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The structure of the male postabdomen and associated sensilla of *Phaneroptera nana* Fieber 1853, and remarks on uniporous sensilla of genitalia (Orthoptera: Tettigoniidae: Phaneropterinae)

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Abstract. The sensilla of the male postabdomen of the Mediterranean Katydid *Phaneroptera nana* were investigated by scanning electron microscope in order to study their involvement in copulatory behaviour. The externally visible parts at the abdominal extremity are the dorsal epiproct and the ventral subgenital plate which together form a kind of pincer, and the highly developed cerci which are curved like a hook. The more internal parts are the paraprocts and the genitalia. The epiproct bears three types of aporous sensilla chaetica and sensilla campaniformia on its external surface, and only aporous sensilla filiformia on its internal surface. The subgenital plate is equipped with aporous sensilla chaetica and aporous sensilla filiformia present on its external surface whereas its internal surface is without sensilla. The cercal sensilla are composed of aporous sensilla filiformia of two subtypes, aporous sensilla chaetica and sensilla campaniformia. The surface of the paraprocts is endowed with aporous sensilla filiformia, two subtypes of aporous sensilla chaetica and sensilla campaniformia. The genitalia comprise uniporous sensilla basiconica with the abruptly narrowed tip. They are joined together by a median small tongue provided with uniporous sensilla basiconica, and are edged with a pad bearing sensilla campaniformia. The possible functions of the above sensilla are proposed in the light of previously published literature: a tactile mechanoreceptive function for sensilla chaetica, a vibroreceptive function for sensilla filiformia, a proprioceptive function for sensilla campaniformia, and a gustative function for uniporous sensilla basiconica. A gustative function appears not to have been mentioned for the male genitalia of Orthoptera or even on those of other insects.

Key words: *Phaneroptera*, Orthoptera, postabdomen, genitalia, mâle, sensilla, aporous, uniporous.

La structure du post-abdomen du mâle et les sensilles associées de *Phaneroptera nana* Fieber 1853 et remarques sur les sensilles unipores des genitalia (Orthoptera: Tettigoniidae: Phaneropterinae).

Résumé. Les sensilles présentes sur le post-abdomen du mâle du Phanéroptère méridional *Phaneroptera nana* ont été étudiées à l'aide du microscope électronique à balayage afin de rechercher leur implication lors du comportement copulatoire. Les pièces visibles extérieurement à l'extrémité abdominale sont l'épiprocte dorsal, le plateau sous-génital ventral qui ensemble constituent une sorte de pince, et les cerques très développés et courbés en forme de crochet. Les pièces plus internes sont les paraproctes et les genitalia. L'épiprocte porte trois types de sensilles chétiformes sans pore et des sensilles campaniformes sur sa face externe, et uniquement des sensilles filiformes sur sa face interne. Le plateau sous-génital est équipé d'un seul type de sensilles chétiformes sans pore qui sont présentes sur sa face externe tandis que sa face interne est dépourvue de sensilles. Les sensilles cercales sont composées de sensilles filiformes sans pore de deux sous-types, de sensilles chétiformes sans pore et de sensilles campaniformes. La surface des paraproctes est pourvue de sensilles filiformes sans pore, de deux sous-types de sensilles chétiformes sans pore et de sensilles campaniformes. Les genitalia comportent des sensilles basiconiques unipores à l'extrémité distale brusquement rétrécie. Elles sont réunies par une languette médiane, pourvue de sensilles basiconiques à l'apex émoussé et perforé d'un pore terminal, et bordée par un bourrelet portant des sensilles campaniformes. Les fonctions possibles des sensilles précédentes sont proposées à la lumière de la littérature scientifique: une fonction mécanoréceptrice tactile pour les sensilles chétiformes, une fonction vibroréceptrice pour les sensilles filiformes, une fonction proprioceptrice pour les sensilles campaniformes et une fonction gustative pour les sensilles basiconiques unipores. Cette fonction ne semble pas avoir été mentionnée en ce qui concerne les genitalia mâles des Orthoptères ni même sur celles d'autres insectes.

Mots-clés : Phaneroptera, Orthoptère, post-abdomen, genitalia, mâle, sensilles, sans pore, unipore.

INTRODUCTION

In insects, the morphology of the female genitalia and their sensilla has often been studied because research of the egg-laying substrat constitutes the final stage of reproductive behaviour. In this respect, different types of sensilla have been described in different orders of insects: chronologically, first the tactile mechanoreceptors, then the gustatory chemoreceptors and finally the olfactory chemoreceptors. On the other hand, literature concerning the male genitalia is less common: Coleoptera (Hammond 1972, Epila-Otara & Triplehorn 1990, Kim *et al*. 1999, Kim & Sota 2004, 2006, Hubweber & Schmitt 2005, Düngelhoef & Schmitt 2006, 2010), Ephemeroptera (Gaino *et al*. 2009), Lepidoptera (Chovet 1982, Davis 1975, Faucheux &d Chauvin 1981, Faucheux 1982, 1999), Hymenoptera (Schlegel 1967). In Coleoptera Phytophaga, Düngelhoef & Schmitt (2010) mention contact chemoreceptors on several aedeagi. In all the other species, only the tactile mechanoreceptors and the proprioceptors have been revealed and not a single chemoreceptor.

