ISSN 0013-8738, Entomological Review, 2022, Vol. 102, No. 1, pp. 20–40. © Pleiades Publishing, Inc., 2022.
Russian Text © The Author(s), 2022, published in Entomologicheskoe Obozrenie, 2022, Vol. 101, No. 1, pp. 29–57.

Seasonal Development of Plant Bugs (Heteroptera, Miridae): Subfamily Phylinae, Tribes Pilophorini, Hallodapini, and Phylini

D. L. Musolin[a,*] and A. Kh. Saulich[b]

[a] *St. Petersburg State Forest Technical University, St. Petersburg, 194021 Russia*

[b] *St. Petersburg State University, St. Petersburg, 199034 Russia*

**e-mail: musolin@gmail.com*

Received October 5, 2021; revised February 14, 2022; accepted February 14, 2022

Abstract—The review analyzes the available literature data on the seasonal development of plant bugs of the subfamily Phylinae distributed in the Holarctic Region. The data set concerns 39 species from 3 tribes: Pilophorini, Hallodapini, and Phylini. The tribe Pilophorini is represented by 5 species, 3 of which complete one generation per year and hibernate at the egg stage. However, there is no reason to believe that their annual cycles are obligatory univoltine, since they have been studied only in regions with a relatively cold climate. Two other species of this tribe, *Pilophorus confusus* and *P. typicus*, are multivoltine in regions with a warmer climate (Spain and Japan, respectively), where they also overwinter at the egg stage. The data on 3 species of the tribe Hallodapini indicate that they have similar seasonal cycles with a single generation per year and overwintering at the egg stage. The greatest diversity of seasonal patterns is known in the tribe Phylini. Two out of 5 *Chlamydatus* species included in this review overwinter as adults, although overwintering at the egg stage is generally characteristic of the family Miridae. Three species of this genus have a multivoltine seasonal cycle, and no data are available on the voltinism and overwintering stage of two other species, *Ch. allii* and *Ch. wilkinsoni*. Of the remaining 26 species of the tribe Phylini, 6 species have a multivoltine seasonal cycle and complete from 2 to 4 generations per year in different climatic zones. The bivoltine *Campylomma verbasci* from the same tribe has a seasonal adaptation unusual for true bugs, namely the shift of host plants during the year realized by different generations: after overwintering, the bugs move from woody plants to herbaceous ones. In general, the subfamily Phylinae is very species-rich and has highly diverse ecological characteristics, such as trophic specialization, voltinism, overwintering stage, seasonal shift of host plants, wing polymorphism, etc.

Keywords: biological control, day length, diapause, nymphal development, seasonal change of food plants, seasonal development, seasonal polymorphism, photoperiodic response, plant protection, true bugs, voltinism

DOI: 10.1134/S001387382201002X

This review continues the series of our publications on the seasonal adaptations of plant bugs (Heteroptera: Miridae) (Saulich and Musolin, 2019, 2020, 2021) and is devoted to species of the subfamily Phylinae, one of the largest in this family. The subfamily Phylinae unites 6 globally distributed tribes with a total of over 440 genera. Its highest species diversity is observed in areas with a Mediterranean climate and also in deserts and semi-deserts. Besides the Mediterranean proper, Asia Minor, and Central Asia in the Palaearctic, these are climatically similar territories in the south of North America in the Nearctic, South Africa, and southern and central Australia. The fauna of the temperate zone mainly includes species of three tribes: Pilophorini (16 genera), Hallodapini (56 genera), and Phylini (over 230 genera) (Schuh and Schwartz, 1988; Cassis and Schuh, 2012; Schuh and Weirauch, 2020).

This review is based on our own database of publications on the seasonal adaptations in Heteroptera and the online database *The Planetary Biodiversity Inventory (PBI) for Plant Bugs* (Schuh, 2012, 2021; Konstantinov

and Namyatova, 2019) containing data on distribution and trophic specialization of plant bug species and on the specimens kept in museum collections (data as of May 2021). The review includes 39 species for which at least basic information on phenology and voltinism is available.

Tribe **PILOPHORINI** Douglas et Scott, 1876

The tribe Pilophorini is represented in the Holarctic by about 150 species in 16 genera. All the studied species are zoophytophages, i.e., predators that additionally feed on plants. They are often associated with certain species of plants or types of vegetation (Schuh, 1991; Cassis and Schuh, 2012; Schuh and Weirauch, 2020).

Genus ***Pilophorus*** Hahn, 1826

The genus *Pilophorus* comprises about 130 species distributed in different zoogeographic regions, mostly in the Holarctic and Oriental regions. The bugs are zoophytophages feeding on aphids and other small insects; many species are myrmecomorphic (Southwood and Leston, 1959; Cassis and Schuh, 2012; Yasunaga et al., 2021).

Pilophorus cinnamopterus (Kirschbaum, 1856)

A Euro-Siberian species, widespread in the Palaearctic (Vinokurov et al., 2010) and unintentionally introduced to North America (Newfoundland) (Wheeler and Henry, 1992).

The bugs occur on pines (*Pinus* spp.) and larch trees (*Larix* spp.) (Southwood and Leston, 1959; Wheeler et al., 2006; Schuh, 2021). They are zoophytophages feeding on aphids (mainly of the tribe Cinarini), immature cones, needles, and resinous secretions of conifers (Kullenberg, 1944; Southwood and Leston, 1959; Wheeler, 2001). The bugs not only externally resemble ants but also mimic their behavior, which is characteristic of true mimicry (Wheeler et al., 2006).

The species is univoltine and overwinters at the egg stage. In Sweden, England, and France adults emerge in the second half of July and usually survive until early October (Kullenberg, 1944; Southwood and Leston, 1959; Ehanno, 1987). According to the label data of museum specimens, adults are predominantly recorded in nature from June to September (Table 1; Schuh, 2021).

Pilophorus clavatus (Linnaeus, 1767)

A Holarctic species (Vinokurov et al., 2010).

Both in European Russia and in the Russian Far East, the species has been recorded on a large number of broad-leaved trees and on shrubs, especially often on willows (*Salix* spp.) (Kerzhner, 1988). In Canada and the US, the species is known on willows (Kelton, 1980; Wheeler et al., 2006), oaks (*Quercus* spp.), and dogwoods (*Cornus* spp.) (Schuh and Schwartz, 1988).

The species is univoltine and overwinters at the egg stage. In England, nymphs occur in June–July, and adults, from July to September (Southwood and Leston, 1959; Schuh, 2021). The same timing of seasonal development was recorded for the Russian Far East (Kerzhner, 1988). Adults are predominantly recorded from July to September (see Table 1; Schuh, 2021).

Pilophorus confusus (Kirschbaum, 1856)

A Euro-Siberian species, unintentionally introduced to North America (Wheeler and Henry, 1992; Vinokurov et al., 2010).

The bugs usually occur on deciduous trees and shrubs (Schuh, 2021).

Diapausing eggs overwinter in young branches of various woody plants. In England, adult bugs commonly occur in July–August (Southwood and Leston, 1959). Adults are predominantly recorded from June to August (see Table 1; Schuh, 2021).

The seasonal cycle of *P. confusus* was studied in the south of Europe (Ramirez-Soria et al., 2018, 2019; as *P. gallicus* Remane, 1954), where this species plays an important role in control of the pear psyllid *Cacopsylla pyri* (L.) (Homoptera: Psyllidae) and other small arthropods damaging pear trees (Rosaceae: *Pyrus communis* L.). In Spain (Murcia Province: 38.4°N, 1.1°W), *P. confusus* completes three overlapping generations a year. Its active stages can be found on pear trees from March to early November (Sanchez and Ortin-Angulo, 2012). The species overwinters at the egg stage. Three years of observations have shown that the earliest nymphs appear from late March to late April, and adults of the first generation emerge in mid-May. These adults account for the first (spring) population peak that occurs at moderate temperatures and an increasing day length.

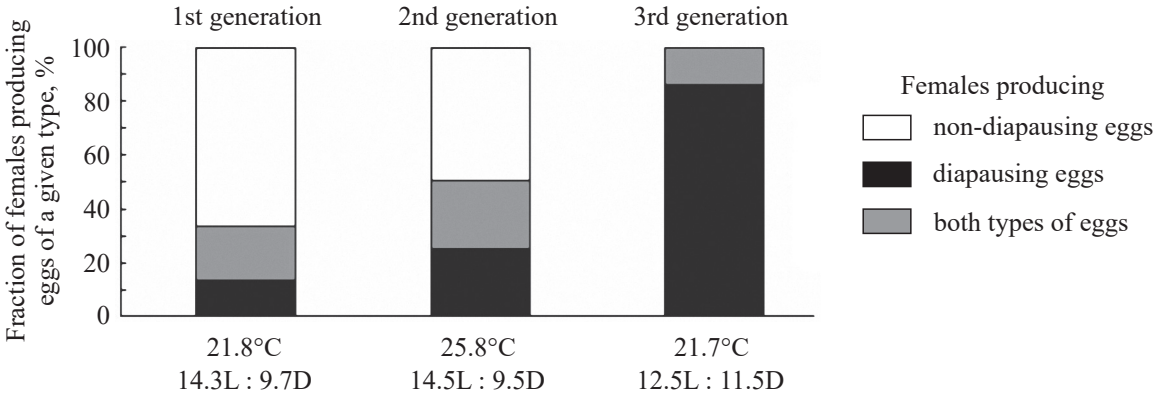

Fig. 1. Fractions of females of *Pilophorus confusus* (Kirschbaum) that produced diapausing eggs, non-diapausing eggs, and both types of eggs (in one batch) under natural conditions in Murcia Province, Spain, 38.4°N, 1.1°W (after Ramirez-Soria et al., 2018; as *Pilophorus gallicus* Remane). The mean temperature (°C) and day length (light : darkness; L : D) for the week preceding the collection of females in nature are indicated under each bar.

