Antennal sensilla of the armoured ground cricket, *Eugaster powysi* Kirby, 1891 (Orthoptera, Tettigoniidae, Hetrodinae)

Sensilles antennaires d'Eugaster powysi Kirby, 1891
(Orthoptera, Tettigoniidae, Hetrodinae)

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Abstract. Sensilla on the antennae of the adult armoured ground cricket, *Eugaster powysi*, were studied using scanning electron microscopy to determine the sensilla morphology and their possible chemo- and mechanoreceptive functions for food detection. Twelve types or subtypes occur in males and thirteen in females: aporous sensilla chaetica (62.6 % of total sensilla in males, 63.5% in females) with a tactile mechanoreceptive function; uniporous sensilla chaetica of three subtypes (12.5-12.7%) with a contact chemoreceptive function; multiporous sensilla trichodea (5.6-7.9%); multiporous sensilla basiconica of three subtypes (13.1-13.9%); multiporous sensilla coeloconica (0.8-0.9%), all multiporous sensilla being olfactory receptors; aporous sensilla coeloconica (2.2%) and aporous sensilla coelocapitula (0.1% in female) with a possible thermo- hygroreceptive function; aporous Böhm sensilla (0.4-0.5%) and sensilla campaniformia (0.5-0.6%) which are proprioceptors. These results are related to the behaviour of *Eugaster* and compared with those obtained in other Orthoptera, Mantodea and Blattodea.

Keywords: *Eugaster*, Tettigoniidae, antenna, sensilla, behaviour.

Résumé. Les sensilles des antennes d'*Eugaster powysi* sont étudiées en microscopie électronique à balayage afin de déterminer leur morphologie et leur fonction chimio- et mécanoréceptrice intervenant lors de la détection de la nourriture. Douze types ou sous-types de sensilles existent chez les mâles et treize chez les femelles : sensilles chétiformes sans pore (62.6 % du total des sensilles chez les mâles, 63.5% chez les femelles) à fonction mécanoréceptrice tactile ; trois sous-types de sensilles chétiformes unipores (12.5-12.7%) à fonction chimioréceptrice de contact ; sensilles trichoïdes multipores (5.6-7.9%), trois sous-types de sensilles basiconiques multipores (13.1-13.9%) ; sensilles coeloconiques multipores (0.8-0.9%), toutes ces sensilles multipores étant des récepteurs olfactifs ; sensilles coeloconiques sans pore (2.2%) et sensilles coelocapitées sans pore (0.1%) avec une fonction thermo-hygroréceptrice possible ; sensilles de Böhm sans pore (0.4-0.5%) et sensilles campaniformes (0.5-0.6%) qui sont des proprioceptrices. Ces résultats sont reliés au comportement d'*Eugaster* et comparés à ceux obtenus chez les autres Orthoptères, les Mantes et les Blattes.

Mots-clés: *Eugaster*, Tettigoniidae, antenne, sensilles, comportement.

INTRODUCTION

The sub-family Hetrodinae includes a large number of African taxa. In North Africa, it is represented by a single genus *Eugaster* Serville, 1839 (armoured ground crickets, armoured katydids). This genuse latter includes large insects which somewhat resemble bush crickets *Ephippiger* Berthold, 1827 but which are easily distinguished by inspection of their thorax, which is covered with large spikes and by the much reduced size of the oviscapt of females (Chopard 1943). In all species, the head is large and the eyes are globular and protruding. The elytra of males are squamiform and hidden beneath the pronotum; those of the females are absent. The hind wings are absent in both sexes. All the legs are short. The anterior tibiae possess a tympanum in the form of a slit. The abdomen is bulky, ovoid and smooth. The cerci are short and blunt. The oviscapt is very short with large upper valves and lower ones that are straight and sharp (Fig. 1).

Eugaster are heavy insects incapable of jumping and easy to capture. Despite their bulky appearance and scary-looking armature, the armoured katydids are completely harmless. Their prothoracic spines and horns likely offer protection against predatory birds and lizards. Their other defence is reflexive bleeding; *Eugaster* sp. responded to handling by squirting haemolymph from pores located on the first two pairs of legs between the coxa and the trochanter (Chopard 1943). But unlike certain beetles which use the mechanism of reflexive bleeding and whose blood haemolymph contains cantharidin that of the armoured katydids is not toxic. They are generally found on the ground or on bushes (Fig. 1). They are mainly herbivorous and they feed on all kinds of plants (Chopard 1943). The males give off a brief muffled stridulation which produces a humming sound that can be heard from quite a distance. Our colleague, Mbarek Agnas, has been of great help and competence in locating these insects.

Eight species of *Eugaster* have been identified in Morocco by Chopard (1943). Later, Grzeschik (1969) distinguished only two species, characterised by the usually whitish colour of the first of these (*E. spinulosa* (Johansson, 1764)) and the brown or black colour of the second (*E. guyoni* (Serville, 1833)), each of them being represented by several subspecies. At the same time, in the same location, individuals specimens that are blackish, or very light in colour and all the intermediary shades can be found together or even in pairs copulating, (Defaut 1988; and our own observations). The individuals captured at Oualidia among White broom *Retama monospema* (Linnaeus) Boissieu, 1840 (Fabaceae) were determined by Bernard Defaut as being *Eugaster powysi* Kirby, 1891.

Figure 1. *Eugaster powysi*. **a**, **b**. habitus of male; **c**. female.

The females, which are relatively rare, possessed very visible abdominal patches of colour; the males were either identical to the females or a shade darker or completely black (Fig. 1)

The antennae of the Caelifera (short-horned grasshoppers), principally the Acrididae family, have been quite thoroughly studied (Slifer *et al*. 1959, Riegert 1960, Bland 1982, 1989, 1991, Ameismeier 1985, Chapman & Greenwood 1986, Ochieng & Hansson 1996, Ochieng *et al*. 1998, Chen *et al*. 2003, Bonsel 2004, Li *et al*. 2007). However, those of Ensifera (long-horned grasshoppers, katydids, bush crickets) have been much less observed (Otte & Cade 1976, Rence & Loher 1977, Hardy & Shaw 1983, Faucheux 1994, Goasmat & Faucheux 2011, Kostromytska *et al*. 2015)

The antennal sensilla of *Ephippiger* sp., whose behaviour compare with that of *Eugaster*, have not to our knowledge been the object of any particular study. It therefore seems worthwhile to compare a wingless and slow-moving species such as *E. powysi* with winged and lively species like most other grasshoppers. Moreover, making use of earlier studies, we shall look for common points and differences among the Orthopteroïds, such as the Mantodea, Blattodea and Orthoptera.

MATERIAL AND METHODS

Adult of *E. powysi* (three males and three females) were collected at Oualidia (Atlantic coast of Morocco) in August 2014 and October 2015, among *Retama monosperma* (Fabaceae). For scanning electron microscopy (SEM) study, the antennae of both sexes were cut into several pieces, cleaned in acetone, dehydrated in pure alcohol, and mounted both on the dorsal and the ventral face, on specimen holders. After coating with gold and palladium, preparations were examined in a Jeol J.S.M. 6 400F SEM at 10 kV.

Counts of the sensilla were made on the dorsal side and the ventral side of the antennae in 3 males and 3 females by using the SEM at different magnifications. The total number of pores on the surface of each sensillum was measured directly from SEM micrographs. To determine whether pore density was even all around the circumference of sensilla, 10 measurements were taken: 5 on the outer surface and 5 on the inner surface of another antenna. Sensillum terminology follows Zacharuk (1980), Altner & Prillinger (1980), and Faucheux (1999).

Gross morphology

According to different authors (Roth & Wallis 1952, Slifer 1968, Goasmat & Faucheux 2011), it is difficult to determine the maximum length of a cockroach's or a cricket's antenna since these insects often bite off the distal portion. The six individuals examined here had antennal tips which had obviously been more or less injured. The males, although smaller than the females, have antennae as long (43 mm, 44.5 mm, 45 mm) as those of the females (40 mm, 45 mm, 46 mm); the numbers of antennomeres are 73, 74, 76 (males) and 68, 73, 76 (females).

The two basal antennomeres are the scape and the pedicel. The scape is a stout cylinder, 1.50-1.52 mm in length and

1.10-1.13 mm in cross section at mid-length. The pedicel is cylindrical and measures 1.03-1.06 mm in length and 0.71-0.73 mm in diameter at the distal tip.

RESULTS

The third antennomere, or first flagellomere, is called the meriston in Blattodea, Mantodea, and Orthoptera (Fig. 2a); it contributes to the formation of new flagellomeres during postembryonic development in these insects and more generally in insects possessing a large number of flagellomeres.

