Faunal make-up, host range and infestation rate of weevils and tephritid flies associated with flower heads of the thistle Cirsium (Cardueae : Astaraceae) in Japan

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ORIGINAL ARTICLE

Faunal make-up, host range and infestation rate of weevils and tephritid flies associated with flower heads of the thistle *Cirsium* (Cardueae: Astaraceae) in Japan

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Abstract

From 1988 to 1998, we collected flower heads of 39 thistle taxa (35 taxa of *Cirsium*, one species each of *Breea*, *Synurus*, *Saussurea* and *Arctium*; Cardueae; Astaraceae) in Japan, mainly from Hokuriku and other parts of central Honshu, and kept them in the laboratory to breed weevils and tephritid flies, the core fauna. We report the faunal make-up, host plants, geographic distribution and the attack levels of the insects. Results indicated that (i) three *Larinus* species (Curculionidae) and three species of tephritid flies (*Tephritis*, *Urophora* and *Xyphosia*) comprised the core fauna; (ii) two insect species belonging to the same taxonomic group (either Curculionidae (*Larinus*) or Tephritidae) tended to use different host plant species; (iii) two sympatric *Larinus* species (*L. latissimus* and *L. meleagris*) segregated the host plants seasonally in central Honshu (*Cirsium* blooming in spring and autumn, respectively); and (iv) two tephritid fly species, *Xyphosia punctigera* and *Urophora sachalinensis*, segregated geographically (the former on the Japan Sea side and the latter on the Pacific Ocean side). In comparison with their European counterparts, the weevils and tephritids of the Japanese *Cirsium* are characterized by a lower species richness and a lower degree of specialization in usage of the thistle flower heads, with gall-formers being distinctly under-represented, and callus tissue-feeders being absent. This reflects the fact that Japanese thistles are so closely related that hybridization frequently occurs, and also that the thistles have had a short history of interaction with the insects since the thistles' arrival in Japan.

Key words: Curculionidae, insect fauna, insect–plant relationship, Japanese thistle flower head, Tephritidae.

INTRODUCTION

Thistles, members of the tribe Cardueae (Astaraceae), are annual or perennial herbaceous plants that occur throughout the Holarctic region from the Mediterranean to East Asia and the Nearctic region (Bremer 1994). All structures of the Cardueae (e.g. roots, stems, leaves, buds and flower heads) are attacked externally as well as internally by a group of phytophagous insects specific to each structure (Zwölfer 1965, 1973; Zwölfer *et al.* 1971; Redfern 1983; Briese *et al.* 1994). The thistle flower head is a rich source of food, packed with achenes, and contains the most varied, specific and best known insect fauna of any part of the plant (Redfern 1983; Zwölfer 1988). The larvae of several herbivorous groups live here – tephritid flies, weevils and moths – together with their parasitoids, and constitute ecological microsystems that offer opportunities to study a variety of ecological and entomological subjects (Zwölfer 1979, 1987, 1988) as follows.

1 The adaptation of phytophagous insects to thistle hosts; for example, phenological synchronization (Romstöck-Völkl & Wissel 1989; Straw 1989a,b, 1991), morphological adaptation to flower head size (ovipositor length of tephritids: Zwölfer 1982, 1987; rostrum length of weevils: Zwölfer & Brandl 1989) and biotype formation (Zwölfer & Romstöck-Völkl 1991; Romstöck-Völkl 1997).

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2 Interspecific interactions among the insects in the flower head (Zwölfer 1979, 1994; Berube 1980).
3 Comparison of insect fauna of European thistle species, which were introduced into North America and have become agricultural weeds, between the original and introduced regions to search for pest control agents (Goeden 1974; Goeden & Ricker 1986a).
4 Major determinant of thistle insect diversity, such as the regional and local species richness of the host thistles and biogeographic history of the Cardueae (Zwölfer 1985).

According to Webb (1976), the Cardueae originated in the Mediterranean and Western Asia where they are most diverse, having 40 genera. From this center, they spread throughout Europe, parts of North Africa and much of Asia, thereafter reaching North America via the Bering Strait land connection (Small 1919). Reflecting this history, the diversity of the tribe decreased from the Mediterranean and Western Asia to North America (Zwölfer & Romstöck-Völkl 1991): in Japan, it is represented by nine genera (Kadota 1995), while in North America, by only three genera (Bremer 1994). In contrast, the genus *Cirsium* Mill. has diversified into more than 60 species in Japan, as many as in all of Europe (Kitamura 1937; Kadota 1995), and into approximately 90 species in North America. In Japan, the species of this genus are mostly endemic. They are often difficult to identify to species not only because different species are often morphologically similar and/or morphologically variable within a population, but also because they easily hybridize. Such situations have prevented us from carrying out studies of insect fauna associated with the thistles, despite these studies being promising.

Since 1988, we have collected thistle flower heads mainly from the Hokuriku district and other areas of central Honshu, the main island of Japan, to study the insect fauna in them. The present paper provides (i) a list of the weevils (Coleoptera: Cucurlionidae) and tephritid flies (Diptera: Tephritidae) obtained from the thistle flower heads, the core fauna associated with the flower heads; (ii) the degree of flower head damage by these insects; and (iii) their geographic distribution. From these data, overlap and/or segregation of host plant usage (thistle species, flowering seasons and geographic distribution) among the insects and the degree of their interactions have been analyzed. Finally, the insect fauna on the Japanese thistle flower head is compared with that in Europe and in North America in terms of species richness and specialization of guild structure.

MATERIALS AND METHODS

Japanese *Cirsium*

From 1988 to 1990 and from 1993 to 1998, thistle flower heads of the genus *Cirsium* (35 taxa consisting of 28 species, one subspecies and six varieties), together with those of the genera *Breea* Less., *Synurus* Iljin., *Saussurea* DC. and *Arctium* L. (one species each) (Table 1), were collected during the flowering seasons at 163 sites from Hokkaido to Okinawa, concentrating on central Honshu (Figs 1,2). Of the thistles studied, *C. japonicum* Fisch. ex DC., which is widespread in Honshu, Shikoku and Kyushu, and *C. brevicaule* A. Gray in Okinawa bloom in spring (hereafter termed 'spring-blooming' species). These two species are the only spring-blooming species in Japan. The flowering seasons of all other thistles collected in Honshu and Kyushu are from late summer to late autumn ('autumn-blooming' species). Flowering seasons of nine thistle species (three genera) collected in Hokkaido were from July to September: we treated these as autumn-blooming species in this study.