The second (summer) peak is the most pronounced and occurs during the period of the highest air temperatures and the longest day. The third (autumn) population peak coincides with a decrease in temperature and day length, and the bugs gradually disappear in nature since mid-October (Ramirez-Soria et al., 2018).

In a laboratory study, all the stages developed actively when kept under long-day (LD) conditions of 16 h of light and 8 h of darkness per day, whereas the embryonic diapause was induced under short-day (SD) conditions of 9 h of light and 15 h of darkness per day. In contrast to many other insects hibernating at the egg stage, the temperature (18 and 23°C) had a weak effect on embryonic diapause induction in *P. confusus*. Females laid two types of eggs: non-diapausing and diapausing. Nymphs hatched from non-diapausing eggs in 15 days at a temperature of 25°C and LD. When diapausing eggs were reactivated for 90 days at a low temperature of 6°C and LD and transferred to the conditions suitable for incubation (25°C and LD), nymphs started hatching on average in 22.3 ± 0.5 days (Ramirez-Soria et al., 2019).

This pattern was also observed under the natural conditions of southeastern Spain. The percentage of actively developing (i.e., non-diapausing) eggs was the greatest in the first generation of *P. confusus* and the lowest in the third generation, whereas that of diapausing eggs was greater in the last generation. Three categories of females were found: females of the first category laid only actively developing (non-diapausing) eggs, those of the second category laid only diapausing eggs, and females of the third category laid both types of eggs simultaneously. The proportion of females laying mixed egg batches only slightly varied between the generations: from 14.3 to 25.0%. In contrast, the proportions of females laying actively developing eggs and diapausing eggs varied strongly between the generations: females of the first category prevailed in the spring generation (66.7%) and their proportion strongly decreased in the autumn generation, while females of the second category were few in the spring generation and their proportion increased in the autumn generation (85.7%) (Fig. 1; Ramirez-Soria et al., 2018).

Pilophorus perplexus
Douglas et Scott, 1875

The species is distributed in Europe, North Africa (Madeira, Algeria, Morocco, Tunisia), and Asia (Georgia, Armenia, Azerbaijan, Iran), and was unintentionally introduced to North America (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999; Schuh, 2021).

The bugs usually occur on deciduous trees and shrubs (Schuh, 2021).

The species was studied in the south of England, where it is commonly found on oaks (*Quercus* spp.). Adults occur in nature from July to October; they feed on aphids (especially of the subfamily Lachninae), eggs and early-instar larvae of the codling moth, spider mites, and other small invertebrates. Eggs are laid in young twigs of the host plants. Nymphs hatch from the over-

Table 1. The main parameters of seasonal development of plant bugs of the subfamily Phylinae

Species	Country or region	Number of generations per year	Records of adults in nature (including data of museum collections)*	Over-wintering stage	Source of data
			Tribe **PILOPHORINI**		
Pilophorus cinnamopterus	England	1	July to early October	Egg	Southwood and Leston, 1959
	Sweden	1	–	Egg	Kullenberg, 1944
	France	1	–	Egg	Ehanno, 1987
	Europe, North America	1	MC: June–September (February: 1)	–	Schuh, 2021 (**115** records)
P. clavatus	England	1	July–September	Egg	Southwood and Leston, 1959
	Europe, North America	1	MC: June–September (January: 1)	–	Schuh, 2021 (**336** records)
P. confusus	England	1	July–August	Egg	Southwood and Leston, 1959
	Spain, France	3	Till mid-October	Egg	Sanchez and Ortin-Angulo, 2012
	Europe, North America	–	MC: June–August (January–June: 1–6 each; September: 6)	–	Schuh, 2021 (**265** records)
P. perplexus	England	1	July–October	Egg	Southwood and Leston, 1959
	Europe, North America	–	MC: June–September (January: 4; May: 2)	–	Schuh, 2021 (**549** records)
P. typicus	Japan	up to 4	Active nearly all year round	None	Yasunaga et al., 2021
	Asia	–	MC: May–December	–	Schuh, 2021 (**29** records)
			Tribe **HALLODAPINI**		
Hallodapus montandoni	England	1	Late July to September	Egg	Southwood and Leston, 1959
	Eurasia	1	MC: May–August (September: 3; October: 1)	–	Schuh, 2021 (**198** records)
H. rufescens	England	1	Early July to September	Egg	Southwood and Leston, 1959
	Eurasia	1	MC: July (June: 6; August: 6)	–	Schuh, 2021 (**25** records)
Systellonotus triguttatus	England	1	Late May to August	Egg	Butler, 1923; Southwood and Leston, 1959
	Eurasia	1	MC: May–August (September: 4)	–	Schuh, 2021 (**231** records)

Table 1. (Contd.)

Species	Country or region	Number of generations per year	Records of adults in nature (including data of museum collections)*	Over-wintering stage	Source of data
			Tribe **PHYLINI**		
Atomoscelis onusta	Kazakhstan	3	–	Egg	Asanova and Iskakov, 1977
	Eurasia, North Africa, North America	–	MC: March–October (January: 2; December: 5)	–	Schuh, 2021 (**2313** records)
Atractotomus magnicornis	England	1	Late June to September	Egg	Southwood and Leston, 1959
	Europe, North America	–	MC: June–August	–	Schuh, 2021 (**733** records)
A. mali	England	1	Late June to early August	Egg	Southwood and Leston, 1959
	Sweden	1	–	Egg	Kullenberg, 1944
	Norway	1	July to mid-August	Egg	Jonsson, 1985
	Canada	1	–	Egg	Ehanno, 1987
	Europe, North America, Central Asia	–	MC: June–August (January: 3; May: 6; September: 2)	–	Schuh, 2021 (**180** records)
Campylomma verbasci	Norway	1	July–October	Egg	Jonsson, 1985
	England	2	June–July and August–October	Egg	Southwood and Leston, 1959
	Spain	2	June–July and August–November	Egg	Torres et al., 1999
	Iran	3	–	–	Pourhadji, 2001
	Canada	2–4	September–October (last generation)	Egg	Thistlewood and Smith, 1996
	Eurasia, North America	–	MC: May–September (January: 5; April: 3; October: 1)	–	Schuh, 2021 (**764** records)
Chlamydatus allii	Kazakhstan	–	–	Adult	Asanova and Iskakov, 1977
	Russia	–	MC: July and September (April: 1; June: 7; August: 4)	–	Schuh, 2021 (**46** records)
Ch. evanescens	England	2	June–July; late August to October	Adult	Southwood and Leston, 1959
	Sweden	2	–	Adult	Kullenberg, 1944
	Eurasia (southeast)	–	MC: August (April: 1; July: 9; September: 1)	–	Schuh, 2021 (**38** records)

Table 1. (Contd.)

Species	Country or region	Number of generations per year	Records of adults in nature (including data of museum collections)*	Over-wintering stage	Source of data
Ch. pulicarius	Kazakhstan	2	May–November	Egg	Asanova and Iskakov, 1977
	Holarctic	–	MC: June–August (January: 1; May: 2; September: 3)	–	Schuh, 2021 (**445** records)
Ch. pullus	England	2	May to early July; late July to September	Egg	Southwood and Leston, 1959
	Kazakhstan	2–3	Late May to November	Egg	Asanova and Iskakov, 1977
	Holarctic	–	MC: May–August (January: 1; September: 8)	–	Schuh, 2021 (**309** records)
Chlamydatus wilkinsoni	England	–	May–August	–	Southwood and Leston, 1959
	Holarctic	–	MC: July–August (June: 4; September: 1)	–	Schuh, 2021 (**106** records)
Compsidolon salicellum	England	1	Late July to October	Egg	Southwood and Leston, 1959; Butler, 1923
	Eurasia, North America	–	MC: July–August (April: 1; June: 4; September: 7)	–	Schuh, 2021 (**102** records)
Europiella artemisiae	Kazakhstan	1–4	–	Egg	Asanova and Iskakov, 1977
	England	2	Late June to July; late August to October	Egg	Southwood and Leston, 1959
	Holarctic	–	MC: April–October (January: 7; February: 6; March: 1; November: 4; December: 2)	–	Schuh, 2021 (**2230** records)
Eu. decolor	England	1	Late June to early August	Egg	Southwood and Leston, 1959
	Holarctic	–	MC: February–October (January: 9; November: 4; December: 3)	–	Schuh, 2021 (**1397** records)
Megalocoleus molliculus	England	1	Early July to September	Egg	Southwood and Leston, 1959
	Eurasia, North America	–	MC: May–August (January: 12; March: 1; April: 1; September: 2; October: 2)	–	Schuh, 2021 (**933** records)
M. tanaceti	England	1	Mid-July to early September	Egg	Southwood and Leston, 1959
	Eurasia	–	MC: June–August (January: 9)	–	Schuh, 2021 (**144** records)

Table 1. (Contd.)

