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Pure-Tone Vibrational Signals in Small Auchenorrhyncha (Homoptera)

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Abstract—Investigation of vibrational calling signals of about 500 species of small Auchenorrhyncha from Russia and adjacent territories has shown that more than 10% of the species studied produce signals fully or partially consisting of pure-tone components. Among these species, there are forms dwelling on various substrates including thick tree branches, slender twigs, grass stems, petioles, and leaves. Therefore, it is impossible to associate the presence of pure-tone signals in any species with the physical properties of the inhabited substrate. Pure-tone signals were recorded both in the largest and the smallest forms. Consequently, the type of signal frequency spectrum is not related to the insect size. Experiments under natural conditions confirm the assumption that pure-tone signals are more resistant to noise than wide-band ones. This property may compensate for the disadvantage of pure-tone signals arising from stronger attenuation in certain substrates. As a result, neither pure-tone nor noise signals give unambiguous advantages for vibrational communication. Since the carrier frequency of pure-tone signals of small Auchenorrhyncha increases with temperature, it seems to be determined by the contraction frequency of tymbal muscles, rather than by the resonance properties of any cavity or cuticular structure. Regular frequency modulations occur in the signals of many species; moreover, the calling signals of some species include both pure-tone and noise components. In most of the species studied, “frequency tuning” of their signals to the physical properties of a particular substrate is impossible because of the presence of frequency modulations, temperature-related variation in the carrier frequency, or the wide host range and the absence of strong preference for any particular plant organ. Sympatric species may differ in the carrier frequency of their pure-tone signals. If the signals occupy the same frequency range they sometimes differ in their frequency modulation pattern. Consequently, conspecific signal recognition not only by amplitude, but also by frequency pattern is possible in this case, which increases the efficiency of intraspecific communication.

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Intraspecific communication in all the representatives of Auchenorrhyncha (Homoptera), except the singing cicadas (Cicadidae), is accomplished not by sounds but by vibrational signals transmitted through solid substrates, such as stems and leaves of plants. Any part of a plant is a complex frequency filter whose parameters are determined by the shape, thickness, elasticity coefficient, mass distribution, and other physical properties of the stem or leaf. Due to the overwhelming diversity of such “filters” in the nature, it is virtually impossible to predict which frequency bands will be absorbed and which will be passed through by a particular stem (Michelsen et al., 1982). At first glance, signals with wide-band, or “noise” frequency spectra would have the best advantage under such conditions, since part of the energy of these signals would almost certainly remain unabsorbed in a substrate with any frequency response. Indeed, most representatives of small Auchenorrhyncha emit noise signals, usually within a range below 2–3 kHz. The use of pure-tone signals with line spectra appears to be nonadaptive in this situation, because in case of coincidence between the main signal frequency and the minimum of the substrate frequency response, the signal will be almost completely absorbed (Michelsen et al., 1982). Still, some Auchenorrhyncha emit pure-tone signals that form regular sine curves in high-speed oscillograms (see, e.g., Tishechkin, 2001, 2007b); therefore, in spite of the drawback considered above, line-spectrum signals may have certain advantages.

Cocroft and Rodríguez (2005) suggested that prolonged pure-tone signals might be advantageous at a high noise level, for example in rainforests where the vibrations induced by the falling rain drops merge into constant background noise. Unfortunately, this hypothesis was never tested experimentally.

Pure-tone vibrational signals were studied in detail only in the American treehoppers of the genus *Enchenopa* (Membracidae). The calling signals of different species were found to differ by their carrier frequencies, the receptive females preferring signals with a species-specific frequency (Rodríguez et al., 2006). Thus, the species emitting pure-tone signals could recognize the signal of a conspecific individual not only by its amplitude-temporal pattern but also by its carrier frequency.

It was also shown by the example of two species of *Enchenopa* that the main frequencies of their signals matched the maxima of the frequency responses of the host plant parts on which the singing males were usually located: stems of *Cercis canadensis* in one species and leaf petioles of *Ptelea trifoliata*, in the other. This correspondence ensured signal propagation with the lowest attenuation rate; in other words, the signal of each species was "tuned" by frequency to the substrate inhabited by that species (McNett and Cocroft, 2008).

Thus, on the one hand, pure-tone signals may attenuate at a higher rate than noise ones when passing through plant substrates; on the other hand, many members of Auchenorrhyncha still use such signals for vibrational communication. The possible adaptive traits of pure-tone signals remain practically unknown since they have been studied in species of only one genus from the family Membracidae (Rodríguez et al., 2006; McNett and Cocroft, 2008).

In view of the above, we have performed a large-scale comparative study of the pure-tone signals of Auchenorrhyncha, using the material from the fauna of Russia and adjacent countries, and tested various hypotheses concerning the possible adaptive significance of this phenomenon.

MATERIALS AND METHODS

The low-amplitude vibrations in plant stems were recorded with a GZP-311 piezoelectric cartridge (a pickup head of a vinyl record player) connected to a recorder (Sony Walkman MZ-NH900 or MZ-RH910 MD recorders, or Elektronika-302-1 cassette tape recorder) via a matching amplifier. The recording level adjustment was done only in the manual mode, to avoid amplitude distortions.

For recording, a small (usually no more than 10–15 cm long) fragment of the plant was fixed with a rubber ring on the cartridge body in such a way that the stylus touched the stem with slight elastic bending. The nylon cage containing the insects was put on the plant; after some time, the insects usually positioned themselves on the stem and started feeding, so that the cage could be removed. The technique of signal recording under field conditions in the presence of natural noise was described in the previous communication (Tishechkin, 2012). The records were analyzed on a computer equipped with an analog/digital converter and the corresponding software.

The material used in this analysis was collected in different regions of Russia and adjacent countries from 1986 to 2011. Altogether, the signals of almost 500 species of small Auchenorrhyncha were studied, among which pure-tone calling signals were found in 62 species. The list of the taxa and the number of genera and species studied are given in Table 1; the oscillograms and sonograms of the signals are presented only for some of them, as an example. The species were selected in such a way as to cover all the higher taxa in which line-spectrum signals are known, and also to reflect the diversity of the signal structure in the best way possible. These species are listed in Table 2, which also contains data on the collection locality, the temperature during signal recording, the host plants, and the body size of the insects; these data will be used in the discussion below.

RESULTS AND DISCUSSION

The acoustic repertoire of small Auchenorrhyncha is quite diverse, including from 2 to 5–6 functional types of signals in the Palaearctic species. In this analysis we will consider only the calling signals, which are spontaneously emitted by the male to attract a conspecific female and which are used for communication over distances many times greater than the insects' body length.

High-speed oscillograms of signals of most Auchenorrhyncha often reveal short fragments containing one or two periods of the sine curve. However, the oscillations in the neighboring fragments are either irregular or have a different frequency, so that the resulting frequency spectrum becomes noise-like even for a relatively short part of the signal (100–200 ms). Therefore, only the signals with a more or less regular sinusoidal carrier, composed of tens of periods of similarly shaped waves, were regarded as "pure-tone" in this analysis. The overlapping irregular low-amplitude vibrations discernible in some oscillograms are usually the result of interference.

Table 1. The list of taxa of Auchenorrhyncha with indication of the total number of the genera and species studied and the number of genera and species in which line-spectrum signals are known

Taxon	Number of genera/species studied	Number of genera/species in which pure-tone signals or signals with line-spectrum fragments are known
SUPERFAMILY MEMBRACOIDEA	135/386	37/57
Family Cicadellidae	132/380	36/54
Subfamily group CICADELLIDES	23/57	19/29
Subfamily Cicadellinae sensu lato	7/11	5/8
Tribe Cicadellini	2/3	1/1
Tribe Evacanthini	2/5	2/5
Tribe Pagaroniini	1/1	1/1
Tribe Bathysmatophorini	1/1	
Tribe Mileewini	1/1	1/1
Subfamily Typhlocybinae	16/46	14/21
Tribe Alebrini	1/3	1/1
Tribe Empoascini	4/19	3/3
Tribe Dikraneurini	4/4	3/3
Tribe Erythroneurini	3/6	3/5
Tribe Typhlocybini	4/14	4/9
Subfamily group IASSIDES	88/217	16/24
Subfamily Xestocephalinae	1/1	
Subfamily Aphrodinae	4/10	
Subfamily Deltocephalinae	80/197	15/23
Tribe Deltocephalini	3/6	
Tribe Paralimnini	22/59	8/14
Tribe Macrostelini	4/11	
Tribe Koebeliini	1/1	
Tribe Opsiini	5/15	
Tribe Goniagnathini	1/1	
Tribe Hecalini	2/4	2/2
Tribe Eupelicini	1/1	
Tribe Dorycephalini	1/2	
Tribe Doraturini	5/16	
Tribe Anoterostemmatini	1/1	
Tribe Scaphytopiini	1/1	1/1
Tribe Athysanini	17/46	
Tribe Cicadulini	4/13	1/3
Tribe Platymetopiini	7/15	1/1
Tribe Fieberiellini	2/2	1/1
Tribe Selenocephalini	3/3	1/1
Subfamily Iassinae	2/6	
Subfamily Penthimiinae	1/3	1/1
Subfamily group ULOPIDES	20/105	
Subfamily Idiocerinae	3/6	

Table 1 (Contd.)

Taxon	Number of genera/species studied	Number of genera/species in which pure-tone signals or signals with line-spectrum fragments are known
Subfamily Macropsinae	6/80	
Subfamily Agalliinae	5/12	
Subfamily Adelungiinae	4/5	
Subfamily Megophthalminae	1/1	
Subfamily Ulopinae	1/1	
Subfamily group LEDRIDES	1/1	1/1
Subfamily Ledrinae	1/1	1/1
Family Membracidae	3/6	1/3
SUPERFAMILY CERCOPOIDEA	20/25	4/5
Family Cercopidae	2/3	
Family Aphrophoridae	9/21	4/5
Tribe Aphrophorini	2/9	
Tribe Lepyroniini	2/4	
Tribe Philaenini	4/8	4/5
Family Machaerotidae	1/1	
SUPERFAMILY FULGOROIDEA	49/85	
Family Delphacidae	24/35	
Family Cixiidae	8/23	
Family Meenoplidae	1/1	
Family Derbidae	1/3	
Family Dictyopharidae	6/10	
Family Tropiduchidae	1/1	
Family Issidae	5/5	
Family Caliscelidae	3/7	
TOTAL	204/496	41/62

As can be seen from Table 1, line-spectrum signals were observed in some but not all the taxa of Auchenorrhyncha.

