

Kontyû, Tokyo, 51 (3): 339-350. September 25, 1983

Host-race Formation and Speciation in the *Henosepilachna vigintioctomaculata* Complex (Coleoptera, Coccinellidae)

II. Geographic Variation of Food Preference in *Henosepilachna vigintioctomaculata**

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Synopsis Food preference of *Henosepilachna vigintioctomaculata* in Japan was examined by food choice tests using eleven species of plants. From the geographic variation in preference for *Schizopepon bryoniaefolius* and *Panax japonicus*, this beetle is divided into three races distributed in Honshu (fpA-1), Hokkaido (fpA-2), and Rishiri and Rebun Islands (fpA-3), corresponding to the morphologically recognized forms V-I, V-II and V-III, respectively. The process of the race formation is reconstructed from the state of differentiation and the geological history of the Japan Archipelago in the Quaternary.

In a previous paper (HOSHIKAWA, 1983) the host ranges of the *Henosepilachna vigintioctomaculata* complex (henceforth abbreviated as the Hv complex) were revised and a tentative classification of the complex was given based on the food preference order. The Hv complex was thus tentatively divided into seven groups: fpA, fpB, ..., fpG. Most of these groups correspond to the forms or species hitherto recognized. This paper deals with one of the seven groups, fpA, which is identified as *H. vigintioctomaculata* (MOTSCHULSKY) (abbreviated as Hv).

The food habit of Hv was intensively studied by KOYAMA (1950a, 1950b, 1951, 1954, 1957, 1975), KUROSAWA (1954) and KATAKURA (1975). From geographic variations in morphological characters, chiefly in elytral shape (MAKI, 1966; KATAKURA, 1973), Hv in Japan was divided into three forms: V-I distributed in Honshu, Shikoku and Kyushu, V-II in Hokkaido and V-III in Rishiri and Rebun Islands (KATAKURA, 1974). On the other hand, the geographic variation in food habit has not been studied as yet.

In this paper, I describe the geographic variation of food preference in fpA (Hv), recognize three host races, and infer the process of host-race formation taking into account the geological evidence in the Quaternary.

The plant names in the text are abbreviated as follows: *R*: *Caulophyllum robustum* MAXIM. *Y*: *Chelidonium japonicum* THUNB. *T*: *Panax japonicus* C. A. MEYER. *A*: *Cirsium* sp. (probably *C. kamtschaticum* LEDEB.). *G*: *Arctium Lappa* L. *Z*: *Breca setosa* (BIEB.) KITAM. *Ch*: *Chrysosplenium japonicum* (MAXIM.)

* Contributions to the knowledge of *Henosepilachna vigintioctomaculata* complex. XIV.

Table 1. Preference orders of samples belonging to fpA, *Hemosepilachna vigintioctomaculata*, obtained by food choice tests for adults (FCTA) and for larvae (FCTL). Plant codes are given in p. 339, 342. Order is expressed as more preferred > less preferred. Plants after “≠” were refused.

Sample code	Plant	Preference order	
		FCTA (No. of ♀♀/♂♂)	FCTL (No. of trials)
601:	P/P ¹⁾	B ≧ P ≧ N	—
2:	P/P	P > B > N > H* > T ¹⁾ > R > A = Y > G	B = P = M = N > H > T > R > A > Y = G (10)
901:	P/P	M > P ≧ B > N > T ¹⁾ > R > Z > A	—
3:	K/P	P > N > T ¹⁾	—
802:	P/P	M > P = B > N > T ¹⁾ > R > A	—
803:	P/P	M > B > P > N > T ¹⁾ > R > A	M > B = P = N > T > R > A > Y > G (3)
RISHIRI & REBUN ISLANDS			
4:	P/P	N > P > B	—
801:	P/P	≠ T, R, A, G	—
12:	P/P	> T ¹⁾ > R > A ≠ G, Y	—
24:	P/P	> T ¹⁾ > R ≧ G = Y ≠ A	N > M = P > B > H > T > R > A > G = Y (6)
606:	P/P	N > P > B > H* > T ¹⁾ > R ≧ Y > G ≠ A	N > P > B > H > T > R > A > G > Y (7)
904:	P/P	N > P ≧ B > T ¹⁾ > R > G > A	—
		M ≧ N > P > B > T ¹⁾ > Z ≠ R, A	—
HOKKAIDO			

