

Interspecific differences in coloration, morphology, and the male calling signal patterns in Palearctic Philaenini (Homoptera: Auchenorrhyncha: Aphrophoridae)

Межвидовые различия в окраске, морфологии и паттерне призывных сигналов самцов у палеарктических Philaenini (Homoptera: Auchenorrhyncha: Aphrophoridae)

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КЛЮЧЕВЫЕ СЛОВА: пенницы, таксономия, идентификация видов, таксономические признаки, изменчивость

ABSTRACT. A comparative study of the external morphology and coloration, the genitalia shape, and the temporal pattern of the male calling signals in 11 species of Palearctic Philaenini from 4 genera revealed that most species are clearly distinguished by the male genitalia shape. The exception is the genus *Neophilaenus*, where coloration is the most reliable species-specific character; the genitalia shape is quite uniform within subgenera, so that some species are indistinguishable by the shape of the aedeagus and styles. Male calling signals of different species of Philaenini are often similar and for this reason cannot be used for species identification. Sometimes, similarity in the calling signal patterns is observed even among species with overlapping ranges and similar ecological preferences. However, we have never found such species in the same biotope, i.e., in conditions where they are potentially capable of acoustic contact.

РЕЗЮМЕ. Сравнительное исследование внешней морфологии и окраски, формы гениталий и временного паттерна призывных сигналов самцов 11 палеарктических видов Philaenini из 4 родов показало, что большинство видов надежно различается по форме гениталий самца. Исключение составляет род *Neophilaenus*, в котором наиболее надежным видовым признаком является окраска; форма гениталий в пределах подродов достаточно однотипна, поэтому некоторые виды неразличимы по форме эдегуса и стилусов. Призывные сигналы самцов разных видов Philaenini нередко бывают сходными и по этой причине непригодны для видовой идентификации.

Иногда сходство сигналов наблюдается даже у видов с перекрывающимися ареалами и сходными экологическими предпочтениями, хотя такие виды никогда не были найдены нами в одном биотопе, т. е. в условиях, при которых они могли бы вступать в акустический контакт.

Introduction

The spittlebug family (Homoptera: Auchenorrhyncha: Aphrophoridae) includes just over 900 species [Dmitriev *et al.*, 2022 onward], about 40 of which are found in Russia and adjacent countries [Emelyanov, 1964; Mityaev, 1971; Nast, 1972; Anufriev, Emelyanov, 1988]. Some Palearctic spittlebugs are among the most common and well-known species of Auchenorrhyncha, found almost everywhere in both natural and anthropogenic landscapes. However, there are many problems in the taxonomy of the Palearctic Aphrophoridae, often concerning long-known and widespread species.

Comparative study of body size, coloration, aedeagus shape, and the male calling signals of *Lepyronia coleoptrata* (Linnaeus, 1758) from different localities in European Russia, Northern Kazakhstan, Siberia, and the Russian Far East showed that all populations studied belong to the same species, and thus, *L. grossa* Uhler, 1896 occurring in Japan and the Russian Far East is a junior synonym of *L. coleoptrata* [Tishechkin, 2019]. A study of the male calling signals of species of the *Aphrophora salicina* (Goeze, 1778) group in Russia, Kazakhstan, and Kyrgyzstan allowed obtaining new data on their dis-

tribution, establishing a new synonym, and revealing a new species from the Lower Volga Region [Tishechkin, 2023].

Investigation of the most common and abundant transpalearctic spittlebug, *Philaenus spumarius* (Linnaeus, 1758), showed, that in the Mediterranean it represents a complex of externally similar species differing only in the shape of the male genitalia and anal tube [Drosopoulos, Asche, 1991; Abdul-Nour, Lahoud, 1995; Drosopoulos, Remane, 2000; Remane, Drosopoulos, 2001]. Recently, new species of this complex were described from Iran [Tishechkin, 2012] and Italy [Bückle, Guglielmino, 2025].

In the cases of *L. coleoptrata* and the *A. salicina* species group, analysis of male vibrational signals proved very useful in solving taxonomic problems. In the genus *Lepyronia* Amyot et Audinet-Serville, 1843 (Cloviini Schmidt, 1920), the signals of different species are distinctly different [Tishechkin, 2019], while in the genus *Aphrophora* Germar, 1821 (Aphrophorini Amyot et Audinet-Serville, 1843) they have more uniform pattern, but nevertheless possess species-specific characters [Tishechkin, 2011, 2023].

This article presents the results of a comparative study of the coloration and appearance, the male genitalia shape, and calling signal patterns in some Palearctic members of the tribe Philaenini Metcalf, 1955. Eleven species from four genera were studied; male calling signals were recorded in ten species.

Material and methods

Spittlebug vibrational 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 (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 stem of the host plant about 10–15 cm in length was attached to the cartridge by a rubber ring with the cartridge needle slightly touching the stem. Then a nylon cage containing a male spittlebug was put on the twig. After some time, the male usually sat on the twig and started singing. Data on collecting sites and temperature during recording are given in the Table.

