On the structure of stridulatory organs in jumping plant lice (Homoptera: Psyllinea)

О строении стридуляционных органов листоблошек (Homoptera: Psyllinea)

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КЛЮЧЕВЫЕ СЛОВА: листоблошки, Psyllinea, вибрационные сигналы, стридуляционные органы, морфология.

ABSTRACT. Stridulatory organs on meso- and metascutellum in 14 species of jumping plant lice were investigated under the scanning electron microscope. Denticulate areas on axillary cords are developed to the same extent both in species, producing vibratory signals and in ones in which no signals were registered. No significant difference in structure of axillary cords between males and females was found. Aphalaridae and Psyllidae are similar in the shape of axillary cords, but differ in this character from Triozidae.

РЕЗЮМЕ. Стридуляционные органы на мезо- и метаскутеллуме у 14 видов листоблошек были исследованы при помощи сканирующего электронного микроскопа. Покрытые зубчиками участки на аксиллярных тяжах развиты в одинаковой степени как у видов, издающих вибрационные сигналы, так и у форм, у которых сигналы зарегистрированы не были. Значимых различий в строении аксиллярных тяжей у самцов и самок не найдено. Aphalaridae и Psyllidae имеют сходную форму аксиллярных тяжей, но отличаются по этому признаку от Triozidae.

Stridulation by jumping plant lice was first reported by Ossiannilsson [1950]. He observed wing vibrations associated with sound production in both sexes of *Trioza nigricornis* Forster, 1848. The amplitude of wing movements did not exceed 10–15°. Heslop-Harrison [1960] detected sounds produced by representatives of six genera of British psyllids and offered rather complex hypothesis concerning the functioning of sound-producing mechanism in these insects. Two years later Taylor [1962] described and illustrated fine corrugations on axillary cords of meso- and metascutellum and corresponding hard flange at the base of the second anal vein on both fore and hind wings in five Australian species of *Hyalinaspis* Taylor, 1960 (Spondyliaspididae). He supposed that the flanges could be drawn over the axillary cords during appropriate wing movements, i. e. they are two parts of frictional mechanism (plectrum and pars stridens respectively). Similar structures were reported in several other genera of Spondyliaspididae [Taylor, 1985].

Closer examination of these organs in two species of *Schedotrioza* Tuthill & Taylor, 1955 (Triozidae) under the scanning electron microscope was performed by Taylor [1985]. The structures on the SEM photographs presented in the paper do not differ principally from these in *Hyalinaspis*. It should be noted, that notwithstanding the fact that certain authors have heard faint buzzing sounds produced by psyllids, neither oscillograms nor sonograms of signals were available in literature until 1986. For this reason the structures described by Taylor [1985] were referred to as "possible stridulatory organs" in his paper.

First descriptions and oscillograms of acoustic signals of a number of species of psyllids were published later by Yang et al. [1986] and Tishechkin [1989, 2005]. Clear association between wing vibrations and signals produced supports the opinion that the structures on wings and thorax, as describer by Taylor [1962, 1985] are stridulatory organs. Singing insect holds the wings closed as in the resting position, but moves them up and down rapidly in an almost vertical plane so that the margins of anal veins could be drawn over the denticulate surface of axillary cords [Tishechkin, 2005].

During the course of recent studies of vibratory communication in Psyllinea I have made recordings of signals of about 30 species of Aphalaridae (including Liviidae), Triozidae and Psyllidae. In most species from first two families males readily sing both in isolation and in the presence of conspecific specimens of either sex. On the contrary, only one species of Psyllidae, namely, *Livilla ulicis* Curtis, 1836 produced signals in my experiments, whereas in six other species studied, as well as in repreTable. List of studied species of jumping plant lice with data on collecting sites and acoustic activity Таблица. Список изученных видов листоблошек со сведениями о местах сбора и акустической активности