Collection of flower heads and insects

In this study, a group of flower heads collected at one time from the same thistle population is referred to as a 'sample'. The attack rate (AR) was calculated for samples with more than 100 flower heads (these are referred to as 'effective samples'), except for those specifically mentioned. Table 1 shows the total number of flower heads collected (NF) and the number of effective samples for each thistle species. A large number of samples were gathered from central Honshu (e.g. *C. japonicum*, 40 samples from 35 sites, NF = 9718; *C. matsumurae* Nakai, 24 samples from 18 sites, NF = 5692; *C. suzukaense* Kitam., 14 samples from 14 sites, NF = 4189; and *C. kagamontanum* Nakai, 13 samples from three sites, NF = 4143). For the species distributed in other regions, only a few samples were obtained (e.g. one sample for *C. uetsuense* Kitam., *C. congestissimum* Kitam. and *C. bitchuense* Nakai, NF = 152, 247 and 345, respectively). For the thistles with large NF, the number of flower heads collected per sample (*nf*) varied greatly among the samples (e.g. *C. japonicum*, 39–665; *C. matsumurae*, 28–854). The number of effective samples of each thistle species varied from 0 to 35 (Table 1).

Rearing of flower head insects

Collected flower heads were brought back to the laboratory and were kept in insect nets (0.5 m in

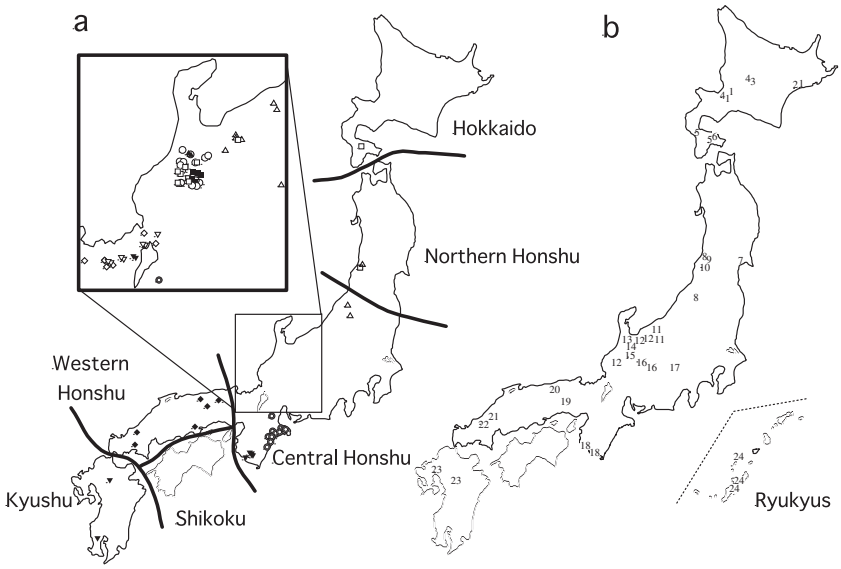

Figure 1 Location of *Cirsium* sampling sites. (a) △, *C. nipponicum*; ○, *C. matsumurae*; □, *C. yezoense*; ▽, *C. ashiuense*; ◇, *C. microspicatum* var. *kiotoense*; ▲, *C. kagamontanum*; ■, *C. purpuratum*; ▼, *C. buergeri*; ◆, *C. nipponicum* var. *yoshinoi*; ◎, *C. suzukaense*. (b) 1, *C. kamtschaticum*; 2, *C. heiianum*; 3, *C. vulgare*; 4, *C. kamtschaticum* subsp. *boreale*; 5, *C. alpicola*; 6, *C. pendulum*; 7, *C. oligophyllum*; 8, *C. dipsacolepis*; 9, *C. amplexifolium*; 10, *C. uetsuense*; 11, *C. microspicatum*; 12, *C. matsumurae* var. *pubescens*; 13, *C. inundatum*; 14, *C. matsumurae* var. *dubium*; 15, *C. otayae*; 16, *C. norikurense*; 17, *C. comocum* var. *yatsugatakense*; 18, *C. maritimum*; 19, *C. congestissimum*; 20, *C. bitchuense* var. *manisaense*; 21, *C. bitchuense*; 22, *C. sieboldii*; 23, *C. suffultum*; and 24, *C. brevicaure*.

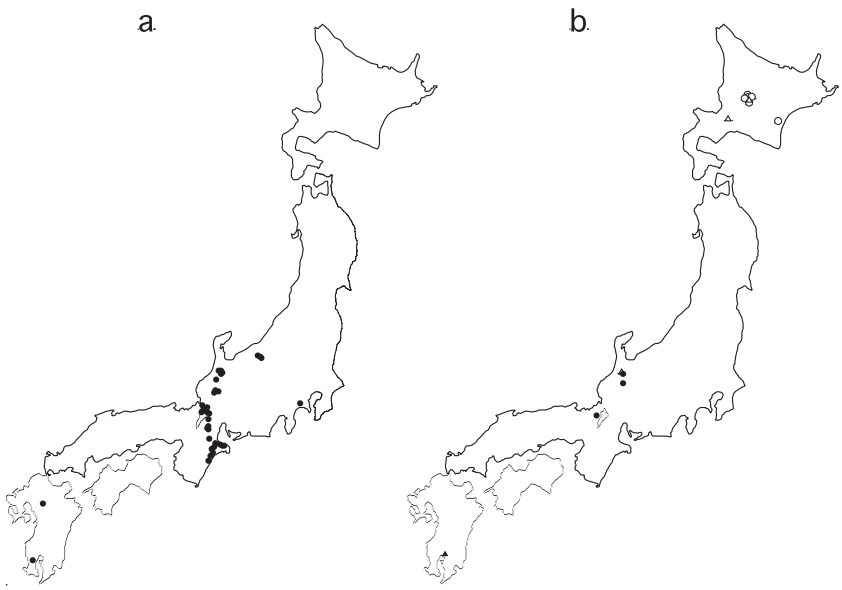

Figure 2 Location of sampling sites. (a) *Cirsium japonicum*. (b) △, *Arctium lappa*; ○, *Breea setosa*; ▲, *Saussurea japonica*; and ●, *Synurus pungens*.

diameter × 0.7 m in length) to obtain adults, which emerged the following autumn and the following spring from the samples collected in spring and autumn, respectively. The total number of individuals in each insect species that emerged from a sample (*ne*) was recorded.