Species	Country or region	Number of generations per year	Records of adults in nature (including data of museum collections)*	Over-wintering stage	Source of data
Monosynamma bohemanni	England	1	Late June to early August	Egg	Southwood and Leston, 1959
	Holarctic	–	MC: June–September (January: 2; April: 3; May: 2)	–	Schuh, 2021 (**861** records)
Parapsallus vitellinus	England	1	Late June to early August	Egg	Southwood and Leston, 1959
Phoenicocoris obscurellus	England	1	Mid-June to late August	Egg	Southwood and Leston, 1959
	Eurasia	–	MC: June–August	–	Schuh, 2021 (**181** records)
Phylus coryli	England	1	Late June to early September	Egg	Southwood and Leston, 1959
	Eurasia, North America	–	MC: June–August (January: 2; May: 1)	–	Schuh, 2021 (**156** records)
Ph. melano-cephalus	England	1	June to early August	Egg	Southwood and Leston, 1959
	Europe	–	MC: June–July (January: 1; March: 1; May: 4; August: 5)	–	Schuh, 2021 (**109** records)
Plagiognathus arbustorum	England	1	July–September	Egg	Southwood and Leston, 1959
	Kazakhstan	1	June–October	Egg	Asanova and Iskakov, 1977
	Holarctic	–	MC: May–September (January: 20; February: 4)	–	Schuh, 2021 (**1313** records)
P. chrysanthemi	England	1	Late June to October	Egg	Southwood and Leston, 1959
	Canada	1	Late June to early September	Egg	Guppy, 1963
Plesiodema pinetella	England	–	Mid-June to late July	–	Southwood and Leston, 1959
	Eurasia	–	MC: May–July (April: 2; August: 5)	–	Schuh, 2021 (**144** records)
P. stlaniki	Japan	1	June–July	Egg	Yasunaga, 2003
	Asia	–	MC: June	–	Schuh, 2021 (**42** records)

Table 1. (Contd.)

Species	Country or region	Number of generations per year	Records of adults in nature (including data of museum collections)*	Over-wintering stage	Source of data
Psallus ambiguus	England	1	Late May to August	Egg	Southwood and Leston, 1959
	Norway	1	Mid-June to mid-July	Egg	Jonsson, 1985
	Eurasia	–	MC: June–July (May: 6; August: 4)	–	Schuh, 2021 (**163** records)
Ps. betuleti	England	1	Late May to August	Egg	Southwood and Leston, 1959
	Holarctic	–	MC: May–September (January: 1)	–	Schuh, 2021 (**318** records)
Ps. falleni	England	–	Late July to September	Egg	Southwood and Leston, 1959
	Holarctic	–	MC: July–August (June: 4; September: 6; October: 1)	–	Schuh, 2021 (**206** records)
Ps. lepidus	England	2	June to early September	–	Southwood and Leston, 1959
	Holarctic	–	MC: July (January: 1; March: 1; May: 4; June: 4; August: 7)	–	Schuh, 2021 (**29** records)
Ps. luridus	England	1	Mid-June to early August	Egg	Southwood and Leston, 1959
	Eurasia	–	MC: July–August (June: 4; September: 1)	–	Schuh, 2021 (**77** records)
Pseudatomoscelis seriatus	USA (Texas)	4–5	May–November	Egg	Gaylor and Sterling, 1977
	North America	–	MC: March–October (January: 1; February: 2; December: 1)	–	Schuh, 2021 (**1126** records)
*Solenoxyphus artemisia*e	Turkmenistan	2	May (?), June to early July	–	Kaplin, 1993
	Asia	–	MC: May	–	Schuh, 2021 (**6** records)
Tytthus pygmaeus	England	1	Mid-July to early September	Egg	Southwood and Leston, 1959
	Holarctic	–	MC: June–August (January: 2; April: 1; May: 1; September: 2)	–	Schuh, 2021 (**149** records)

* The records of adult bugs in museum collections were obtained from the online database *The Planetary Biodiversity Inventory (PBI) for Plant Bugs* (Schuh, 2021) as of May 8, 2021. These records are preceded by "MC:" and have the following layout: first the range of months when 10 or more adults per month were recorded, then (in parentheses) the number of records for those months when less than 10 adults were recorded. Data for January may be less accurate than those for other months because, when the collection date is absent in the label but the corresponding *Collection Date* field of the database cannot be left blank, the problem is often circumvented by entering the conditional date 01.01. The total number of records in the database as of May 8, 2021 is given in bold in the "Source of data" column for each species. Dash indicates the absence of data.

wintered eggs in May–June of the following year. The species has one generation a year (Southwood and Leston, 1959). Adults are predominantly recorded from June to September (see Table 1; Schuh, 2021).

Pilophorus typicus (Distant, 1909)

The species is distributed in Southeast Asia (Kerzhner and Josifov, 1999; Yasunaga et al., 2014, 2021; Schuh, 2021).

The bugs feed on various herbaceous plants, including such vegetable crops as cucumbers, eggplants, red peppers, pumpkins, etc., and often act as greenhouse pests. Nymphs occur on plants of the families Acanthaceae, Asteraceae, Convolvulaceae, Ericaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Rutaceae, Solanaceae, and Urticaceae. This is a zoophytophagous species attacking thrips, whiteflies, leafhoppers, and spider mites, and ecologically closely associated with ants (Yasunaga et al., 2021).

In the south of Japan (Kyushu and Ryukyu islands), *P. typicus* is active almost year-round, all the stages of development occurring throughout the year. According to many-year observation data, in Nagasaki (32.8°N, 129.9°E) the species completes four generations a year (Yasunaga et al., 2021). Adults are mainly recorded from May to December (see Table 1; Schuh, 2021).

Pilophorus typicus was studied in Japan (Shikoku Island: Nankoku, Kochi Prefecture, 33.6°N, 133.6°E) as a promising control agent to be used against the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), the main pest of tobacco in Southeast Asia. In the laboratory the bugs were fed on leaves of *Sedum rubrotinctum* (Saxifragales: Crassulaceae) and frozen eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), and the developmental parameters of all the stages from egg to adult were studied within a wide range of temperatures: from 17.5 to 30.0°C (Nishikawa et al., 2010). It was found out that the developmental time of individual stages strongly depended on the temperature but was close in different sexes. The duration of development from egg to adult was 72.0 ± 4.5 days at 17.5°C and 20.7 ± 1.1 days at 30.0°C (mean ± SD) (Nishikawa et al., 2010).

The following regression equations for the development rate were determined within the temperature range 17.5–30.0°C: $1/Y = -0.0337 + 0.0028T$, $r^2 = 0.9953$ for females and $1/Y = -0.0340 + 0.0028T$, $r^2 = 0.9854$ for males, where Y is the developmental time and T is the temperature. The lower temperature thresholds and the sums of effective temperatures required for completion of development from egg to adult were also determined: 12.0°C and 357.1 degree-days for females; 12.1°C and 357.1 degree-days for males. The cited researchers concluded that the most favorable temperatures for rearing *P. typicus* were close to 25.0–27.5°C. At the same time, since the food used in rearing the bugs under the experimental conditions was too expensive, an alternative food source should be found before *P. typicus* can be effectively used as a biological control agent (Nishikawa et al., 2010).

Tribe **HALLODAPINI** Van Duzee, 1916

This is a relatively small, globally distributed tribe including 64 genera (Cassis and Schuh, 2012). Most of its species are associated with ants, and many are myrmecomorphic.

Genus ***Hallodapus*** Fieber, 1858

Hallodapus montandoni Reuter, 1895

The species is distributed in Europe, the Caucasus, and Central Asia, as far eastward as Mongolia and Northwest China (Kerzhner and Josifov, 1999; Konstantinov and Vinokurov, 2011).

In England the bugs can be found in meadows, usually on bare ground between grass sods. They attack the ants *Myrmica scabrinodis* Nylander (Hymenoptera: Formicidae), with which they usually co-occur. Long-winged individuals are extremely rare.

The species is univoltine and overwinters at the egg stage. Nymphs appear in early June; adults emerge in late July and usually survive until September (Southwood and Leston, 1959). Judging by the museum collections, adults are predominantly recorded from May to August (see Table 1; Schuh, 2021).

Hallodapus rufescens (Burmeister, 1835)

A Euro-Siberian species (Vinokurov et al., 2010).

These bugs are typical inhabitants of the soil surface, preferring open, well heated biotopes; in particular, in

Siberia they are common in meadows (Vinokurov and Kanyukova, 1995). In England, they occur in heathlands. The short-winged form predominates in the populations, while long-winged individuals are rare (Southwood and Leston, 1959).

The species is univoltine. In England, adults emerge in early July and survive until September. Hibernation occurs at the egg stage (Southwood and Leston, 1959). Adults are recorded from June to August (see Table 1; Schuh, 2021).

Genus ***Systellonotus*** Fieber, 1858

Systellonotus triguttatus (Linnaeus, 1767)

The species is distributed in Europe; within Asia, it has been recorded in Armenia, Kazakhstan, and Tyumen Province of Russia (Vinokurov and Kanyukova, 1995; Kerzhner and Josifov, 1999; Konstantinov and Namyatova, 2008).

In England, the bugs inhabit open sandy areas overgrown with heather, usually co-occurring with the ants *Formica fusca* L. or *Lasius niger* (L.) which they externally resemble. Nymphs and adults are zoophytophages that consume both plant and animal food but never attack living ants. Their plant diet includes sap from the buds, young shoots, and immature fruits of heather and sheep fescue *Festuca ovina*; the bugs also suck honeydew and can feed on galls on willows. Their animal food consists mainly of aphids. Males are always long-winged; the myrmecomorphic females are usually short-winged (Southwood and Leston, 1959).

The species is univoltine and overwinters at the egg stage. Eggs are laid in bark fissures, in particular, of the creeping willow *Salix repens*. Nymphs hatch in the spring of the following year, and adults can be found in nature from late May to mid-August. Adults are predominantly recorded from May to August (see Table 1; Schuh, 2021).

Tribe **PHYLINI**
Douglas et Scott, 1865

This is one of the largest tribes of the subfamily Phylinae, comprising over 136 Palaearctic genera and over 100 Nearctic genera (Cassis and Schuh, 2012; Schuh and Weirauch, 2020).

Genus ***Atomoscelis*** Reuter, 1875

Atomoscelis onusta (Fieber, 1861)

A West-Central Palaearctic species, unintentionally introduced to North America (Wheeler and Henry, 1992; Vinokurov et al., 2010).

