FEMALE GENITALIA AND COPULATION OF THE PLANTHOPPER
HYALESTHES OBSOLETUS SIGNORET
(HEMIPTERA : FULGOROMORPHA : CIXIIDAE)

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Résumé. — Accouplement et morphologie de l’appareil génital femelle de Hyalolesthes obsoletus Signoret (Hemiptera : Fulgoromorpha : Cixiidae). — L’étude des genitalia femelles du genre Hyalesthes (Cixiidae) à ovipositeur court, montre que tous les structures gonocoxales que gonophyses et ones ont subi un phénomène de réduction, par rapport au genre Cixius à ovipositeur long. La paroi de la bourse copulatrices présente des ornamentations circulaires, connues chez de nombreux Fulgoromorphes. Ces différenciations cuticulaires sont vraisemblablement liées à des formations glandulaires. La dissection de spécimens en copula montre également que, durant la copulation, des structures d’appareil génital mâle sont introduites dans le vagin : l’édéage, le périantridium, ainsi que le processus latéral gauche du pygophore.

Abstract. — Female genitalia morphology in the cixiid genus Hyalesthes — with a short ovipositor — is described in comparison with another long ovipositor cixiid genus Cixius. In Hyalesthes, gonocoxal structures and not only gonophyses ones are reduced. The circular sclerotized ornamentations of the bursa copulatrix wall, widely distributed in the Fulgoromorph, seem to be linked to glandular units. Dissection of Hyalesthes obsoletus Signoret in copula shows that not only the aedeagus and the periantrium are inserted into the vagina but also the left lateral process of the pygophore.

The Southwest Palearctic cixiid genus Hyalesthes consists of more than thirty species the revision of which has been undertaken by Hoch & Remane in 1985 and completed by Hoch (1986a, 1990) and Remane & Hoch (1986). In these studies, monophyly of the genus was established and at least five monophyletic groups of species were recognized within it. Hyalesthes obsoletus Signoret, 1865, is the type species of the genus and belongs to the obsoletus group restricted mainly to the Northern Mediterranean countries (Hoch, 1986b).

H. obsoletus is known for several years as a major vector of the stolbur phytoplasma (previous MLO, mycoplasma-like organism), a wall-less bacteria located in phloem. This bacteria causes serious diseases in many crops : tomato, tobacco, grapevine, etc, both in European and Mediterranean countries (Suchov & VEEN, 1948 ; FOS et al., 1992 ; MAIXNER 1994 ; SFORZA et al., 1996, submitted). In France, adults of this monovoltine species is observed from May to August with an abundance peak around the end of June. In France, bindweed (Convolvulus arvensis Linne) and lavender (Lavandula angustifolia Mill.) were first

recognized as host-plants (Leclaire, 1988; Fox et al., 1992). Recently, honey cress (Lepidium draba Linne) was also added to this list (Sporza & Bourgoin, 1996; Sporza et al., submitted). Several other host-plants are known in other countries (Guelu & Oztek, 1988; Hoch & Remane, 1985).

The engagement of male and female genitalia during copulation is poorly documented in Fulgoromorpha. In the cicadas: Cicala (Weber, 1930) and Hyalodeshes (Hoc'h & Remane, 1985), and in the delphacid: Steanoecus (Aroche, 1985) and Prokelisia (Heady & Wilson, 1990). These observations were summarized in Bourgoin & Huang (1991) who gave also information for the tetrigomorid genus Tettigomorpha and provided a more complete description of the copulatory mechanism in the ditrusian tropidochilid genre Trypetomorpha.

The present study provides a description of the female genitalia of Hyalodeshes which bears a short regressed ovipositor, with special attention paid to the sclerotized ovisacs (Bourgoin, 1993) of the bursa copulatrix in different species. The engagement of male and female genitalia during copulation is described for the species H. obsoletus to complete the description given by Hoch & Remane (1985).

Materials and methods

Female genitalia were examined from dried or alcohol preserved specimens of Hyalodeshes obsoletus Signoret and H. leucophala Feiniger. This last species represents another monophyletic group of species recognized by Hoch & Remane (1985).

Engagement of male and female genitalia was investigated by dissection of 5 pairs of H. obsoletus in copula according to Bourgoin & Huang's materials and methods already published (1991). Two stains were used: eosinol black E and Pergon Blue (Bourgoin, 1993). Drawings were made using a camera lucida with specimens placed in glycerine. For morphological studies using scanning electron microscopy (SEM), insects were first cleaned using a ultrasonic cleaner by soaking specimens in a chloroform bath (3 min) and then cleaned twice in 70% alcohol or distilled water (2 min). Specimens were then dehydrated through increasing concentrations of alcohol, critical point dried and coated with a 65-70 nm film of gold-palladium. They were examined using a Joel JSM 840 scanning electron microscope. Terminology for male and female genitalia follows Bourgoin & Huang (1990) and Bourgoin (1993).

