Zootaxa 4801 (3):591–599
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4801.3.12
http://zoobank.org/urn:lsid:zoobank.org:pub:30961FC3-22CD-47D1-88C0-7EB4D06E8D25

A new structure on the frons of male adults of the Asian rice spittlebug *Callitettix versicolor* (Hemiptera: Auchenorrhyncha: Cercopidae)

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Abstract

A new structure, here tentatively named the "frontal gland," specifically found on frons of male adults of the Asian rice spittlebug, *Callitettix versicolor* (Fabricius, 1794) (Hemiptera: Auchenorrhyncha: Cercopidae), is reported. Adult *C. versicolor* is distinctly dimorphic in frons morphology. The frons in female adults, like that in most cercopid species, is normally swollen and nearly bulbose and is covered with short pilosity, while the frons in male adults is visibly different, with the lower 3/5 of the postclypeus and anteclypeus being centrally flat, bare and smooth on the surface. SEM observations revealed that the flat frons surface of the male adults is covered with numerous, very fine pores. In total, each frons has over 4500 pores on the central flat area, with an average density of 55.5 ± 1.50 pores per 100 μm^2. The distance among the pores averages 10.63 ± 1.8 µm. Each pore unit is composed of a round, deep cavity in which one central conical process is set. The cavity is delimited by a cuticular rim and the opening of the cavity averages 2.89 ± 0.20 µm in diameter. The central, conical process has a sponge-like apex and measures 2.52–2.70 µm in diameter. In addition, one or two (two in most cases) extremely fine pits (0.42–0.56 µm in diameter) are located on the marginal cuticle rim surrounding the cavity and its central conical process. These cuticular, fine pits are located proximal to the pores, at a distance of 0.98–1.96 µm. These porous structures are not present on the frons in female adults. They are assumed to be an exocrine gland system and are possibly the male sex pheromone-releasing glands, as they are only present in male adults. Observations of mating behavior showed that it is likely that the secretions made by the frontal gland constitute short-range attractants and may fulfil aphrodisiac functions to stimulate mating. The species of Auchenorrhyncha were previously thought to communicate via acoustic signals, but the findings described here suggest that at least one Auchenorrhynchan species also uses chemicals for sexual communication.

Key words: *Callitettix versicolor*, Homoptera, dimorphism, secondary sexual structures, male sex pheromone glands, chemical communication

Introduction

Cercopidae (Hemiptera: Auchenorrhyncha: Cercopoidea) comprise the largest group of plant xylem-feeding insects, with approximately 1,500 described species classified in about 150 genera worldwide (Liang & Webb 2002). The group is distributed predominantly in the tropical and subtropical regions of the world. Cercopid nymphs, or spittlebugs, protect themselves from predators by secreting masses of spittle, which they surround themselves with on host plants at their feeding sites. Their adults, commonly known as froghoppers for their quick jumps and putative resemblance to tiny frogs, which are named in parallel to other Auchenorrhyncha such as the leafhoppers, planthoppers and treehoppers, do not produce spittle but rely on their jumping ability and warning coloration for defense as they move about and feed on same or other host plants (Peck & Thompson 2008; AP Liang 2019, unpublished data). Both life stages feed on plant saps mostly from xylem of their host plants (Goodchild 1966; McGavin 1993). Adults feed on the leaves and stems of a variety of plants, whereas nymphs may also feed on roots, at or below ground level (Liang & Fletcher 2002; Liang & Webb 2002). In addition to the poor knowledge in basic taxonomy,

Accepted by C. Dietrich: 4 May 2020; published: 19 Jun. 2020

the biology, ecology and behaviour of most cercopid species are unknown (Cobben 1987; Thompson 1994, 1997; Liang & Webb 2002).

Callitettix versicolor (Fabricius, 1794) (Fig. 1), known as the rice spittlebug, is a polyphagous species, and represents a serious pest on rice, maize, wheat, sugarcane, soybean and other food crops in China as well as other Asian countries, including India, east Pakistan, Myanmar, Sikkim, Laos, Vietnam, Cambodia, Thailand and Malaysia (Hoffmann 1942; Pawar & Bhalla 1976; Lim & Pan 1980; Yuan 1986; Guan *et al.* 1991; Morris & Waterhouse 2001; Luo & Xu 2011). The species has polymorphic markings on its forewings (Distant 1908). The populations from China can be recognized by the following combination of characters: body elongate, nearly parallel-sided, length 11.0–14.0 mm; colour shining black, frons of males with the middle area brown; fore wings black, with a subtransverse spot on clavus beyond apex of scutellum, and a subtransverse spot on corium between costal margin and claval margin before the middle of the fore wings, white; and two spots on corium beyond middle of fore wings: external one large and transverse (present in both female and male), internal one very small (usually present in female and absent in male), sanguineous (Fig. 1a). In some populations from Vietnam, all markings in the fore wings are white; while in some other populations from Vietnam, the fore wings have only two sanguineous spots on apical 1/3 in males. In the population from Thailand, the internal white spot on corium of fore wings in males are usually present (Vinton Thompson, personal communication; AP Liang 2020, unpublished data).

Due to its broad distribution, *C. versicolor* causes considerable damage to rice and maize in south and central China (Li *et al.* 2001; Li *et al.* 2010; Liao *et al.* 2010). As its distribution area is expanding towards to northern parts of China due to changes in the farming system and the warmer climate, the economic losses are increasing (Chen & Liang 2012; Chen *et al.* 2018).