The bugs are trophically associated with wild chenopods (Amaranthaceae) and also damage many crops: beets, corn, pumpkins, and melons (Asanova and Iskakov, 1977; Vinokurov and Kanyukova, 1995; Schuh, 2021).

The species overwinters at the egg stage. In Kazakhstan, it has three generations a year, with pre-adult development taking about one month (Asanova and Iskakov, 1977). Adults are commonly recorded from March to October (see Table 1; Schuh, 2021).

Genus ***Atractotomus*** Fieber, 1858

Atractotomus magnicornis
(Fallén, 1807)

A European species, unintentionally introduced to North America (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999).

According to observations in England, the bugs usually live on spruces (*Picea* spp.) and rarely occur on other conifers (Southwood and Leston, 1959). They have been found on many species of pines (*Pinus* spp.) (Schuh, 2021).

The species overwinters at the egg stage. Adults emerge in late June or early July and survive until September. Eggs are laid on the host plants, and nymphs hatch in the following spring. The species is univoltine (Southwood and Leston, 1959). Adults are predominantly recorded in nature from June to August (Table 1; Schuh, 2021).

Atractotomus mali (Meyer-Dür, 1843)

A Palaearctic species, unintentionally introduced to North America (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999).

The bugs are phytozoophages feeding on spider mites, aphids and their sugary secretions, lepidopteran larvae and pupae, and other small insects. In Kazakhstan

they are known as predators destroying apple ermine larvae in their nests (Asanova and Iskakov, 1977). They may also feed by cannibalism (Collyer, 1953). The main host plants are trees and shrubs of the family Rosaceae, though the bugs have been found on plants of many other families, including conifers (Schuh, 2021).

The seasonal cycle is univoltine in Europe and the northern regions of North America (Canada) (Kullenberg, 1944; Jonsson, 1985; Ehanno, 1987). According to observations in England, the species also has one generation a year; eggs overwinter, and adults occur in nature from late June to early August (Southwood and Leston, 1959). Adults are predominantly recorded from June to August (see Table 1; Schuh, 2021).

Genus ***Campylomma*** Reuter, 1878

Campylomma verbasci (Meyer-Dür, 1843)
(mullein plant bug)

A West-Palaearctic species, distributed in the entire North Africa, Europe, Transcaucasia, Turkey, Central Asia, and northeastern China (Konstantinov and Vinokurov, 2011). It was discovered on the British Isles as late as the 1930s (Wheeler and Henry, 1992). This is an adventive species in North America (Kerzhner and Josifov, 1999).

In Europe, the species used to be considered of no importance to agriculture, but in 1990 significant damage was reported in apple orchards in the Netherlands, Belgium, and Bulgaria (Wheeler, 2000a, 2000b). The bugs are phytozoophages feeding on small insects: thrips, whiteflies, aphids, and small lepidopteran larvae. In Kazakhstan, they reach high densities on cotton plants where they feed on spider mites (Asanova and Iskakov, 1977). The species has been found on many deciduous trees (Schuh, 2021).

The species completes 2 generations a year over most of its European range (Southwood and Leston, 1959; Niemczyk, 1978; Torres et al., 1999), 1 generation in Norway (60°N) (Skanland, 1980; Jonsson, 1983, 1985), and 3 generations in Iran (Pourhadji, 2001). Eggs overwinter in diapause (Thistlewood and Smith, 1996). Adults are predominantly recorded from May to September (see Table 1; Schuh, 2021).

This species is characterized by a change of host plants during the season. Nymphs of the first (overwintered) generation feed on woody plants. Adults of this generation emerge in June–July and migrate to herbaceous plants, more often to the great mullein *Verbascum thapsus*, where they give rise to the second generation that develops entirely on herbaceous plants. In August–October, adults of the second generation return from grasses to woody plants, mainly to apple and pear trees, where they lay eggs to overwinter in the young stems (Southwood and Leston, 1959).

The seasonal development of *C. verbasci* was extensively studied in Canada, because after naturalization of this species in North America it became an important pest of orchard trees. The punctures made by the feeding early-instar nymphs in the setting apple and pear fruits appear later as dark corky scars, reducing the quality and commercial value of fruit. The nymphs of *C. verbasci* also feed as predators and destroy small insects; however, in the overall balance the damage caused by nymphs feeding on apple trees outweighs their utility as predators. In contrast, on pear trees *C. verbasci* is the most important predator of the pear psyllid *Psylla pyri* L.; therefore, it was recommended to preserve this bug in pear crops (Thistlewood and Smith, 1996).

In Canada (Richmond, British Columbia, 49.2°N, 123.1°W; Ontario, Quebec, 46.8°N, 71.2°W), the species usually produces 2 or 3, and rarely even 4 generations a year. Nymphs of the first generation hatch from overwintered eggs in early May, when apple and pear trees start blossoming. In some years, up to 50% of the nymphs hatch within 3–4 days. The nymphs live in inflorescences or in silky nests of lepidopteran larvae. In early June, most of the emerging adults migrate to herbaceous plants and form several generations there; adults of the last generation return to fruit trees in September–October and lay overwintering eggs (Thistlewood et al., 1990; Thistlewood and Smith, 1996).

The developmental time of *C. verbasci* nymphs was estimated by different authors under laboratory conditions. The nymphal stage was completed in 23 days at 21°C (McMullen and Jong, 1970), in 21 days at 22°C (Smith and Borden, 1991), and in 16 days at 23°C (Niemczyk, 1978). Animal food is required for nymphal development, although pollen can partly compensate for the lack of proteins (Bartlett, 1996).

The results of laboratory studies at different constant temperatures were used in developing a model to predict

the timing of nymphs hatching from overwintered eggs under natural conditions (Judd and McBrien, 1994).

Genus ***Chlamydatus*** Curtis, 1833

Chlamydatus allii V.G. Putshkov, 1959

A Eurasian steppe species (Vinokurov et al., 2010).

In European Russia, the bugs have been recorded on wild garlic (*Allium* spp.), and they are known to damage the leek *Allium porrum* L. (Vinokurov et al., 2010).

The species overwinters at the adult stage (Asanova and Iskakov, 1977). In Russia adults are recorded in July and September, and sporadically in other months (see Table 1; Schuh, 2021).

Chlamydatus evanescens (Boheman, 1852)

A Eurasian species (Kerzhner and Josifov, 1999)

The bugs feed on *Lepidium* spp., less commonly on *Sedum* spp. (Southwood and Leston, 1959).

In England, the species completes two generations a year. Adults of the summer generation emerge in June and early July, those of the autumn generation, in late August and September and even in October; they overwinter and reactivate in May of the following year. Eggs are laid on the leaves of the host plant. The color of the hatching nymphs matches that of the young leaves (Southwood and Leston, 1959). Overwintering of the species at the adult stage was also observed in Sweden (Kullenberg, 1944). Adults are commonly recorded in August (see Table 1; Schuh, 2021).

Chlamydatus pulicarius (Fallén, 1807)

A Holarctic species (Schuh and Schwartz, 2005; Schuh, 2021).

In Siberia, the bugs are more often found in meadows (Vinokurov and Kanyukova, 1995). Similar to *Ch. pullus*, *Ch. pulicarius* is a polyphagous species (Putshkov, 1972; Schuh, 2021). In Kazakhstan, the bugs also occur on corn, beets, and buckwheat.

The species is bivoltine and overwinters at the egg stage (Asanova and Iskakov, 1977). Adults are predominantly recorded from June to August (see Table 1; Schuh, 2021).

Chlamydatus pullus (Reuter, 1870)

A Holarctic species (Schuh and Schwartz, 2005; Vinokurov et al., 2010).

The bugs damage many field and vegetable crops, being more common on alfalfa, sainfoin, and clover.

The species largely produces 2 generations a year in Kazakhstan, and 3 generations in the southern regions. It overwinters at the egg stage. Adults occur from late May to late autumn (Asanova and Iskakov, 1977).

The species was studied in England, where the bugs can often be found on sorrels (*Rumex* spp.) and the common knotgrass *Polygonum aviculare* L., though their main host plants are the white clover *Trifolium repens* L. and the hop clover *Medicago lupulina* L. Two generations are completed in a year. Adults of the first generation emerge in late May and early June, those of the second generation, in late July, and some of them survive until late September. The species overwinters at the egg stage. Adults of both sexes are always long-winged (Southwood and Leston, 1959).

Adults are predominantly recorded from May to August (see Table 1; Schuh, 2021).

Chlamydatus wilkinsoni
(Douglas et Scott, 1866)

A Holarctic circumpolar species (Vinokurov et al., 2010; Schuh, 2021).

In Siberia, the bugs occur on goosefoots, often in wetlands and mountain tundra (Vinokurov and Kanyukova, 1995).

In England, adults can be found from May to August. They are usually short-winged, while long-winged individuals of both sexes are very rare (Southwood and Leston, 1959). Adults are most commonly recorded in July and August in different parts of the species' range (see Table 1; Schuh, 2021).

Genus ***Compsidolon*** Reuter, 1899

Compsidolon salicellum
(Herrich-Schaeffer, 1841)

A Euro-Siberian species, unintentionally introduced to North America (Wheeler and Henry, 1992; Vinokurov et al., 2010).

The bugs live on blackberries and other herbaceous and woody plants, including the common hazel *Corylus avellana* (L.) H. Karst., willows (*Salix* spp.), alders (*Alnus* spp.), and apple trees (*Malus* spp.) (Schuh, 2021). They are zoophytophages feeding on small insects and mites.

In England, the species can be found from late July to October. It overwinters at the egg stage (Southwood and Leston, 1959).

Genus ***Europiella*** Reuter, 1909

Europiella artemisiae (Becker, 1864)

A Holarctic species (Schuh, 2004; Vinokurov et al., 2010).

The bugs damage vegetable and field crops. In the wild they are trophically associated only with various wormwoods (*Artemisia* spp.) (Asanova and Iskakov, 1977).