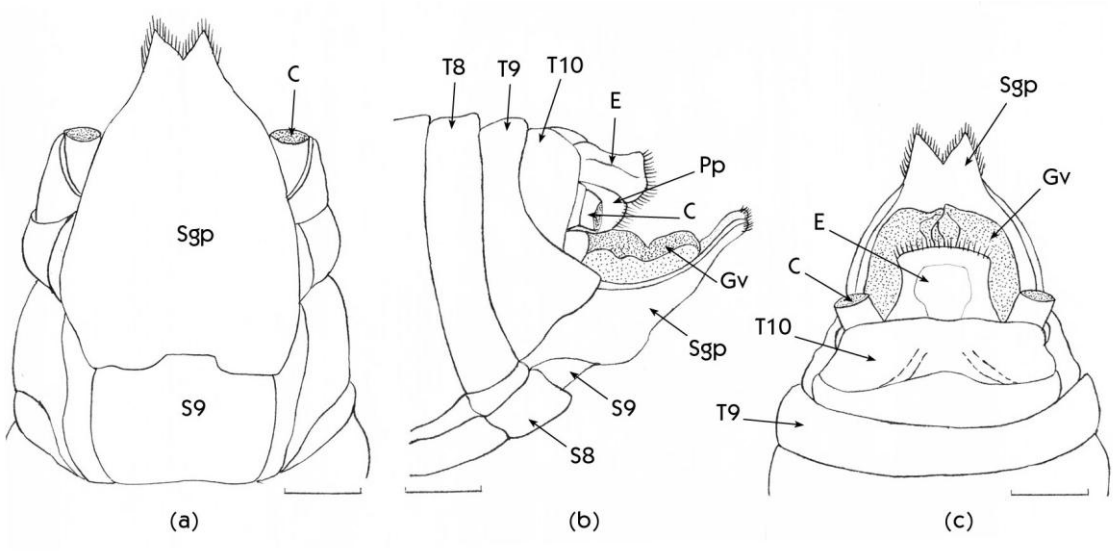

Figure 1. Male postabdomen of *Phaneroptera nana*, line drawings. **a**, ventral view; **b**, lateral view; **c**, dorsal view. C, cercus; E, epiproct; Gv, genital valve; P, paraproct; Sgp, subgenital plate; S8, 8th sternite; S9, 9th sternite; T8, 8th tergite; T9, 9th tergite; T10, 10th tergite.

However, in the course of the study of the sensory equipment of a grasshopper *Phaneroptera nana* Fieber 1853 (Phaneropterinae), we have been led to observe the posterior end of the males (cerci and genitalia) and have discovered an usual sensillum type in this position. These data obtained with the scanning electron microscopy will subsequently be verified with ultrastructural descriptions and electrophysiological techniques.

MATERIAL AND METHODS

The specimens of *Phaneroptera* were captured on the littoral dunes of Essaouira (Morocco) in 2008. Their determination has been verified by François Dusoulier (Gap, France). For the study with scanning electron microscope (SEM), the post-abdominal parts of insects (n = 5) were dissected, dehydrated in a graded ethanol series, mounted on specimen holders and coated with a thin layer of gold and palladium in a JFC 1100 sputter coater. Preparations were examined in a Jeol JSM 6400 SEM at 10 kV. The terminology of Zacharuk (1985) is used in naming the types of sensilla.

RESULTS

General morphology of the post-abdomen

In *Phaneroptera*, the last sternite visible in the male is the 9th, it is the subgenital plate which is elongated, pointed, curved upwards and bifid at its apex (Fig. 1a). The styli, present in other Ensifera, have disappeared. The 10th tergite pushes back a process, the epiproct, which forms with the subgenital plate a kind of pincer (Fig. 1b). The epiproct in the shape of a compressed blade in the sagittal plane is clearly separated from the10th tergite in *Phaneroptera* (Fig. 1c). Two paraprocts are placed on each side of the epiproct.

The cerci are inserted in a laterodorsal position, near the 10th tergite; in the male, they possess a short, sharp point which abruptly narrows (Defaut 1988). They are unisegmented and ostensibly curved in the form of a hook (Fig. 2a).

The genitalia which protrude from the subgenital plate, are always symetrical and are reduced to 4 membranous valves arranged around the gonopore: the two upper valves are rounded and more or less lobed, the lower valves are triangular. Only the upper valves are visible on the micrographs (Fig. 2b). These parts are joined together by a membranous small tongue. In Tettigoniidae, there also exists a chitinous element situated between the genital valves and the paraprocts. This element or epiphalle which is often divided into two parts named titillators is missing from many Phaneropterinae and in particular in *P. nana*. There is no real penis and the copulation takes place without the introduction of a copulatory organ.