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

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

Species	Locality	Air temperature during recording, °C
<i>Aphilaenus ikumae</i> (Matsumura, 1915)	The Russian Far East, Primorskiy Krai, W shore of the Khanka Lake, 10 km S of Turiy Rog, 16.VII.2002.	21–22
<i>Paraphilaenus notatus</i> (Mulsant et Rey, 1855)	1. Russia, Rostov Oblast, Oblivskiy District, env. Sosnovy Village on the Chir River, 16, 18.VIII.1991. 2. Russia, Volgograd Oblast, env. Ilovlya Town, 2.VII.2025. 3. Kyrgyzstan, Western Tien-Shan Mts., mountain steppes about 20 km north of Tash-Kumyr Town, 4.VII.2011.	25–26 22 21–22
<i>Philaenus signatus</i> (Melichar, 1896)	Greece, Korfu Island, environs of Nissaki Village, ca 12 km N of Kerkyra, 9, 12.IX.2019.	25
<i>Ph. spumarius</i> (Linnaeus, 1758)	1. Russia, Moscow Oblast, env. Pushkino, 24.VII.1993. 2. Kyrgyzstan, Chatkal Mtn. Range, env. Arkyt Village, 30.VI.2011. 3. The Russian Far East, Primorskiy Krai, ca. 15 km SW of Slavyanka, env. Ryazanovka Village, 15.VII.2012.	27 22 24
<i>Neophilaenus (Neophilaenus) lineatus</i> (Linnaeus, 1758)	Russia, Moscow Oblast, Voskresensk District, env. Beloozerskiy Town, 2.VIII.2022.	24
<i>N. (Neophilaenus) minor</i> (Kirschbaum, 1868)	Russia, Volgograd Oblast, env. Ilovlya Town, 30.VI.2025.	23
<i>N. (Neophilaenus) campestris</i> (Fallén, 1805)	1. Russia, Moscow Oblast, Voskresensk District, env. Beloozerskiy Town, 14.VII.2017. 2. SE Azerbaijan, Talysh Mts., env. Lerik Village, 14.VII.1987.	24–27
<i>N. (Neophilaenus) sachalinensis</i> (Matsumura, 1915)	Russia, Buryatia, the Irkut River Valley W of Mondy Village (about 80 km W of Kyren), 30.VI.2007.	29–30
<i>N. (Neophilaenus) haupti</i> (Zakhvatkin, 1925)	Kyrgyzstan, S shore of the Issyk-Kul Lake, env. Ton (=Tong) Village, 10.VII.2013.	20
<i>N. (Neophilaenus) infumatus</i> (Haupt, 1917)	1. Russia, Saratov Oblast, Khvalynskiy District, env. Ulyanino Village, 16.VII.2005. 2. Russia, Saratov Oblast, Krasnokutskiy District, env. Dyakovka Village, 14.VII.2004. 3. Russia, Volgograd Oblast, Kamysinskiy District, env. Shcherbatovka Village, 11.VII.2005. 4. Russia, North Ossetia, Alagirskiy District, env. Tsey Village, 1.VIII.1990. (misidentified as <i>N. (Neophilaenus) exclamationis</i> in Tishechkin [2003]).	29–30 31 23–25 20

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**.

Digital images of male genitalia were obtained with a Micromed 3 LED M microscope equipped with a MiChrome 5 Pro camera (Tucsen). For morphological studies and illustrations, specimens whose signals had been recorded were used, as far as possible. Materials studied are deposited in the collection of the Zoological Museum of M.V. Lomonosov Moscow State University.

Results

1. External morphology and coloration

Some species of Philaenini have distinctive coloration and can be easily recognized by appearance in combination with the body size. Among species studied, these include *Aphilaenus ikumae* (Matsumura, 1915) (Fig. 1), *Paraphilaenus notatus* (Mulsant et Rey, 1855) (Figs 5–6), *Neophilaenus* (*Neophilaenulus*) *campestris* (Fallén, 1805) (Figs 28–29), *N.* (*Neophilaenulus*) *exclamationis* (Thunberg, 1784) (Figs 35–36), and *N.* (*Neophilaenulus*) *sachalinensis* (Matsumura, 1915) (Figs 44–45).

Neophilaenus (*Neophilaenus*) *lineatus* (Linnaeus, 1758) (Fig. 20), *N.* (*Neophilaenus*) *minor* (Kirschbaum, 1868) (Fig. 24), and *N.* (*Neophilaenulus*) *haupti* (Zakhvatkin, 1925) (Fig. 40) have a uniform light brown coloration with lighter costal margins of the forewings and, as a rule, a dark longitudinal stripes along them; sometimes there are also dark spots on the apices of the forewings. Similar color form is sometimes found in *N.* (*Neophilaenulus*) *infumatus* (Haupt, 1917) (Figs 49–51). Despite this, these species also differ quite clearly in appearance.

N. (*Neophilaenus*) *minor* differs from the other three similar species by its smaller body size and greater relative crown length. *N.* (*Neophilaenulus*) *haupti* has lighter coloration than *N.* (*Neophilaenus*) *lineatus* and *N.* (*Neophilaenulus*) *infumatus*. The last two species are sometimes somewhat similar in appearance, although *N.* (*Neophilaenulus*) *infumatus* is usually darker than *N.* (*Neophilaenus*) *lineatus* and does not have such a distinct stripes along costal margins of the forewings.

Members of the genus *Philaenus* Stål, 1864 (Figs 13–14, 17), especially, *Ph. spumarius* (Linnaeus, 1758), are well-known for their extremely variable coloration. For this reason, in this genus differences in coloration cannot be used for species diagnostics. Since color polymorphism in *Philaenus* was described in detail by other authors [Ossiannilsson, 1981: 249; Drosopoulos *et al.*, 2010, etc.], we do not provide photographs of all the numerous color variations here.

2. Male genitalia

Members of the different genera of Philaenini differ, among other characters, in the shape of their genitalia (e.g., Figs 2–4, 7–12, 15–16), but the features of their structure are rarely, if at all, used in keys to genera of the fauna of Russia and adjacent countries [Emelyanov, 1964; Mityaev, 1971; Anufriev, Emelyanov, 1988].

Traditionally, the shape of the male genitalia is the primary character in Auchenorrhyncha species diagnostics. Most identification keys to species are based mainly on differences in the genitalia shape; external morphology and coloration are often omitted, even when species are clearly distinguished by their appearance.

