

Comparison of interspecific differences in coloration, morphology, and male calling signal patterns in two genera of *Idiocerini* (Homoptera: Cicadellidae: Eurymelinae)

Сравнение межвидовых различий в окраске, морфологии и паттернах призывных сигналов самцов в двух родах *Idiocerini* (Homoptera: Cicadellidae: Eurymelinae)

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KEY WORDS: Homoptera, Cicadellidae, *Idiocerini*, *Populicerus*, *Idiocerus*, morphology, coloration, vibrational signals, diagnostic traits.

КЛЮЧЕВЫЕ СЛОВА: Homoptera, Cicadellidae, *Idiocerini*, *Populicerus*, *Idiocerus*, морфология, окраска, вибрационные сигналы, диагностические признаки.

ABSTRACT. Comparison of interspecific differences in coloration, morphology, and male calling signals in six species of *Populicerus* and three species of *Idiocerus* revealed similar patterns. Species within each genus, with the exception of *P. ambigenus*, are almost indistinguishable by the shape of male genitalia, differ only partly by the shape of the abdominal apodemes, but are easily distinguishable by coloration. Male calling signals in different species of *Idiocerus* are distinctly different; in *Populicerus*, they are more similar, and in some species are almost indistinguishable. All species studied are reproductively isolated due to geographic allopatry, different host specialization, or, in case of overlapping ranges and the same host, due to differences in calling signal temporal patterns. Thus, some leafhopper taxa distinctly differ from each other only in coloration, but are different biological species in spite of similar shape of male genitalia, abdominal apodemes and, occasionally, even of male calling signal patterns. In leafhopper taxonomy, such cases should be taken into account when clarifying the status of dubious forms of species rank.

РЕЗЮМЕ. Сравнение межвидовых различий в окраске, морфологии и временном рисунке призывных сигналов самцов у шести видов *Populicerus* и трёх видов *Idiocerus* выявило сходные закономерности. Виды в пределах каждого рода, за исключением *P. ambigenus*, практически неразличимы по

строению гениталий самца, лишь частично различаются по форме брюшных аподем, но легко различимы по окраске. Призывные сигналы самцов у разных видов *Idiocerus* отчётливо различаются по временному паттерну; у *Populicerus* они более схожи, а у некоторых видов почти неразличимы. Все изученные виды репродуктивно изолированы за счёт географической аллопатрии, разной кормовой специализации или, в случае симпатрии и обитания на одном и том же кормовом растении, за счёт различий в паттерне призывных сигналов. Таким образом, некоторые таксоны цикадок могут отчётливо различаться только по окраске, но, несмотря на сходство гениталий и аподем, а иногда даже призывных сигналов самцов, представляют собой разные биологические виды. В систематике цикадовых такие случаи следует учитывать при выяснении статуса сомнительных форм видového ранга.

Introduction

Typically, in leafhoppers (Homoptera: Cicadellidae), genera and long-diverged species distinctly differ in external appearance, primarily, in coloration. More closely related species in most cases are externally similar, but usually differ in the shape of male genitalia and abdominal apodemes. Also, as a rule, closely related species, even almost indistinguishable in the shape of genitalia, differ in the temporal pattern of the male

calling signals. This is completely consistent with the assumption that in the process of speciation, the differences in the specific mate recognition system (SMRS), i. e. in the signal pattern, arise first. Then differences in structures directly related to copulation and to the signal producing, i.e. in the shape of genitalia and abdominal apodemes, respectively, evolve. Finally, differences in coloration and external morphology appear. This is also reflected in practical taxonomic work. Identification of easily distinguishable leafhopper species is possible based on external appearance and coloration, for identification of closely related species investigation of genitalia is necessary, and for recognition of cryptic species or for clarifying the taxonomic status of dubious forms acoustic analysis is used.

However, exceptions to this rule are also known. Among leafhoppers, almost identical calling signals in congeneric species differing in coloration or/and genitalia shape were described in *Limotettix* Van Duzee, 1894 [Tishechkin, 2019a], *Macropsis* Lewis, 1836 [Tishechkin, 2019b], and in several genera of Paralimnini [Tishechkin, 2007]. In other insect taxa, such examples are known, inter alia, in *Reptalus* Emeljanov, 1971 (Homoptera: Cixiidae) [Emelyanov, Tishechkin, 2012], *Cicadetta* Kolenati, 1857 (Homoptera: Cicadidae) [Popov, 1998], and *Euchorhippus* Tarbinskii, 1926 (Orthoptera, Acrididae) [Ragge, Reynolds, 1984].

From a theoretical point of view, such exceptions are interesting, since they demonstrate that in certain cases speciation can occur without divergence of SMRS. Such forms with similar SMRS are good illustrations of the recognition species concept proposed in a number of works by Paterson [e. g., Lambert, Paterson, 1984; Paterson, 1985]. According to Paterson, species are “groups of organisms which are tied together by a

common *Specific-Mate Recognition System*” [Lambert, Paterson, 1984: 504]. The main idea of his concept is that the primary function of SMRS is a finding conspecific mate and, thus, providing conspecific fertilization. Providing precopulatory reproductive barrier, i. e. isolation from heterospecific individuals is a secondary function, which in some cases may not be realized at all. In the above examples, SMRS performs only its recognition function, but in principle cannot provide interspecific isolation due to the similarity of signal patterns.

In taxonomic practice, such examples should be taken into account when clarifying the status of dubious forms. If reproductive isolation is provided not by differences in SMRS, but by other factors, closely related taxa can be similar in signal patterns or/and in the genitalia shape, but nevertheless may represent good biological species.

Below we describe examples of good species distinctly differing in coloration, but similar in male genitalia shape and, partially, in shape of male abdominal apodemes and calling signal patterns in two genera of Idiocerini (Homoptera: Cicadellidae: Eurymelinae), *Populicerus* Dlabola, 1974 and *Idiocerus* Lewis, 1834.

