

On the similarity of temporal pattern of vibrational calling signals in different species of Fulgoroidea (Homoptera: Auchenorrhyncha)

О сходстве временного рисунка вибрационных призывных сигналов у разных видов Fulgoroidea (Homoptera: Auchenorrhyncha)

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КЛЮЧЕВЫЕ СЛОВА: Auchenorrhyncha, Fulgoroidea, Delphacidae, вибрационная коммуникация, призывные сигналы, каналы связи, акустическая ниша.

ABSTRACT. Examples of similarity of calling signal temporal pattern in different species of Fulgoroidea are considered, possible reasons of this phenomenon are discussed. In all cases the similarity of signals occurs only in acoustically isolated forms occupying different acoustic niches. It is suggested that the signal temporal pattern is determined not only by phylogenetic relationships of the particular species, but also by its acoustic environment, i.e. by the presence or absence of sympatric forms producing songs with similar structure.

РЕЗЮМЕ. Рассмотрены примеры сходства временного рисунка призывных сигналов у разных видов Fulgoroidea, обсуждаются возможные причины этого явления. Во всех случаях сходство наблюдается только у акустически изолированных форм, занимающих разные акустические ниши. Предполагается, что временной рисунок сигнала определяется не только филогенетическими связями вида, но и его акустическим окружением, т.е. наличием или отсутствием симпатрических форм, издающих сигналы со сходной структурой.

In insects using acoustic communication for recognition and locating of potential mate interspecific differences in temporal pattern of calling signals provide main precopulatory barrier of reproductive isolation. For this reason calling signals (songs) as a rule differ distinctly even in most closely related, morphologically similar species. This makes acoustic analysis a useful tool for discrimination between cryptic species or for elucidation of taxonomic status of dubious forms. On the other hand, there is increasing evidence that temporal pattern of calling songs in different species sometimes can be almost identical. Such examples are known among grasshoppers (Orthoptera: Acrididae) [Bukhvalova, 2006],

jumping plant lice (Homoptera: Psyllinea) [Tishechkin, 2006, 2007a], and small Auchenorrhyncha (Homoptera) [Tishechkin, 2003, 2007b]. Special investigation of these cases showed that such species are always allopatric or have different ecological preferences and thus never come into acoustic interactions with each other.

In grasshoppers producing air-borne sounds the forms having similar song patterns are either allopatric or inhabit different biotopes [Bukhvalova, 2006]. In small Auchenorrhyncha and in jumping plant lice such species sometimes are formally sympatric, i.e. can be found in the same locality and biotope. However, they always dwell on different host plants and do not perceive the songs of each other, since vibrational signals cannot be transmitted from plant to plant without physical contact between them.

Among small Auchenorrhyncha, signals with uniform temporal pattern were presently described in certain Fulgoroidea and in a number of Paralimnini (Cicadellidae: Deltocephalinae). Considerable part of species of Paralimnini produce songs consisting of short syllables with simple structure [Tishechkin, 2007b]. The number of signal parameters which can vary is restricted to syllable duration and pulse repetition period. The latter has close values in different species; moreover, in certain cases pulses become almost indistinguishable because of distortions of signal during transmission via substrate. Syllable repetition period is very variable and depends much on ethological situation, i.e. presence or absence of receptive female or competing males, etc. Thus, this parameter for the most part is not species-specific. As a result, in species having close values of syllable duration calling signals become almost identical in their temporal patterns. This is the case in *Sorhoanus medius* (Mulsant et Rey, 1855) and *S. hilaris* (Melichar, 1900), *Diplocolenus frauenfeldi* (Fieber, 1869), *D. suttholli* Vilbaste,

1980 and *D. bohemani* (Zetterstedt, 1840) and in certain other Paralimnini [Tishechkin, 2007b].

In the most part of studied representatives of Fulgoroidea with the exception of Delphacidae and Caliscelidae calling signals are successions of short pulses following each other with constant intervals. For this reason signal temporal patterns occasionally are similar in different species. In representatives of Delphacidae the structure of calling signals is highly diverse. In a number of species signals consist of simple syllables, whereas in other ones these are prolonged complex phrases. Still, in spite of this diversity, signals of different species quite often have the

same general scheme of temporal pattern and occasionally are almost indistinguishable. In the present paper examples of similarity of signal pattern in certain groups of Fulgoroidea are discussed and illustrated.