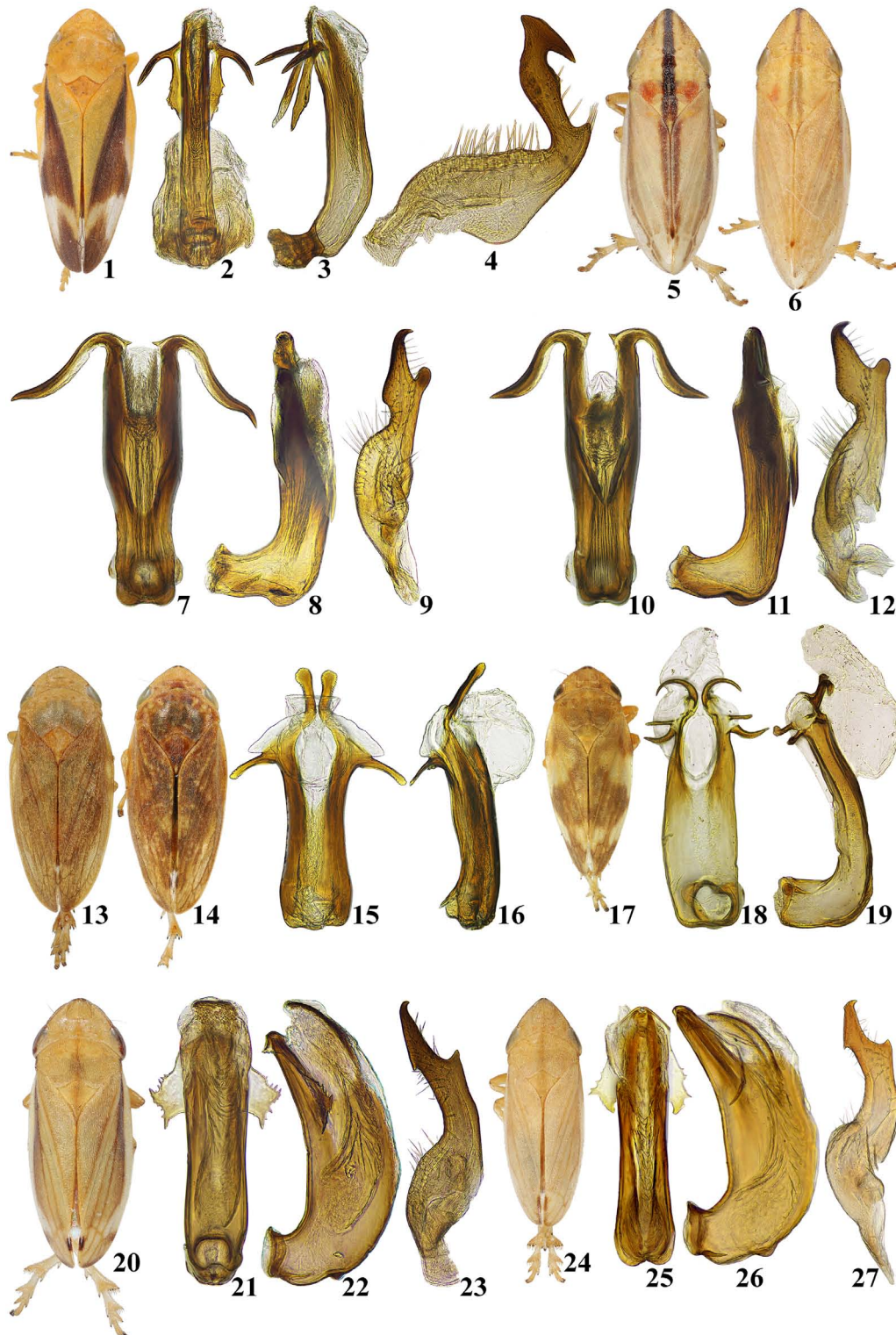
In the genus *Philaenus*, the shape of the male genitalia is species-specific (Figs 15–16, 18–19), and it is precisely the differences in the shape of aedeagus that made it possible to reveal a significant number of new species in this genus (e.g., Drosopoulos [1991]; Drosopoulos, Remane [2000]; Bückle, Guglielmino [2025]).

In the genus *Neophilaenus*, distinct differences in the shape of the aedeagus and styles are observed at the subgeneric level. In *Neophilaenus* (*Neophilaenus*) *Haupt*, 1935, the aedeagal shaft is wide, especially in lateral view, with two rather small side lamellar lobes having irregularly identified margins (Figs 21–22, 25–26). In *Neophilaenus* (*Neophilaenulus*) *Emelyanov*, 1964, the aedeagal shaft is narrow, with large side lobes of more or less triangular outlines (Figs 30–31, 37–38, 41–42, 46–47, 52–53). Also, in *Neophilaenus* (*Neophilaenus*), the distal notch on the inner margin of the style is wide (Figs 23, 27), whereas in *Neophilaenus* (*Neophilaenulus*), it is very small, of approximately the same width as the base of the distal denticle (Figs 32, 39, 43, 48, 54).

In two members of the nominotypical subgenus, the aedeagus shape is almost identical (Figs 21–22 and 25–26). Minor differences are observed only in the shape of styles. In *N.* (*Neophilaenus*) *lineatus*, external denticle of the style is somewhat closer to basal internal one than in *N.* (*Neophilaenus*) *minor* (Figs 23, 27).

