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

I. Host-plant Ranges and Food-preference Types*

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Synopsis Host-plant ranges of the *Henosepilachna vigintioctomaculata* complex are reviewed with some new host records. Food-preference orders in 112 samples collected from 83 populations in Japan are determined by food choice tests both for adults and larvae. Based on the similarity of preference order the complex is tentatively divided into seven groups.

The *Henosepilachna vigintioctomaculata* complex (abbreviated as the Hv complex) consists of phytophagous ladybird "forms" more variable in food habit than in morphology. Since 1940's this complex has been studied from various aspects, being suitable for studying speciation problems. We can recognize four "forms" in the complex, *H. vigintioctomaculata* (MOTSCHULSKY) (=Hv), *H. pustulosa* (KÔNO) (=Hp), the *Caulophyllum robustum* feeder or the "Towada form" (=Hr), and the questionable "Tokyo western form" (=Ht). Except for Hv the morphological differentiation is not very clear among them (KATAKURA, 1977; YASUTOMI, 1973)**, while their food habits differ from one another conspicuously. It seems that Hp, Hr and Ht are characterized by their different food habits. However, the results of previous studies on the food habit are difficult to compare (KATAKURA *et al.*, 1977) because of different populations and methods involved. The present work deals with the geographic variation in food preference and attempts to establish the classification and phylogeny of the Hv complex. This is the first report of a series and aims at three points: revision of host ranges, description of procedures to determine the food preference, and a tentative classification of the complex based on food preference.

I. Host-Plant Ranges

The beetles of the Hv complex feed on various plants such as Solanaceae, Compositae, Berberidaceae, etc., which are not related to one another.

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

** Recently, KATAKURA (1981) reviewed the taxonomy of the complex. Closer comparison between his system and the present one is intentionally postponed until all preference types are described.

Table 1. A list of host plants of the *Henosepilachna vigintioctomaculata* complex, with codes used in the text. Two non-host plants, *K* and *G*, are included to give their codes.

Plant species	(codes)	Hv	Hp	Hr	Ht
Berberidaceae					
Caulophyllum robustum MAXIM.	(*R*)	+	+++	+++	+++
Papaveraceae					
Chelidonium japonicum THUNB.	(*Y*)	+	++	+	+++
Araliaceae					
Panax japonicus C. A. MEYER	(*T*)	++	×	+++	+
Cucurbitaceae					
Schizopepon bryoniaefolius MAXIM.	(*N*)	+++	++	++	+
Cucurbita moschata DUCH.	(*K*)	++	+	++	
Compositae					
Arctium Lappa L.	(*G*)	+	+	+	+
Breea setosa (BIEB.) KITAM.	(*Z*)	+	+++	+	+
Cirsium spp.	(*A*)	+	+++	×	++
Solanaceae					
Lycium chinensis MILL.	(*C*)	+++	++	++	+
Scopolia japonica MAXIM.	(*H*)	++	+++?	++	+++
Solanum megacarpum KOIDZ.	(*M*)	+++	+++	++	+
S. nigrum L.	(*B*)	+++	+	++	+
S. melongena L.	(*E*)	+++	++	++	+++
S. tuberosum L.	(*P*)	+++	+++	++	+++
Physaliastrum japonicum (FR. et SAV.) HONDA	(*F*)	+++?	++	+++	
Lycopersicon esculentum MILL.	(*L*)	+++	++	++	+
Datura stramonium L.	(*D*)	+++	++		

+++: host plant, ++: food plant, +: edible plant, ×: not accepted, blank: unknown.

In a previous paper, these plants are tentatively divided into three categories (KATAKURA *et al.*, 1977):

a) Host plants: those allowing successful growth of larvae in the field.

b) Food plants: those allowing growth of at least some larvae only under rearing conditions.

c) Edible plants: those observed to be eaten by either adults or larvae under natural or rearing conditions but not belonging to the first two categories.

Mainly referring to the host plants, the general trends in host specificity of the four ladybird forms are summarized in Table 1, with codes for the plant species used in the text. Plants of the three categories hitherto confirmed or inferred (with question marks) are listed below for each form with some remarks.

