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Oviscapt and associated sensilla of the armoured ground cricket, *Eugaster powysi* Kirby, 1891 (Orthoptera: Tettigoniidae: Hetrodinae)

Oviscapte et sensilles associées d'Eugaster powysi Kirby, 1891 (Orthoptera: Tettigoniidae: Hetrodinae)

Michel J. Faucheux

Laboratoire d'Endocrinologie des Insectes Sociaux, Faculté des Sciences et des Techniques, 2 rue de la Houssinière, B.P. 92208, 44322 Nantes Cedex 3, France (faucheux.michel@free.fr)

Abstract. Sensilla on the oviscapt 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 egg-laying. The very shortened oviscapt bears uniformly distributed sensilla on the three pairs of valves. 6 types and 27 subtypes are recognized: trichodea (5 subtypes), basiconica (13 subtypes), campaniformia (6 subtypes), coeloconica, digitiformia, and cylindrica. Except for some subtypes, most of them are characteristic of each pair of valves and of their faces, external and internal. Sensilla campaniformia and digitiformia, which are described for the first time on the oviscapts of Orthoptera, were probably capable of recording both the cuticular stress and the mechanical contact of the oviscapt, from the initial through the final steps of penetration in the soil. Most sensilla trichodea and basiconica are contact chemoreceptors and the sensilla coeloconica are probably hygroreceptors. These results are related to the behaviour of *Eugaster powysi* and compared with those obtained in other Orthoptera.

Keywords: *Eugaster*, Ensifera, oviscapt, sensilla, campaniformia, behaviour.

Résumé. Les sensilles de l'oviscapte d'*Eugaster powysi* sont étudiées en microscopie électronique à balayage afin de déterminer leur morphologie et leur fonction chimio- et mécanoréceptrice intervenant lors du comportement de ponte. L'oviscapte exceptionnellement court porte des sensilles uniformément réparties sur les trois paires de valves. 6 types et 27 sous-types de sensilles ont été identifiés : trichoïdes (5 sous-types), basiconiques (13 sous-types), campaniformes (6 sous-types), coeloconiques, digitiformes et cylindriques. À part quelques sous-types, la plupart d'entre eux sont caractéristiques de chacune des paires de valves et de leurs faces, externe et interne. Les sensilles campaniformes et digitiformes, qui sont décrites pour la première fois sur les oviscaptes des Orthoptères, sont capables d'enregistrer à la fois les stress de la cuticule et le contact mécanique de l'oviscapte durant les différentes étapes de sa pénétration dans le sol. La plupart des sensilles trichoïdes et basiconiques sont des chimiorécepteurs de contact tandis que les sensilles coeloconiques sont probablement des hygrorécepteurs. Ces résultats sont reliés au comportement d'*Eugaster powysi* et comparés à ceux obtenus chez les autres Orthoptères.

Mots Clés: *Eugaster*, Ensifera, oviscapte, sensilles, campaniforme, comportement.

INTRODUCTION

The oviposition is the last step of the reproductive behaviour of insects on which the future of the offspring depends (Faucheux 1987, Desouhant 1997). The laying organ, named ovipositor (in Latin: *positor* = to place, to set down) or oviscapt (in Greek: *skaptein* = to dig) as the case may be (Faucheux 2009a) plays simultaneously a mechanical and a sensory role.

In a number of Orthoptera Ensifera belonging to groups of insects which leave their eggs in the soil, the oviscapt is so shortened that it becomes almost nonfunctional (Chopard 1938). The case of *Eugaster* was studied by Favrelle (1936): however the females dig a small cavity with their rudimentary oviscapt and introduce at least half of their abdomen in the wet sand as do the locusts. The eggs were found at a depth of 2 or 3 centimeters. They are separate from one another, and can be isolated or irregularly piled up; the maximum number of eggs at the same place being ten. The eggs are elongated, rounded at two ends, with a flat face and a convex face opposite.

In the present article, we aim to discover whether the sensory equipment of the oviscapt of the armoured ground cricket *Eugaster powysi* Kirby, 1891 is affected by the laying mode in the soil as regards the types and the number of sensilla. Then we compare it to other Orthoptera which lie in the ground or on plants. The morphology of the oviscapt of an armoured ground cricket, *Acanthoplus speiseri* Brancsik 1895 (Hetrodinae) has previously been studied but its sensilla were not listed (Mbata 1985).

MATERIAL AND METHODS

Female adults of *E. powysi* 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 valves of the oviscapt were separated, cleaned in acetone, dehydrated in pure alcohol, and mounted either on the external face, or on the internal face, on specimen holders. After coating with gold and palladium, preparations were examined in a Jeol J.S.M. 6400F SEM at 10 kV.

Counts of the sensilla were made on the external face and the internal face of each pair of valves in 3 females by using SEM at different magnifications. Sensillum terminology follows Zacharuk (1980), and Faucheux (1999).

RESULTS

General morphology

According to Chopard (1920), the abdominal end of female *Eugaster* sp. is thick and short. The 10th tergite is rudimentary and bears the cerca which are short and conical; the epiproct is short and curved, the paraprocts are wide and flat (Fig. 1). The valvifers are short sclerotized pieces which are situated at the base of the upper and lower valves.

The oviscapt of the Orthoptera Ensifera typically comprises 6 pairs of valves (upper, lower, and inner) (Chopard 1949). It is exceptionaly short in the subfamily Hetrodinae as in *Eugaster* sp. The upper valves which are wide at the base, are suddenly incurved at right angles and terminated by a small hook curved upwards. Their surface is roughly dotted and undulated near the edges (Fig. 1). They measure 5.6 mm in length and 4.2 mm in their greatest width; they are very thick and sclerotized. Their external face is slightly convex (Fig. 3a) whereas their internal face is hollowed at its proximal part (Fig. 4a).

The lower valves are straight, sharp and smooth; they are thick and sclerotized like the upper valves. They are 6.6 mm long and 1.8 mm in width at the base. The two faces are slightly bumpy (Figs. 3a, 4a). Upper and lower valves tend to deviate towards the apex; the upper ones directed upward, the lower downward (Fig. 1).

The inner valves are short (3.7 mm in length), very narrow (1.1 mm in width at the most) and slightly sclerotized; they are curved and sharp towards the apex (Fig. 4a). The external face shows a smooth base but the whole of the valve is folded, particularly in the upper part (Fig. 9a). The internal face is clearly folded and deformable (Figs. 4a and 8a).

Figure 1. *Eugaster powysi*, lateral view (a, b) and posterior view (c) of female last abdominal segments; LV, lower valve of oviscapt; UV, upper valve of oviscapt; Vf, valvifers; Ce, cercus; Ep, epiproct; Pp, paraproct; ST8, sternite 8 ; T7-10, tergites 7-10 (scale bars = 2 mm) (photographs André Lequet).

Sensilla

Six types of sensilla are present on the valves: sensilla trichodea (5 subtypes), sensilla basiconica (13 subtypes), sensilla campaniformia (6 subtypes), sensilla digitiformia (1 subtype), cylindrical sensilla (1 subtype), and sensilla coeloconica (1 subtype). As the majority of subtypes are characteristic of one of the three pairs of valves, they will be studied in relation to their location.

Table 1 – Morphological characteristics of sensilla trichodea (T) of oviscapt in *Eugaster powysi* (in µm): ?, presumed; ??, unknown; ---, absence (n = 10).

Sensilla	T1	T2	T3	T4	T5
Length	42.0	10.6	37.0	??	??
basal diameter	7.0	2.5	7.9	10.0	4.8
collar: outer dia.	17.0	9.0	12.0	---	---
Cavity: diameter	---	10.0	16.0	11.0	6.6
pores	TP?	NP	TP?	?	?

Table 2 – Morphological characteristics of sensilla basiconica (B1 – B13) of oviscapt in *Eugaster powysi* (in µm): ?, unknown (collar) or probable (pores); -- absent; tp, terminal pore; wp, wall pores (n = 10).