Species	Locality	Vibratory signals were registered /not registered (-/)
	Family Aphalaridae	
Livia funcorum (Lett.)	South Siberia, South Tuva, env. Erzin Village, <i>Juncus</i> sp. in the flood-land of Erzin Riv.	+
Craspedolepia campestrella Oss.	Moscow Area, Serpukhov District, env. Luzhki Village, Artemisia campestris L. on the bank of Oka River.	+
C. dracuncull Log.	Irkutsk Area, Kosaya Step' Village about 50 km E of Bayanday, A. dracunculus L.	+
C. gloriosa Log.	Moscow Area, Serpukhov District, env. Pushchino-na-Oke Town, A. abrotanum L.	+
C. malachilica (Dhlb.)	Moscow Area, Serpukhov District, env. Luzhki Village, A. absimination L. on the bank of Oka River.	+
C. amissa Wagn.	Volgograd Area, env. Shcherbatovka Village about 50 km N of Karnyshyn Town, <i>A. vulgaris</i> L.	+
Calliardia anabasidis Log.	Astrakhan' Area, western shore of Baskunchak Lake, <i>Anabasis aphylla</i> L. in steppe.	+
Rhinocola aceris (L.)	Moscow Area, Serpukhov District, env. Pushchino-na-Oke Town	-
	Family Psyllidae	
Arytaina maculata (Löw)	Volgograd Area, env. Shcherbatovka Village about 50 km N of Karnyshyn Town, <i>Cytisus ruthenicus</i> Fisch, ex Wołoszcz.	-
Livilla korvathi (Scott)	North of Saratov Area, steppe on hills about 15 km SE of Khvelynsk Town, Genista tinctoria L.	Ι
L. ulicis Curtis	Moscow Area, Serpukhov District, env. Luzhki Village, G. thetoria.	+
Psylla alni L.	Moscow Area, Chashnikovo in the environs of Zelenograd Town, <i>Alnus incana</i> (L.) Moench.	_
	Family Triozidae	
Trichochermes walkeri (Först.)	North of Saratov Area, steppe on hills about 15 km SE of Khvalynsk Town, Rhamnus cathartica L.	-
Bactericera perrisi Put.	Dosang railway station about 60 km N of Astrakhan', Ariemisia arenaria DC and A. scoparia Waldst. et Kit. in desert.	+

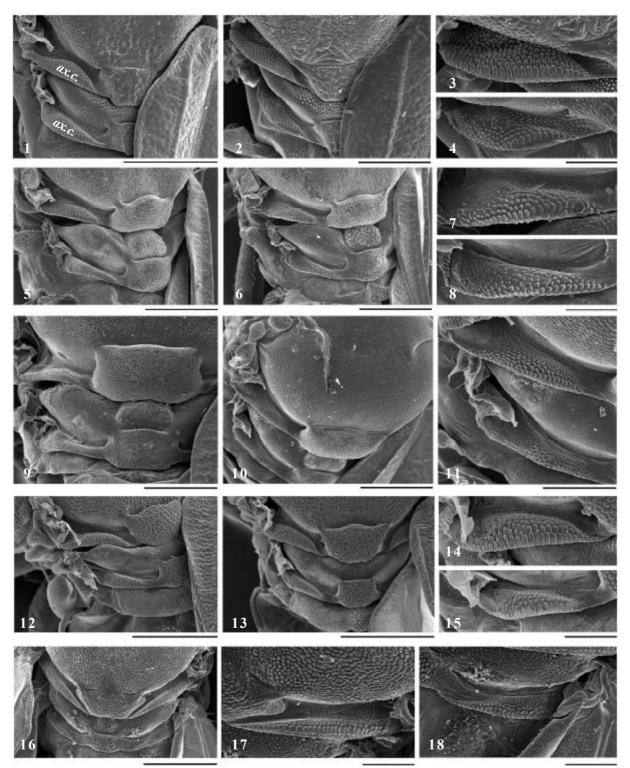
sentatives of *Trichochermes* Kirkaldy, 1904 (Triozidae) and in *Rhinocola aceris* (L., 1758) (Aphalaridae) no signals were heard. This raises the question of whether such species are capable of signals production, i.e. do they possess stridulatory mechanism. The main task of the present study was to ascertain this problem. In addition, comparative investigation of stridulatory organs in different groups makes it possible to elucidate potentials of application of characters of their structure in taxonomy on species and superspecies level. Moreover, only Australian species were investigated until now, and no information on sound-producing organs of Palaearctic psyllids exists in the literature.