Material and methods

Leafhopper vibrational calling signals were recorded by means of portable recording equipment consisting of a piezocrystal gramophone cartridge GZP-311 connected to the microphone input of a cassette recorder Elektronika-302-1 (before 2005), minidisk recorder Sony Walkman MZ-NH900 (2005–2016), or Roland R-05 wave/mp3 recorder (since 2017) via a custom-made matching amplifier. For recording, a twig of the host

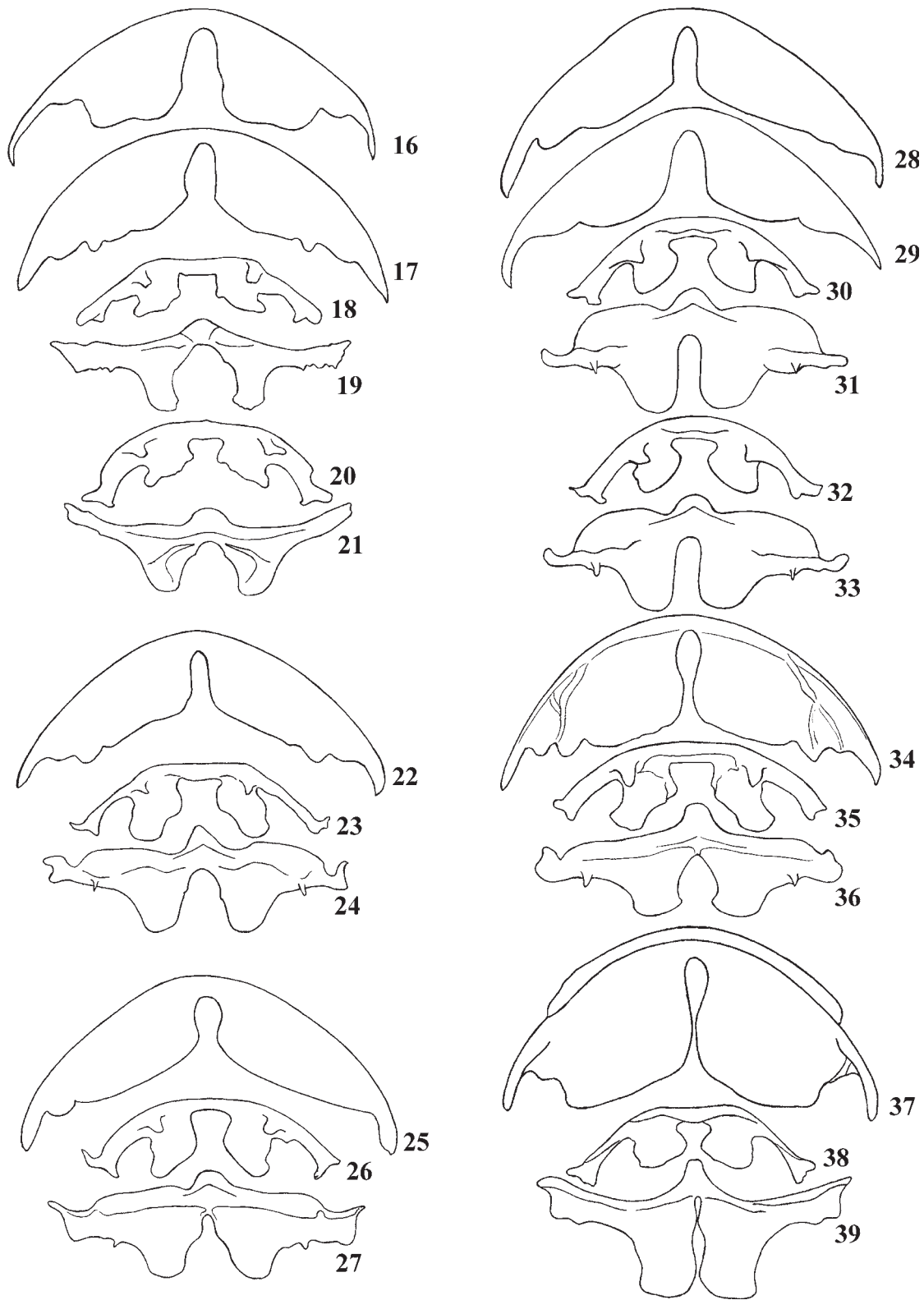
Table. Data for recordings of calling signals of the studied species of Idiocerini.
Таблица. Данные о записях призывных сигналов изученных видов Idiocerini.

Species	Locality	Air temperature during recording, °C
<i>Populicerus confusus</i> (Fl.)	Russia, Moscow Oblast, Voskresensk District, env. Beloozersky Town, from <i>Salix cinerea</i> L.	21–24
<i>P. albicans</i> (Kbm.)	Same locality, from <i>Populus alba</i> L.	25
<i>P. populi</i> (L.)	Same locality, from <i>P. tremula</i> L.	23–24
<i>P. nitidissimus</i> (H.-S.)	Same locality, from <i>P. nigra</i> L.	25–27
<i>P. laminatus</i> (Fl.)	Russia, Moscow Oblast, Serpukhov District, env. Luzhki Village, from <i>P. tremula</i> .	19–20
<i>P. ambigenus</i> (Dub.)	Kyrgyzstan, Central Tien Shan, the Dzhungal River Valley E of Chaek, from <i>Salix</i> sect. <i>Helix</i> (Figs 91, 107).	26
	Kyrgyzstan, Alay Mtn. Range, the Kurshab River Valley ca. 10 km NW of Gul'cha Town, from <i>S. alba</i> L. (Figs 92, 108–109).	24
<i>Idiocerus lituratus</i> (Fall.)	Russia, Moscow Oblast, Voskresensk District, env. Beloozersky Town, from <i>S. cinerea</i> .	23–24 (Figs 110, 112) 28 (Figs 111, 113)
<i>I. herrichii</i> (Kbm.)	Same locality, from <i>S. euxina</i> I.V. Belyaeva.	28–29
<i>I. stigmatalis</i> (Lew.)	Russia, Moscow Oblast, the Ucha River S of Pushkino Town, from <i>S. euxina</i> .	24–25