The species is multivoltine and overwinters at the egg stage. It produces 1 or 2 generations a year in the northern regions of Kazakhstan, and 3 or 4 generations in the south (Asanova and Iskakov, 1977). The species was studied in England, where it also has two generations a year. Adults of the first generation appear in late June and July, those of the second generation, from late August to October (Southwood and Leston, 1959). Adults are predominantly recorded from April to October in different parts of the species' range (see Table 1; Schuh, 2021).

Europiella decolor (Uhler, 1893)

A Holarctic species (Schuh, 2004; Vinokurov et al., 2010).

The main host plants belong to the genera *Artemisia* and *Chrysothamnus* (Asteraceae), although in the Palaearctic the bugs also feed on Lamiaceae. Unlike most species of the subfamily Phylinae, these bugs are commonly found on plants that are not yet in bloom (Schuh, 2004).

In England, adults emerge in late June and early July and become already rare in early August. The species produces one generation a year, with eggs overwintering and nymphs hatching in May of the following year (Southwood and Leston, 1959). These observations are not quite consistent with the label data of museum specimens, according to which adults are predominantly recorded from February to October, with a peak of occurrence in June–August (see Table 1; Schuh, 2021).

Genus ***Megalocoleus*** Reuter, 1890

Megalocoleus molliculus (Fallén, 1807)

A trans-Palaearctic species, unintentionally introduced to North America (Wheeler and Henry, 1992; Vinokurov et al., 2010).

The bugs are common on yarrows (*Achillea* spp.) and other composites (Southwood and Leston, 1959; Vinokurov and Kanyukova, 1995; Matocq, 2004).

The seasonal cycle of the species was studied in England, where it overwinters at the egg stage; nymphs hatch in early June, and adults emerge in early July and can be found until September. One generation a year is produced (Southwood and Leston, 1959). Adults are predominantly recorded from May to August (Table 1; Schuh, 2021).

Megalocoleus tanaceti (Fallén, 1807)

A Euro-Siberian species (Matocq, 2004; Vinokurov et al., 2010).

In England, the bugs commonly occur on buds, flowers, and immature fruits of tansy (*Tanacetum* spp.; Asteraceae).

Adults can be found from mid-July to early September. Females lay overwintering eggs in the stems of blossoming plants, usually at the base of the secondary corymbs. Nymphs hatch the following summer. One generation a year is produced (Southwood and Leston, 1959). Adults are predominantly recorded from June to August (see Table 1; Schuh, 2021).

Genus ***Monosynamma*** Scott, 1864

Monosynamma bohemanni (Fallén, 1829)

A Holarctic species (Vinokurov et al., 2010; Schuh, 2021).

In Siberia, the bugs live on willows (*Salix* spp.) (Vinokurov and Kanyukova, 1995); in England, they also

inhabit willows, but only those growing on coastal sand dunes. The species is also known from legumes, composites, and other herbaceous and some woody plants (Schuh, 2021).

Adults occur from late June to early August. The species is univoltine and overwinters at the egg stage (Southwood and Leston, 1959). Adults are predominantly recorded from June to September (see Table 1; Schuh, 2021).

Genus ***Parapsallus*** Wagner, 1952

Parapsallus vitellinus (Scholtz, 1847)

A trans-Eurasian species, unintentionally introduced to North America (Wheeler and Henry, 1992; Vinokurov et al., 2010).

The bugs commonly occur on conifers, often on larch trees (*Larix* spp.).

In England, adults occur from late June to early August. The species is univoltine and overwinters at the egg stage (Southwood and Leston, 1959).

Genus ***Phoenicocoris*** Reuter, 1875

Phoenicocoris obscurellus (Fallén, 1829)

A Euro-Siberian species, widespread from the west of Europe, including the British Isles, Portugal, and Italy, to the Russian Far East (Kerzhner and Josifov, 1999; Schwartz and Stonedahl, 2004; Vinokurov et al., 2010).

The bugs commonly occur on the Scots pine *Pinus sylvestris* L.; in France, also on the common juniper *Juniperus communis* L. (Schwartz and Stonedahl, 2004).

In England, the earliest adults appear in mid-June and can be found until the end of August. The species is univoltine and overwinters at the egg stage (Butler, 1923; Southwood and Leston, 1959). Adults are predominantly recorded from June to August (see Table 1; Schuh, 2021).

Genus ***Phylus*** Hahn, 1831

Phylus coryli (Linnaeus, 1758)

A species widespread in Europe, recorded in Transcaucasia and Turkey, and unintentionally introduced to North America (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999; Aukema et al., 2013).

The bugs usually live on hazel and feed on aphids, psyllids (Psyllidae), and other small insects (Southwood and Leston, 1959).

Eggs are laid in the young shoots near the stipules. Nymphs hatch in late May and early June. The earliest adults emerge in late June, and only a few of them survive until mid-August or early September. The species is univoltine (Butler, 1923; Southwood and Leston, 1959). Adults are predominantly recorded from June to August (Table 1; Schuh, 2021).

Phylus melanocephalus (Linnaeus 1767)

A European species; within Asia, it was recorded in Georgia, Armenia, and Turkey (Kerzhner and Josifov, 1999; Aukema et al., 2013).

The bugs commonly occur on oaks (*Quercus* spp.). They are phytozoophages feeding on aphids and other small insects.

Adults appear in the first half of June and survive until early August. Overwintering eggs are laid near the buds of young oaks. Nymphs hatch in mid-May. The species is univoltine (Southwood and Leston, 1959). Adults are predominantly recorded in June and July (see Table 1; Schuh, 2021).

Genus ***Plagiognathus*** Fieber, 1858

Plagiognathus arbustorum (Fabricius, 1794)

A Holarctic species (Schuh, 2001; Vinokurov et al., 2010). This is one of the commonest species of the family Miridae in England.

The bugs occur on various herbaceous plants, especially often on nettles (*Urtica* spp.) (Southwood and Leston, 1959; Schuh, 2021). In Kazakhstan, they prefer humid habitats. The species is phyzootophagous (Southwood and Leston, 1959) and polyphagous. The bugs damage peas and alfalfa (Asanova and Iskakov, 1977).

According to observations in England, nymphs hatch in May, and the earliest adults emerge in early July; in Kazakhstan, adults appear in mid-June and die off by the end of September. The species is univoltine and overwinters at the egg stage (Southwood and Leston,

1959; Asanova and Iskakov, 1977). Adults are predominantly recorded from May to September (Table 1; Schuh, 2021).

Plagiognathus chrysanthemi
(Wolff, 1804)

A trans-Palaearctic species, unintentionally introduced to North America (Wheeler and Henry, 1992; Schuh, 2001; Vinokurov et al., 2010).

At high densities the bugs damage alfalfa, clover, and sainfoin crops; the species is regarded as a minor pest of herbaceous legumes (Putshkov, 1972; Asanova and Iskakov, 1977). In Canada, the bugs strongly damage legumes, especially the deervetch *Lotus corniculatus* L. that is usually grown for seeds (Guppy, 1963). In England, the species can be found in wastelands on ragworts (*Senecio* spp.), mayweeds (*Anthemis* spp.), yarrows (*Achillea* spp.), and other composites (Southwood and Leston, 1959).

According to observations in England, nymphs hatch in late May. The earliest adults emerge in late June, and some adults survive until October. Eggs are laid in July–August and overwinter, so that nymphs hatch in the spring of the following year. The species is known to be univoltine both in England (Southwood and Leston, 1959) and in the northern regions of North America (Canada) (Guppy, 1963).

Genus ***Plesiodema*** Reuter, 1875

Plesiodema pinetella (Zetterstedt, 1828)

A West-Central Palaearctic species (Schwartz, 2006; Vinokurov et al., 2010).

Adults can be found on various conifers (*Pinus* spp., *Picea* spp., *Larix* spp.) (Schwartz, 2006) from mid-June to late July (Southwood and Leston, 1959).

There is no exact information about the overwintering stage, though other species of this genus are known to overwinter as eggs (Yasunaga, 2003). Adults are predominantly recorded from May to July (see Table 1; Schuh, 2021).

Plesiodema stlaniki Kerzhner, 1979

The species is distributed in Siberia and the Russian Far East (Kerzhner and Josifov, 1999; Vinokurov et al., 2010), and also in Japan (the islands of Hokkaido and Honshu: Yasunaga, 2003).

In Japan, the bugs were found in the alpine belt on *Pinus pumila* Regel (Kerzhner, 1978, 1979).

The species is univoltine and overwinters at the egg stage. Nymphs occur in June and July (see Table 1; Yasunaga, 2003; Schuh, 2021).

Genus ***Psallus*** Fieber, 1858

Psallus ambiguus Fallén, 1807

A European-East Mediterranean species that is known, besides Europe, also from Georgia, Azerbaijan, Turkey, and Iran (Kerzhner and Josifov, 1999; Aukema et al., 2013).

The species was studied in detail in England, where it is widespread. The bugs commonly occur on apple trees (*Malus* spp.), hawthorns (*Crataegus* spp.), willows (*Salix* spp.), and other, predominantly woody plants. They are phytozoophages, both nymphs and adults consuming not only plant food but also aphids and other small insects (Southwood and Leston, 1959; Schuh, 2021).

Adults occur from late May to August in England and from mid-June to mid-July in Norway. Eggs are laid in young twigs of trees; nymphs hatch in May of the following year. The species is univoltine (Southwood and Leston, 1959; Jonsson, 1985). Adults are predominantly recorded in June and July (see Table 1; Schuh, 2021).

Psallus betuleti (Fallén, 1826)

A Holarctic species (Vinokurov et al., 2010; Schuh, 2021).