Morphological analysis of *C. versicolor* revealed that the frons of this species is dimorphic, with males exhibiting a smooth and flat frons absent in females. Using scanning electron microscopy, it was revealed that this flat surface of the male frons is covered with numerous fine pores of high density. This dimorphic feature suggests that it represents a pheromone-releasing structure.

In this paper, I present a description of the morphological ultrastructure, the number and distribution of this new porous structure found in *C. versicolor*, and provide a brief discussion on its possible function.

Materials and methods

Specimens studied. Dry, pinned museum specimens were obtained from the Insect Collection at the Institute of Zoology, Chinese Academy of Sciences, Beijing, P. R. China. The identity of *C. versicolor* was based on a comparison with syntype specimens of *Cercopis versicolor* Fabricius, 1794 housed at the Zoological Museum, University of Copenhagen, Copenhagen, Denmark. In total, fourteen males and six females were examined. They were collected from Napo and Fangcheng located in the Guangxi Zhuang Autonomous Region in southwest China, during July, 2003.

Light microscopy. External morphology was observed with a Zeiss (Stemi SV 11) optical stereomicroscope (Carl Zeiss, Göttingen, Germany). Photographs in figure 2 were taken with a Nickon D7000 digital camera mounted on a Leica M205 C microscope (Leica Microsystems Inc., Buffalo Grove, Illinois, United States). The digital images were then imported into Adobe Photoshop 8.0 for labeling and plate composition. The length, diameter and size of the frontal gland structure were measured using Image J 1.X software (Schneider et al. 2012).

Scanning electron microscopy. For scanning electron microscopy (SEM) studies, dry, pinned museum specimens were examined for frons gland structures. To this end, the heads were dissected from the body and washed with 10% KOH for 1–2 minutes, then cleaned using a fine bristle brush, before being washed in distilled water. Next, the heads were mounted on aluminum stubs with double-sided carbon sticky tape (SPI Supplies, Division of Structure Probes, Inc.), air-dried at room temperature, and then three times sputter-coated with gold-palladium over a 45-s period while rotating the stub using an E–1010 sputter ion instrument (Hitachi Koki Co. Ltd., Tokyo, Japan). Structures were analyzed using a JEOL JSM–6301F (Japanese Electronic and Optical Ltd., Tokyo, Japan) scanning electron microscope, operated at accelerating voltages of 15 kV.

Morphological terminology. The morphological terminology used in this paper follows that of Metcalf & Horton (1934) and Lallemand (1949).