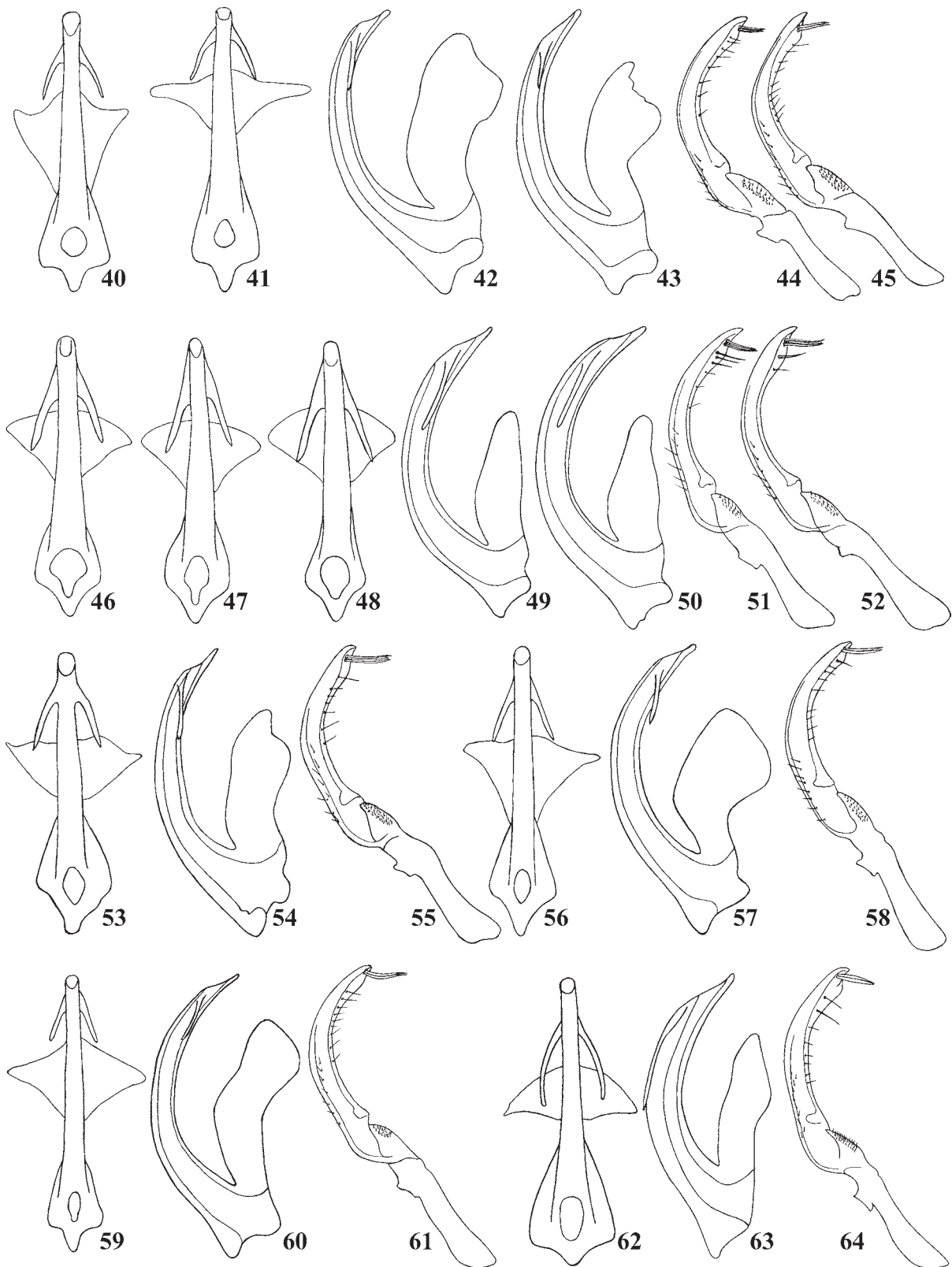
Figs 1–15. Idiocerini, dorsal view. 1–2 — *Populicerus confusus*; 3–4 — *P. albicans*; 5–6 — *P. populi*; 7–8 — *P. nitidissimus*; 9–10 — *P. laminatus*; 11–12 — *P. ambigenus*; 13 — *Idiocerus lituratus*; 14 — *I. herrichii*; 15 — *I. stigmaticalis*.

Рис. 1–15. Виды трибы Idiocerini, сверху. 1–2 — *Populicerus confusus*; 3–4 — *P. albicans*; 5–6 — *P. populi*; 7–8 — *P. nitidissimus*; 9–10 — *P. laminatus*; 11–12 — *P. ambigenus*; 13 — *Idiocerus lituratus*; 14 — *I. herrichii*; 15 — *I. stigmaticalis*.



Figs 16–39. Male abdominal apodemes of species of *Populicerus*. 16–21 — *P. confusus*; 22–24 — *P. populi*; 25–27 — *P. laminatus*; 28–33 — *P. albicans*; 34–36 — *P. nitidissimus*; 37–39 — *P. ambigenus*; 16–17, 22, 25, 28–29, 34, 37 — apodemes of the 3rd tergum; 18, 20, 23, 26, 30, 32, 35, 38 — same, 1st sternum; 19, 21, 24, 27, 31, 33, 36, 39 — same, 2nd sternum.

Рис. 16–39. Аподемы брюшных сегментов самцов *Populicerus*. 16–21 — *P. confusus*; 22–24 — *P. populi*; 25–27 — *P. laminatus*; 28–33 — *P. albicans*; 34–36 — *P. nitidissimus*; 37–39 — *P. ambigenus*; 16–17, 22, 25, 28–29, 34, 37 — аподемы III тергита; 18, 20, 23, 26, 30, 32, 35, 38 — аподемы I стернита; 19, 21, 24, 27, 31, 33, 36, 39 — аподемы II стернита.

