

# ANTENNAL CUTICULAR SENSILLA IN SOME MAYFLIES (EPHEMEROPTERA)

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A survey at ultrastructural level on the antennal sensilla of several mayfly species is presented. The species here considered belong to Leptophlebiidae (*Choroterpes picteti*, *Habroleptoides confusa*, *Habrophlebia eldae*), Heptageniidae (*Ecdyonurus venosus*, *E. helveticus*, *Electrogena grandiae*, *Epeorus sylvicola*, *Rhithrogena loyolaea*), Baetidae (*Cloeon dipterum*), Caenidae (*Caenis luctuosa*), Siphlonuridae (*Siphlonurus lacustris*). Sensilla are categorized on the basis of their fine external morphology. Their diversification and relative position is illustrated in nymphs and adults. Nymphs show a vast variety of sensilla, mainly located on pedicel and flagellum. Adult antennae are strongly reduced and their morphology changes even from subimago to imago; sensilla are few and less diversified. The functional and taxonomic relevance of mayfly sensilla is discussed in consideration of the role performed by the sensory systems in insects.

## INTRODUCTION

Numerous studies have been carried out on insect sensilla with particular attention to antennae (KEIL & STEINBRECHT, 1984; ALTNER & LOFTUS, 1985; McIVER, 1985; ZACHARUK, 1985; SOLINAS *et al.*, 1987; FAUCHEUX, 1990; KAPOOR, 1991; ROSS, 1992; OLSON & ANDOW, 1993; BOURGOIN & DEISS, 1994; CATALÀ & SCHOFIELD, 1994; PRAKASH *et al.*, 1995).

As far as Ephemeroptera are concerned, sensilla and related structures have been studied in the past (EASTHAM, 1936) and repeatedly taken into some consideration for taxonomic purposes (MÜLLER-LIEBENAU, 1969; PETERS & EDMUNDS, 1970; AGNEW, 1980; SARTORI & THOMAS, 1991; SOLDÁN & LANDA, 1991). Nevertheless, investigation on their fine architecture is limited to the description of mechanoreceptors in the pedicel of a few species (SCHMIDT, 1974). A recent scanning electron microscopy study concerns the antennal sensilla in the ephemerellid *Vietnamella dabieshanensis* (SU & CAI, 1994). We have considered the main kind of mayfly antennal sensilla on the basis of their fine external morphology. Our interest has been focused mostly on aquatic stages, since, in comparison with adults, nymphs show a greater variety of their receptors.

## MATERIALS AND METHODS

Representatives of Leptophlebiidae (*Choroterpes picteti*, *Habroleptoides confusa*, *Habrophlebia eldae*), Hepta-

geniidae (*Ecdyonurus venosus*, *E. helveticus*, *Electrogena grandiae*, *Epeorus sylvicola*, *Rhithrogena loyolaea*), Baetidae (*Cloeon dipterum*), Caenidae (*Caenis luctuosa*), Siphlonuridae (*Siphlonurus lacustris*) were considered in this study. Antennae were essentially examined under interference phase contrast and scanning electron microscopes (SEM). Selected material was dissected from anesthetized specimens collected in the Scrivia river (Casella, Liguria), Verde stream (Isoverde, Liguria), Berlino stream (Rossiglione, Liguria), Erro stream (Arzello, Piemonte). Samples were fixed in KARNOVSKY's medium (1965) for 1 hour and rinsed in cacodylate buffer.

For SEM analysis antennae were critical point dried using a CO<sub>2</sub> Pabisch CPD 750 apparatus, mounted on stubs with silver conducting paint and coated with gold palladium in a Balzers Union evaporator. Specimens were observed with a Philips EM 515 scanning electron microscope.

A preliminary investigation with transmission electron microscope (TEM) was carried out on the antennae of *Ch. picteti*, after having postfixed them for 1 hour in osmium tetroxide, rinsed in cacodylate buffer, dehydrated in graded ethanol series and finally embedded in Epon-Araldite mixture resin. Thin sections, obtained with a Reichert ultratome, were collected on formvar-coated copper grids, stained with uranyl acetate and lead citrate, and observed with a Philips EM 400 electron microscope. The basic descriptive terminology used by ZACHARUK (1985) is followed in the present paper.