609:	N/N	$N > P \geq B$	$> T^1 > R > G = A$	(8/7)	—	$N > P > B = H = T > R > A \neq G, Y$	(4)
20:	N/N	$N > P > B > H > T^1 > R$	$\neq A, G, Y$	(4/1)	—	$N = P > B > H > T > R > A \neq G, Y$	(5)
31:	P/P	$N > P > B > H^* > T^1 > R > A \geq Y \neq G$		(15/16)			
HONSHU							
34:	K+G/P	$P > B$	$> N > A \neq T, R, G$	(8/6)	—		
806:	P/P	$P > B = M > N > T$		(10/9)	—		
807:	E/P	$P > B = M > N > T$		(6/2)	—		
37:	P/P	$P > B > N = H^* > T > A > G \neq R, Y$		(13/12)	—	$P = M = B > H > N > T > R > A > Y = G$	(14)
910:	P/P	$P > B > M > N > T > Z \geq R > A$		(4/2)	—		
40:	P/P	$P > B > N \geq H \neq T, R, Y, G, A$		(5/4)	—	$P > B = H = M > N > T > R > A > Y = G$	(8)
912:	P/P	$P > B > N > T$		(8/3)	—		
913:	Ch/Ch	$P > N$	$> T \neq A$	(10/8)	—		
41:	P/P	$P > N \neq R$		(2/2)	—		
49:	P/P	$P > R > T \neq A, G$		(2/0)	—	$P = B = M > N > T > R = A > G \neq Y$	(3)
50:	P/P	$P > B > H > N > T > R \neq Y, A, G$		(10/6)	—	$P = B > H > N > T > R > Y > A = G$	(14)
53:	F/P	—			—	$P > B > H > N = T \neq R, Y, A, G$	(3)
54:	P/P	—			—	$M = P > B > N > T > R > A \neq Y, G$	(4)
57:	P/P	$P > B > N > H > R > G > Y > A \neq T$		(22/8)	—	$P = M > B > N > H > T > R > Y > A > G$	(15)
60:	P/P	$P > B > H > N > T > R > Y = G \neq A$		(13/3)	—	$P > B > M = N = H > T > R > G > A \neq Y$	(12)
63:	P/P	$P > B > H = N > T = R > G \neq Y, A$		(12/11)	—	$P > B > H > N > T > R > G \neq Y, A$	(9)

1) Plant from which the sample was collected/plant given as food in rearing.

2) T¹: "Panax burst" (explanation in text). The rank of asterisked H was decided only by feeding intensity on it.

KITAM. *H*: *Scopolia japonica* MAXIM. *F*: *Physaliastrum japonicum* (FR. et SAV.)
 HONDA. *M*: *Solanum megacarpum* KOIDZ. *P*: *S. tuberosum* L. *B*: *S. nigrum* L.
E: *S. melongena* L. *N*: *Schizopepon bryoniaefolius* MAXIM. *K*: *Cucurbita moschata*
 DUCH.

Materials and Methods

Of 112 samples of the Hv complex tested, 31 from 28 populations (Table 1, Fig. 1) were clustered in fpA (see the next section).

Preference order was determined by food choice test for adults (FCTA: repeated food choice tests with removal of the most preferred plant) and food choice test for larvae (FCTL: continuous feeding on leaf discs of various plants) (HOSHIKAWA, 1983).

I. Geographic Variation of Food Preference

Populations of fpA are all characterized by the preference for *P*, *B*, *M*, *H*, *N* and by the virtual rejection of *A*, *Y* and *G*. *T*, *R* and *Z* are also not preferred but less rejectable than *A*, *Y* or *G*. The preference orders obtained are given in Table 1.

