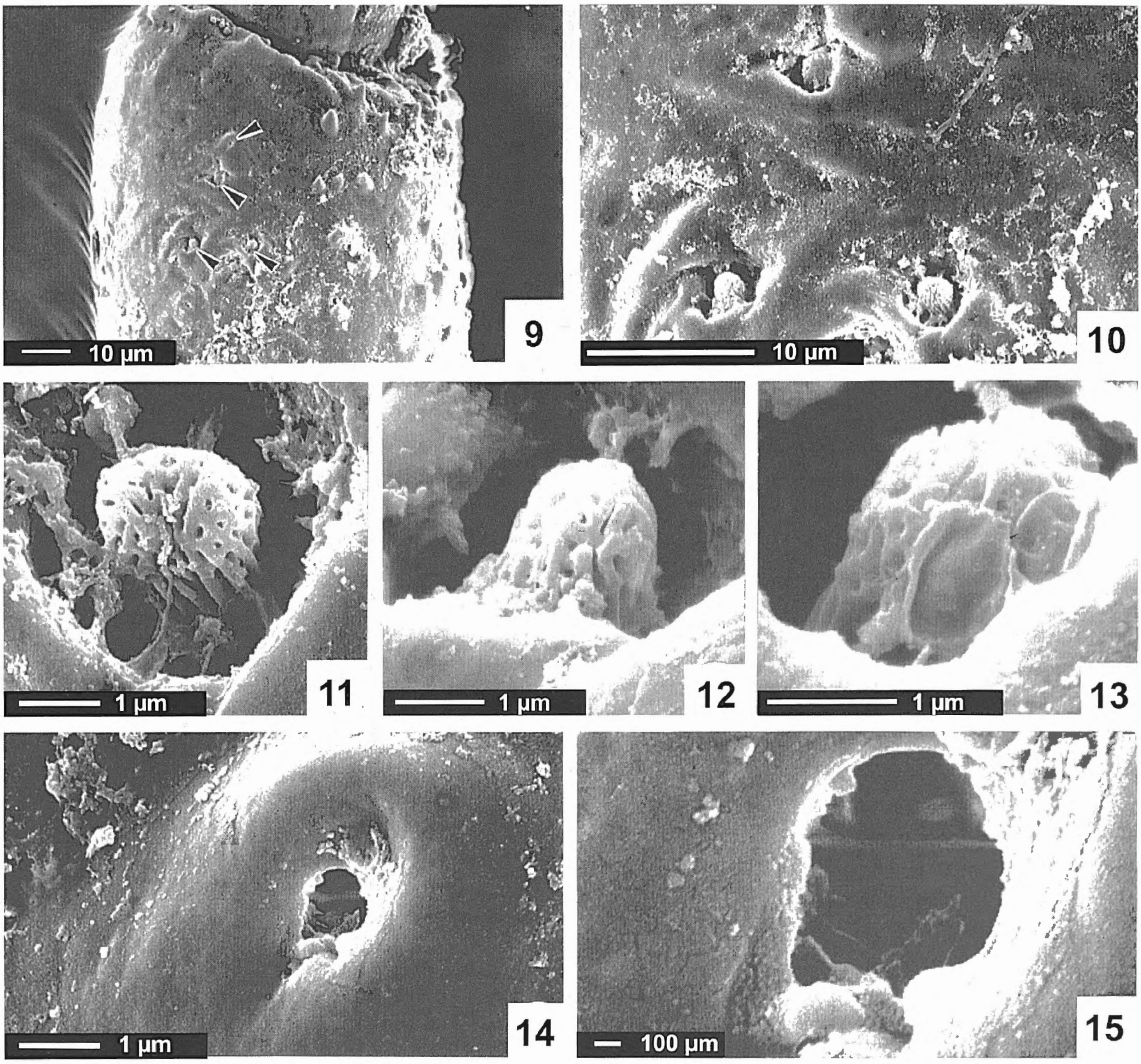
Figs 1-8 — Larval antennae and sensilla of *Epiophlebia superstes*. **1.** dorsal face of the head showing the antennae (arrows); **2.** dorsal face of left antenna showing scape (S), pedical (P) and flagellomeres (1-3); **3.** apex of pedicel showing the rows of curved sensilla chaetica (arrows); **4.** four curved sensilla chaetica; **5.** base of curved sensillum chaeticum; **6.** distal part of third flagellomere showing two sensilla filiformia (arrows); **7.** sensilla filiformia (arrows); **8.** base of sensillum filiformium.

from 80 to 125 nm; they are generally circular but are sometimes elongated and are lengthen when they reach the ridges at the pedicel of the sensillum. The shape of the peg varies (Figs 12, 13).