Among Cicadellidae, such signals are emitted by many representatives of the group Cicadellides that includes the subfamilies Cicadellinae s. l. and Typhlocybinae (Figs. 1, 2); the signals of 36 species of these subfamilies were described in an earlier communication (Tishechkin, 2001). It should be noted that many authors quite reasonably exclude a number of tribes from the subfamily Cicadellinae s. l., leaving only Cicadellini and Proconiini in it. However, to avoid taxonomic discussion, we consider this subfamily in the "broad" sense, following the interpretation of Anufriev and Emeljanov (1988).

The pure-tone calling signals were recorded in all the representatives of Cicadellinae s. l. studied by us, except two species of the genus *Cicadella* and *Bathysmatophorus reuteri* J. Sahlberg, 1871 in which only the courtship signal contains some line-spectrum elements (Tishechkin, 2001). The calling signals of *Kolla atramentaria* (Motschulsky, 1859) (Fig. 1, *1–2*) (Cicadellini), *Onukia onukii* Matsumura, 1912 (Evacanthini) (Fig. 1, *7–8*), and *Epiacanthus stramineus* (Motschulsky, 1861) (Pagaroniini) (Fig. 1, *9–10*) consist of single or repeated simple pulses, whereas those of species of the genus *Evacanthus* (Evacanthini) are complex phrases (Fig. 1, *3–6*). However, in all the cases the signals are completely or partly composed of elements with regular sinusoidal fill. The pure-tone

Table 2. Collection localities, conditions of signal recording, trophic specialization, and body size of some species of Auchenorrhyncha emitting pure-tone signals

Species	Collection locality and temperature during signal recording	Trophic specialization	Body length, mm
Family Cicadellidae Subfamily group Cicadellides Subfamily Cicadellinae Tribe Cicadellini			
Kolla atramentaria (Motsch.)	Chita Prov., the Ingoda valley near the Talacha outfall (15 km E of Urul'ga, Karymskiy Distr.); 25 and 31–32°C	Polyphagous, feeding on stems of herbaceous plants	5.5–7.2
Tribe Evacanthini			
Evacanthus interruptus (L.)	1. Moscow Prov., env. of Pushkino, bank of the Ucha; 26°C. 2. Moscow, Sokolniki Park; 21°C. 3. Moscow Prov., Sergiev Posad; 39°C	Polyphagous, feeding on stems of herbaceous plants; in particular, collected on the nettle *Urtica dioica* (Urticaceae) and the goutweed *Aegopodium podagraria* (Apiaceae)	5.2–7.0
E. asiaticus (Osh.)	Kyrgyzstan, Chatkal Range, Sary-Chelek Reserve; 20–23, 28, 30, 43°C	Collected on the nettle *Urtica* sp.; feeds on stems	5.1–6.4
Onukia onukii Mats.	S Primorskii Terr., Kedrovaya Pad' Reserve; 25–26°C	Collected on grasses; feeds on stems and blades	4.7–5.8
Tribe Pagaroniini			
Epiacanthus stramineus (Motsch.)	S Primorskii Terr., env. of Andreevka, Khasan Distr.; 27–28°C	Collected on the trailplant *Adenocaulon himalaicum* (Asteraceae); feeds on stems or large leaf veins	7.2–8.7
Tribe Mileewini			
Mileewa dorsimaculata (Mel.)	S Primorskii Terr., env. of Barabash-Levada, Pogranichnyi Distr.; 22–23°C	Polyphagous, feeding on stems or large leaf veins of herbaceous plants	5.2–6.2
Subfamily Typhlocybinae Tribe Alebrini			
Alebra albostriella (Fall.)	Moscow Prov., env. of Pirogovo; 26–27°C	Feeds on leaf laminae of the oak *Quercus robur* (Fagaceae)	4.3–4.7
Tribe Empoascini			
Austroasca vittata (Leth.)	Moscow Prov., env. of Pirogovo; 18°C	Feeds on leaf laminae of wormwoods *Artemisia* spp. (Asteraceae)	3.0–3.4
Tribe Dikraneurini			
Igutettix oculatus (Lindb.)	Moscow, Vorob'evy Gory; 30°C	Collected on the Hungarian lilac *Syringa josikaea* (Oleaceae); feeds on leaves	4.4–4.9
Tribe Typhlocybini			
Aguriahana germari (Zett.)	Moscow Prov., env. of Pirogovo; 22–23°C	Feeds on needles of the pine *Pinus sylvestris* (Pinaceae)	3.9–4.7
Subfamily group Iassides Subfamily Deltocephalinae Tribe Paralimnini			
Aglena ornata (H.-S.)	Saratov Prov.: (1) 4–5 km N of Ozinki, the Chalykla floodland; 28°C; (2) env. of Dyakovka, Krasnokutskii Distr.; 32–34°C, recorded with natural background noise	Feeds on stems and blades of the sea clubrush *Bolboschoenus maritimus* (Cyperaceae)	8.0–10.0

Table 2 (Contd.)

Species	Collection locality and temperature during signal recording	Trophic specialization	Body length, mm
Calamotettix taeniatus (Horv.)	Astrakhan Prov., Bogdo-Baskunchak Reserve, W bank of Lake Baskunchak; 30–33°C	Feeds on blades of the common reed *Phragmites australis* (Poaceae)	5.0–6.1
Cosmotettix paludosus (Ball.)	East Siberia, Buryatia, the Irkut valley, ca 80 km W of Kyren; 27°C	Feeds on blades of sedges *Carex* spp. (Cyperaceae)	3.2–3.7
Sorhoanus xanthoneurus (Fieb.)	Same locality; 26–28°C	The same	3.5–3.7
S. hilaris (Mel.)	East Siberia, Buryatia, the Bryanka valley ca 10 km E of Onokhoi; 31°C	Feeds on grasses (Poaceae)	3.7–4.2
Paralimnus elegans Em.	Saratov Prov., 4–5 km N of Ozinki, the Chalykla floodland; 24°C	Feeds on reed blades	3.4–4.2
Hebecephalus changai Dlab.	East Siberia, Buryatia, the Irkut valley, ca 80 km W of Kyren; 32°C	Feeds on grasses (Poaceae)	2.7–3.2
Tribe Hecalini			
Hecalus lineatus (Horv.)	S Primorskii Terr., env. of Primorskii, Khasan Distr.; 25–27°C	Feeds on blades of *Miscanthus* (Poaceae)	6.3–7.0
Glossocratus foveolatus Fieb.	Chita Prov., the Ingoda valley near the Talacha outfall (15 km E of Urul'ga, Karymskiy Distr.); 26°C	Feeds on grasses (Poaceae)	6.8–10.0
Tribe Scaphytopiini			
Stymphalus rubrolineatus (Stål)	S Primorskii Terr., env. of Primorskii, Khasan Distr.; 25°C	Feeds on blades of *Miscanthus* (Poaceae)	5.0–6.0
Tribe Cicadulini			
Cicadula persimilis (Edw.)	Moscow Prov., env. of Pirogovo; 23°C	Feeds on blades of grasses (Poaceae)	4.5–5.5
Tribe Platymetopiini			
Scaphoideus festivus Mats.	S Primorskii Terr., Kedrovaya Pad' Reserve; 27–28°C	Feeds on stems of herbaceous plants	4.5–6.0
Tribe Fieberiellini			
Phlogotettix cyclops (M.R.)	S Primorskii Terr., Kedrovaya Pad' Reserve; 26°C	The same	4.5–5.5
Tribe Drabescini			
Drabescus vilbastei Zhang, Webb	S Primorskii Terr., Lake Khanka coast, 10–15 km S of Turii Rog; 23°C	Feeds on leaf stalks and large veins of the Mongolian oak *Quercus mongolica* (Fagaceae)	7.0–8.5
Subfamily Penthimiinae			
Penthimia scutellata Mel.	SW of Khabarovsk Terr., 10 km N of Obluchie; 30°C	Collected on willows; feeds on leaf stalks and large veins	4.7–5.4
Subfamily group Ledrides Subfamily Ledrinae			
Ledra auditura Walker	S Primorskii Terr., Kedrovaya Pad' Reserve; 24°C	Feeds on branches from 4–5 to 10–15 mm in diameter and thicker of the Mongolian oak *Quercus mongolica* (Fagaceae) and maples *Acer* spp. (Aceraceae)	12.5–16.0

Table 2 (Contd.)

Species	Collection locality and temperature during signal recording	Trophic specialization	Body length, mm
		Family Membracidae	
Gargara mongolica Dlab.	S Primorskii Terr., Lake Khanka coast, 10–15 km S of Turii Rog; 27°C	Collected on *Lespedeza bicolor* (Fabaceae); feeds on branches	3.9–5.3
G. genistae (F.)	Saratov Prov., env. of Dyakovka, Krasnokutskii Distr.; 34°C, recorded with natural background noise	Collected on *Cytisus ruthenicus* (Fabaceae); feeds on branches	4.0–5.3
	Kyrgyzstan, Chatkal Range, Sary-Chelek Reserve; 24 and 30°C	Collected on *Caragana arborescens* (Fabaceae); feeds on branches	
		Family Aphrophoridae	
Neophilaenus sachalinensis (Mats.)	East Siberia, Buryatia, the Irkut valley, ca 80 km W of Kyren; 29–30°C	Feeds on blades of grasses (Poaceae)	4.3–6.3
Philaenus spumarius (L.)	Kyrgyzstan, Chatkal Range, Sary-Chelek Reserve; 22°C	Polyphagous; feeds on stems of herbaceous plants	5.0–6.7
Aphilaenus ikumae (Mats.)	S Primorskii Terr., Lake Khanka coast, 10–15 km S of Turii Rog; 21–22°C	Feeds on stems and leaf stalks of wormwoods of the section *Artemisia* (Asteraceae)	6.3–7.7

and noise fragments are combined in the calling signals of *E. stramineus* and *Mileewa dorsimaculata* (Melichar, 1902) (Mileewini), as well as of some other Cicadellidae (Figs. 1, *9–10*; 2, *1–2*).

The subfamily Typhlocybinae, closely related to Cicadellinae, includes the smallest leafhoppers with narrow bodies and delicate integuments. Species emitting pure-tone signals were found in all the five tribes studied in this respect: Alebrini, Empoascini, Dikraneurini, Erythroneurini, and Typhlocybini (Tishechkin, 2001); the oscillograms of the signals of three of them are given here as an example (Fig. 2, *3–8*).