Cercal sensilla

Three types of sensilla are found on the cerci: sensilla filiformia, s. chaetica, s. campaniformia.

Aporous sensilla filiformia are long, very flexible and delicately as well as longitudinally grooved aporous sensilla, inserted in a very large cuticular cavity which permits ample displacement of the hair (Fig. 3a). Two morphological subtypes are distinguished according their length. Sensilla filiformia of subtype 1 are very long sensilla which measure 200-250 µm in length and 3.3-3.5 µm in width at the base. The inner diameter of the cavity measures 16 µm and the outer diameter of the alveolus 32 µm (Figs 3 b, c). They are more numerous than short sensilla. Sensilla of subtype 2 are short sensilla of 30-50 µm in length and 1.7 µm in width at the base. The basal socket has an exterior diameter of 20 µm and an interior diameter

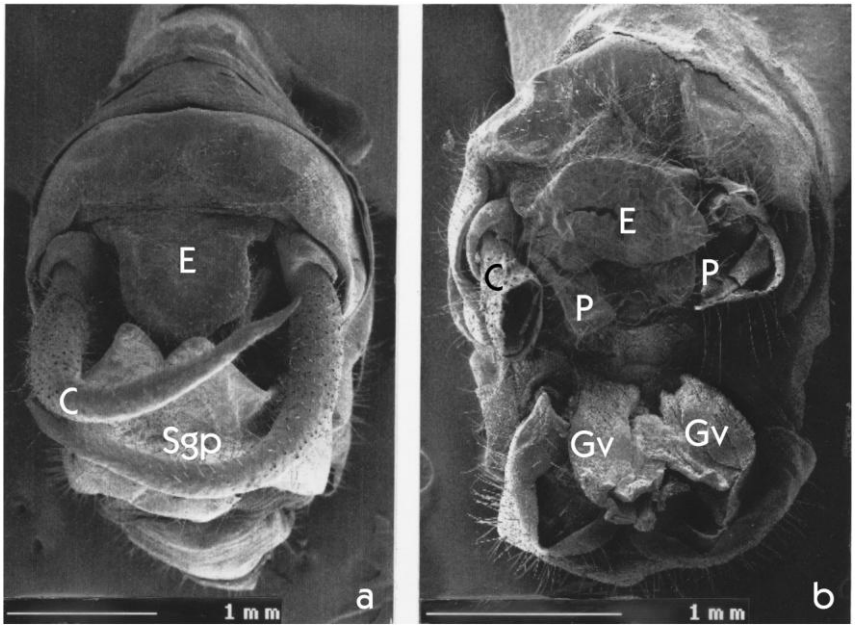

Figure 2. Male postabdomen of *Phaneroptera nana*. **a**, dorsal view; **b**, dorsal view with folded epiproct and subgenital plate severed. C, cercus; E, epiproct; Gv, genital valve; P, paraproct; Sgp, subgenital plate.