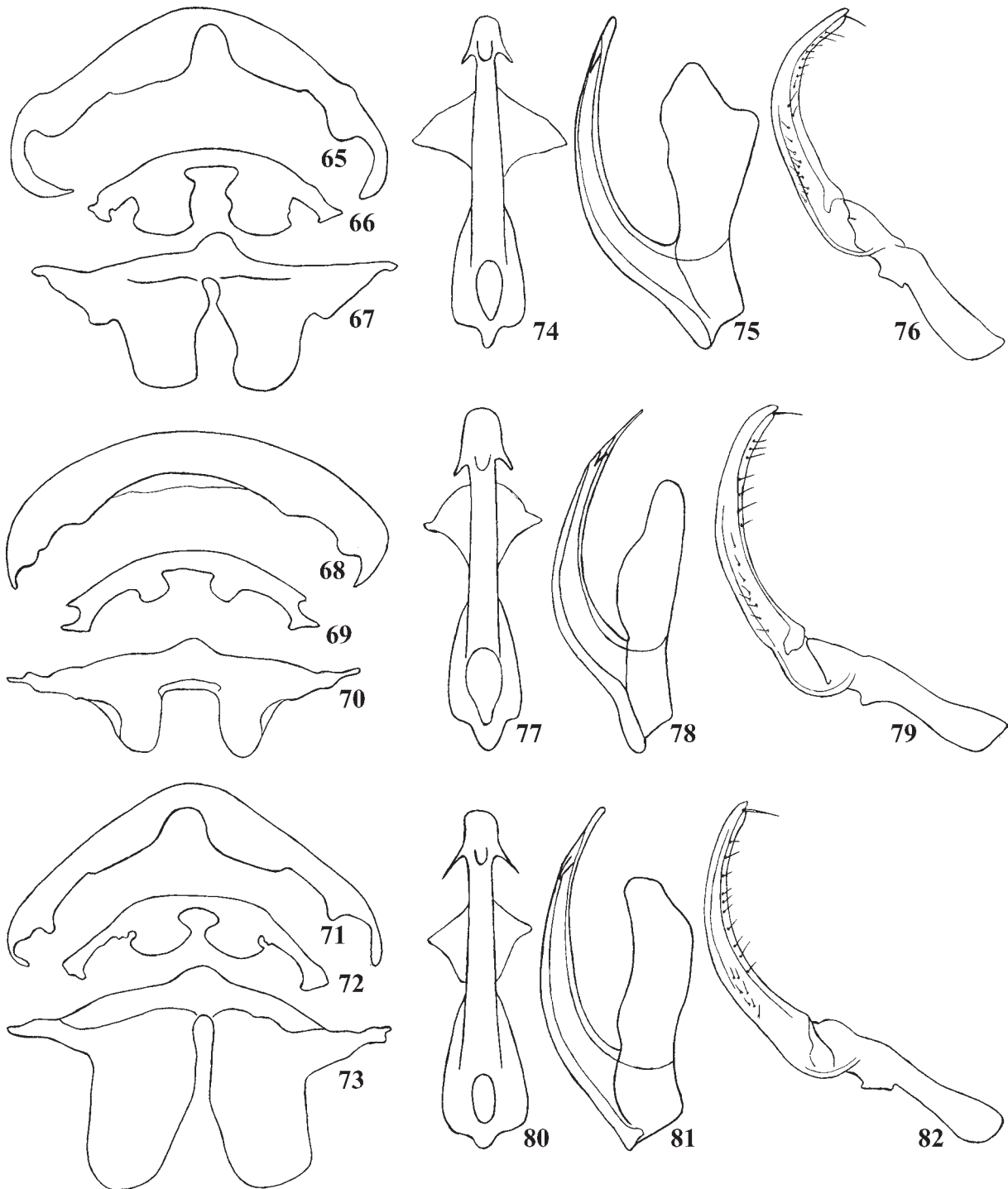


Figs 40–64. Male genitalia of species of *Populicerus*. 40–45 — *P. confusus*; 46–52 — *P. albicans*; 53–55 — *P. populi*; 56–58 — *P. nitidissimus*; 59–61 — *P. laminatus*; 62–64 — *P. ambigenus*; 40–41, 46–48, 53, 56, 59, 62 — penis, back view; 42–43, 49–50, 54, 57, 60, 63 — same, side view; 44–45, 51–52, 55, 58, 61, 64 — style.

Рис. 40–64. Гениталии самцов *Populicerus*. 40–45 — *P. confusus*; 46–52 — *P. albicans*; 53–55 — *P. populi*; 56–58 — *P. nitidissimus*; 59–61 — *P. laminatus*; 62–64 — *P. ambigenus*; 40–41, 46–48, 53, 56, 59, 62 — пенис, сзади; 42–43, 49–50, 54, 57, 60, 63 — то же, сбоку; 44–45, 51–52, 55, 58, 61, 64 — стилус.

plant about 10–15 cm in length was attached to the cartridge by a rubber ring so that the cartridge needle touched the stem slightly. Then a nylon cage containing a male leafhopper was put on the twig. After a time, the

male usually sat on the twig and started singing. Data on collecting sites and temperature during recording for the signals presented on oscillograms are given in the Table.



Figs 65–82. Male abdominal apodemes and genitalia of species of *Idiocerus*. 65–67, 74–76 — *I. lituratus*; 68–70, 77–79 — *I. herrichii*; 71–73, 80–82 — *I. stigmatalis*; 65, 68, 71 — apodemes of the 3rd tergum; 66, 69, 72 — same, 1st sternum; 67, 70, 73 — same, 2nd sternum; 74, 77, 80 — penis, back view; 75, 78, 81 — same, side view; 76, 79, 82 — style.

Рис. 65–82. Аподемы брюшных сегментов и гениталии самцов *Idiocerus*. 65–67, 74–76 — *I. lituratus*; 68–70, 77–79 — *I. herrichii*; 71–73, 80–82 — *I. stigmatalis*; 65, 68, 71 — аподемы III тергита; 66, 69, 72 — аподемы I стернита; 67, 70, 73 — аподемы II стернита; 74, 77, 80 — пенис, сзади; 75, 78, 81 — то же, сбоку; 76, 79, 82 — стилус.

Oscillograms of signals were produced with Cool Edit Pro 2.1 software.

For elements of signal temporal pattern the following terms are used. **Pulse** is a brief elementary fragment of signal (or succession of sine waves) with rapid increase and subsequent decrease of amplitude, i.e. separated from similar fragments by amplitude minimums. Short fragments with constant temporal pattern usually repeated with regular intervals and consisting of uniform or different pulses are referred to as **syllables**. Any more or less prolonged signal with complex pattern (e.g. succession of similar or different syllables) is referred to as a **phrase**.

The drawings of male genitalia and abdominal apodemes were made by tracing the outlines of digital photographs on a glass table lighted from underneath. All specimens investigated are deposited in the collection of the Zoological Museum of M.V. Lomonosov Moscow State University.

Results

Six studied species of *Populicerus* distinctly differ from each other in background coloration and, in case of *P. populi* (Linnaeus, 1761) and *P. laminatus* (Flor, 1861), in a light pattern of forewings (Figs 1–12). All species of *Idiocerus* have similar background coloration, but distinctly differ from each other in black and white pattern (Figs. 13–15). It should be added that, in these genera, coloration is considered most reliable diagnostic trait by many authors and is used in identification keys [Ossiannilsson, 1981; Biedermann, Niedringhaus, 2009].