In the subfamily group Iassides, signals with line frequency spectra were recorded in representatives of several tribes of Deltocephalinae and in one of the three studied species of the genus *Penthimia* (Penthimiinae). Among Deltocephalinae, many species of Paralimnini emit such signals. Pure-tone signals are known in species of 8 out of the 22 studied genera: *Aglena*, *Paralimnus*, *Sorhoanus*, *Cosmotettix*, *Diplocolenus*, *Calamotettix*, *Hebecephalus*, and *Rosenus* (Fig. 3); the signals of *Sorhoanus medius* (Mulsant et Rey, 1855) and *Diplocolenus frauenfeldi* (Fieber, 1869) were described in an earlier communication (Tishechkin, 2007b).

In the group of closely related tribes including Doraturini, Eupelicini, Dorycephalini, Anoterostemmatini, and Hecalini, whose representatives, like those of Paralimnini, mostly occur on grasses, pure-tone signals were recorded only in two species of Hecalini (Fig. 4, *1–4*). The calling signal of *Hecalus lineatus* (Horvath, 1899) consists only of pure-tone elements (Fig. 4, *1–2*), whereas that of *Glossocratus foveolatus* Fieber, 1866 includes noise fragments (Fig. 4, *3–4*).

Signals with regular sinusoidal fill were also found in the only studied representative of the mostly tropical tribe Scaphytopiini, *Stymphalus rubrolineatus* (Stål, 1855) (Fig. 4, *5–6*).

Species of the small tribe Cicadulini are also associated with grasses and sedges. In this group, signals with pure-tone components were recorded only in three species of the nominotypical subgenus of the genus *Cicadula* (Fig. 4, *7–8*). The studied representatives of the genera *Paluda*, *Rhopalopyx*, *Taurotettix*, and *Cicadula* (*Cyperana*) emit signals with noise frequency spectra.

In the tribe Platymetopiini, signals with line spectra were recorded only in *Scaphoideus festivus* Matsumura, 1902 (Fig. 5, *1–2*). Signals with some pure-tone components were also described in *S. titanus* Ball, 1932 (Mazzoni et al., 2009), all the other studied representatives of this group emitting wide-band calling signals (Tishechkin, 2000). It should be noted that the composition of this tribe is still obscure; here, we follow the interpretation of Emeljanov (1999).

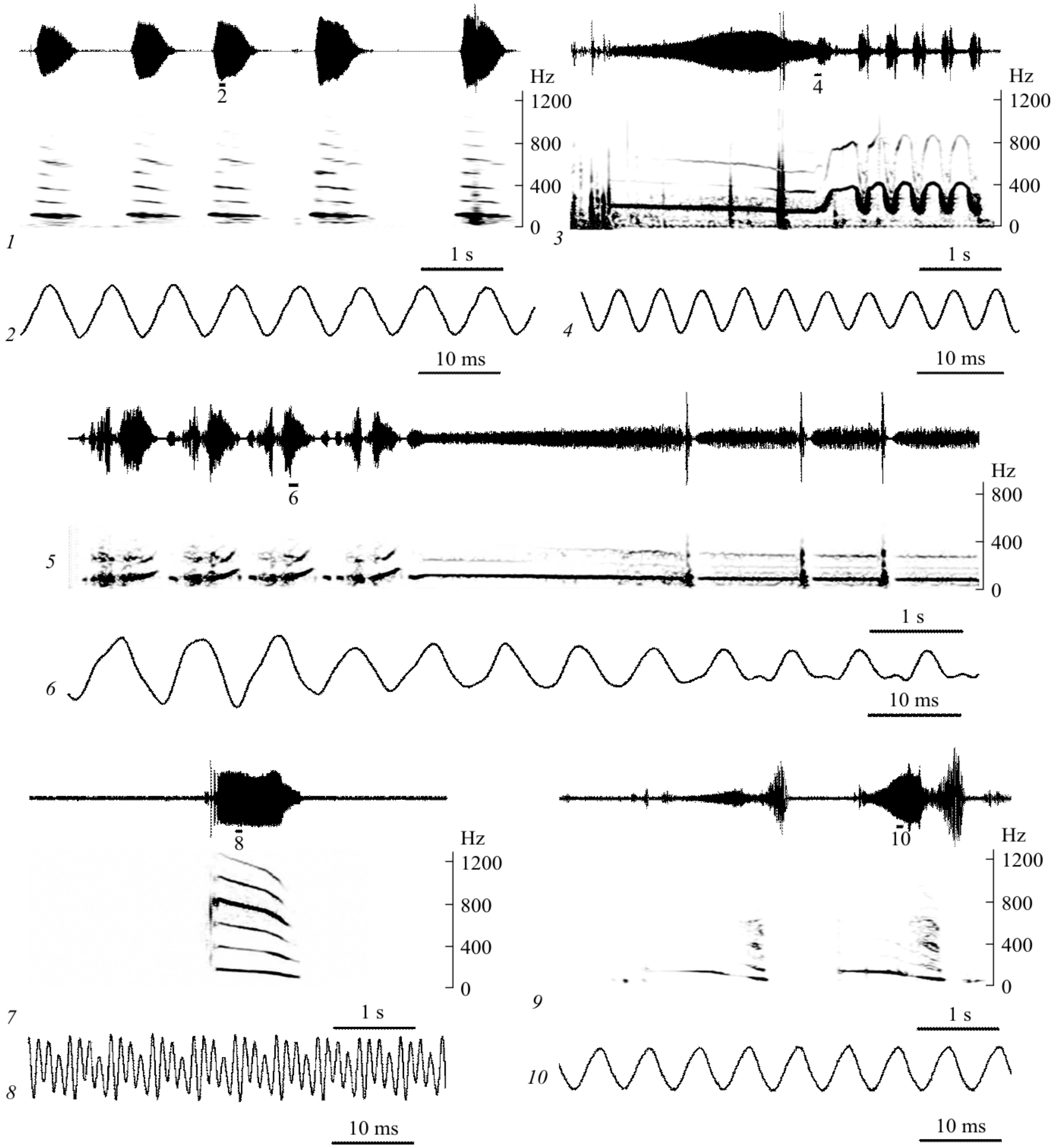

Fig. 1. Vibrational signals of Auchenorrhyncha: (*1*, *2*) *Kolla atramentaria*; (*3, 4*) *Evacanthus interruptus*; (*5, 6*) *E. asiaticus*; (*7, 8*) *Onukia onukii*; (*9, 10*) *Epiacanthus stramineus* [(*1*, *3*, *5*, *7*, *9*) total view of the signal: oscillogram and sonogram at the same scale; (*2*, *4*, *6*, *8*, *10*) oscillogram showing the wave shape in the signal]. The fragments of signals designated by numbers *2*, *4*, *6*, *8*, and *10* are shown in oscillograms under the same numbers.

In the tribe Fieberiellini, closely related to Platymetopiini, pure-tone signals were recorded in *Phlogotettix cyclops* (Mulsant et Rey, 1855) (Fig. 5, *3–4*).

Among the three studied species of Selenocephalini (including Drabescini), signals with line spectra are emitted only by *Drabescus vilbastei* Zhang, Webb,

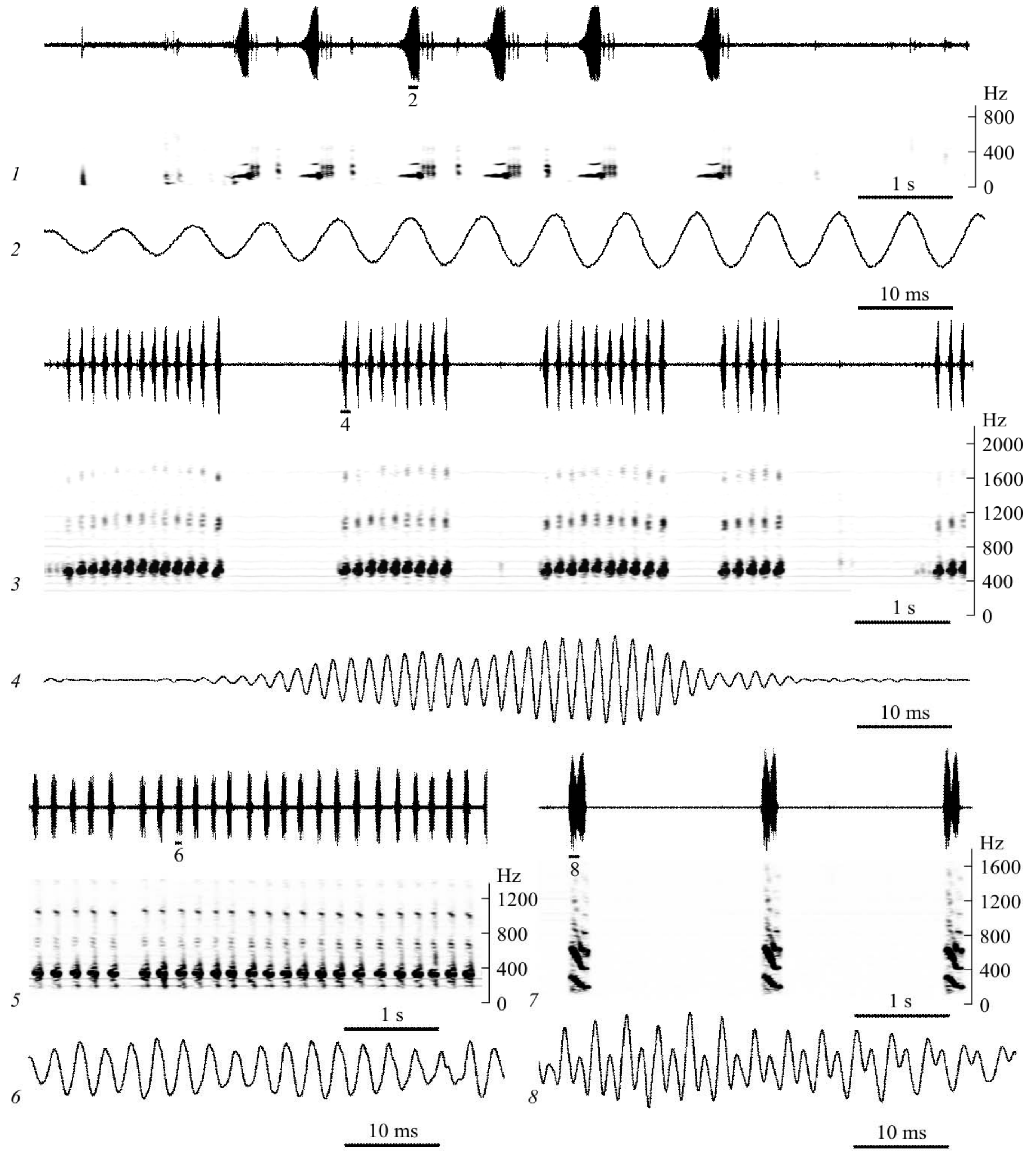

Fig. 2. Vibrational signals of Auchenorrhyncha: (*1, 2*) *Mileewa dorsimaculata*; (*3, 4*) *Alebra albostriella*; (*5, 6*) *Austroasca vittata*; (*7, 8*) *Aguriahana germari* [(*1, 3, 5, 7*) total view of the signal: oscillogram and sonogram at the same scale; (*2, 4, 6, 8*) oscillogram showing the wave shape in the signal]. The fragments of signals designated by numbers *2*, *4*, *6*, and *8* are shown in oscillograms under the same numbers.