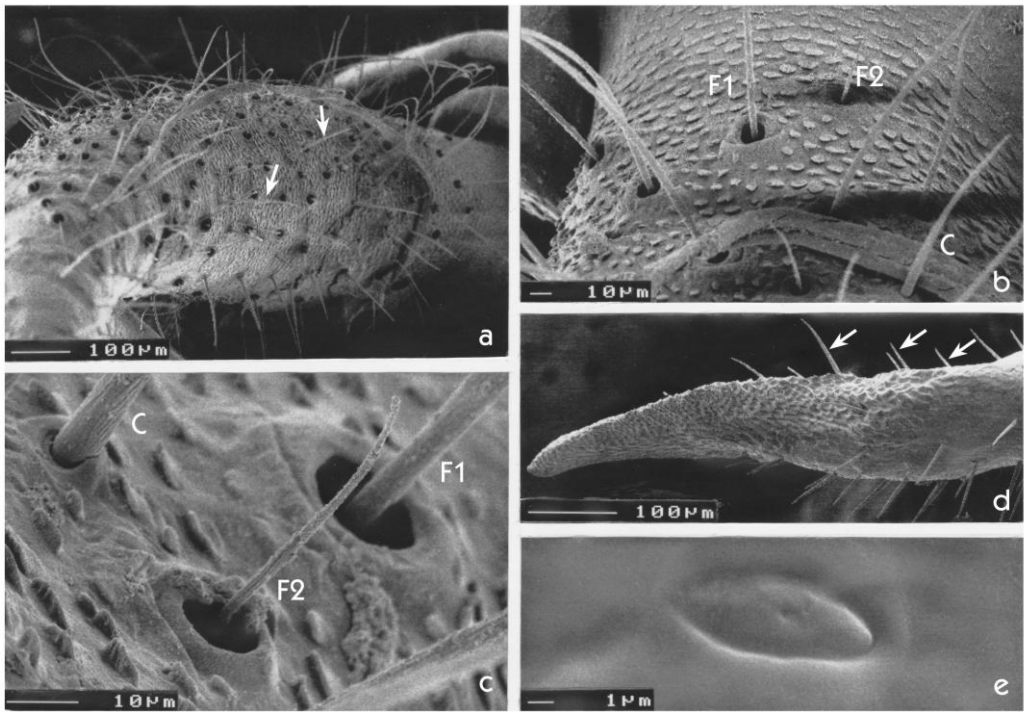

Figure 3. Cercus of male *Phaneroptera nana*. **a**, basal part showing numerous sensilla; **b**, long sensilla filiformia F1, short sensilla filiformia F2, sensilla chaetica C; **c**, detail of sensilla; **d**, distal part of cercus with sensilla chaetica (arrows); **e**, sensillum campaniformium with ecdysial pore.

of 12 µm (Fig. 3c). The two subtypes are disposed in circles of 12-14 sensilla situated close to one another. They are more numerous on the upper surface of cerci. Most of them occupy the proximal half in which the two subtypes are mixed but, in the median region, only the short sensilla are present. We estimate at 200 the total number of sensilla filiformia for each cercus.

In contrast to the previous sensilla, the *aporous sensilla chaetica* are nearly straight and extend out from the cercal surface so that their long axis tends to form a right angle with the long axis of the cercus. Their surface is grooved longitudinally. They are of variable length (30-110 µm) and have a basal diameter of 5.3-5.5 µm. They are inserted in a flexible socket of 12 µm for the outer diameter and have an

