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Seasonal Development of Plant Bugs (Heteroptera, Miridae): Subfamily Orthotylinae, Tribes Halticini and Orthotylini

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Abstract—The paper reviews the available data on seasonal development of the best studied species of the subfamily Orthotylinae inhabiting the Palaearctic and Nearctic regions and included in 2 of the 6 tribes of this subfamily: Halticini and Orthotylini. All the 12 species of the tribe Halticini studied to date and included into this review are phytophagous with a wide range of host plants; all of them are characterized by wing polymorphism with long-winged males and, as a rule, short-winged females. Of these 12 species, 11 have a univoltine seasonal cycle and overwinter at the embryonic stage. When a species with a univoltine seasonal cycle penetrates beyond its native range, its seasonal development pattern remains close to the original one adapted to the environmental conditions of the species' native range. *Microtechnites bractatus* stands apart in the tribe Halticini because it represents the only genus in this tribe in which all the species are restricted to the Western Hemisphere, have a multivoltine seasonal cycle, and are zoophytophagous. Almost all the species of the tribe Orthotylini, regardless of their geographic distribution, have a univoltine seasonal cycle and are zoophytophagous, with the exception of *Orthotylus flavosparsus*, which has a multivoltine seasonal cycle and is phytophagous, preferring plants of the subfamily Chenopodioideae throughout most of its Holarctic range. Analysis of the data indicates that the seasonal development of Orthotylinae is still poorly understood, although among them there are many species that have great economic importance and invasive potential.

Keywords: biological control, day length, diapause, nymphal development, seasonal development, photoperiod, seasonal polymorphism, plant protection, true bugs, voltinism

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The family of plant bugs (Miridae) is the largest family of true bugs (Heteroptera). Many plant bugs are serious agricultural pests, while a number of other species are used as biological agents of plant protection. The family comprises 7 or 8 subfamilies, 46 tribes, over 1500 genera, and over 11 300 species (Cassis and Schuh, 2012; Namyatova et al., 2016; Henry, 2017; Konstantinov et al., 2018; Schuh and Weirauch, 2020).

In our previous publications (Saulich and Musolin, 2019, 2020, 2021) we analyzed the phenological patterns of development and the underlying seasonal adaptations in species of the subfamilies Bryocorinae and Mirinae (tribes Mirini and Stenodemini). This paper is devoted to the similar adaptations in bugs of the subfamily Orthotylinae Van Duzee, 1914, one of the largest subfamilies of Miridae, along with Phylinae Douglas et Scott, 1865 and Mirinae Hahn, 1833. According to the modern views, the subfamily Orthotylinae includes 6 tribes, of which only 2 are represented in the Holarctic fauna: Halticini and Orthotylini (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*, containing data on distribution and trophic specialization of plant bug species and on the specimens kept in museum collections (Schuh, 2021; data as of May 1, 2021).

Tribe **HALTICINI** Costa, 1853

The tribe Halticini includes about 25 genera, 18 of which unite the Palaearctic species and only 5, the Nearctic ones. The highest species diversity of the tribe is observed in the Mediterranean area (Cassis and Schuh, 2012; Tatarnic and Cassis, 2012; Schuh and Weirauch, 2020). The great majority of its species are phytophages, mostly feeding on herbaceous plants (Schuh and Slater, 1995; Wheeler, 2001).

Genus ***Halticus*** Hahn, 1832

Halticus apterus (Linnaeus, 1758)

A Holarctic species, unintentionally introduced to North America (Kerzhner and Josifov, 1999; Schuh, 2021).

The bugs mostly feed on *Vicia striata* (Fabaceae) (Tatarnic and Cassis, 2012), but are also known from a number of other plants (Schuh, 2021). The species is a minor pest of herbaceous legumes (Fabaceae) (Putshkov, 1972).

The phenology of *H. apterus* was studied in England. The species has a univoltine seasonal cycle, with eggs overwintering in diapause. Nymphs hatch in the middle of spring and develop for about two months. Adults emerge in late June and in July, lay eggs that enter diapause, and gradually die out by the end of August (Southwood and Leston, 1959). This seasonal cycle is confirmed by the collection dates of museum specimens (Table 1; Schuh, 2021).

Wing dimorphism is typical of both sexes, but short-winged individuals are more common among females (Southwood and Leston, 1959).