Hv. Host plants: *P*, *M*, *C*, *B*, *E*, *L*, *D*, *F*? (Solanaceae); *N* (Cucurbitaceae). *P* is the main host plant for Hv. *M*-dependent (NAKANO, pers. comm.) and *N*-dependent populations (KATAKURA, 1975) are found only in Hokkaido. Other plants should be subsidiary hosts so far as the complete dependence on them has never been confirmed. Since Hv is fundamentally a Solanaceae feeder as shown above, some wild *Solanum* species such as *S. maximowiczii*, *S. japonence*, etc. may be added to the host-plant list. In the Far East (Primorie in USSR), *Solanum dulcemara* and *Thladiantha dubia* (Cucurbitaceae) are wild host plants (IVANOVA, 1962).

Food plants: *H*; *K*, *Cucumis Melo*, *C. sativus*, *Citrullus vulgaris* (Cucurbitaceae); *Carduas crispus* (Compositae); *T*. Hv can complete its larval growth on some cucurbitacean plants. It is remarkable that a composite species *Carduas crispus* is recorded as a food plant (KOYAMA, 1962). *T* is also a food plant but causes high mortality (HOSHIKAWA, in prep., TOMIOKA, pers, comm.).

Edible plants: 9 spp. of Solanaceae, 5 Cucurbitaceae, 8 Leguminosae, 6 Cruciferae, 4 Compositae and 10 spp. of other families are known in Japan. Cultivated plants are 22 out of the 42 edible species. List of edible plants was compiled by KOYAMA (1954) and KATAKURA *et al.* (1977). In addition to this list, feeding on *Physalis heterophylla* or *Actinostemma lobatum* was observed by KATAKURA (pers. comm.), on *Galinsoga parviflora* or *Humulus japonicus* by KIRYU (1970)* and on *Solanum japonence*, *Trichosanthes Kirilowii* or *Elaeagnus multiflora* by TOMIOKA (pers. comm.). Even stems of the fern *Pteridium aquilinum* was observed to be eaten by the beetle (KOYAMA, 1950, 1954). I observed *Chrysosplenium japonicum* (Saxifragaceae) infested by many adults gathering on its flowers, leaves and stems at Kammata, Fukushima Pref., on May 7, 1979 when *P* did not yet sprout. IVANOVA (1962) also noted the beetle feeding on a species of *Chrysosplenium* in the Soviet Far East.

Other records: Ripe seeds of *Zea Mays* (Gramineae) were eaten by prehibernating adults (SAKAGAMI, pers. comm.). Fluid from extrafloral nectaries of *Sambucus Sieboldiana* was sucked in May, at Sapporo (KATAKURA *et al.*, 1977). Honey dew from an aphid colony on *Larix leptolepis* was sucked by four adults on Oct. 3, 1979 at Tomakomai, Hokkaido (HOSHIKAWA, unpubl.). Eggs of Hv are sometimes devoured by conspecific adults and larvae. This cannibalism is not unusual in Coccinellidae including other forms of the Hv complex. KOYAMA (1957) obtained an adult female which had been given only eggs as food.

Hp. Host plants: *A*, *Z*; *R*; *P*, *M*, *H*?. The main host plant for Hp is *A*. *R*-dependent and *M*-dependent populations are found in Hokkaido. *Z* and *P* are subsidiary host plants. *H* should be a host plant at least in the southwestern part of Honshu, since many adults and egg masses were collected from *H* where there were few plants of *A* (Mitoku, Tottori Pref.). SHINBO (1977) also collected Hp from *H* and *A* at Nakakawachi, Shiga Pref.

Food plants: *N*; *C*, *E*, *L*, *D*, *F*; *Y*. Hp can grow on solanaceans and cucurbitaceans. *Y* is a low quality food plant, causing high mortality (HOSHIKAWA, unpubl., TOMIOKA, pers. comm.).

* Although KIRYU (1970) has reported the feeding beetles as Hv, they may or may not be Ht because of the observed locality (Sagamiwara City).

Edible plants: 3 spp. of Compositae, 6 Solanaceae, 4 Cucurbitaceae, 4 Leguminosae, 3 Cruciferae and 6 spp. of other families are known. Cultivated plants are 16 out of the recorded 26 species. In and near Sapporo, Hp feeds on various plants which are neither hosts nor food plants, especially in late summer when the host plants become withered: *Kalopanax pictus* (Araliaceae) (KATAKURA *et al.*, 1977), *Smilacina japonica* (Liliaceae) (HOSHIKAWA, unpubl.), *Pachysandra terminalis* (Buxaceae) (HOSHIKAWA, unpubl., TSURUSAKI, pers. comm.), *Physalis heterophylla* (KATAKURA, pers. comm.), *G*, and a fern, a species of Aspidiaceae (HOSHIKAWA, unpubl.).