4 – A sensillum ampulliformium is located above the sensilla coeloconica towards the apex of the first flagellomere (Fig. 9). It consists of a cuticular dome of 5 µm in diameter, pierced in the centre by a pit of 0.8 µm in diameter, within which can be seen a cuticular structure which is difficult to describe (Figs 14, 15).

5 – A group of six sensilla basiconica is situated at the most distal part of the first flagellomere, near the joint between this flagellomere and the second one (Fig. 16). The basal diameter of sensilla varies from 1 µm to 1.5 µm (Fig. 17). Their surface is irregular; the presumed pores could not been shown with only scanning electron microscopy technology.

The larvae preceding the final larval stadium possess sensilla filiformia and curved sensilla chaetica identical to those of adult larvae, but in reduced numbers; the sensilla coeloconica, ampullacea and basiconica have not been identified in the young larvae.



Figs 9-15 — Sensilla on the first larval flagellomere of *Epiophlebia superstes*. **9**. distal part of first flagellomere showing the location of sensillum ampullaceum (upper arrow) and sensilla coeloconica (other arrows); **10**. group of three sensilla coeloconica; **11-13**. different views of sensillum coeloconicum; **14**. sensillum ampullaceum; **15**. detail of the cavity of sensillum ampullaceum.

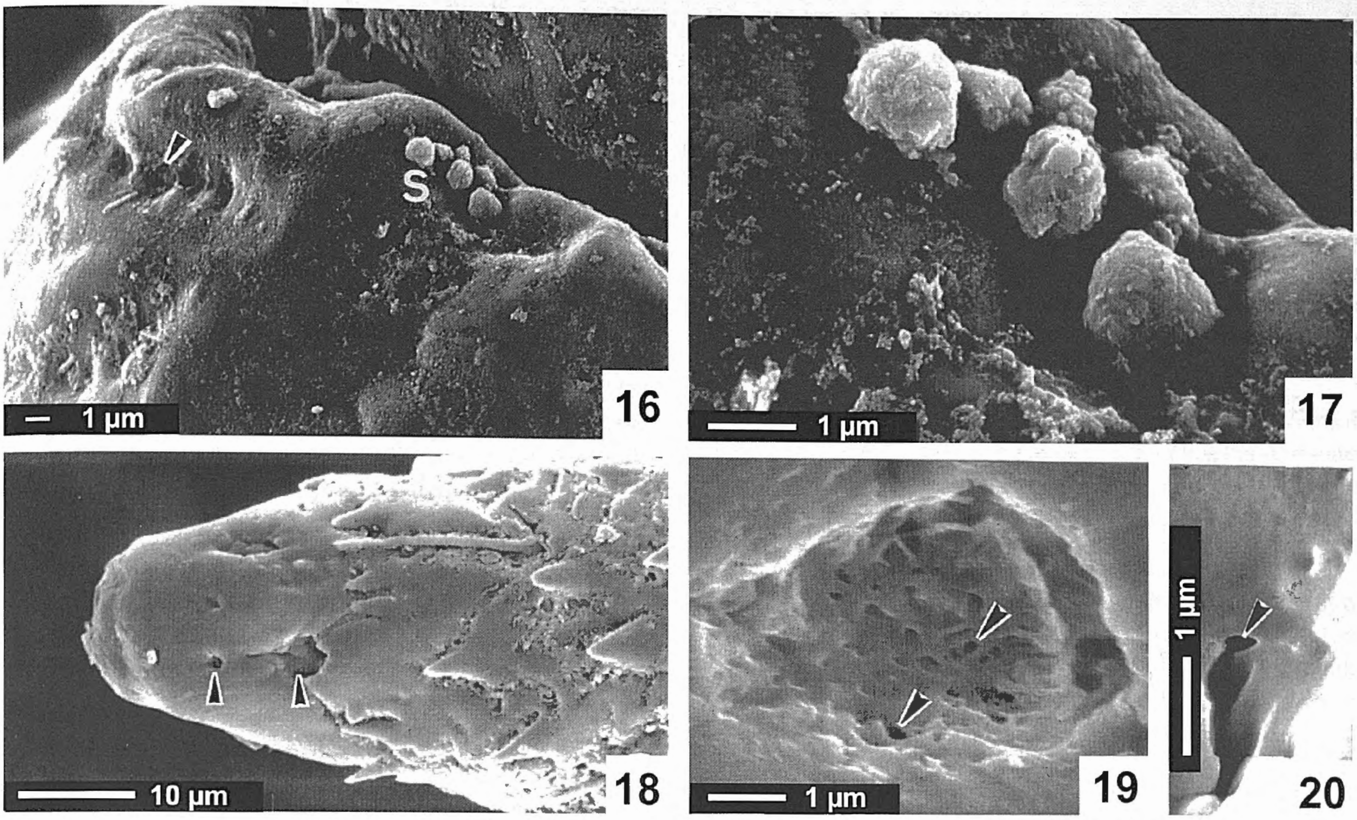
B – Glandular pores

The terminal part of the third flagellomere comprises two rings of flat bottomed cavities containing glandular pores: an apical ring of five cavities (two dorsal, three ventral), a subapical ring of four large cavities (two dorsal, two ventral) (Fig. 18). The small cavities possess three or four pores (Fig. 20); the large cavities have as many as 30 pores (Fig. 19). A row of five small cavities is present near the sensilla basiconica on the first flagellomere (Fig. 16).