The seasonal cycle described above is characteristic of most species of Halticini, including *Halticus saltator* (Geoffroy, 1785) and *H. luteicollis* (Panzer, 1804) (see Table 1). All of them are phytophagous, have a univoltine seasonal cycle, and overwinter in the state of embryonic diapause (Southwood and Leston, 1959; Tatarnic and Cassis, 2012).

Genus ***Microtechnites*** Berg, 1883

Microtechnites bractatus (Say, 1832) (garden fleahopper)

This species is widely distributed in the USA, Canada, Mexico, and also in Central and South America as far as Argentina (Henry and Wheeler, 1988; Tatarnic and Cassis, 2012; Schuh, 2021).

The species is broadly polyphagous, damaging crop plants from many families, including Cucurbitaceae, Solanaceae, Fabaceae, and Brassicaceae, and also various trees and ornamental plants (Schuh, 2021). These bugs may be zoophytophagous (Capinera, 2001).

Microtechnites bractatus is one of the few species in the tribe Halticini that have a multivoltine seasonal cycle. In particular, it produces 5 or 6 generations a year in South Carolina (USA), 5 generations in Virginia, and 3 in New Jersey (Day and Saunders, 1990; Wheeler, 2000a). The generations usually overlap, so that adults and nymphs of different instars belonging to different generations can be found simultaneously during the entire warm season. The developmental time of one generation in Virginia is about one month, while temperatures above 32°C are unfavorable for all the stages of development. Nymphs hatch from overwintered eggs in April. In Florida adults can be found all the year round except December, the warm winters of the region favoring year-round activity of the bugs (Day and Saunders, 1990; Capinera, 2001). This seasonal cycle is confirmed by the collection dates of museum specimens (see Table 1; Schuh, 2021).

Genus ***Labops*** Burmeister, 1835

Labops burmeisteri Stål, 1858

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

In Yakutia the species is regarded as a potential pest of grasses (Poaceae) (Vinokurov et al., 2010). It inhabits dry meadows, steppes, and mountain tundra (Vinokurov and Kanyukova, 1995).

There are no data on the seasonal development of the species; however, the label data of museum specimens suggest that, similar to most other species of this tribe, *L. burmeisteri* produces one generation a year and overwinters at the egg stage (see Table 1; Schuh, 2021).

Labops hesperius Uhler, 1872

This species is native to North America and distributed from British Columbia, Ontario, and Quebec (Canada) in the north to California and New Mexico (USA) in the south (Wheeler, 2000a; Schuh, 2021).

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

Species	Over-wintering stage	Number of generations per year	Number of adults collected monthly in different parts of the species' range (based on the labels of museum specimens)*												
			I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Tribe Halticini															
Halticus apterus	Egg	1	46	0	0	0	19	**313**	**1044**	**630**	16	1	0	0	2096
H. saltator	Egg	1	0	0	0	0	2	**20**	**20**	**0**	0	0	0	0	42
H. luteicollis	Egg	1	6	0	0	0	2	**30**	**29**	**9**	0	0	0	0	76
Microtechnites bractatus	Egg	3–6 or homodynamic development	2	7	21	26	15	**131**	**186**	**216**	89	28	3	4	728
Labops burmeisteri	Egg	1	0	0	7	0	3	**177**	**415**	**37**	1	0	0	0	640
L. hesperius	Egg	1	0	0	0	3	117	**496**	**237**	**42**	2	0	0	0	897
L. sahlbergi	Egg	1	9	0	0	0	6	**206**	**179**	**53**	27	0	0	0	480
Orthocephalus bivittatus	Egg	1	12	0	0	1	265	**999**	**70**	**17**	1	0	0	0	1365
O. coriaceus	Egg	1	0	0	0	0	2	**164**	**133**	**12**	0	0	0	0	311
O. saltator	Egg	1	6	0	0	15	57	**265**	**372**	**64**	2	0	0	0	781
Strongylocoris leucocephalus	Egg	1	24	0	0	3	81	**460**	**422**	**23**	0	0	1	0	1014
S. luridus	Egg	1	1	0	0	0	0	**9**	**2**	**0**	0	0	0	0	12
Tribe Orthotylini															
Blepharidopterus angulatus	Egg	1	4	0	0	0	1	**11**	**218**	**780**	12	3	1	0	1030
Cyllecoris histrionius	Egg	1	3	0	1	1	28	**99**	**18**	**0**	0	0	0	0	150
Cyrtorrhinus caricis	Egg	1	0	0	0	0	28	**22**	**102**	**138**	21	0	37	0	348
Excentricus planicornis	Egg	1	0	0	0	0	5	**27**	**53**	**3**	0	0	0	0	88
Globiceps flavomaculatus	Egg	1	17	0	0	1	3	**144**	**324**	**81**	1	0	0	0	571
Heterotoma merioptera	Egg	1	0	0	0	0	2	**6**	**17**	**8**	0	0	0	0	33
H. planicornis	Egg	1	0	0	0	0	0	**7**	**268**	**136**	3	1	0	0	415
Mecomma ambulans	Egg	1	3	0	0	0	0	**97**	**204**	**81**	0	1	0	0	386
M. dispar	Egg	1	2	0	0	0	0	**1**	**21**	**34**	0	0	0	0	58
Orthotylus bilineatus	Egg	1	0	0	0	0	0	**6**	**40**	**47**	3	0	0	0	96
O. flavosparsus	Egg	1–5	13	1	0	33	126	**515**	**919**	**640**	189	24	1	0	2461
O. interpositus	Egg	1	0	0	0	0	1	**17**	**80**	**11**	0	0	0	0	109
O. marginalis	Egg	1	1	0	0	0	4	**168**	**160**	**48**	0	0	0	0	381
O. pallens	Egg	1	0	0	0	0	0	**3**	**69**	**17**	0	0	0	0	89
O. parvulus	Egg	1	0	0	0	0	1	**18**	**6**	**103**	13	4	0	0	145