Sensilla

Twelve types or subtypes of sensilla are present on the antennae in males and thirteen in females (Fig. 2g, h): aporous sensilla chaetica ASC, uniporous sensilla chaetica comprising three subtypes USC1, 2, 3, multiporous sensilla trichodea MST, multiporous sensilla basiconica comprising three subtypes MSB1, 2, 3, multiporous sensilla coeloconica MSCo, aporous sensilla coeloconica ASCo, aporous sensilla coelocapitula ASCc (only in females), aporous Böhm sensilla ABS, and aporous sensilla campaniformia ASCa. The number of sensilla varies in relation to the situation of the flagellomere on the antenna (Fig. 2d-f).
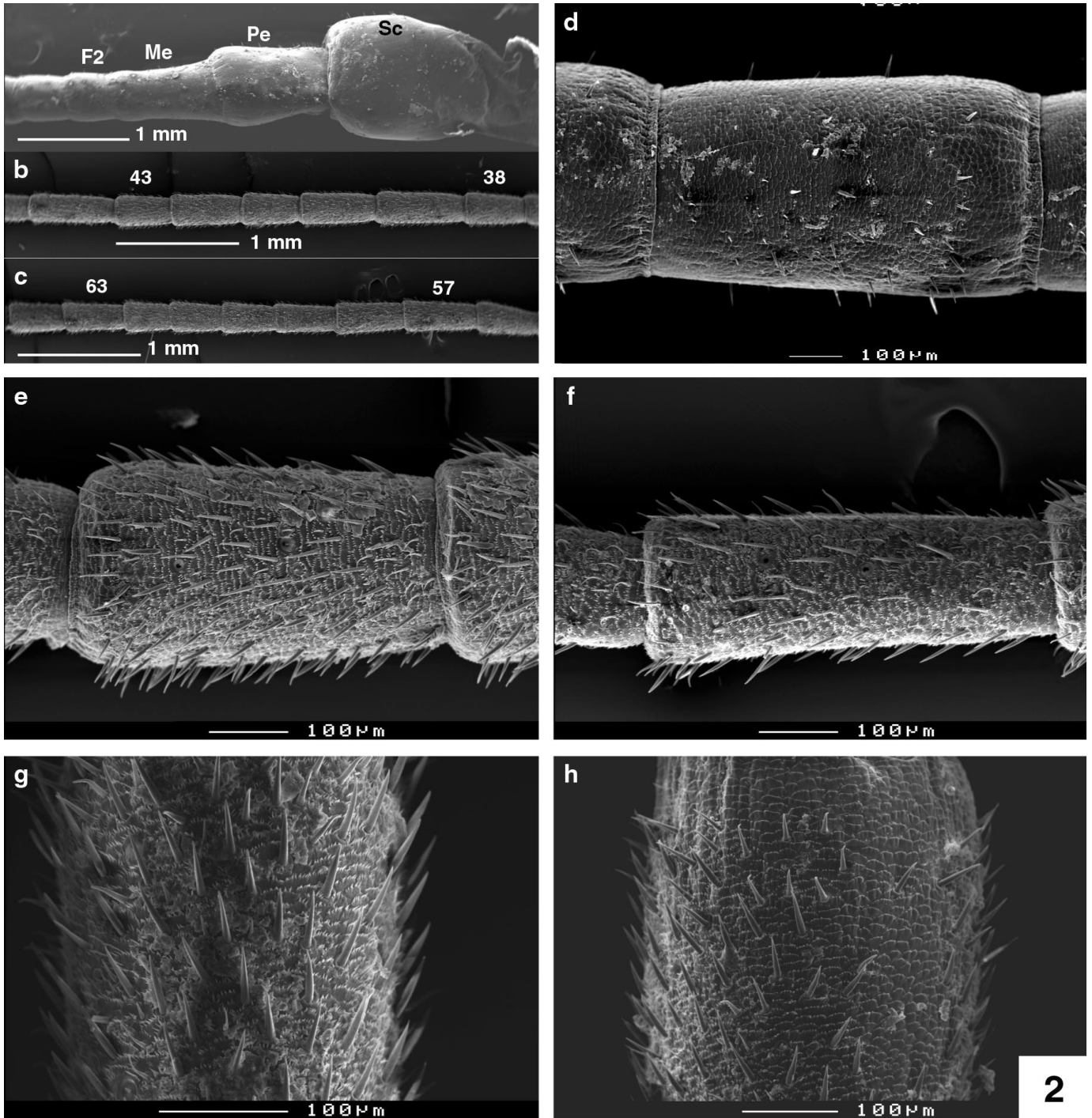

Figure 2. *Eugaster powysi*, **a-f**. male antenna, dorsal face; **a**. base showing scape Sc, pedicel Pe, meriston Me, 2nd flagellomere F2; **b**. 38-43th flagellomeres; **c**. 57-63th flagellomeres; **d**. 11th flagellomere; **e**. 40th flagellomere; **f**. 68th flagellomere; **g**. 47th flagellomere, male ventral face; **h**. 47th flagellomere, female ventral face.

Aporous sensilla chaetica (ASC)

The ASC are the commonest sensilla (C1, Fig. 3a, b, c); they are present from the first antennomeres onwards. They are 46.0-48.0 µm in length and 7.5-8.0 µm in basal diameter (Fig. 3d). They maintain their diameter from the base to mid-length but then it diminishes regularly up to the apex of the hair. The ASC are inserted in a short socket measuring 12.2 µm in outer diameter and 9.5 µm in inner diameter. They have a length close to that of the uniporous sensilla chaetica, but they differ by their slight flattened form and above all by their sharp tip measuring less than 0.2 µm (C1, Fig. 3d, e). No wall pores or terminal pore were observed. However, an ecdysial pore is visible at mid-length in some sensilla. Their wall possesses 25-30 ribs which are parallel at the base but then become oblique (C1, Fig. 3c, d). The ASC are all directed towards the distal part of the flagellomeres, forming an angle of 45° with the antennal integument (Fig. 3c).

Uniporous sensilla chaetica (USC) C2 C3 C4

Three subtypes of USC (C2, C3 and C4) are present on the antennae of both sexes. They can be confused with the previous sensilla; however, they are never sharp-ended but blunt-tipped (Fig. 3b).

USC subtype 1 are identifiable on the lateral edges of the flagellomeres seen dorsally (C2, Fig. 3a, b). They are lined up and regularly spaced out. Unlike the ASC and other subtypes of USC, these sensilla are set up at a right angle in relation to the antennal integument (Fig. 3a). They are 36.9-37.8 µm long, and 4.8-5.4 µm in basal diameter. These slender sensilla frequently possess a curved tip and are endowed with a transversal furrow (C2, Fig. 4a). This apex has a cylindrical form and a diameter of between 1.2 and 1.5 µm which corresponds to a ¼ of the basal diameter (Fig. 4b). The apical pore has a diameter of 0.32-0.36 µm. Their basal socket resembles that of the aporous sensilla chaetica C1.

The wall possesses about 26 ribs at the base and 16 ribs at the apex. These sensilla are situated almost exclusively on the dorsal face of flagellomeres and their number is about 15 per flagellomere.

USC subtype 2 is the most numerous of the three subtypes (C3, Fig. 3a, b). They are thick-set sensilla, 32.0-55.0 µm long, and 7.5 µm in basal diameter, and are inserted in a basal socket with 15.0 µm outer diameter and 10.0 µm inner diameter (C3, Fig. 4c).
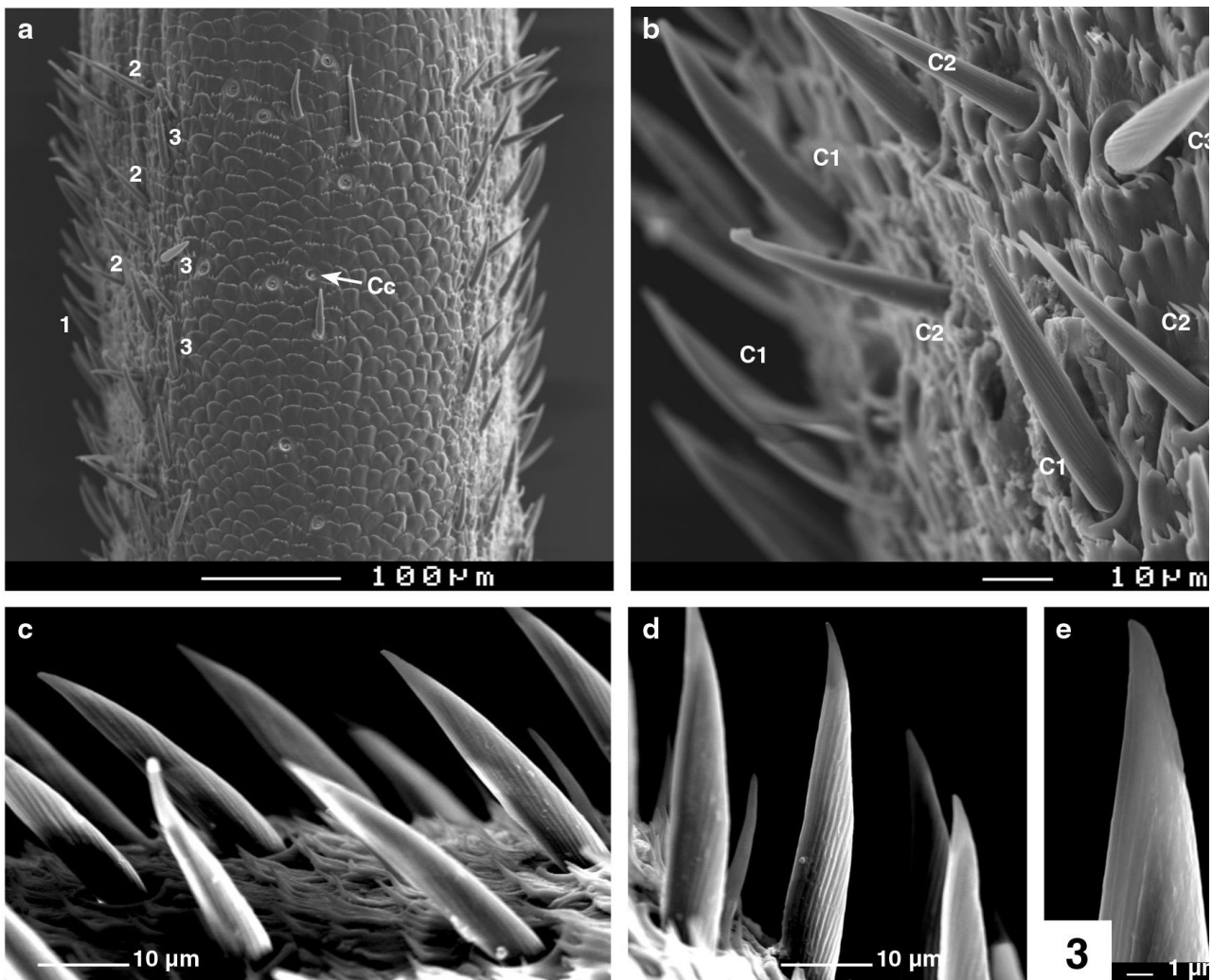