## RESULTS

This study illustrates sensilla diversification in shape and arrangement on the antennae, also in consideration that a drastic modification of the antennae occurs at the emergence from water.

### *Leptophlebiidae*

The flagellum of nymphs of *Choroterpes picteti*, *Habroleptoides confusa*, *Habrophlebia eldae*

*eldae* shows sensilla trichodea (Figs 1-4). They emerge isolated and in groups of three elements as well; in both cases they jut out from a discrete socket (Figs 1-3). In spite of the species belonging to different genera, a uniform pattern in morphology and distribution of antennal sensilla is evident.

Longitudinal sections of the sensilla of *Ch. picteti* examined under TEM reveal the association of a tubular body (Fig. 4) with the dendrites extending along the lumen of the shaft (inset of Fig. 4).

Along the distal border of the pedicel of the nymph of this species, campaniform sensilla are present (Fig. 5). At SEM level (Fig. 5) they appear as simple depression of the cuticle (Fig. 6).

In the subimaginal stage of *Habrophlebia eldae*, scape and pedicel are uniformly covered by microtrichia (Fig. 7). The unsegmented flagellum is decorated with densely packed ribs (Fig. 8).

#### Heptageniidae

In the nymphs of *Rhithrogena loyolaea* and *Epeorus sylvicola* flat-tipped sensilla occur (Figs 9-12). They are located on the distal portion of the flagellar segments together with sensilla basiconica (Figs 11, 12). Most of the flat-tipped sensilla protrude beyond the border of the segment but they only occasionally touch the surface of the next segment. Their apical portion has an arrowhead shape and bears a pore (Fig. 10). In *Epeorus sylvicola* a groove extends from the base to the top of each sensillum (Fig. 12).

The nymphs of *Ecdyonurus helveticus* have different kinds of sensilla present along the distal portion of each flagellar segment (Figs 13-15). Together with sensilla basiconica, other coeloconic-like sensilla are present (Figs 14, 15). Both are completely included in their socket but show a different morphology: one type is round-shaped (Fig. 14) and the other is slightly elongated with a pore located in its upper region (Fig. 15).

The subimago of *Electrogena grandiae* has its pedicel uniformly covered by microtrichia, while the flagellum shows a ribbed decoration (Fig. 16). Sensilla coeloconica are interspersed among ribs (Fig. 17) and emerge isolated or in

pairs. Sometimes a pore at their apex is evident (inset of Fig. 17). At the imaginal stage, microtrichia, which cover the scape and pedicel of the subimago, disappear and are replaced by scales (Fig. 18). The initial part of the flagellum is covered by fan-like cuticular projections that gently enlarge giving rise to irregular folds towards the distal portion of the flagellum. Sensilla coeloconica are scattered among folds along the ventral side of the flagellum (Fig. 19).

#### Baetidae

The nymphs of *Cloeon dipterum* have sensilla trichodea on the flagellum (Fig. 20). In the imago, scape and pedicel are covered by scales; the flagellum has a folded appearance and shows sensilla coeloconica among folds (Fig. 21).

#### Siphlonuridae

The nymphs of *Siphlonurus lacustris* have sensilla placodea included in a wide socket and mainly located along the lateral surfaces of the flagellum (Fig. 22). In these nymphs sensilla chaetica with a slight groove in the middle occur. They are located along the distal border of the pedicel (Fig. 23).