14 species in total from 3 families of jumping plant lice mentioned above were studied. For investigation on SEM dry material was used. In all species attempts to register vibratory signals were undertaken, but in certain ones I failed to hear any signals. The list of species with data on collecting sites and acoustic activity recorded is given in the table.

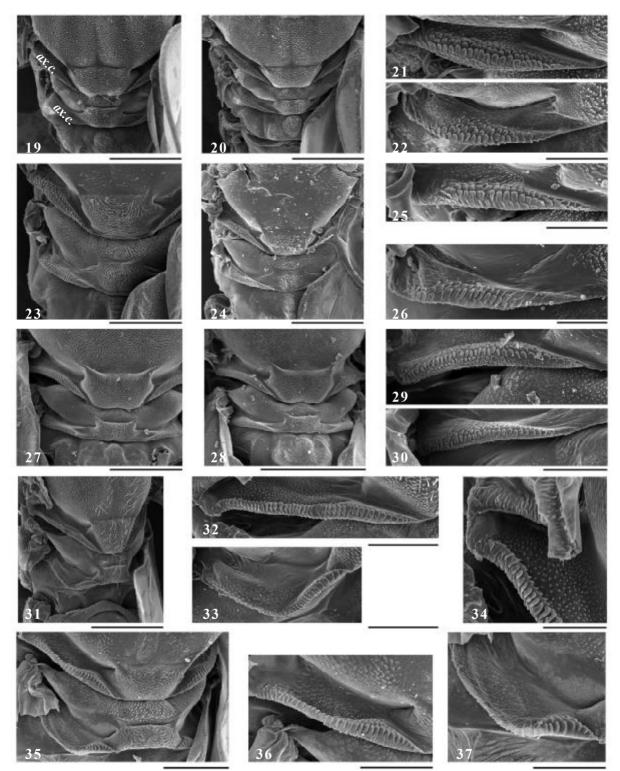
Every frictional sound-producing mechanism necessarily consists of two parts. One part is a row of pegs or denticles usually referred to as "file" or "pars stridens", another is a matching hard ridge or knob, so called, "scraper" or "plectrum". Moving of plectrum over pars stridens results in producing sounds or/and vibrations. According to Taylor [1985], denticulate areas on axillary cords of meso- and metascutellum in psyllids play the role of pars stridens, whereas sclerotized area on the second anal veins act as a plectrum.

In all species studied axillary cords are covered with scale-like denticles. They are developed to the same extent both in species, producing vibratory signals and in ones in which no signals were registered (Figs 1–49). For investigation on SEM specimens were placed so, that sclerotization on the second anal veins cannot be seen on photographs, still in certain cases it is clearly visible, that veins can be drawn over denticulate surface of axillary cords during wings movements (Figs 5–6, 13, 20, 35). Therefore, all species possess morphological structures, which can be used for producing of signal.

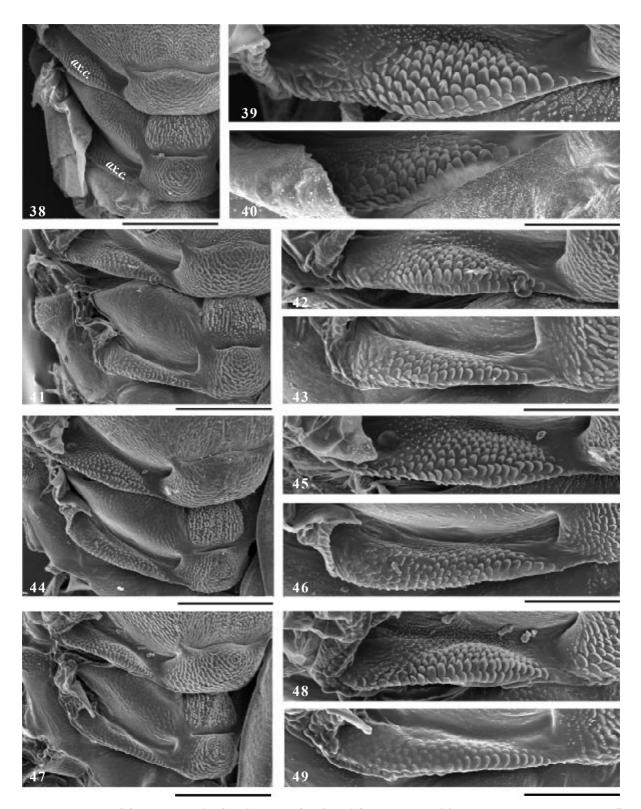
Do they actually use this mechanism, this is a question, however. Unlike most other insects, producing of