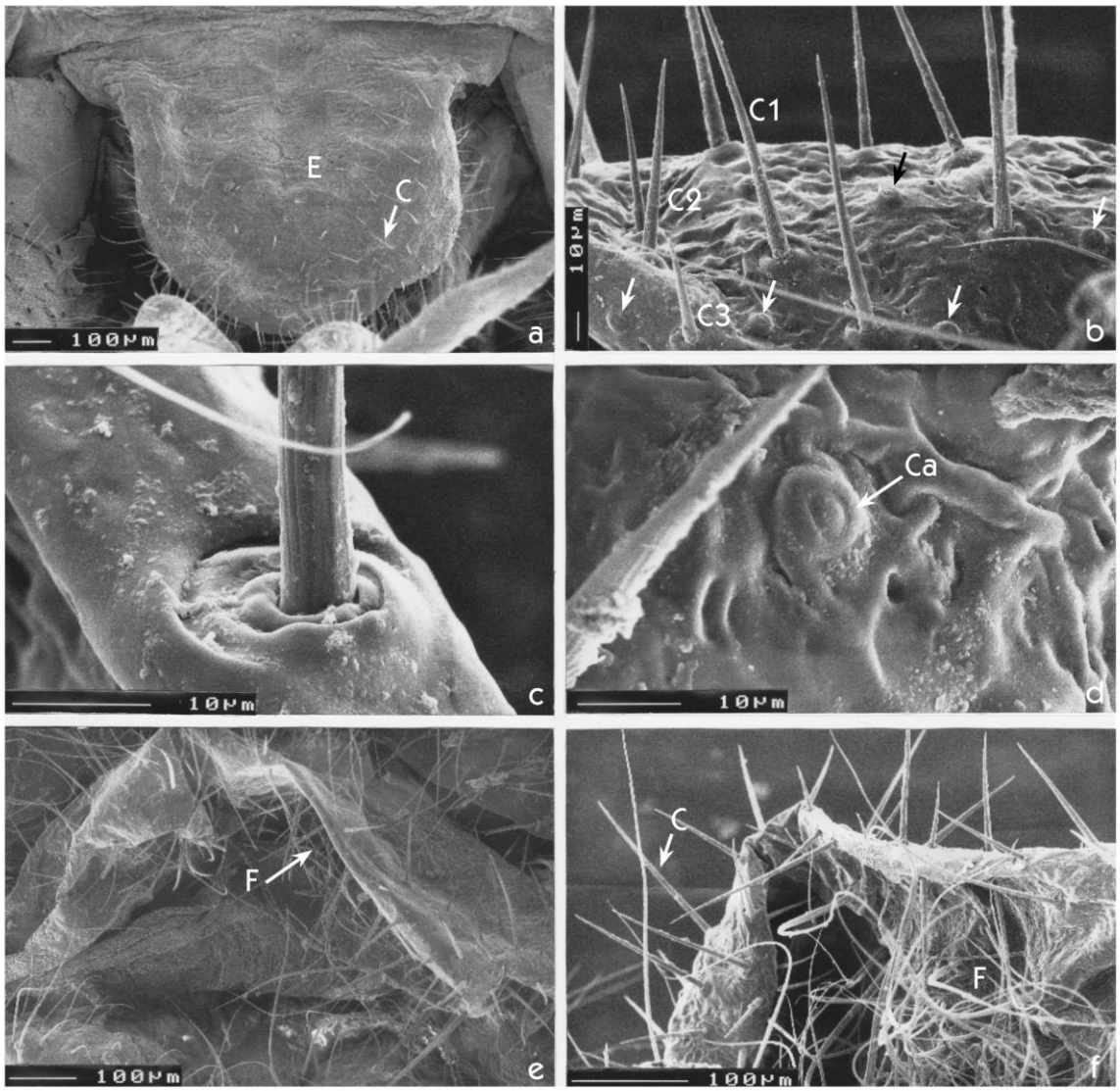

Figure 4. Epiproct of *Phaneroptera nana*. **a**, dorsal view of epiproct E showing sensilla chaetica C; **b**, sensilla chaetica of 3 subtypes C1, C2, C3; the arrows show sensilla campaniformia; **c**, base of sensillum chaeticum C1; **d**, sensillum campaniformium Ca; **e**, folded epiproct showing sensilla filiformia F on the inner face; **f**, distal part of epiproct showing outer face with sensilla chaetica C and inner face with sensilla filiformia F.

inner diameter of 6.0-6.5 µm which permits only minor displacements of the hair (Fig. 3c). They are sensilla with a thick wall of 2.3 µm and with a lumen of 0.9 µm in diameter. Their number per cercus is about 180. They are longer and more numerous on the lateral edges of cerci. The sensilla chaetica are mingled with sensilla filiformia on some proximal 2/3 of the cercus but they subsist alone and in large numbers in the distal region (Fig. 3d).

Aporous sensilla campaniformia though rarer than the previous sensilla are frequently met with on the distal half of the cercus and they are more numerous on the internal face than on the external face. They are oval in shape and their main axis is orientated in the longitudinal sense of cercus. Their elliptical dome of 6 µm in length and 2.5 µm in width is surrounded by a bulge of 8 µm in diameter (Fig. 3e).

Sensilla of epiproct, paraprocts and subgenital plate

The external face of the epiproct bears *aporous sensilla chaetica* whose hair shaft is evenly tapered towards the distal part that forms a pointed tip (Fig. 4a). Three subtypes are distinguished: long sensilla C 1, 80-100µm in length, with longitudinal ridges; median sensilla, 45-60 µm long, with oblique ridges C 2; short sensilla, 15-30 µm long with longitudinal ridges C 3. All these sensilla are distributed mainly on the lateral regions of the epiproct (Fig. 4a). *Sensilla campaniformia* are spread out on the distal edge of the epiproct (Fig. 4d). The internal face comprises *aporous sensilla filiformia*, 250-300 µm long (Figs 4e, f).

Aporous sensilla filiformia, chaetica and sensilla campaniformia exist on the surface of the paraprocts. *Sensilla filiformia*, 100-150 µm in length are distributed

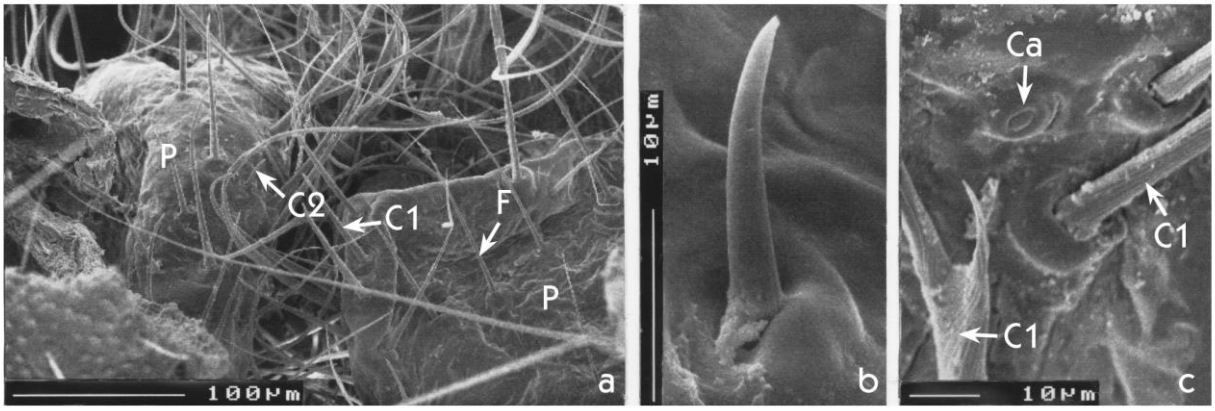

Figure 5. Paraprocts of *Phaneroptera nana*. **a**, paraprocts P with two types of sensilla chaetica C1 and C2 and sensilla filiformia F; **b**, sensillum chaeticum C2; **c**, sensilla chaetica C1 and sensillum campaniformium Ca.