Figure 3. *Eugaster powysi*, female antenna; **a**. distribution of aporous sensilla chaetica (1) and uniporous sensilla chaetica (2, 3) on a flagellomere; Cc, sensilla coelocapitula; **b**. detail showing aporous sensilla chaetica C1, uniporous sensilla chaetica (C2, C3); **c. d**. some aporous sensilla chaetica C1; **e**. detail of apex of C1 without pore.

USC subtype 2 is the most numerous of the three subtypes (C3, Fig. 3a, b). They are thick-set sensilla, 32.0-55.0 µm long, and 7.5 µm in basal diameter, and are inserted in a basal socket with 15.0 µm outer diameter and 10.0 µm inner diameter (C3, Fig. 4c). They possess the form of an elongated cone sometimes with a sudden narrowing towards the distal third of the sensillum. The wall reveals 15 to 20 contiguous ribs, at times separated from one another by a delicately striated space; they are V-shaped at the base and on the external surface, but oblique towards the apex. An ecdysial pore is located in the proximal third of the sensillum (C3, Fig. 4c). A terminal, apical or subapical, pore, 0.4 µm long, is clearly visible in most sensilla (Fig. 4d). When the pore is subapical, it is visible only on one side of the hair. Thus, even when present, this pore may escape attention. Since all these sensilla chaetica are identical as regards their overall morphological characteristics, we can reasonably assume that they all possess a terminal pore.

USC subtype 3 is the rarest of the three subtypes. They are short sensilla, 18.4-20.6 µm long, with a basal diameter of 6.1-6.5 µm and a distal diameter of 3.6-3.7 µm (C4, Fig. 4e). The hair is inserted into a socket (17.5 µm in outer diameter, 12.5 µm in inner diameter), which forms an internal cuticular fold whose inner diameter of 9.4 µm limits the movements of the hair (Fig. 4e). A terminal pore, 0.42 µm in diameter, is present at the truncated tip (Fig. 4f). The wall cuticle possesses some twenty somewhat less raised ribs that are less visible than those of previous sensilla and are frequently obstructed by a transversal cuticular network (Fig. 4e).

Distribution and number of sensilla chaetica (ASC and USC)

There is no difference in the arrangement of sensilla between male and female antennae. The sensilla chaetica appear progressively from the 8th flagellomere (F8). On F11, the dorsal surface of the male antenna bears 27-30 sensilla chaetica concentrated on the distal region (Fig. 2d). From F20 to F35, 110 to 120 sensilla are present all over each segment. From F36 to F45, the number of sensilla is close to 105 per segment (Fig. 2e). It increases from F46 to F60 by 105 to 120 sensilla. From F65 on, this number diminishes and it amounts to 60 sensilla on F68 (Fig. 2f). The ventral surface of male antenna possesses more sensilla chaetica than the dorsal surface. On F65, there are about 92 dorsal sensilla and 20 ventral ones. In both sexes, the flagellomeres sometimes have on their dorsal face a media-longitudinal zone that is poorly endowed by sensilla, but on the remainder of this surface, the density of the sensilla is greater; the lateral sensilla chaetica are then closer together.

The female antenna is less richly endowed with sensilla chaetica than that of the male (Fig. 2g, h). For example, the dorsal face of F45 comprises 105 sensilla for the male and 90 for the female. The total numbers of sensilla chaetica (ASC + USC) per antenna has been estimated for the male at 6460 (dorsal face) and 8100 (ventral face) with a total of 14560 sensilla; with, for the female, 6390 (dorsal face) and 7930 (ventral face) for a total of 14320 sensilla. The aporous sensilla chaetica C1 are the most numerous antennal sensilla: 62.6% in males and 63.5% in females. The uniporous sensilla chaetica of all types represent 12.5% of total sensilla in males and 12.7% in females (Tab. 1).

Sensilla	Male	Female
Aporous sensilla chaetica	12140 (62.6%)	11930 (63.5%)
Uniporous sensilla chaetica(all types)	2420 (12.5%)	2390 (12.7%)
Multiporous sensilla trichodea	1430 (7.9%)	1050 (5.6%)
Multiporous sensilla basiconica (all types)	2540 (13.1%)	2610 (13.9%)
Multiporous sensilla coeloconica	170 (0.8%)	165 (0.9%)
Aporous sensilla coeloconica	430 (2.2%)	420 (2.2%)
Aporous sensilla coelocapitula		20 (0.1%)
Aporous Böhm sensilla	80 (0.4%)	80 (0.5%)
Aporous sensilla campaniformia	110 (0.5%	110 (0.6%)
Total	**19320**	**18775**

Table 1. Average numbers and percentages of sensilla on a male and a female antenna of *Eugaster powysi* (3 individuals of each sex).

Multiporous sensilla trichodea (MST)

The sensilla trichodea are the longest of the multiporous sensilla and they are characterized by a diameter which diminishes progressively from the base to the sharp apex; they possess an obvious curved shape (Tr, Fig. 5a). They measure 28.0 µm in length, 3.6 µm in basal diameter and 1.7 µm at mid-length. The basal socket has an outer diameter of 10.0 µm and an inner one of 4.5 µm. Some twenty longitudinal striae are spread over the whole of the hair.

They are oblique at the base and barely visible in the middle of the hair. The wall pores are longitudinally lined up, oval and measure from 117 nm to 176 nm. The pore density is 10-11 pores per μm^2 (Fig. 5b).