Total number of insect individuals that emerged from a single flower head

The total number of insect individuals that emerged from a single flower head (n^*) was derived only from the flower heads that were attacked by the insects. In this study, n^* could not be derived directly from *nf* and *ne*, because collected flower heads were not kept separately. However, n^* was assessed for the following three thistle species: *C. japonicum*, *C. matsumurae* and *C. kagamontanum* collected in Kanazawa. Flower heads were individually kept in cups (100 mm in diameter × 40 mm deep) under laboratory conditions to record the number of individuals that emerged.

Table 1 List of weevils and tephritids associated with flower heads of Japanese Carduae, together with the average attack rate (AR) to the host plant

Plant species	Geographical distribution[†]	Total no. flower heads collected (NF)	No. effective samples[‡]	Weevils			Tephritids			
				Ll[§]	Lm	Lg	Tm	Xp	Us	Or
Cirsium kamtschaticum	HK	461	3	–	1[¶] (1.8)[††]	–	3 (22.8)	2 (6.0)	–	–
C. kamtschaticum subsp. *boreale*	HK	573	2	–	1 (1.4)	–	2 (4.8)	1 (7.3)	–	–
C. alpicola	HK and NH	320	2	–	–	–	1 (0.7)	1 (4.2)	1 (0.3)	–
C. heiianum	HK and NH	48	0	–	–	–	–	–	–	–
C. pendulum	HK and CH	138	1	–	–	–	–	1 (10.9)	–	–
C. yezoense	HK, NH and CH	835	3	–	2 (4.9)	–	–	*(1.4)	–	–
C. inundatum	NH	713	2	–	2 (0.5)	–	1 (1.3)	–	–	–
C. uetsuense	NH	152	1	–	–	–	–	–	–	–
C. nipponicum	NH and CH	2305	10	–	4 (0.5)	–	7 (1.6)	3 (0.4)	–	–
C. amplexifolium	NH and CH	385	1	–	–	–	–	–	–	–
C. oligophyllum	CH	759	1	–	–	–	–	1 (0.1)	1 (1.3)	–
C. comocum var. *yatsugatakense*	CH	33	0		*(3.0)	–	–	–	–	–
C. purpuratum	CH	381	1	–	1 (3.7)	–	–	–	–	–
C. norikurense	CH	74	0	–	*(13.5)	–	*(4.1)	–	–	–
C. matsumurae	CH	5692	20	–	13 (4.2)	–	12 (3.8)	6 (0.7)	–	–
C. matsumurae var. *pubescens*	CH	342	1	–	1 (2.5)	–	1 (20.6)	1 (1.3)	–	–
C. matsumurae var. *dubium*	CH	84	0	–	–	–	–	–	–	–
C. otayae	CH	479	3	–	–	–	–	1 (0.2)	–	–
C. suzukaense	CH	4189	14	–	–	–	–		1 (0.02)	–

C. microspicatum	CH	290	1	–	1 (0.5)	–	–	1 (0.8)	–	–
C. microspicatum var. *kiotoense*	CH	1727	5	–	–	–	1 (0.09)	5 (3.5)	–	–
C. kagamontanum	CH	4143	13	–	3 (0.07)	–	8 (0.5)	7 (0.6)		
C. ashiuence	CH	3257	9	–	2 (0.9)	–		3 (0.8)	–	–
C. buergeri	CH, WH and KS	995	5	–	–	–	4 (24.1)	–	–	–
C. nipponicum var. *yoshinoi*	WH	957	6	–	–	–	2 (0.4)	4 (3.2)	–	–
C. congestissimum	WH	247	1	–	–	–	1 (2.4)	1 (1.6)	–	–
C. bitchuense	WH	345	1	–	–	–	–	1 (2.6)	1 (0.3)	–
C. bitchuense var. *manisaense*	WH	117	1	–	–	–	–	1 (6.8)	–	–
C. suffultum	SK and KS	101	0	–	*(1.0)	–	–	*(6.9)	–	–
C. japonicum	HS, SK and KS	9718	35	9 (1.1)	3 (0.09)	–	–	25 (13.9)	5 (10.3)	–
C. dipsacolepis	HS, SK and KS	379	2	–	–	–	–	2 (4.0)	–	–
C. sieboldii	HS, SK and KS	61	0	–	–	–	–	*(3.3)	–	–
C. maritimum	HS, SK and KS	103	0	–	–	*(7.8)	–	–	*(116.5)	–
C. brevicaule	RK	837	3	3 (26.1)	–	–	–	–	–	–
C. vulgare	Europe (introduced to HK)	53	0	–	–	–	–	–	–	–
Breea setosa	HK and NH	2209	4	–	–	–	–	2 (0.1)	–	1 (0.03)
Saussurea japonica	KS	288	1	–	–	–	–	–	–	–
Synurus pungens	HK and CH	427	2	–	–	–	–	1 (0.5)	–	–
Arctium lappa	Europe (introduced)	1156	4	–	–	–	–	–	–	–
Number of thistle species utilized				2	15	1	13	24	6	1

[†]Abbreviations refer to the districts shown in Figure 1: CH, Central Honshu; HK, Hokkaido; HS, all of Honshu; KS, Kyushu; NH, Northern Honshu; RK, Ryukyus; SK, Shikoku; WH, Western Honshu; [‡]see the text for an explanation of 'effective samples'; [§]abbreviations refer to each weevil and tephritid species: Ll, *Larinus latissimus*; Lm, *Larinus meleagris*; Lg, *Larinus griseopilosus*; Tm, *Tephritis majuscula*; Xp, *Xyphosia punctigera*; Us, *Urophora sachalinensis*; Or, *Orellia ruficauda*; [¶]number of effective samples; and [††]the average attack rate (AR) (the values with <100 flower heads are shown by an asterisk).

Estimation of attack rate of insects

The attack rate (AR) of weevil and tephritid species for individual samples was derived as follows:

$$AR_{ij} = (ne_{ij}/nf_j) \times 100$$

where AR_{ij} is the attack rate by insect species i for sample j, nf_j is the number of flower heads in the jth sample, and ne_{ij} is the number of individuals of insect species i that emerged from sample j. Table 1 shows the average AR calculated for each thistle species that had effective samples (except for those specifically mentioned: see the footnote of Table 1). Table 2 shows the average AR for each insect species on the spring- and autumn-blooming thistles. When only one individual of species i emerged from a single flower head ($n^* = 1$), AR_{ij} was exactly the same as the ratio of flower heads infested by species i; however, when n individuals emerged from one flower head, the value was n-fold of the true ratio of damaged flower heads. In this paper, AR will be used as an approximation measure.

Similarity in insect host range

The degree of overlap of insect species i and j in host plant usage was examined by two indices. First, the Jaccard coefficient of community (S_{ij}) (Krebs 1999) was calculated for all pairs of insect species as follows:

$$S_{ij} = a/(a + b + c)$$

where a is the number of thistle species utilized by both insect species i and j, and b and c are numbers of thistle species used only by i and j, respectively.