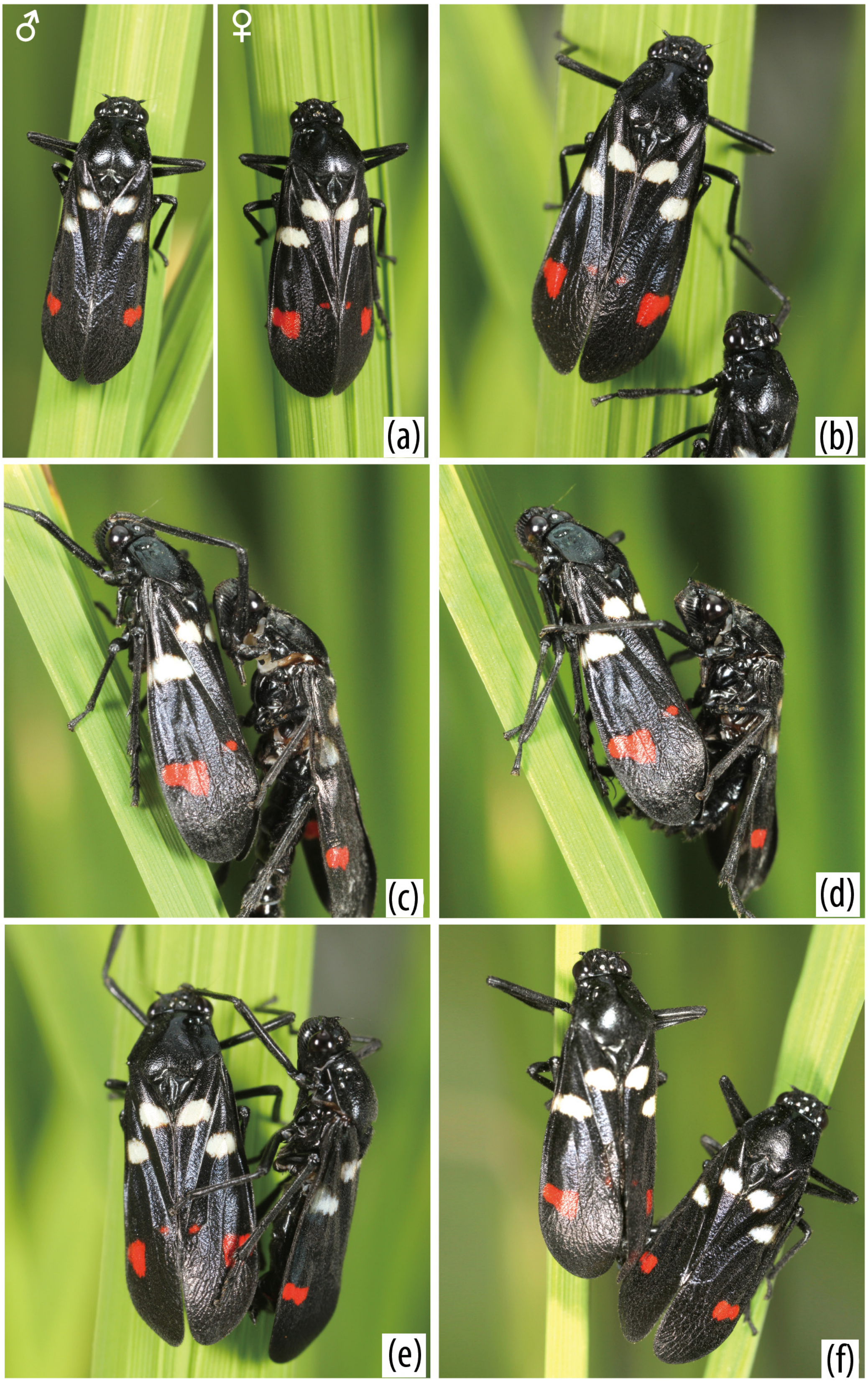

FIGURE 1. *Callitettix versicolor* (Fabricius, 1794) (China: Henan, Wugan), sequence of mating behavior. (a) A couple of pre-mating adults, male on left, female on right; (b) Male approaches female from below; (c) Male mounts the female, touches the female's dorsum with his left foreleg and presses his frons on the female's pronotum; (d) Male aligns his body on the lateral area of the female and pulls the end portion of her abdomen allowing insertion of his aedeagus, initiating copulation; (e) In copulation; and (f) Feeding while in copulation.

Results

Gross morphology of the frons. The frons of *C. versicolor* in ventral aspect consists of the upper, distinctly larger postclypeus (pc in Figs. 2a, 2c, 3a, 3b) and the lower, distinctly smaller anteclypeus (ac in Figs. 2a, 2c, 3a, 3b) which are separated by the clypeal suture. *C. versicolor* distinguishes itself by clear sexual dimorphism, both in terms of morphology as well as color and shape of the frons.

Like other cercopid species, female *C. versicolor* display a convex, swollen postclypeus and anteclypeus, which are not in a same plane in ventral or ventrolateral aspect and are covered with short pilosity (Figs. 2c, 2d, 3a). Unlike most other cercopid species, the lower 3/5 of the postclypeus as well as the entire anteclypeus of the frons of male *C. versicolor* in ventral aspect are broad and visibly flat, bare and smooth without pilosity on surface. In addition, the middle areas of both postclypeus and anteclypeus are positioned on the same plane in both ventral and lateral aspect (Figs. 2a, 2b, 3b). In females, the frons is completely black (Figs. 2c, 2d), while in the male the flat and bare area of the frons is brown (Fig. 2a), thus clearly distinguishable from the black ground color of the frons. This sexual dimorphism of the frons (Figs. 2a–2d, 3a, 3b) provides a simple way to separate the males and females of *C. versicolor* without having to examine the genitalia.

It should be noted that the frons of males in other species of the genus *Callitettix*, namely *C. braconoides* (Walker, 1858) (the type species of *Callitettix* Stål, 1865) (Figs. 2e–h), *C. coomani* Lallemand 1946 and *C. costalis* Lallemand 1933 (Lallemand 1949; Metcalf 1961) are normal and are not flattened.