I-1. Results of FCTA

Two distinct features are recognized in Fig. 1: (i) There are two types as to *N* preference; in one type *N* is ranked top while in the other ranked 3rd or 4th. (ii) There are two types concerning the feeding intensity of *T*; it is high in one type but very low in the other. *T* was scarcely eaten by all fpA populations when offered with solanaceans or cucurbitacean (Fig. 1). Removal of these in consecutive tests causes a clear increase of *T* consumption (*Panax* burst, T^1 in Table 1) in some samples but not in others. This phenomenon did not appear in tests using one or a few adults, suggesting a kind of aggregation effect (HOSHIKAWA, unpublished). By these differences fpA is divided into three subgroups:

fpA-1: prefers *P* to *N* and does not show *Panax* burst. Samples 34, 37, 40, 50, 57, 60, 63, 806, 807, 910, 912, 913, 41?, 49?, all these samples are from Honshu.

fpA-2: prefers *N* to *P* and shows *Panax* burst. Samples 12, 20, 24, 31, 606, 609, 801, 904, 4?, from the main island of Hokkaido.

fpA-3: prefers *P* to *N* and shows *Panax* burst. Samples 2, 3, 601, 802, 803, 901, from Rishiri and Rebun Islands.

T or *R* was completely refused in some samples of fpA-1. In the extreme case (No. 40) *T*, *R*, *Y*, *A* and *G* were not eaten through three consecutive tests. Even when they were eaten, the consumed amount was almost negligible in most cases. All samples of fpA-2 and fpA-3 took both *T* and *R* except that No. 904 rejected *R* and No. 4 both. Similar tendencies were observed for *Y* and *A*. In general, samples belonging to fpA-1 showed a stronger stenophagy than fpA-2 or fpA-3. *M* pre-

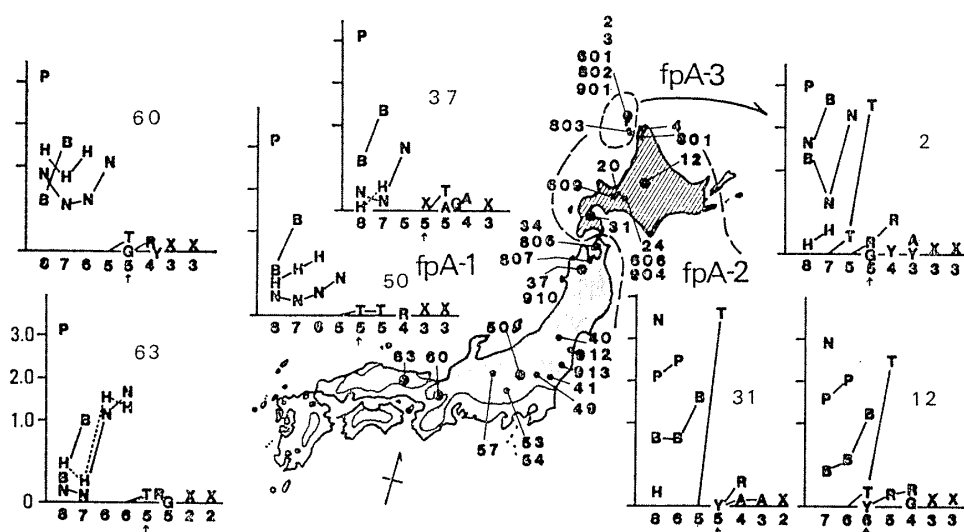


Fig. 1. Typical results of food choice test for adults (FCTA) with fpA populations (Nos. 2, 12, 31, 37, 50, 60, 63). Ordinate: feeding intensity, i.e. the area consumed (cm^2)/individual. Abscissa: number of plant species offered in consecutive tests (Arrow indicates addition of Y). x: no intake. The map shows sample localities, with distribution areas of Hv in Japan by KATAKURA *et al.* (1977).