Second, the percentage similarity (PS_{ij}) (Krebs 1999) was calculated as follows:

$$\mathrm{PS}_{ij} = \sum\nolimits_{\mathrm{min.}} (\mathrm{P}_{ix}\mathrm{P}_{jx})$$

$$P_{ix} = n_{ix}/N_i, \quad P_{jx} = n_{jx}/N_j$$

where N_i and N_j are the total number of individuals of insect species i and j emerged, respectively, and n_{ix} and n_{jx} are the number of individuals of insect species i and j which emerged from thistle species x. In this study, the number of thistle flower heads sampled was variable among the species; therefore, to derive P_{ix} and P_{jx}, AR_{ix} was used for n_{ix} and AR_{jx} for n_{jx}, $\sum AR_{ix}$ and $\sum AR_{jx}$ were used for N_i and N_j, respectively.

UPGMA cluster analysis was carried out on the two similarity matrixes derived by S_{ij} and PS_{ij}.

RESULTS

Weevils and tephritids that emerged from thistle flower heads and their attack rate

In this study, a total of six species – three *Larinus* species (Curculionidae) and three tephritid fly species – were recorded from *Cirsium*. More than one of these insect species was recorded from 30 *Cirsium* taxa collected in 111 (142 samples) of 149 sampling sites (192 samples in total). Two and one tephritid fly species were recorded from *Breea* and *Synurus*, respectively, in four (four samples) of 14 sampling sites (14 samples). Neither weevils nor tephritids were recorded from *Saussurea* or *Arctium* (Table 1). *Cirsium* had a richer insect fauna than other genera. Below are brief notes on host thistle species, distribution of collection sites and AR for each insect species.

Family Curculionidae: genus *Larinus*

Larinus latissimus *Roelofs*

Host plant. This weevil emerged from *C. japonicum*, the only spring-blooming species widespread in Honshu, Kyushu and Shikoku, and *C. brevicaule*, which is also a spring-blooming species and is locally distributed in Ryukyu (from the Amami-oshima to the Sakishima islands (Kadota 1995) (Table 1). The *C. brevicaule* feeding population was recognized as *L. latissimus kuroiwai* Kono (Morimoto, pers. comm., 1995). Of the 43 samples (38 sites) of *C. japonicum* (Fig. 2a), this weevil species was found in central Honshu (12 samples) and also in Fukuoka Prefecture, Kyushu (one sample) (Fig. 3a). In central Honshu, the species emerged from the samples collected on both the Japan Sea side (Ishikawa Prefecture, six samples from three sites) and the Pacific Ocean side (Mie Prefecture, five samples from five sites), but it was not found in the samples (13 samples from 12 sites) collected in the inland area between Fukui and the northern part of Lake Biwa (Figs 2a,3a). In *C. brevicaule*, the weevil emerged from all three samples collected in Okinawa Prefecture (Fig. 3a).

Attack rate. The average value of AR was low in *C. japonicum* (1.1) and high in *C. brevicaule* (26.1) (Table 1), although AR of *C. japonicum* was high for one sample from Mie and in Fukuoka Prefecture: 11.3 and 11.9, respectively.

Remarks. In central Honshu, the fact that spring-blooming *C. japonicum* was the only host and also the fact that the adult weevils emerged at the end of the flowering season from early to late July suggests that

Table 2 Geographical distribution, number of thistle species utilized and average attack rate (AR) of weevil and tephritid species on spring- and autumn-blooming thistles

		Host plants							
		Spring-blooming				Autumn-blooming			
			AR				AR		
Insect species	Geographical distribution	No. species (species)	Average[†]	*n*[‡]	Range	No. species (species)	Average	*n*	Range
Weevils									
Larinus laitssimus	Widespread	2 (*Cirsium japonicum*, *C. brevicaule*)	10.4	13	0.2–60.0				
Larinus meleagris	Widespread	1 (*C. japonicum*)	1.0	3	0.3–1.7	14 (e.g. *C. nipponicum*, *C. yezoense*, *C. matsumurae*)	4.3	30	0.1–30.9
Larinus griseopilosus	Local (Wakayama Prefecture)					1 (*C. maritimum*)	17.0[§]	–	–
Tephritids									
Tephritis majuscula	Widespread					13 (e.g. *C. kamtschaticum*, *C. matsumurae*, *C. buergeri*)	7.6	43	0.4–58.7
Xyphosia punctigera	Widespread	1 (*C. japonicum*)	19.4	25	1.4–113.5	21 (e.g. *C. kamtschaticum*, *C. matsumurae*)	3.4	43	0.1–15.0
	(Hokkaido)					1 (*B. setosa*)	0.2	2	0.2–0.3
	(Ishikawa Prefecture)					1 (*S. pungens*)	1.1	1	–
Urophora sachalinensis	Widespread	1 (*C. japonicum*)	71.8	5	0.3–203.8	5 (e.g. *C. maritimum*, *C. oligophyllum*)	0.6	4	0.2–1.3
Orellia ruficauda	Local (Hokkaido)					1 (*B. setosa*)	0.1	1	–

[†]Based on the effective samples infested by each insect species; [‡]the number of samples for which average attack rate (AR) was calculated; [§]AR was calculated from the sample with 47 flower heads.

this weevil is univoltine and overwinters as adults. The *n** was 1 or 2 (average 1.2) in *C. japonicum* (Table 3). In addition, one or two larvae or pupae were found from 69 of 150 flower heads of *C. brevicaule* dissected.