* The records of adult bugs in museum collections for each month and for the whole year were obtained from the online database *The Planetary Biodiversity Inventory (PBI) for Plant Bugs* (Schuh, 2021) as of May 1, 2021. 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. For clarity, data for the summer months are shown in bold.

These bugs have been collected on various grasses (Poaceae) and on arboreal plants: willows *Salix* sp. and junipers *Juniperus* sp. (Schuh, 2021).

The species was studied in detail in Oregon (Corvallis, 44°N, 123°W). It has a univoltine seasonal cycle (see Table 1; Schuh, 2021). Nymphs hatch from overwintered eggs in late March (Todd and Kamm, 1974) and develop to adults in about four weeks (Higgins et al., 1977). The feeding nymphs pierce the plant tissues and cause the yellowing of leaves, as is generally typical of Halticini (Ling et al., 1985). The earliest adults appear at the end of April, and mass emergence occurs two weeks later. The preoviposition period lasts about two weeks. Eggs overwinter in the state of diapause that is formed at late stages of embryogenesis. Only one generation is produced annually. Thus, the bugs are active approximately during 3 months in summer, while the diapause lasts for more than 9 months. It was experimentally shown that termination of embryonic diapause required exposure to low positive temperatures (from 3 to 9°C) for at least 60 days, followed by 2 weeks of incubation at 15°C. The effect of the day length at low temperatures was manifested in inconsiderable speeding-up of diapause termination (Fuxa and Kamm, 1976b).

Labops hesperius is characterized by wing polymorphism. Most males in the studied population from Oregon are long-winged, while most females are short-winged, with no more than 4% of long-winged individuals. The long-winged females mature on average 3 weeks later than short-winged ones, probably as the result of morphological and physiological preparation for migratory activity (Fuxa and Kamm, 1976a).

Labops sahlbergi (Fallén, 1829)

A Euro-Siberian species (Vinokurov et al., 2010; Schuh, 2021).

These bugs are potential pests of gramineous crops and other grasses (Poaceae); they are commonly found on timothy grass *Phleum* sp.

There are no data on the seasonal development of the species; however, the label data of museum specimens (see Table 1; Schuh, 2021) suggest that, similar to most other species of this tribe, *L. sahlbergi* overwinters at the egg stage and produces one generation a year.

Males are long-winged; females can be both long- and short-winged (Asanova and Iskakov, 1977).

Genus ***Orthocephalus*** Fieber, 1858

Orthocephalus bivittatus Fieber, 1864

A West-Central Palaearctic species (Vinokurov et al., 2010; Namyatova, 2020; Schuh, 2021).

The bugs feed on wormwoods *Artemisia* spp. and other composites (Asteraceae) (Vinokurov and Kanyukova, 1995; Schuh, 2021).

The seasonal cycle of the species was studied in Kazakhstan. It overwinters at the egg stage. Adults emerge in June and occur on wheatgrass *Agropyron* sp., brome grasses *Bromus* sp., and alfalfa *Medicago* sp.; the bugs usually disappear in August. Only one generation is produced annually (Asanova and Iskakov, 1977). The seasonal cycle is confirmed by the label data of museum specimens (see Table 1; Schuh, 2021).