Provenance of samples (sample code, locality and date in parenthesis). Nos. 601–609, Nos. 2–63, Nos. 801–807, Nos. 901–913 were collected in 1976, 1977, 1978, and 1979, respectively. *Rishiri and Rebun Islands*: 601, Lake Kushu, Rebun (IX/2); 2, do. (VI/15); 901, do. (VI/24); 3, Motochi (IX/23); 802, Kahuka (VII/3); 803, Oshidomari, Rishiri (VII/3). *Hokkaido*: 4, Hujimi chō, Wakkanai (VI/14); 801, Yūchi (VII/4); 12, Kagura, Asahikawa (VI/16); 24, Hiroshima chō, near Sapporo (VII/2); 606, Todoyama (VIII/24); 904, Nopporo (VII/22); 609, Usubetsu, Sapporo (VIII/19); 20, Kobetsuzawa, Sapporo (VII/23); 31, Yakumo, Oshima (VI/8). *Honshu*: 34, Kusō-domari, Shimokita (VIII/22); 806, Wakinosawa (VII/23); 807, Kita-Nojiri, Aomori (VIII/12); 37, Jōnan chō, Hirosaki (V/24); 910, Ichinowatari (VII/12); 40, Sakamaki, near Yamagata (V/22); 912, Souma (V/9); 913, Kammata, near Takine (V/7); 41, Daigo chō (V/29); 49, Izumi, Nikkō (V/27); 50, Tsukuda (V/18); 53 & 54, Ohmukawa, near Kobuchizawa (V/29); 57, Shimashima, near Matsumoto (V/17); 60, Seriu, Kyōto (V/16); 63, Mitoku, near Kurayoshi (V/14).

ference may also differ between fpA-1 and the others, i.e. the former has a lower preference for *M*, but this should be further confirmed by taking more population samples.

Other minor differences observed are: (i) *B* was eaten slightly more by fpA-3 than the others. (ii) Samples collected from *N* (Nos. 20, 609) ingested *N* more than other samples of fpA-2 collected from *P*. (iii) Samples from southwestern Honshu (Nos. 60, 63) took *H* slightly more than the others, though the preference rank of *H* was constantly the lowest in the solanaceans tested. These may reflect historical or ecological differences among the tested populations, but the present results are not sufficient for closer analysis since the feeding intensities fluctuated in FCTA (cf. KOYAMA, 1950 b). No consistent geographic tendency was observed as to *P* preference or occasional feeding on *G*.

I-2. *Results of FCTL*

The mean preference order determined by FCTL (HOSHIKAWA, 1983) also varies geographically though less conspicuously than in FCTA, i.e. $P \geq B > N$ in fpA-1, $N > P > B$ in fpA-2 and $B = P = N$ in fpA-3 (Table 1, Fig. 2A). The difference is statistically significant despite occasional shifts of the rank in 2–10% of the tests.

To compare the feeding responses of these samples in more detail, the speed of disc consumption was evaluated by an nh index, $n \times h/100$ (n : the number of larvae tested, h : hours required to consume half of a leaf disc). Tests including either H or M were taken into account, since the influence of the presence/absence of the disc upon nh indices of the other plants was negligible. The variation in consumption speed for each plant are given in Table 2. The preference order and consumption speed agree with each other in general, but there are some discrepancies as in No. 12 (B, T), No. 40 (P, B) and No. 50 (P, B).

On N and T , consumption speed was quicker in fpA-2 and fpA-3 than in fpA-1. In the latter, northern samples (fpA-1N: Nos. 37, 40, 50) consumed quicker than did southwestern ones (fpA-1S: Nos. 57, 60, 63), showing a gentle cline. Complete rejection of T was observed in 16% of the tests with fpA-1, while never in fpA-2 and fpA-3. An R disc was often eaten more than half by fpA-2 and fpA-3 (Table 2), while never by fpA-1. In fpA-1, a maximum consumption rate of only 30% was observed in No. 37, and the leaf disc was just nibbled in 60% of the tests. B was discriminated from P only by fpA-2. Exchange of its rank with T sometimes occurred (23% of the tests) in fpA-2 but not in fpA-1 or fpA-3. The rejection ratio of A was 23, 50, 50, 62% in fpA-3, fpA-2, fpA-1N and fpA-1S, respectively, being higher in southern samples. Slight variation was found as to the preference for P, Y and G . H and M were consumed as quickly as P or B , and the data are still insufficient to detect the geographic variation.