Hr. Host plants: *R*; *T*; *F*. The principal host plant is *R*. *T* is utilized only in Honshu as a subsidiary host plant. Some solanaceans such as *P* or *H* may be included in the host range since Hr sometimes infests them.

Food plants: *P*, *H*, *M*, *C*, *E*, *L*, *B*, *Solanum carolinense*; *N*, *K*, *Citrullus vurgaris*, *Cucumis Melo*. Most of these were observed to be food plants by TOMIOKA (1981; pers. comm.) in the Hirosaki population, Aomori Pref. Hr can grow on solanaceans or cucurbitaceans, including *B* and *M* (HOSHIKAWA, unpubl.).

Edible plants: *G*, *Z*; *Y*; *Pachysandra terminalis*; *Coniogramme intermedia*. I observed *P. terminalis* eaten by an adult at Ohnuma, Hokkaido and a fern *C. intermedia* by final instar larvae at Hirosaki.

Ht. Host plants: *P*, *H*, *E*; *Y*; *R*. Ht was first found as a pest of *P*. Recent discoveries of Ht populations on wild host plants have elucidated a difference in food habit between Ht and Hv. A *Y*-dependent population was found at Takaozan, Tokyo (YASUTOMI, 1973). An *R*-dependent population was also found at Takaozan (TOMIOKA, 1980), and *H*-dependent populations by TACHIKAWA (pers. comm.) at Okutama, Tokyo and by SHINBO (1977) at Urayama, Saitama Pref. Some solanaceans may be added to the host plants such as *C*, *B*, etc.

Food plants: TOMIOKA (pers. comm.) confirmed *Solanum carolinense* to be a food plant in the Bôsô population, Chiba Pref. WATANABE and SUZUKI (1965) and HINOMIZU (1976) obtained adult Ht reared with *A* leaves. Although food plants of Ht are poorly known, most of solanaceans or cucurbitaceans listed below as edible plants should be transferred to food plants.

Edible plants: *C*, *B*, *L*, *M*; *N*, *Cucumis sativus*; *Z*, *G*; *T*; *Pterostyrax hispidus* (Styracaceae) (INOUE, 1955).

Questionable populations: 1) A *Y*-dependent population at Izumi, near Nikko, Tochigi Pref. (KATAKURA *et al.*, 1978). 2) A $Y+R+T$-dependent population at Daigo-cho, Ibaraki Pref. In the field the numbers of adults on these plants were $Y>R>T$ on May 17, 1981. 3) An *H*-dependent population at Ohmukawa, Yamanashi Pref. (KATAKURA *et al.*, 1978). *H*-dependent populations were also found at several places in Nagano Pref. (HARA & YAMAGUCHI, 1979; SHIRAI, pers. comm.), one of which utilized *Phyladelphus coronarius* (Saxifragaceae) as an edible plant (SHIRAI, pers. comm.). These populations are morphologically similar to either Hr or Ht.

To summarize, numbers of species of host/food/edible plants hitherto known are as follows: Hv (10/7/42), Hp (6/7/26), Hr (3/12/5), Ht (5/2/10) and the Hv complex as a whole (15/6/46) (*Cirsium* spp. are counted as a single species). Of these 67 species, 29 are crop plants, 7 are exotics, and 3 are regarded as "prehistoric exotics" (MAEKAWA, 1943). The other 28 species are native to Japan, including *R*, *Y*, *T*, *Z*, *A*, *N*, *H*, *M*, *C* and *F*. In spite of the wide variety of hosts utilized by the Hv complex (Table 1), the main host constantly used over a wide area by each form is restricted to a single species, i. e. *P* for Hv, *A* for Hp, *R* for Hr, and *P* for Ht.

Generally speaking, all forms can grow on solanaceans and cucurbitaceans in rearing tests, conforming to the common tendency in Epilachninae (SHILDER & SHILDER, 1929). Actual host selection, however, is rather form-specific as mentioned above. The existence of some host plants being utilized in limited areas (e. g. *N* in Hv) or of unique subsidiary host plants (*T* in Hr) suggests that the host race formation is an important factor causing diversity in the Hv complex.

II. Determination of Preference Order

The materials and methods for this series of studies are described here.