Vibrational signals were registered by means of piezo-electric crystal gramophone cartridge connected to the microphone input of cassette recorder "Elektronika-302-1" or minidisk recorder Sony Walkman (models MZ-NH900 or MZ-RH910) via the custom-made matching amplifier. Signals of insects collected in Moscow Area were recorded in the laboratory; in other regions

Table. Data for recordings of calling signals of the studied species of Fulgoroidea
Таблица. Данные о записях призывных сигналов изученных видов Fulgoroidea

Species*	Locality	Air temperature during recording, °C
Family Cixiidae		
<i>Cixius nervosus</i> (L.)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	24–25
Family Issidae		
<i>Alloscelis vittifrons</i> (Ivanov)	South of European Russia, Rostov Area, Oblivskiy District, env. Sosnovy (=Oporny) vill. on Chir River.	30–31
Family Derbidae		
<i>Cedusa sarmatica</i> (Anufr.)	NW Caucasus, Krasnodar Province, env. Aderbievka vill. east of Gelendzhik Town.	27–30
<i>C. mesasiatica</i> (Dub.)	Kyrgyzstan, W Tien-Shan Mts., Chatkal'skiy Ridge, Sary-Chelekiy Nature Reserve, env. Arkit vill.	23–24
<i>C. ussurica</i> (Anufr.)	Russian Far East, Maritime Province, 30 km north of Chuguevka, env. Zametnoe vill.	28
Family Delphacidae		
<i>Criomorphus albomarginatus</i> (Curtis)	Moscow Area, Serpukhov District, env. Luzhki vill.	22
<i>Megamelus notula</i> (Germ.)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	20
<i>Stiroma bicarinata</i> (H.-S.)	Moscow Area, Mytishchi District, env. Pirogovo Town.	25–26
<i>Herbalima eforiae</i> (Dlab.)	Lower Volga Region, Dosang Railway Station about 60 km north of Astrakhan'.	26
<i>H. mongolica</i> (Kusn.)	E Siberia, Buryatia, Temnik River 4–5 km north of Selenduma Town.	23–24
<i>Eurybregma nigrolineata</i> Scott	Moscow Area, Serpukhov District, env. Luzhki vill.	20–21
<i>Javesella obscurella</i> (Boh.)	Moscow Area, Voskresensk District, env. Beloozerskiy Town.	22–24
<i>Struebingianella lugubrina</i> (Boh.)	Moscow Area, env. Naro-Fominsk Town.	26–27
<i>Metropis achnatheri</i> Em.	E Siberia, Buryatia, Selenga River 5 km north of Novoselenginsk Town.	32–34
<i>Dicranotropis hamata</i> (Boh.)	Moscow Area, Serpukhov District, env. Luzhki vill.	25–26
<i>Ribautodelphax bogdul</i> Dlab.	E Siberia, Buryatia, Irkut River valley west of Mondy vill. (about 80 km west of Kyren).	22–23
<i>R. angulosa</i> (Rib.)	Moscow Area, Mytishchi District, env. Pirogovo Town.	24
<i>R. albostrata</i> (Fieb.)	Moscow Area, Serpukhov District, env. Luzhki vill.	24–25
<i>R. flavicans</i> Vilb.	E Siberia, Buryatia, about 10 km east of Onokhoy.	23–24
<i>Muirodelphax aubei</i> (Perr.)	Lower Volga Region, Saratov Area, Krasnokutskiy District, env. Dyakovka vill.	23
<i>Acanthodelphax spinosa</i> (Fieb.)	Moscow Area, Serpukhov District, env. Luzhki vill.	25–26
<i>Xanthodelphax xantha</i> Vilb.	Altai Mts., S shore of Teletskoe Lake, mouth of Kyga River.	23
<i>Ditropsis flavipes</i> (Sign.)	Moscow Area, Serpukhov District, env. Luzhki vill.	26–26
<i>Falcotoya simulans</i> (Dlab.)	Lower Volga Region, Astrakhan' Area, Bogdinsko-Baskunchakskiy Nature Reserve.	30–31
<i>Megamelus flavus</i> (Crawford)	S Siberia, S Tyva, env. Erzin vill., the valley of Tes-Khem River.	23
<i>Metropis mayri</i> Fieb.	Moscow Area, Serpukhov District, env. Luzhki vill.	20–21
<i>Stiroma affinis</i> Fieb.	Altai Mts., S shore of Teletskoe Lake.	24

* Species are listed in the same order as on illustrations.

* Порядок перечисления видов соответствует иллюстрациям.

recordings were made under field conditions, usually, in a tent. Data on collecting sites and temperature during recording for signals presented on oscillograms are given in the Table. All specimens investigated are deposited in the collection of the Zoological Museum of M.V. Lomonosov Moscow State University.

As mentioned above, calling songs with simple and uniform structure occasionally are quite similar in different species. In Fulgoroidea, which signals are successions of short pulses following each other with more or less constant period this is not a rare case. Comparative analysis of signals of a sufficient number of species almost always allows revealing the pairs of non-related forms which signals are hardly distinguishable. It may be safely suggested that in these cases such resemblance is accidental. Undoubtedly, similarity of a general scheme of signal temporal pattern in different families of Fulgoroidea is a result of their phylogenetic relationship. Still calling songs of congeneric species as a rule differ from each other to a greater extent, than in such superficially similar forms. By way of illustration let us consider two species from different families, *Cixius nervosus* (Linnaeus, 1758) (Cixiidae) and *Alloscelis vittifrons* (Ivanov, 1885) (Issidae). Calling signals of both species are short successions of pulses (Figs 1–2 and 3–6). Signal duration as well as pulse repetition period have close values in both species. The shape of pulses cannot be used for discrimination between the signals of these species because it varies greatly depending upon physical properties of a substrate, i.e. particular stem or twig on which the insect sings (Figs 5–6). Since *C. nervosus* is a forest-dwelling species, whereas *A. vittifrons* inhabits steppes of Southern Ukraine and European Russia, evidently they do not come into acoustic interaction and never hear the signals of each other. Thus, the similarity of the signals is no barrier for successful intraspecific communication.