The shape of the male abdominal 1st and 2nd sternal apodemes and of the 3rd tergal ones is partially similar in different species, but sometimes provides good diagnostic traits and thus can also be used in identification keys. *P. confusus* (Flor, 1861), *P. populi*, and *P. laminatus* are similar in apodeme shapes (Figs 16–21, 22–24, 25–27). *P. albicans* (Kirschbaum, 1868), *P. nitidissimus* (Herrich-Schäffer, 1835), and *P. ambigenus* (Dubovskiy, 1966) are partially similar to each other in the shape of one or another pair of apodemes (Figs 28–33, 34–36, 37–39). For example, *P. albicans* and *P. ambigenus* have similar shape of 1st sternal apodemes (Figs. 30, 32 and 38), whereas *P. nitidissimus* and *P. ambigenus* are similar in shape of 3rd tergal apodemes (Figs. 34 and 37). Still, these species can be easily identified by combination of traits of three pairs of apodemes. In the studied species of the genus *Idiocerus*, 3rd tergal apodemes are poorly developed and similar (Figs. 65, 68, 71), but sternal ones have species-specific shape (Figs. 66–67, 69–70, 72–73).

Shapes of penis and style within each of these genera as a rule are very similar (Figs. 40–64, 74–82). For this reason, the possibility of using these traits for species diagnostics is extremely limited [Ossiannilsson, 1981; Biedermann, Niedringhaus, 2009]. As we have shown earlier, the proportions of the penis, the position of the

subapical processes, and the number and size of small setae situated on the style proximal to subapical large ones can vary within the species [Tishechkin, 2018]; variability of these traits in two species of *Populicerus* is also illustrated on Figs 40–52. Thus, in species under consideration, small interspecific differences in genitalia shape as a rule are masked by their intraspecific variation. The only exception is *P. ambigenus* distinctly differing from congeneric species by longer and stronger curved subapical processes of penis (Fig. 62). Also, *P. albicans* has somewhat wider penis stem with longer preapical processes (Figs 46–48), but it is impossible to clearly describe these differences and use them in a key (for example, differences between Figs 46 and 53). Identification of species of *Idiocerus* based on genitalia shape is also impossible (Figs 74–82).

In a comparative analysis of leafhopper vibrational signals, it should be taken into account that their wave shape strongly depends on a frequency response of a particular twig or, more precisely, of a part of a twig between the singing insect and the gramophone cartridge needle, since each twig is, in fact, a frequency filter with its own individual physical properties [Michelsen et al., 1982]. As a result, the appearance of different signals of the same species or even of the same individual on oscillograms can vary greatly.

First, different signals can differ in carrier frequencies, so that in some oscillograms sinusoidal oscillations are visible, whereas in other ones they merge with each other (cf. Figs 97 and 98, 100 and 101). Second, the relative amplitude of low- and high-frequency components varies depending on whether the substrate functions as a high-pass or low-pass filter. In a signal subjected to low-pass filtering, high-frequency components have very low amplitude and are hardly discernible on oscillograms. If the attenuation of the low frequencies is stronger than that of the high frequencies, the high-frequency components have much higher relative amplitude. (cf. the amplitude of short discrete pulses in the ends of syllables on Figs 93 and 94–95, 100–101 and 102).

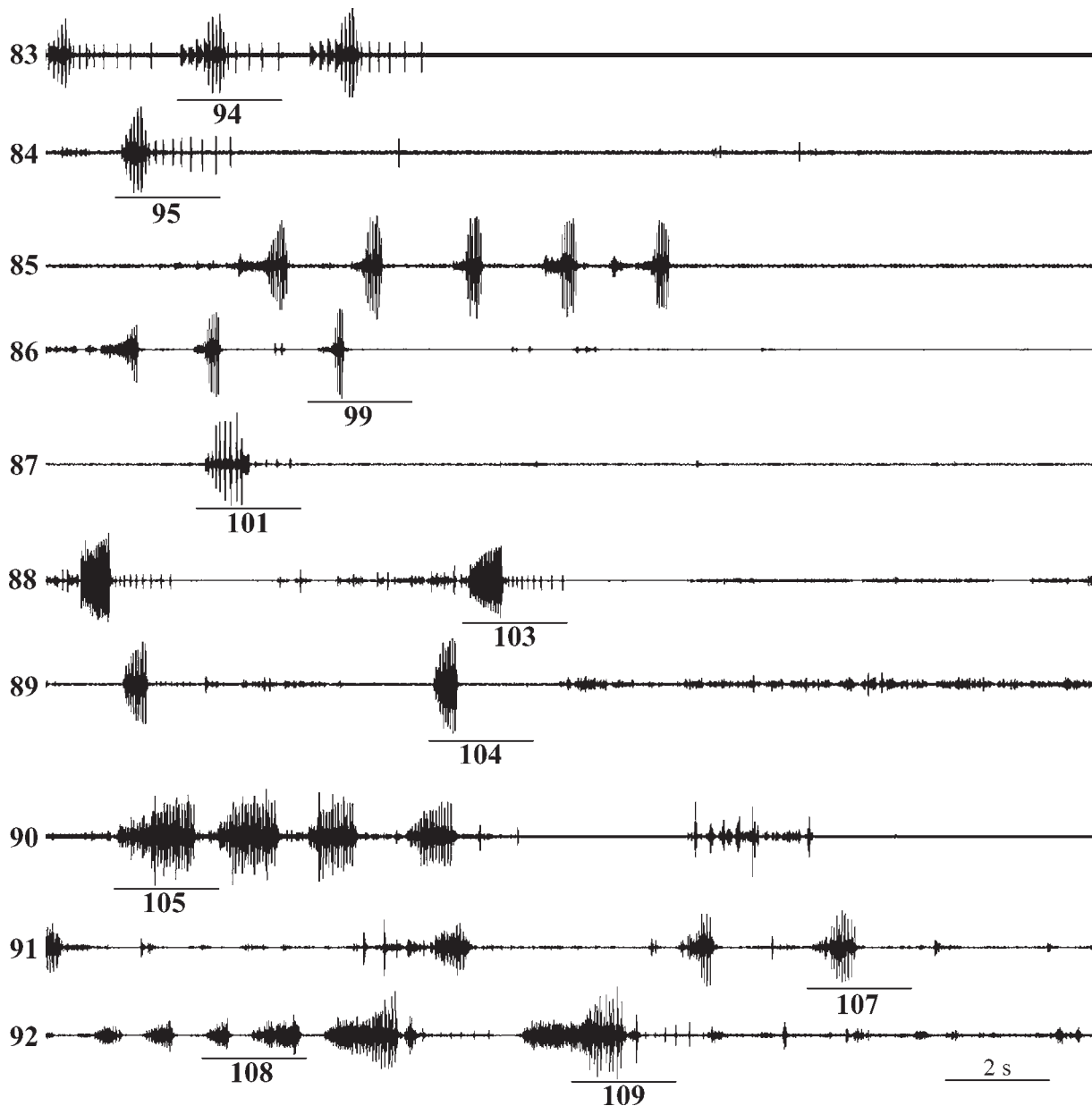
The variability of the signal due to individual characteristics of the singing individual is mainly manifested in the change in the repetition period, duration, and number of signal elements. For example, signals of the same species can consist of a sequence of syllables following each other with constant repetition period or of separate syllables following each other with very long irregular gaps (cf. Figs 91 and 92). Syllable duration in the same species can differ by two to three times due to different number of pulses in syllable (cf. Figs 96–97 and 99, 105 and 106). Occasionally, some component of a signal can be partially or fully reduced. For example, in *P. confusus*, the succession of longer pulses at the beginning of a syllable can be well developed (consists of 7–8 pulses, Fig. 93), partially reduced (consists of 3–4 pulses, Fig. 94), or almost absent (represented by one low-amplitude pulse, merged with the subsequent elements of a syllable, Fig. 95). In *Idiocerus lituratus* (Fallén, 1806), the initial part of a phrase can