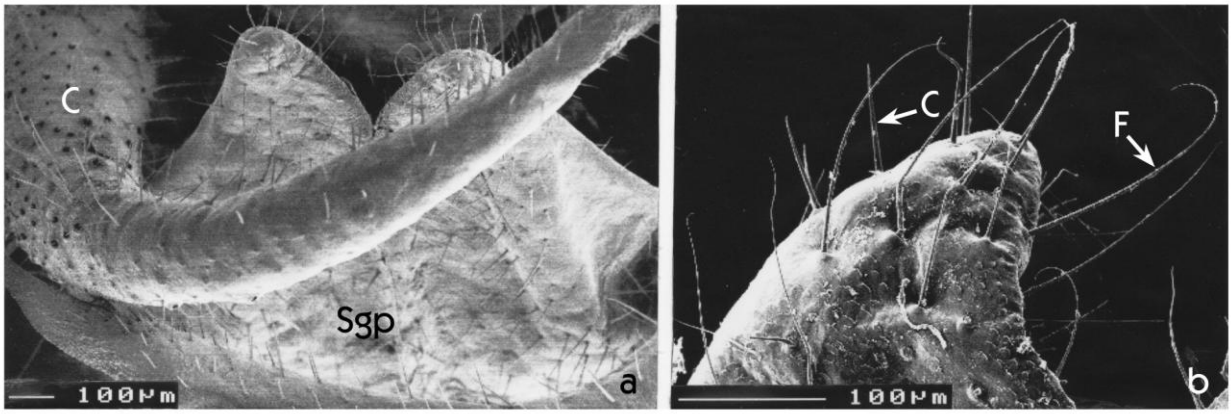

Figure 6. Subgenital plate of *Phaneroptera nana*. **a**, subgenital plate Sgp partly covered by cercus; **b**, distal part showing sensilla chaetica C and filiformia F.

over the whole surface (Fig. 5a). Two subtypes of *sensilla chaetica* are present: the first comprises long and stout sensilla, 60-100 µm in length located on the internal edge of paraprocts (C 1) (Figs 5a, c); the second consists of short sensilla 60-70 µm long scattered on the paraprocts (C 2) (Fig. 5b). Some *sensilla campaniformia* occur on the distal edge (Fig. 5c).

The external face of the subgenital plate is visible on the Fig. 6a on which the distal region of the plate is folded dorsally. This face bears slender *aporous sensilla chaetica* whose length varies from 60 µm to 85 µm, and aporous sensilla filiformia 110-160 µm in length. All these sensilla are evenly spaced over the whole surface of the plate, and occur predominantly on the distal part where they are more numerous (Figs 6a, b). The internal face is smooth, without sensilla.

Sensilla of genitalia

The surface of the valves (Fig. 7a) bears *uniporous sensilla basiconica* (subtype 1) whose cone which measures 1.8 µm in height and 1.7 µm in basal width is prolonged by a narrow process (Fig. 7b). The cone is surrounded by a socket of 11 µm in diameter. Laterally, some ten sensilla are present per valve.

The triangular median small tongue (Fig. 7a) comprises two types of sensilla: sensilla basiconica and sensilla campaniformia. *Uniporous sensilla basiconica* (subtype 2) possess cones of 3.5 µm in height with a basal diameter of 4 µm, surrounded by a socket of 16 µm in diameter and of 6 µm in height (Fig. 7d). The cone is broadly rounded at its tip with a definite terminal pore of 0.3 µm in diameter. Some 30 sensilla are situated on the largest part of the small tongue (Fig. 7c). About a dozen of *sensilla campaniformia* are found on the swollen lateral edges of the small tongue (Fig. 7e). They have the shape of a flattened dome of 0.7 µm in height, with a basal diameter equal to 3 µm; their basal socket has a diameter of 11 µm and measures 3 µm in height (Fig. 7f). The ecdysial pore, visible here, has a diameter of 0.15 µm.

DISCUSSION

The sensilla chaetica without pores [NP (no pore)-sensilla, aporous sensilla] of insects are tactile mechanoreceptors whereas a gustative function is attributed to sensilla with a terminal pore and an inflexible socket [TP (terminal pore)-sensilla, uniporous sensilla] (Altner 1977, Zacharuk 1980, 1985). Aporous sensilla filiformia are deflected by faint air currents and low frequency sounds or