Materials. A total of 112 samples from 83 populations were studied, including all forms of the Hv complex so far known in Japan. They will be referred to by code numbers (Fig. 1). Two samples of *Henosepilachna vigintioctopunctata* (FABRICIUS) and one of *Epilachna admirabilis* CROTCH were also used for comparison. Many samples were collected from Hokkaido because a clear variation was found there in preliminary tests. As Hp sometimes invades potato fields (cf. EHARA, 1955), a few doubtful adults with black femora (KATAKURA, 1977) were excluded from Hv samples.

Adults were reared at room temperature (18–29°C) and 17L7D or 18L6D photoperiod (0–1500 lux.), and provided with fresh leaves renewed every other day.

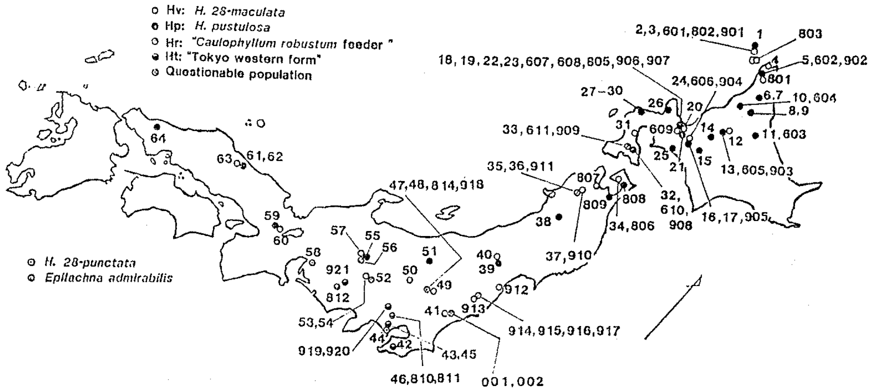

Fig. 1. Localities where samples were collected for the present study. Further details and locality names will be given in subsequent papers.

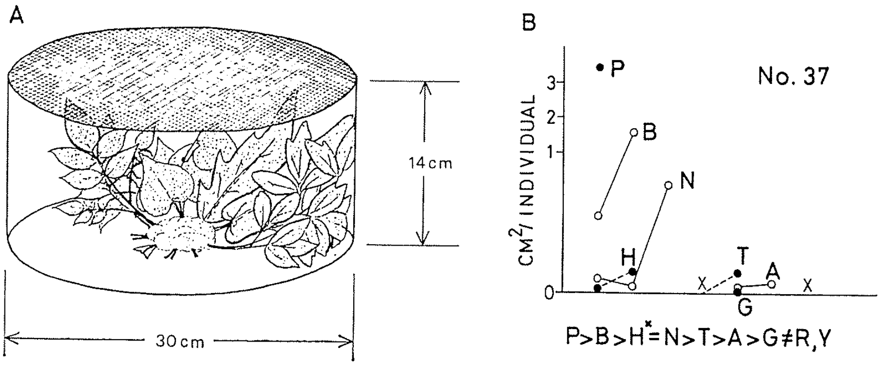

Fig. 2. —— A, Experimental setting of a food choice test for adults (Four plants in foreground are omitted. Further explanations in the text.); B, an example of the result of a serial test obtained with a sample (No. 37) of beetles (Letters in the figure are plant codes as shown in Table 1). × : no feeding was observed. Abscissa: the sequence of a serial test; Ordinate: feeding intensity; Bottom: a preference order obtained.

About 10–30 individuals were put in a plastic case of 25×18×20 (h) cm, the bottom of which was covered with moist filter paper. Some offspring larvae were also tested.

A total of 11 plant species were used. Main tests covered 9 spp. (*R*, *Y*, *T*, *H*, *B*, *P*, *N*, *A*, *G*, see Table 1), but *H* or *Y* was not always used. *M* and *Z* were included only in some tests. These plants were chosen to include the host plants of each form of the Hv complex and also by their availability. *R*, *T*, *N*, *A** were collected in the suburbs of Sapporo City chiefly Kobetsuzawa, and *M*, *P***, *B*, *Z*, *G* on the campus of Hokkaido Univ. *Y* and *H* were transplanted from Izumi, Nikko City and from Zatoishi, Hirosaki City, respectively, on the campus of Hokkaido Univ. *H* in Experimental Station of Medicinal Plant Studies, Hokkaido Univ., was also used. Plants were kept alive either by soaking the stems in water and used within 24 hrs of collecting or by preserving in a refrigerator packed in vinyl bags for several days.