The MST, easily recognizable from their length and their curved appearance, are grouped together and lined up for the most part near the proximal edge (Fig. 2e, f) and sometimes on the distal edge of the flagellomere as well. Their number is estimated as 1430 sensilla per antenna in males and 1050 sensilla in females, i.e. 7.9-5.6% of antennal sensilla (Tab. 1).
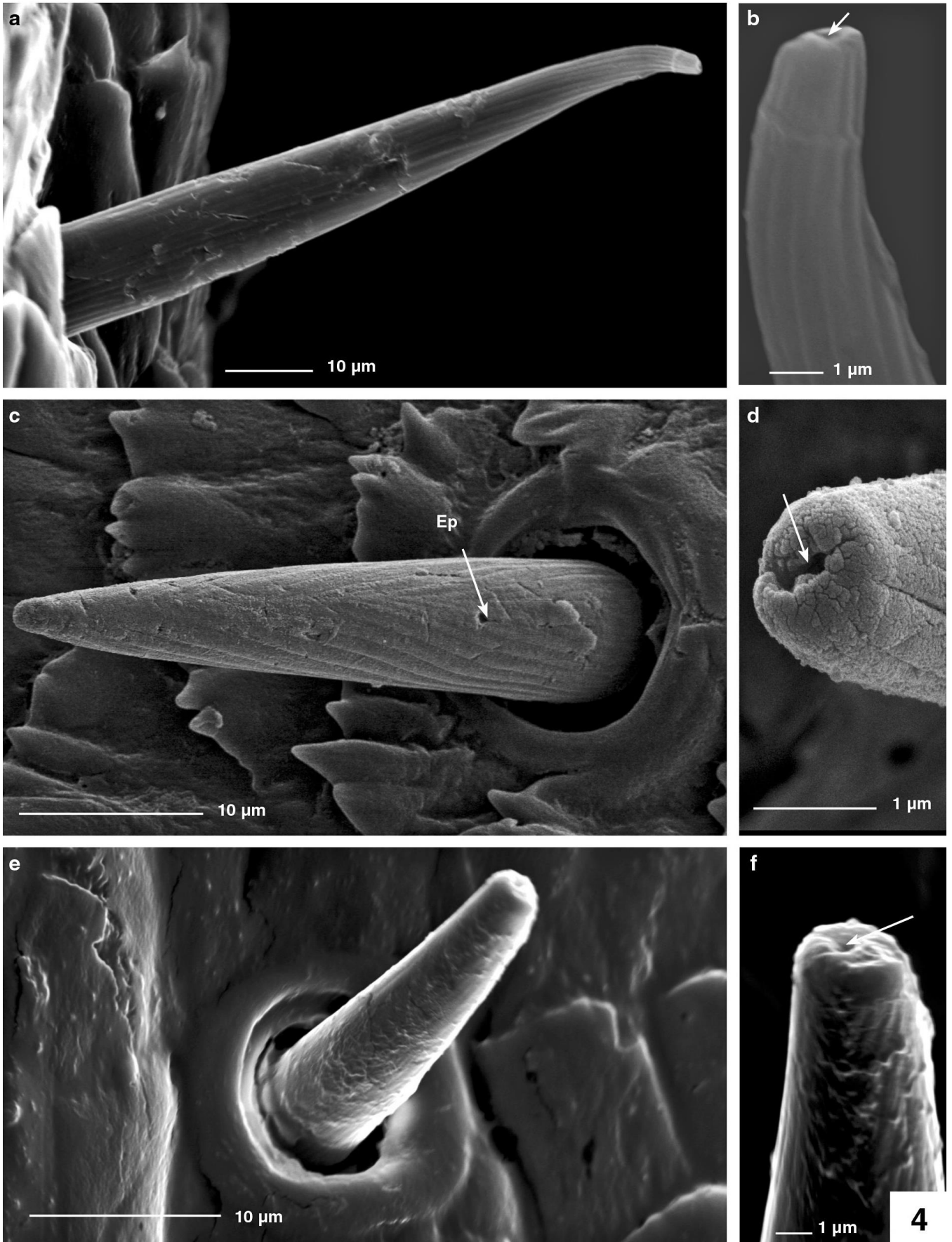
Figure 4. *Eugaster powysi*, female antenna, uniporous sensilla chaetica; **a**, **b**. sensillum C2 and detail of terminal pore (arrow); **c**, **d**. sensillum C3 with detail of terminal pore (arrow) and ecdysial pore Ep; **e**, **f**. sensillum C4 and detail of terminal pore (arrow).
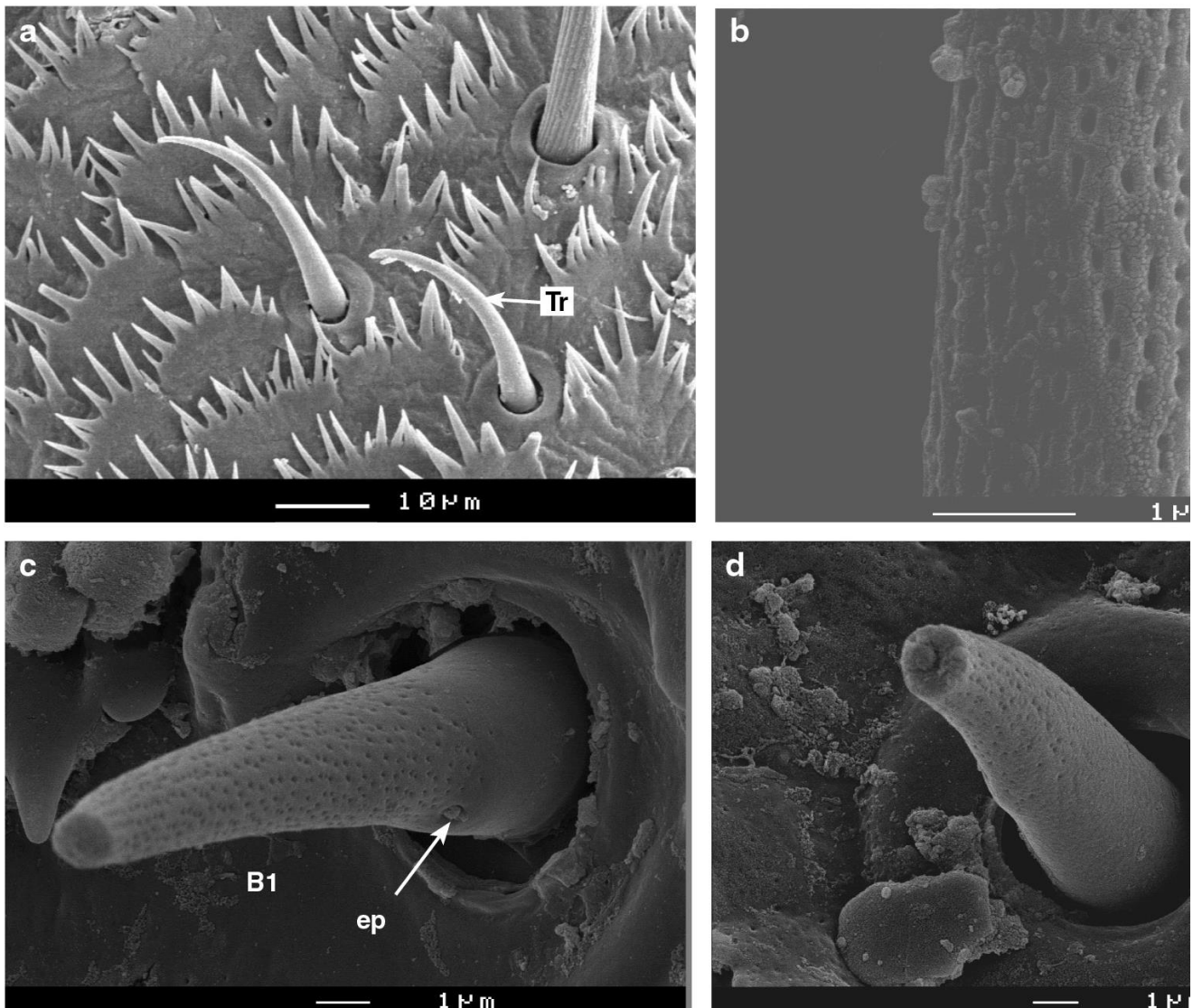
Figure 5. *Eugaster powysi*, male antenna; **a**. group of 2 multiporous sensilla trichodea Tr; **b**. wall pores of Tr; **c**. multiporous sensillum basiconicum subtype 1, B1 showing the ecdysial pore ep; **d**. wall pores of B1.

Multiporous sensilla basiconica (subtype 1) (MSB1)

Three subtypes of multiporous sensilla basiconica can be distinguished; they differ by their length, and the diameter and density of wall pores. MSB1 are 10.3 μm long, 3.8 μm in basal diameter and 2 μm at mid-length (B1, Fig. 5c). They are inserted in a basal socket of 6.4 μm in outer diameter and 5.7 μm in inner diameter. The wall pores, longitudinally lined up, appear only at 2 μm of the base, at the level of the ecdysial pore (Fig. 5c). They are circular and show a variable diameter from 59 nm to 117 nm (Fig. 5d). The pore density at mid-length is 16-18 pores per μm^2. An ecdysial pore is present at the base of the peg (ep, Fig.5c).

Multiporous sensilla basiconica (subtype 2) (MSB2)

MSB2 are rarer than the MSB1 and are always spread about unlike the previous sensilla which exist in groups (B2, Fig. 6a). They are curved like the preceding ones but much shorter (10-13 μm), and flattened at the base which measures 3.6 μm; they narrow suddenly towards the truncated-tipped apex (Fig. 6b). The ecdysial pore is situated at 4 μm from the base (ep, Fig. 6b). The wall pores are not lined up; they have a diameter of 45-90 nm and the pore density is 8-13 pores per μm^2 (Fig. 6c).

Multiporous sensilla basiconica (subtype 3) (MSB3)

MSB3 are short, cone-shaped sensilla of 6.5 μm in length with a diameter of 3.0 μm at the base and 2.6 μm at mid-length (B3, Fig. 6d). The cone narrows at mid-length from an ecdysial pore (ep) of great size onwards (ep, Fig. 6d, e). The basal socket, 8.6 μm in outer diameter and 5.0 μm in inner diameter, appears very wide in relation to the sensory cone. The wall pores, of 42-82 nm in diameter, have a density of 10-12 pores per μm^2 (Fig. 6e). These sensilla are easily identifiable because of their short length and are rare and grouped together in twos (Fig. 6a).

Distribution and number of sensilla basiconica

In the male, subtypes B1 and B2 sensilla basiconica appear together from the 10th flagellomere F10 onwards. On F11, some 15 sensilla occur on the proximal region of the segment (Fig. 2d). MSB3 appear from F12. On the following flagellomeres, the three types of sensilla basiconica are present. For instance, the flagellomeres F28, F40, F48 and

F68 of the male bear respectively 20, 27, 45 and 25 dorsal sensilla. The ventral sensilla are slightly fewer in number but the differences are largely insignificant. The female antenna shows a distribution of MSB identical to that of the male: for the same segment, 27 sensilla were counted in the male and 19 sensilla in the female. MSB1 and MSB2 are scattered on each flagellomere. MSB3 are always rare (no more than 4 per segment) and grouped together in the median region. The total number of sensilla basiconica, all types, per antenna is 2540 in males and 2610 in females, i.e. 13.1-13.9% of total sensilla (Tab. 1).