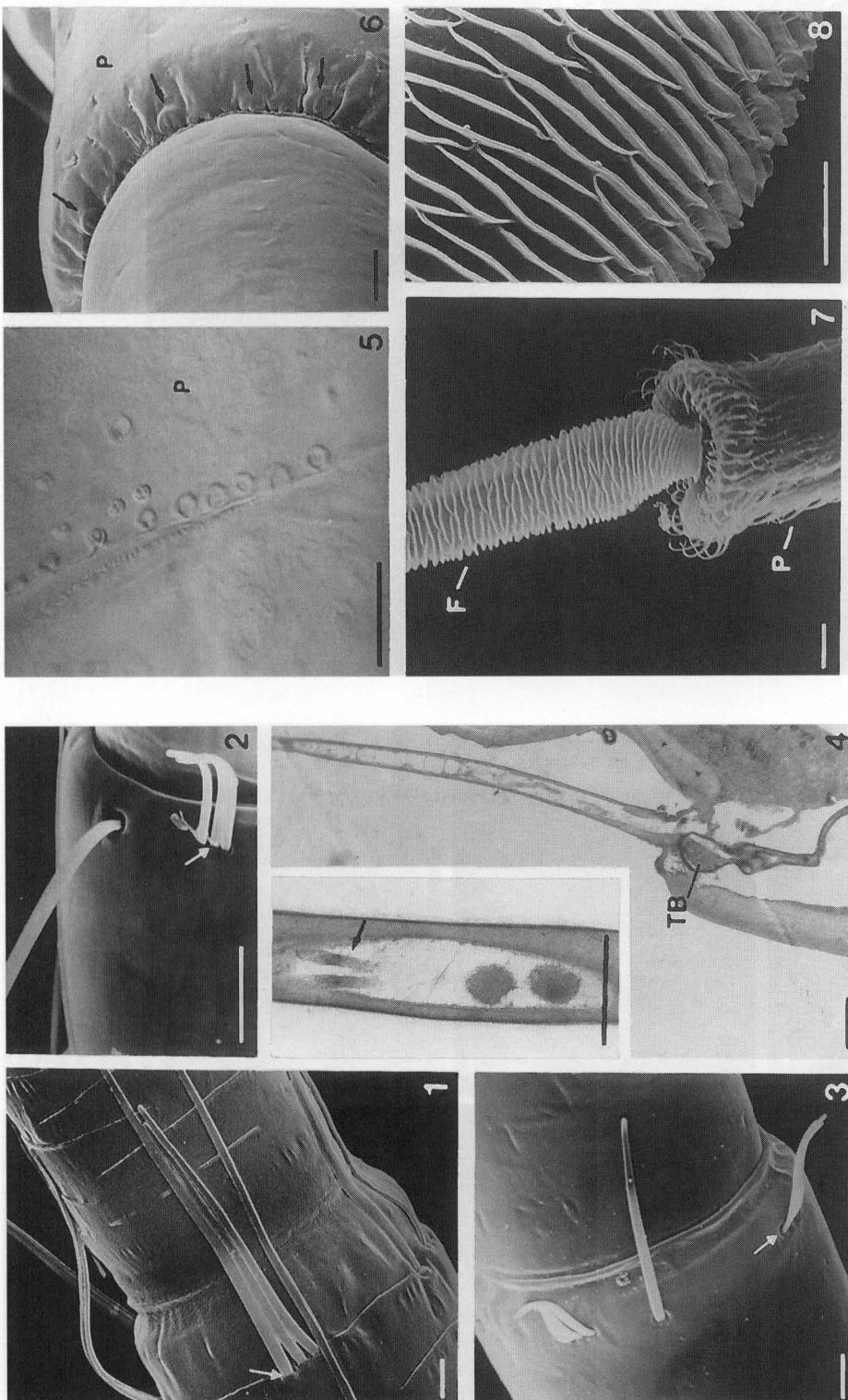
#### Ephemerellidae

Sensilla trichodea emerge in groups in the antennae of the nymphs of *Torleya major* (Fig. 24). The subimago exhibits the cuticular ribs (Fig. 25).

In the imago of *Ephemera ignita*, the pedicel is covered by scales compressing towards the flagellum (Fig. 26). Sensilla trichodea are present among the scales (Fig. 27).