Table 2. Consumption speed for each plant in FCTL, represented by nh index.

	fpA-3				fpA-2				fpA-1				
	2	12	24	20	31	37	40	50	57	60	63	fpA-1	
<i>P</i>	2.0	2.5	2.9	2.0	1.7	2.4	2.4	2.9	1.8	2.1	2.0	2.2	2.2
<i>B</i>	1.8	4.0	3.2	3.0	3.1	3.4	2.6	2.0	1.7	2.7	2.4	2.7	2.4
<i>N</i>	2.2	1.2	2.0	0.9	1.3	1.5	4.0	5.0	4.6	5.5	5.5	6.0	4.9
<i>T</i>	3.7	3.3	4.6	3.0	3.2	3.7	5.5	5.4	5.3	6.5	7.4	10.1	6.2
	(90)						(93)		(50)	(73)	(83)	(44)	(74)
<i>R</i>	5.2	4.2	7.6	4.0	5.7	5.9	—	—	—	—	—	—	—
	(60)	(67)	(71)	(50)	(40)	(59)	—	—	—	(0)	—	—	—
<i>A</i>	9.6	9.8	—	—	—	9.8	—	—	—	—	—	—	—
	(20)	(17)	—	(0)	—	(5)	—	—	—	(0)	—	—	—
<i>Y</i> or <i>G</i>	(0)												

Percentages of tests in which more than half the area was consumed are given in parenthesis. When such percentages were 100% they were not shown.