Multiporous sensilla coeloconica) (MSCo)

MSCo are pegs 6.0 μm long, 2.0 μm in basal diameter and 1.5 μm large at mid-length; they are smooth in the proximal half and covered by some twenty ribs or finger-shaped processes in the distal half (Co1, Fig. 7b). They possess a barely raised basal ring of 6.0 μm in diameter. Each peg is situated in a circular pit with a flat bottom of 16 μm in diameter and 1.5 μm in depth (Fig. 7a).The microtrichia, which prolong the cuticular scales of the integument surround the pit and resemble the fringe of microtrichia of the multiporous sensilla coeloconica of lepidopterans. They are frequently associated with sensilla coeloconica subtype 2 (Fig. 6f) and are present on the dorsal and ventral faces in both sexes but are always found in small numbers: 1-3 per flagellomere (Fig. 6f). Their number per antenna is 170 in males and 165 in females, i.e. 0.8-0.9% of total sensilla (Tab. 1).
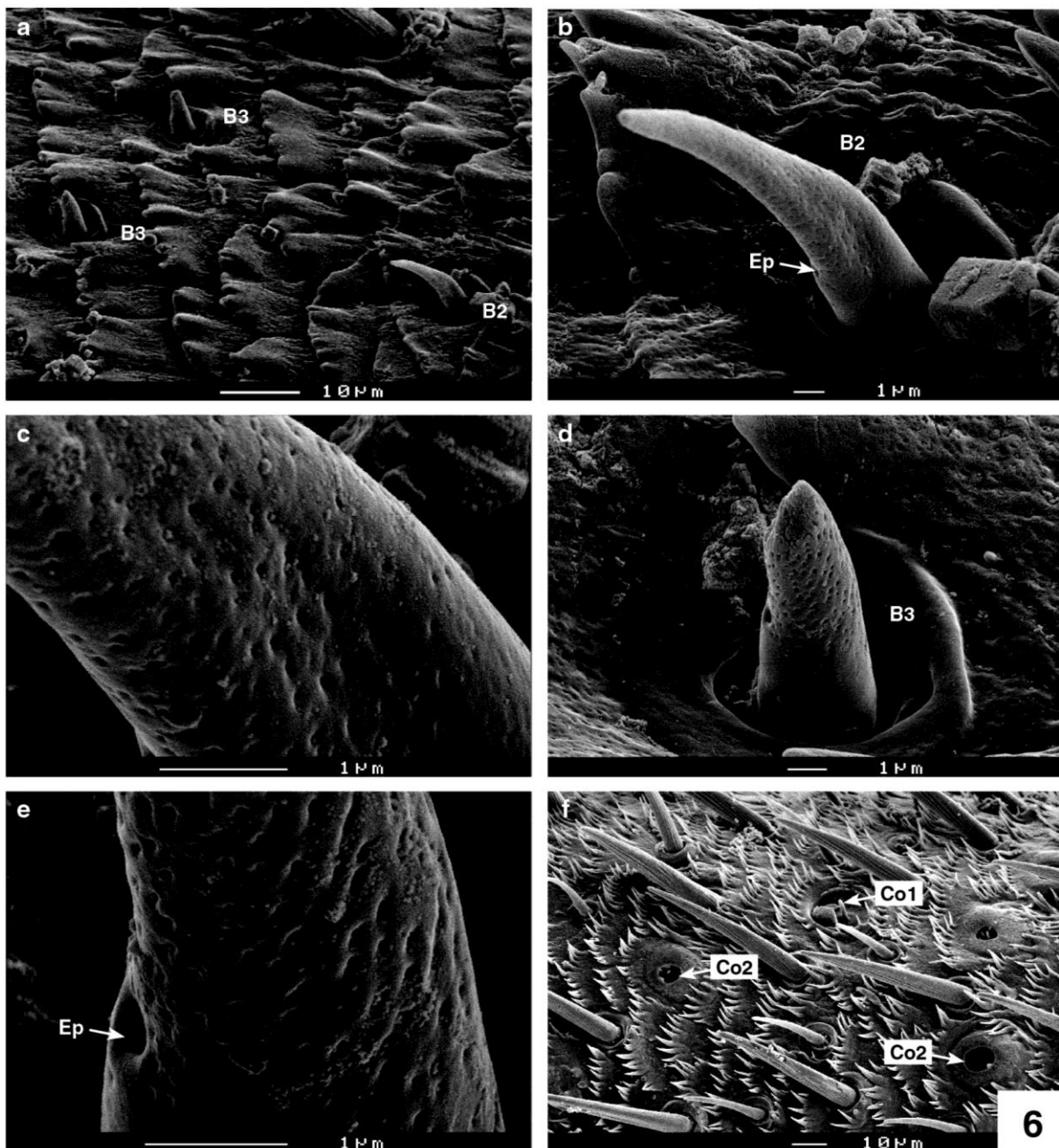

Figure 6. *Eugaster powysi*, male antenna; **a**. multiporous sensilla basiconica subtypes 2 and 3, B2 and B3; **b**. sensillum B2 with ecdysial pore Ep; **c**. wall pores of B2; **d**. sensillum B3; **e**. wall pores and ecdysial pore Ep of B3; **f**. multiporous sensillum coeloconicum Co1 and aporous sensilla coeloconica Co2.
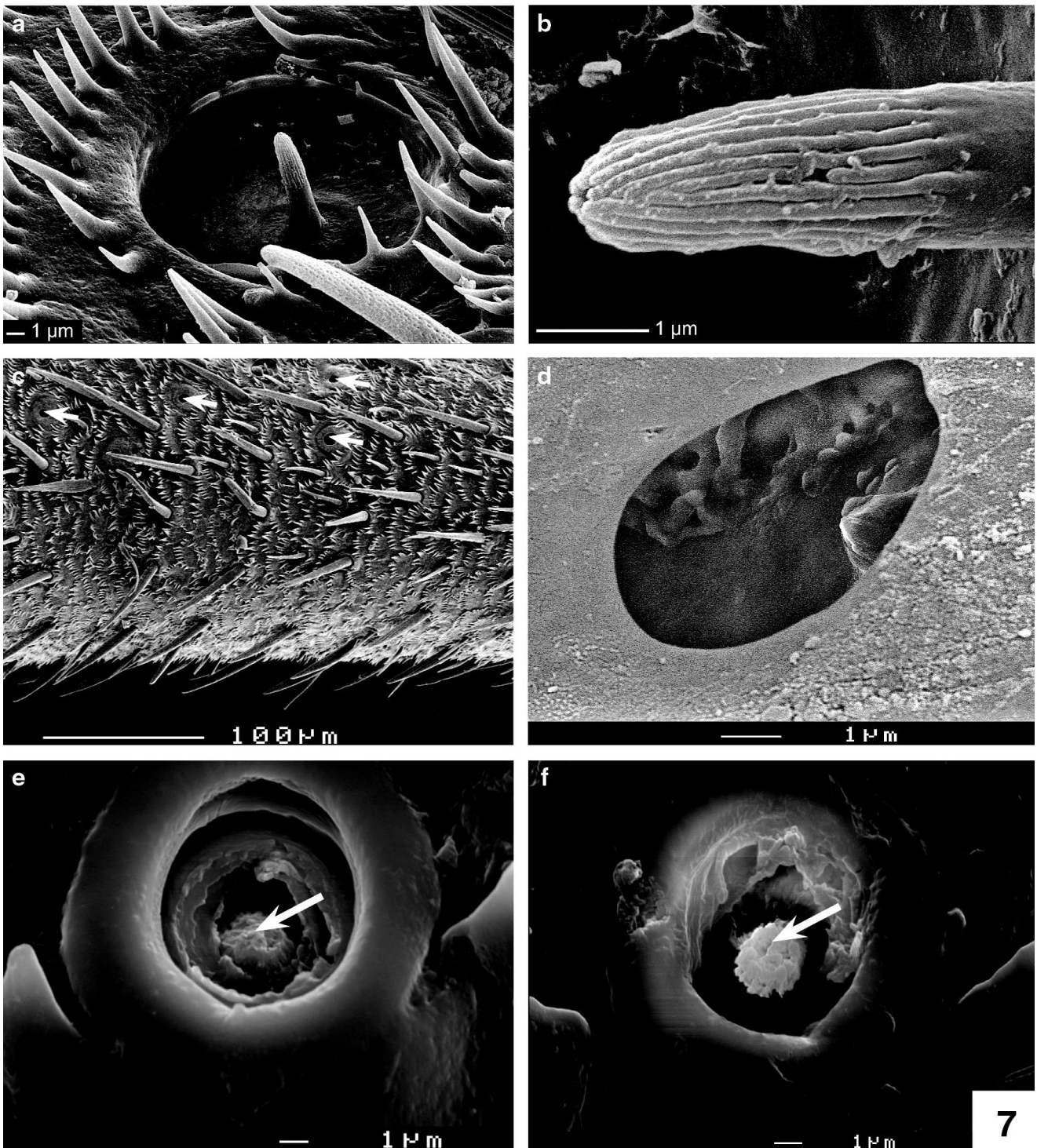
Figure 7. *Eugaster powysi*, male antenna; **a**. multiporous sensillum coeloconicum Co1 surrounded by a fringe of microtrichia; **b**. detail of grooves of Co1; **c**. aporous sensilla coeloconica Co2 (arrows); **d**, detail of the structure in the pit of Co2; **e**, **f**, sensilla coelocapitula with sensory cone (arrow).