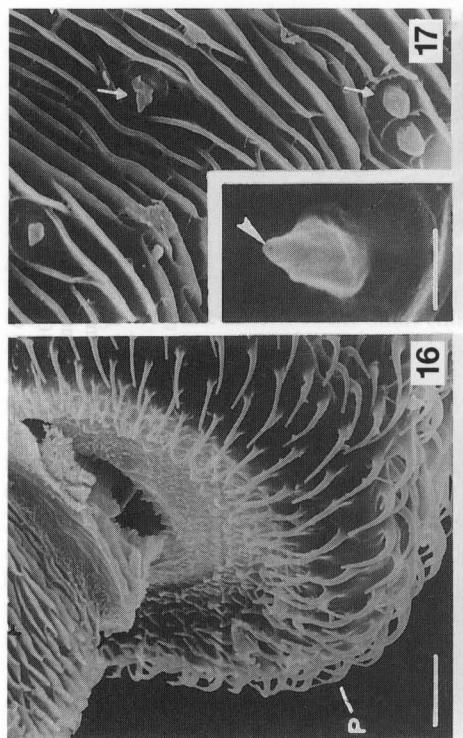
#### Caenidae

In the imago of *Caenis luctuosa*, scape and pedicel apparently lack sensilla. The pedicel has a wrinkled surface (Fig. 28) and shows a smooth cuticular ring in its apical region (Fig. 29). The flagellum shows a honeycomb-like cuticle (Fig. 29). Pits with emerging coeloconic sensilla are present along the ventral side of the flagellum (Fig. 30). The terminal region of the antenna has a tapered and pleated cuticle (Fig. 31).

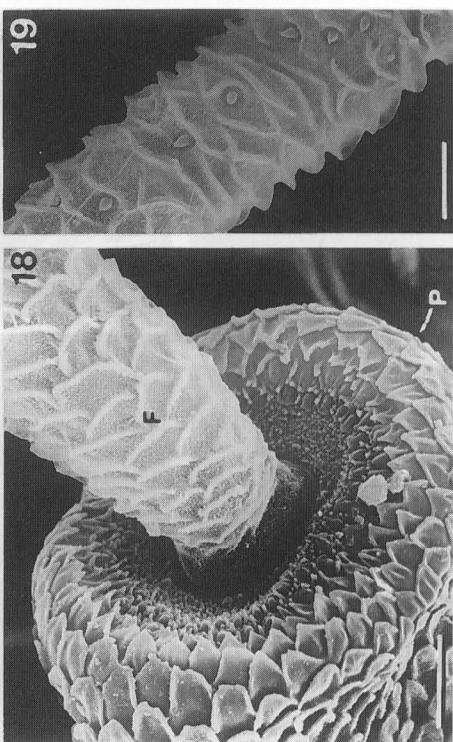
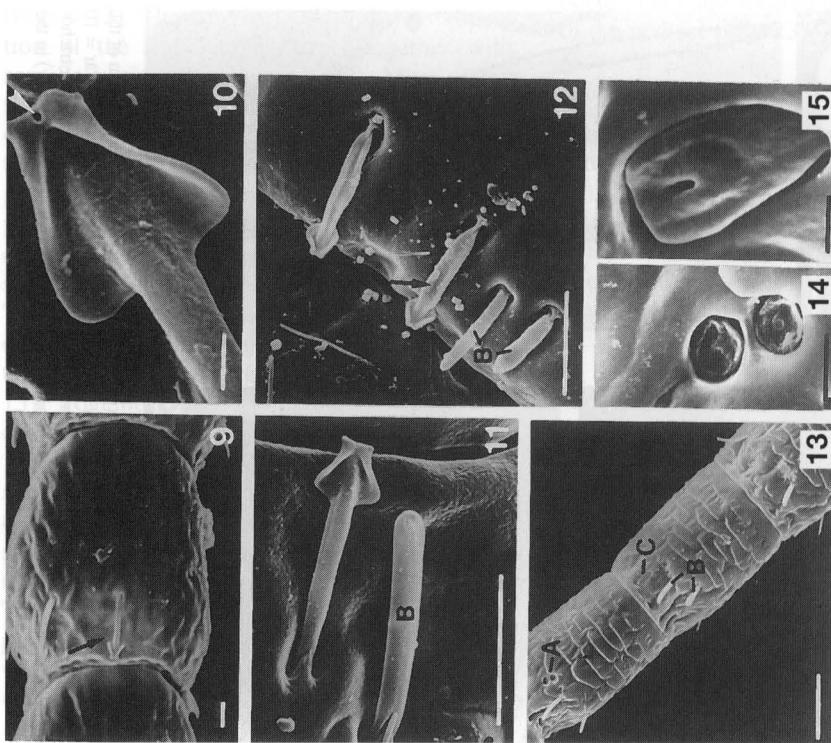