consist of a succession of syllables with a distinct and constant temporal pattern (Fig. 110) or strongly reduced and has irregular pattern (Fig. 111).

Taking into account all the above, it is sometimes quite difficult to reveal interspecific boundaries by the structure of signals, despite the fact that individual signals of different species may differ quite clearly.

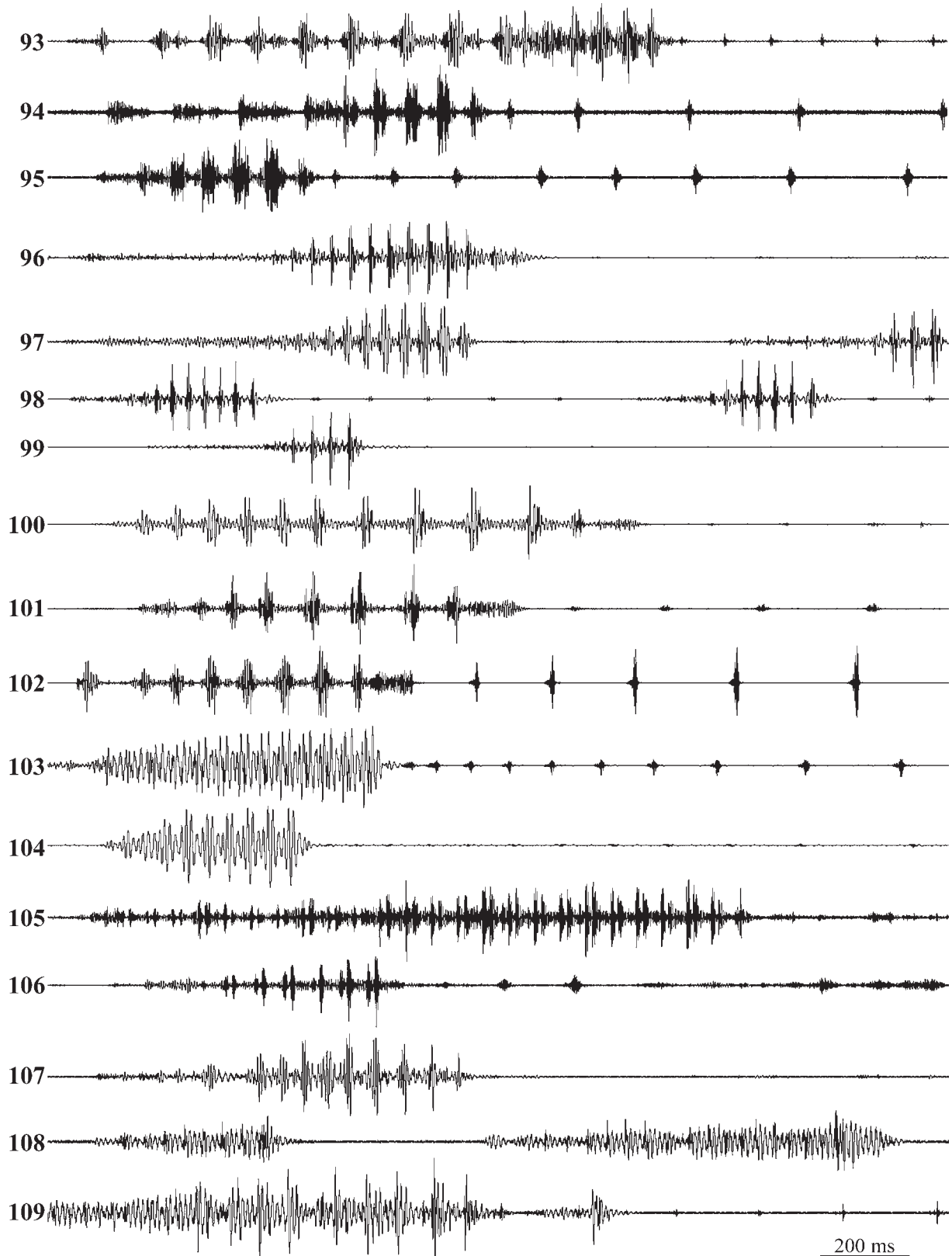
In the genus *Populicerus*, calling signals consist of syllables each including a succession of partially merged pulses followed by several short discrete ones; the latter often have much lower amplitude and are hardly distin-

guishable on oscillograms (Figs 83–109). Syllables can be separated by short gaps of the same duration or follow with very long irregular gaps (Figs 83–92). In all species studied, both regularly and irregularly produced syllables were registered. In this genus, there are two groups of species producing similar and sometimes almost identical calling signals. The first group includes *P. confusus* feeding on willows (Figs 83–84, 93–95) and *P. populi* feeding on aspen (*Populus tremula* L.) (Figs 87, 100–102); these species are geographically sympatric throughout their ranges. The second group