Sensilla	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13
Length	3.6	3.0	7.7	4.6	2.6	16.1	8.0	7.0	12.5	5.5	6.1	5.0	4.1
Basal diameter	2.2	2.5	2.3	4.5	3.8	5.6	5.3	3.0	6.0	2.4	2.2	3.0	2.7
Collar, outer dia.	?	5.4	10.0	--	6.2	8.0	?	5.6	?	5.5	6.6	5.7	4.9
Cavity diameter	8.0	8.0	11.0	5.0	6.6	10.2	10.6	8.2	10.7	7.7	6.8	7.8	5.0
Pores	wp	tp	?	?	?	wp?	wp?	wp?	wp?	tp	wp?	tp	tp ?

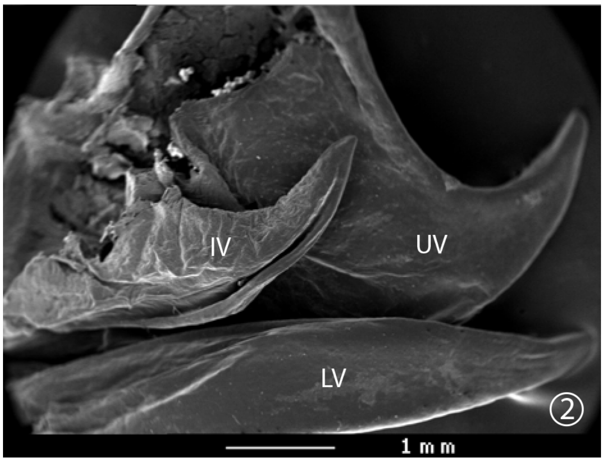

Figure 2. *Eugaster powysi*, oviscapt, internal view of right valves. UV, upper valve; LV, lower valve; IV, internal valve.

The morphological characteristics of the different oviscapt sensilla of *E. powysi* are given in Table 1 (sensilla trichodea), Table 2 (sensilla basiconica) and Table 3 (sensilla campaniformia).

Table 3 – Morphological characteristics of sensilla campaniformia (Ca) of oviscapt in *Eugaster powysi* (in µm): length and width of cap, outer diameter of ring, diameter of cavity, outer diameter of cuticular bulge, position of sensillum (n = 10).

Sensilla	length	cap width	ring diam.	cavity diam.	bulge diam.	Sunken Raised
Ca1	8.6	4.0	10.6	11.4	----	S
Ca2	12.0	5.5	14.0	14.2	22.5	R
Ca3	9.1	2.1	----	10.0	----	S
Ca4	5.8	2.1	9.1	9.2	14.5	S
Ca5	5.5	2.2	7.3	----	13.4	R
Ca6	2.3	1.8	8.8	----	19.1	R

Sensilla of the upper valves

- on the external face (6 subtypes) (Fig. 3)

The punctuations visible on Fig. 3a correspond to the cavities of the sensilla present on the external face of the upper left valve.

Sensilla trichodea T1 are the longest sensilla of the oviscapt. They have a blunt tip which appears to be truncated with a presumed terminal pore; the wall bears about thirty thin longitudinal striae. Their base is surrounded by a flat collar leaving a space with hair and allowing for the movement of the latter (Fig. 3b). They are towards the back of the valve. *Sensilla trichodea T2* are sharp-tipped and four times shorter than the previous sensilla. Their wall possesses about twenty longitudinal striae and no pores are visible. The base is surrounded by a collar in the shape of a truncated cone, 1.9 µm in height, and sunken into the integument (Fig. 3c). *Sensilla trichodea T3* have an intermediate size between the sensilla T1 and T2; they are erected at right angle in relation to the integument, blunt-tipped and furrowed by thirty oblique striae (Fig. 3d, e). They are inserted into a funnel-shaped cavity.

Sensilla basiconica B1 are small, notched at their tips, sunken into the integument, with an invisible but plausible collar. Lines of wall pores are visible at the base of the peg (Fig. 3f). *Sensilla basiconica B2* are stouter than sensilla B1 and blunt-tipped; they possess a basal collar, 1.6 µm height, whose surface is widely wrinkled, and are located in a circular cavity provided with a clear rim (Fig. 3g). *Sensilla campaniformia Ca1* resemble small, oval and flat cuticular cap surrounded by a cuticular ring; the whole is closely sunken into the integument. The cap shows a depression and a central plug closing the ecdysial pore (Fig. 3h). The distribution of sensilla is shown on Figure 3i.

- on the internal face (8 subtypes) (Figs. 4 and 5)

On the internal face of the upper right valve, the proximal part seems to be dug in because of the swelling of the upper edge, whereas the hook of the valve is raised (Fig. 4a). On this latter part, the punctuations correspond to sensilla which are regularly spaced (Fig. 4b).

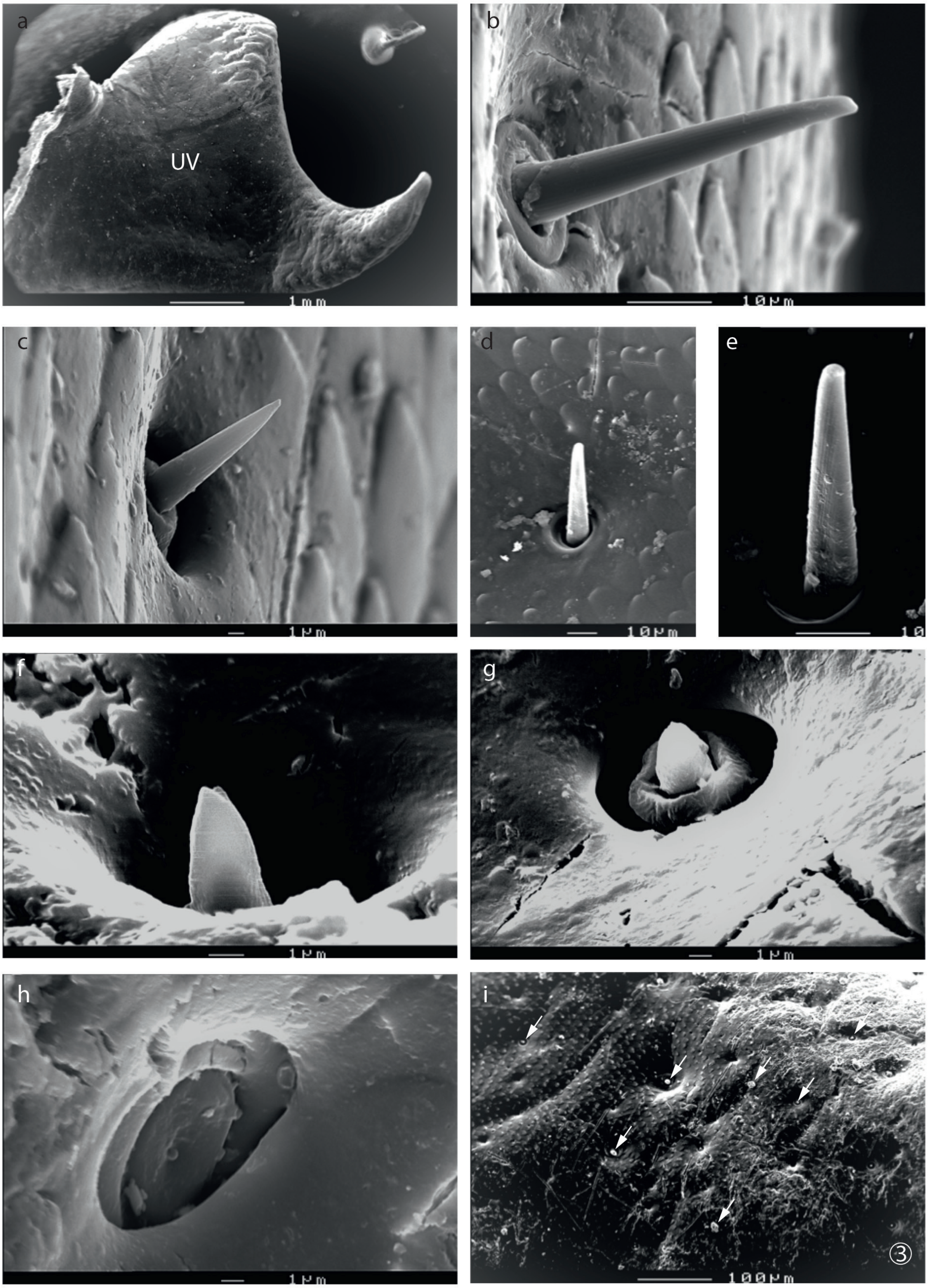

Figure 3. *Eugaster powysi*, oviscapt sensilla, left upper valve, outer face; **a**. whole valve; **b**. sensillum trichodeum subtype 1, T1; **c**. sensillum trichodeum subtype 2, T2; **d**, **e**. sensillum trichodeum subtype 3, T3; **f**. sensillum basiconicum subtype 1, B1; **g**. sensillum basiconicum subtype 2, B2; **h**. sensillum campaniformium subtype 1, Ca1; **i**. distribution of sensilla (arrows).