Males are long-winged; females are usually short-winged, rarely long-winged (Namyatova and Konstantinov, 2009).

Orthocephalus coriaceus (Fabricius, 1777)

This species is distributed in Western and Central Europe (Schuh, 2021) and Kyrgyzstan; it was recently found in Tunisia (Namyatova and Konstantinov, 2009; Namyatova, 2020) and unintentionally introduced to North America (Wheeler, 1985).

The bugs inhabit open and dry sandy landscapes and feed on composites (Asteraceae). In Sweden they commonly occur on *Achillea millefolium* and *Tanacetum vulgare* (Kullenberg, 1944), and in more southern areas they have a much wider range of host plants (Namyatova and Konstantinov, 2009; Schuh, 2021). In North America the species is often found on ruderal vegetation (Wheeler, 1985).

Eggs are laid in the middle and lower parts of the plant stems and overwinter in diapause. In England and Sweden adults emerge in the second half of June and can be found till August (Kullenberg, 1944; Southwood and Leston, 1959). In Pennsylvania (USA) the earliest nymphs hatch at the end of April; adults emerge at the end of May and can usually be found till the end of June. Males usually die out earlier than females (Wheeler, 1985). Thus, the species remains univoltine in both the native and the secondary range (see Table 1; Schuh, 2021). The timing of appearance of individual developmental stages varies depending on the local climate.

Wing dimorphism is manifested in both sexes (Southwood and Leston, 1959).

Orthocephalus saltator (Hahn, 1835)

A West-Central Palaearctic species, introduced to North America (Wheeler, 1985; Henry and Kelton, 1986; Vinokurov et al., 2010; Namyatova, 2020; Schuh, 2021).

The bugs are broadly polyphagous, occurring on plants of the families Asteraceae, Fabaceae, Lamiaceae, Poaceae, Rosaceae, and Salicaceae (Namyatova and Konstantinov, 2009; Schuh, 2021).

The seasonal development of *O. saltator* was studied in England. The species overwinters at the egg stage. Adults emerge in early July and usually live till the beginning of September. Only one generation is completed annually. Judging by the museum collection data (see Table 1; Schuh, 2021), in more southern regions adult bugs were also found in April–May, but the species still seems to have one generation a year.

Males are always long-winged, while females are commonly short-winged and only rarely long-winged (Southwood and Leston, 1959).

Genus ***Strongylocoris*** Blanchard, 1840

Strongylocoris leucocephalus (Linnaeus, 1758)

A trans-Palaearctic species (Vinokurov et al., 2010; Schuh, 2021).

The bugs commonly occur on herbaceous plants from various families, in particular on those of the genera *Galium*, *Vicia*, *Urtica*, *Campanula*, and many others.

In England nymphs were recorded since early May, and adults are commonly found from early June to August; they gradually die out after laying eggs that overwinter. The species invariably produces only one generation a year (see Table 1; Schuh, 2021).

A similar seasonal cycle is observed in one more species of the same genus, *S. luridus* (Fallén, 1807) (see Table 1; Butler, 1923; Southwood and Leston, 1959; Schuh, 2021).

Tribe **ORTHOTYLINI** Van Duzee, 1916 (1865)

According to the modern views, the tribe Orthotylini comprises about 260 species, grouped in about 37 genera in the Palaearctic fauna and 57 genera in the Nearctic fauna (Cassis and Schuh, 2012).

Genus ***Blepharidopterus*** Kolenati, 1845

Blepharidopterus angulatus (Fallén, 1807)
(black-kneed capsid)

A trans-Palaearctic species, unintentionally introduced to North Africa (Drapolyuk, 2017) and North America (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999; Vinokurovet al., 2010; Schuh, 2021).

This is a zoophytophagous and a broadly polyphagous species. The bugs feed on small insects, mostly of the order Homoptera, and on eggs and larvae of Lepidoptera. They also hunt spider mites (Tetranychidae) and are believed to be the main predators of the European red mite *Panonychus ulmi* (Huffaker et al., 1970; Austreng and Sømme, 1980; Wheeler, 2000b). During its nymphal development, a male of *B. angulatus* consumes up to 1500 spider mites, and a female, twice as many. These bugs are widespread in apple orchards and also occur on many wild trees (elm, aspen, birch, linden) and rarely, on forb vegetation (Southwood and Leston, 1959; Drapolyuk, 2017; Schuh, 2021).