Figs 5-8. Sensilla of the nymph of *Choroterpes picteti* (5, 6) and of the subimago of *Habrophlebia eldae* (7, 8). 5: sensilla campaniformia on the distal part of the pedicel (P), under interference phase contrast microscope. Bar = 10 µm; 6: pedicel (P) showing the ring of sensilla campaniformia (arrows). Bar = 10 µm; 7: pedicel (P) with microtrichia and flagellum (F) with ribs. Bar = 10 µm; 8: ribs of the flagellum. Bar = 5 µm.

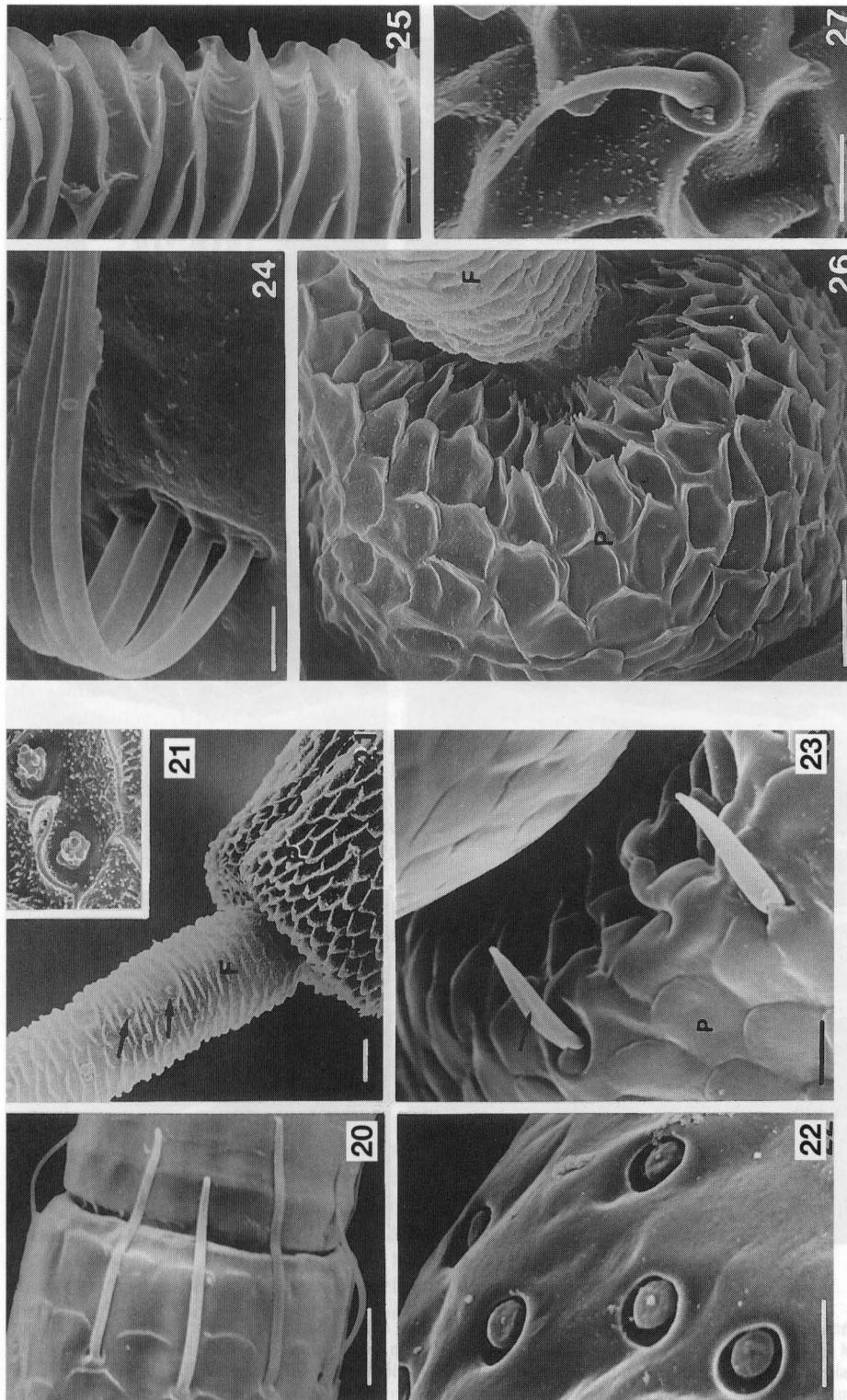
Figs 1-4. Sensilla trichodea emerging from their sockets (arrows) on the flagellum of the nymphs of *Habrophlebia eldae* (1). Bar = 1 µm; *Habroleptoides confusa* (2). Bar = 1 µm; *Choroterpes pectinata* (3). Bar = 2 µm; 4, longitudinal section of a sensillum trichodeum in *C. picteti* showing the tubular body (TB). Note the two dendrites (arrow) in the inset. Bars = 1 µm.