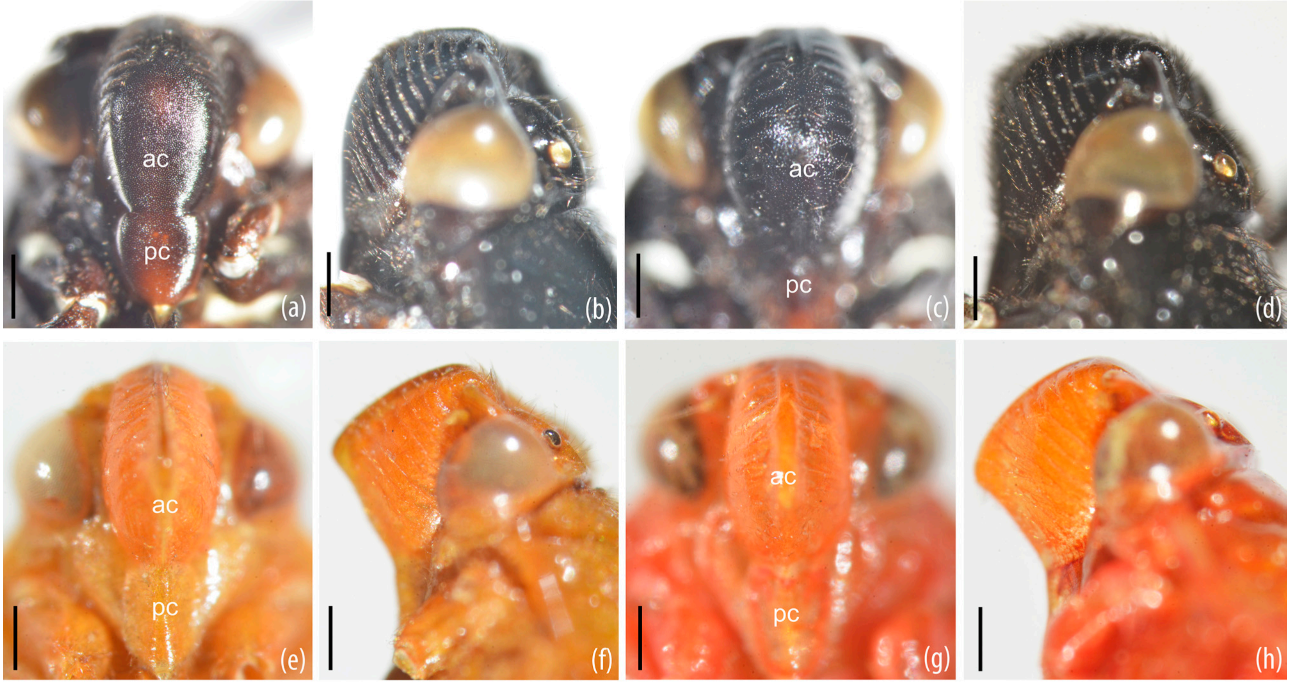

FIGURE 2. Head of *Callitettix* species. a–d. *C. versicolor* (Fabricius, 1794) (China: Henan, Wugang). (a) Male adult, ventral view; (b) Male adult, lateral view; (c) Female adult, ventral view; (d) Female adult, lateral view; e–h. *C. braconoides* (Walker, 1858). (e) Male adult (China: Guizhou, Chishui), ventral view; (f) Male adult (China: Guizhou, Chishui), lateral view; (g) Female adult (China: Yunnan, Xishuanbanna, Mengla), ventral view; (h) Female adult (China: Yunnan, Xishuanbanna, Mengla), lateral view. Abbreviations: ac, anteclypeus. pc, postclypeus. Scale bar = 0.5 mm.

Description of the frontal gland. When the flattened and bare surface of the postclypeus and anteclypeus of the male *O. versicolor* was examined by scanning electron microscopy, numerous, fine, micro-scaled pores were clearly visible on the bare, smooth surface (Figs. 3c–3h). These pores are nearly rounded, and form shallow cuticular depressions (cavities) delimited by cuticle rims. Each pore unit is composed of a round, deep cavity in which one central conical process is set (Figs. 3c–3h). The central, conical process possesses very fine longitudinal grooves on its surface (Figs. 3g–3h). In addition, one or two (two in most cases) extremely fine pits are located on the marginal cuticle rim surrounding the central conical process (Figs. 3g–3h). These fine porous structures are not present on the surface of the postclypeus and anteclypeus in female *O. versicolor*.