The univoltine seasonal cycle of *B. angulatus* was studied in England (Southwood and Leston, 1959; Muir, 1966) and Sweden (Austreng and Sømme, 1980). Females lay eggs singly in thin one- or two-year-old twigs, damaging the plant in the process and inducing characteristic knots. In England oviposition continues from late July to October. Nymphs hatch from overwintered eggs from mid-May to late July or early August. Nymphal development lasts about 5 weeks, so that adults can be found from late June to October. The adult lifespan of males is 3–4 weeks, and that of females is twice as long. This seasonal cycle is confirmed by the collection dates of museum specimens from different regions (see Table 1; Schuh, 2021).

A laboratory study (Muir, 1966) showed that the winter embryonic diapause was terminated during 14–16 weeks of exposure to low temperatures (+4.4 and +7.2°C). The lower temperature threshold of nymph hatching was estimated at 4.7°C; the earliest nymphs hatched in the laboratory when the sum of effective temperatures above this threshold reached 409 degree-days. In another experiment, 50% of the nymphs hatched when the sum of effective temperatures reached 727 degree-days, and the calculated lower temperature threshold of hatching was close to 3.4°C.

In order to test the validity of laboratory data for predicting the phenology of *B. angulatus*, the earliest dates of nymph hatching were recorded for 7 years during field experiments in England (Kent, 51°12′N, 0°42′E). The predictions based on the lower temperature threshold of 4.7°C proved to be more reliable (Muir, 1966).

Males of *B. angulatus* are represented by two morphological forms. The more common form *angulatus* has elongated antennae and hind tibiae. Individuals of the form *brevicornis*, with shorter antennae and hind tibiae, are rarer and can be found only in large samples of the species (Southwood and Leston, 1959).

Genus ***Cyllecoris*** Hahn, 1834

Cyllecoris histrionius (Linnaeus, 1767)

A European species, introduced to Siberia (Vinokurov et al., 2010; Schuh, 2021).

The bugs occur on various species of oak *Quercus* sp. (Southwood and Leston, 1959). Nymphs and adults feed on unexpanded catkins and young acorns. Adult bugs are phytozoophagous; they hunt small insects, mostly of the order Homoptera, and actively consume the larvae of the European oak leafroller *Tortrix viridana* (L.) and also various inhabitants of oak leaf galls (Butler, 1923; Southwood and Leston, 1959; Drapolyuk, 2017).

According to the observations made in England, the species overwinters at the egg stage. Nymphs hatch in mid-May, and the earliest adults emerge in early June. Their numbers decline already by late July, though some adults survive till September (see Table 1; Schuh, 2021). Only one generation is completed annually (Southwood and Leston, 1959). A univoltine life cycle was also observed in this species in Azerbaijan (Drapolyuk, 2017).

Genus ***Cyrtorrhinus*** Fieber, 1858

Cyrtorrhinus caricis (Fallén, 1807)

A Holarctic species; in the Caucasus it is known only from Azerbaijan (Vinokurov et al., 2010; Drapolyuk, 2017; Schuh, 2021).

The bugs occur on paludal plants of the sedge family (Cyperaceae) (Vinokurov and Kanyukova, 1995), and were recorded on other plants as well (Schuh, 2021). They feed as predators, mostly consuming eggs of various Homoptera (Southwood and Leston, 1959).

In England nymphs hatch in late May or early June; adults emerge in July and live till October. Thus, the species has one generation a year (see Table 1; Southwood and Leston, 1959; Schuh, 2021).

Genus ***Excentricus*** Reuter, 1878

Excentricus planicornis (Herrich-Schäffer, 1836)

A trans-Palaearctic species (Vinokurov et al., 2010; Drapolyuk, 2017; Schuh, 2021).

The bugs are phytophagous and occur on Rosaceae (*Rosa acicularis*, *R. myriacantha*, etc.), including hawthorn *Crataegus* sp. In Iran they were recorded on broom plants *Cytisus* sp. (Linnavuori, 2007).

In the Caucasus nymphs can be found in June (Drapolyuk, 2017). There are no detailed data on the seasonal development of the species, but the label data of museum specimens (see Table 1; Schuh, 2021) suggest that, similar to most other species of this tribe, *E. planicornis* overwinters at the egg stage. Thus, one generation is completed annually.