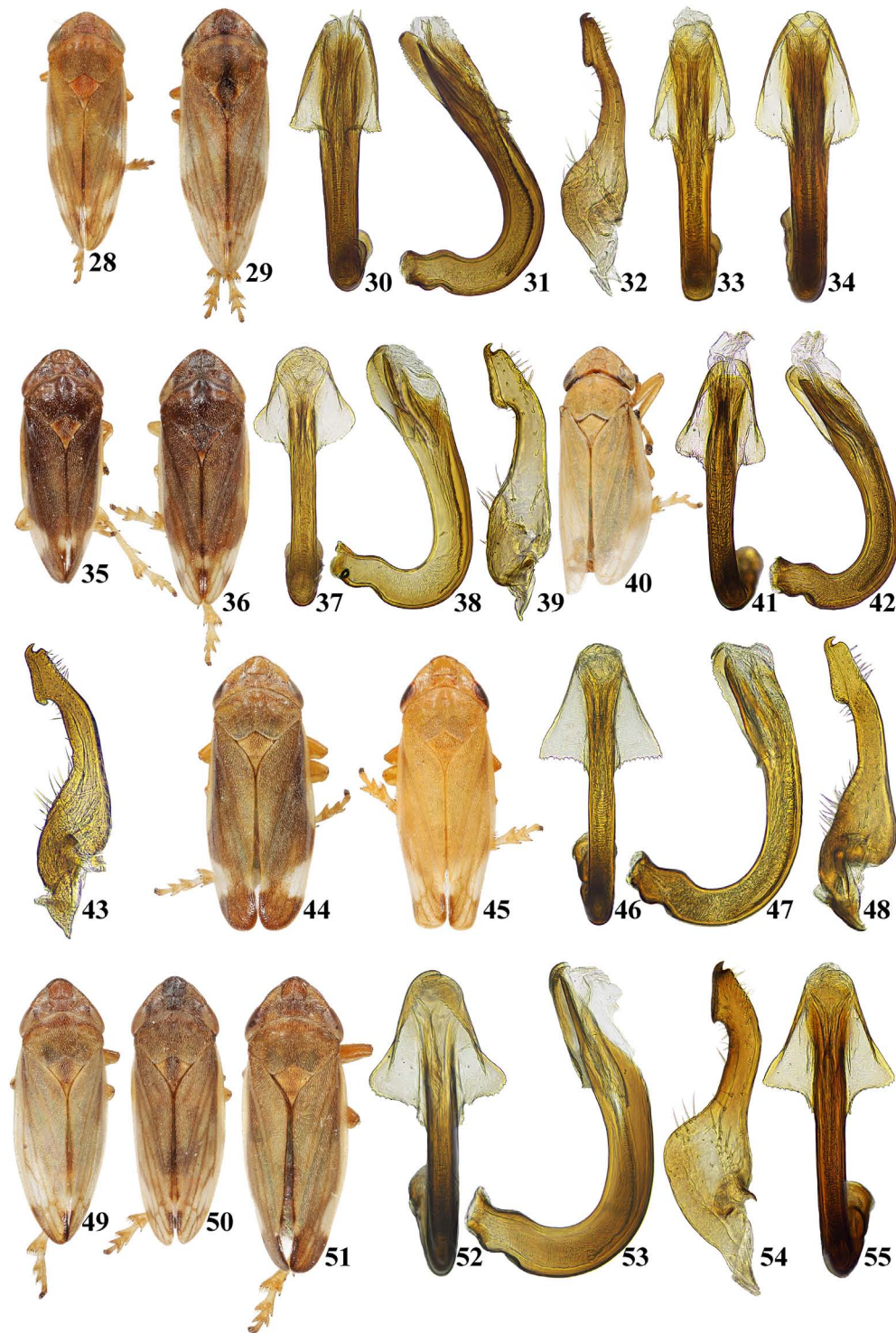
In five studied members of *Neophilaenus* (*Neophilaenulus*), the style shape does not have constant interspecific differences and provides no reliable characters for species identification (Figs 32, 39, 43, 48, 54). Aedeagus in lateral view in all species is also similar (Figs 31, 38, 42, 47, 53). In *N.* (*Neophilaenulus*) *campestris*, aedeagal shaft is rather thick and lateral margins of aedeagal lamellar lobes are slightly convex (Figs 30, 33–34), whereas in four other species they are more or less concave (Figs 37, 41, 46, 52, 55). In *N.* (*Neophilaenulus*) *exclamationis*, side lobes are slightly shorter than in other species (Fig. 37), but this difference is not always distinct. In *N.* (*Neophilaenulus*) *haupti*, side lobes are somewhat narrower than in other species (Fig. 41), but this character cannot always be interpreted with certainty. In *N.* (*Neophilaenulus*) *sachalinensis* and *N.* (*Neophilaenulus*) *infumatus*, the shape of aedeagus is almost identical (Figs 46, 55).

No significant differences in genitalia shape were found between individuals from different localities.



Figs 1–27. Philaenini. 1–4 — *Aphilaenus ikumae*; 5–12 — *Paraphilaenus notatus* (5–9 — specimens from Volgograd Oblast, 10–12 — specimen from Western Tien Shan); 13–16 — *Philaenus signatus*; 17–19 — *Ph. spumarius*; 20–23 — *Neophilaenus (Neophilaenus) lineatus*; 24–27 — *N. (Neophilaenus) minor*. 1, 5–6, 13–14, 17, 20, 24 — dorsal habitus, 2, 7, 10, 15, 18, 21, 25 — aedeagus, caudal view, 3, 8, 11, 16, 19, 22, 26 — aedeagus, lateral view, 4, 9, 12, 23, 27 — style.

Рис. 1–27. Philaenini. 1–4 — *Aphilaenus ikumae*; 5–12 — *Paraphilaenus notatus* (5–9 — экземпляры из Волгоградской обл., 10–12 — экземпляр с Западного Тянь-Шаня); 13–16 — *Philaenus signatus*; 17–19 — *Ph. spumarius*; 20–23 — *Neophilaenus (Neophilaenus) lineatus*; 24–27 — *N. (Neophilaenus) minor*. 1, 5–6, 13–14, 17, 20, 24 — вид сверху, 2, 7, 10, 15, 18, 21, 25 — эдеагус сзади, 3, 8, 11, 16, 19, 22, 26 — эдеагус сбоку, 4, 9, 12, 23, 27 — стилус.