Figs 1–18. Stridulatory organs of jumping plant lice: 1–4 — *Livia juncorum*; 5–8 — *Craspedolepta omissa*; 9–11 — *Calliardia anabasidis*; 12–15 — *Rhinocola aceris*; 16–18 — *Arytaina maculata*; 1, 5, 9, 12 — female, dorsal view of thorax, both wings on the left side are removed (*ax.c.* — axillary cords); 2, 6, 10, 13, 16 — same, male; 3, 7, 14, 17 — same, axillary cord of mesoscutellum; 4, 8, 15, 18 — same, axillary cord of metascutellum; 11 — same, axillary cords of mesoscutellum and metascutellum. Scale bars: 1, 5–6, 9–10, 12–13, 16 — 300 µm; 2 — 200 µm; 3–4, 7–8, 14–15 — 80 µm; 11 — 150 µm; 17, 18 — 100 µm. Рис. 1–18. Стридуляционные органы листоблошек: 1–4 — *Livia juncorum*; 5–8 — *Craspedolepta omissa*; 9–11 — *Calliardia anabasidis*; 12–15 — *Rhinocola aceris*; 16–18 — *Arytaina maculata*; 1, 5, 9, 12 — самка, грудной отдел, сверху, оба крыла с левой стороны удалены (*ax.c.* — аксиллярные тяжи); 2, 6, 10, 13, 16 — то же, самец; 3, 7, 14, 17 — то же, аксиллярный тяж мезоскутеллума; 4, 8, 15, 18 — то же, аксиллярный тяж метаскутеллума; 11 — то же, аксиллярные тяжи мезоскутеллума, 4, 8, 15, 18 — то же, аксиллярный тяж метаскутеллума; 11 — то же, аксиллярные тяжи мезоскутеллума, 11 — 150 µm; 11 — 150 µm; 11 — 150 µm; 17, 18 – 100 µm. 18 — 100 µm.



Figs 19–37. Stridulatory organs of jumping plant lice: 19–22 — *Livilla horvathi*, 23–26 — *L. ulicis*, 27–30 — *Psylla alni*, 31– 34 — *Trichochermes walkeri*, 35–37 — *Bactericera perrisi*, 19, 23, 27 — female, dorsal view of thorax, both wings on the left side are removed (*ax.c.* — axillary cords); 20, 24, 28, 31, 35 — same, male; 21, 25, 29, 32, 36 — same, axillary cord of mesoscutellum, 22, 26, 30, 33, 37 — same, axillary cords); 20, 24, 28, 31, 35 — same, male; 21, 25, 29, 32, 36 — same, axillary cord of mesoscutellum, 22, 26, 30, 33, 37 — same, axillary cords); 20, 24, 28, 31, 35 — same, male; 21, 25, 29, 32, 36 — same, axillary cord of mesoscutellum, 22, 26, 30, 21–22, 25, 34, 37 — 80 µm; 26 — 60 µm; 27, 31 — 400 µm; 28 — 600 µm; 29–30 — 120 µm; 32–33, 35 — 150 µm; 36 — 100 µm. Puc. 19–37. Стридуляционные органы листоблошек: 19–22 — *Livilla horvathi*, 23–26 — *L. ulicis*; 27–30 — *Psylla alni*; 31– 34 — *Trichochermes walkeri*; 35–37 — *Bactericera perrisi*; 19, 23, 27 — самка, грудной отдеа, сверху, оба крыла с левой стороны удалены (*ax.c.* — аксиллярные тяжи); 20, 24, 28, 31, 35 — то же, самец; 21, 25, 29, 32, 36 — то же, аксиллярный тяж мезоскутеллума; 22, 26, 30, 33, 37 — то же, аксиллярный тяж метаскутеллума; 34 — то же, передняя часть аксиллярного тяжа метаскутеллума. Масштаб: 19–20, 23–24 — 300 µm; 21–22, 25, 34, 37 — 80 µm; 26 — 60 µm; 27, 31 — 400 µm; 28 — 600 µm; 29–30 — 120 µm; 32–33, 35 — 150 µm; 36 — 100 µm.