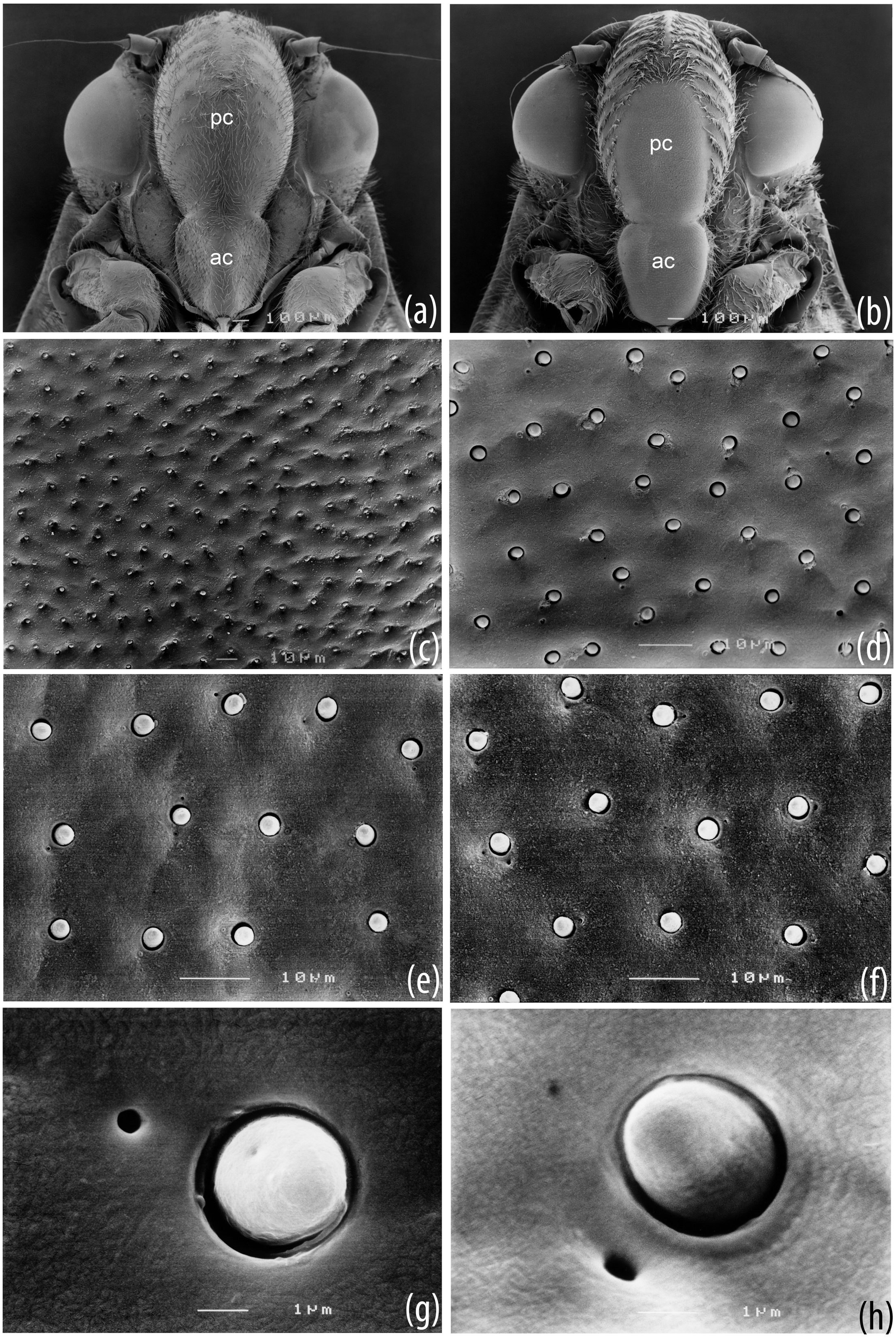

FIGURE 3. *Callitettix versicolor* (Fabricius, 1794), scanning electron micrographs of the frontal glands in male adults. (a) Head of female adult, ventral view, showing bulbose, pilose frons; (b) Head of male adult, ventral view, showing flat, bare median region of frons; (c–f) Fine gland pores on the surface of frons of male adult; (g, h) One gland pore on frons of male adult, showing a central conical process located on the cavity bordered with one or two fine pits on rim. Abbreviations: ac, anteclypeus. pc, postclypeus.

In *O. versicolor*, a total of over 4500 pores are present on the flatted, smooth area of the male frons. They have an average density of 55.5 ± 1.50 (n=6) pores per 100 μm^2, and the distance among the pores averages 10.63 ± 1.8 μm (n=11) (Figs. 3c–3f). The opening of the cuticular cavity averages 2.89 ± 0.20 μm (n= 6) in diameter. The central process is conical and nearly papillate and measures about 4.10–4.56 μm in length and 2.52–2.70 μm in median diameter. There are indistinct longitudinal grooves superficially (Fig. 3h). The one or two extremely fine pits on the marginal cuticle rim surrounding the central conical process are approximately 0.42–0.56 μm wide in diameter. These cuticular, fine pits are located proximal to the pores, at a distance of approximately 0.98–1.96 μm.

No previous reports appear to have been published describing a similar structure on the frons in any other known cercopid species. Either this structure has been overlooked or it possesses no known homologues amongst the Cercopidae. On the basis of our detailed morphological and ultrastructural analysis, we hypothesize that these porous structures play a role in either olfactory, mechanoreceptive or secretory processes.

The central, conical process morphology and their seemingly flexible insertion suggest a secretory function. It is very likely that the central conical process is eversible in the live insect and the longitudinal grooves on its surface may be used to enhance secretory evaporation (Fig. 3h). These cuticular pores seem to be structures disseminating chemicals and might represent/constitute a path for pheromone release, namely from the epidermal secretory gland cells to the outside environment (see Percy-Cunningham & MacDonald 1987). Importantly, these porous structures are absent in immature males of *C. versicolor* (AP Liang 2019, unpublished data). Thus, we propose that these pores are likely to function as pheromone glands involved in courtship behavior. Here I tentatively name this type of putative male pheromone-producing structure the frontal gland.

Discussion

Pheromones are a primary method of chemical communication in insects, where the chemicals function to identify members of the same species and thus possible mates. They are widespread in insects and have been reported in many groups (Birch & Haynes 1982; Cardé 1997).

In the order Hemiptera, sex pheromones have been chemically identified for scale insects (Margarodidae and Diaspididae), mealybugs (Pseudococcidae), and aphids (Aphididae) among Sternorrhyncha and for plant bugs (Miridae), assassin bugs (Reduviidae), stink bugs (Pentatomidae), and shield bugs (Scutelleridae) in the Heteroptera (see review by Aldrich 1996). No reports, however, have been published on the pheromones in Cercopidae and other groups of Auchenorrhyncha, with the exception of Boulard & Boulard (1979) who reported a ‘ventral organ’ in the females of species of the African cercopid genus *Locris* as a possible sexual pheromone system.

The males of some shield bugs species (Heteroptera: Scutelleridae) possess either hypertrophied dorsal abdominal glands or sternal glands, each homologous to those glands in asopine bugs (Pentatomidae: Asopinae) (Carayon 1984; Knight *et al.* 1985). The secretions of two scutellerid species (one for each gland type) have been chemically analyzed (Fig. 8 in Aldrich’s 1996 review). Behavioral data as to the reason for the secretions are lacking, but it is likely that one or both secretions constitute long-range attractants. The crystalline sternal gland secretion of cotton harlequin bug *Tectocoris diophthalmus* (Thungberg) males was originally postulated to be an aphrodisiac (Carayon 1984). Although rubiginol (Fig. 8B in Aldrich’s 1996 review) is a solid, it readily sublimes (Gough *et al.* 1986), hence the assumption this compound also represents an attractant pheromone. In addition, males of the Middle Eastern wheat pest *Eurygaster integriceps* Putnam attract nearby females with vanillin, ethyl acrylate, and a novel homosesquiterpenoid compound produced by hitherto unidentified glands (Ubik *et al.* 1975; Zdárek & Kontev 1975; Vrkoc *et al.* 1977; Staddon *et al.* 1994). It is important to note that the structure of the frontal gland found here in *C. versicolor* is very similar to that of the male-specific exocrine gland in the cotton harlequin bug *T. diophthalmus* (Thungberg) (Heteroptera: Scutelleridae) and that this gland has been demonstrated to secrete 3,5-dihydroxy-4-pyrone onto sternal gland setae (Carayon 1984; Gough *et al.* 1986).