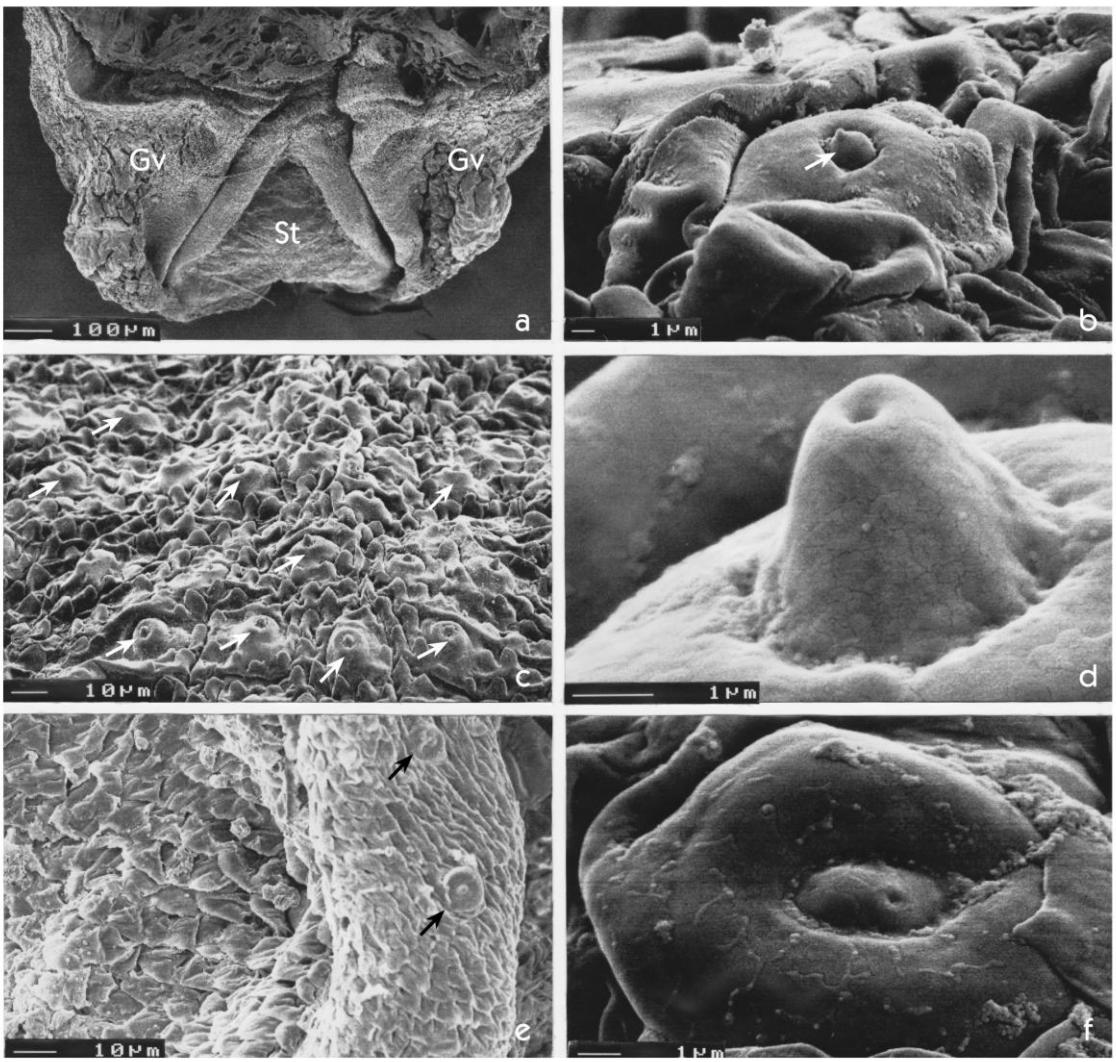

Figure 7. Genital valves of *Phaneroptera nana*. **a**, whole view showing genital valves Gv and small tongue St; **b**, sensillum basiconicum subtype 1 on the genital valve (arrow); **c**, sensilla basiconica subtype 2 on the small tongue (arrows); **d**, sensillum basiconicum subtype 2; **e**, sensilla campaniformia (arrows) on the edge of small tongue; **f**, sensillum campaniformium.

medium vibrations and therefore, are considered as vibroreceptors (Gnatzy & Schmidt 1971, Dumpert & Gnatzy 1977). Sensilla campaniformia perceive stress in the cuticle resulting from mechanical deformation (McIver 1985, Zacharuk 1985).

The intervention of tactile mechanoreceptors and vibroreceptors of cerci and genitalia may be explained during copulatory behaviour. There is no real mating in the Ensifera but simply a juxtaposition of the sexual orifices as a result of which the spermatophore is introduced at the base of the oviscapt, in relation to the female spermatheca (Chopard 1920). In the course of mating in Phaneropterinae, the male takes place under the female lying on her back, the heads of the two individuals being lined up in the same direction. The male cerci used as prehensile organs form an authentic pincer which seizes the female subgenital plate. The latter possess tubercles which facilitate hold by the male. Subsequently, the male straightens up with a leap. He then emits a voluminous spermatophore comprising two small spherical bulges and a mucous mass, the spermatophylax which contains a liquid devoid of spermatozoon (Chopard 1952). The spermatophore which contains the sperm is setting at the base of the oviscapt, in relation to the spermatheca.