The bugs have been found on Betulaceae, mainly on birches (*Betula* spp.) and alders (*Alnus* spp.) (Kerzhner, 1978; Schuh, 2021). They are phytozoophages feeding on small insects, including aphids (Butler, 1923; Southwood and Leston, 1959).

In England, nymphs hatch in late April and early May. Adults emerge in late May and the first half of June and can be found until August (Southwood and Leston, 1959). Similar dates of adult emergence were recorded in the Netherlands (Aukema, 2008). Eggs are laid in young shoots of birch trees and overwinter. The species is univoltine (Southwood and Leston, 1959). Adults are

predominantly recorded from May to September (see Table 1; Schuh, 2021).

Psallus falleni Reuter, 1883

A Holarctic species (Vinokurov et al., 2010).

The bugs occur on plants of the family Betulaceae (Kerzhner, 1978; Yasunaga and Vinokurov, 2000; Schuh, 2021).

In England, adults are especially numerous from late July to September, and occasional nymphs can be found even in early August. The species probably overwinters at the egg stage (Butler, 1923; Southwood and Leston, 1959). Adults are predominantly recorded from May to September (see Table 1; Schuh, 2021).

Psallus lepidus Fieber, 1858

The species is distributed in Europe and North Africa; within Asia it is known from Armenia and Azerbaijan. It was unintentionally introduced to North America (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999).

In England, adults occur on ash trees (*Fraxinus* spp.) from mid-June to early September, and nymphs can be found even as late as August. In the opinion of Southwood and Leston (1959), the species probably produces two generations a year. Adults are mostly recorded from May to September (see Table 1; Schuh, 2021).

Psallus luridus Reuter, 1878

A Euro-Siberian species (Vinokurov et al., 2010).

In England, the bugs inhabit young trees of European larch *Larix decidua*. Adults can be found from mid-June to early August. The species is univoltine and overwinters at the egg stage (Southwood and Leston, 1959). Adults are predominantly recorded in July and August (see Table 1; Schuh, 2021).

Genus ***Pseudatomoscelis*** Poppius, 1911

Pseudatomoscelis seriatus (Reuter, 1876)
(cotton fleahopper)

A Nearctic species (Schuh, 2021).

The bugs damage cotton plants in the USA. They are polyphages feeding on over 35 plant species and preferring species of the genus *Croton* (Snodgrass et al., 1984).

The species is multivoltine (Gaylor and Sterling, 1977). The seasonal development of its population was studied in Texas, USA (30.6°N, 96.3°W). From September to November females concentrate on blossoming hogworts *Croton capitatus* Michx. and lay diapausing eggs in their stems. Nymphs hatch in March and April, and newly emerged adults of the first generation migrate to various species of early-spring ephemeroid plants. As these plants become less attractive to bugs, the adults migrate to cotton fields and produce several generations there. In autumn the bugs migrate back to hogwort plants (Gaylor and Sterling, 1977; Breene et al., 1989).

The onset of facultative embryonic diapause in this species was found to depend on the living conditions of nymphs of the maternal generation. The highest sensitivity to day length was observed in early-instar nymphs (up to the III instar). The production of diapausing egg was controlled by the photoperiodic response of a long-day type with a threshold between 12 and 13 h at 26.7°C. If early-instar nymphs developed at a photophase shorter than the threshold one, the females laid diapausing eggs (Fig. 2; Gaylor and Sterling, 1977).

The embryonic diapause was terminated under the influence of low temperatures. The greatest proportion of nymphs hatched from the diapausing eggs stored at about +4°C (Gaylor and Sterling, 1977).

Adults are predominantly recorded from March to October (Table 1; Schuh, 2021).

Genus ***Solenoxyphus*** Reuter, 1875

Solenoxyphus artemisiae Putshkov, 1978

The species is distributed in Turkmenistan and Uzbekistan (Konstantinov, 2008).

The species was originally described by Putshkov (1978) based on specimens collected from *Artemisia badghysi* Krasch. et Lincz. ex Poljakov (Asteraceae). According to observations in the eastern part of the Kara-Kum Desert (Kaplin, 1993), its main host plants are *Kochia odontoptera* Schrenk, *Londesia eriantha* Fisch. et C.A. Mey., *Salsola sclerantha* (C.A. Mey.) Akhani et Roalson, and *S. carinata* C.A. Mey. (Chenopodiaceae).

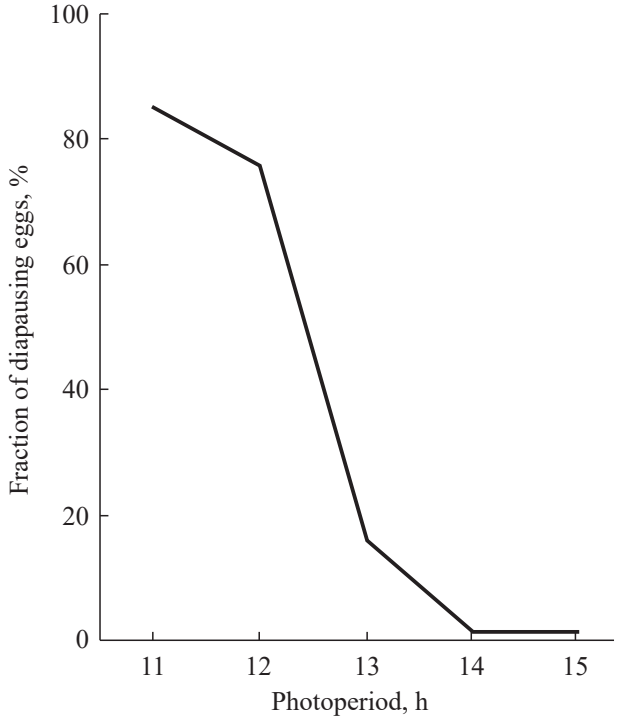

Fig. 2. Photoperiodic induction of embryonic diapause in *Pseudatomoscelis seriatus* (Reuter) at 26.7°C (Texas, USA, 30.6°N, 96.3°W; after Gaylor and Sterling, 1977). Bugs of the maternal generation were kept at constant day lengths and temperatures.

Two generations are produced annually; nymphs of the second generation can be found until late June, and adults that develop from them, in early July (Kaplin, 1993). The few adults kept in museums were collected in May (see Table 1; Schuh, 2021).

Genus ***Tytthus*** Fieber, 1864

Tytthus pygmaeus (Zetterstedt, 1838)

A Holarctic species (Vinokurov et al., 2010; Schuh, 2021).

The bugs live on sedges in humid biotopes in Siberia (Vinokurov and Kanyukova, 1995). The same information was reported for Canada (Kelton, 1980).

Adults emerge since mid-July and usually survive until early September. The species overwinters at the egg stage. Adults are always long-winged. Both nymphs and adults are predators feeding on eggs and small nymphs of leafhoppers (Cicadellidae) (Southwood and Leston, 1959). Adults are predominantly recorded from June to August (see Table 1; Schuh, 2021).

DISCUSSION

Analysis of the currently available data on voltinism and phenology of the 39 most studied species of the subfamily Phylinae in the Holarctic fauna show that most of the studied species are those of economic importance: either biological control agents or pests of economically important crops. The ecophysiological responses controlling the seasonal development of bugs, e.g., the pre-adult development rate, diapause induction and termination, and wing dimorphism, remain practically unstudied even in such a species-rich subfamily as Phylinae.

Five Holarctic species of the tribe **Pilophorini** have been studied in this respect. Three of them, distributed in the temperate zone, complete one generation a year and hibernate at the egg stage. This is clearly confirmed by their phenology: adults are the last to appear during the season, and only nymphs but not adults are present in the spring of the following year. However, there is still no reason to believe that their annual cycles are obligatorily univoltine, because the obligate nature of their diapause has not been proven experimentally and there is no data indicating that the species remain univoltine under the climatic conditions that allow more than one generation a year. The seasonal cycle of these species was studied only in regions with a boreal climate, where the sum of effective temperatures above the developmental threshold seems to be sufficient for only one generation per season.

The seasonal cycles of *Pilophorus confusus* and *P. typicus* have been studied in regions with a warmer climate: Spain and Japan, respectively. These species are multivoltine; depending on environmental conditions, they produce a greater number of generations (*P. confusus*) or are active all the year round, i.e., homodynamic (*P. typicus*).

The three studied species of the tribe **Hallodapini** have similar seasonal cycles with one generation per year and overwintering at the egg stage. However, the available data are insufficient to characterize the ecophysiological basis of univoltinism for the entire tribe.

The tribe **Phylini** is the largest in the subfamily Phylinae; some of its genera, such as *Psallus* and *Campylomma*, comprise up to 140 species each (Duwal et al., 2012; Konstantinov et al., 2015). This tribe also shows a higher diversity of seasonal patterns. Although overwintering at the egg stage is generally characteristic of the family Miridae, two species of the genus *Chlamydatus* of the tribe Phylini are known to overwinter as adults: *Ch. allii* in Kazakhstan (Asanova and Iskakov, 1977) and *Ch. evanescens* in England (Southwood and Leston, 1959) and Sweden (Kullenberg, 1944). Three out of five studied *Chlamydatus* species have a multivoltine seasonal cycle, and no data are available on the voltinism and overwintering stage of two other species, *Ch. allii* and *Ch. wilkinsoni*.

Of the remaining 26 species of the tribe Phylini listed in Table 1, six species have multivoltine seasonal cycles and complete from 2 to 4 generations a year in different climatic zones.

Species of this tribe also demonstrate a seasonal adaptation quite unusual for true bugs, namely the shift of host plants during the season. As described above, nymphs of the first (overwintering at the egg stage) generation of *Campylomma verbasci* feed on woody plants, and the emerging adults of this generation migrate to herbaceous plants, on which the second generation develops. Adults of the second generation return from herbaceous vegetation to woody plants in late summer or early autumn and lay overwintering eggs in the young stems (Southwood and Leston, 1959). Such a seasonal cycle is more typical of Homoptera than of Heteroptera, although it is also known in *Lygocoris pabulinus* from the tribe Mirini of the subfamily Mirinae (Saulich and Musolin, 2020).