The similar pore pattern found in some Heteropteran true bugs and in the male *C. versicolor* here, especially the presence of numerous pores, suggests that the fine pores on the frons of male *C. versicolor* possibly carry out a similar function in disseminating the male sex pheromones. In *O. versicolor*, males appear to play the more active part during mate selection and courtship (Figs. 1b–1f, AP Liang 2019, unpublished data). Our own unpublished observations of mating behavior showed that male adults of *O. versicolor* approach the immobile females from below. When the male reaches the female, the former usually uses its forelegs to touch the dorsum of the female

(Figs. 1c–1d) (see also Fonseca *et al.* 2013). Another distinct action taken by the male is that it presses its frons on the dorsum of female before mating (Fig. 1c). It is likely that the secretions made by the frontal gland constitute short-range attractants and may fulfil aphrodisiac functions to attract female adults and to stimulate mating. Aphrodisiac pheromones act as close-range sex pheromones to mediate courtship behaviors. They can function both as contact pheromones and volatile attractants that function over very short distances. In comparison with most sex pheromones, these signals are often perceived through contact alone, produced in staggeringly large quantities, and are by and large more structurally diverse. They are commonly produced by males of Lepidoptera and are also present in some beetles and flies (Ginzel 2010).

While our study provides strong ultrastructural evidence, more detailed studies, e.g. histological, ultramorphological, electrophysiological, chemoreceptive, and behavioral studies, are necessary before drawing final conclusions on the exact function of the porous structures described here. If this structure proves to function as a male pheromone-releasing organ, it could provide a suitable target for controlling this agricultural pest by developing suitable pheromone-based attractants against female *C. versicolor*.

Acoustic signals are now widely known to be almost exclusively used in intraspecific sexual communication by Hemipteran Auchenorrhyncha. Male cicadas (Cicadidae) are familiar for their unique, loud airborne calls used in mate recognition and courtship, while other much smaller species of Auchenorrhyncha, including leafhoppers and treehoppers (Membracoidea), planthoppers (Fulgoroidea) and spittlebugs (Cercopoidea), produce low intensity, substrate-transmitted acoustic signals in mate location and courtship (Ossiannilsson 1949; Claridge 1985a,b; Claridge 1990; Morgan & Claridge 1993; Claridge *et al.* 1999; Machado *et al.* 2001). The discovery of apparent male pheromone glands in *C. versicolor* in the present study shows that at least one Auchenorrhynchan species may also use chemical pheromones in intraspecific communication in addition to their well-known physical acoustic signal communication systems. Recent investigation on rice spittlebug *O. versicolor* have shown that the nymphs of this pest species can use an aggregation pheromone in controlling the number of the nymphs in each spittle foam (Chen & Liang 2015). This fact should be considered as a starting point in a better understanding of pheromone communication in both Cercopidae and Auchenorrhyncha.

Acknowledgments

I am grateful to Yongjie Yan and Linfeng Fu (Electron Microscope Unit, Advanced Materials Laboratory, Ministry of Education of China, Tsinghua University, Beijing, China) for providing technical assistance with the scanning electron microscopy. I thank Dianjie Zhang and Xu Chen (Institute of Zoology, Chinese Academy of Sciences, Beijing, China) for the preparations of figures 1 and 2, respectively. I wish also to extend my appreciation to André Quennedey, Laboratoire de Zoologie, Université de Bourgogne, Dijon, France, Michael F. Claridge, School of Pure and Applied Biology, University of Wales, Cardiff, U.K., and Chris H. Dietrich, Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, IL, USA, for giving much welcome discussions during the preparation of the manuscript. The two anonymous reviewers are also gratefully acknowledged for their constructive comments and suggestions. The work on which this paper is based was supported by the following sources: National Natural Science Foundation of China (grant nos. 30530110, 31872279, 31561163003) and the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (grant no. 2019HJ2096001006).

Conflict of Interest Statement

The author declares that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

References

Aldrich, J.R. (1996) Sex pheromones in Homoptera and Heteroptera. *In:* Schaefer, C.W. (Ed.), *Studies on Hemipteran Phylogeny. Thomas Say Publications in Entomology*. Entomological Society of America, Lanham, Maryland, pp. 199–233.

Birch, M.C. & Haynes, K.F. (1982) *Insect Pheromones. The Institute of Biology's Studies in Biology No. 147*. Edward Arnold (Publishers) Ltd., London, 57 pp.

Boulard, M. & Boulard, J. (1979) Un organe énigmatique chez les femelles de *Locris* (Homoptera Cercopidae). *Annales de la Société entomologique de France*, Nouvelle Série, 15, 513–523.

Carayon, J. (1984) Les androconies de certains Hémiptères Scutelleridae. *Annales de la Société entomologique de France*, Nouvelle Série, 20, 113–134.