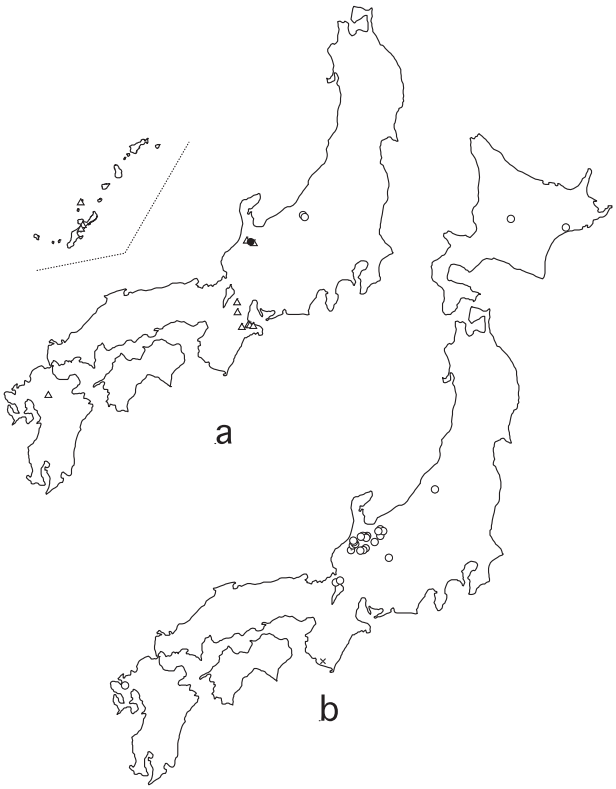

Figure 3 Distribution maps of three Japanese species of the genus *Larinus* for (a) spring-blooming thistles and (b) autumn-blooming thistles. △, *L. latissimus*; ○, *L. meleagris*; ×, *L. griseopilosus*; ●, *L. latissimus* and *L. meleagris* (coemerged from the same sample).

Larinus meleagris *Petri*

Host plant. This weevil species emerged from both spring-blooming *C. japonicum* and 14 autumn-blooming *Cirsium* taxa (Table 1). On *C. japonicum*, the weevil emerged in a small number from only three samples collected on the Japan Sea side of central Honshu (Niigata Prefecture, two samples from two sites; Ishikawa Prefecture, one sample) (Fig. 3a). In contrast, on autumn-blooming thistle species, the weevil emerged from a total of 42 samples collected from 30 sites, which were sporadically distributed from Hokkaido to Kyushu (Fig. 3b).

Attack rate. AR was very low in *C. japonicum* samples (0.3–1.7) (Table 2). In autumn-blooming thistles, the average AR was also low (4.3) (Table 2), with high values for some samples; for example, 15.7 and 30.9 in *C. matsumurae* samples and 10.2 in a *C. yezoense* sample collected in Ishikawa Prefecture.

Remarks. In central Honshu, the distribution of this weevil seemed biased on the Japan Sea side, based on the fact that thistles growing on the Pacific Ocean side, for example *C. suzukaense* collected in Mie Prefecture and *C. maritimum* Makino in Wakayama Prefecture, were not utilized by the weevil.

The weevil mostly utilized autumn-blooming thistles and it also used the spring-blooming thistle, but with a very low frequency. Of seven sites where we collected both spring- (13 samples) and autumn-blooming (26 samples) thistles, at six sites, the weevil emerged from either one of the seasonal blooming thistles, suggesting univoltinism depending on only one seasonal thistle. However, at the remaining site, it emerged from both spring- and autumn-blooming thistles, indicating the possibility of bivoltinism, depending on both seasonal thistles. The voltinism of this species is thus still

Table 3 Number of individuals of weevils and tephritid flies emerged from a flower head (*n**)

Insect species	No. individuals: Average	No. individuals: Range	*n*†	Examined host
Weevils				
Larinus latissimus	1.2	1–2	18	*Cirsium japonicum*
Larinus meleagris	1	1	90	*C. matsumurae*
	1	1	2	*C. kagamontanum*
Tephritids				
Tephritis majuscula	1	1	39	*C. matsumurae*
	1	1	9	*C. kagamontanum*
Xyphosia punctigera	1.3	1–5	378	*C. japonicum*
	1.2	1–3	13	*C. matsumurae*

†Number of flower heads from which adults emerged (see text).

unknown. On autumn-blooming thistles, the adults emerged from October to early November, so that this species seems to overwinter as adults. The n^* was 1 in *C. matsumurae* and *C. kagamontanum* (Table 3).

In Japan, *L. latissimus* and *L. meleagris* partitioned hosts by season: one used a spring-blooming thistle species and the other an autumn-blooming one. In Europe and North America, seasonal segregation in host plant usage has not been reported.

Larinus griseopilosus *Roelofs*

Host plant. This species emerged only from *C. maritimum* collected in Wakayama Prefecture (one site, one sample) (Table 1; Fig. 3b).
Attack rate. Eight *L. griseopilosus* adults emerged from 47 flower heads (AR = 17.0) (Table 2).

Family Tephritidae

Tephritis majuscula *Hering and Ito*

Host plant. The fly emerged from 13 autumn-blooming *Cirsium* taxa growing in Hokkaido (*C. kamtschaticum*. Ledeb. ex DC.), central Honshu (e.g. *C. nipponicum*, *C. matsumurae* and *C. kagamontanum*), Kyushu (*C. buergeri* Miq.) and other sites to a total of 49 samples from 39 sites (Table 1; Fig. 4b).
Attack rate. AR was frequently high: 14.8–30.8 for three *C. kamtschaticum* samples in Hokkaido; 11.7 and 24.0 for two *C. matsumurae* samples in Hokuriku (in addition, 16 adults emerged from one sample with 72 flower heads, AR = 22.2); 20.8 and 38.6 for two *C. buergeri* samples on the Pacific Ocean side of central Honshu (in addition, 29 adults emerged from a sample with 51 flower heads, AR = 56.9); and 58.7 for one *C. buergeri* sample in Kyushu.
Remarks. This tephritid species utilized only autumn-blooming *Cirsium* species and adults emerged at the end of the flowering period from late October to early November, and the species seems to be univoltine and overwinter as adults. Some species of European *Tephritis* feed on callus (Zwölfer 1985), but *T. majuscula* larvae did not form a callus. Most larvae of all European *Tephritis* species are gregarious in flower heads, but in this study, only one adult of *T. majuscula* emerged from a flower head ($n^* = 1$) of *C. matsumurae* and *C. kagamontanum* (Table 3).