1996 (Fig. 5, *5–6*); the calling signals of *Selenocephalus obsoletus* (Germar, 1817) and *Athysanopsis salicis* Matsumura, 1905 have noise frequency spectra (Tishechkin, 2000, 2010).

Signals with line spectra were also recorded in *Penthimia scutellata* Melichar, 1902 from the subfamily Penthimiinae, closely related to Deltocephalinae (Fig. 5, *7–8*).

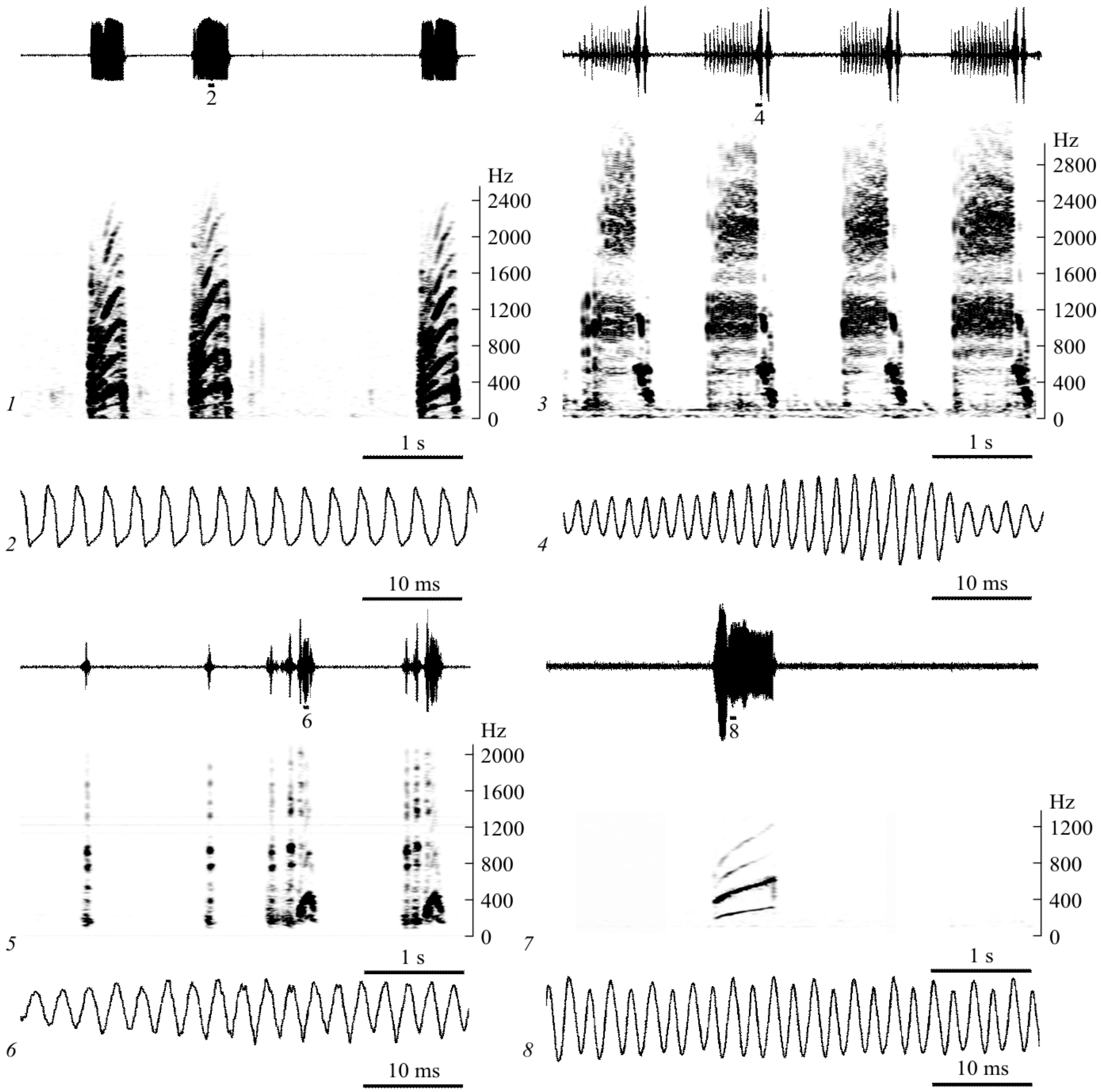

Fig. 3. Vibrational signals of Auchenorrhyncha: (*1, 2*) *Aglena ornata*; (*3, 4*) *Paralimnus elegans*; (*5, 6*) *Calamotettix taeniatus*; (*7, 8*) *Hebecephalus changai* [(*1*, *3*, *5*, *7*) total view of the signal: oscillogram and sonogram at the same scale; (*2*, *4*, *6*, *8*) oscillogram showing the wave shape in the signal]. The fragments of signals designated by numbers *2*, *4*, *6*, and *8* are shown in oscillograms under the same numbers.

Among the rest of Cicadellidae, pure-tone signals were recorded by us only in *Ledra auditura* Walker, 1858 from a very peculiar subfamily Ledrinae which is sometimes considered as a separate family (Fig. 6, *1–2*). In addition, signals with pure-tone components were described in one Australian representative of this group (Percy and Day, 2005). No such signals were found in the subfamily group Ulopides despite the extensive material studied (Table 1).

Pure-tone signals are also emitted by many representatives of the family Membracidae, related to Cicadellidae (Cocroft and McNett, 2006); the signals of two Palaearctic species of the genus *Gargara* are described below.

In the other taxa of Auchenorrhyncha, species emitting signals with line spectra are present only as rare exceptions. In the superfamily Cercopoidea, the only

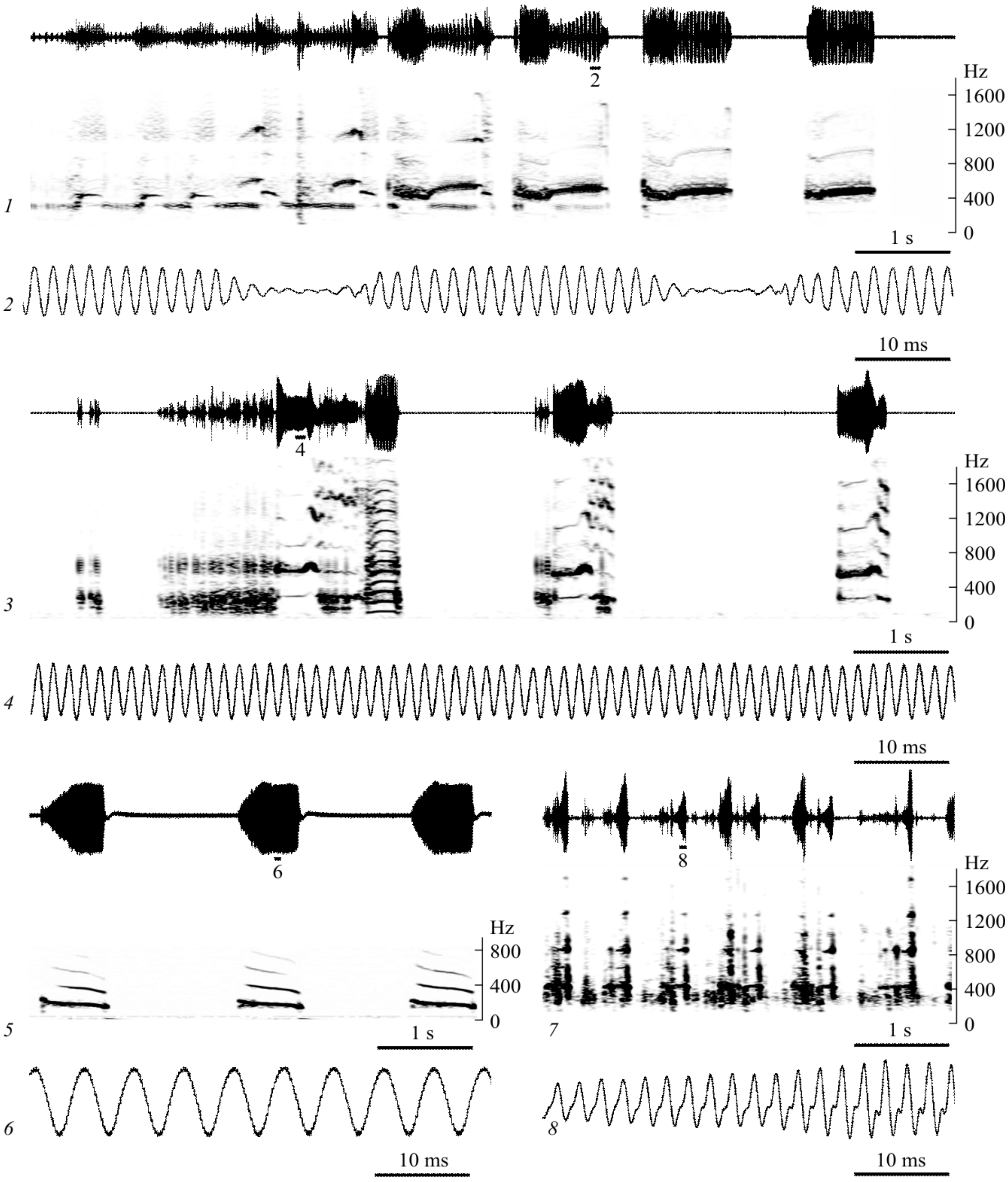

Fig. 4. Vibrational signals of Auchenorrhyncha: (*1, 2*) *Hecalus lineatus*; (*3, 4*) *Glossocratus foveolatus*; (*5, 6*) *Stymphalus rubrolineatus*; (*7, 8*) *Cicadula persimilis* [(*1, 3, 5, 7*) total view of the signal: oscillogram and sonogram at the same scale; (*2, 4, 6, 8*) oscillogram showing the wave shape in the signal]. The fragments of signals designated by numbers *2, 4, 6,* and *8* are shown in oscillograms under the same numbers.