In conclusion, it should be noted that the large subfamily Phylinae shows a considerable diversity of ecophysiological characteristics, such as trophic specialization, seasonal shift of host plants, voltinism, and the overwintering stage. The subfamily includes many agricultural pests and also species whose economic status and invasion potentials may change following climate warming and transformation of agricultural practices.

ACKNOWLEDGMENTS

We thank F.V. Konstantinov (St. Petersburg State University; Zoological Institute of the Russian Academy of Sciences, St. Petersburg) and A.A. Namyatova (All-Russian Institute of Plant Protection; Zoological Institute of the Russian Academy of Sciences, St. Petersburg) for thorough examination and criticism of the manuscript.

FUNDING

Development of the database of seasonal adaptations in Heteroptera was partly supported by the Inessa Charitable Foundation (A.Kh. Saulich). This work (data analysis and manuscript preparation) was supported by the Russian Science Foundation (project 21-16-00050; https://rscf.ru/project/21-16-00050/).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

REFERENCES

Asanova, R.B. and Iskakov, B.V., *Vrednye i poleznye poluzhestkokrylye Kazakhstana. Opredelitel'* (A Key to Harmful and Beneficial True Bugs of Kazakhstan), Alma-Ata: Kainar, 1977.

Aukema, B., *Psallus* (*Apocremnus*) *montanus* Josifov, 1973 in The Netherlands (Heteroptera, Miridae), in *Advances in Heteroptera Research (Festschrift in Honour of 80th Anniversary of Michail Josifov)*, Grozeva, S. and Simov, N., Eds., Sofia: Pensoft, 2008, p. 9.

Aukema, B., Rieger, Ch., and Rabitsch, W., *Catalogue of the Heteroptera of the Palaearctic Region. Vol. 6. Supplement*, Amsterdam: The Netherlands Entomological Society, 2013.

Bartlett, D., *Feeding and Egg Laying Behaviour in Campylomma verbasci Meyer (Hemiptera: Miridae). M.Sc. Thesis*, Burnaby, British Columbia, Canada: Simon Fraser University, 1996.
https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=&ved=2ahUKEwjRueGyqP31AhXrl-

IsKHTQmBUkQFnoECAUQAQ&url=http%3A%2F%2Fsummit.sfu.ca%2Fsystem%2Ffiles%2Firitems1%2F6905%2Fb17825969.pdf&usg=AOvVaw0kV-v4wnkLmHjYpMV7wD2-6

Breene, R.G., Martin, W.R., Jr., Dean, D.A., and Sterling, W.L., Rearing methods for the cotton fleahopper, *Southwest. Entomol.*, 1989, vol. 14, no. 3, p. 249.

Butler, E.A., *Biology of the British Hemiptera-Heteroptera*, London: Witherby, 1923.

Cassis, G. and Schuh, R.T., Systematics, biodiversity, biogeography, and host associations of the Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha), *Annu. Rev. Entomol.*, 2012, vol. 57, p. 377.
https://doi.org/10.1146/annurev-ento-121510-133533

Collyer, E., Biology of some predatory insects and mites associated with the fruit tree red spider mite (*Metatetranychus ulmi* (Koch)) in south-eastern England III. Further predators of the mite, *J. Hortic. Sci.*, 1953, vol. 28, p. 98.

Duwal, R.K., Yasunaga, T., Jung, S., and Lee, S., The plant bug genus *Psallus* (Heteroptera: Miridae) in the Korean Peninsula with descriptions of three new species, *Eur. J. Entomol.*, 2012, vol. 109, no. 4, p. 603.
https://doi.org/10.14411/eje.2012.074

Ehanno, B., *Les Hétéroptères Mirides de France. Tome II A: Inventaire et synthèses écologiques*, Paris: Muséum National d'Histoire Naturelle, 1987.

Gaylor, M.J. and Sterling, W.L., Photoperiodic induction and seasonal incidence of embryonic diapause in the cotton fleahopper, *Pseudatomoscelis seriatus*, *Ann. Entomol. Soc. Am.*, 1977, vol. 70, no. 6, p. 893.
https://doi.org/10.1093/aesa/70.6.893

Guppy, J.C., Observation on the biology of *Plagiognathus chrysanthemi* (Hemiptera: Miridae), a pest of birdsfoot trefoil in Ontario, *Ann. Entomol. Soc. Am.*, 1963, vol. 56, p. 804.

Jonsson, N., The bug fauna (Hem. Heteroptera) on apple trees in south-eastern Norway, *Fauna Norv. Ser. B*, 1983, vol. 30, p. 9.

Jonsson, N., Ecological segregation of sympatric heteropterans on apple trees, *Fauna Norv. Ser. B*, 1985. 32: 7–11.

Judd, G.J.R. and McBrien, H.L., Modeling temperature-dependent development and hatch of overwintered eggs of *Campylomma verbasci* (Heteroptera: Miridae), *Env. Entomol.*, 1994, vol. 23, no. 5, p. 1224.
https://doi.org/10.1093/ee/23.5.1224

Kaplin, V.G., *Otkrytozhivushchie chlenistonogie semennykh rastenii Garagumov* (Openly Living Arthropod Pests of Seed Plants in the Kara-Kum Desert), Ashgabat: Ylym, 1993.

Kelton, L.A., The plant bugs of the prairie provinces of Canada. Heteroptera: Miridae. Part 8, in *The Insects and Arachnids of Canada* (*Publ. 1703*), Hull: Agriculture Canada Research Branch, 1980.

Kerzhner, I.M., Heteroptera of Sakhalin and the Kuril Islands, *Tr. Biol.-Pochv. Inst. Nov. Ser.*, 1978, vol. 50, p. 31.

Kerzhner, I.M., New Heteroptera from the Far East of the USSR, *Tr. Zool. Inst. Akad. Nauk SSSR*, 1979, vol. 81, p. 14.

Kerzhner, I.M., 21. Family Miridae, in *Opredelitel' nasekomykh Dal'nego Vostoka SSSR* (Key to Insects of the Far East of the USSR), Vol. 2: *Ravnokrylye i poluzhestkokrylye* (Homoptera and Hemiptera), Lelej, A.S., Ed., Leningrad: Nauka, 1988, p. 778.

Kerzhner, I.M. and Josifov, M., Family Miridae Hahn, 1833, in *Catalogue of the Heteroptera of the Palaearctic Region*, *Vol. 3*, Aukema, B. and Rieger, Ch., Eds., Amsterdam: The Netherlands Entomological Society, 1999.

Konstantinov, F.V., Review of *Solenoxyphus* Reuter, 1875 (Heteroptera: Miridae: Phylinae), *Am. Mus. Novit.*, 2008, vol. 3607, p. 1.

Konstantinov, F.V. and Namyatova, A.A., New records of Phylinae (Hemiptera: Heteroptera: Miridae) from the Palaearctic Region, *Zootaxa*, 2008, vol. 1870, p. 24.
https://doi.org/10.11646/zootaxa.1870.1.2

Konstantinov, F.V. and Namyatova, A.A., Taxonomic revisions and specimen database in the Internet age: dealing with a species rich insect taxon, *Entomol. Rev.*, 2019, vol. 99, no. 3, p. 340.
https://doi.org/10.1134/S0013873819030072

Konstantinov, F.V. and Vinokurov, N.N., New species and new records of plant bugs (Hemiptera: Heteroptera) from Northwestern China, *Zootaxa*, 2011, vol. 2836, p. 27.
https://doi.org/10.11646/zootaxa.2836.1.2

Konstantinov, F.V., Neimorovets, V.V., and Korzeev, A.I., The genus *Campylomma* Reuter, 1878 (Hemiptera: Heteroptera: Miridae: Phylinae): two new synonyms and discussion of the diagnosis, *Zootaxa*, 2015, vol. 3974, no. 2, p. 203.
https://doi.org/10.11646/zootaxa.3974.2.5

Kullenberg, B., Studien über die Biologie der Capsiden, *Zool. Bidrag Uppsala*, 1944, vol. 23, p. 1.

Matocq, A., Revue des espèces attribuées au genre *Megalocoleus* Reuter, 1890 (Heteroptera: Miridae), *Ann. Soc. Entomol. Fr. N. S.*, 2004, vol. 40, no. 1, p. 69.
https://doi.org/10.1080/00379271.2004.10697407

McMullen, R.D. and Jong, C., The biology and influence of pesticides on *Campylomma verbasci* (Heteroptera: Miridae), *Can. Entomol.*, 1970, vol. 102, p. 1390.

Niemczyk, E., *Campylomma verbasci* Meyer-Dür (Heteroptera, Miridae) as a predator of aphids and mites in apple orchards, *Pol. Pismo Entomol.*, 1978, vol. 48, p. 221.

Nishikawa, H., Shimada, T., Nakahira, K., and Arakawa, R., Thermal effect on the development and reproduction of an indigenous mirid bug, *Pilophorus typicus* Distant (Heteroptera: Miridae), a potential biological control agent in Japan, *Appl. Entomol. Zool.*, 2010, vol. 45, no. 2, p. 313. https://doi.org/10.1303/aez.2010.313

Pourhadji, A., Biology of *Campylomma verbasci* (Meyer-Dür) (Hemiptera: Miridae) and its injury in apple orchards of West Azerbaijan, *J. Entomol. Soc. Iran*, 2001, vol. 20, no. 2, p. 47.