Aporous sensilla coeloconica (ASCo)

ASCo comprise small domes of 17 μm in outer diameter, pierced apically by a large rather round orifice of 4.2-6.0 μm in diameter through which their structure can be observed (Fig. 7c, d). The internal structure reveals a sinuous, irregular form sometimes pierced by pores (Fig. 7d).

These sensilla are generally grouped, and are more or less lined up on the flagellomeres (Fig. 7c). Their number varies from 3 to 6 on a face of flagellomere; they occur on both faces of the antenna and show no sexual dimorphism. Their number does not vary between sexes: 430-420 sensilla per antenna, i.e. 2.2% of total sensilla (Tab. 1).

Aporous sensilla coelocapitula (ASCc)

Sensilla coelocapitula appear as small peg-like projections whose diameter is 2.2-3.0 μm sitting in the centre of a large pit, 7.0-8.5 μm in diameter, around which there is a circular thick bulge of the surrounding cuticle of 13.9-15.7 μm in outer diameter (Fig. 7e, f). The external

surface of the peg is highly convoluted with spongy looking globular irregularities with no visible pores. Unlike other sensilla coelocapitula described in the literature in which the space between the peg and the cuticular bulge is narrow (see discussion), the space of the sensillum in *Eugaster* is very large and is occupied by a series of four successive membranous folds, each of which is situated at a different depth inside the pit (Fig. 7e). Each membrane issued from the internal wall of the pit is perforated in the centre and therefore creates a ring of varying size whose inner diameter diminishes in size from the most superficial to the most deeply imbedded, situated near the distal region of the peg. As concerns the sensillum of Fig. 7e, the diameters are the following: 6.1, 5.4, 4.6 and 3.0 μm. Together these rings form a kind of diaphragm which progressively limits the diameter of the pit. The peg itself is not a cylindrical shaft but seems to widen and become grooved between the apex and the base.

These sensilla are found on three flagellomeres but only in females and are always few in small numbers (0.1%). However, when they do occur on a flagellomere, they exist in significant numbers and are lined longitudinally on a zone with few other sensilla (n = 9 on Fig. 3a). As Ramirez-Esquivel *et al.* (2014) have also noticed on the antenna of an ant, the sensilla coelocapitula cannot immediately be identified because they resemble the stumps left behind by broken sensilla chaetica. Nevertheless, their diameter which is much smaller than that of the latter sensilla leaves no doubt as to their identity. What is more, their particular internal structure makes them distinguishable from sensilla coeloconica type 2.

Aporous Böhm sensilla (ABS)

The ABS which are typically spread out over two or three areas at the base of the scape in most insects do not exist in *Eugaster*. A group of 30-35 short aporous sensilla chaetica is visible on the internal surface of the scape (Fig. 8a, b); it is located in the proximal half of the scape and covers a third of that region. These sensilla resemble the ABS of the pedicel (Fig. 8c, d); thus, this group may be considered as a median area of the scape.
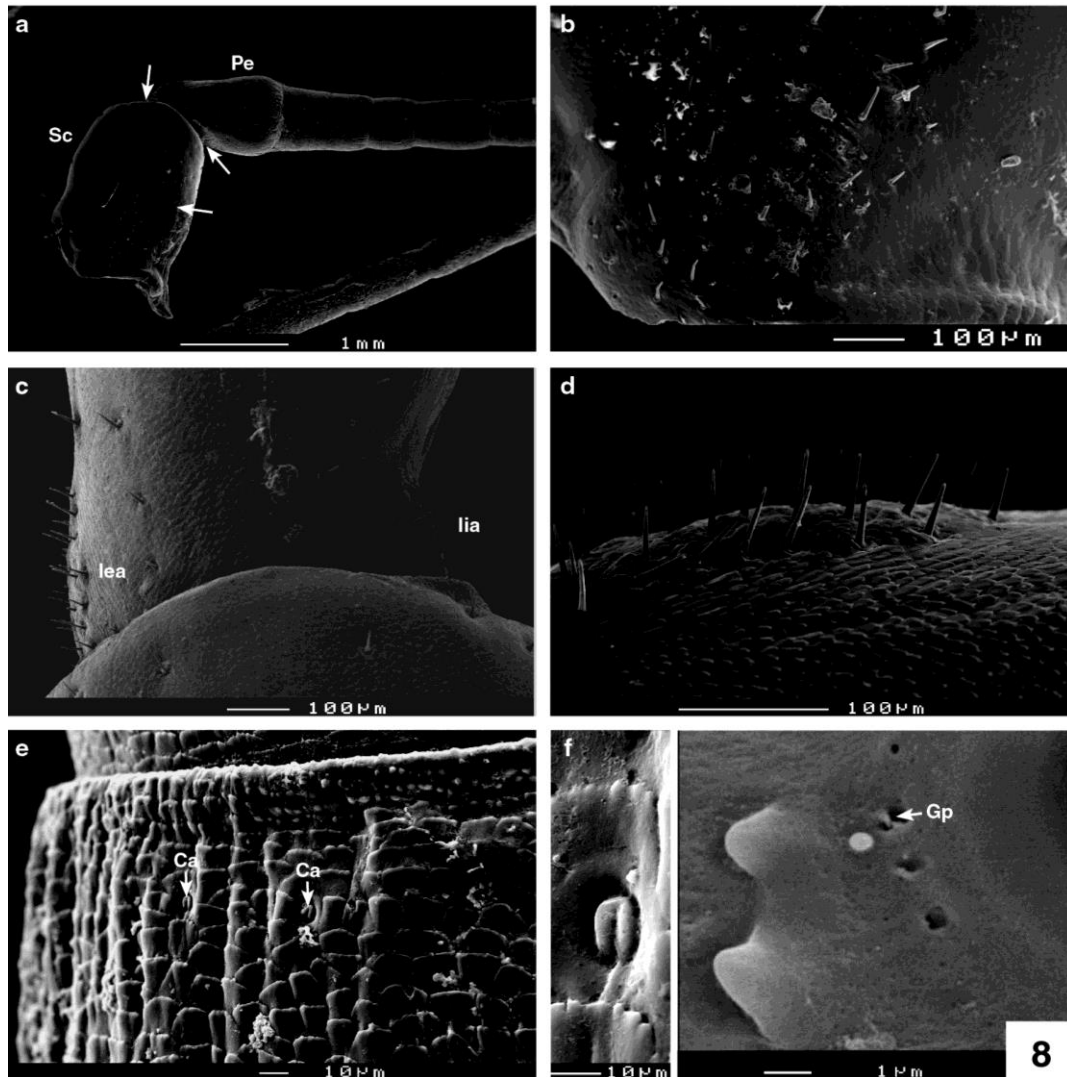

Figure 8. *Eugaster powysi*, female antenna; **a-d**. aporous Böhm sensilla; **a**. internal surface of left antenna showing the location of sensilla on scape Sc, and pedicel Pe (arrows); **b**. sensilla on the base of scape; **c**. latero-external area lea and latero-internal area lia of pedicel; **d**. detail of sensilla of latero-external area; **e**. **f**. two sensilla campaniformia Ca on the distal part of flagellomere and detail of sensillum; **g**, glandular pores Gp.

Aporous sensilla chaetica (ASC)

We have found it difficult to distinguish the ASC C1 from the USC subtype C3 for they closely resemble them. The sharp tip of the C1 marked their difference from the C3 and amounted a priori to a criterion of the absence of a terminal pore but the presence of a subapical pore on one of the faces of a "sensillum chaeticum" with a large base on the cerci of *Acheta domestica* (Linnaeus, 1758) (Faucheux 1990) advises prudence. That is why we have examined both faces of a very large number of sensilla C1 and proved the absence of pores, wall pores or terminal pore.

According to their morphology and their distribution, the scattered aporous sensilla chaetica of *Eugaster* are mechanoreceptive (Zacharuk 1980, Faucheux 1999).

Other Orthoptera (Ensifera) and Mantodea possess long aporous sensilla chaetica whose morphology and distribution suggest mechanoreceptory functions (Faucheux 2006, 2008a, 2009a; Goasmat & Faucheux 2011; Kostromytska *et al.* 2015). The ASC form from 94.5% (female) to 99.5% (male) of all sensilla and are presumably mechanoreceptors in the Gryllacrididae *Bothriogryllacris pinguipes* Rentz, 1983 (Bland & Rentz 1994). Their arrangement in rows perpendicular to the antennal axis suggest their sensitivity to very fine air movements, media flow and/or low frequency sounds and vibrations (Keil 1999, Barth 2004, Humphrey & Barth 2008, Kostromytska *et al.* 2015). The presence of these long sensilla chaetica explained the characteristic tendency to flee of these species.