Calling songs of different species of *Cedusa* Fowler, 1904 (Derbidae) are prolonged successions of syllables (Figs 7–13). In certain cases shorter syllables occasionally alternate with longer ones (Figs 7–10). Duration of the song as a whole as well as a number of syllables, their repetition period and arrangement of shorter and longer ones vary greatly both within and between the songs, whereas a shape of syllables in different species is quite similar (Figs 8, 10–11 and 13). As a result, signals of three species studied sometimes are almost indistinguishable. It is reasonable to assume that in the case under consideration the similarity is a result of close relationships between species studied rather than a mere incident. As in the case with *C. nervosus* and *A. vittifrons*, the three species studied do not compete with one another for communication channels because they are allopatric. The range of *Cedusa sarmatica* (Anufriev, 1966) includes Crimea, North Caucasus and Transcaucasia, *C. mesasiatica* (Dubovsky, 1966) is widespread in Southern Kazakhstan and Central Asia, *C. ussurica* (Anufriev, 1968) was found only in Maritime Province (the Russian Far East).

Calling signals of Delphacidae are much more diverse and often have complicated temporal pattern. Still, examples of similarity can be found even among the signals with elaborate structure.

Comparative investigation of signals of Delphacinae allowed revealing four types of temporal pattern including from 2 to 8 species from our material each. In total, at least 19 of 32 representatives of the subfamily studied by the author (i.e. about 60%) can be attributed to one of the types. Signals of the remaining 13 species are unique in their pattern. They have no analogues in our material and can neither be attributed to one of four types with certainty, nor grouped into any additional type(s). In this paper we present oscillograms of only three such species; descriptions of signals of seven more ones (two species of *Chloriona* Fieber, 1866, *Delphax crassicornis* (Panzer, 1796), *Hyledelphax elegantula* (Boheman, 1847), and three species of *Javesella* Fennah, 1963) can be found in Tishechkin [2003].

The first type includes signals consisting of short discrete syllables following each other with irregular intervals (Figs 14–23). Signals of this type were recorded in *Criomorphus albomarginatus* (Curtis, 1833), *Megamelus notula* (Germar, 1830), *Stiroma bicarinata* (Herrich-Schäffer, 1835), *Herbalima eforiae* (Dlabola, 1961) and *H. mongolica* (Kusnezov, 1929). As a rule syllables begin quietly reaching maximum intensity near the middle. Duration of syllables varies from about 150 up to 250–300 ms in all species. In *M. notula* and *S. bicarinata* signals sometimes are almost identical (Figs 16–17 and 18–19). On the other hand, differences between two species of *Herbalima* Emeljanov, 1972 are more pronounced (Figs 20–21 and 22–23).