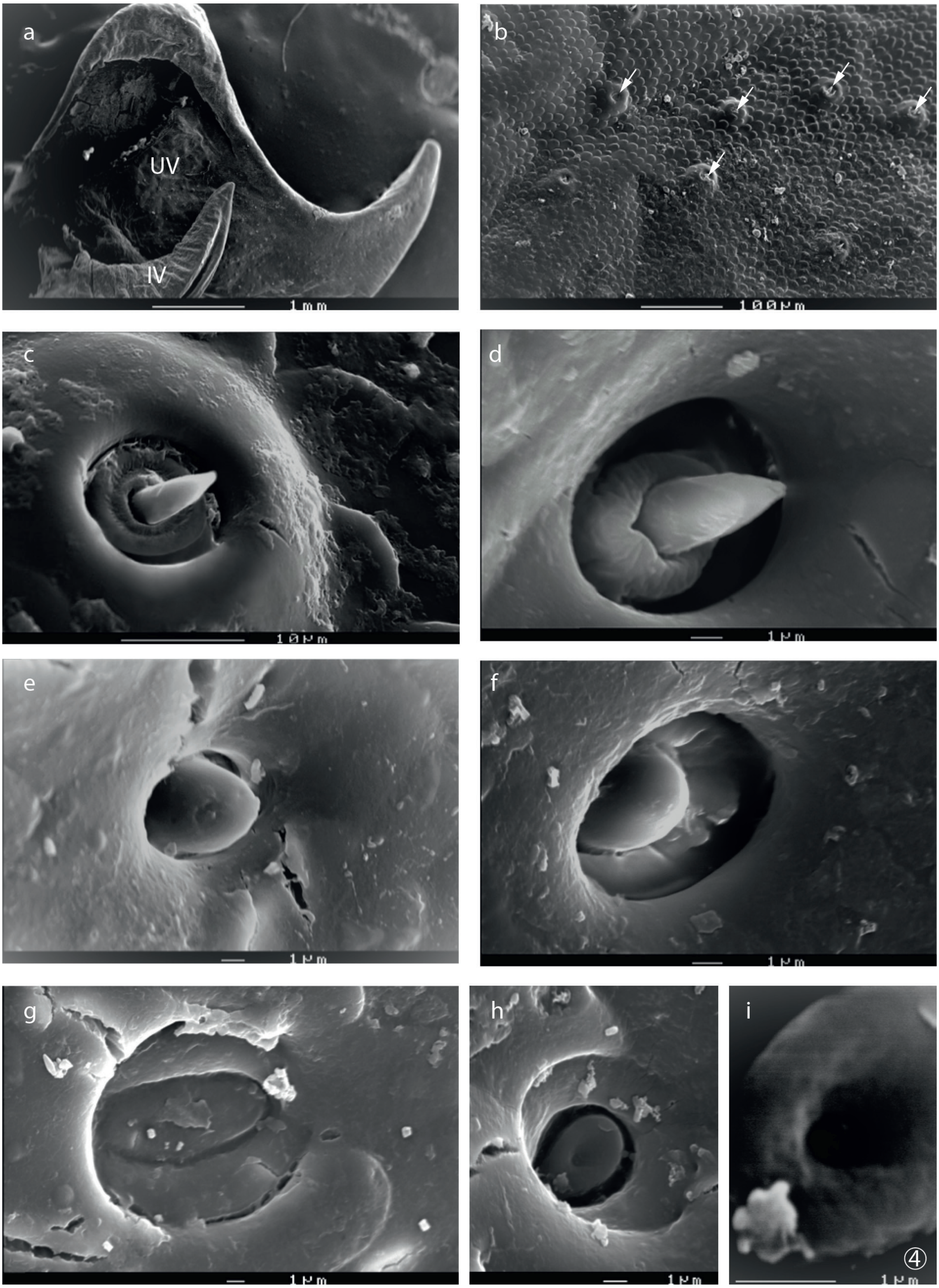

Figure 4. *Eugaster powysi*, oviscapt sensilla, right upper valve, inner face; **a**. whole upper UV and internal IV valves; **b**, distribution of sensilla basiconica (arrows); **c**. sensillum basiconicum subtype 3, B3; **d**. sensillum basiconicum subtype 2, B2; **e**. sensillum basiconicum subtype 4, B4; **f**. sensillum basiconicum subtype 5, B5; **g**. sensillum campaniformium subtype 2, Ca2; **h**. sensillum campaniformium subtype 3, Ca3; **i**. detail of pores on P3.

Sensilla basiconica B2 which are present on the external face are also found on the internal one (Fig. 4d). The sensory cone is longer (4.7 µm instead of 3.0 µm), and both the outer diameter of the collar and the diameter of the cavity are smaller. Another difference is the existence of a large prominent cuticular bulge (40 µm in outer diameter, 16 µm in height) raising the sensillum which, although housed in a cavity, is in relief compared to the valve (Fig. 4b). Sensilla B2 are often grouped in the zone of the hook. *Sensilla basiconica B3* resemble sensilla B2 as regards their position above the valve cuticle and the presence of a peripheral bulge (30 µm in outer diameter) but they differ by the greater length of the sensory cone and the presence of a basal flat collar made of two concentric rings whose outer diameter is 5 µm and 19 µm respectively (Fig. 4c). *Sensilla basiconica B4* are thickset cones partly sunken into a cavity barely wider than the cone; no basal collar is visible (Fig. 4e). *Sensilla basiconica B5* are spherical and the smallest of the sensilla basiconica. They are surrounded by a large basal collar and sunken into a relatively narrow cavity bordered by a cuticular bulge; the tip of the cone does not exceed the cavity (Fig. 4f). *Sensilla campaniformia Ca2* are the widest sensilla campaniformia and are not sunken into the integument. The cuticular bulge surrounding the sensillum forms an incomplete ring (Fig. 4g, Table 3).

Sensilla digitiformia D may be confused with sensilla campaniformia but they differ by their position in a cavity surrounded by a cuticular ring situated slightly below the valve cuticle and surrounded itself by a bulge (Fig. 4h). Compared to typical sensilla digitiformium, the sensillum of *Eugaster* is rather short (length: 3.8 µm, width: 2.5 µm) and resembles a sensillum auricillicum. Its proximal part is inserted into an internal cavity that is more or less circular (diameter: 4.1 µm); the diameter of the external cavity measures 7.7 µm in its greatest dimension. The sensillum seems thick, it has a central hollow and is perforated with presumed large pores 0.09 µm in diameter (Fig. 4i).

Sensilla trichodea T4. All the rare observed sensilla trichodea T4 are broken at the base probably because of their position on the internal surface of the upper valves (Fig. 5a). They are identified by their large diameter of 10.0 µm, the largest of sensilla trichodea (Table 1) and by their thick wall of 3.4 µm corresponding to one third of the sensillum diameter, and the internal lumen of 3.1 µm. The sensillum base is sunk into the integument of the valve; the narrow cavity, here 11.0 µm in diameter, only allows limited movements. *Sensilla trichodea T5* are rare sensilla broken at the base and inserted into a relatively spacious cavity (Table 1) (Fig. 5b). They are without internal lumen. Like sensilla T4, the edge of the cavity is without a cuticular bulge.