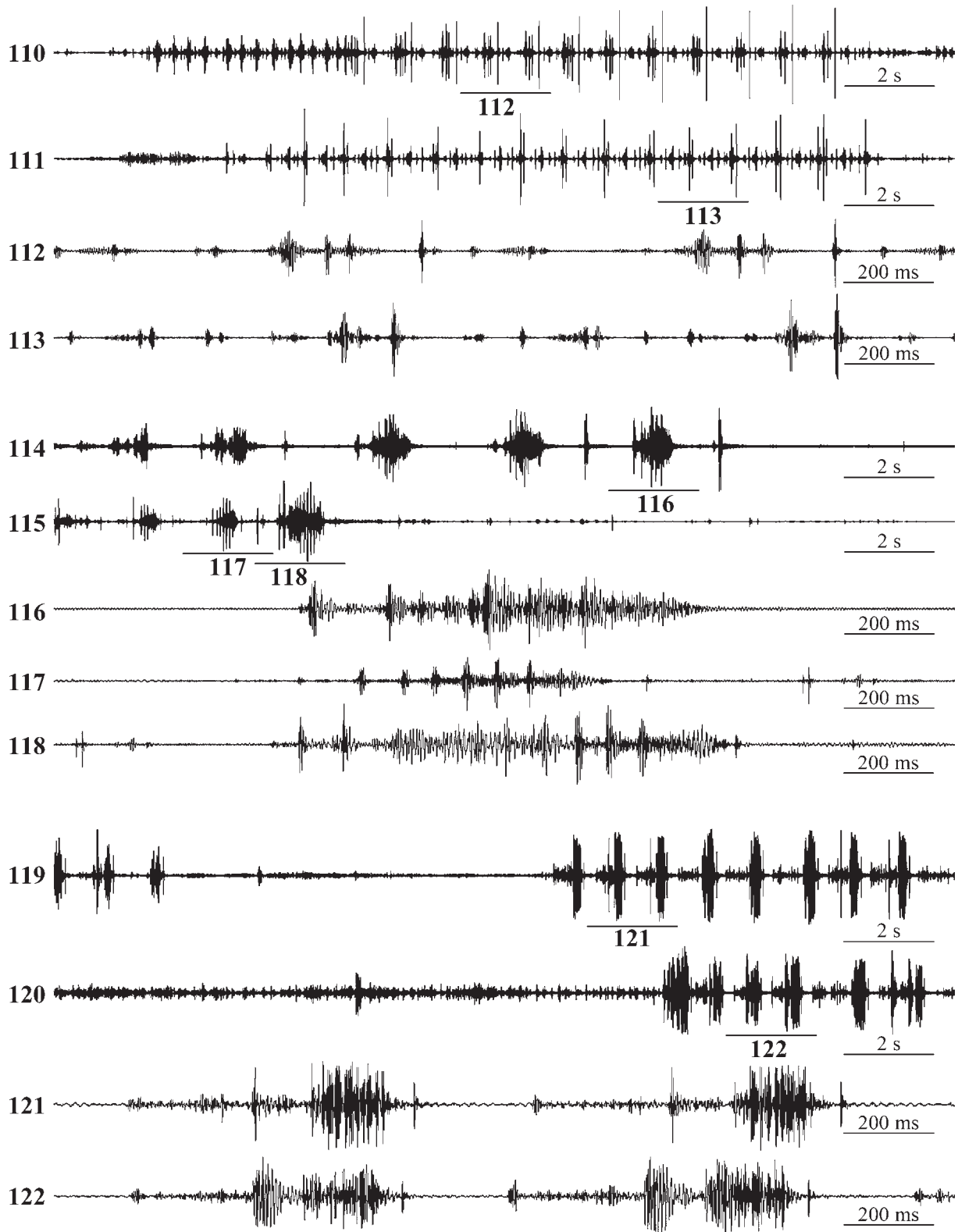
Figs 83–92. Oscillograms of male calling signals of species of *Populicerus*. 83–84 — *P. confusus*; 85–86 — *P. albicans*; 87 — *P. populi*; 88–89 — *P. nitidissimus*; 90 — *P. laminatus*; 91–92 — *P. ambigenus*. Faster oscillograms of the parts of signals indicated as “94–95”, “99”, “101”, “103–105”, and “107–109” are given under the same numbers. Scale mark at the bottom on the right is the same for all oscillograms.

Рис. 83–92. Осциллограммы призывных сигналов самцов *Populicerus*. 83–84 — *P. confusus*; 85–86 — *P. albicans*; 87 — *P. populi*; 88–89 — *P. nitidissimus*; 90 — *P. laminatus*; 91–92 — *P. ambigenus*. Фрагменты сигналов, обозначенные цифрами “94–95”, “99”, “101”, “103–105” и “107–109”, представлены на осциллограммах под такими же номерами. Отметка времени внизу справа – общая для всех осциллограмм.



Figs 93–109. Oscillograms of male calling signals of species of *Populicerus*. 93–95 — *P. confusus*; 96–99 — *P. albicans*; 100–102 — *P. populi*; 103–104 — *P. nitidissimus*; 105–106 — *P. laminatus*; 107–109 — *P. ambigenus*. Scale mark at the bottom on the right is the same for all oscillograms.

Рис. 93–109. Осциллограммы призывных сигналов самцов *Populicerus*. 93–95 — *P. confusus*; 96–99 — *P. albicans*; 100–102 — *P. populi*; 103–104 — *P. nitidissimus*; 105–106 — *P. laminatus*; 107–109 — *P. ambigenus*. Отметка времени внизу справа – общая для всех осциллограмм.



Figs 110–122. Oscillograms of male calling signals of species of *Idiocerus*. 110–113 — *I. lituratus*; 114–118 — *I. herrichii*; 119–122 — *I. stigmatalis*. Faster oscillograms of the parts of signals indicated as “112–113”, “116–118”, and “121–122” are given under the same numbers.

Рис. 110–122. Осциллограммы призывных сигналов самцов *Idiocerus*. 110–113 — *I. lituratus*; 114–118 — *I. herrichii*; 119–122 — *I. stigmatalis*. Фрагменты сигналов, обозначенные цифрами “112–113”, “116–118” и “121–122”, представлены на осциллограммах под такими же номерами.

includes *P. albicans* feeding on *Populus alba* L. (Figs 85–86, 96–99), *P. nitidissimus* feeding on so-called black poplars (*P. nigra* L. and some cultivated introduced species and hybrids) (Figs 88–89, 103–104), and *P. ambigenus* feeding on willows (*Salix* spp.) (Figs 91–92, 107–109). *P. albicans* and *P. nitidissimus* are geographically sympatric throughout Europe, but allopatric with *P. ambigenus* occurring in Southern Kazakhstan and Central Asia. Unlike abovementioned species, in *P. laminatus*, pulses in the signal are grouped by two (Figs 105–106), which is found in other species only as a rare exception (Fig. 94).