such forms are spittlebugs of the tribe Philaenini (Aphrophoridae) (Fig. 6, *3–8*; see also Tishechkin, 2003). Pure-tone signals of several species of singing cicadas (Cicadoidea, Cicadidae) were described in the literature (Moulds, 1975; Young and Josephson, 1983); however, they are not considered here since

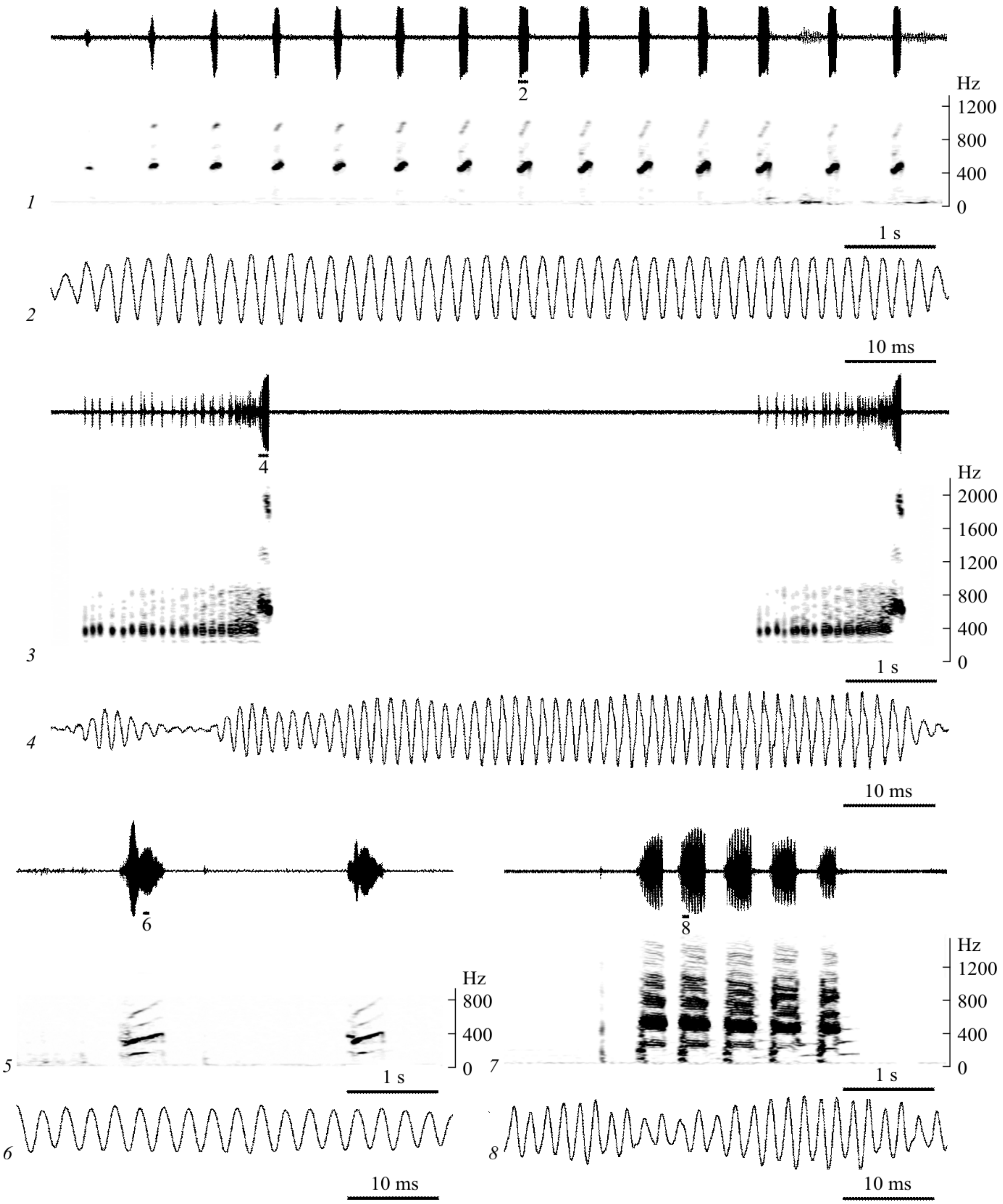

Fig. 5. Vibrational signals of Auchenorrhyncha: (*1, 2*) *Scaphoideus festivus*; (*3, 4*) *Phlogotettix cyclops*; (*5, 6*) *Drabescus vilbastei*; (*7, 8*) *Penthimia scutellata* [(*1*, *3*, *5*, *7*) total view of the signal: oscillogram and sonogram at the same scale; (*2*, *4*, *6*, *8*) oscillogram showing the wave shape in the signal]. The fragments of signals designated by numbers *2*, *4*, *6*, and *8* are shown in oscillograms under the same numbers.

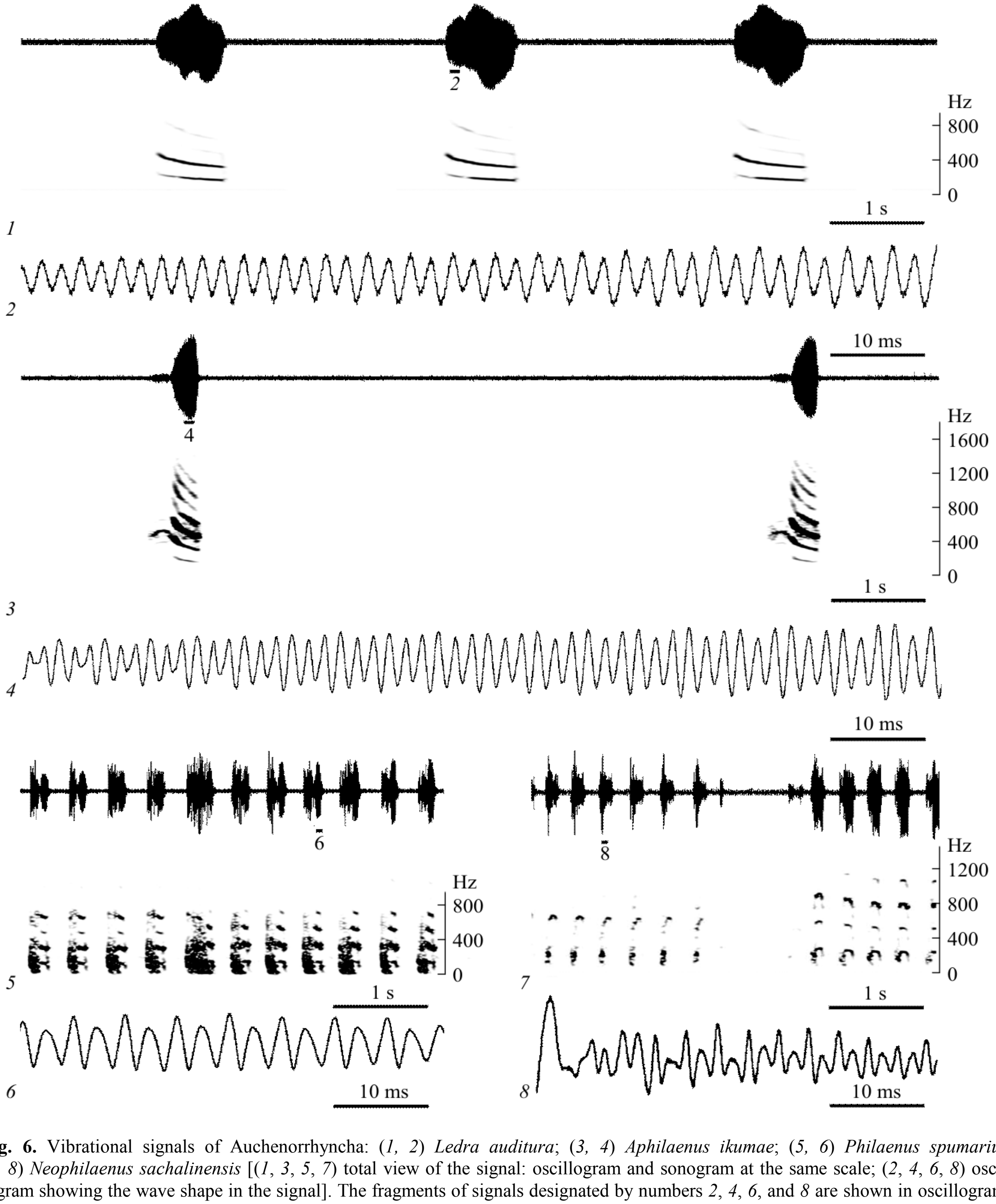

Fig. 6. Vibrational signals of Auchenorrhyncha: (*1, 2*) *Ledra auditura*; (*3, 4*) *Aphilaenus ikumae*; (*5, 6*) *Philaenus spumarius*; (*7, 8*) *Neophilaenus sachalinensis* [(*1*, *3*, *5*, *7*) total view of the signal: oscillogram and sonogram at the same scale; (*2*, *4*, *6*, *8*) oscillogram showing the wave shape in the signal]. The fragments of signals designated by numbers *2*, *4*, *6*, and *8* are shown in oscillograms under the same numbers.

these insects use sound rather than vibrational communication. No signals with line spectra were recorded in representatives of the eight families of Fulgoroidea studied by us (Table 1).

Thus, although pure-tone vibrational signals are quite common in some groups of Auchenorrhyncha, they have not been found in other groups despite the extensive material studied. A question arises, what is the reason for such differences among these taxa?

The Trophic Specialization of the Representatives of Auchenorrhyncha Emitting Pure-tone Signals

It may be assumed that the use of signals with line spectra may be advantageous on substrates with certain physical properties, for example, on stems of a particular thickness, on the leaf lamina, etc. This assumption is indirectly supported by the main signal frequency matching the maxima of the substrate frequency response in two species of *Enchenopa* (Membracidae) (McNett and Cocroft, 2008). However, as can be seen even from the limited data in Table 2, species emitting pure-tone signals occur on practically all the types of substrates on which Auchenorrhyncha can exist. For example, *Ledra auditura* lives on large lignified branches of trees, *Drabescus vilbastei* and species of the genus *Gargara* are also associated with trees or shrubs but occur on slenderer twigs, and most of the remaining species feed on herbaceous plants. These hortobionts also vary strongly in their biology: some of them (in particular, Cicadellinae s. l.) mainly occur in tall and humid herbage where they feed on plants with relatively thick and sappy stems, such as nettles, goutweed, or *Adenocaulon himalaicum*, whereas others (most of Deltocephalinae) occur on sedges and grasses. The latter group includes both the species associated with reeds or *Miscanthus* spp. which may grow 2 m tall (e.g., *Stymphalus rubrolineatus*, *Calamotettix taeniatus* Horvath, 1911, and *Hecalus lineatus*), and those living on short steppe grasses (in particular, *Hebecephalus changai* Dlabola, 1965 and some species of *Sorhoanus*) or sedges (*Aglena ornata* Herrich-Schäffer, 1838, *Cosmotettix* spp.).