Figs 28–55. *Neophilaenus* (*Neophilaenulus*) spp. 28–34 — *N. (N.) campestris* (28–32 — specimens from Moscow Oblast, 33 — specimen from North Ossetia, Northern Caucasus, 34 — specimen from Talysh Mts., SE Azerbaijan); 35–39 — *N. (N.) exclamationsis*; 40–43 — *N. (N.) haupti*; 44–48 — *N. (N.) sachalinensis*; 49–55 — *N. (N.) infumatus* (49, 52–54 — specimens from Saratov Oblast, 50–51, 55 — specimens from North Ossetia, Northern Caucasus). 28–29, 35–36, 40, 44–45, 49–51 — dorsal habitus, 30, 33–34, 37, 41, 46, 52, 55 — aedeagus, caudal view, 31, 38, 42, 47, 53 — aedeagus, lateral view, 32, 39, 43, 48, 54 — style.

Рис. 28–55. *Neophilaenus* (*Neophilaenulus*) spp. 28–34 — *N. (N.) campestris* (28–32 — экземпляры из Московской обл., 33 — экземпляр из Северной Осетии, Северный Кавказ, 34 — экземпляр с Талышских гор, ЮВ Азербайджан); 35–39 — *N. (N.) exclamationsis*; 40–43 — *N. (N.) haupti*; 44–48 — *N. (N.) sachalinensis*; 49–55 — *N. (N.) infumatus* (49, 52–54 — экземпляры из Саратовской обл., 50–51, 55 — экземпляры из Северной Осетии, Северный Кавказ). 28–29, 35–36, 40, 44–45, 49–51 — вид сверху, 30, 33–34, 37, 41, 46, 52, 55 — эдеагус сзади, 31, 38, 42, 47, 53 — эдеагус сбоку, 32, 39, 43, 48, 54 — стилус.

For example, genitalia shape in *P. notatus* males from the Lower Volga Region and the Western Tien Shan does not consistently differ (Figs 7–9 and 10–12). In *N. (Neophilaenus) campestris*, the shape of aedeagus differs slightly between males from the Moscow Oblast (Fig. 30), the lowlands of North Ossetia (Fig. 33), and the Talysh Mountains, southeastern Azerbaijan (Fig. 34), but retains species-specific characters: a relatively thick shaft and convex lateral margins of the lamellar lobes. The aedeagus shape in males of *N. (Neophilaenus) infumatus* from Khvalynsk, the northern Saratov Oblast (Fig. 52) and from the mid-mountain regions of North Ossetia (Fig. 55) also does not significantly differ.

3. Male calling signals

As shown by ethological experiments, in insects using sounds or substrate-born vibrations for conspecific mate recognition, it is the differences in the male calling signal patterns that constitute the main precopulatory reproductive barrier. Therefore, when differentiating closely related taxa by their signal patterns, one can actually discriminate between the biological species based on the very criterion of their reproductive isolation. For this reason, signal analysis is often used to distinguish closely related taxa and determine their status (review: Tishechkin [2013]).

Signals of all studied members of Philaenini have similar general scheme of the temporal pattern. They are single or regularly repeated syllables, each of which consists of two parts. The first part is a sequence of partially or almost completely merged pulses with a noise frequency spectrum. The second part is a pure-tone component with a line spectrum. Differences in the waveform between the two components of the syllable are not always distinctive on oscillograms, but they are clearly visible on sonograms (Figs 58, 74, 77). The amplitude and duration ratios of the two parts of a syllable can vary even in the song of the same male (Figs 70, 83). Sometimes the first, i.e., the noise part of the syllable is almost completely reduced (cf. Figs 83 and 84). In species with syllable durations of approximately 0.5 s or more, syllables are typically separated by long, often irregular gaps (Figs 56–68, 76–81). In species with syllable durations of no more than 200–300 ms, syllables are usually separated by short, regular gaps, thus forming phrases (Figs 69, 73, 82, 89, 91).

A. ikumae (Figs 56–58), *P. notatus* (Figs 59–65), and *Philaenus signatus* (Melichar, 1896) (Figs 66–68) produce syllables separated by long gaps. The average syllable duration in these three species is different. However, since the syllable duration in each species varies greatly, overlapping of extreme values in different species is possible (cf. Figs 61 and 68). This does not prevent recognition of conspecific mate, as *A. ikumae* occurs in the Far East, *P. notatus* inhabits steppes of Eastern Europe and Central Asia, and *Ph. signatus* is found in East Mediterranean.

The two species of *Neophilaenus* from the nominotypical subgenus also produce signals consisting of sin-

gle or irregularly repeated syllables. They are similar in temporal pattern and differ in the syllable duration with only small overlapping in extremes (Figs 76–78 and 79–81). The ranges of these two species considerably overlap, but *N. (Neophilaenus) lineatus* prefers mesophytic vegetation, whereas *N. (Neophilaenus) minor* inhabits dry habitats and is especially common in steppes; thus, they normally cannot perceive each other's signals.

The signals of *N. (Neophilaenus) haupti* (Figs 86–88) are similar in duration to those of *N. (Neophilaenus) minor* (Figs 79–81); as mentioned above, the amplitude ratio of the first and second parts of a syllable in Philaenini varies widely within the same species, so the differences in the amplitudes of the second parts of the syllables in Figs 80–81 and 87–88 can be ignored. These species have overlapping ranges and similar ecological preferences.

Ph. spumarius, *N. (Neophilaenus) campestris*, *N. (Neophilaenus) sachalinensis*, and *N. (Neophilaenus) infumatus* produce regularly repeated syllables forming phrases lasting from 2–3 up to 10–15 s and more. In *N. (Neophilaenus) campestris*, the syllable duration usually exceeds 200 ms (Figs 83–85), while in the other three species it rarely reaches this value and is usually around 150 ms (Figs 70–72, 74–75, 90, 92–94). No significant interspecific differences were found between the signals of *Ph. spumarius*, *N. (Neophilaenus) sachalinensis*, and *N. (Neophilaenus) infumatus* (Figs 69–75, 89–90, and 91–94). *N. (Neophilaenus) sachalinensis* and *N. (Neophilaenus) infumatus* are allopatric, but transpalearctic *Ph. spumarius* is sympatric with each of these species in different parts of its range.