Genus ***Globiceps*** Lepeletier et Serville, 1825

Globiceps flavomaculatus (Fabricius, 1794)

A Euro-Siberian species (Vinokurov et al., 2010; Schuh, 2021).

In Siberia the species prefers humid biotopes and often occurs under the forest canopy (Vinokurov and Kanyukova, 1995). In the Caucasus it was recorded on Rosaceae, especially hawthorn *Crataegus* sp., loquat *Eriobotrya japonica*, and cherry plum *Prunus cerasifera* (Gidayatov, 1965). The bugs are phytozoophagous; the early-instar nymphs feed on plants, predominantly on legumes, while the late-instar nymphs and adults hunt aphids.

In England the species produces one generation a year. Adults can be found from June to September; eggs are laid in the bark fissures of old trees and shrubs (prune, blackthorn) (Southwood and Leston, 1959). The seasonal cycle with most probable overwintering at the egg stage is also confirmed by the collection dates of the museum specimens from different regions (see Table 1; Schuh, 2021).

Males are always long-winged; females are usually short-winged, rarely long-winged.

Genus ***Heterotoma*** Lepeletier et Serville, 1825

Heterotoma merioptera (Scopoli, 1763)

This species is distributed in Europe and also recorded in Turkey, Israel, and Iraq (Kerzhner and Josifov, 1999; Kment and Bryja, 2006; Schuh, 2021).

This is a broadly polyphagous species, occurring on nettle *Urtica* sp. and on various shrubs and trees. The bugs often suck sap from buds and young fruits. In the Czech Republic the species was recorded on 19 species of plants from 12 families (Kment and Bryja, 2006). Both nymphs and adults feed on aphids and other small insects.

The species is univoltine, always producing only one annual generation and overwintering at the egg stage (see Table 1; Schuh, 2021). In England nymphs hatch in late May or early June, and adults emerge in the second half of July, some individuals surviving till October (Southwood and Leston, 1959).

Heterotoma planicornis (Pallas, 1772)

A European species, unintentionally introduced to North America and the Hawaii (Kerzhner and Josifov, 1999; Schuh, 2021).

This is a zoophytophagous and broadly polyphagous species. Its nymphs feed on 11 species of plants from 7 families, consuming small insects, their eggs, and also young fruits of various plants (Kment and Bryja, 2006).

According to the observations in the Czech Republic, the earliest adults appear in the last third of June; the first peak of adult abundance falls on the middle third of July, the second peak, on the middle third of August, after which the adult bugs start to die out and completely disappear by the end of September (Kment and Bryja, 2006). Despite this record of more than one abundance peak, the seasonal cycle appears to be univoltine, with overwintering at the egg stage (see Table 1; Schuh, 2021).

Genus ***Mecomma*** Fieber, 1858

Mecomma ambulans (Fallén, 1807)

A trans-Palaearctic species (Vinokurov et al., 2010; Schuh, 2021).

In Siberia the bugs commonly occur in wet meadows and under the forest canopy on common reed *Phragmites australis*, bulrush *Scirpus* sp., and cattail *Typha* sp. (Vinokurov and Kanyukova, 1995); in England they are more often found at forest edges and in glades (Southwood and Leston, 1959).

The overwintering stage is the egg. Nymphs hatch in the second half of May and usually keep to the lower parts of their host plants. Adults can be found from late June to early September. Only one generation seems to be produced annually (see Table 1; Schuh, 2021).

Males are always long-winged; females are usually short-winged, but some individuals from northern and mountainous regions have wings of intermediate length (Southwood and Leston, 1959).

Mecomma dispar (Boheman, 1852)

A Euro-Siberian species (Vinokurov et al., 2010; Schuh, 2021).

The species is polyphagous (Drapolyuk, 2017). The bugs mostly occur in the forest zone, in bogs among the tussocks of grasses (Poaceae) and sedges (*Carex* sp.), and also in meadows in mountainous regions (Azerbaijan, İstisu, 2225 m above sea level) (Gidayatov, 1971).

Adult bugs were often recorded in great numbers, especially in June and July (Gidayatov, 1971). There is no other information on the seasonal development of the species, but the data of museum specimens (see Table 1; Schuh, 2021) suggest that *M. dispar* produces one generation a year and overwinters at the egg stage.

Males are long-winged, while females are usually short-winged, very rarely long-winged (Southwood and Leston, 1959).