Cardé, R.T. (1997) *Insect Pheromone Research: New Directions*. Chapman and Hall, New York, 684 pp. https://doi.org/10.1007/978-1-4615-6371-6

Chen, X. & Liang, A.-P. (2012) Laboratory rearing of *Callitettix versicolor* (Hemiptera: Cicadomorpha: Cercopidae), with descriptions of the immature stages. *Annals of the Entomological Society of America*, 105, 664–670. https://doi.org/10.1603/AN12052

Chen, X. & Liang, A.-P. (2015) Identification of a self-regulatory pheromone system that controls nymph aggregation behavior of rice spittlebug *Callitettix versicolor*. *Frontiers in Zoology*, 12, 10. https://doi.org/10.1186/s12983-015-0102-4

Chen, X., Meyer-Rochow, V.B., Fereres, A., Morente, M. & Liang, A.-P. (2018) The role of biofoam in shielding spittlebug nymphs (Insecta, Hemiptera, Cercopidae) against bright light. *Ecological Entomology*, 43, 273–281. https://doi.org/10.1111/een.12496

Claridge, M.F. (1985a) Acoustic signals in the Homoptera. *Annual Review of Entomology*, 30, 297–317. https://doi.org/10.1146/annurev.en.30.010185.001501

Claridge, M.F. (1985b) Acoustic behaviour of leafhoppers and planthoppers: species problems and speciation. *In:* Nault, L.R. & Rodriguez, J.G. (Eds.), *The Leafhoppers and Planthoppers*. John Wiley & Sons, New York, pp. 103–125.

Claridge, M.F. (1990) Acoustic recognition signals: barriers to hybridisation in Homoptera Auchenorrhyncha. *Canadian Journal of Zoology*, 68, 1741–1746. https://doi.org/10.1139/z90-255

Claridge, M.F., Morgan, J.C. & Moulds, M.S. (1999) Substrate-transmitted acoustic signals of the primitive cicada, *Tettigarcta crinita* Distant (Hemiptera Cicadoidea, Tettigarctidae). *Journal of Natural History*, 33, 1831–1834. https://doi.org/10.1080/002229399299752

Cobben, R.H. (1987) What do we really know about host selection in Auchenorrhyncha? *In:* Vidano, C. & Arzone, A. (Eds.), *Proceedings of the 6th Auchenorrhyncha Meeting, CNR-IPRA*, *Turin, Italy*, 1987, pp. 81–92.

Distant, W.L. (1908) Rhynchota, Homoptera and Appendix (Pt.). *In*: Bingham, C.T. (Ed.), *The Fauna of British India including Ceylon and Burma. Vol. IV.* Taylor & Francis, London, pp. i–xv + 1–501.

Fonseca, M.G., Silva, S.E.B., Auad, A.M., Paiva, I.G. & Borges, C.A. (2013) Mating behavior of *Mahanarva spectabilis* (Hemiptera: Cercopidae) under laboratory conditions. *Journal of Insect Behavior*, 26, 824–831. https://doi.org/10.1007/s10905-013-9394-4

Ginzel, M.D. (2010) Olfactory signals. *In:* Breed, M.D. & Moore, J. (Eds.), Encyclopedia of Animal Behavior. Academic Press, Oxford, pp. 584–588. https://doi.org/10.1016/B978-0-08-045337-8.00268-0

Goodchild, A.J.P. (1966) Evolution of the alimentary canal in the Hemiptera. *Biological Reviews of the Cambridge Philosophical Society*, 41, 97–139. https://doi.org/10.1111/j.1469-185X.1966.tb01540.x

Gough, A.J.E., Games, D.E., Staddon, B.W., Knight, D.W. & Olagbemiro, T.O. (1986) C9 aliphatic adelhydes: possible sex pheromone from male tropical West African shield bug, *Sphaerocoris annulus*. *Zeitschrift für Naturforschung*, 41C, 93–96. https://doi.org/10.1515/znc-1986-11-1221

Guan, S.-Q., Zhang, B.-L. & Zuo, Y.L. (1991) Preliminary study on the occurrence and control of *Callitettix versicolor* Fabricius and *Abidama liuensis* Metcalf. *Plant Protection*, 17 (3), 10–12.

Hoffmann, W.E. (1942) Bugs or Homoptera. The cicadas, plant hoppers, plant lice, scale insects, and others. *Special Publication of Lingnan Natural History Survey and Museum*, 9, 1–20, pls. 1–30.

Knight, D.W., Staddon, B.W. & Thorne, M.J. (1985) Presumed sex pheromon from androconical glands of male cotton harlequin bug *Tectocoris diophthalmus* (Heteroptera: Scutelleridae) identified as 3,5-dihydroxy-4-pyrone. *Zeitschrift für Naturforschung*, 40C, 851–853. https://doi.org/10.1515/znc-1985-11-1217

Lallemand, V. (1949) Révision des Cercopinae (Hemiptera Homoptera). Première partie. *Mémoires d'Institut Royal des Sciences Naturelles de Belgique*, Series 2, 32, 1–193.