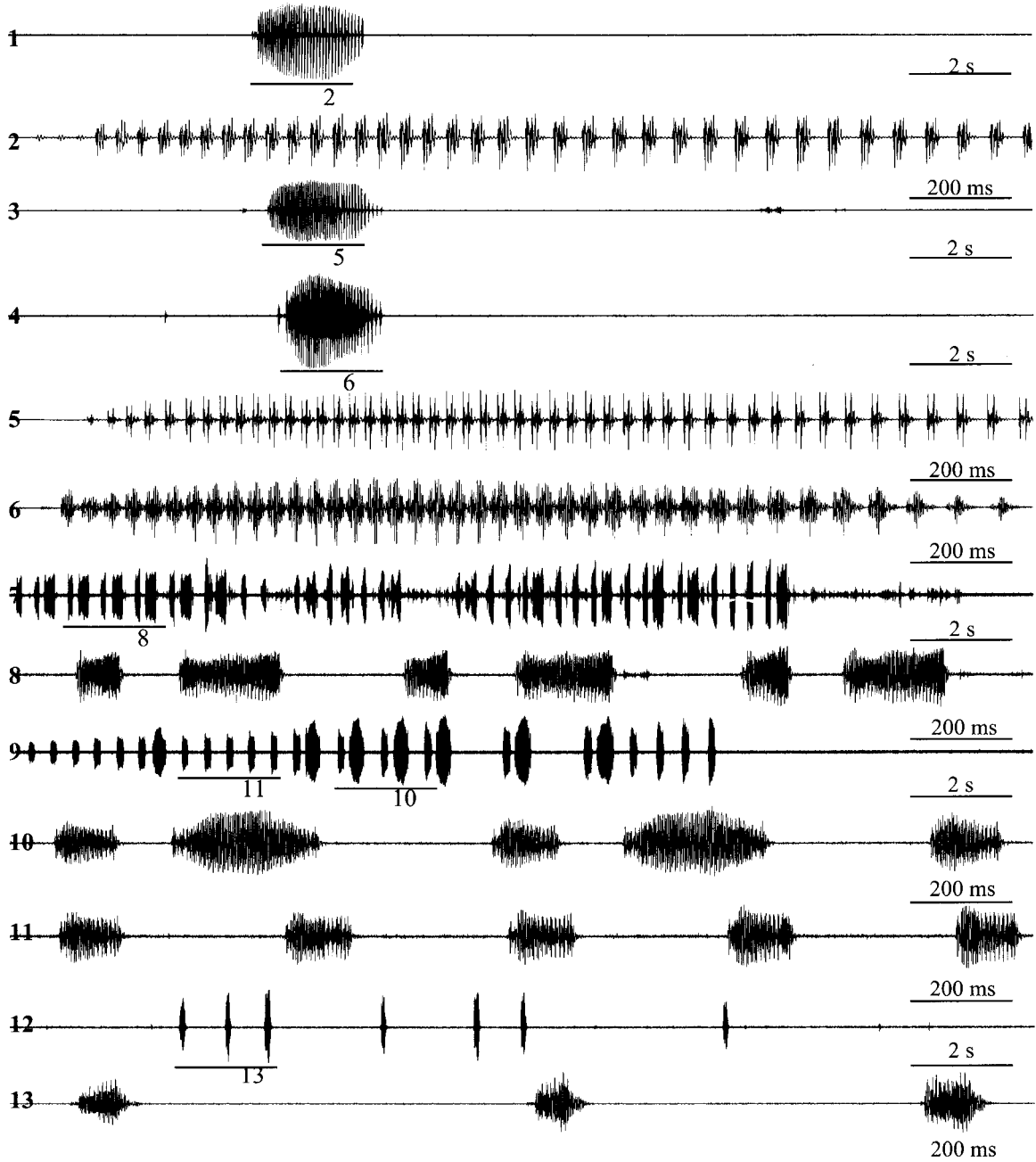
Signals of the second type are echemes consisting of regularly repeated uniform syllables having almost the same temporal pattern as in the songs of the previous type (Figs 24–27). Signals with such structure were recorded in *Javesella obscurella* (Boheman, 1847) and *Eurybregma nigrolineata* Scott, 1875. In the former species both echemes and syllables usually are somewhat shorter than in the latter one, but in certain cases their signals are quite similar.

Calling signals of *Struebingianella lugubrina* (Boheman, 1847), *Metropis achnatheri* Emelyanov, 1964, *Dicranotropis hamata* (Boheman, 1847), *Ribautodelphax bogdul* Dlabola, 1968, *R. angulosa* (Ribaut, 1953), *R. albostrata* (Fieber, 1866), *R. flavicans* Vilbaste, 1965, and *Muirodelphax aubei* (Perris, 1857) belong to the third type (Figs 28–44). These are phrases, each consisting of a short succession of syllables, followed by more or less prolonged monotonous fragment. Usually phrases follow each other with irregular intervals, but in *S. lugubrina* and *M. achnatheri* calling songs quite often consist of a train of phrases repeated with constant period. Signals of different species within this type differ from each other mainly in duration of the components of a phrase and in the shape of syllables in the initial part. In representatives of *Ribautodelphax* Wagner, 1963 and in *M. aubei* signals are most similar with each other, moreover in *R. flavicans* and *M. aubei*

the patterns of phrases are almost identical (Figs 41–42 and 43–44).

Signals of the fourth type in general structure are similar with these from the third one, but typically have more complex pattern of syllables in the first part of the

phrase and somewhat longer pulses repetition period in the second one. The type includes the songs of four species (Figs 45–54). In *Acanthodelphax spinosa* (Fieber, 1866), *Xanthodelphax xantha* Vilbaste, 1965, and *Ditropsis flavipes* (Signoret, 1865) the song as a rule