Sensilla of the lower valves

- on the external face (8 subtypes) (Figs. 6 and 7)

Sensilla trichodea T3 are located on the basal part of the lower valves (Fig. 6a) and are regularly distributed (Fig. 6b). They resemble T3 of the upper valves: the basal diameter is identical but the length decreases (26 µm instead of 37 µm), the hair is more sparse towards the apex (Fig. 6c).

Sensilla basiconica B6 are, like sensilla T3, located on the basal part of the valve. With a length of 16 µm, they are the longest sensilla basiconica of all valves (Fig. 6d). They are not sunken into the integument, have a thin basal collar and are inserted into a narrow cavity. They have 50-60 longitudinal striae which are probably alignments of wall pores. *Sensilla basiconica B2* like the sensilla B7 and B8 are found on the distal part of the lower valves, in a zone without scales and whose surface is very bumpy (Fig. 6e). They resemble sensilla B2 of the upper valves and clearly show a laterally located terminal pore (Fig. 6f, g). *Sensilla basiconica B7* are strong pegs of identical length to sensilla B3, with a large basal diameter and a fluted wall (about 30 ribs) (Fig. 6h). *Sensilla basiconica B8* are long, blunt-tipped pegs with a basal collar about 2 µm in height; wall pores are hypothesized (Fig. 6i). *Sensilla basiconica B9* have a massive form which recalls sensilla B7; they are longer and rounded at the tip. They are inserted into a cavity without a visible basal collar (Fig. 7a). *Sensilla campaniformia Ca3* are oval caps, with dimensions comparable to Ca1, showing a central hollow and a plug which conceals the ecdysial pore (Fig. 7b). Unlike other campaniformia, Ca3 are without annular ring and are inserted into a shallow cavity of 10.0 X 4.2 µm. *Sensilla cylindrica Cy* are different from other sensilla (Fig. 7c): they are 9.4 µm in length, 6.2 µm in basal diameter, and are inserted in a cavity of 10.0 µm in diameter. The cylindrical part has irregular striae; the distal part is swollen.

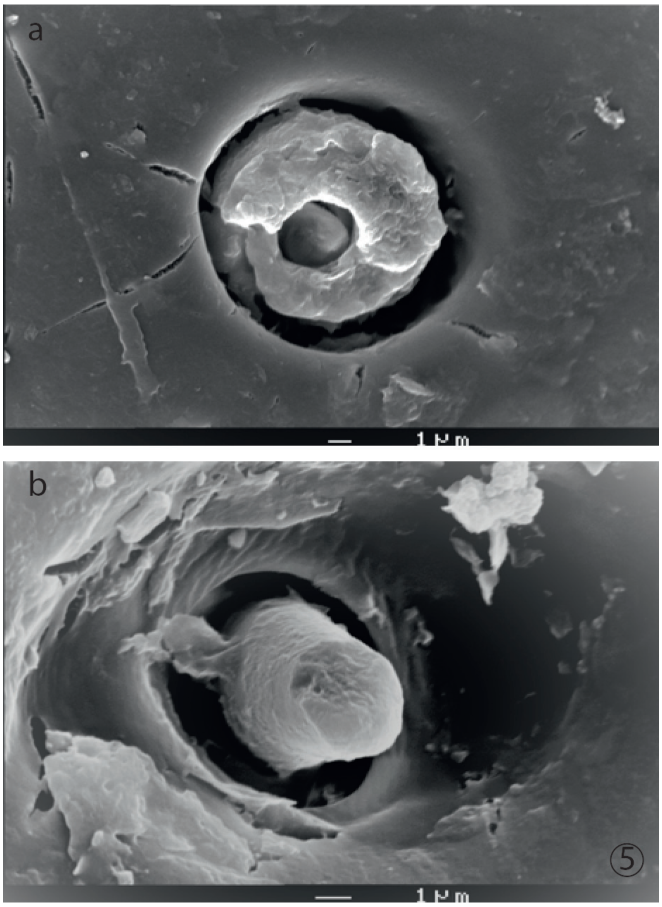

Figure 5. *Eugaster powysi*, oviscapt sensilla, right upper valve, inner face; **a**. sensillum trichodeum subtype 4, T4, broken at the base; **b**. sensillum trichodeum subtype 5, T5, broken near the base.

- on the internal face (3 subtypes) (Fig. 8)

Sensilla coeloconica Co have the form of a more or less circular cavity of 2.0 µm X 1.4 µm, and are borderless. The inner structure of the cavity shows nipples and a pore (Fig. 8b). *Sensilla campaniformia Ca4* have oval caps only twice the dimensions of Ca1 and Ca2 (Table 3), and are surrounded by a ring of raised cuticle, slightly sunken into the integument. This structure is surrounded by a cuticular bulge forming a second ring (Fig. 8e). *Sensilla basiconica B10* are blunt-tipped short pegs with the same diameter from the base to the tip. They have a flat basal collar and are

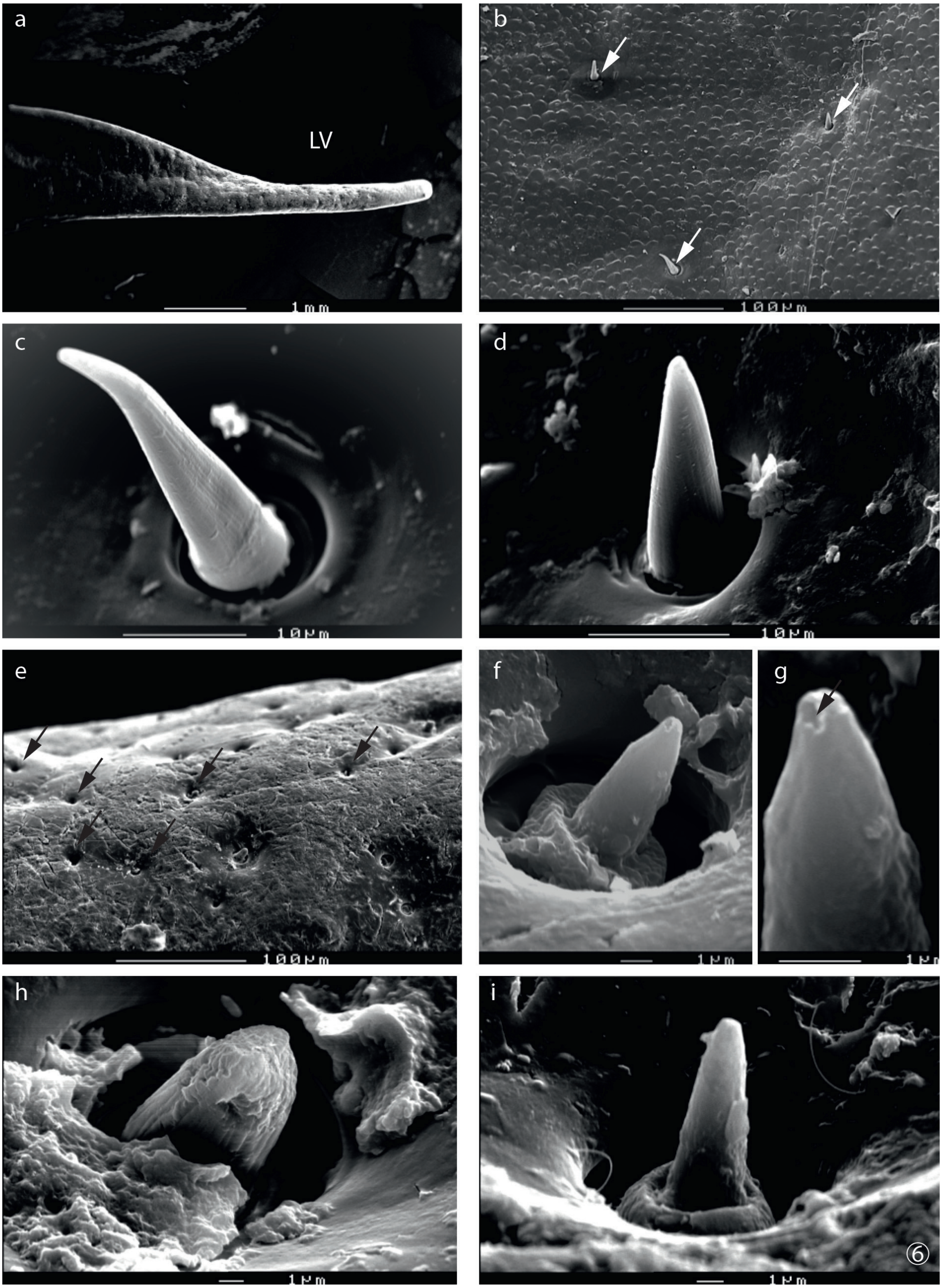

Figure 6. *Eugaster powysi*, oviscapt sensilla, left lower valve, outer face; **a**. distal part of valve LV; **b**. distribution of some sensilla on basal part (arrows); **c**. sensillum trichodeum subtype 3, T3, on basal part; **d**. sensillum basiconicum subtype 6, B6, on basal part; **e**. distribution of sensilla on distal part (arrows); **f**. sensillum basiconicum subtype 2, B2, on distal part; **g**. terminal pore of B2 (arrow); **h**. sensillum basiconicum subtype 7, B7, on distal part; **i**. sensillum basiconicum subtype 8, B8, on distal part.

inserted into a large cavity. The wall is smooth and does not possess any pore (Fig. 8f).