Discussion

The larval antenna of *E. superstes*, which consists of only five segments, is unique; they are seven in the majority of Odonata (Denis & Bitsch, 1973).

The curved sensilla chaetica of *E. superstes* are morphologically similar to the sensilla of *E. lindenii* (Faucheux, 2006) and *C. viridis* (Faucheux & Meurgey, 2006) and of the anisopteran *A. cyanea* (Faucheux & Meurgey, 2007). However, their distribution is different: scape and pedicel of *E. superstes*, apex of



Figs 16-20 — Larval antenna of *Epiophlebia superstes*. **16**. joint between the first and the second flagellomere showing the location of six sensilla basiconica (S) and a group of glandular pores (arrow); **17**. group of sensilla basiconica; **18**. apical and subapical circles of glandular pores (arrows) on the third flagellomere; **19**. glandular pores of the subapical circle (arrows); **20**. glandular pores of the apical circle.

flagellomeres in the other odonats, except two sensilla on the scape of *E. lindenii* (Meurgey & Faucheux, 2006). The sensilla located only near the joints of flagellomeres in Zygoptera and Anisoptera act as proprioceptors assuring the positioning of flagellomeres. Such a function cannot be attributed to the sensilla of *E. superstes* which no doubt possess a tactile function. It is interesting that the sensilla of the latter species are frequently lined up transversally, reminding one of their circular arrangement characteristic on the flagellomeres of Zygoptera and Anisoptera.

The presence of multiporous sensilla coeloconica is common to both *E. superstes* and *L. depressa* (Gaino & Rebora, 2001). According to Zacharuk (1985), an olfactive function may be attributed to the sensilla coeloconica. In *E. superstes*, these sensilla function equally well in water or in the air, when he larva is out of the water; they are useful for detecting predators. Sine the sensilla which are thought to be olfactive are only present in the final-stadium larvae, one must suppose that olfaction plays a preponderant role only during the life out of water of the larvae.

The particular morphology of sensilla coeloconica in *E. superstes* recalls that of *L. depressa*. Indeed, the interruptions of the cuticle described in *Epiophlebia* are very similar to the wall-pores of simple and compound coeloconic pit pegs located on the antennal flagella of adult damselflies and dragonflies, and interpreted as chemosensory sensilla by Slifer and Sekhon (1972). The SEM micrographs of these authors are not demonstrative but we have observed these sensilla on the adult antennae of the anisopteran *Brachythemis leucosticta* Burmeister, 1839 (Faucheux, unpublished) and their resemblance with the sensilla of *E. superstes* is very striking. The number of pores is closely similar: about 50 in *E. superstes* as against 65 in *B. leucosticta*; the pore diameter is as wide: 80-125 nm in larval *Epiophlebia* (see above), 55-166 nm in adult *Brachythemis* (pers. obs.). In both cases, the pore diameter is larger than that described in the other insect orders. Indeed, it reaches 40 nm in the sensilla coeloconica of Lepidoptera (Cuperus, 1985) and 20 nm in Diptera (Shanbhag *et al.*, 1999). This large diameter is not dependant on the environment, whether aquatic or terrestrial, in which the odonats live since it is more or less the same in both the aquatic larvae and the