Unlike previously studied species, the ASC of *Eugaster* are relatively short, non-deformable and rather rigid. Their sensitivity to air currents is therefore unlikely. This absence of function may be linked to the behaviour of this insect which is incapable of jumping or fleeing. Indeed, in contrast to other katydids who try to nibble you if handled, armoured katydids never bite, no matter how roughly they are treated. Covering the two faces of antennal flagellum, the ASC show an effective tactile sensitivity which intervenes in the search for food, contact with plants and also in antennal contacts between conspecifics. Sure enough, the description of copulation in *Eugaster nigripes* Chopard, 1937 and *E. spinulosa* by Favrelle (1936) and Bleton (1940) desmonstrates the importance of antennal contact which presumably leads to stimulation of the ASC and the USC of both sexes.

Uniporous sensilla chaetica (USC)

The "sensilla chaetica" of *S. gregaria* antennae and the "medium sensillum chaetica" of the *Locusta migratoria* (Linnaeus, 1758) cerci are identical (shape, size) to USC subtype 2 of *Eugaster* (Ochieng *et al.* 1998, Yu *et al.* 2011). They have the structure of the bimodal mechano-chemoreceptive sensilla with a double lumen, one with four dendrites and another without dendrites (Gaffal 1979). This internal structure and other features, i.e. a flexible socket, a thick non-porous cuticular wall and an apical pore, suggest a gustative function of these sensilla and consequently for the USC of *Eugaster* (Altner & Prillinger 1980, Zacharuk 1980). Our findings and those obtained by Kostromytska *et al.* (2015) for the mole cricket are identical to the previous results in other insect taxa (Hallberg 1981, Jorgensen *et al.*

2007, Crook *et al.* 2008). But the USC of these studied insects are always filiform unlike those of *Eugaster*.

The gustatory sensilla of the antennae in insects are always less numerous than tactile sensilla and they possess a specific distribution related to their function which is frequently in a circle around the flagellomere (Faucheux 1999, Kostromytska *et al.* 2015). Moreover, they differ by their general form and their blunt tip. However in *Eugaster*, ASC and USC are mixed on the flagellomeres. In the mole cricket, although identical in appearance, two different functional types were reported: aporous with a mechanoreceptive function, and terminal-pore that are innervated with additional gustatory neurons (Kostromytska *et al.* 2015). The prevalence of sensilla chaetica was also documented for cockroaches such as *P. americana*, *Paratemnopteryx* spp. Electrophysiological recordings have shown that these sensilla respond to chemical and mechanical stimulation, especially to a conspecific tergal secretion, which is a component of the mating process (Hansen-Delkeskamp 1992, Bland *et al.* 1998). The role of contact chemoreception in *Eugaster* mate recognition has not been studied, but many crickets use cuticular pheromones in close range intraspecific recognition (Otte & Cade 1976, Rence & Loher 1977, Hardy & Shaw 1983, Tregenza & Wedell 1997, Kostromytska *et al.* 2015). In mole crickets, intersexual and interspecific differences in composition of cuticular lipids suggest their involvement in inter- and intraspecific recognition (Castner & Nation 1984). If this is the case for *Eugaster*, the considerable number of USC uniformly spread out on both faces of flagellomeres would appear to be amply justified. In addition to producing courtship song, the male field crickets like many other orthopterans, frequently stroke the body of the females with their antennae (Alexander 1961, Leroy 1966). In the cricket *Teleogryllus oceanicus* (Le Guillou), Balakrishnan & Pollack (1997) confirm the importance of the antenna for the female responses to courting males. By relatively disrupting different antennal sensilla, they show that the crucial modality for mounting responses is contact chemoreception.

The regular distribution of the USC over the whole of the flagellum in *Eugaster* is both surprising and exceptional because in the acridid *S. gregaria*, whose sensory equipment is close to that of the armoured ground cricket, the USC exist in small numbers on all flagellomeres except the terminal one where they are numerous and concentrated (Ochieng *et al.* 1998).

Multiporous sensilla trichodea (MST)

MST are present in other Orthoptera, i.e. "single-walled wall-pore type B" of *L. migratoria* (Ameismeier 1987), "sensilla trichodea" of *S. gregaria* (Ochieng *et al.* 1998), and "multiporous sensilla trichodea" of *P. nana* (Goasmat & Faucheux 2011). The structural features of sensilla trichodea are typical of olfactory receptors as described by Altner & Prillinger (1980) and Zacharuk (1980).

Olfactory cues are known to be important in the courtship behaviour of insects. In tree crickets and cockroaches, there is evidence that female response during courtship may involve olfactory cues (Belle 1980, Moore & Breed 1986, Sreng 1990). Similarly, in response to the male acoustic signal (courtship song) recorded by the female

tympana, the antennal MST of *Eugaster* could possible intervene during the courtship. Along with sensilla basiconica, sensilla trichodea may be involved in the search for food in the armoured ground cricket which is essentially herbivorous. Rogers & Simpson (1997) in *L. migratoria* show that insects fed for the final two stadia on nutritionally adequate synthetic foods have fewer chemosensory sensilla on the antennae (and maxillary palps) than insects fed on the usual rearing diet of seedling wheat.

Multiporous sensilla basiconica (MSB1-3)

The presence of an ecdysial pore in all subtypes of sensilla basiconica requires explanation. In a surface view by SEM, it may appear as a distinct pore and could be easily be interpreted as evidence of a permeable pore that is open or extruded a liquor. Consequently, the ecdysial pore does not intervene in the function of the sensilla. Sensilla basiconica on the adult male and female antennae of the desert locust, *S. gregaria*, were found to house receptor neurons sensitive to all the potential aggregation pheromone components (Anton & Hansson 1996). If this type of pheromone exists in *Eugaster*, at least one of three subtypes of sensilla basiconica could be a pheromone receptor.

Chemical cues are widely used among insects for food-finding (Dethier 1970, Eisner & Meinwald 1995). The other subtypes can be involved in the search at a distance for food. The existence of different subtypes in *Eugaster* must be related to a specificity of olfactory receptor cells of sensilla. Indeed, in the cockroach *P. americana,* Selzer (1984) has studied the antennal olfactory receptor cells by extracellular recordings. The stimuli used were compounds of the naturally occurring food sources of the cockroach. On the basis of similarities between the reaction spectra, the cells were classified into reaction groups. The morphology of the sensilla basiconica, which housed the recorded cells, was investigated by scanning electron microscopy and transmission electron microscopy. Thus, the alcohol-sensitive and terpene-sensitive cells were seen only in smooth, single-walled hairs (multiporous sensilla basiconica), whereas the cyclohexylamine cells were found in single-walled hairs (multiporous sensilla basiconica) as in grooved, double-walled hairs (multiporous sensilla coeloconica).

Multiporous sensilla coeloconica (MSCo)

Sensilla morphologically similar to the MSCo of *Eugaster* are present in other orthopterans: "multiporous sensilla coeloconica type I" of *P. nana* (Goasmat & Faucheux 2011) and *T. viridissima* (unpublished observations), "sensilla coeloconica" of eight species of Acrididae (Li *et al*. 2007) and also in the praying mantids: "sensilla coeloconica" of *Mantis religiosa* (Linnaeus 1758) (Faucheux 2005) and *Sphodromantis viridis occidentalis* (Werner 1906) (Faucheux 2006), "multiporous sensilla basiconica subtype 1" of *Oxyothespis maroccana* Bolivar 1908 (Faucheux 2008a), "sensilla coeloconica subtype 1" of *Iris oratoria* (Linnaeus 1758) and *Rivetina baetica tenuidentata* La Greca & Lombardo 1982 (Faucheux 2009), "grooved pegs" of *T. aridifolia* (Carle *et al*. 2014a).

In the orthopteran *L. migratoria*, sensilla coeloconica similar to those of *Eugaster* are double-walled wall pore (dw wp) sensilla according the terminology of Altner & Prillinger (1980) and house chemo- and probably thermoreceptors (Boeckh 1967, Kafka 1970, Altner *et al*. 1981). In the praying mantids, the fact that these sensilla coeloconica appear in very great numbers in the adult males confirms that this type of sensilla is involved in sex-pheromone detection in mantids (Faucheux 2009, Carle *et al*. 2014a, b). This constitutes the unique case of double-walled sensilla which were not thought to play a role in this function until now (Carle *et al*. 2014a).

Now, the MSCo of three studied tettigoniids (*P. nana* (Goasmat & Faucheux 2011), *T. viridissima* (personal observations), *E. powysi* (this study) are rare and reveal no sexual dimorphism. These facts are in accordance with the absence of sex-pheromone detection in these three species of Tettigoniidae in which sexual approach takes place by acoustical means thanks to the male stridulating apparatus. The few rare MSCo which exist in both sexes of *Eugaster* are multiporous sensilla whose probably olfactory role needs to be made clear. According to Boeckh (1967) and Kafka (1970), olfactory receptor neurons located in sensilla coeloconica are tuned to a large variety of plant volatiles, which probably play an important role in food localization.