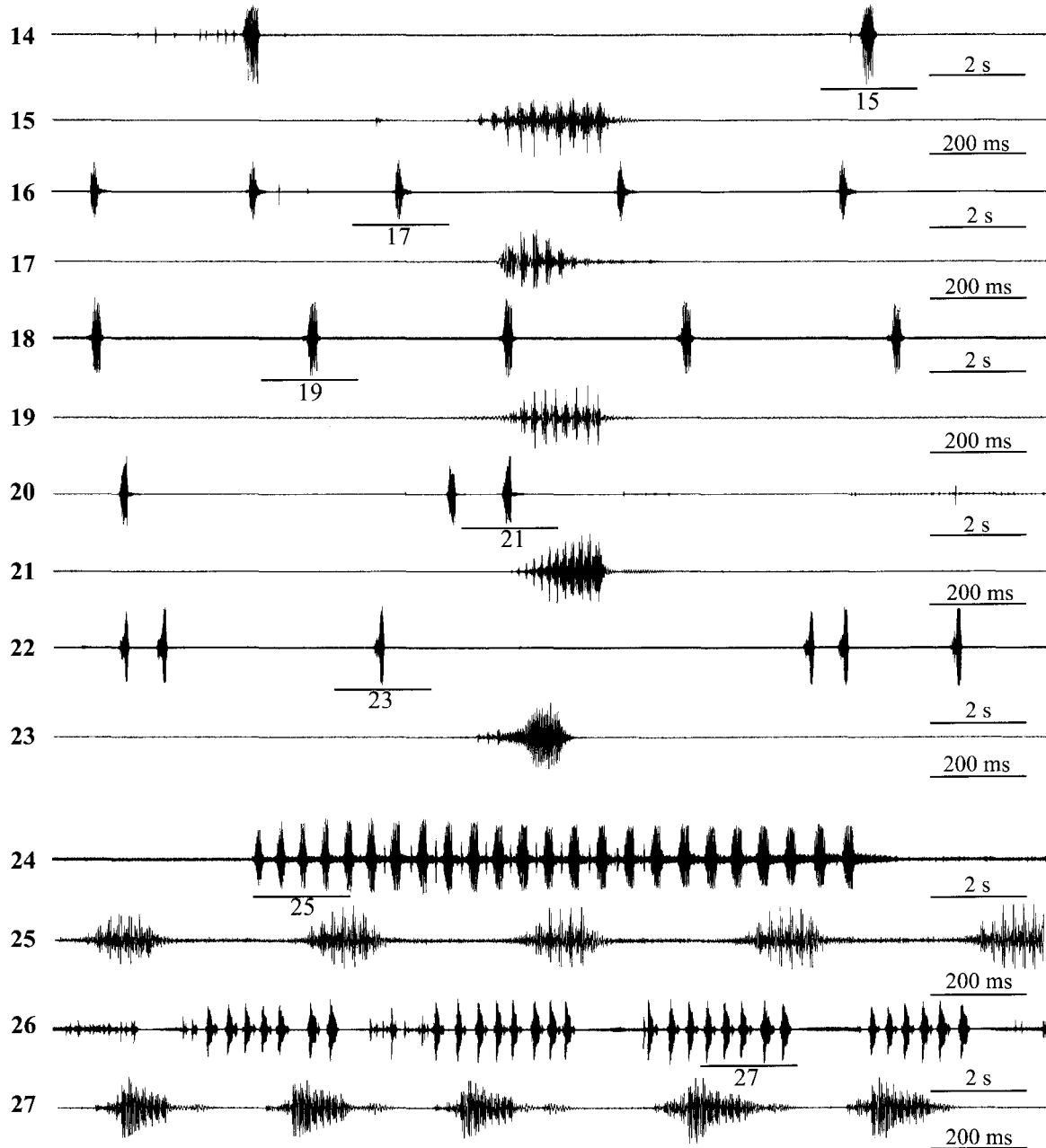


Figs 1–13. Oscillograms of calling signals of representatives of Fulgoroidea: 1–2 — *Cixius nervosus* (Cixiidae); 3–6 — *Alloscelis vittifrons* (Issidae); 7–8 — *Cedusa sarmatica* (Derbidae); 9–11 — *C. mesasiatica*, 12–13 — *C. ussurica*. Faster oscillograms of the parts of songs indicated as 2, 5–6, 8, 10–11 and 13 are given under the same numbers.

Рис. 1–13. Осциллограммы призывных сигналов представителей Fulgoroidea: 1–2 — *Cixius nervosus* (Cixiidae); 3–6 — *Alloscelis vittifrons* (Issidae); 7–8 — *Cedusa sarmatica* (Derbidae); 9–11 — *C. mesasiatica*, 12–13 — *C. ussurica*. Фрагменты сигналов, помеченные цифрами 2, 5–6, 8, 10–11 и 13, представлены при большей скорости развёртки на осциллограммах под такими же номерами.