Urophora sachalinensis *Shiraki*

Host plant. Six *Cirsium* taxa, including both spring-blooming *C. japonicum* (eight samples from eight sites) and five autumn-blooming taxa (six samples from six sites) (Table 1) were used as host plant. This fly species

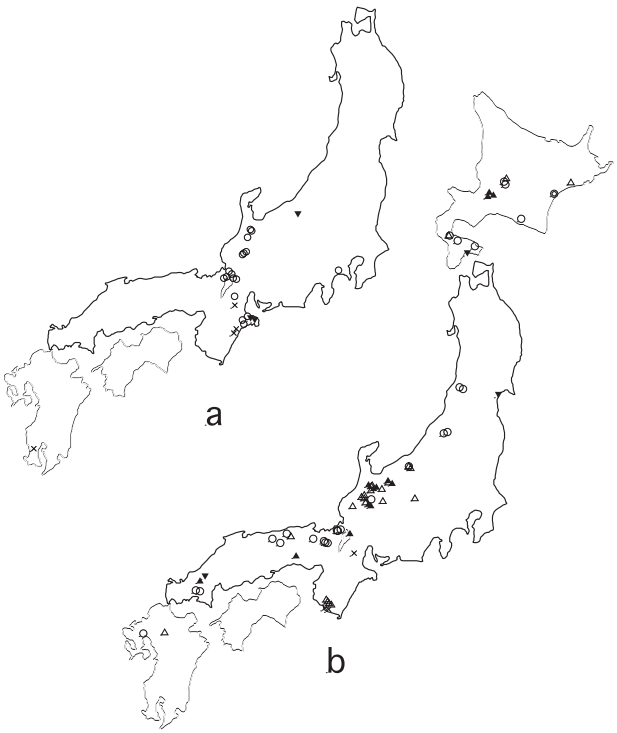

Figure 4 Distribution maps of four Japanese species of tephritids for (a) spring-blooming thistles and (b) autumn-blooming thistles. △, *Tephritis majuscula*; ○, *Xyphosia punctigera*; ×, *Urophora sachalinensis*; ◎, *Orellia ruficauda*; ▼, *X. punctigera* and *U. sachalinensis* (emerged from the same sample); ▲, *T. majuscula* and *X. punctigera* (emerged from the same sample).

was widespread from Hokkaido to Kyushu, but its occurrence was sporadic (Fig. 4a,b). On the Japan Sea side, it was not recorded from the Hokuriku or San'in districts, except in one site (Niigata Prefecture, *C. japonicum*), while the species was commonly collected on the Pacific Ocean side of central Honshu (six of 11 *C. japonicum* samples in Mie Prefecture; both of two *C. maritimum* samples in Wakayama Prefecture) (Fig. 4a,b).
Attack rate. AR of a few samples was extremely high on the Pacific Ocean side of central Honshu (e.g. 149.8 and 203.8 for *C. japonicum* collected in Mie Prefecture; 92.9 and 144.7 for *C. maritimum* collected in Wakayama Prefecture, where the number of flower heads was only 52 and 68, respectively), but AR in other areas was generally low (average: 1.1; range: 0.3–1.3).
Remarks. This species utilized both spring- and autumn-blooming thistle species. However, all of these samples were collected from different locations. The

voltinism of this species is to be studied. Larvae of this fly formed lignified, cup-shaped ovary-receptacle galls in flower heads, in which an average of 2.9 (SD: 3.2; range: 1–26 ($n = 88$), Mie Prefecture) cells were found, and they overwintered as mature larvae in the galls.

Xyphosia punctigera *Coquillett*

Host plant. This species emerged from more than one host genus, which was the only such case among the weevils and tephritids recorded in this study. It emerged from 22 *Cirsium* taxa (spring-blooming *C. japonicum* and 21 autumn-blooming taxa), *Breea setosa* (M. Bieb.) Kitam. and *Synurus pungens* (Franch. and Sav.) Kitam. (Table 1): these were distributed widely from Hokkaido to Kyushu (80 samples from 62 sites) (Table 1; Fig. 4a,b). However, the distribution in central Honshu was concentrated on the Japan Sea side, as shown partly by the fact that the species emerged neither from *C. maritimum* nor *C. buergeri* in Wakayama Prefecture, nor from *C. suzukaense* in Mie Prefecture (Fig. 4a,b).

Attack rate. In *C. japonicum*, AR was frequently high (average 18.3, range 10.4–113.5 on 17 of 29 samples) (Table 2) with the highest value (113.5) in Mie Prefecture. In 21 autumn-blooming *Cirsium* taxa, AR was generally low (average 3.4, range 0.1–15.0) (Table 2) except for a few samples (e.g. 15.0 in *C. kamtschaticum*; 14.6 in *C. kamtschaticum* ssp. *boreale* (Kitam.) Kitam.; 10.9 in *C. pendulum* Fisch. ex DC.; and 11.0 in *C. microspicatum* var. *kiotoense* Kitam.). AR was also low in *B. setosa* (0.2) and *S. pungens* (1.1) (Table 2).

Remarks. At many sampling sites, this fly species utilized both spring-blooming *C. japonicum* and autumn-blooming thistle species; for example, in Kanazawa it emerged from *C. japonicum* and autumn-blooming *C. matsumurae* growing nearby. This fact shows that the species is bivoltine. Adults emerged at the end of the flowering season of *C. japonicum* from early to late in July, and mature larvae of this species hibernated within the flower heads of autumn-blooming *Cirsium* hosts. The n^* was 1–5 (average: 1.3) (Table 3).

As mentioned above, *U. sachalinensis* and *X. punctigera* emerged from both spring- and autumn-blooming thistle species, but these two species were rarely recorded simultaneously (one sample in Niigata Prefecture and two in Mie Prefecture on spring-blooming *C. japonicum*, and one sample each in Hokkaido, Miyagi and Shimane prefectures on autumn-blooming *Cirsium* species) (Fig. 4a,b). The former was collected mainly on the Pacific Ocean side, and the latter mainly on the Japan Sea side.

Orellia ruficauda *F.*

Only one individual emerged from one of six samples of *B. setosa* collected from six sites in Hokkaido. AR was 0.1 (Table 2).

Similarity in insect host range

Jaccard coefficient of community

The similarity matrix based on the Jaccard coefficient of community (Table 4) showed that the index was highest, 0.42, between *L. meleagris* and *X. punctigera*, each utilizing 15 and 25 *Cirsium* species, respectively, and

Table 4 Similarity matrices of Jaccard coefficient and percent similarity index

	Larinus latissimus	*Larinus meleagris*	*Larinus griseopilosus*	*Tephritis majuscula*	*Xyphosia punctigera*	*Urophora sachalinensis*
Jaccard coefficient						
L. latissimus	1	–	–	–	–	–
L. meleagris	0.06	1	–	–	–	–
L. griseopilosus	0	0	1	–	–	–
T. majuscula	0	0.4	0	1	–	–
X. punctigera	0.04	0.42	0	0.4	1	–
U. sachalinensis	0.14	0.05	0.17	0.06	0.17	1
Percent similarity index						
L. latissimus	1	–	–	–	–	–
L. meleagris	0.001	1	–	–	–	–
L. griseopilosus	0	0	1	–	–	–
T. majuscula	0	0.23	0	1	–	–
X. punctigera	0.18	0.14	0	0.19	1	–
U. sachalinensis	0.07	0.001	0.91	0.002	0.08	1

sharing 11 of these species (C. *japonicum* and 10 autumn-blooming thistle species). The second highest index was 0.4 for two combinations: between *L. meleagris* and *T. majuscula* (utilizing 13 autumn-blooming thistle species), and between *X. punctigera* and *T. majuscula*, sharing eight and 10 thistle species, respectively. The third highest similarity, 0.17, was found between *U. sachalinensis*, utilizing *C. japonicum*, *C. maritimum* and four other thistle species, and two insect species: first with *X. punctigera*, sharing five thistle species, including *C. japonicum*; and second with *L. griseopilosus*, recorded only from *C. maritimum* (Table 2).