Methods. Food choice tests for adults (FCTA) were undertaken as follows. Plant leaves of approximately 200 cm² were arranged in a circle on the bottom of a plastic case fastened with wet absorbent cotton (Fig. 2, A). About 10–30 adults were released in the center and permitted to feed for 24 hrs under illumination with a fluorescent lamp ca. 20 cm above. The area of leaves of each plant consumed by the adults was measured by scales of 1/4 cm² (for large areas) and of 1 mm² (for small areas). Characteristic stripes left in the consumed area were ignored. The area consumed per adult was calculated in each test. After an interval of more than 24 hrs, the next test was carried out with the same adults in the same way except that the most preferred plant was removed. The tests were repeated by removing the most preferred plant in the previous test until only unedible plants were left.

* Probably *Cirsium kamtschaticum* LEDEB.

** Cultured on the campus; race: Norin No. 1 (1976–1978), Danshaku (1979) and unknown (1980).

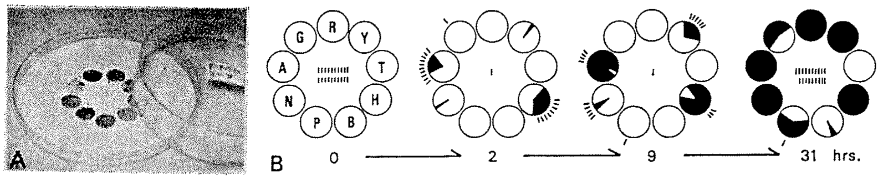

Fig. 3. —— A, Experimental setting of a food choice test for larvae (Leaf discs are arranged in circle and larvae are put in the center.); B, diagram showing a typical course of the test (Circles are leaf discs and enclosed letters identify the plant species as shown in Table 1. Larvae are represented by bars. Those around leaf discs indicate larvae on the discs. The consumed areas of discs are shown as pie-graphs. Further explanations in the text.)

The rank of preference was represented by the order of removal in the serial tests described above (Fig. 2, B) and expressed as more preferred>less preferred. When two (A, B) or more plants were eaten almost equally, the test was repeated without removing them, and the preference order was determined either as A≧B (A was eaten more than B in most but not all trials), or A=B (indistinguishable). Refused plants are preceded by symbol "≠."

A difficulty in FCTA was to ensure enough supply of plants. Since the used plant species differ in their phenologies, all tested plants were available only in the period from late June to early July in Sapporo. Owing to this restriction, some samples were tested without certain plants. When a plant became unavailable before the completion of a serial test, its rank of preference was inferred only from the consumed area in the preceding test and indicated by an asterisk (cf. Fig. 2, B, *H*). This method might overestimate the preference for plants with thinner leaves since measurements are based on area and not on volume. The sexes of adults were ignored since no significant sexual difference was found in preliminary tests.

In food choice test for larvae (FCTL) leaf discs (9.5 mm in diameter; ca. 71 mm^2) of each plant were arranged in a circle in a petri-dish, the bottom of which was covered with moist filter paper (Fig. 3, A). All discs were put upside down. In the center, 10–40 larvae (ca. 30 in most cases) 10–24 hrs after hatching (ca. 20 hrs in most cases) and without feeding experience (cf. KOYAMA, 1957) were released (Fig. 3, B, 0). Larvae started feeding, gathered on some leaf discs (Fig. 3, B, 2), soon ate up them and moved to others (Fig. 3, B, 9). The maximum number of larvae observed on a disc was 18. The consumption rate (area consumed/area of whole disc) was estimated by eye at ca. 4–11 hrs interval. The intervals were adjusted according to the speed of consumption, and generally shorter at the earlier stage. The test was continued until most larvae wandered in the petri-dish and left all discs (ca. 36–48 hrs; Fig. 3, B, 31). The test was carried out in a dark box, except for the time of observation, because larvae were restless and did not stay on any disc under illumination.