**Figs 9-15.** Antennal sensilla on the flagellar segments of the nymph of *Rhithrogena loyola* (9-11), *Epeorus sylvica* (12), *Ecdyonurus hevericus* (13-15). 9: flat-tipped sensillum (arrow). Bar = 10 µm; 10: apical pore (arrowhead) of a flat-tipped sensillum. Bar = 1 µm; 11: a flat-tipped sensillum with a sensillum basiconicum (B). Bar = 10 µm; 12: flat-tipped sensilla with a groove in their middle (arrow) and sensilla basiconica (B). Bar = 10 µm; 13: two kinds of coeloconic-like sensilla (A, C) on the distal portion of each antennal segment associated with sensilla basiconica (B). Bar = 20 µm; 14: enlarged view of porous sensilla (A in Fig. 13). Bar = 2.5 µm; 15: enlarged view of porous sensilla (C in Fig. 13). Bar = 1 µm.

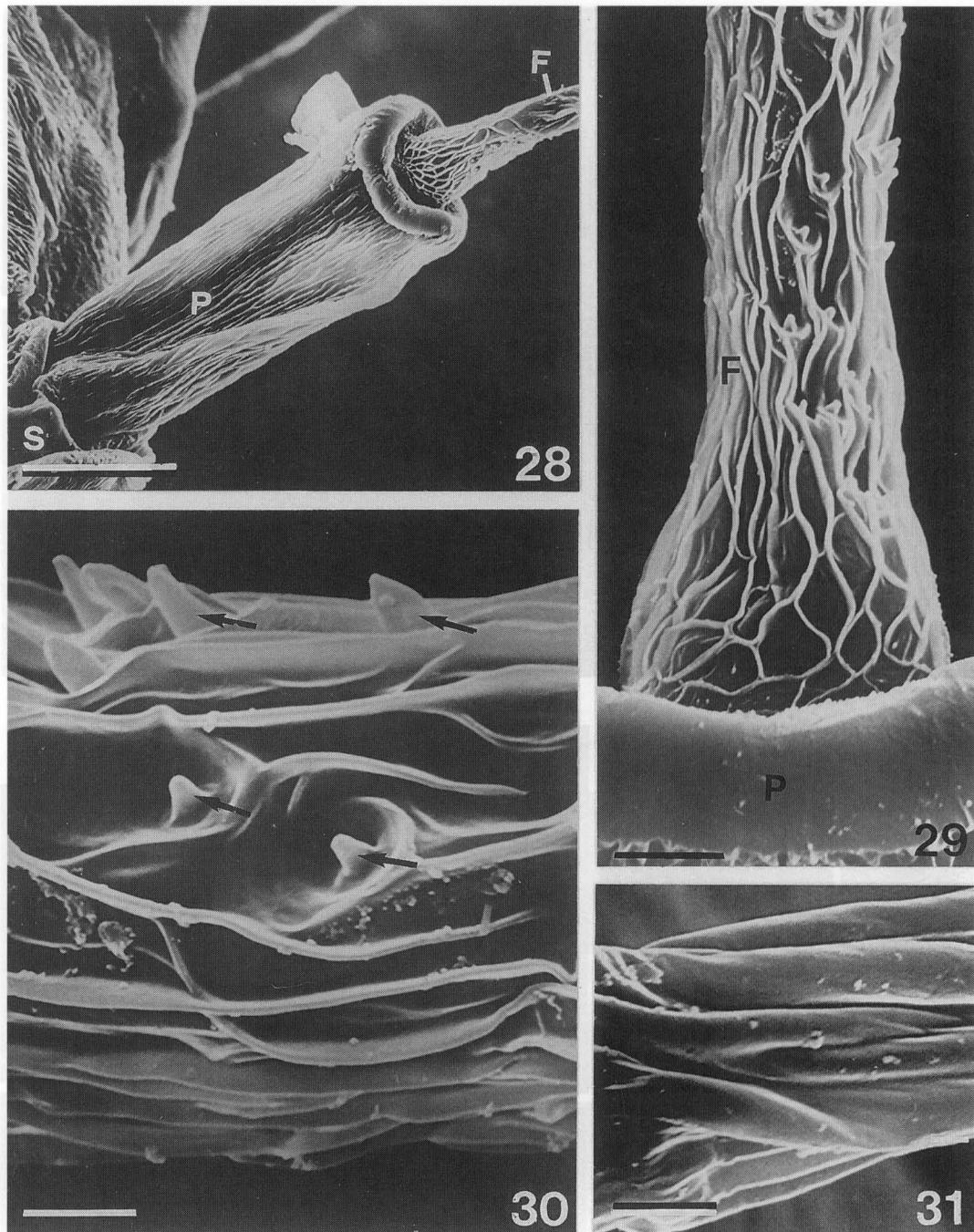


**Figs 16-19.** Antenna of the subimago (16, 17) and of the imago (18, 19) of *Electrogena grandiae*: 16: pedicel (P) covered by microtrichia and flagellum (F) uniformly ribbed. Bar = 10 µm; 17: sensilla coeloconica (arrows) on the ventral side of the flagellum. Bar = 5 µm. Magnification of one of them