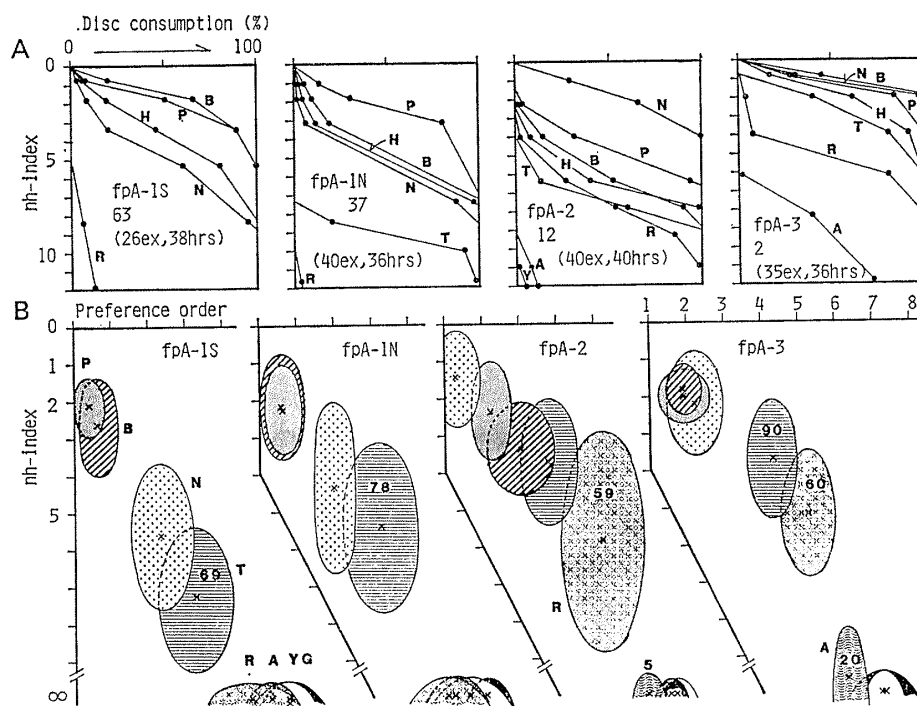


Fig. 2. A: Typical results of food choice test for larvae (FCTL). B: Preference order and consumption speed for each plant in FCTL. Long and short axes of ellipses show SD's of nh indices (number of larvae \times hours required to consume half of the leaf disc/100) and preference orders, and crosses (\times) means. Numerals in ellipses are percentages of the test in which more than half of the leaf disc was consumed; 0 and 100% are not shown. Several samples, fpA-1S (63, 60, 57), fpA-1N (50, 40, 37), fpA-2 (31, 20, 24, 12) and fpA-3 (2) are lumped together.

Thus, the three races are also recognized by FCTL, though fpA-2 and fpA-3 are hardly distinguished by the *B*-consumption rate. The stronger tendency of polyphagy northwards is also observed in the consumption rate of *N*, *T*, *R* and *A*. Another remarkable feature is the clinal variation in consumption speed of *N* and *T* by fpA-1. The general trend of variation in food preference of the host races shown by FCTL are summarized in Fig. 2B.

II. Reconstruction of Evolutionary History of fpA, *H. vigintioctomaculata* in the Japan Archipelago

Although the food habit of *Hv* may seem to be stabilized because it is an important pest of *P*, the food choice tests have shown intraspecific variations in food preference. The three races referred to above occur in Honshu (fpA-1), Hokkaido (fpA-2), and Rishiri and Rebun Islands (fpA-3), respectively. Each of them is isolated from the others by the Tsugaru or Rishiri Strait. This distinction of the host races well corresponds to that of the morphological forms, V-I, V-II and V-III

(KATAKURA, 1974). By extrapolation we can infer that V-II in southern Saghalien and western Kunashiri Island is similar in food preference to fpA-2. Morphologically V-II differs from V-I and V-III by its elytral shape, while the latter two are hardly distinguished from each other with slight statistic differences in degree of melanism (KATAKURA, 1974). On the other hand, the host races differ from one another in food preference as summarized as follows:

Distribution	:	Honshu	Rishiri· Rebun	Hokkaido
Food preference	{	FCTA:	fpA-1 ≠ fpA-3 ≠ fpA-2	
		FCTL:	fpA-1 ≠ fpA-3 ≐ fpA-2	
Morphology	:	V-I	≐ V-III	≠ V-II

The differentiation of Hv populations suggests that the straits are effective geographic barriers.

II-1. *Chorological interpretation*

Hv is distributed in the cool regions of East Asia, whereas other species of the Hv complex are endemic to Japan so far as known. The state of their distribution suggests that the complex in Japan has been formed by multiple invasion of the continental stock, and that Hv itself invaded Japan in a relatively recent time (KATAKURA, 1976).

Invasion: Straits surrounding the Japan Archipelago repeatedly closed and opened during the ice age (MINATO, 1966, 1972)*. It is likely that Hv is practically unable to migrate across the sea, and also that the straits around the Japan Archipelago have not undergone substantial topographical changes since the ice age. Hv should have therefore invaded Japan *via* the closed Korea Strait but not the closed Tatar Strait because of the cold northern climate at that time. Even at present Hv does not reach northward to the latitude of the Tatar Strait (STUNDJUK, 1966). The present geographic variation itself either in morphology or in food habit must not be used as a cue to elucidate the invasion route unless the speed of differentiation is known. Based on geological evidence (MINATO, 1972; GOHARA, 1976, cf. Fig. 3, A), the time of the invasion is presumed to be the Late Würm, ca. 22000 years B.P.** Since the Rishiri Strait opened ca. 17500 ys. B.P., Hv migrated with an average speed of more than 0.3 km/year (=1500 km/4500 years) along the archipelago to reach the northernmost islands. This seems to be a reasonable assumption as Hv is relatively vagile among the species of the Hv complex (NAKAMURA & OHGUSHI, 1981).