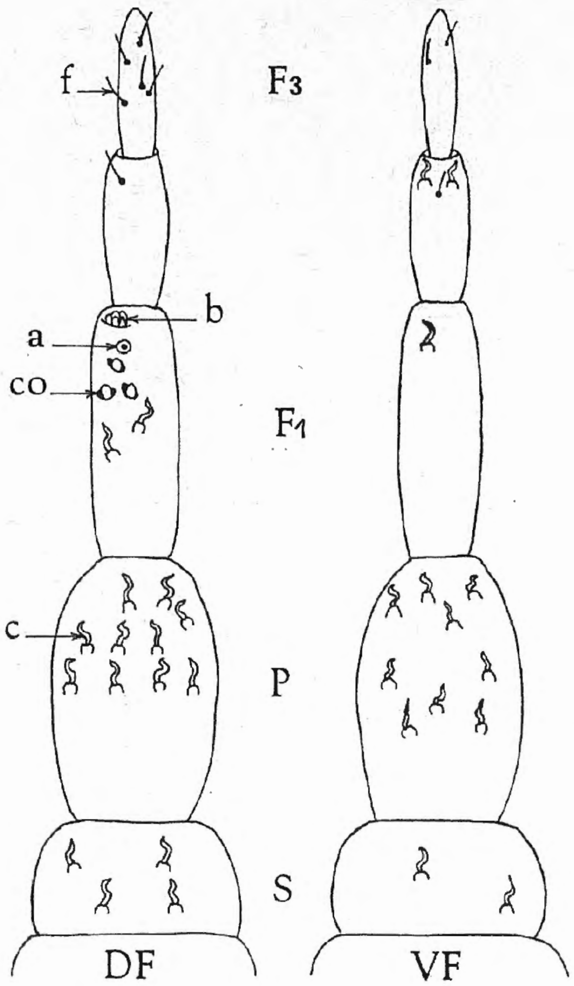


Fig. 21 — Schematic view of larval antenna of *Epiophlebia superstes* showing the distribution of sensilla on the dorsal face (DF) and the ventral face (VF). S, scape; P, pedicel; F1, first flagellomere; F3, third flagellomere; a, sensillum ampullaceum; b, sensillum basiconicum; c, curved sensillum chaeticum; co, sensillum coeloconicum.

terrestrial adults.

In a preliminary investigation of the sensilla coeloconica of *L. depressa*, GAINO and REBORA (1999) proposed a chemosensory function. But the internal structure of these sensilla reminds one of the general morphology of hygroreceptors (REBORA *et al.*, 2006). The presence of hygroreceptors would not be surprising in *E. superstes*, whose a long larval period is supposed to be about seven or eight years, because the mature larva shows terrestrialization in that it leaves its usual habit, the rushing water, about four or five months before the transformation in adult, and can occupy microhabitats where the ambient humidity is continuous and high (ASAHINA, 1954). Likewise, larvae of *L. depressa* often live in small temporary pools and appear resistant to dehydratation (KNAPP *et al.*, 1983).

Sensilla basiconica have not been described in the other odonat larvae (FAUCHEUX, 2006; FAUCHEUX & MEURGEY, 2006, 2007). Future ultrastructural studies would be needed to confirm the presence of wall pores.

Sensilla ampulliformia have not been observed on the larval antenna of odonats previously described but they are present in small numbers on the caudal lamellae of *E. lindenii* (FAUCHEUX, submitted). Similar sensilla exist on the adult antennal flagella of *B. leucosticta* (pers. obs.). A chemoreceptive function may be assigned to them (ZACHARUK, 1985).

The presence of sensilla filiformia on the antenna of *E. superstes* is surprising for these sensilla are only efficient in a calm aquatic environment in which the slightest vibrations can be perceived. What is more, the final-stadium larvae of *Epiophlebia* leave the water about 20 days before emergence, concealing itself under small stones or fallen leaves near where emergence will take place. During this period, the sensilla filiformia would be useless and, out of water, would adhere to the antenna because they are less rigid than those of terrestrial insects (FAUCHEUX, 2006).

Curiously, the most characteristic sensilla in *E. superstes* (coeloconica, ampulliformia, basiconica) are located only on the first flagellomere. This is perhaps related to the fact that frequently the third flagellomere is absent or the first and second flagellomeres are merged into a single segment.

Although the antennal sensilla of adult *E. superstes* have not been studied, one may suppose, judging by the results of SLIFER and SEKHON (1972) concerning 6 species of Zygoptera and 11 species of Anisoptera, that the sensilla coeloconica and ampulliformia are likewise present in this dragonfly. In that case, there would be a striking resemblance between the sensilla of the larvae and of the adults. ASAHINA (1954) already indicated that the number of segments of the adult flagellum of *E. superstes* was the same as that of the full-grown larva. Therefore, larvae and adults could have the same types of sensilla, thus being active in different environments. Indeed, JENSEN and ZACHARUK (1992) have described sensilla working in different environments, on the antennae of the diving beetle, *Graphoderus occidentalis*. They are multiporous olfactory sensilla sensitive to low concentrations of chemicals in both air and water. Previous electrophysiological investigations carried out by BEHREND (1971) on the multiporous sensilla of the aquatic beetle, *Dytiscus marginatus*, gave identical results to the previous ones.

The presence of groups of glandular pores, often lined up, is frequent in the larvae of odonats as has already been pointed out in *E. lindenii* (MEURGEY & FAUCHEUX, 2006).

Conclusion

The originality of the sensory equipment of the larval antennae of *E. superstes* consists in the presence of chemoreceptive or hygroreceptive multiporous sensilla and the reduced number of vibroreceptive sensilla filiformia, as well as a morphological resemblance with that of the antennae of adult odonats. The presence of sensilla coeloconica and ampulliformia allows us to relate *Epiophlebia* to Anisoptera and to distinguish this species from Zygoptera.

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