The glandular pores are often very numerous at the base and between two adjacent cuticular scales (Fig. 8c). They have the shape of a hole 0.7 µm in diameter, located at the bottom of a funnel-shaped cuticular hollow measuring 2 µm in diameter (Fig. 8d).

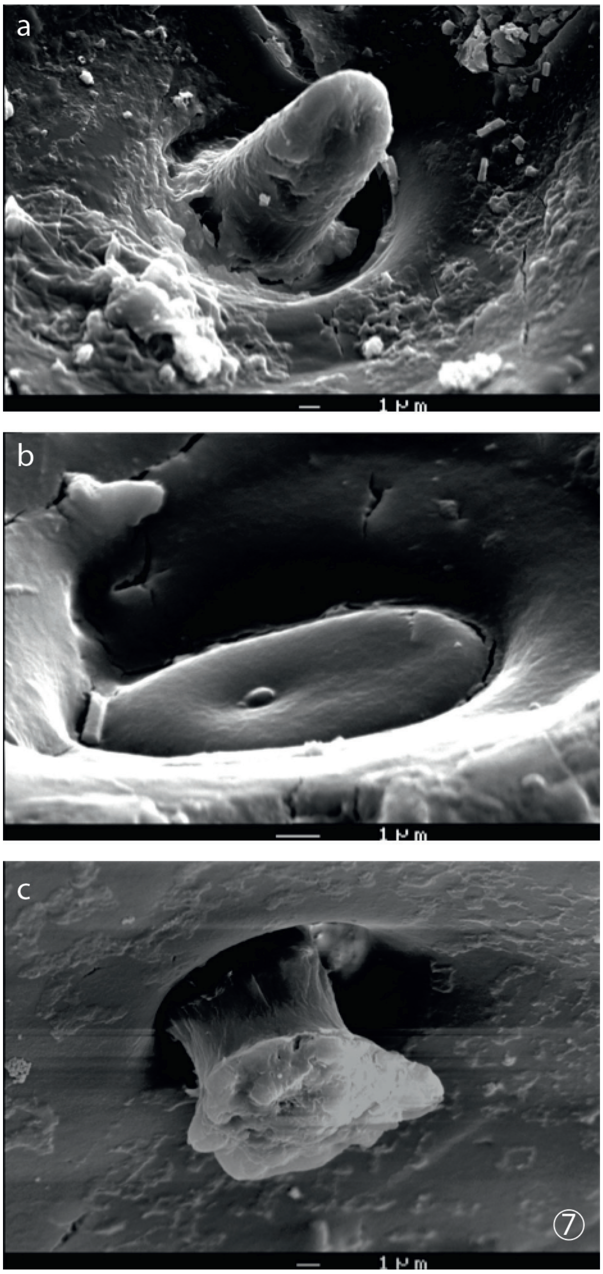

Figure 7. *Eugaster powysi*, oviscapt sensilla, left lower valve, outer face, distal part; **a**. sensillum basiconicum subtype 9, B9; **b**. sensillum campaniformium subtype 4, Ca4; **c**. sensillum cylindricum Cy.

Sensilla of the inner valves

- on the external face (1 subtype) (Fig. 9)

Sensilla campaniformia Ca5 are sensilla, of identical dimensions to Ca4, whose cap is slightly sunken and the ring and the bulge merge about half of their length with the scales of the valve (Fig. 9c). They are the only sensilla which are present in the distal part of the external surface (Fig. 9a) and are regularly distributed (Fig. 9b).

- on the internal face (5 subtypes) (Fig. 10)

Sensilla trichodea T3 are relatively short blunt-tipped sensilla. They are inserted in a large socket with raised edges on a zone without scales (Fig. 10a). The cavity contains an internal ring tightening the base of the hair while allowing it to move. A terminal pore is probable. *Sensilla basiconica B11*. Two slightly different subtypes are here grouped because their sensory cones are of identical length (Fig. 10b, c) and seem to possess wall pores (Fig. 10b). The cones are inserted into a large cavity provided with an internal membrane more or less tightening the base of the cones. This membrane is pleated in both cases: it has waves which are either concentric and close together (Fig. 10b) or radiating (Fig. 10c). *Sensilla basiconica B12* are rather similar to sensilla B11 but are stockier (Fig. 10d); they have a sinuous terminal pore (Fig. 10e) described in some insects. *Sensilla basiconica B13* stand in the middle of a raised structure which, merging with the surrounding scales, has the shape of a flower of 19.4 µm-22.2 µm (Fig. 10f). The olive-shaped sensory cone is located in a cavity bordered by a large bulge and provided with an internal membrane with radiant folds forming a ring around the cone (Fig. 10g). *Sensilla campaniformia Ca6* possess the smallest cap of all the sensilla campaniformia of the oviscapt (Table 3). They are sunken at the bottom of a funnel surrounded by a very large cuticular bulge which has the same shape as B13 (Fig. 10h, i).

Distribution and number of sensilla

The distribution of sensilla is regular and spaced on each valve and each face. No significant concentration of a type or subtype has been noticed on any valve. The position of the sensilla is characterized by punctuations on Fig. 1, white dots, hollows or blisterings of the cuticle on the micrographs (Figs. 2, 3a, 4a, 8a).

The numbers of sensilla depend both on the surface of the valve and the numbers of types and subtypes present. They reach the following values for each valve: upper valve: 240-250 (external face), 260-270 (internal face); lower valve: 120-130 (external face), 70-80 (internal face); inner valve: 25-30 (external face), 55-60 (internal face). In terms of the highest values, the three pairs of valves of the oviscapt bear about 820 X 2 = 1640 sensilla.