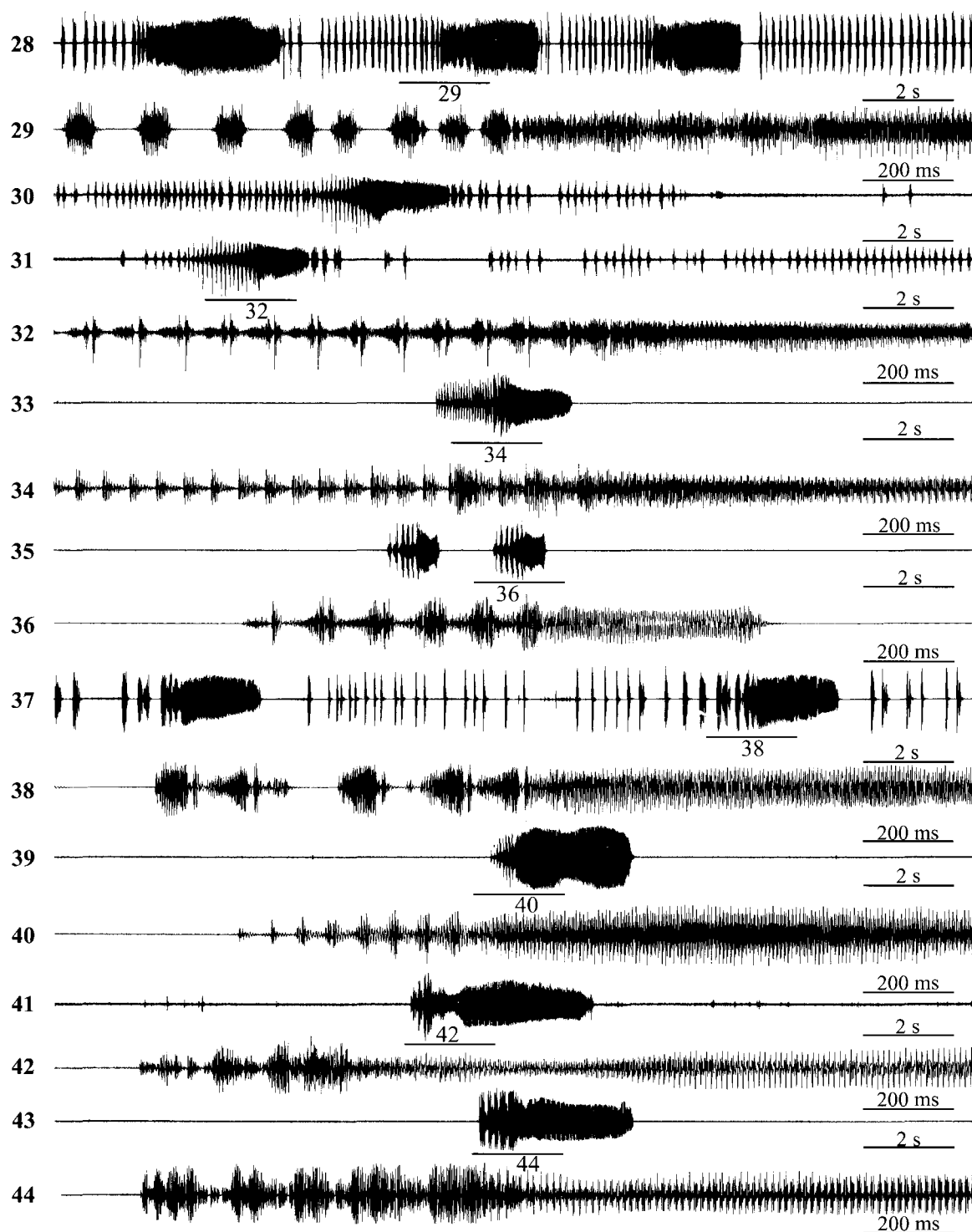
consists of a train of phrases (Figs 45, 47 and 50), but in the last two ones single phrases were occasionally recorded as well (Fig. 48). In *Falcotoya simulans* (Dlabola, 1958) phrases follow each other with prolonged irregular intervals (Figs 53–54).

Undoubtedly, the types described are artificial groups. The boundaries between them are a matter of convention. As new information on planthopper signals will be available, they will possibly shift. Segregation of different types only means that the signals with similar



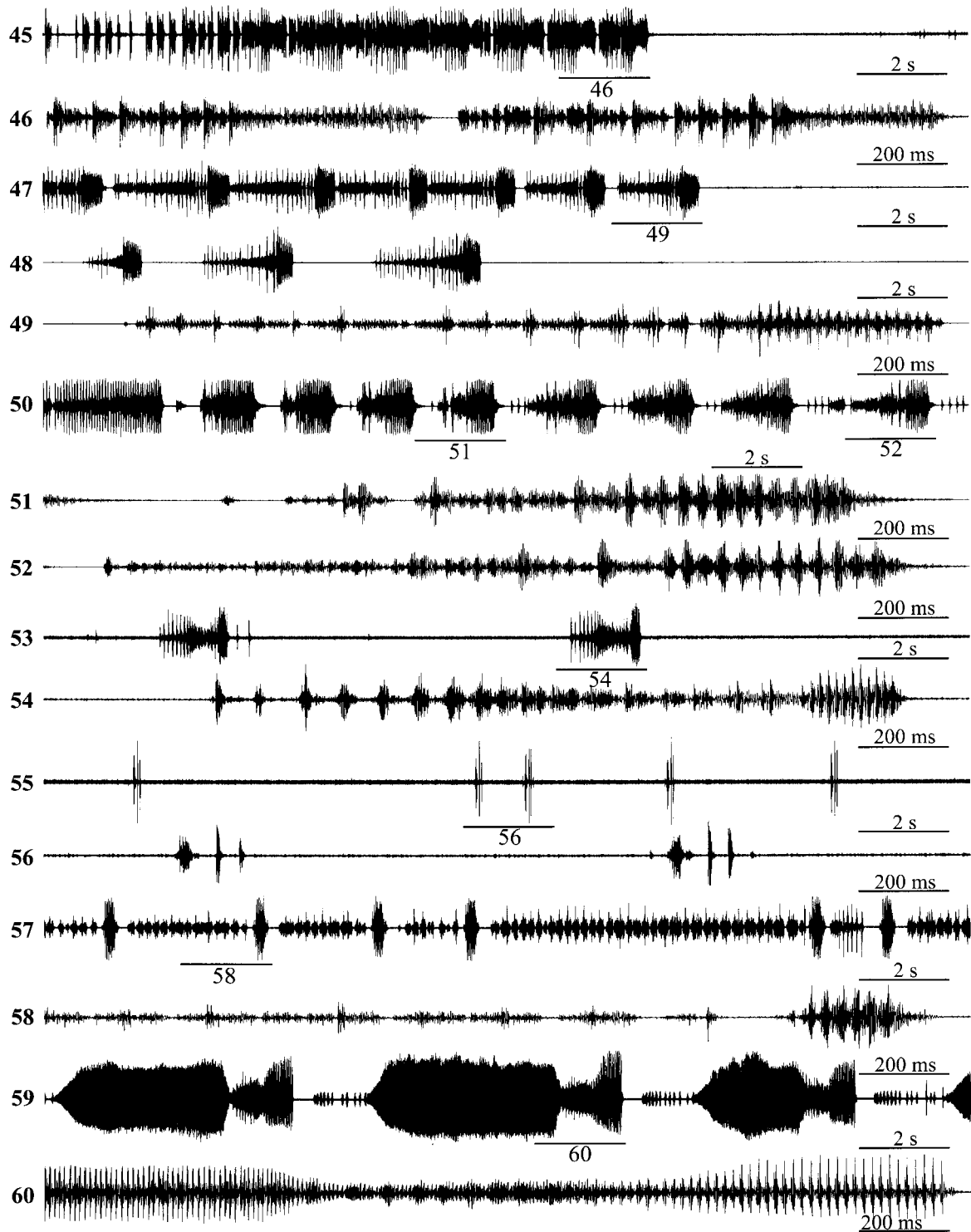
Figs 14–27. Oscillograms of calling signals of planthoppers (Delphacidae): 14–15 — *Criomorphus albomarginatus*; 16–17 — *Megamelus notula*; 18–19 — *Stiroma bicarinata*; 20–21 — *Herbalima eforiae*; 22–23 — *H. mongolica*; 24–25 — *Eurybregma nigrolineata*; 26–27 — *Javesella obscurella*. Faster oscillograms of the parts of songs indicated as 15, 17, 19, 21, 23, 25 and 27 are given under the same numbers.