Differentiation: It is obvious that the three races of fpA had differentiated after the formation of the straits. The Tsugaru Strait opened ca. 18500 ys. B.P. and the Rishiri Strait ca. 17500 ys. B.P. Although V-II is distributed in Saghalien

* OHSHIMA (1976-1977) presented another interpretation, both Tsugaru and Korea Straits having never been closed after the Riss stage. This opinion is not supported by the present chorological state of differentiation in the Hv complex as will be discussed in a forthcoming paper.

** Reasons why Riss stage is excluded will be described in a subsequent paper.

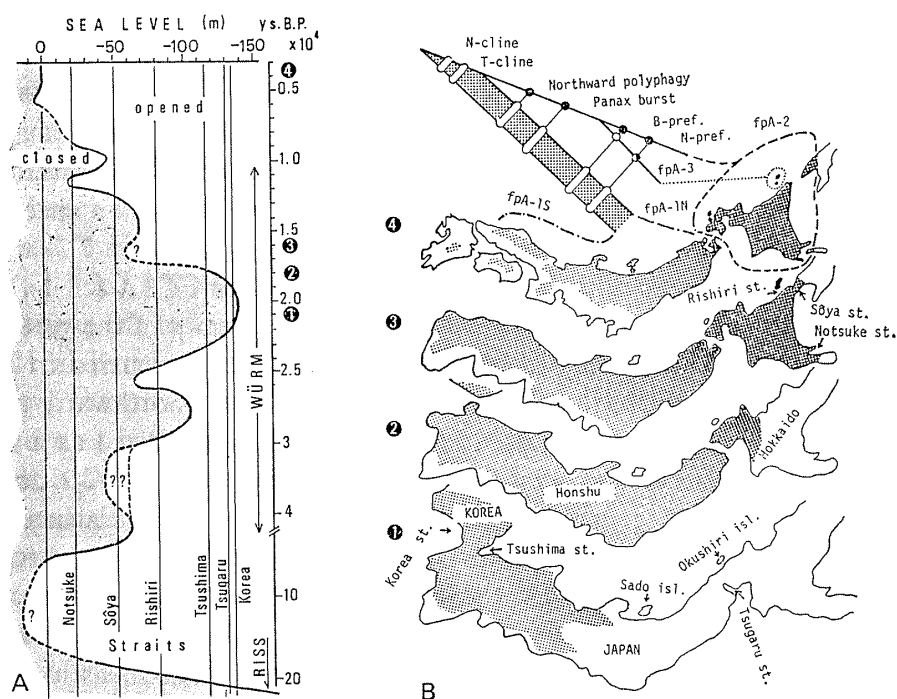


Fig. 3. Reconstruction of the process of host-race formation in fpA. A: Fluctuation of sea level during the Japanese Würmian and Early Holocene (after GOHARA, 1976) and the depths of the straits. B: Reconstructed process of differentiation of fpA in Japan, with a cladogram showing food niche shift. Further explanation in text.

and Kunashiri, the Sôya (Saghalien/Hokkaido) and Notsuke (Kunashiri/Hokkaido) Straits opened later, ca. 12500 and 9000 ys. B.P., respectively. Therefore, V-II should have differentiated in the period between 18500 and 12500 ys. B.P. Thus, from the geological history of the Japan Archipelago, especially the chronology based on relationship between sea level change and depths of the straits, the process of differentiation of the geographic races of Hv is reasonably inferred (Fig. 3B). There remains problems of the origin of a few insular populations such as V-I in Sado Island and V-II in Okushiri Island. These islands are separated by the straits more than 200 m deep, which have never been closed after the Riss stage. These populations are tentatively regarded as the descendants of artificially introduced stocks in quite recent times.

II-2. Ecological interpretation

The present food preference should have been evolved through the process of natural selection and adaptation. Since fpA is primarily a solanaceous feeder (HOSHIKAWA, 1983) migrants from the continent should depend on these plants. What changes occurred in the food habit of Hv in the course of its northward extension? The present geographic variation shows three trends: 1) northward increase in polyphagy, 2) a gentle cline in fpA-1 and 3) differentiation of the host

races.