Cluster analysis, carried out on Jaccard coefficients (Fig. 5a), indicated *L. meleagris*, *X. punctigera* and *T. majuscula* composed the first cluster (a-1) by sharing many autumn-blooming thistle species. *Larinus latissimus*, *U. sachalinensis* and *L. griseopirosus* formed the second cluster (a-2) by sharing *C. japonicum* (*L. latissimus* and *U. sachalinensis*) and *C. maritimum* (*U. sachalinensis* and *L. griseopirosus*).

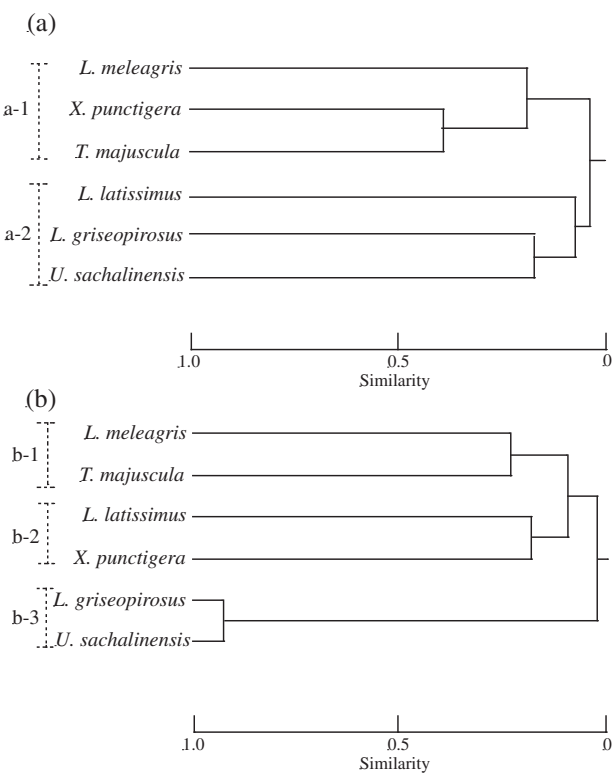

Figure 5 Cluster diagrams for host plant similarity of the insects associated with the flower head of Japanese *Cirsium*. Cluster analyses were carried out on the Jaccard coefficient (a) and percentage similarity (b).

Percentage similarity

The similarity matrix based on percentage similarity (Table 4) indicates that the index was highest between *L. griseopilosus* and *U. sachalinensis* (0.91), and was second highest for *L. meleagris* and *T. majuscula*, which shared eight species (0.23). The third and fourth highest similarity (0.19 and 0.18) was found in *T. majuscula* and *X. punctigera* (sharing 10 autumn-blooming thistle species), and *L. latissimus* and *X. punctigera* (sharing only *C. japonicum*), respectively.

The percentage similarity index (PS_{ij}), calculated on the basis of relative abundance using AR (Table 4), was somewhat different from similarity indices based on Jaccard coefficients: *L. griseopilosus* and *U. sachalinensis* had a closer relationship in percentage similarity (0.91, highest) than that in Jaccard coefficients (0.17, third highest), because they shared only *C. maritimum*, but their relative abundances were extremely high on this host (1 and 0.91, respectively). The percentage similarity between *L. latissimus* and *X. punctigera* (0.18, fourth highest) was also higher than that calculated by Jaccard coefficients (0.05, ninth highest), because their relative abundances on *C. japonicum,* the only shared host, were high (1 and 0.18, respectively). In contrast, the percentage similarity between *L. meleagris* and *X. punctigera* (0.14, fifth highest) was lower than that in Jaccard similarity (0.42, highest), because these species shared 11 thistle species, but their relative abundance was not simultaneously high for the same thistle species. For example, the relative abundance of *L. meleagris* was high only on *C. matsumurae* (0.21), but extremely low on 10 other species (0.001–0.08), and that of *X. punctigera* was high on *C. japonicum* and *C. suffultum* (0.18 and 0.1, respectively), but extremely low on eight other species (0.002–0.07).

Cluster analysis carried out on the percentage similarity mentioned above showed different results from that in the Jaccard coefficient analysis (Fig. 5b): *L. meleagris* and *T. majuscula* formed the first cluster (b-1), *L. latissimus* and *X. punctigera* a second cluster (b-2), and *L. griseopilosus* and *U. sachalinensis* a third (b-3).

In summary, the combination of a weevil and a tephritid (i.e. *L. latissimus* and *X. punctigera*, *L. meleagris* and *T. majuscula* or *L. griseopilosus* and *U. sachalinensis*) showed strong similarity, forming a cluster in both similarity indices, while the combination of two species in the same taxonomic group (weevil–weevil or tephritid–tephritid) showed a lower host plant similarity. These facts suggest that the two species, utilizing the *Cirsium* flower heads in a similar way, may

segregate the host plants through interference (or competition).

DISCUSSION

Species richness of weevils and tephritid flies associated with flower heads of the Japanese *Cirsium*

In the present study, we recorded three *Larinus* species (Curculionidae) and three tephritid fly species (*Tephritis*, *Urophora* and *Xyphosia*) from the flower heads of 35 taxa of Japanese *Cirsium*. Two other tephritid flies, *Chaetostomella stigmataspis* (Zwölfer 1973) and *Tephritis longicauda* (Sueyoshi 1998), were also recorded from Japanese *Cirsium* but they were not found in the present study. In total, five tephritid fly species (four genera) were recorded from Japanese *Cirsium*. In this study, we examined more than half of the Japanese *Cirsium* species. However, we collected the samples mainly from central Honshu, particularly from Hokuriku: samples from other regions were limited. Among the three *Larinus* species, two were widespread, but the other two were locally distributed. All three tephritid species were widespread and utilized various thistle species. We probably recorded a substantial portion of the widespread insect species, but the species with localized distribution, such as *L. griseopirosus*, might have been overlooked. In the future, we should examine thistles in regions other than central Honshu more extensively.