OBSERVATIONS

Female genitalia

Segmental and appendicular structures (figs. 1-2)

In H. obsoletus, gonocoxae VIII (Gv VIII) are almost elliptical and feebly sclerotized plates. Each gonocoxa is linked ventrally to a more or less quadrangular plate pointing anteriorly, the endogastronotal lobe (GAL). Each one bears the reduced and membranous gonapophysis VIII (Gv VIII), in its inner side, the anterior fibula of the gonapophysis VIII is short, feebly marked, and probably not functional.

Posteriorly, the gonocoxae IX are rod-like. Gonapophyses IX are short and membranous, not fused on their inner margins. Gonoplaques (Gp) are represented by two processes of rounded section not enveloping the gonapophyses. A wide wax gland area closes posteriorly the genital area. Internally (fig. 2) gonocoxae IX are divided by the fulcrum (F) into an anterior part bearing the gonapophyses IX and a posterior part developing into the gonoplaque. On each side, two strong apodemes for attachment of the retractor muscle (mR Gv IX) and of the extensor muscle (mE Gv IX) of gonapophysis IX are observable. Dorsally to the anterior part of each gonocoxa IX, the gonangulum is limited to a thin rod-like sclerite. It joins anteriorly the gonapophysis VIII.

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**Complex of the ectodermal genital ducts (figs. 2-3)**

*H. obsoleta* is monogynous and the complex of the ectodermal genital ducts opens externally by the gonopore via an enlarged vestibulum. The vestibulum (*V*st) is limited anteriorly by a short triangular sclerotized sternal plate (fig. 1, *St. VIII*) and posteriorly by a more or less quadrangular plate, the basil apodem (*B.A*). The vestibulum opens widely into the posterior vagina (*V*P) which bears in its anterior part a wide bursa copulatrix ductus (*BCd*) opening into the bursa copulatrix (*BC*). Limits between the posterior and the anterior (*VA*) vagina are poorly marked. Anteriorly, the anterior vagina (*VA*) receives a long spermathea and the common oviduct (*CO*). As in most fulgoromorphs, the spermathea is divided into orificium receptaculi (placed ventro-laterally), ductus receptaculi (*Dr*), a wide and long diverticulum ductus (*Dd*), a short pars intermedia (*Pi*) and the glandula apicalis (*G.A*) of which only the cuticular ducts are observable.

**Fig. 1. Hyleodes hylodes* Signoret, female genitalia ventral view. *Gp* : gonopores; *Gx VIII* : gonocoxa VIII; *Gx IX* : endogonocoxal lobe; *Gy VII* : gonopophysis VIII; *Gy IX* : gonopophysis IX; *Lig IX* : intertergite IX; *St VIII* : sternal VIII; *V*st : vestibulum.

**Fig. 2. Hyleodes hylodes* Signoret, female genitalia internal semi-diagramatic view (left side). *BA* : basil apodem; *MG* IX : exterior muscle of gonopophysis IX; *F* : furca; *Ga* : gonangium; *Gx IX* : gonocoxa IX; *Ph IX* : phragma IX; *nG* IX : retractor muscle of gonopophysis IX; *V*P : posterior vagina. Other as previous figure.
Sclerotized ornamentations of the bursa copulatrix (fig. 4)

As in many fulgoroidea, small sclerotized ornamentations (So) are present in the wall of the bursa copulatrix. In Hyalesthes obsoletus these ornamentations are distributed on the whole wall of the bursa copulatrix. They are rounded structures of 15 μm in diameter limited externally by a sclerotized ring. The median part of the ring is a multimecropunctated ciliate area as shown by small white spots. In H. luteus these sclerotized ornamentations were not observable.

Copulatory mechanism (fig. 3)

During copulation male and female are side by side but facing in opposite direction; male is slightly inclined in comparison with the female. If they have to move, it is the female which leads the pair during the displacement. This copulatory position involves the twist of the male genital segments. When specimens in copula are killed, the abdominal twist is lost and one of the specimens faces dorsal while the other remains facing ventral. Contractions of the abdomen were observed. For two copula observed, duration of the mating were about forty minutes.

During mating, the male anal tube (AM) is turned up and applied on the abdominal sternum area of the female. The male genitalia in Hyalesthes are everted and both the aedeagus and paramandrum structures are inserted together into the female vagina. The paramandrum process (PP) is located in the dorsal part of the vagina (posterior vagina) and the aedeagus (A) into the anterior vagina but it does not enter into the bursa copulatrix. The male gonostylus (Gn) are inserted between the female gonapophysis. Together with the genitalia structures, the lateral processes of the pygofer are also inserted inside the vestibulum and the longer left process (LPP) reaches the posterodorsal part of the vagina.