Three studied species of *Idiocerus* are geographically sympatric throughout their ranges, and distinctly differ from each other in calling signal patterns. In all three species, calling signals are rather long phrases consisting of repeated syllables, but their shape is species-specific (Figs 110–122). In addition, in *I. lituratus* and *I. stigmatalis* (Lewis, 1834), prolonged lower-amplitude signal usually precedes the main part of a phrase (Figs 110, 120). *I. lituratus* feeds on *Salix* spp. from the section *Cinerella*, whereas *I. herrichii* (Kirschbaum, 1868) and *I. stigmatalis* (Lewis, 1834) feed on *Salix* spp. from the nominotypical section and are therefore strictly sympatric.

Discussion

Comparative investigation of different traits revealed similar patterns in two genera of *Idiocerini*. Species within each genus, with the exception of *P. ambigenus*, are almost indistinguishable by the shape of male genitalia, differ only partly by the shape of the abdominal apodemes, but are easily distinguishable by coloration. Male calling signals in different species of *Idiocerus* are distinctly different in temporal pattern; in *Populicerus*, they are more similar, and in some species are almost indistinguishable.

Three species of *Idiocerus* have overlapping ranges. Two of them feed on the same willow species, i.e. are strictly sympatric, still, differences in the signal patterns, apparently, provide reliable reproductive isolation between them.

In the genus *Populicerus*, situation is more complex. *P. ambigenus* occurs in Southern Kazakhstan and Central Asia and is thus allopatric with other species. The latter five ones are geographically sympatric and inhabit the western half of the Palaearctic; eastern boundaries of their ranges are obscure. Among them, *P. albicans*, *P. nitidissimus*, and *P. confusus* are acoustically isolated due to different host specialization because vibrational signals cannot transmit from one plant to another without physical contact between them. *P. populi* and *P. laminatus* feed on aspen and, therefore, are strictly sympatric, but distinctly differ from each other in signal patterns (Figs 100–102 and 105–106).

As a result, all species studied are reproductively isolated due to geographic allopatry (*P. ambigenus* and other species), different host specialization (*I. lituratus*

and two other *Idiocerus* species; *P. albicans*, *P. nitidissimus*, *P. confusus* and two species of *Populicerus* feeding on aspen), or, in case of a strict sympatry (overlapping ranges and the same host specialization in *I. herrichii* and *I. stigmatalis* and in *P. populi* and *P. laminatus*), due to differences in calling signal temporal patterns.

Interspecific morphological differences within each genus are small. All species of *Idiocerus* and some species of *Populicerus* differ in abdominal apodeme shape. Genitalia shape within each genus is similar with the only exception, *P. ambigenus*.

At the same time, all the species under consideration clearly differ from each other in coloration. The differences in coloration between species of *Populicerus* are probably adaptive, because each species has the same coloration as the young twigs of its host plant. Species dwelling on aspen are greenish or yellowish with reddish brown dorsal side of a body (Figs 5–6, 9–10), species dwelling on willows are green or yellowish green (Figs 1–2, 11–12), *P. albicans* dwelling on silver poplar has greyish green coloration (Figs 3–4), and *P. nitidissimus* dwelling on black poplar is yellow with a brownish tinge (Figs 7–8).

All species of *Idiocerus* have yellowish grey coloration with a highly developed contrasting black and white pattern (Figs 13–15); therefore, this explanation does not apply to them. Even if we assume that this coloration makes them inconspicuous on the bark of old trunks, in the cracks of which they hibernate (although they live and feed on young green twigs during summer), this still does not explain the interspecific differences in the shape and number of black and white spots.

It is often considered that in the process of speciation, the first differences arise in traits that ensure the recognition of a conspecific mate (in our case, in the signal patterns), or in genitalia (indeed, species similar in external appearance usually differ in genitalia shape). Nevertheless, the example of *Populicerus* shows that this is not always the case. After transition to different hosts, reproductive isolation in leafhoppers is provided mainly due to differences in host specialization, which can result in speciation [Wood, 1980; Wood, Guttman, 1981]. In such case, male calling signals provide only a finding of a conspecific mate and, thus, conspecific fertilization, which, according to Paterson [Lambert, Paterson, 1984; Paterson, 1985], is their primary function. Their secondary function, i. e. providing precopulatory isolation between closely related species, is not necessary due to the presence of other isolating mechanism, difference in host specialization. Apparently, for this very reason, signal patterns in some *Populicerus* species remained almost identical in spite of divergence in coloration. On the other hand, signals of species of *Idiocerus* living on willows from different sections differ quite clearly. Similarly, closely related species of *Macropsis* Lewis, 1836 (Homoptera: Cicadellidae: Eurytelinae: Macropsini) as a rule distinctly differ from each other in the signal temporal patterns although dwell on different host plants [e. g. Tishechkin, 2002].

For the same reason, differences in the shape of male genitalia (as well as in any other morphological structures) are also not necessary for existence of such forms as biological species. Indeed, the shape of genitalia within each genus of Idiocerini is similar or their evolution is not directly related to the reproductive isolation, since the only species of *Populicerus* that differs in genitalia traits is allopatric with all other ones. The same is true for the abdominal apodemes. Most of species studied are similar, at least, in shape of one pair of apodemes, and some species of *Populicerus* are indistinguishable in shape of all three apodeme pairs. Again, in the genus *Macropsis* situation is similar, most species being almost indistinguishable in male genitalia shape and species feeding on Rosaceae, *Urtica dioica* L., and *Hippophae rhamnoides* L. differing from each other only in coloration and signal patterns [Tishechkin, 2002, 2015].

Thus, the degree of divergence by different traits in different taxa of Cicadellidae can vary greatly: in some taxa, species differ better in signal patterns, in others, in coloration, etc. Some differences are clearly adaptive in nature; for example, these are differences in coloration between *Populicerus* species or in the signal patterns between two strictly sympatric species of this genus. In other cases, their reasons are not obvious; examples include differences in coloration between species of *Idiocerus*, or distinct difference in the penis shape in *P. ambigenus*, which is geographically allopatric with other species of this genus.

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