Putshkov, V.G., Order Hemiptera (Heteroptera), true bugs, in *Nasekomye i kleshchi – vrediteli sel'skokhozyaistvennykh kul'tur* (Insects and Mites as Agricultural Pests), *Vol. 1*, Kryzhanovsky, O.L. and Danzig, E.M., Eds., Leningrad: Nauka, 1972, p. 222.

Putshkov, V.G., Species of the genus *Solenoxyphus* Reuter, 1874 (Heteroptera, Miridae) in the fauna of the USSR, *Dokl. Akad. Nauk USSR Ser. B*, 1978, vol. 5, p. 470.

Ramirez-Soria, M.J., López-Gallego, E., La-Spina, M., and Sanchez, J.A., Population dynamics and seasonal variation in the embryonic dormancy of *Pilophorus gallicus* (Hemiptera: Miridae): 'don't put all your eggs in one basket,' *Agr. Forest Entomol.*, 2018, vol. 20, no. 2, p. 191. https://doi.org/10.1111/afe.12243

Ramirez-Soria, M.J., Wäckers, F., and Sanchez, J.A., When natural enemies go to sleep: diapause induction and termination in the pear psyllid predator *Pilophorus gallicus* (Hemiptera: Miridae), *Pest Manage. Sci.*, 2019, vol. 75, no. 12, p. 3293. https://doi.org/10.1002/ps.5451

Sanchez, J.A. and Ortin-Angulo, M.C., Abundance and population dynamics of *Cacopsylla pyri* (Hemiptera: Psyllidae) and its potential natural enemies in pear orchards in southern Spain, *Crop Prot.*, 2012, vol. 32, p. 24.

Saulich, A.Kh. and Musolin, D.L., Seasonal development of plant bugs (Heteroptera, Miridae): subfamily Bryocorinae, *Entomol. Rev*., 2019, vol. 99, no. 3, p. 275. https://doi.org/10.1134/S0013873819030011

Saulich, A.Kh. and Musolin, D.L., Seasonal development of plant bugs (Heteroptera, Miridae): subfamily Mirinae, tribe Mirini, *Entomol. Rev*., 2020, vol. 100, no. 2, p. 135. https://doi.org/10.1134/S0013873820020013

Saulich, A.Kh. and Musolin, D.L., Seasonal development of plant bugs (Heteroptera, Miridae): subfamily Mirinae, tribe Stenodemini, *Entomol. Rev*., 2021, vol. 101, no. 2, p. 147. https://doi.org/10.1134/S0013873821020019

Schuh, R.T., Phylogenetic, host and biogeographic analyses of the Pilophorini (Heteroptera: Miridae: Phylinae), *Cladistics*, 1991, vol. 7, p. 157.

Schuh, R.T., Revision of New World *Plagiognathus* Fieber, with comments on the Palearctic fauna and the description of a new genus (Heteroptera: Miridae: Phylinae), *Bull. Am. Mus. Nat. Hist.*, 2001, vol. 266, p. 1. https://doi.org/10.1206/0003-0090(2001)266%3C0001:RONWPF%3E2.0.CO;2

Schuh, R.T., Revision of *Europiella* Reuter in North America, with the description of a new genus (Heteroptera: Miridae: Phylinae), *Am. Mus. Novit.*, 2004, vol. 3463, p. 1.

Schuh, R.T., Integrating specimen database and revisionary systematics, *ZooKeys*, 2012, vol. 209, p. 255.

Schuh, R.T., On-line Species Pages of Heteroptera (Insecta), 2021 (accessed 3.10.2021). http://research.amnh.org/pbi/heteropteraspeciespage/

Schuh, R.T. and Schwartz, M.D., A revision of the New World Pilophorini (Heteroptera: Miridae: Phylinae), *Bull. Am. Mus. Nat. Hist.*, 1988, vol. 187, no. 2, p. 101.

Schuh, R.T. and Schwartz, M.D., Review of North American *Chlamydatus* Curtis species, with new synonymy and the description of two new species (Heteroptera: Miridae: Phylinae), *Am. Mus. Novit.*, 2005, vol. 3471, p. 1.

Schuh, R.T. and Weirauch, C., *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History. 2nd Edition*, Manchester: Siri Scientific Press, 2020.

Schwartz, M.D., Review of *Plesiodema* Reuter and a description of a new genus to accommodate *Psallus sericeus* Heidemann (Heteroptera: Miridae: Phylinae), *Russ. Entomol. J.*, 2006, vol. 15, no. 2, p. 211.

Schwartz, M.D. and Stonedahl, G.M., Revision of *Phoenicocoris* Reuter with descriptions of three new species from North America and a new genus from Japan (Heteroptera: Miridae: Phylinae), *Am. Mus. Novit.*, 2004, vol. 3464, p. 1. https://doi.org/10.1206/0003-0082(2004)464%3C0001:ROPRWD%3E2.0.CO;2

Skanland, H.T., Studies on the arthropod fauna of a Norwegian apple orchard, *Fauna Norv. Ser. B*, 1980, vol. 28, p. 25.

Smith, R.F. and Borden, J.H., Fecundity and development of the mullein bug, *Campylomma verbasci* (Meyer) (Heteroptera: Miridae), *Can. Entomol.*, 1991, vol. 123, p. 595. https://doi.org/10.4039/Ent123595-3

Snodgrass, G.L., Scott, W.P., and Smith, J.W., A survey of the host plants and seasonal distribution of the cotton fleahopper (Hemiptera: Miridae) in the delta of Arkansas, Louisiana, and Mississippi, *J. Georgia Entomol. Soc.*, 1984, vol. 19, p. 34.

Southwood, T.R.E. and Leston, D., *Land and Water Bugs of the British Isles*, London: Frederick Warne and Co., 1959.

Thistlewood, H.M.A. and Smith, R.F., Management of the mullein bug, *Campylomma verbasci* (Heteroptera: Miridae), in pome fruit orchards of Canada, in *Zoophytophagous Heteroptera: Implications for Life History and Integrated Pest Management*, Alomar, O. and Wiedenmann, R.N., Eds.

(*Thomas Say Publications in Entomology*), Lanham: Entomological Society of America, 1996, p. 119.

Thistlewood, H.M.A., Borden, J.H., and McMullen, R.D., Seasonal abundance of the mullein bug, *Campylomma verbasci* (Meyer) (Heteroptera: Miridae), on apple and mullein in the Okanagan Valley, *Can. Entomol.*, 1990, vol. 122, no. 11, p. 1045.

Torres, X., Sarasua, M.J., and Avilla, J., The role of *Campylomma verbasci* (Herrich-Schäffer) in pear and apple orchards, *Bull. Org. Int. Lutte Biol.*, 1999, vol. 22, no. 7, p. 139.

Vinokurov, N.N. and Kanyukova, E.V., *Poluzhestkokrylye nasekomye (Heteroptera) Sibiri* (Heteroptera of Siberia), Novosibirsk: Nauka, 1995.

Vinokurov, N.N., Kanyukova, E.V., and Golub, V.B., *Katalog poluzhestkokrylykh nasekomykh (Heteroptera) Aziatskoi chasti Rossii* (Catalogue of Heteroptera of Asian Russia), Novosibirsk: Nauka, 2010.

Wheeler, A.G., Jr., Plant bugs (Miridae) as plant pests, in *Heteroptera of Economic Importance*, Schaefer, C.W. and Panizzi, A.R., Eds., Boca Raton, Florida: CRC Press, 2000a, p. 37.

Wheeler, A.G., Jr., Predacious plant bugs (Miridae), in *Heteroptera of Economic Importance*, Schaefer, C.W. and Panizzi, A.R., Eds., Boca Raton, Florida: CRC Press, 2000b, p. 657.

Wheeler, A.G., Jr., *Biology of the Plant Bugs (Hemiptera: Miridae): Pests, Predators, Opportunists*, Ithaca, New York: Cornell Univ. Press, 2001.

Wheeler, A.G., Jr. and Henry, T.J., *A Synthesis of the Holarctic Miridae (Heteroptera): Distribution, Biology, and Origin, with Emphasis on North America (Thomas Say Foundation Monographs. Vol. 15)*, Lanham, Maryland: Entomological Society of America, 1992.

Wheeler, A.G., Jr., Henry, T.J., and Hoebeke, E.R., Palearctic plant bugs (Hemiptera, Miridae) in Newfoundland, Canada: First North American records for *Phytocoris longipennis* Flor and *Pilophorus cinnamopterus* (Kirschbaum), new records of eight other species, and review of previously reported species, *Denisia*, 2006, vol. 19, p. 997.
https://www.zobodat.at/pdf/DENISIA_0019_0997-1014.pdf

Yasunaga, T., A review of Japanese species of the genus *Plesiodema* Reuter (Heteroptera: Miridae: Phylinae), *Tijdschr. Entomol.*, 2003, vol. 146, p. 371.

Yasunaga, T. and Vinokurov, N.N., The phyline plant bug genus *Psallus* Fieber in Japan (Heteroptera: Miridae: Phylinae), *Entomol. Sci.*, 2000, vol. 3, no. 4, p. 653.

Yasunaga, T., Yamada, K., and Artchawakom, T., Additional records and descriptions of the ant-mimetic plant bug genus *Pilophorus* from Thailand (Hemiptera: Heteroptera: Miridae: Phylinae: Pilophorini), *Zootaxa*, 2014, vol. 3795, no. 1, p. 1. https://doi.org/10.11646/zootaxa.3795.1.1

Yasunaga, T., Duwal, R.K., and Nakatani, Y., Reclassification of the plant bug genus *Pilophorus* in Japan and key to the genera and species of Japanese Pilophorini (Hemiptera: Heteroptera: Miridae: Phylinae), *Zootaxa*, 2021, vol. 4942, no. 1, p. 1.
https://doi.org/10.11646/zootaxa.4942.1.1