DISCUSSION

Female genitalia in Hyalesthes show some slight differences from the description given by Bourguin (1955) for another cixiid genus, Cixius. These differences are related to the reduction of both gonoxoan and gonapophysis structures linked to an invagination of the sclerotized plates surrounding the gonoporus. For instance reduction of gonapophyses
IX is linked with the absence of their fusion on their inner sides, the absence of the intergutereal plate and of the postgonopodophophy tail. The basal apoderm which is considered as a synapomorphy for the Fulgoromorpha with an enteropod-type ovipositor (BOURGON, op. cit.) is also strongly reduced, feebly sclerotized and shifted inside the body closing posteriorly the vestituculum. Internally, apodemas of muscles are also comparatively strongly reduced. This is particularly the case for the extensor muscle of gonopods IX which apoderm is rod-like while it is wide and fringed in Eristalis. These morphological modifications have to be related to the fact that Hylastes lays the eggs on the soil surface or in the ground close to the plant crown but does not insert them into the host-plant.

In the Fulgoromorpha, the sclerotized ornamentations of the bursa copulatrix show a great diversity in their conformation. They are probably present in all the Fulgoromorpha families but not in all the species (BOURGON, op. cit.). They are present in H. absolonius while they seem to be absent in H. lutulipes or they could not have been observed with the techniques used here. They have also been mentioned and illustrated in some Derbidae by YANG & WU (1983) (Primosia Kukalkey, Sheska Matsamura, Neogona Yang & Wu, Panendorfia Distinct, Helesta Stahl, Zengoria Westwood). In Tettigoniidae, they are generally present except in some Helidinae (BOURGON, 1985). In Membracidae, their absence seems to be apomorphic for the New-Caledonian genus Suanisra (BOURGON, 1997).

The sclerotized ornamentations present in the wall of the bursa copulatrix correspond much probably to glandular units - but they may be associated also to a sensory function - as it has already been histologically described by BOLLARD (1965) in cicadas (Cicadomorpha). The numerous microstructures of the median area are probably the place through which secretions are discharged. But what could be the role of such glandular units?

In Fulgoromorpha spermatozoa are generally deposited at the bursa copulatrix basis and they must be transferred secondarily into the spermaphore (SOUILLER-PERRINS & BOURGON, submitted). One possible role for these structures should be to allow the spermatozoa migration thanks to chemical secretions. Another role should be to destroy spermatozoa in excess as it has been already shown by BOLLARD (1990) in cicadas where the corso-vaginal pouch (= bursa copulatrix) has a glandular function and a destructive role of spermatozoa in excess. This should be also the case in the Fulgoromorpha even if it has never been studied. However the role of these structures remains unclear: what happens when they are absent? A another possible role should be that they are connected to the presence of a spermaphore. While spermatozoa are generally considered as absent in Hemiptera (TOZAT, 1977; MAUER, 1958) a spermaphore has been described by STRONG (1955) in the diptera Drosophila. It has also been observed in the derbid Diastrophus (BOURGON, unpublished). In this last genus the bursa copulatrix is divided into two successive rooms. The spermaphore is stored in the first basal one which shows sclerotized ornamentations in its wall while they are absent in the second room. One could make the hypothesis that these structures could inform the insect on the presence of the spermaphore and allow its destruction thanks to glandular secretions. Clearly an ultrastructural study of these glandular-sensory structures, their role after deposit and storage of spermatozoa and the occurrence of spermatozoa in Fulgoromorpha would need special attention and investigation.

The copulatory position observed here is close to the description given by HECIN & REMANE (1985) but no information was provided about the male and female engagement and the relative positions of genital structures. To maintain the copulatory position between male and female during copulation, these authors have observed that the paired asymmetric spine-like processes of the pygofer come to settle in the membranous sternal fold between
the sternite VIII and the gonocoxa VIII. However, in the different pairs in copula studied, the pygofer processes are also inserted inside the female genitalia, with the genitalia structures. This difference is probably imputable to the moment when the pair has been killed during copulation. Engagement involving not only genitalia structures but also processes of the pygofer is important to note and will have to be analysed in the frame of the hypothesis of short cuts of mating behaviour suggested by SOUTHERN-PERKINS & BOUROIGN (submitted). Internally, the study shows that the bursa copulatrix is never reached by the aestegus which is located only into the posterior vagina during copulation. Such behaviour seems to be the most common within the Fulgoromorpha (SOUTHERN-PERKINS & BOUROIGN, op. cit.).

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LITERATURE CITED