The preference order was determined by the sequence of disc consumption for each test. The mean order for each plant was obtained from several trials, since

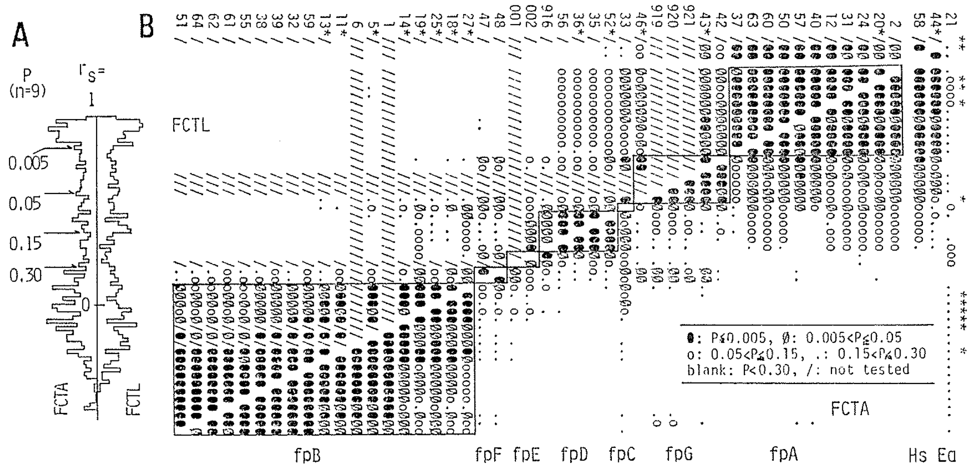

Fig. 4. —— A, Distribution of rank correlation coefficients (r_s) among preference orders of 46 local samples of the Hv complex; B, similarity matrix for the preference order (Pairs including asterisked sample were calculated with ranks of 8 spp. plants, others 9 spp. Sample code Nos. (top) are in accrod with Fig. 1).

reproducibility of the result was somewhat lower in FCTL than in FCTA (cf. additional note, 2). When two or more plants had similar mean values (difference$\leqq$ 0.3), they were equally ranked. In most FCTL 8 spp. of plant (*R*, *Y*, *T*, *B*, *P*, *N*, *A*, *G*) were offered, and some included *H* or *M*, whereas *Z* was used only in a few cases.

III. A Tentative Classification of Food Preference Types

A tentative classification of food preference types based on the results of experiments described above is proposed here. Comparison of such a classification system with the morphological one proposed previously (KATAKURA, 1981) will be the subject of a future paper.

Similarity of the preference orders between any two given samples was calculated, using SPEARMAN's rank correlation coefficient, $r_s=1-6d^2/(n^3-n)$, where n is the number of plant species ranked, and d^2 the sum of squared difference in rank of each plant between the two paired samples. When there were equally ranked plants, they were given the mid value between the adjacent ranks, i. e. when $N=P>$ . . . . ., $N=P=1.5$.

In the similarity matrix thus obtained (Fig. 4, B), distribution of r_s values among 46 samples of the Hv complex (Fig. 4, A) shows a bimodal pattern with weak peaks near 0 without correlation and near +1 with a high positive correlation. Results of cluster analysis (Fig. 5) by UPGMA (unweighted pair-group method using aritthemetic average) (SNEATH & SOKAL, 1973) show that these samples are clustered to 5 groups in FCTL and 8 groups in FCTA, at P=0.05 (r_s=0.68). Discrepancies