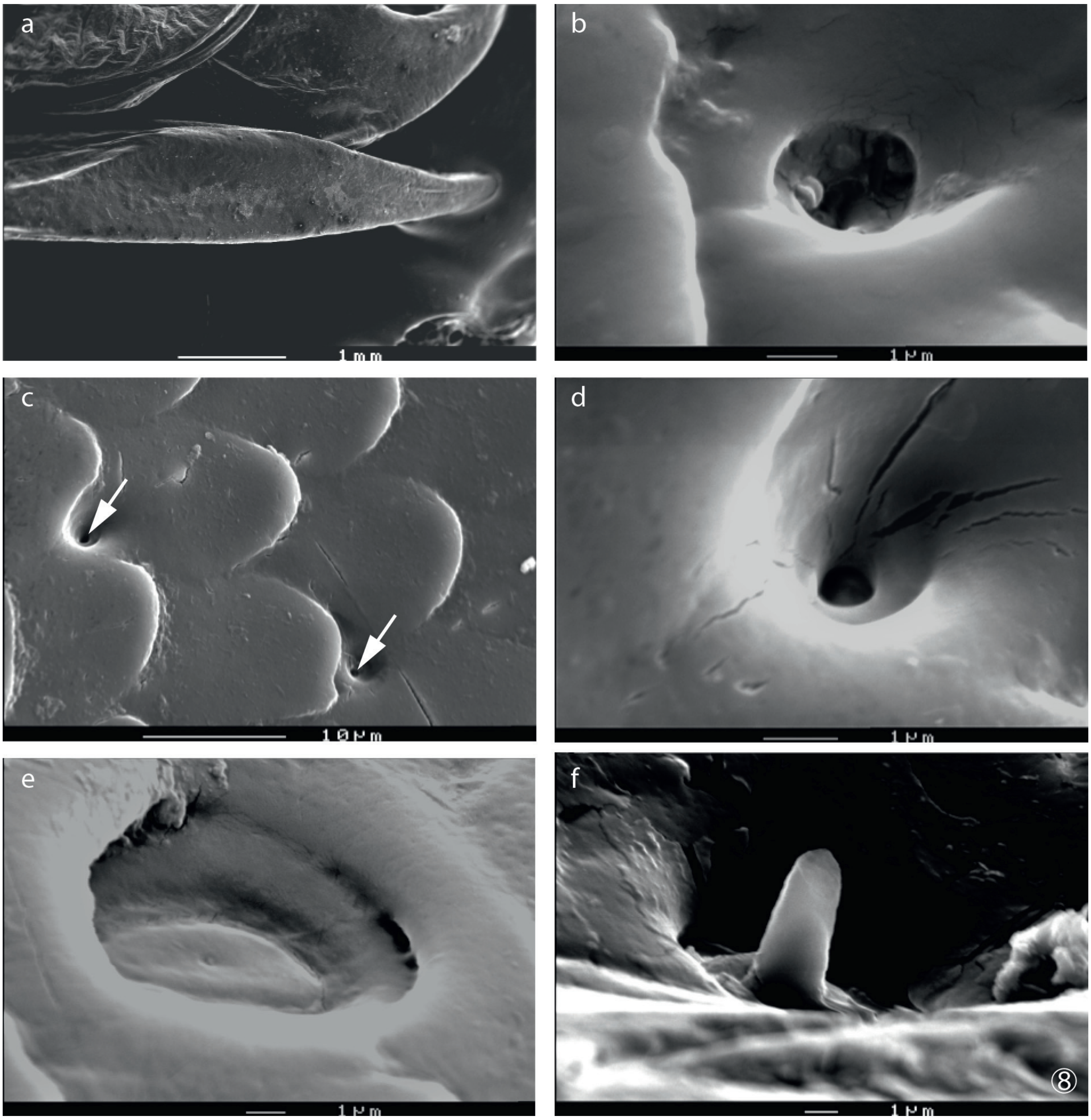

Figure 8. *Eugaster powysi*, oviscapt sensilla, right lower valve, inner face; **a**. whole view of valve LV; **b**. sensillum coeloconicum Co; **c**. cuticular scales and two glandular pores (arrows); **d**. glandular pore; **e**. sensillum campaniformium subtype 5, Ca5; **f.** sensillum basiconicum subtype 10, B10.

Table 4 – Distribution of sensilla (presence: +) on the external face (ef) and the internal face (if) of oviscapt valves.

Sensilla	Upper	valve	Lower	valve	Inner	valve
	ef	if	ef	if	ef	if
Trichodea 1	+	–	–	–	–	–
Trichodea 2	+	–	–	–	–	–
Trichodea 3	+	–	+	–	–	+
Trichodea 4	–	+	–	–	–	–
Trichodea 5	–	+	–	–	–	–
Basiconica 1	+	–	–	–	–	–
Basiconica 2	+	+	+	–	–	–
Basiconica 3	–	+	–	–	–	–
Basiconica 4	–	+	–	–	–	–
Basiconica 5	–	+	–	–	–	–
Basiconica 6	–	–	+	–	–	–
Basiconica 7	–	–	+	–	–	–
Basiconica 8	–	–	+	–	–	–
Basiconica 9	–	–	+	–	–	–
Basiconica 10	–	–	–	+	–	–
Basiconica 11	–	–	–	–	–	+
Basiconica 12	–	–	–	–	–	+
Basiconica 13	–	–	–	–	–	+
Campaniformia 1	+	–	–	–	–	–
Campaniformia 2	–	+	–	–	–	–
Campaniformia 3	–	–	+	–	–	–
Campaniformia 4	–	–	–	+	–	–
Campaniformia 5	–	–	–	–	+	–
Campaniformia 6	–	–	–	–	–	+
Coeloconica		–	–	–	+	–
Digitiformia		–	+	–	–	–
Cylindrica		–	–	+	–	–

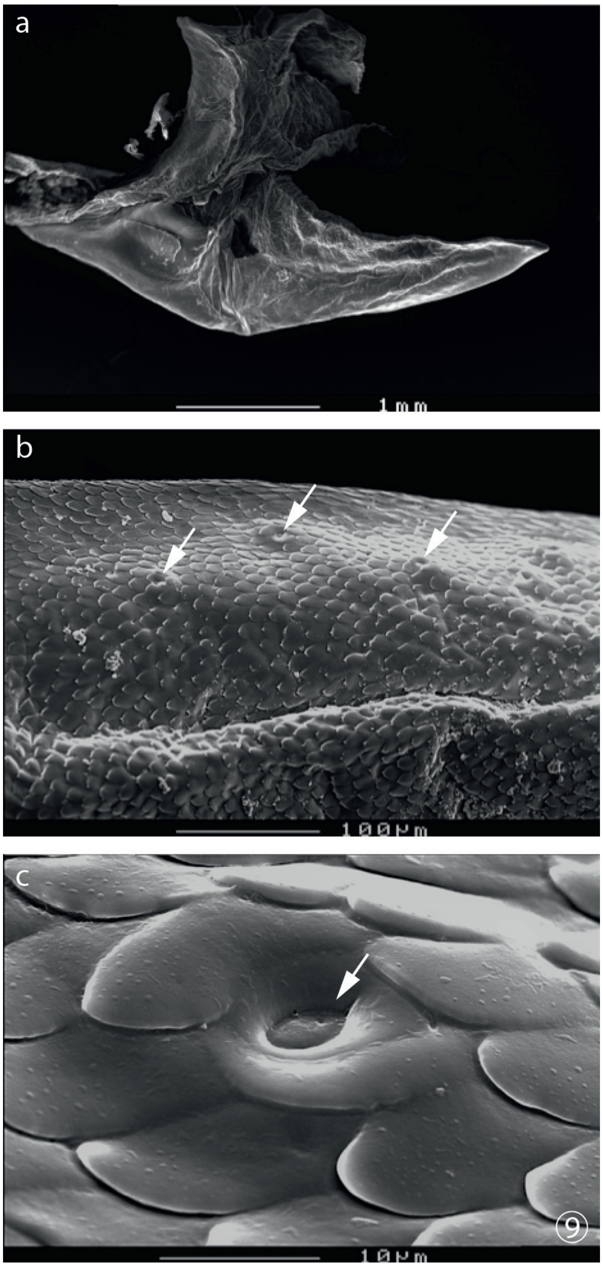

Figure 9. *Eugaster powysi*, oviscapt sensilla, left internal valve, outer face; **a**. whole view of valve IV; **b**. distribution of sensilla (arrows); **c**. sensillum campaniformium subtype 5, Ca5 (arrow).