Li, D.-Y., Liao, G.-H. & He, C.-J. (2010) Growth and decline regulation of *Callitettix versicolor* and its control in paddy field. *Southwest China Journal of Agricultural Sciences*, 23, 1370–1373. [in Chinese with English abstract]

Li, J.-Q., Zhao, Z.-M., Wu, S.-Y., Ming, K. & Hou, L.-N. (2001) Biology and ecology of rice spittle bug (*Callitettix versicolor*). *Journal of Southwestern Agricultural University*, 23, 156–159. [in Chinese with English abstract]

Liang, A.-P. & Fletcher, M.J. (2002) Morphology of the antennal sensilla in four Australian spittlebug species (Hemiptera: Cercopidae) with implications for phylogeny. *Australian Journal of Entomology*, 41, 39–44. https://doi.org/10.1046/j.1440-6055.2002.00266.x

Liang, A.-P. & Webb, M.D. (2002) New taxa and revisionary notes in Rhinaulacini spittlebugs from southern Asia (Homoptera: Cercopidae). *Journal of Natural History*, 36, 729–756.

https://doi.org/10.1080/00222930110062336

Liao, G.-H., Li, D.-Y. & He, C.-J. (2010) Distribution and injury of *Callitettix versicolor* in rice. *Guizhou Agriculture Science*, 38, 96–99. [in Chinese]

Lim, G.T. & Pan, Y.C. (1980) Entomofauna of sugarcane in Malaysia. *Proceedings of the International Society of Sugar Cane Technologists*, 17, 658–1679.

Luo, Q.Y. & Xu, S.M. (2011) The occurrence and integrated control of *Callitettix versicolor* (Fabricius). *Hubei Plant Protection*, 2011 (2), 29–30. [in Chinese]

Machado, F.E.L., Peck, D.C. & Lerma, J.M. (2001) Importancia de la comunicación vibracional en el comportamiento reproductivo del salivazo de los pastos (Homoptera: Cercopidae). *Revista Colombiana de Entomologia*, 29, 9–15.

McGavin, G.C. (1993) *Bugs of the World*. Blandford, London, 192 pp.

Metcalf, Z.P. (1961) *General Catalogue of the Homoptera. Fasc. VII. Cercopoidea. Part 2. Cercopidae, Paper No. 1278*. North Carolina State College, Raleigh, North Carolina, pp. 1–607.

Metcalf, Z.P. & Horton, G. (1934) The Cercopidae (Homoptera) of China. *Lingnan Science Journal*, 13, 367–429, pls. 37–43.

Morgan, J.C. & Claridge, M.F. (1993) Acoustic signals and life history of *Machaerota rastrata*. *In:* Drosopoulos, S., Petrakis, P.V., Claridge, M.F. & de Vrijer, P.W.F. (Eds.), *Proceedings of the 8th Auchenorrhyncha Congress, Delphi, Greece*, 9–13 August 1993, pp. 91–92.

Morris, H. & Waterhouse, D.F. (2001) *The Distribution and Importance of Arthropod Pests and Weeds of Agriculture in Myanmar*. ACIAR, Canberra, 73 pp.

Ossiannilsson, F. (1949) Insect drummers. A study on the morphology and function of the sound-producing organ of Swedish Homoptera Auchenorrhyncha. *Opuscula Entomologica*, 10 (Supplementum), 1–146.

Pawar, A.D. & Bhalla, O.P. (1976 [1974)) Pest complex of rice in Himachal Pradesh. *Indian Journal of Entomology*, 36, 358–359.

Peck, D.C. & Thompson, V. (2008) Spittlebugs (Hemiptera: Cercopoidea). *In:* Capinera, J.L. (Ed.), *Encyclopedia of Entomology*. Springer, Dordrecht, pp. 3512–3516.

Percy-Cunningham, J.E. & MacDonald, J.A. (1987) Biology and ultrastructure of sex pheromone-producing glands. *In:* Prestwich, G.D. & Blomquist, G.J. (Eds.), *Pheromone Biochemistry*. Academic Press, Orlando, Florida, pp. 27–69.
https://doi.org/10.1016/B978-0-12-564485-3.50007-5

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675.
https://doi.org/10.1038/nmeth.2089

Staddon, B.W., Abdollahi, A., Parry, G., Rissiter, M. & Knight, D.W. (1994) Major component in male sex pheromone of cereal pest *Eurygaster integriceps* Puton (Heteroptera: Scutelleridae) identified as a homosesquiterpenoid. *Journal of Chemical Ecology*, 20, 2721–2731.
https://doi.org/10.1007/BF02036203

Stål, C. (1865) Homoptera nova vel minus cognita. *Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar, Stockholm*, 22, 145–165.

Thompson, V. (1994) Spittlebug indicators of nitrogen-fixing plants. *Ecological Entomology*, 19, 391–398.
https://doi.org/10.1111/j.1365-2311.1994.tb00257.x

Thompson, V. (1997) Spittlebug nymphs (Homoptera: Cercopidae) in *Heliconia* flowers (Zingiberales: Heliconiaceae): preadaptation and evolution of the first aquatic Homoptera. *Revista de Biologia Tropical*, 45, 905–912.

Ubik, K., Vrkoc, J., Zdárek, J. & Kontev, C. (1975) Vanillin: possible sex pheromone of an insect. *Naturwissenschaften*, 62, 348.
https://doi.org/10.1007/BF00608902

Vrkoc, J., Ubik, K., Zdárek, J. & Kontev, C. (1977) Ethyl acrylate and vanillin as components of the male sex pheromone complex in *Eurygaster integriceps* (Heteroptera: Scutelleridae). *Acta Entomologica Bohemoslov*, 74, 205–206.

Yuan, F. (1986) Family Cercopidae. *In:* Deng, G.-F. (Ed.), *Agricultural Insects of China.* Science Press, Beijing, pp. 154–157. [in Chinese]

Zdárek, J. & Kontev, C. (1975) Some ethological aspects of reproduction in *Eurygaster integriceps* (Heteroptera: Scutelleridae). *Acta Entomologica Bohemoslov*, 72, 239–248.