Рис. 14–27. Осциллограммы призывных сигналов Delphacidae: 14–15 — *Criomorphus albomarginatus*; 16–17 — *Megamelus notula*; 18–19 — *Stiroma bicarinata*; 20–21 — *Herbalima eforiae*; 22–23 — *H. mongolica*; 24–25 — *Eurybregma nigrolineata*; 26–27 — *Javesella obscurella*. Фрагменты сигналов, помеченные цифрами 15, 17, 19, 21, 23, 25 и 27, представлены при большей скорости развёртки на осциллограммах под такими же номерами.



Figs 28–44. Oscillograms of calling signals of planthoppers (Delphacidae): 28–29 — *Strucbingianella lugubrina*; 30–32 — *Metropis acbmatberi*; 33–34 — *Dicranotropis hamata*; 35–36 — *Ribautodelphax bogdul*; 37–38 — *R. angulosa*; 39–40 — *R. albostrata*; 41–42 — *R. flavicans*; 43–44 — *Muirodelphax aubei*. Faster oscillograms of the parts of songs indicated as 29, 32, 34, 36, 38, 40, 42 and 44 are given under the same numbers.

Рис. 28–44. Осциллограммы призывных сигналов Delphacidae: 28–29 — *Strucbingianella lugubrina*; 30–32 — *Metropis acbmatberi*; 33–34 — *Dicranotropis hamata*; 35–36 — *Ribautodelphax bogdul*; 37–38 — *R. angulosa*; 39–40 — *R. albostrata*; 41–42 — *R. flavicans*; 43–44 — *Muirodelphax aubei*. Фрагменты сигналов, помеченные цифрами 29, 32, 34, 36, 38, 40, 42 и 44, представлены при большей скорости развёртки на осциллограммах под такими же номерами.



Figs 45–60. Oscillograms of calling signals of planthoppers (Delphacidae): 45–46 — *Acanthodelphax spinosa*; 47–49 — *Xanthodelphax xantha*; 50–52 — *Ditropsis flavipes*; 53–54 — *Falcotoya simulans*; 55–56 — *Megamelus flavus*; 57–58 — *Metropsis mayri*; 59–60 — *Stiroma affinis*. Faster oscillograms of the parts of songs indicated as 46, 49, 51–52, 54, 56, 58 and 60 are given under the same numbers.

Рис. 45–60. Осциллограммы призывных сигналов Delphacidae: 45–46 — *Acanthodelphax spinosa*; 47–49 — *Xanthodelphax xantha*; 50–52 — *Ditropsis flavipes*; 53–54 — *Falcotoya simulans*; 55–56 — *Megamelus flavus*; 57–58 — *Metropsis mayri*; 59–60 — *Stiroma affinis*. Фрагменты сигналов, помеченные цифрами 46, 49, 51–52, 54, 56, 58 и 60, представлены при большей скорости развёртки на осциллограммах под такими же номерами.

scheme of temporal pattern in different species of Delphacinae actually exist. Since this phenomenon is not a rare case, evidently such similarity is not accidental.