Finally, representatives of Typhlocybinae clearly differ in their biology from the rest of Auchenorrhyncha since they feed not on the sap from the plant vascular system but on the contents of the mesophyll cells; correspondingly, they mostly occur on the leaf laminae and not on the stems. Some species of the genus *Aguriahana*, including *A. germari* (Zetterstedt, 1840) considered herein, represent a certain exception in that they are trophically associated with various pines (*Pinus* spp.) and feed on the needles.

Thus, no correlation can be revealed between the presence of pure-tone signals in a particular species and the physical properties of the substrate on which the species dwells. Species emitting line-spectrum signals develop on plants of various life forms, from trees (both leaved and coniferous) to short grasses, and feed on stems of various length, diameter, and shape as well as on leaf stalks or laminae. Moreover, species emitting signals with noise frequency spectra often occur nearby on the same plants.

Noise Resistance of Pure-tone Signals

Another possible advantage of pure-tone signals over noise ones is the fact that their energy is concentrated within a narrow frequency range. Correspondingly, a line-spectrum signal can be more easily distinguished against the background noise than a wideband signal with the same energy. This property of pure-tone signals is used, for example, in electronic alarm clocks and similar “beeping” devices whose signal appears quite loud whereas the energy consumption is low. Therefore, the use of pure-tone signals may be advantageous, first, for the smallest representatives of Auchenorrhyncha in which the muscles of the sound-producing apparatus are too weak, and second, for the species living at a high level of noise.

However, no correlation can be observed between the size of a particular species and the presence of pure-tone signals in its repertoire. Among the species emitting pure-tone signals there are insects of different size, from the largest members of the subfamily Ledrinae to Typhlocybinae, most of which are minute and slender forms with delicate integuments (Table 2). Within the tribe Paralimnini, pure-tone signals were recorded both in the largest of the Palaearctic species, *Aglena ornata* (body length 8.0–10.0 mm) and in the smallest representatives, such as *Rosenus stepposus* Vilbaste, 1965 (body length 2.4–2.6 mm). Besides, there are many species of Auchenorrhyncha comparable in size with the smallest members of Paralimnini (for example, many Delphacidae), which emit signals with a noise frequency spectrum.

The main source of vibrational noises in plant stems is the wind (Tishechkin, 2007, 2012). The vibrations are mainly produced by collisions of stems and leaves of densely growing plants, rather than by the wind itself. We analyzed the signals of two species of Auchenorrhyncha recorded in the nature against the background of natural noise at moderate wind speeds. The signals of *Aglena ornata* were recorded in the thickets of the sea clubrush *Bolboschoenus maritimus* (Cyperaceae) 60–70 cm tall, and those of *Gargara* *genistae* (Fabricius, 1775, Membracidae), in a bush of the broom shrub *Cytisus ruthenicus* (Fabaceae) about 1 m tall. In both cases, recording was done in an open landscape in the steppe zone (see Table 2) at wind speeds varying from 1–3 to 5–6 m/s; the vibrations were mostly produced by collisions and frictions of the stems. During the gusts of wind, the tips of the broom shrub stems moved with an amplitude of 10–15 cm; the maximum amplitude of the clubrush blades was 4–5 cm.

The signals of both species are practically indiscernible in the oscillograms, i.e., their amplitude does not exceed that of the noise. At the same time, the signals can be easily distinguished in the sonograms due to their energy being concentrated within a narrow frequency range (Fig. 7, *1*, *3*). The signals of *G. genistae* consist of noise and pure-tone components (Fig. 7, *2*). In the sonograms of the records made in the nature, the latter component is clearly discernible whereas the former is almost indistinguishable from the noise produced by plants (Fig. 7, *3*). This fact confirms the assumption of Cocroft and Rodríguez (2005) that pure-tone signals should have a higher noise resistance as compared to wide-band ones.

This property seems to compensate for the drawback of pure-tone signals related to their strong attenuation in case of their main frequency matching the frequency response minimum of the substrate. Thus, any of the two types of frequency spectrum can hardly have an indisputable advantage. This is additionally confirmed by the fact that species emitting pure-tone and noise signals coexist in all the regions of Russia, including the steppe and semi-desert zones where strong winds are common.

Frequency Modulations in the Pure-tone Signals of Auchenorrhyncha

As mentioned above, the study of pure-tone signals in the cryptic species complex *Enchenopa binotata* (Say, 1824) has shown that the main frequency of the signal, first, acts as one of the key characters in the process of signal recognition by the conspecific female and, second, coincides with the maximum of the frequency response of the substrate occupied by a particular species (Rodríguez et al., 2006; McNett and Cocroft, 2008). It is evident that both the "frequency tuning" to a particular substrate and the segregation of communication channels ("acoustic niches") by frequency are possible only if each species is characterized by a more or less constant frequency. Therefore, in order to find out whether the trends described in *Enchenopa* represent a special case or a phenomenon common to all the Auchenorrhyncha, we should determine how stable the carrier frequency is in the signals of these insects.

Comparison of the sonograms has allowed us to subdivide all the species studied into four groups.

The first group is formed by the species in which the frequency remains almost constant along the entire signal. It includes, in particular, a number of Typhlocybinae whose signals consist of short uniform pulses (Fig. 2, *3*, *5*), *Penthimia scutellata* (Penthimiinae) (Fig. 5, *7*), and, with some reservations, *Gargara mongolica* Dlabola, 1965 (Membracidae).

The second group unites the species whose signals demonstrate a gradual increase or decrease in the frequency along a pulse or a syllable. It includes *Kolla atramentaria* (Fig. 1, *1*), *Igutettix oculatus* (Lindberg, 1929), *Aguriahana germari* (Fig. 2, *7*), most Paralimnini (Fig. 3, *1*, *7*), *Stymphalus rubrolineatus* (Fig. 4, *5*), *Scaphoideus festivus* (Fig. 5, *1*), *Drabescus vilbastei* (Fig. 5, *5*), *Ledra auditura* (Fig. 6, *7*), and many other species. The most abrupt changes in the frequency may occur within several tens of milliseconds of a single pulse. This phenomenon is observed, for example, in *I. oculatus*: the carrier frequency is about 560 Hz at the beginning of each pulse and about 200 Hz at the end of it (Fig. 8, *1*). The drop of frequency can be seen in the high-speed oscillogram as well (Fig. 8, *2*). More often, similar changes occur during longer fragments (for example, Fig. 8, *5*, *7*).

The third group includes the species showing a more complex pattern of frequency modulation, for example, an increase followed by a drop of frequency within a syllable, or a signal consisting of several components with different frequency spectra. Such signals are emitted, for example, by *Evacanthus interruptus* (Linnaeus, 1758) (Fig. 1, *3*), *Hecalus lineatus* (Fig. 4, *1*), *Neophilaenus sachalinensis* (Matsumura, 1915), and *Aphilaenus ikumae* (Matsumura, 1915) (Fig. 6, *3*, *7*).

Finally, the fourth group is formed by the species whose signals combine pure-tone and noise fragments, in particular *Mileewa dorsimaculata* (Fig. 2, *1*), *Paralimnus elegans* Emeljanov, 1964 (Fig. 3, *3*), *Calamotettix taeniatus* (Fig. 3, *5*), *Glossocratus foveolatus* (Fig. 4, *3*), *Cicadula persimilis* (Edwards, 1920)