Aporous sensilla coeloconica (ASCo)

ASCo have been described from a few Lepidoptera, Coleoptera and Orthoptera. They are named "cupuliform organs" in the lepidopterans *Homoeosoma nebullella* Denis & Schiffermüller 1775 (but they are absent in the congeneric *Homoeosoma electellum* (Hulster, 1887)), in *Micropterix calthella* (Linnaeus, 1761) and *Apoplania valdiviana* Davis & Nielsen, 1985 (Faucheux 1992, 1995, 1997; Faucheux *et al*. 2006); "discoidal sensilla coeloconica" or "multiporous sensilla coeloconica" in the coleopterans *Ceroglossus buqueti cupreus* Faz 1925 (Jaffrézic & Faucheux 2006) and *Ceroglossus buqueti valvus* Géhin 1885 (Faucheux & Jaffrézic 2007).

In the orthopterans, they are "sensilla coeloconica subtype IV" in *P. nana* (Goasmat & Faucheux 2011) and *T. viridissima* (unpublished observations), and "cavity sensilla" in eight species of Acrididae (Li *et al*. 2007). They are named "sensilla coeloconica subtype III" in the praying mantids *I. oratoria* and *M. religiosa* (Faucheux 2009a). These sensilla are no doubt more common in Lepidoptera because they can easily be confused with scale sockets, which is probably the reason why they have rarely been identified. Their resemblance to a sensillum ampullaceum suggests an olfactory function, but this is yet to be proved. However, the ASCo resemble the "organe cupuliforme" located on the antenna of a Dipluran whose ultrastructure is that of an olfactory chemoreceptor (Bareth 1971). But, in the orthopteran *L. migratoria*, this type of poreless sensillum houses thermo - and hygroreceptors (Altner *et al*. 1981, Ameismeier & Loftus 1988) and this is probably the case for *Eugaster*.

Aporous sensilla coelocapitula (ASCc)

Sensilla coelocapitula are known in Hymenoptera (Yokohari *et al*. 1982, Yokohari 1983, Nakanishi *et al*. 2009, Ramirez-Esquivel *et al*. 2014), Coleoptera Carabidae and Lampyridae (Giglio *et al*. 2008, Iwasaki *et al*. 1995), and

Mantophasmatodea (Drilling & Klass 2010), as well as in the house cricket *Acheta domestica* (Linnaeus, 1758) (Itoh *et al*. 1984) and the desert locust *Locusta migratoria* (Linnaeus, 1758) (Ameismeier 1985). In the two Orthoptera, they are called sensilla coeloconica.

The sensillum coelocapitulum of *Eugaster* differs from the sensilla of Hymenoptera which have a funnel-form at the bottom of which is to be found the sensory peg. It is also distinguishable from all the other sensilla coelocapitula (Hymenoptera, Coleoptera, and other Orthoptera) by the presence of a very large space around the peg, a space which is narrow in the other sensilla. The existence of successive membranes in *Eugaster*, which have never been described in other insects, can also be justified. Sensilla coelocapitula act both as hygro- and thermoreceptors (Yokohari *et al*. 1982, Yokohari 1983). Thus, their function interferes with that of the aporous sensilla coeloconica which are also hygroreceptors but are present in both sexes. Their existence exclusively limited to females could establish a relation with egg-laying in the substrates necessitating a certain degree of humidity.

Aporous Böhm sensilla (ABS)

The ABS of the scape and the pedicel, grouped in hair-plates, inform *Eugaster* about antennal position and movements (Moran *et al*. 1971, Zacharuk 1985, Keil 1999). The gradations of joint movements may be detected in the central nervous system of the insect by a summation of the responses of several displaced sensilla (Toh 1981). A particular location of the ABS has been revealed on the scape of *P. nana* (Faucheux & Goasmat 2011). *Eugaster* which offers the same arrangement is thus a second example. It would be wise to examine other Orthoptera Ensifera to see whether this localization is general. As a matter of fact, a double longitudinal lining up of ABS has been represented on a large part of the scape in the mole cricket (Kostromytska *et al*. 2015) but these authors have not questioned the interest of this arrangement. This longitudinal distribution may be a characteristic of the Orthoptera because the hair plates on the labial palps of *A. domestica* reveal a similar arrangement of sensilla (Gurgel *et al*. 1987).

The absence of the two proprioceptive areas at the base of the scape of *Eugaster* points to a certain rigidity of the antenna and a reduced mobility of its base; it tells us that the ground cricket is not informed of the movements and position of its scape. The mobility of the antenna is thus discerned by the insect in the area of the joint between the scape and the pedicel. The proprioceptive areas of the pedicel inform the insect of the often very ample movements of the antenna. The blunt appearance of the sensillum tip is noteworthy because the ABS of insects are usually sharp ended sensilla (Faucheux 1999). A blunt tip makes contact between the pedicellar sensilla and the distal extremity of the scape less harsh than if the tip was sharp ended.

The lateral proprioceptive area of the scape is stimulated by the more or less insistent contact of its sensilla on the head capsule. This lateral contact on a large surface provides information about the position of the scape in relation to the head. The control of the position of the two scapes in relation to the insect's body and more precisely its head is probably related to the great length of the antennae.

Aporous sensilla campaniformia (ASCa)

The particular form of the sensilla campaniformia, in which the ring of raised cuticle surrounding the cap is swollen and incomplete, has also been mentioned for other Orthoptera, i.e. on the palps of *S. gregaria* (Blaney & Chapman 1969), the labium of *A. domestica* (Gurgel *et al*. 1987), and the antennae of *P. nana* (Goasmat & Faucheux 2011). This shape is likely correlated with the flexibility of the cuticle (McIver 1985). Sensilla campaniformia are mechanoreceptors which detect stresses applied to the surface of the cuticle and function as proprioceptors (Keil 1997). Three distal circles of sensilla campaniformia are present on the distal part of the pedicel of *P. nana* near the joint with the flagellum (Goasmat & Faucheux 2011). This disposition is frequent in other Orthoptera (Gewecke 1972), Blattodea (Toh 1981) and Mantodea (Faucheux 2006). These sensilla detect the curve of the flagellum on the pedicel. Their abundant number is related to the great flexibility of the flagellum and their circular disposition suggests that they can detect flagellum movements in any direction. This numerical importance of the sensilla campaniformia of the pedicel is a frequently described characteristic in orthopteroids.

The pedicel of *Eugaster* possesses only a single sensillum campaniformium, which may imply a feeble control of the mobility of the flagellum with regard to the pedicel. However, the presence of a sensillum campaniformium at the distal end of each flagellomere probably indicates a permanent control of the position of the flagellomeres in relation to one another. The segmented cerci of *P. americana* show a similar localization of the sensilla campaniformia (Füller & Ernst 1977).

Distribution and numbers of sensilla

We have found no difference between the sensillum arrays in both sexes of *Eugaster*, a result similar to that of *L. migratoria* (Greenwood & Chapman 1984) and *S. gregaria* (Ochieng *et al*. 1998). The total numbers of sensilla per antenna in *Eugaster* are an average of 19320 in males and 18775 in females (Tab. 1). This feeble sexual dimorphism points up the absence of olfactory sexual communication in this species in which sexual approach takes place essentially by acoustic signal. Of all the antennae of Orthoptera Ensifera studied so far (*A. domestica*, *P. nana*, *T. viridissima*) (Faucheux 1994, Goasmat & Faucheux 2011, pers. observ.), *Eugaster* alone possesses a large number of sensilla. This numerical advantage has several explanations: larger antennae (diameter of 290 µm in *Eugaster*, 85 µm in *P. nana*), closer together and more numerous sensilla in *Eugaster* (two hundreds per flagellomere), more widely spaced and less numerous in *P. nana* (twenty or so per flagellomere). We have not found in *Eugaster* the sensilla digitiformia pointed out on the antennae of the house cricket (Faucheux 2009b).

Glandular pores and epidermal glands

Masses of large unicellular glands with an elaborate collecting vesicle within the cytoplasm of each and a duct leading from it to the surface of the antennal cuticle are present in the epidermis of antennomeres of Blattodea (Slifer 1968). These glandular pores can be observed in most

insects' antennae and bodies (Noirot & Quennedey 1974). Sutcliffe & Mitchell (1980) think that the epidermal glands secrete a substance that coats the mouthparts (and the antennae) and prevents them from being stuck together by a fluid ejected from the mouth or any part of the body.

CONCLUSION

The types and abundance of sensilla on armoured ground cricket antennae differ greatly from those found in other ground orthopterans (Bland 1989, 1991). Only 21.8% (male) and 20.4% (female) of *Eugaster* flagellar sensilla have olfactory functions, whereas many other insect species have above all olfactory sensilla. The importance of contact chemoreception, or taste, is obvious when observing the antennae of *Eugaster* (12%). The tactile mechanoreceptors represent the largest percentage of sensilla (63%) as in other Ensifera. Antennae are used to palpate surfaces and thus gain information from mechanoreceptors and also contact chemoreceptors. This predominance of aporous sensilla chaetica distinguishes *Eugaster* from certain Caelifera Acrididae such as *S. gregaria* (Ochieng *et al.* 1998). The absence of long sensilla chaetica with a vibroreceptive function may explain the lack of reactivity of *Eugaster* in which the absence of functional wings and of hindlegs adapted to jumping as well as the voluminous abdomen do not facilitate fleeing. In spite of the predominance of the mechanoreceptors and contact chemoreceptors, *E. powysi* possesses complex olfactory capabilities thanks to five types or subtypes of sensilla.

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