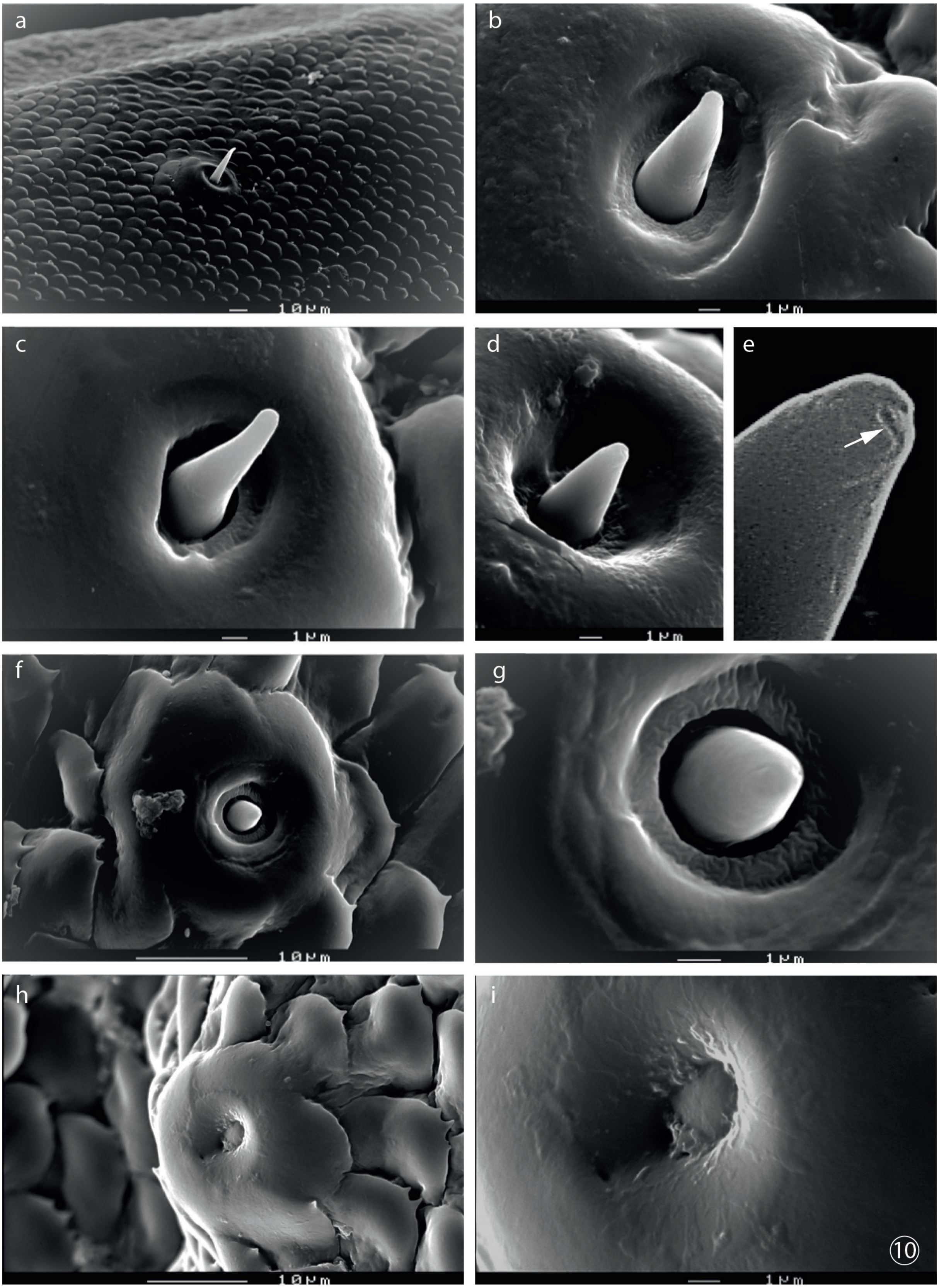

Figure 10. *Eugaster powysi*, oviscapt sensilla, right internal valve, inner face; **a**. sensillum trichodeum subtype 3, C3; **b**. sensillum basiconicum subtype 11, B11; **c**. another aspect of B11; **d**. sensillum basiconicum subtype 12, B12; **e**. detail of terminal pore (arrow); **f**. sensillum basiconicum subtype 13, B13; **g**. detail of B13; **h**. sensillum campaniformium subtype 6, Ca6; **i**. detail of Ca6.

DISCUSSION

Summary of results

The bristle-shaped sensilla trichodea are especially present on the upper valves (all 5 subtypes T1-T5) and only 1 subtype (T3) is found on the lower and inner valves. They are more numerous on the external faces; their presence on the internal faces is more random due to the friction of valves between them. Sensilla T2 with their sharp tips and the absence of pores are tactile mechanoreceptors (Altner 1977, Zacharuk 1985). Blunt-tipped sensilla trichodea T1 and T3 are candidates for the contact chemoreception (Altner & Prillinger 1980). Sensilla T3 are found on the three pairs of valves. Thus, contact chemoreception is provided by all the valves of the oviscapt.

The sensilla basiconica are frequent on the valves: 5 subtypes on the upper valves, 5 subtypes on the lower valves, and 3 subtypes on the inner valves. The variety of subtypes is partly due to the presence of each of them on the different types of valves, and to the diversity of sensory stimuli perceived by each sensillum. The inner valves are important during the expulsion of the egg because, with their thin wall, they are a little rigid and tend to stick to the wall of the egg (Cappe de Baillon 1919). The existence of 3 subtypes of sensilla basiconica on the internal face of these valves shows that the chemoreception is still important during the emergence of the egg.

The presence of wall pores in 6 subtypes of sensilla basiconica (B1, B6, B7, B8, B9, B11) is assumed. If this is so, an olfactory function could be attributed to the oviscapt of *E. powysi*, as has been demonstrated for the ovipositors of certain Lepidoptera (Klinner *et al*. 2016).

Comparison with Orthoptera Caelifera (Acrididae)

Mechanical role

In *Locusta migratoria* and *Schistocerca gregaria*, two pairs of shovel-shaped appendages, the ovipositor valves on the abdomen tip, excavate the soil for the egg-laying (Thompson 2018). In an appropriate site, desert locust *S. gregaria* lay their eggs at depth in soil by digging their abdomen into the substrate using rhythmic movements of their abdomen and hard, sclerotized ovipositor valves (Newland & Yates 2008). According to Favrelle (1936) the females of *Eugaster* act identically. The ovipositor valves of desert locust and migratory locust have different functions: the lower pair levers the abdomen down, the upper pair digs the hole (Vincent 1976). Similar functions can be attributed to the valves of *Eugaster*, especially as the upper pair is very large. The inner pair of valves protected by the two other pairs is not involved in the digging. Signs of wear and scratches are frequently observed on the oviscapt of insects laying eggs in the ground or in hard soils such as *Julodis aequinoctialis* (Olivier, 1790) (Coleoptera: Buprestidae) (Faucheux 2016). The oviscapt of *E. powysi* shows no sign of wear which confirms the egg-laying of *Eugaster* in soft substrates. The lack of sclerotization in the inner valves allows them to fit the elongated shape of the egg, with both its flat face and its convex face , as well as the polygonal network in relief of the surface.

Sensory role

Locusta migratoria possesses contact chemoreceptors (sensilla basiconica) located on the ovipositor valves and genital segments which serve to control the chemical features of the substrate before and during oviposition. They occur dispersed and crowded in fields between mechanosensory exteroreceptors sensitive to touch or wind (sensilla trichodea and sensilla filiformia). The sensilla basiconica of the ovipositor valves usually contact the substrate during the pre-oviposition probing movements (Tousson & Hustert 2000). Likewise, on the upper valves of *L. migratoria*, Rice & McRae (1976) report the presence of six morphological types. Among them, three types are long, medium, and short setae which all appear to be tactile receptors; one type has a well-marked terminal pore which classifies it as a contact chemoreceptor (50 sensilla per valve); two types are pits and papillae whose function is hard to define.

The role of contact chemoreceptors on egg-laying behaviour and on the rhythmic digging movements of the ovipositor valves has been analysed in *S. gregaria*. All chemicals tested (sucrose, lysine-glutamate salt, …) acted aversively and reduced both the duration spent egg-laying and the number of eggs laid (Newland & Yates 2008). On the lower ovipositor valves of the acridid *Taeniopoda eques* (Burmeister, 1838), Tousson (2004) observes a large number of contact chemoreceptors. These receptors play an important role in many aspects of grasshopper life such as detecting the chemical composition of the soil before and during oviposition. Observation of the lower valves of the lubber grasshopper revealed the presence of uniporous basiconic contact chemoreceptors in addition to different types of trichoid mechanoreceptors. The sensilla basiconica contain one mechanosensory neuron and four chemosensory neurons which characterize the bimodal sensilla. The «tip recording technique» from single sensillum demonstrated mechanosensory responses to deflections of the sensillum as well as a gustatory activity when in contact with different chemical solutions. These sensilla basiconica serve as contact chemoreceptors and not as olfactory receptors (Tousson 2004).