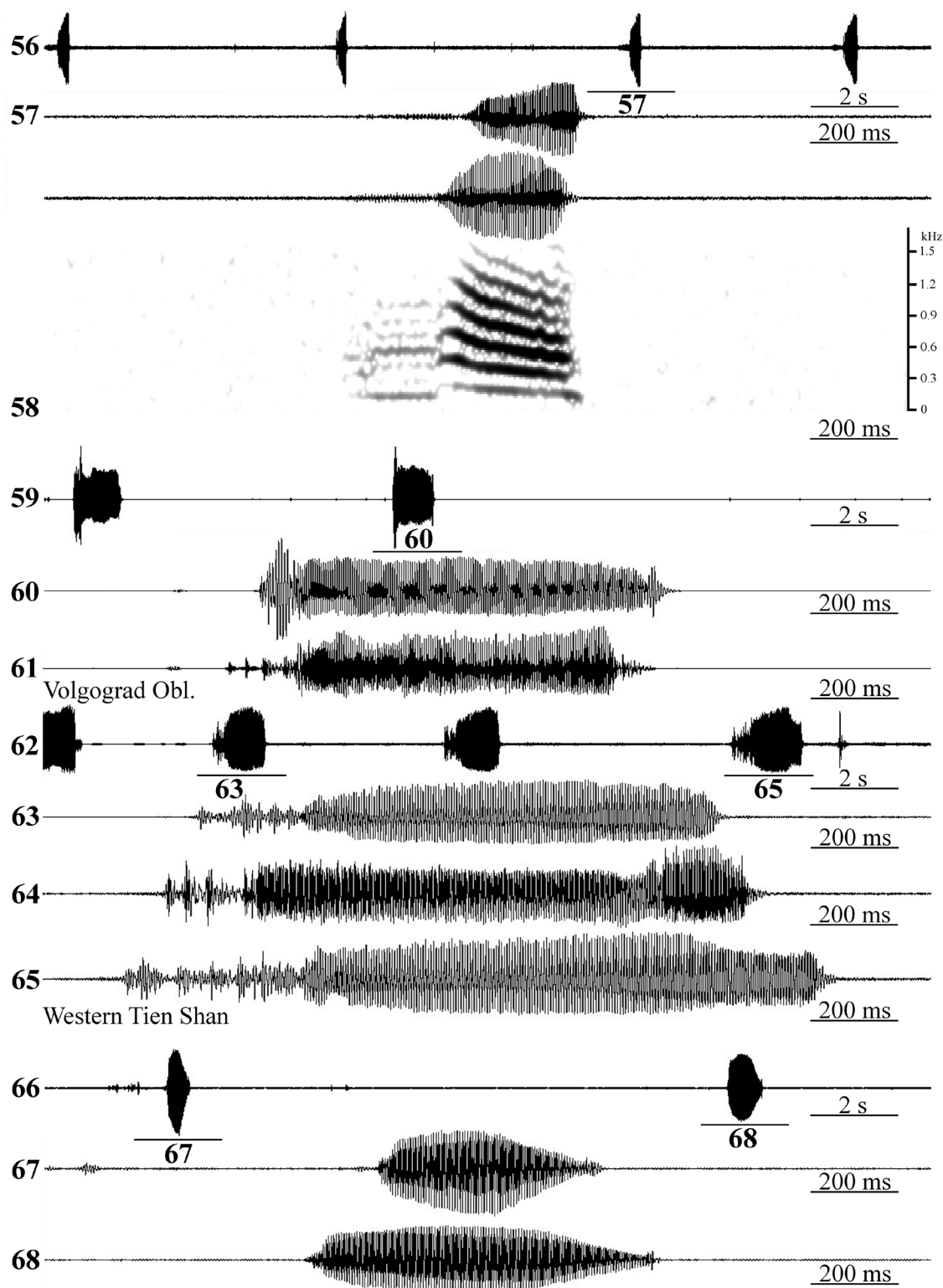
Interspecific differences in the signal frequency spectra, including second, pure-tone parts of syllables, were not revealed.

In four species from three genera, signals of individuals from two or more geographical points were studied (Table), but no constant differences between signals of males from different localities were found (Figs 59–65, 69–75, 83–85, 92–94).