in the inset. Note the apical pore (arrowhead). Bar = 1.5 µm; 18: pedicel (P) with scales and flagellum (F) ribbed. Bar = 10 µm; 19: sensilla coeloconica among folds of the ventral side of the flagellum. Bar = 10 µm.



Figs 20-23. Antenna of the nymph (20) and of the imago (21) of *Cleon dipterum* and of the nymph of *Siphlonurus lacustris* (22, 23). 20: sensilla trichodea on the flagellum. Bar = 10 µm; 21: pedicel (P) with scales and flagellum (F) with folds. Bar = 10 µm. Sensilla coelocnica (arrows) are magnified in the inset; 22: sensilla placodea on the flagellum. Bar = 5 µm; 23: sensilla chaetica on the distal portion of the pedicel (P). Note the slight groove (arrow) in their middle. Bar = 5 µm.

Figs 24-27. Antenna of the nymph (24) and of the subimago of *Tortueya major* (25) and of the image of *Ephemerella ignita* (26, 27). 24: sensilla trichodea on the flagellum. Bar = 2.5 µm; 25: ribs on the flagellum. Bar = 5 µm; 26: pedicel (P) with scales compressing towards the flagellum (F). Bar = 10 µm; 27: a sensillum trichodeum on the pedicel. Bar = 2.5 µm.