Genus ***Orthotylus*** Fieber, 1858

Orthotylus bilineatus (Fallén, 1807)

A trans-Palaearctic species, mostly inhabiting the forest zone (Yasunaga, 1999; Schuh, 2021).

The bugs feed predominantly on aspens, willows, and poplars (Salicaceae) (Southwood and Leston, 1959; Yasunaga, 1999; Drapolyuk, 2017).

The seasonal development of the species was studied in the Caucasus and in England, and its phenology was found to be largely similar in the two regions. The overwintering stage is the egg. Nymphs hatch since the end of June; adults emerge in the second half of July and can be found till the middle or end of August. One generation a year is produced throughout the species' range (see Table 1; Southwood and Leston, 1959; Putshkov, 1972; Drapolyuk, 2017; Schuh, 2021).

Orthotylus flavosparsus C.R. Sahlberg, 1841

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

The bugs were recorded on many plant species (Schuh, 2021). They are known as pests of beets and vectors of the beet mosaic virus (Putshkov, 1972). In the Caucasus the species is associated only with wild chenopods (Chenopodioideae: *Chenopodium* sp., *Atriplex* sp., etc.) (Drapolyuk, 2017).

In different regions the species produces up to 4 or 5 generations a year (Putshkov, 1972). Its nymphs appear in late April or early May and occur in nature till September (Putshkov, 1972; Drapolyuk, 2017). Only two annual generations were observed in England; adults of the first generation emerged in the middle and at the end of June, and those of the second generation, at the end of August, although nymphs could be often found as late as September (Southwood and Leston, 1959). On Hokkaido Island (Japan) the species also develops in two annual generations, with adults of the first generation emerging in June and those of the second generation, in September (Yasunaga, 1999). Similar to all the plant bugs, females of *O. flavosparsus* lay overwintering eggs in plant stems. In Kazakhstan the species produces three generations a year (Asanova and Iskakov, 1977). Adult bugs were recorded practically all the year round in different parts of the range (see Table 1; Schuh, 2021).

Orthotylus interpositus Schmidt, 1938

A Euro-Siberian species (Vinokurov et al., 2010; Schuh, 2021).

The bugs feed on willows (*Salix* spp.) and are sometimes captured in light traps (Yasunaga, 1999; Schuh, 2021).

There are almost no data on the seasonal development of this species, apart from the report that in Japan the late-instar nymphs appear in mid-July (Yasunaga, 1999). The label data of museum specimens (see Table 1; Schuh, 2021) suggest that *O. interpositus* overwinters at the egg stage and has one generation a year throughout its range.

Orthotylus marginalis Reuter, 1883

A Euro-Siberian species, unintentionally introduced to North America (Vinokurov et al., 2010; Schuh, 2021).

The bugs are zoophytophagous, feeding on psyllids, aphids and other insects, and also spider mites. This is a dendrobiotic species, commonly found on willows, alder, linden, birch, and other trees (Putshkov, 1972). In England it occurs on apple trees, less commonly on currant and blackthorn shrubs.

The overwintering stage is the egg. Nymphs hatch in late April or early May. Adults emerge starting from mid-June, and some individuals survive till the end of August. Only one generation is produced annually (see Table 1; Southwood and Leston, 1959; Schuh, 2021).

In Switzerland *O. marginalis* mostly occurs on apple trees. Nymphs hatch in spring from the overwintered eggs and, as in all plant bugs, develop with five instars. As the result of laboratory experiments, the lower temperature thresholds of development (± S.E.) were determined for the eggs (9.2 ± 0.13°C) and for different nymphal instars (N2: 11.0 ± 0.66°C; N3: 10.7 ± 0.17°C; N4: 10.8 ± 0.20°C; N5: 10.7 ± 0.17°C), the sum of effective temperatures corresponding to the lower temperature threshold of each developmental stage, and many other parameters were determined. These data were used to analyze the phenology of *O. marginalis* population under natural conditions (Schaub and Baumgartner, 1989).

Orthotylus pallens (Matsumura, 1911)

This species is distributed in the south of the Russian Far East (Sakhalin Island and the Kuril Islands) and in Japan (Yasunaga, 1999; Vinokurov et al., 2010; Schuh, 2021).

Adults and late-instar nymphs feed on the larvae of Lepidoptera and Diptera (Yasunaga, 1999).

The species is univoltine. Adults emerge at the end of June and lay eggs in the young shoots of willows *Salix* spp.; the overwintering stage is the eggs (see Table 1; Schuh, 2021).