Discussion

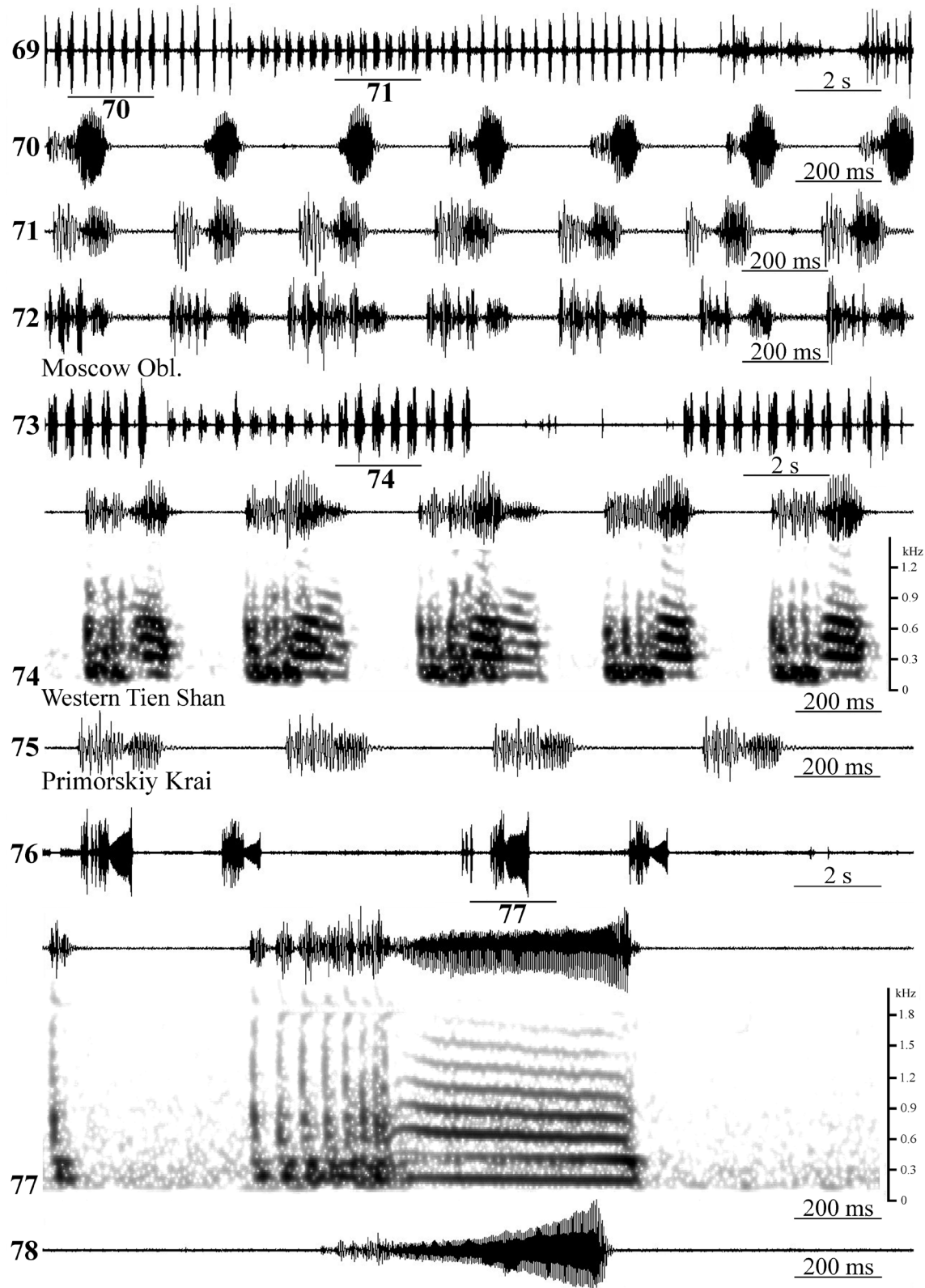
A comparison of external morphology and coloration, genitalia shape, and the male calling signal patterns in different species revealed that there are no universal characters for species identification in Philaenini.

Members of most genera studied are fairly reliably distinguished by the male genitalia shape. *Neophilaenus*, which is the most diverse genus of Philaenini in Russia and adjacent countries, is the only exception in this regard. The shape of the aedeagus and styles in certain species of this genus is almost identical. On the other hand, the members of the nominotypical subgenus differ in the body size and crown shape. The members of the subgenus *Neophilaenus* (*Neophilaenus*) are distinguished by the forewing coloration because the arrangement of spots and stripes on forewings retains species-specific pattern despite the variability of the degree of dark pigmentation. Forewing coloration is also used for



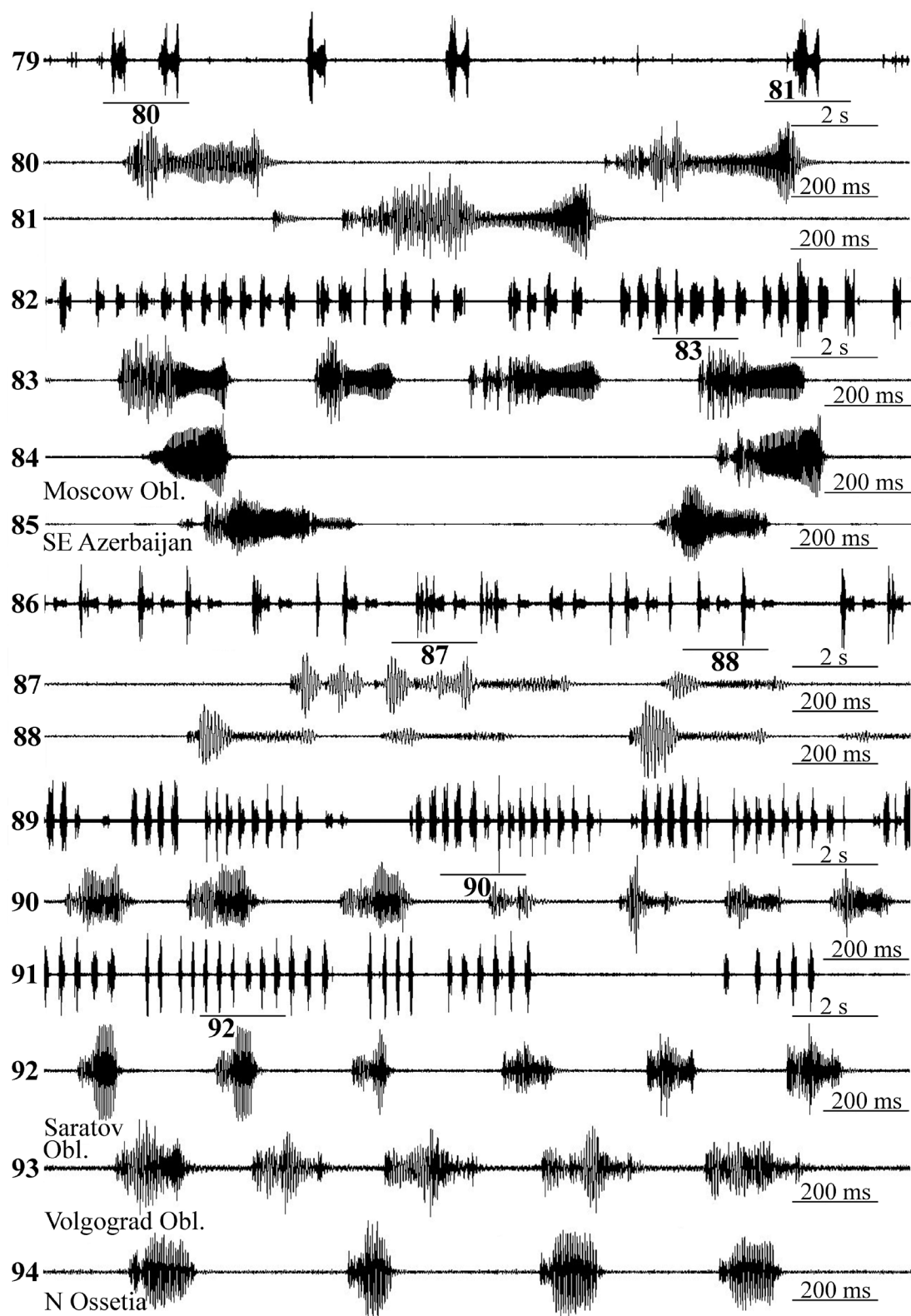
Figs 56–68. Male calling signals of Philaenini. 56–58 — *Aphilaenus ikumae*; 59–65 — *Paraphilaenus notatus*; 66–68 — *Philaenus signatus*. 56–57, 59–68 — oscillograms, 58 — oscillogram and sonogram at the same speed. Faster oscillograms of the parts of signals indicated as “57”, “60”, “63”, “65”, and “67–68” are given under the same numbers. Here and below, for species for which signal recordings from more than one locality are available, the signal recording localities are given under oscillograms.