In Blattodea and Orthoptera Gryllidae in which the male cerci have no prehensile role, the sensilla filiformia are uniformly distributed over all the cerci of cerci. In *P. nana*, they are present only on the proximal half of cerci, the distal half being devoid of them wherever they are replaced by sensilla chaetica. Since the sensilla filiformia are stimulated by slight draughts, their displacement causes the insects to take to flight (Dumpert abd Gnatzy 1977). They probably assume the same function in the male of *P. nana* but they do not intervene during mating. On the other hand, it is the sclerotized distal part of cerci, transformed into hooks which allows males to grasp the female subgenital plate. In this respect, on the internal face the aporous sensilla chaetica are stimulated by the contact between the two individuals. Some sensilla chaetica have likely a terminal pore and therefore might be involved in contact chemoreception processes (Yu *et al*. 2011). The sensilla campaniformia of cerci monitor the pressure

exerted by the cerci on the subgenital plate. The importance of cerci during copulation in Tettigoniidae was pointed out by Chopard (Chopard 1938). Subsequently, the male subgenital plate with its sensilla chaetica is pressed against the base of oviscapt. The epiproct and the paraprocts enter firmly into contact with the posterior margin of the 7th female sternite. The sensilla chaetica and campaniformia of these three pieces perceive this contact and transmit positional information to the male. All the available information on the copulatory behaviour of *P. nana* indicate the predominance of tactile stimuli recording by male and female postabdominal structures.

The intervention of gustative sensilla during mating is original and does not appear to have mentioned in any insect. Their presence in the male of *P. nana* is difficult to explain. Nevertheless, several hypotheses may be offered. In Gryllidae, the titillators appear to play an important role in fixing the spermatophore in the female genitalia (Bitsch 1979). As well as a mechanical role, we think that these parts are capable of recognising female secretions by means of contact chemoreceptors. The titillators are absent in *P. nana* but the genitalia with their uniporous sensilla may perhaps assume this function.

Copulatory attempts between different species or between two conspecific males are frequent in Orthoptera (Chopard 1938). If this is the case for *Phaneroptera*, the uniporous sensilla basiconica of the male probably perceive the gustatory qualities of glandular secretions specific to females (glands situated at the base of oviscapt with a duct emerging above the female gonopore (Chopard 1949)) and allow mating to continue (in the case of a conspecific female) or, on the contrary, put an end to it if the female is of a different species. In the case of an attempt at mating between two conspecific males, the gustatory sensilla of each are not stimulated and the males separate.

Coupling is repeated in males as in females of Orthoptera (Chopard 1938). However, Arnaud (1999) has revealed the importance of the sperm competition in insects. The competition between the spermatozoon of several males in order to fecundate the ovules of a female may be very intense. Thus, in the Phaneropterinae *Metaplastes ornatus* Ramme, Von Helverson & Von Helverson (1991) have shown that a second male is capable of extracting from the vulva the sperm of a previous rival, before transferring its own sperm. If this is the case in *P. nana*, it is possible that uniporous sensilla basiconica perceive the rival sperm and can thus inform the male about the existence of a previous copulation by his partner and encourage him to remove the rival sperm.

In other Orthoptera, such as Grylllidae, by inseminating large quantities of sperm, certain males dilute the sperm of previous males and thus increase their chances of fecundation (Von Helverson & Von Helversen 1991). The amount of sperm contained in the vulva can be estimated in relation to the greater or lesser number of stimulated sensilla basiconica. "Like the TP-sensilla with inflexible sockets of the maxillary palp of cockroaches (Altner 1977), the sensilla of *P. nana* are crowded together within a field comprising about 70 pegs. The whole cuticle of the field is flexible and held convex by hemolymph pressure, making it elastic when it comes into contact with the substrate. The contact with the substrate is not controlled individually" (Altner 1977). Knowledge of a previous copulation is essential as it is generally considered that the last male to fecundate the female has the advantage (Parker 1970). All the precedent hypotheses presuppose contact between the genitalia bearing sensilla and the glandular secretions of the female or rival's sperm.

A preliminary research of uniporous sensilla on the male genitalia of two other grasshoppers *Leptophyes punctatissima* (Bosc, 1792) (Phaneropterinae) and *Meconema thalassinum* (De Geer, 1773) (Meconematinae) has been fruitless (pers. obs.).

CONCLUSION

The majority of sensilla situated on the male postabdominal structures show a morphology compatible with a mechanosensory function, particularly tactile but also related to pressure stimulations. The presence of mechanoreceptors is coherent with the necessity for the male to receive mechanosensory information about the female during mating. The proprioceptors are frequent on the cerci, the epiproct, the paraprocts and the genitalia. The intervention of presumably gustative sensilla is more difficult to explain. Precise observations of partners in copula may contribute to a better understanding of the role played by the gustatory stimuli.

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