Figs 28-31. Antenna of the imago of *Caenis luctuosa*. 28: scape (S), pedicel (P) and flagellum (F). Bar = 50 µm; 29: distal portion of the pedicel (P) along its smooth cuticular ring and flagellum (F) with a honeycomb-like organization of the cuticle. Bar = 10 µm; 30: sensilla coeloconica (arrows) on the ventral side of the flagellum. Bar = 2,5 µm; 31: distal portion of the flagellum. Bar = 2,5 µm.

## DISCUSSION

Larval stages and adults of mayflies live in different habitats and they require specialized sensillar devices adapted to work in both aquatic and air condition. Under SEM, mayfly sensilla show a wide range of diversification but, at present, it is difficult to establish a clear relationship between the morphology and the specific function they perform. Indeed, it is well known that sensory systems can be tested only by means of TEM investigation coupled with electrophysiological analysis (ZACHARUK, 1985).

In the present study, mayfly sensilla have been tentatively classified on the basis of their external morphology and included into the general categorization proposed for insects (SCHNEIDER, 1964; ZACHARUK, 1985). Since a mechano-chemosensitive function has been assessed only for the sensilla trichodea of *Choroterpes picteti*, the probable functions of the other sensilla can be suggested from analogy with receptors of known function described in other insect species. The morphological traits are consistent with the occurrence of sensilla trichodea (Leptophlebiidae, Heptageniidae, Baetidae, Ephemerallidae), campaniformia (Leptophlebiidae), coeloconica (Baetidae, Caenidae), basiconica (Heptageniidae), placodea and chaetica (Siphlonuridae). Sensilla campaniformia are mechanoreceptors and they probably sense the movements of the flagellum over the pedicel (KAPOOR, 1991). Sensilla coeloconica and basiconica perform different functions and their internal organization is crucial for assessing a specific task. Sensilla placodea are reported to be chemosensory (ZACHARUK, 1985). The occurrence of an apical pore in the peculiar flat-tipped sensilla found in *Rhithrogena loyolaea* and *Epeorus sylvicola* might be consistent with a gustatory function (GAINO & REBORA, 1996).

Compared with adults, mayfly nymphs show more numerous types of sensilla. This feature is in agreement with previous investigations carried out by KAPOOR (1985) on the stonefly *Paragnetina media*. In this species the absence of nymphal sensilla in the adults reflects a specialization of the sensory system for different environmental requests.

Mayfly nymphs are strictly aquatic and require diversified sensilla in order to acquire informa-

tion about environmental conditions. During the short and unfeeding adult phases, hygrosensitivity is of paramount importance to avoid dehydration. It seems acceptable to assume that the aporous sensilla coeloconica of the flagellum could be hygrosensory. This in view of the external morphological characteristics exhibited by this kind of receptors (ALTNER & LOFTUS, 1985).

As far as mating is concerned, sight seems to allow males to reach females (BRINCK, 1956); the presence of pheromones is hypothesized only in species with small eyes that mate at night (MCCAFFERTY & BLOODGOOD, 1989). We found no evidence of sexual dimorphism in antennal receptors, which are notoriously involved in intersexual communication (HARBACH & LARSEN, 1977; CUPERUS, 1985; FAUCHEUX, 1991; NEWMAN *et al.*, 1993; MELLOR & ANDERSON, 1995; JOURDAN *et al.*, 1995). This feature agrees with the predictions of the lack of reception of sex attractant in mayflies whose distinct and finite timing of emergence (BRITAIN, 1982) could favor mating and swarming.

Comparative studies on antennal sensilla have evidenced the taxonomic applications of such receptors (ROSS, 1992; WCISLO, 1995), sometimes utilized to resolve difficult questions (CATALÁ & SCHOFIELD, 1994). The occurrence of two very similar kinds of flat-tipped sensilla in *Rhithrogena* and *Epeorus* stresses the relationship between these genera considered to be adelphotaxa (TOMKA & ELPERS, 1991).

In conclusion, SEM analysis of the antennal sensilla highlighted the morphological variety of these sensory systems in mayflies. This diversification, other than reflecting the taxonomic position of the species, represents a starting point for further investigations in such a field. This in order to ascertain the relationship between these insects and their environment together with the possible intra- and interspecific communication.

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