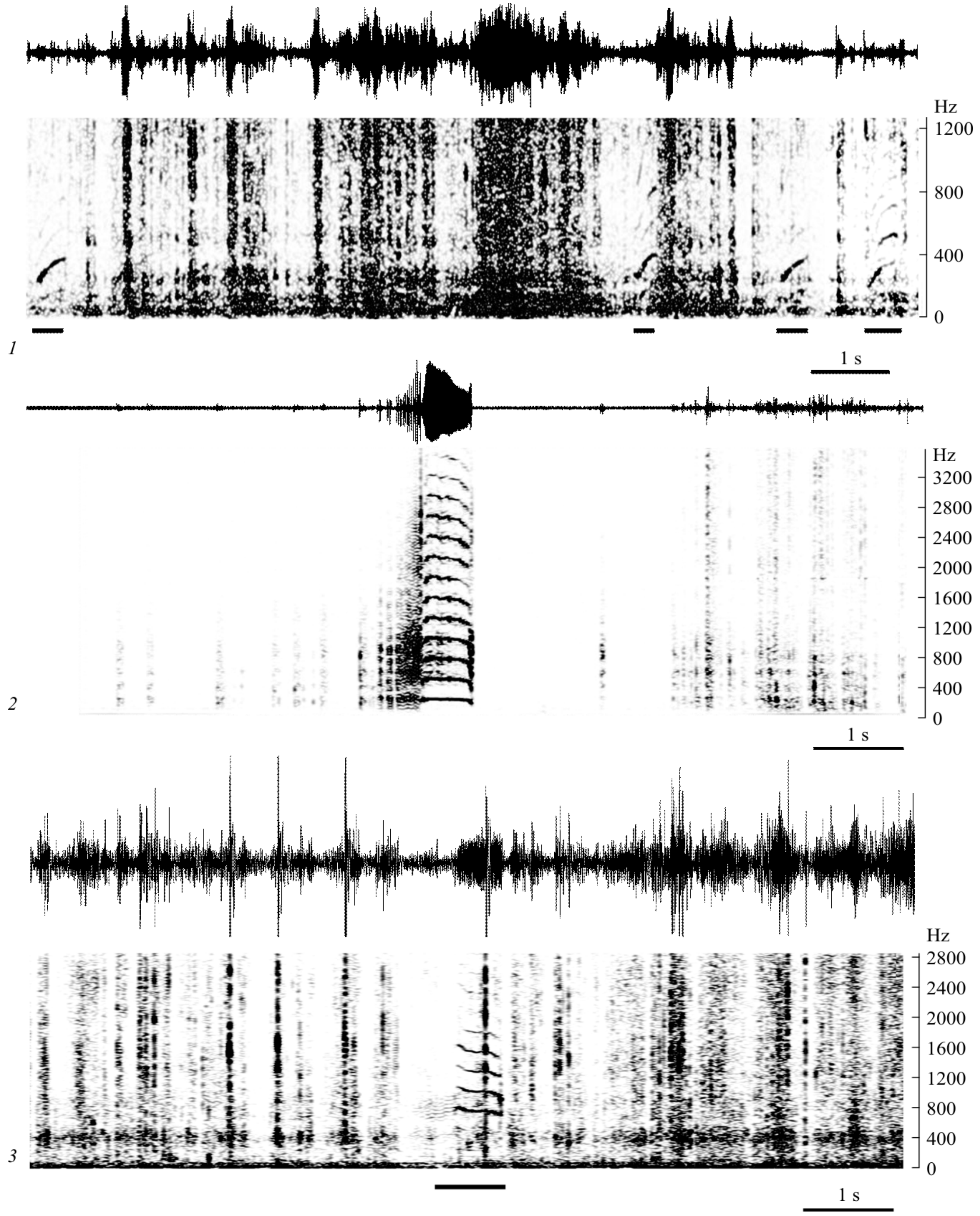

Fig. 7. Vibrational signals of Auchenorrhyncha: (*1*) *Aglena ornata*, oscillogram and sonogram at the same scale; (*2, 3*) *Gargara genistae*, oscillogram and sonogram at the same scale. Signals *1* and *3* were recorded in the nature with wind noise in the background; signal *2* was recorded in the laboratory. The signals are marked with horizontal bars in sonograms *1* and *3*.

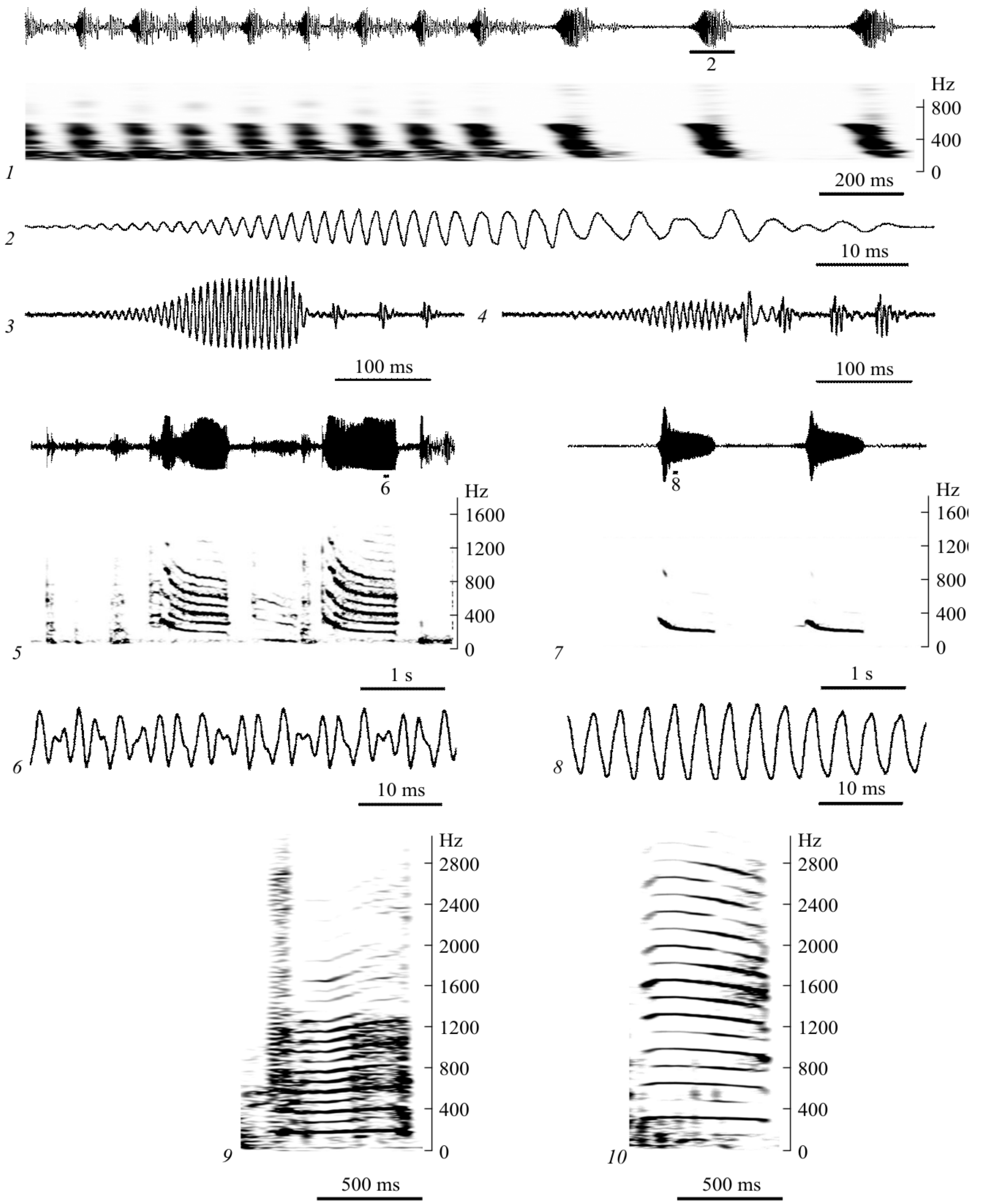

Fig. 8. Vibrational signals of Auchenorrhyncha: (*1*) *Igutettix oculatus*, oscillogram and sonogram at the same scale; (*2*) the wave shape in the signal of the same species; (*3, 4*) *Mileewa dorsimaculata*, fragments of signals of the same male recorded on different substrates; (*5–8*) *Sorhoanus hilaris*: (*5, 6*) and (*7, 8*) are signals of two different males from the same geographic locality; (*5, 7*) oscillogram and sonogram at the same scale; (*6, 8*) the wave shape in the signal; (*9, 10*) *Gargara genistae*, sonograms of signals recorded at 24°C (*9*) and at 30°C (*10*). The fragments of signals designated by numbers *2*, *6*, and *8* are shown in oscillograms under the same numbers.

(Fig. 4, *7*), *Phlogotettix cyclops* (Fig. 5, *3*), *Gargara genistae* (Fig. 7, *2*), and *Philaenus spumarius* (Linnaeus, 1758) (Fig. 6, *5*).

In our material, these four groups are represented by 27, 40, 13, and 20% of the species, respectively. Thus, species emitting signals with constant frequencies are in the minority (27%), whereas most representatives of Auchenorrhyncha reveal regular frequency modulations in their signals.

Modulation usually occurs within the range of 100–150 Hz, which may correspond to a twofold change in the frequency. The differences in the frequency of different parts of the signal in some species exceed 200 Hz: about 360 Hz in *Igutettix oculatus*, 240–280 Hz in *Aguriahana germari*, about 400 Hz in *Aglena ornata*, 240 Hz in *Cosmotettix paludosus* (Ball, 1899), 230–250 Hz in *Hebecephalus changai*, and 230–240 Hz in *Aphilaenus ikumae*.

When singing, nearly all the representatives of Auchenorrhyncha perform dorso-ventral movements with their abdomen synchronously with certain elements of the signal. In singing cicadas such movements may change the volume and, consequently, the resonant properties of the air sacs. According to some authors, it is in this way that frequency modulations of the signals are produced (Gogala et al., 2004). However, since small Auchenorrhyncha do not have abdominal air sacs, such movements in them may affect the tension and curvature of the tymbals or the apodemes to which the tymbal muscles are attached.

It should be noted that signal distortion in the substrate does not usually affect its frequency-temporal pattern, although the amplitude ratio of the signal components with different carrier frequencies may change even as the result of movements of the singing insect relative to the sensor, due to selective attenuation of certain frequencies (Fig. 8, *3–4*). However, individuals of the same species sometimes emitted signals clearly different both in the wave shape and in the number of harmonic components (Fig. 8, *5–8*; see also Tishechkin, 2007b). Although this phenomenon was not specially studied, it may result from resonance in the substrate.

Thus, over 70% of the species studied emit signals with regularly changing frequencies. Since such changes obviously hamper recognition of conspecific signals by their carrier frequency, this character is unlikely to play any significant role in most Auchenorrhyncha.

The Dependence of the Carrier Frequency of Pure-tone Signals on the Temperature

In order to estimate correctly the variation of signals depending on the temperature, one should compare the signals of the same individual recorded at different temperatures. The use of artificial heat sources, such as a filament bulb, is undesirable in this case because such sources form a steep temperature gradient within which the actual value is difficult to measure. The dependence of the frequency of pure-tone signals on the temperature was studied in *Gargara genistae*. We compared the signals of the same male recorded indoors at 24°C and outdoors at noon, at 30°C, with an interval of about 1 h; altogether, 4 males were studied. In all the cases, as the temperature grew by 6°C, the signal frequency (the first harmonic in the sonograms in Fig. 8, *9–10*) increased from 190–220 to 310–330 Hz, i.e., approximately by 1.5 times, and the intervals between the harmonics increased correspondingly.

Temperature-dependent variation in the pure-tone signals of singing cicadas was studied by the example of *Magicicada septendecim* (Linnaeus, 1758) from the group of American "periodical cicadas" (Young and Josephson, 1983). A single inflection of the ribbed tymbal was shown to produce one pulse consisting of several periods of sinusoidal waves. When the two tymbals worked in turns, the pulses partly merged into a continuous pure-tone signal with slight amplitude modulations, their period coinciding with the total frequency of contraction of the right and left tymbal muscles. The original assumption that each period of the sinusoid within a pulse might correspond to inflection of one rib of the tymbal, i.e., a single click in the pulse, was not confirmed. As the temperature grew by 15°C, the pulse repetition period was considerably reduced but the signal carrier frequency remained the same. Therefore, the cited authors concluded that this frequency was determined not by the frequency of muscle contraction but by the resonant properties of the tymbal itself and possibly of the abdominal air sacs.

A completely different situation was observed in *G. genistae*: the carrier frequency of the signal increased with temperature. We may therefore suggest that it was determined by the frequency of the tymbal muscle contraction, rather than by the resonant properties of any cuticular structures or air-filled cavities.

The Possibility of "Frequency Tuning" of Pure-tone Signals to the Parameters of the Substrate

The frequency responses of different stems are highly non-linear, the signal attenuation being the smallest within their optimum zones. For example, the frequency response of the stem of *Thesium bavarum* (Santalaceae) has two maxima at about 100–220 and 1700–2050 Hz; thus, the width of the frequency ranges optimal for communication will be 120 and 350 Hz, respectively (Michelsen et al., 1982, fig. 8).