Northward increase in polyphagy has been confirmed by both FCTA and FCTL. Selection should favor polyphagy in the north where the food supply was seasonally more restricted than in the south. A potential polyphagy of this species is inferable from the number of plant species edible for Hv (HOSHIKAWA, 1983). Of the ten plant species tested by FCTL, the consumption speed for both *N* and *T* changes gradually among populations of fpA-1. *N* and *T* are just the plants of which preference differed among the host races in FCTA (cf. I-1). Therefore, fpA-3 and fpA-2 might have been derived from extremes of the graded change in fpA-1. The food niche shift to utilize *N* as a new host occurred in Hokkaido presumably in 16000 ± 2000 ys. B.P. on the basis of the northward polyphagy. In northern Honshu, *N* is rarely eaten in the field and not utilized as a host plant (TOMIOKA, 1981). The reason why fpA-3 prefers *N* less than fpA-2 does should be either stagnancy or degeneration of the niche shift due to the absence of *N* in Rishiri and Rebun Islands. The flora of these islands includes only two species which might become the host for fpA, *Solanum macrocurpum* (probably synonymous with *M*) and *B* in Rebun (TATEWAKI, 1934) and *M* in Rishiri (TATEWAKI, 1941). Since IVANOVA (1962) listed a cucurbitacean, *Thladiantha dubia*, as a host of Hv in the Soviet Far East, a similar niche shift might have occurred also in the continent, but the continental Hv should have hardly differentiated into host races probably because of the absence of effective barriers. *T* is a problematical food plant of Hv. Why is there geographic variation in the preference for *T*, despite *T*-feeding by Hv has never been observed under natural conditions? It is still difficult to explain this.

Until recent times since the differentiation, each host race should have de-

Table 3. A chronological table of the presumed host-race formation in fpA, Japan.

Times (ys. B.P.)	Geological events	Process of host-race formation
22000	Korea St. closed.	Invasion of immigrants depending on solanaceans in Japan occurred <i>via</i> the closed Korea Strait.
—	—	Northward extension and intensification of the polyphagy trend.
19000	Korea St. opened.	Cessation of new immigrant supply. Arrival of pioneers at Hokkaido.
18500	Tsugaru St. opened.	Start of differentiation into fpA-2 in Hokkaido.
17500	Rishiri St. opened.	Start of differentiation into fpA-3 in Rishiri and Rebun Islands.
—	—	Completion of these differentiations. Inclusion of <i>N</i> as a host of fpA-2.
12500	Sôya St. opened.	} Separation of V-II (fpA-2) into some disjunct populations.
9000	Notsuke St. opened.	
100	<i>P</i> -cultivation started.	
—	—	Artificial colonization to Sado/Okushiri Islands.

pended on different *menu*, presumably fpA-1 lived on solanaceans such as *F*, *M*, *C* and/or *H*, fpA-2 on *N* and *M*, and fpA-3 on *M*. Most populations of these races have become potato pests throughout their territories without changing the basic food preference with the expansion of *P* cultivation started ca. 100 ys. B.P. The process of the host-race formation is summarized in Table 3.

Acknowledgements I wish to express my sincere gratitude to Professor Shôichi F. SAKAGAMI (Institute of Low Temperature Science, Hokkaido University) for his reading through the manuscript. My special thanks goes to anonymous reviewers for their valuable criticisms upon earlier drafts of this paper.

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* In Japanese. ** In Japanese with English summary. *** In Russian.

Erratum and addendum

Number of host-plant species for Hv in the previous paper (HOSHIKAWA, 1983, p. 258, line 2) should be corrected to 9 instead of 10. Although KOYAMA (1954) had presumed that *H* should be a native host for Hv, this plant has never been confirmed as a host of Hv despite that a few adults were rarely found on *H* (KOYAMA, pers. comm.). So, *H* can not be regarded as a host of Hv at the present. I thank Professor N. KOYAMA for his kind advice.