Zwölfer (1985) mentioned that the major determinants of insect diversity in *Cirsium* flower heads are the regional and local species richness of the host thistles and the biogeographic history of the Cardueae. Zwölfer (1965) recorded six weevil species (two genera) and 12 tephritid fly species (seven genera) from 16 *Cirsium*, approximately one quarter of the European *Cirsium* species, collected from seven countries. In North America, four tephritid fly species and no weevils were recorded (Goeden & Ricker 1986b, 1987a,b) (Fig. 6a). The average numbers of insect species on a *Cirsium* species in Europe, Japan and North America were 1.8 ± 1.1, 1.0 ± 0.7 and 0 weevils, and 2.7 ± 1.6, 1.8 ± 0.4 and 1.6 ± 1.4 tephritids, respectively (Fig. 6b) (the figures for Europe were derived from Zwölfer (1965), for North America from Goeden & Ricker (1986b, 1987a,b) and for Japan from this study). Species richness of weevils and tephritids attacking *Cirsium* in Japan was lower than that in Europe and higher than that in North America. This gradient in the richness of these insects is contrary to the species richness of the genus *Cirsium*, which could be explained by (i) lower species richness of the tribe Cardueae in Japan and (ii) shorter history of insect–thistle interactions than in Europe, the place of origin of the thistles.

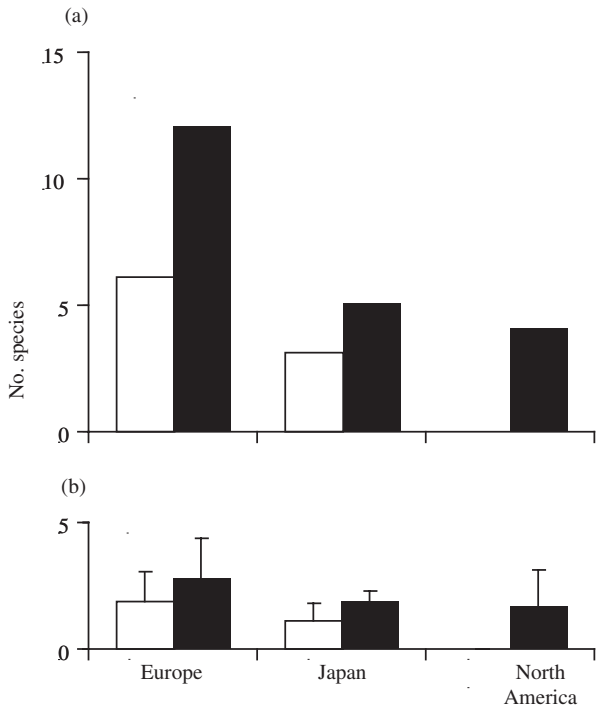

Figure 6 Number of insect species associated with the flower head of the *Cirsium* genus in Europe, Japan and North America. Total number of species (a) and average number of insect species per *Cirsium* species (b). □, Weevils; ■, tephritids.

Specialization in host usage

The degree of specialization was considered from the following two aspects: host specificity and guild structure.

In insects associated with the flower head, host range becomes narrower as the host plant–herbivore interactions advance (Zwölfer & Romstöck-Völkl 1991). In Europe, the average number of *Cirsium* species utilized by a single insect species was 3.6 (SD: 2.8; range: 1–10) in Tephritidae (12 species in seven genera) and 4.7 (SD: 3.5; range: 1–10) in weevils (six species in two genera) (derived from Zwölfer 1965). In North America, all tephritid species attack not only the genus *Cirsium*, but also other genera of Cardueae (Goeden & Ricker 1986b, 1987a,b). In Japan, comparable values for Tephritidae and weevils were 13.7 species (SD: 8.0; range: 6–22) and 6.0 species (SD: 6.4; range: 1–15),

respectively. Compared to the European species, the host range in Japan was broader in Tephritidae, but it was similar in the weevils, and both insect groups were more specialized than in North America.

In Japan, there are only two spring-blooming thistle species (*C. japonicum* and *C. brevicaule*), so that insects that reproduce only on the spring-blooming thistles can utilize up to two host species (e.g. *L. latissimus* utilized *C. japonicum* and *C. brevicaule*). In contrast, the autumn-blooming thistles are usually closely related, each occupying only a narrow area and being replaced successively by other species. Therefore, widespread insect species reproducing on autumn-blooming thistles can utilize many thistle species (e.g. *L. meleagris* utilized *C. kamtschaticum* and *C. kamtschaticum* ssp. *boreale* in Hokkaido, *C. matsumurae* and *C. nipponicum* in Hokuriku district and *C. suffultum* in Kyushu; Table 1). The exception is *U. sachalinensis*. It is widespread but utilized only five autumn-blooming species (Table 2). The gall-forming habit of this fly may limit its host range.

In the majority of *Cirsium* species in Europe, the herbivore fauna in flower heads showed a distinct niche structure with three complementary trophic strategies, namely guild structure: (i) an early attack on the closed buds of flower heads, usually combined with the formation of structural galls or callus growth on which the larvae feed; (ii) feeding on maturing or ripe achenes and receptacle without the induction of abnormal tissue growth; and (iii) oviposition after flower heads have opened or even in an early postbloom stage by polyphagous lepidopterous species with relatively mobile larvae that feed on plant tissues and develop carnivorous or cannibalistic tendencies when they come into contact with other inhabitants of the flower head (Zwölfer 1988). This study dealt with the weevils and tephritids, thus guild (iii) is not discussed here. In the majority of the European Cardueae, Zwölfer (1988) has found complete guilds with representatives of the two complementary guilds of the weevils and tephritids (41 host plant species with complete guilds, six with incomplete guilds). Our study showed that only *U. sachalinensis*, forming galls in six *Cirsium* species, belongs to guild (i), and callus tissue-feeder was lacking. The other five insect species recorded in this study belong to guild (ii). Thus guild (i) is not saturated in Japanese *Cirsium*. In North America, *Cirsium* flower heads also lack the insect guild (i) (Headrick & Goeden 1998).

From these viewpoints, the weevils and tephritids of the Japanese *Cirsium* are characterized by a lower species richness and a lower degree of specialization in usage of the thistle flower heads.

Further study

In Europe, local populations of weevils and tephritids associated with thistle flower heads (e.g. *T. conura*) are often recognized as 'biotypes', showing a different host preference and morphological adaptation to host structure (Zwölfer & Romstöck-Völkl 1991; Romstöck-Völkl 1997). In this study, however, we noticed morphological differences according to size differences in flower heads among host species neither in the length of the tephritid ovipositor nor in that of the weevil rostrum. The morphology of the insects is to be measured quantitatively in our next study.

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