Figs 38–49. Stridulatory organs of males of jumping plant lice of the genus *Craspedolepta* (s.str.): 38–40 — *C. campestrella*; 41–43 — *C. dracunculi*; 44–46 — *C. gloriosa*; 47–49 — *C. malachitica*; 38, 41, 44, 47 — dorsal view of thorax, both wings on the left side are removed (*ax.c.* — axillary cords); 39, 42, 45, 48 — same, axillary cord of mesoscutellum; 40, 43, 46, 49 — same, axillary cord of metascutellum. Scale bars: 38, 41, 44, 47 — 200 µm; 39, 40 — 60 µm; 43, 45–46, 48–49 — 100 µm. Рис. 38–49. Стридуляционные органы самцов листоблошек рода *Craspedolepta* (s.str.): 38–40 — *C. campestrella*; 41–43 — *C. dracunculi*; 44–46 — *C. gloriosa*; 47–49 — *C. malachitica*; 38, 41, 44, 47 — грудной отдел, сверху, оба крыла с левой стороны удалены (*ax.c.* — аксиллярные тяжи); 39, 42, 45, 48 — то же, аксиллярный тяж мезоскутеллума; 40, 43, 46, 49 — то же, аксиллярный тяж мезоскутеллума. Масштаб: 38, 41, 44, 47 — 200 µm; 39, 40 — 60 µm; 43, 45–46, 48–49 — 100 µm.

acoustic signals in psyllids is not a necessary stage of mating behaviour. Normally, male spontaneously produce calling signals when ready for copulation. Receptive conspecific female sings in reply to calling male remaining stationary, whereas male after hearing reply signals immediately starts searching her emitting calling from time to time. In such a way partners find each other. Nonetheless, under experimental conditions at high density of insects on the plant male can find female and mate successfully not producing calling signals [Tishechkin, 2005]. Many species of Psyllinea live in dense aggregations, so it is not unlikely that this situation can exist in nature. Maybe, in certain species acoustic communication was fully reduced, but observations of mating behaviour under different conditions are necessary for solving the question.

There is no any significant difference in structure of axillary cords of males and females (Figs 1–2, 5–6, 9–10, 12–13, 19–20, 23–34, 27–28). This agrees well with the fact that receptive females sing actively and their signals are similar in temporal pattern with these of conspecific males [Tishechkin, 2005].

In certain taxa the structures associated with soundproducing organs provide reliable taxonomic characters on species level. For example, in Gomphocerinae grasshoppers (Orthoptera: Acrididae) the number and density of pegs in stridulatory file on hind femur are often species-specific. Comparison of photographs of axillary cords in males of four species of *Craspedolepta* (s.str.) Enderlein, 1921 does not revealed any distinct species-specific characters, however (Figs 38–49). Number of denticles in longitudinal rows is approximately equal in all four species. Moreover, denticles in peripheral part of axillary cords are reduced to some extent and are difficult to count for certain. The shape of axillary cords is also similar both within the genus *Craspedolepta* and within Aphalaridae as a whole (Figs 1–15, 38–49).

Aphalaridae (including *Livia* Latreille, 1804 — Figs 1–4) are rather similar with Psyllidae in structure of stridulatory organs. In representatives of both families (Figs 1–15, 38–49 and 16–18, 19–30) axillary cords are

more or less straight and wide and as a rule possess at least 3–4 longitudinal rows of teeth on the dorsal surface. In studied representatives of Triozidae, axillary cords are more narrow (Figs 31–37); moreover, axillary cord of metascutellum is strongly arched (Figs 33, 37). This fact is in agreement with viewpoint of Burckhardt [1987] uniting Psyllidae and Aphalaridae, but regarding Triozidae as a separate family.

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