In the study of two species of *Enchenopa* it was shown that the maxima of the frequency responses of the plant organs favored by the singing males occupied the ranges of about 50–170 and 200–500 Hz, whereas the signals of these species had the carrier frequencies of 140 and 340 Hz (McNett and Cocroft, 2008). As a result, the carrier frequency of each species was within the range of the lowest signal attenuation rate. Based on these data, the cited authors concluded that the possibility of "frequency tuning" to the parameters of the host plant of a particular species might be one of the adaptive traits of pure-tone signals.

In view of these findings, one may assume that the maxima of the frequency responses of stems of other plants will also occupy a frequency range of a similar width (i.e., 120–350 Hz). In this case, the frequency range of signals of at least some of the studied species will extend beyond the optimum zone of the substrate frequency response, due to frequency modulations in the signal.

According to our observations and the data of other researchers (De Vrijer, 1984), high acoustic activity of small Auchenorrhyncha in the temperate zone is preserved at temperatures ranging approximately from 20 to 35°C. Since the frequency of pure-tone signals changes with temperature, it cannot remain within the maximum of the stem frequency response when the temperature varies so widely. This is particularly true of signals with frequency modulation, since the range of this modulation may exceed the width of the substrate response optimum even at a constant temperature.

Besides, the group of species emitting pure-tone signals includes many polyphagous forms which develop on various plant species and can feed on stems as well as on stalks and large veins of leaves (in particular, most Cicadellini s. l.). Moving within the same plant or flying from stem to stem in the dense herbage, the singing male inevitably visits substrates with different frequency response parameters.

Finally, species associated with the same host plant and occurring on the same plant organs may emit signals with different frequencies. The most vivid example of this kind is given by the two species of *Gargara* studies by us: both species can develop on *Caragana arborescens* and mostly occur on young twigs, but their signal frequencies differ by almost 3 times (Fig. 9, *1–4*).

In view of the above, we can state that the coincidence between the carrier frequency of the signal of *Enchenopa* spp. and the maximum of the frequency response of their host plants appears to be particular case. Such coincidence would be impossible for a considerable part of the species studied by us, due to the presence of frequency modulations and temperature-related changes in the carrier frequency, and also due to the absence of strict preferences for particular species and organs of host plants.

Besides, if adaptation of Auchenorrhyncha to the physical properties of their host plants had occurred by "tuning" to the frequency response of the substrate, the signal frequency ranges would have become very narrow. In reality, however, most of the species studied emit signals which have regularly changing frequencies and sometimes include not only pure-tone but also noise fragments.

The Differences in the Frequency Patterns of Pure-tone Signals in the Sympatric Species of Auchenorrhyncha

It is known that in the assemblages of animals using acoustic communication, signals of different species may become separated by their frequencies (see, e.g., Sueur, 2002). In particular, in treehoppers of the *Enchenopa binotata* group the carrier frequencies of the signals of closely related species differ on average by 100–150 Hz (Rodríguez et al., 2006). It is the carrier frequency, rather than the amplitude-temporal pattern of the signal, that plays the key role in signal recognition by the conspecific female in these species.

We have compared the frequency patterns of signals in several pairs of species occurring on the same host plant or inhabiting the same biotope. It should be noted that in dense herbage, vibrational signals can be easily transmitted from stem to stem by contacts of both aerial and underground parts of plants; therefore, the insects can perceive one another's signals even if

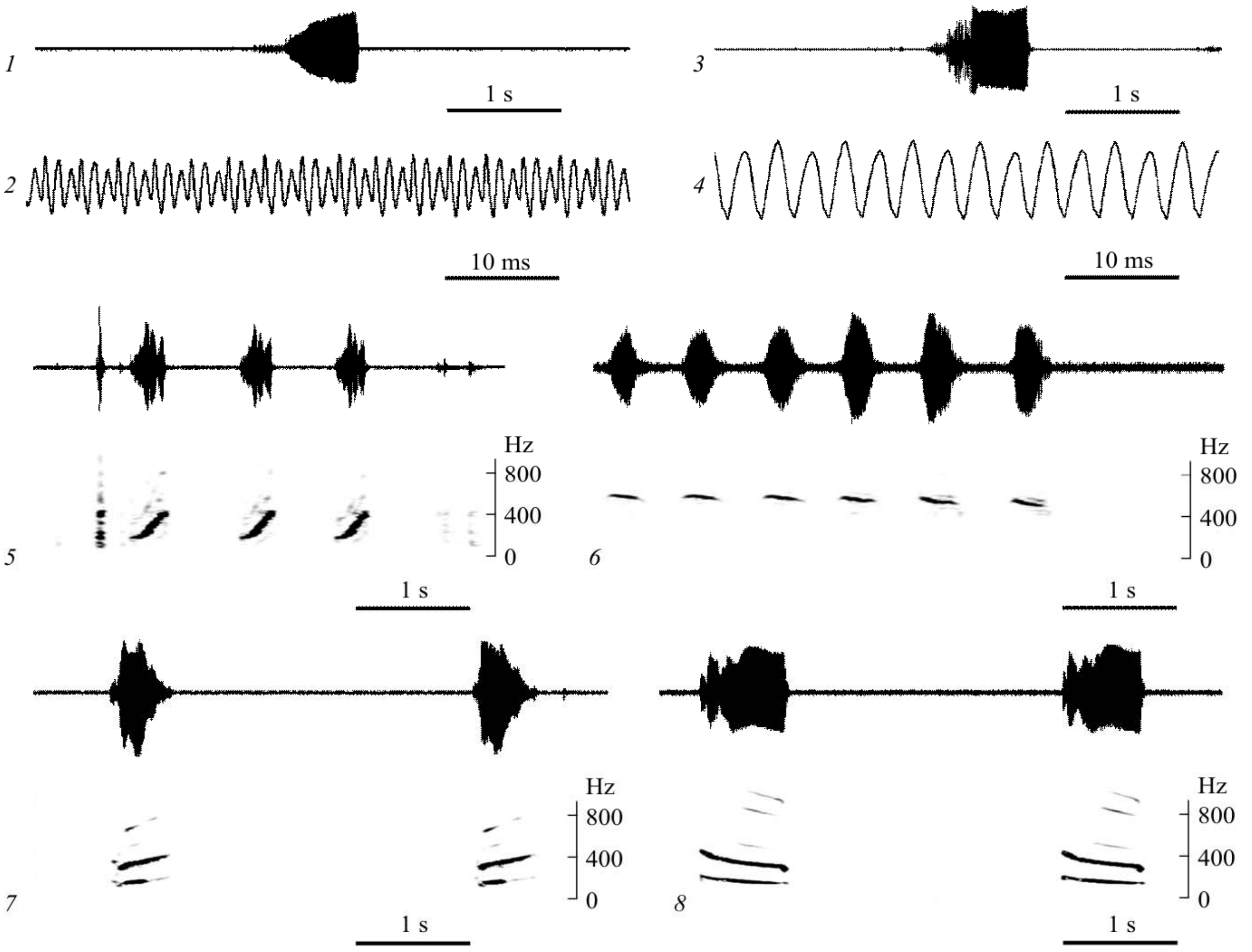

Fig. 9. Vibrational signals of Auchenorrhyncha: (*1, 2*) *Gargara mongolica*; (*3, 4*) *G. genistae*; (*5*) *Cosmotettix paludosus*; (*6*) *Sorhoanus xanthoneurus*; (*7*) *Drabescus vilbastei*; (*8*) *Ledra auditura* [(*1, 3*) total view of the signal; (*2, 4*) the wave shape in the signal; (*5–8*) oscillogram and sonogram at the same scale].

they are positioned on different plants (Tishechkin, 2011). It should also be noted that, since the signal frequency increases proportionally with temperature in all the species in the given biotope, temperature-related variation can hardly affect the signal recognition in this case.

The signals of two morphologically similar species of the genus *Gargara* (Membracidae) considered above have no reliable differences in their amplitude-temporal patterns, whereas their carrier frequencies differ by almost three times: 930–940 Hz in *G. mongolica* and about 330 Hz in *G. genistae* at 27–30°C (Fig. 9, *1–4*). Thus, in some species of Auchenorrhyncha the main species-specific character of the signal may be the carrier frequency, rather than the amplitude-temporal pattern.

The leafhoppers *Cosmotettix paludosus* and *Sorhoanus xanthoneurus* (Fieber, 1869) were collected on sedges (*Carex* spp.) in swamped areas within the Irkut river valley (Buryatia) (Tishechkin, 2009). In the former species the signal frequency increases gradually from about 180 to 420 Hz during the syllable, whereas in the latter the signal frequency is maintained at the mean level of about 600 Hz during the syllable and only slightly reduced by its end (Fig. 9, *5–6*).

The frequency ranges of the signals of *Drabescus vilbastei* and *Ledra auditura*, living on the Mongolian oak *Quercus mongolica* in the south of Primorskii Territory, overlap almost completely. At the same time, in *D. vilbastei* the frequency increases from the beginning to the end of the signal, whereas in *L. auditura* it decreases in the same manner (Fig. 9, *7–8*).

Since the signals of these two species are quite similar in their amplitude-temporal pattern, their frequency modulation becomes the main species-specific character.

These examples show that channels of vibrational communication of small Auchenorrhyncha can be separated by their carrier frequency or by the frequency modulation pattern, even though the signals of different species usually differ in their amplitude-temporal parameters as well. In species emitting signals with a complex frequency structure (such as *Evacanthus* spp., *Hecalus lineatus*, *Glossocratus foveolatus*, etc.), the frequency modulation pattern may also act as an additional character by which the conspecific signal can be more easily distinguished against the background of signals emitted by the numerous sympatric species.

The insects using vibrational communication face intense competition for the available communication channels. Even in European Russia, as many as 20–30 species of Auchenorrhyncha can often be found in the same biotope. Since each species has contacts with different sets of sympatric forms in different parts of its range, the total number of signals among which the conspecific calling signal has to be distinguished may be more than a hundred. Moreover, vibrational communication is much more common among insects than sound one: vibrational signals are emitted by many true bugs, psyllids, neuropterans, dipterans, and representatives of a number of other groups which compete with Auchenorrhyncha for the "acoustic niches." In this situation, recognition of the conspecific signal based not only on the amplitude-temporal pattern but also on the frequency pattern may significantly increase the efficiency of intraspecific communication.

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