Рис. 56–68. Призывные сигналы самцов Philaenini. 56–58 — *Aphilaenus ikumae*; 59–65 — *Paraphilaenus notatus*; 66–68 — *Philaenus signatus*. 56–57, 59–68 — осциллограммы, 58 — осциллограмма и сонограмма при одной скорости развертки. Фрагменты сигналов, помеченные цифрами “57”, “60”, “63”, “65” и “67–68”, представлены на осциллограммах под соответствующими номерами. Здесь и далее для видов, по которым имеются записи сигналов из нескольких точек, места записи сигналов указаны под осциллограммами.



Figs 69–78. Male calling signals of Philaenini. 69–75 — *Philaenus spumarius*; 76–78 — *Neophilaenus (Neophilaenus) lineatus*. 69–73, 75–76, 78 — oscillograms, 74, 77 — oscillogram and sonogram at the same speed. Faster oscillograms of the parts of signals indicated as “70–71”, “74”, and “77” are given under the same numbers.

Рис. 56–68. Призывные сигналы самцов Philaenini. 69–75 — *Philaenus spumarius*; 76–78 — *Neophilaenus (Neophilaenus) lineatus*. 69–73, 75–76, 78 — осциллограммы, 74, 77 — осциллограмма и сонограмма при одной скорости развертки. Фрагменты сигналов, помеченные цифрами “70–71”, “74” и “77”, представлены на осциллограммах под соответствующими номерами.



Figs 79–94. Oscillograms of the male calling signals of *Neophilaenus* spp. 79–81 — *N. (Neophilaenus) minor*; 82–85 — *N. (Neophilaenus) campestris*; 86–88 — *N. (Neophilaenus) haupti*; 89–90 — *N. (Neophilaenus) sachalinensis*; 91–94 — *N. (Neophilaenus) infumatus*. Faster oscillograms of the parts of signals indicated as “80–81”, “83”, “87–88”, “90”, and “92” are given under the same numbers.

Рис. 79–94. Осциллограммы призывных сигналов самцов *Neophilaenus* spp. 79–81 — *N. (Neophilaenus) minor*; 82–85 — *N. (Neophilaenus) campestris*; 86–88 — *N. (Neophilaenus) haupti*; 89–90 — *N. (Neophilaenus) sachalinensis*; 91–94 — *N. (Neophilaenus) infumatus*. Фрагменты сигналов, помеченные цифрами “80–81”, “83”, “87–88”, “90” и “92”, представлены на осциллограммах под соответствующими номерами.

identification of *Neophilaenus* species in Biedermann & Niedringhaus [2009].

The calling signal patterns in Philaenini are quite variable within each species and, at the same time, can be similar between congeneric species and even between species from different genera. In particular, the signals of *Ph. spumarius*, *N. (Neophilaenus) sachalinensis*, and *N. (Neophilaenus) infumatus* are indistinguishable (Figs 69–75, 89–90, and 91–94); on the other hand, the signals of congeneric *Ph. spumarius* and *Ph. signatus* are fundamentally different (Figs 66–68 and 69–75). This once again confirms the fact that in insects, ethological (in the case under consideration, acoustic) and morphological characters can evolve quite independently, so that species similar in morphology can distinctly differ in the signal patterns and *vice versa*; similar cases were described previously in other insect taxa (e.g., Heller [2006]; Tishechkin [2022]).

The signal pattern similarity is observed not only in allopatric species but also in species with overlapping ranges and similar ecological preferences. *Ph. spumarius*, being a transpalearctic species, common in both natural and anthropogenic landscapes in a wide variety of plant communities, could well be strictly sympatric with *N. (Neophilaenus) sachalinensis* and *N. (Neophilaenus) infumatus*. Thus, it is potentially capable of acoustic contact with each of these species, which could interfere with successful recognition of conspecific mates through vibrational communication. However, we have never collected these species in the same biotope. The same situation is observed in *N. (Neophilaenus) haupti* and *N. (Neophilaenus) minor* also producing similar signals. Despite geographical sympatry and similar habitat preferences, we have never found them in the same habitat. Evidently, they somehow avoid acoustic interactions, although this mutual avoidance mechanism is still unknown.

Thus, in Philaenini, unlike *Lepyronia* (Clovini) and *Aphrophora* (Aphrophorini), coloration and/or the male genitalia shape appears to be the most reliable characters for species identification. The use of the signal analysis for this purpose is limited because of numerous cases of the signal pattern similarity in different species.

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