Orthotylus parvulus Reuter, 1879

A Eurasian steppe-dwelling species (Vinokurov et al., 2010; Schuh, 2021).

The bugs occur in saline lands on plants of the family Chenopodiaceae (Kerzhner, 1988; Vinokurov and Kanyukova, 1995).

There are no data on the seasonal development of the species, but the label data of museum specimens (see Table 1; Schuh, 2021) suggest that *O. parvulus* overwinters at the egg stage and produces one generation a year.

CONCLUSIONS

All the studied species of the tribe Halticini are phytophagous and have a wide range of host plants; all of them are characterized by wing polymorphism with long-winged males and usually short-winged females. Analysis of the literature and the online database (see Table 1; Schuh, 2021) has revealed considerable similarity in the seasonal development patterns of Halticini species. Of the 12 species considered in this review, 11 overwinter at the egg stage and have a univoltine seasonal cycle: their populations produce only one complete generation a year in any part of their ranges. When these species expand beyond their native ranges, they retain the original pattern of seasonal development. Having crossed geographic barriers (in the process of natural invasion or as the result of unintentional or deliberate introduction by man), the species end up in territories with new climate conditions; however, their seasonal cycle does not undergo any essential transformation but remains close to the original cycle, i.e., the one adapted to the native living conditions. Examples of such stable seasonal cycles can be found in two species unintentionally introduced from Eurasia to North America: *Halticus apterus* and *Orthocephalus coriaceus*. In such cases, univoltinism may be considered obligatory and treated as a species-specific trait.

Microtechnites bractatus, distributed from Canada to Argentina, stands apart in the tribe Halticini since it represents the only genus of this tribe that is totally restricted to the Western Hemisphere. Different geographic populations of *M. bractatus* can complete a different number of generations a year, depending on the climate. In addition, *M. bractatus* is zoophytophagous, as opposed to the purely phytophagous species of the genus *Halticus*.

Little is known on the seasonal development in the genus *Labops*, but the label data of museum specimens suggest that, similar to most members of Halticini, species of this genus overwinter at the egg stage and produce one generation a year.

Most species of the tribe Orthotylini also have a similar pattern of seasonal development. All the studied members of this tribe except *Orthotylus flavosparsus* have a univoltine seasonal cycle, regardless of their geographic distribution. They always complete only one annual generation even in the regions with a long and warm summer season, where the sum of effective temperatures would be sufficient for development of several generations. As opposed to Halticini, all the species of the tribe Orthotylini are zoophytophagous and, correspondingly, deserve attention as potential agents of biological pest control.

Similar to Halticini, the tribe Orthotylini includes one species that clearly differs from others in its ecological characteristics. *Orthotylus flavosparsus* is a phytophagous species with a multivoltine seasonal cycle, comprising from 1 to 5 annual generations in different regions. It overwinters at the egg stage, as is typical of most Miridae. Both nymphs and adults of this species prefer host plants of the subfamily Chenopodioideae throughout the greatest part of its vast range, extending from England to Japan.

On the whole, the seasonal development of bugs of the subfamily Orthotylinae is still poorly understood, although many of them have great economic importance and invasive potential. Most publications on this taxon are focused on systematics, taxonomy, distribution, and trophic associations of its species. At the same time, there are few publications devoted to analysis of the seasonal development of Orthotylinae and experimental study of the ecological responses controlling their seasonal cycle.

Our earlier analysis of seasonal adaptations in shield bugs (Heteroptera: Pentatomidae) (Saulich and Musolin, 2018) showed that even in this well-studied taxon, phylogenetic reconstructions based solely on morphological characters could not be used to predict the parameters of seasonal development in individual species, let alone their populations. Similar complexes of seasonal adaptations were observed only within some genera, small tribes or small subfamilies. However, in some cases data on the ecology and seasonal cycle of a species may help to clarify its taxonomic position. For instance, *Dybowskyia reticulata* (Dallas, 1851) was placed in the tribe Tarisini by some authors (Vinokurov et al., 2010) and in the tribe Graphosomatini by others (Gapon, 2008); at the same time, in ecological characteristics *D. reticulata* more closely resembles the species of the tribe Graphosomatini. It is quite possible that a study of the specific ecological features of *O. flavosparsus* would serve as a prerequisite to taxonomic revision of the genus *Orthotylus*.

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COMPLIANCE WITH ETHICAL STANDARDS

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

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