In *Eugaster,* we have not observed a terminal pore as accurate as the one represented by Rice & McRae (1976) in *L. migratoria* but certain sensilla basiconica of the upper valves (B1 and B2), lower valves (B2), and inner valves (B12, B13) possess a more or less visible terminal pore, and can be considered as contact chemoreceptors. Sensillum B12 has a terminal pore whose shape recalls that of the labellar taste hair of blow flies (Stürckow *et al*. 1973). The sensillum B13 of *Eugaster*, whose terminal pore is not visible, is similar to the contact chemoreceptors described by Rice & McRae (1976). The short sensilla trichodea T1 and T3 with a blunt apex, present on the external face of upper valves, show the characteristic features of uniporous sensilla (Zacharuk 1980, 1985). The variety of the morphological subtypes of sensilla basiconica proposed as gustatory in *Eugaster* implies specific sensitivity to various chemicals. Sensilla filiformia described in *L. migratoria* by Tousson & Hustert (2000) are absent from the oviscapt of *Eugaster* but they may be replaced functionally by the sensilla filiformia of cerci.

Comparison with Orthoptera Ensifera

Most Orthoptera Ensifera lay their eggs in plants. Their oviscapt has been little studied, because of their low economic interest: *Gryllus campestris* Linnaeus, 1758 (Sellier 1971), *Phaneroptera nana* Fieber, 1853 (Faucheux & Goasmat 2012), *Tettigonia viridissima* (Linnaeus, 1758) (unpublished pers. obs.). In *G. campestris* that lays its eggs in the soil, Sellier (1971) reports sensilla trichodea of very different sizes, the smallest of which are treated as sensilla basiconica or sensilla coeloconica. In *P. nana*, that lays its eggs in the leaves of various plants , the upper valves bear numerous aporous sensilla coeloconica and aporous sensilla chaetica (= trichodea), 20-40 µm long, some of which are bifurcate, on both two faces; the lower valves have aporous sensilla chaetica (= trichodea), 20-30 µm long, on the external face, but no sensilla on the internal face; the inner valves possess no sensilla on their external face, but numerous aporous sensilla chaetica, 10-40 µm long, and sensilla basiconica (type B of *Eugaster*) on their internal face (Faucheux & Goasmat 2012). Unpublished personal observations in *T. viridissima* shows the presence: 1 – on the upper valves, of numerous sensillla coeloconica, rare sensilla trichodea 10-30 µm long and sensilla basiconica (1 type) on the external face; whereas the internal face is entirely covered with sensilla coeloconica; 2 – on the lower valves, are found rare sensilla basiconica (1 type) and numerous sensilla coeloconica but no sensilla trichodea; 3 – on the inner valves, there are sensilla trichodea 20 µm long, sensilla basiconica (1 type) on the external face, and rare basiconica on the internal face. In summary, the three precited Ensifera possess sensilla trichodea, basiconica and coeloconica on their oviscapt. These sensillum types are present in *E. powysi*.

Sensilla common to the other Orthoptera and original sensilla

The *sensilla trichodea and basiconica* of the oviscapts are common to all Orthoptera. The sensilla coeloconica reported in many Orthoptera are rare in *Eugaster* and only present on the internal face of the lower valves.

Sensilla coeloconica on the internal face of lower valves of *E. powysi* belong to a special type because they have no characteristic sensory cone . This sensillum type is present on the antennae of Orthoptera and Mantodea. They are “sensilla coeloconica subtype IV” in *P. nana* (Goasmat & Faucheux 2011), “cavity sensilla” in eight species of Acrididae (Li *et al*. 2007), and “sensilla coeloconica subtype 2” on the antennae of *E. powysi* (Faucheux 2017). They are named “sensilla coeloconica subtype III” in the praying mantids *I. oratoria* and *M. religiosa* (Faucheux 2009a). In *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 the sensilla of the oviscapt of *Eugaster*. According to Cappe de Baillon (1919), the lower valves in the grasshoppers are perforating blades whereas the upper valves serve primarily to occupy space. During penetration into the ground, the sensilla coeloconica could appreciate its humidity rate which is vital for the survival and the development of eggs.

Sensilla campaniformia seem not to have been cited on the oviscapts of crickets and locusts by previous authors. They are characteristic and recognizable on both external and internal faces of upper, lower, and inner valves of *Eugaster*. The sensilla campaniformia of insects are frequently concentrated on structures subject to cuticular distorsions (McIver 1985). They are mechanoreceptors which detect stresses applied to the surface of the cuticle and function as proprioceptors (Keil 1997). Furthermore in *E. powysi*, they show a certain diversity in relation to the type and the face of valves. This variety, present in the same organ, here the oviscapt, was reported by McIver (1975) but on different organs. The cap may be circular (inner valve, internal face) or oval (upper and lower valves, both faces), raised or sunken (inner valve, internal face), and flat (all the types in *Eugaster*). The ring of raised cuticle surrounding the cap may be incomplete as occurs in sensilla on the palps of a locust (Blaney & Chapman 1969), on the antennae of *P. nana* (Goasmat & Faucheux 2011), and on the oviscapt of *Eugaster* (upper valve, internal face, this paper); it may be absent (inner valve, internal face). This reduction is most likely correlated with the flexibility of the socket (McIver 1985); it shows differences in the sclerotization of three pairs of valves. All these variations in the size and structure of the cuticular portions, which are common, determine the mechanics of coupling relating to the specific characteristics of the stimulus perceived at the particular location of the sensillum. The variable depth of the sinkage of sensilla campaniformia is related both to the thickness of the cuticle (McIver 1975) and to the intensity of the pressure on the sensilla when digging the egg-laying hole and during the progression of the eggs. The shape of the cap has a functional importance because campaniform sensilla with round caps respond to stress in the cuticle from all directions, whereas oval sensilla are directionally selective (Pringle 1961). The central pore present in the cap of certain sensilla in *Eugaster* is not a sensory pore. This pore which corresponds to the ecdysial canal is sometimes observed in hemimetabolous and holometabolous insects (Moeck 1968, McIver 1985). It is often closed by a cuticular plug (upper valve, external face; both faces of lower valves) as oberved on the pedicellar sensilla of the antenna in *P. nana* (Goasmat & Faucheux 2011).

Sensilla digitiformia observed on the internal face of upper valves were not cited on the oviscapts of orthopterans. In the oviscapt of *E. powysi*, these valves are naturally in contact with their internal faces and therefore, the sensilla can be stimulated during this contact. In the coleopteran *Ctenicera destructor*, the sensilla digitiformia on the labial palp respond electrophysiologically to contact and vibratory stimuli (Zacharuk *et al*. 1977). According to the observations of Cappe de Baillon (1919) in the Tettigoniidae, during the penetration of the oviscapt in the soil, there are alternative movements of the external valves (upper and lower) which slide over one another. The upper and lower valves act separately. The vibratory stimuli produced by these movements will be recorded by the sensilla digitiformia. The presence of vibroreceptors is known in palps of Coleoptera (see Faucheux 2013). Schmitt (1994) suspects that the primary biological role of the sensilla digitiformia is the detection of stretching forces acting upon the cuticular surface of the terminal maxillary or labial palpal segment of coleopterans. However, according to Giglio *et al.* (2003), sensilla digitiformia can be both mechanoreceptors and chemoreceptors, though hygroreception may also be postulated on the basis of their abundance on the mouthparts of hygrophilous species.

The glandular secretion released by glandular pores, which are numerous on the lower valves, can help the sliding of the valves and play the role of lubricant facilitating the expulsion of the eggs.

CONCLUSION

Although the oviscapt of *Eugaster powysi* is short compared to other Ensifera, it possesses a diversity of subtypes of sensilla greater than that of other studied species. Each pair of valves often has its own subtypes. The morphological diversity of sensilla campaniformia must be linked to the thickness of the valve and its position in the oviscapt. Sensilla campaniformia, digitiformia and coeloconica observed on the oviscapt are specific to the armoured ground cricket *Eugaster powysi.* Proprioception, contact chemoreception and hygroreception are functions well provided for by the oviscapt.

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