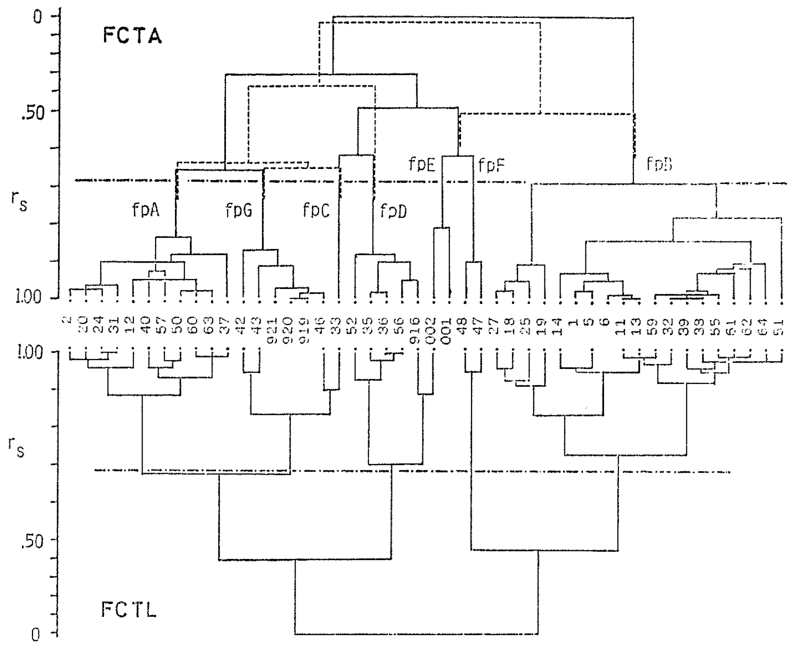

Fig. 5. Cluster analysis of the similarities among preference orders (UPGMA using SPEARMAN's rank correlation coefficients; chain lines: r_s=0.68 (P=0.05)). As to FCTA, an alternative dendrogram is also possible when experimental errors are taken into consideration, as shown by broken lines.

between the larval and adult clusters are found in samples No. 33, No. 002, No. 916 and the grouping from No. 27 to No. 51. Samples No. 33 and No. 002 are tentatively regarded as distinct. Thus, the Hv complex is divided into 7 types as follows (plants with variable rank are parenthesized):

Preference type	Sample code No.	Preference (High ——— Low)	Forms so far recognized
fpA:	2, 20, 50, etc.	: *P*, *B*, *H*, (*N*), *T*, *R*, *Y*, *A*, *G* :	Hv
fpB:	11, 18, 55, etc.	: *A*, *H*, (*R*, *N*), *P*, *Y*, *G*, *B*, *T* :	Hp
fpC:	33	: *R*, *H*, *N*, *P*, *B*, *Y*, *T*, *A*, *G* :	Hr
fpD:	52, 35, 916, etc.	: *R*, *T*, *H*, *N*, *P*, *B*, *Y*, *A*, *G* :	Hr
fpE:	002, 001	: *R*, *Y*, *T*, *H*, *N*, *P*, *B*, *A*, *G* :	?
fpF:	47, 48	: *Y*, *R*, *H*, *N*, *P*, *B*, *T*, *A*, *G* :	?
fpG:	42, 43, 46, etc.	: *P*, *B*, *H*, *R*, (*Y*), *N*, *T*, *A*, *G* :	Ht

In these 7 types, fpB includes weakly correlated pairs, and extreme members (r_s= 0.33–0.68) are more dissimilar than between types fpA and fpG, fpC and fpG, or fpC and fpD, suggesting a high variability. The preference types generally correspond to the forms hitherto recognized, although Hr is splitted into types fpC and fpD. Type fpC is similar in the preference order not only to fpD but also to fpG.

The dendrograms in Fig. 5 show general similarities or dissimilarities in the preference order but not the phylogenetic relationships. Intragroup geographic variations were recognized in types fpB and fpA. Therefore, analysis of the geographic variation in food preference is indispensable. In subsequent papers, geographic variations in each food preference type will be described, together with probable phylogenetic relationships among host races in the Hv complex.

Additional notes: 1. The preference orders in adults and larvae in the same population are closely correlated. The mean r_s between the results of FCTA and FCTL is 0.93 (s. d.=0.05; range: 0.75–1.00; n=40).

2. Reproducibility of FCTA was calculated by comparing preference orders of two samples collected from the same population. Mean r_s value is 0.96 (s. d.=0.06; range: 0.75–1.00; n=16), while that of FCTL is 0.86 (s. d.=0.12; 0.40–1.00; n=431). The lower correlation in FCTL is chiefly due to pairs belonging to fpB (0.80±0.14; 0.40–1.00; n=223). If they are excluded, a relatively high correlation (0.92±0.06; 0.69–1.00; n=208) was obtained. This shows a plasticity in food preference of the larvae of fpB.

3. Although the food preference by *Epilachna admirabilis* was examined in only one sample by FCTA, they did not feed any plants except for *N*, showing a narrow food preference. On the other hand, the preference order of *Henosepilachna vigintioctopunctata* showed a remarkable similarity to fpA, $P>B>H>N>T>A \neq R, Y, G$, though feeding intensities for *N*, *T* and *A* were low. Nevertheless KOYAMA (1957) pointed out a clear difference in the preference for *Physalis Alkekengi* L. (Solanaceae) between this species and Hv. The similarity in food preference may reflect the phylogenetic relationship between *Epilachna* and *Henosepilachna*, or may be due to their parallel adaptations to similar niches.

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