As is seen from oscillograms presented, the structure of calling signals does not always correlate with relationships between different species. True enough, in all studied species of *Ribautodelphax* including west-european forms [den Bieman, 1986] signals are quite similar and differ from each other mainly in quantitative parameters (Figs 35–42). This is also the case in two species of *Herbalima* (Figs 20–23). On the other hand, signals of studied species of *Stiroma* Fieber, 1866 bear no resemblance to each other (Figs 18–19 and 59–60). In *M. notula* and *M. flavus* (Crawford, 1914) (Figs 16–17 and 55–56) as well as in *M. achnatheri* and *M. mayri* Fieber, 1866 (Figs 30–32 and 57–58) calling songs are also quite different. High diversity of signal patterns is observed in the genus *Javesella* [de Vrijer, 1986; Tishechkin, 2003].

At the same time the cases of similarity of calling signals in species from different genera are not rare. Among species producing signals of the first type (syllables repeated with irregular period) these are *M. notula*, *S. bicarinata* and *H. eforiae* (Figs 16–21). They never inhabit the same biotope, because the first species feeds on sedges (*Carex* spp.) growing in bogs and on river banks, the second one dwells on grasses on glades and forest edges in forest zone and the third lives on saline lands and salted meadows in steppes and semi-deserts.

Signals of *R. flavicans* and *M. aubei* are also almost identical in spite of the fact that they are rather complex phrases (Figs 41–44). The former species occurs in South Siberia and in the Russian Far East, whereas the range of the latter one includes Western Europe, Ukraine, European Russia, South Urals, Caucasus, Transcaucasia, Kazakhstan and Central Asia; record from Mongolia [Dlabola, 1967] was not confirmed by Emelyanov [1982]. Thus, these two species are evidently allopatric and never come into acoustic interactions.

Songs of *M. achnatheri* and *D. hamata* in certain cases are also quite similar (Figs 31–32 and 33–34); certain differences in the shape of syllables or pulses in the first part of phrase (Figs 32, 34) is of no concern since it depends upon the properties of a substrate (see Figs 5–6 as an illustration). These species are partly sympatric, still they hardly can occur in the same biotope because the former one is monophagous on *Achnatherum splendens* (Trin.) Nevski, 1937 (Poaceae) growing only in open dry habitats (steppes, semideserts, saline lands), whereas the latter feeds on mesophilious gramineous vegetation on forest edges, glades, etc.

Groups of genera formed basing on signal similarity are in contradiction with traditional order of genera. For instance, *Eurybregma* Scott, 1875, *Metropis* Fieber, 1866 and *Stiroma* as a rule follow one after another in keys and check-lists [Logvinenko, 1975; Emelyanov, 1982; Anufriev & Emelyanov, 1988], still the signals of the studied representatives of these genera are dissimilar. The genera *Ribautodelphax*, *Struebingianella* Wag-

ner, 1963 and *Javesella* are also placed together by certain authors [Emelyanov, 1982; Anufriev & Emelyanov, 1988], still in two former ones signals belong to the third type (phrases consisting of succession of syllables, followed by monotonous fragment), whereas in the latter genus signal patterns are different. The same is true of *Falcotoya* Fennah, 1969 (Figs 53–54) and *Criomorphus* Curtis, 1833 (Figs 14–15) (placed one near another in [Logvinenko, 1975]), *Ditropsis* Wagner, 1963 (Figs 50–52) and *Criomorphus* (Figs 14–15) (the former follows the latter in Emelyanov [1982]), etc.

Thus, phylogenetic relationships in Fulgoroidea can be traced in acoustic characters only within certain genera (e.g. *Cedusa* from Derbidae, *Ribautodelphax* and *Herbalima* from Delphacidae), but not between them. By contrast, in species from different genera and even from different families calling signals sometimes are similar, whereas in congeneric species their patterns quite often are completely unlike each other. It is probable that a number of kinds of motorial programs controlling the working of timbals (i.e. contractions of tymbal muscles) appeared at early stages of evolution of planthoppers. In sympatric forms producing similar signals these programs diverged and substantially changed due to competition for communication channels (acoustic niches). If the acoustic niche of any species remained unoccupied by other ones, his motorial program and, consequently, signal pattern remained unchanged in spite of evolution of other characters (biochemical, morphological, etc.). As a result, temporal patterns of calling songs occasionally remain quite alike in morphologically different forms. Similar hypothesis concerning calling songs of grasshoppers (Orthoptera: Acrididae: Gomphocerinae) has recently been proposed by Savitsky [2007].

To summarize briefly, the similarity of calling signal temporal patterns in different species can result from at least three different reasons. First is accidental resemblance of signals having simple and uniform structure in forms from highly diverged phylogenetic lines, e.g. from non-related families. Second reason is close relation between species; this is usually the case in congeneric ones. The third reason, apparently, is retaining of the same motorial program of timbals in species diverged in other characters, including morphological ones. Anyway, in all cases the similarity of signals occurs only in acoustically isolated forms occupying different acoustic niches. Thus, signal temporal pattern is determined not only by phylogenetic relationships of the species, but also by its acoustic environment, i.e. by the presence or absence of sympatric forms producing similar signals.

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