Morphology and Distribution of the Forms of *Henosepilachna vigintioctomaculata* Complex in Hokkaido

By

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(With 11 Text-figures and 3 Tables)

By the remarkable variability in both morphology and biology *Henosepilachna vigintioctomaculata* complex (Hv-complex) is one of the most promising materials for the study of intra- and interspecific relations (cf. Katakura 1974). The complex involves two distinct groups, *H. vigintioctomaculata* (Motschulsky) (Hv) and *H. pustulosa* (Kôno) (Hp), together with some questionable forms so far known only in Honshu (Yasutomi 1973). Several local forms have been recognized both in Hv and Hp by the difference in elytral structure. The morphology and distribution of two forms of Hv, Honshu and Hokkaido forms, were recently discussed by Maki (1966). But the morphology and distribution of the forms of Hp were referred to by several authors only tentatively (Ehara 1953, '55; Koyama 1962; Watanabe and Sakagami 1948; Yasutomi 1954, '66). The present paper mainly deals with the distinction of various forms inhabiting Hokkaido and their distribution as a basis for further studies of this fascinating group.

1. Distinction of Hp and Hv

The distinction of Hp and Hv by morphological characters has been repeatedly discussed by several authors, i.e. Ehara 1953, '55; Koyama 1962; Watanabe and Sakagami 1948; Yasutomi 1954, '66. Synthesizing previous contributions and my own observations, the diagnostic adult characters are summarized in Table 1. Among these characters I and II are fairly stable while IV shows considerable local variations and fading in preserved specimens. Character III seems fairly constant but can not be used for dried specimens. In addition to these characters, the

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1) Contributions to the knowledge of *Henosepilachna vigintioctomaculata* complex.

2) Usage of these scientific names is explained in Katakura (1974).

Table 1. Diagnostic adult characters between *H. pustulosa* (Hp) and *H. vigintioctomaculata* (Hv).

<table>
<thead>
<tr>
<th>Characters (cf. Fig. 1)</th>
<th>Hp</th>
<th>Hv</th>
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<tbody>
<tr>
<td>I. Coloration of hind leg</td>
<td>Entirely black except both ends of tibia and terminal end of femora which are reddish brown (Hokkaido), or at least femora entirely black except both ends (Honshu)</td>
<td>Reddish brown with a black mark on femora</td>
</tr>
<tr>
<td>II. Shape of elytral maculation</td>
<td>Spot 5 fused on suture, spot 8 entirely fused on suture, spots 13, 14 larger than Hv, spot 12 smaller and elliptical</td>
<td>Spot 5 not fused or fused but upper part biconvexed, spot 8 not or only partly fused, spots 13, 14 small (Honshu), often minute or evanescent (Hokkaido), spot 12 largest and curved</td>
</tr>
<tr>
<td>III. Shape of spermatheca</td>
<td>Apex generally swollen</td>
<td>Apex not swollen</td>
</tr>
<tr>
<td>IV. Coloration and tint of elytra</td>
<td>Deep reddish brown with weak metallic tint</td>
<td>Pale reddish brown without metallic tint</td>
</tr>
</tbody>
</table>

Specific difference is also recognized in the number of spicules of adult mandibles in some local populations (Koyama 1962) and the anomaly tendency of elytral maculation (Katakura 1974). On the other hand, Yoshida (1948) and Takenouchi (1955) failed to find any significant difference in chromosomal features between them. All so far known questionable forms are identified with Hp by these characters, but their food plant in natural condition is definitely different from that of Hp, namely the latter feeds on thistles (*Cirsium* spp., *Compositae*) while the former on potato (*Solanum tuberosum*, *Solanaceae*) as Hv or *Caulophyllum thalictroides robustum*, *Berberidaceae* (Fukuda 1970, Yasutomi 1973). In other words, questionable forms go morphologically to Hp while biologically rather to Hv.

The distinction of Hp and Hv is thus not difficult by using these characters as far as questionable forms are ignored. As to the specimens from Hokkaido, the separation is more easy by the differentiation in elytral structures as mentioned subsequently.

2. Forms of Hp: Revision and variation analysis

2.1. Forms of Hp. Hitherto four basic forms have been recognized in Hokkaido: Typical (Kôno 1937), Sapporo (Watanabe and Sakagami 1948), Sounkyô (Yasutomi 1952) and Ohnuma (Katakura 1973) forms. Further the intermediate forms are recorded between Typical and Sapporo forms (Watanabe and Sakagami op. cit.), as well as between Typical and Sounkyô forms (Yasutomi
Fig. 1. Morphological diagnostic characters between *H. pustulosa* (P) and *H. vigintioctomaculata* (V): 1) Leg coloration; 2) shape of elytral spots; 3) shape of spermatheca (modified from Ehara 1953).

1954). These four basic forms were reconfirmed from the morphological studies of the specimens from numerous localities given in Appendix at the end of the paper. Due to the occurrence of intermediate forms, the classification of particular specimens into the forms is occasionally difficult. At the sample level, however, the identification is possible by the relative stability of morphological features in most specimens involved. When the sample size was small, the identification was made tentatively, leaving the confirmation for the future.

In this section, various forms are revised and their geographical distribution is given by the code numbers given in the appendix (cf. also Fig. 2). The morphological comparison of these forms is presented in 2.2.

A. Basic forms

1) Form P-I (Sōunkyō form, Fig. 3-I): Elytra without tubercles, not expand-
Fig. 2. Distribution of various forms of *H. pustulosa* in Hokkaido. Code numbers for localities listed in Appendix and the samples used for variation analysis are shown by Arabic abbreviations. Explanation of form symbols, P-I etc. see in Fig. 3.

ed at hind edge, in profile sharply curved and part between summit and apex nearly linear with hind edge not bent downward, in posterior view contour somewhat angular, as if shrunk along body axis.

**Distribution:** Northeastern part. Localities, 6, 7, 8, 9, 10, 11, 12, 25.

Two types are recognized. P-Ia (Fig. 3-Ia), elytral curvature conspicuous with summit postward; P-Ib (Fig. 3-Ib), elytral curvature less conspicuous with summit forward. Type P-Ia distributed in the south to central part of the distribution area of form P-I (loc., 10, 11, 12, 25), while P-Ib in the northern part (loc., 6, 7, 8, 9). Although the name, Sōunkyō, has been applied to by the first discovery of the form from this locality situated at the northern outskirt of Mts. Taisetsuzan (Fig. 2, code no. 18), the specimens from Sōunkyō are intermediate between P-I and P-II given below.

2) Form P-II (Typical form, Fig. 3-II): Elytra provided with prominent tubercles and remarkably expanded at apex, in profile moderately curved with hind edge bent downward, in posterior view contour somewhat triangular.
Morphology and Distribution of H. vigintioctomaculata Complex


Elytral curvature in lateral and posterior views variable. The specimens from the type locality, Soeushinai (40) and the vicinity, sometimes very sharply curved in profile (cf. Ehara 1953). Elytra generally upheaved along the posterior half of the suture, but this feature variable in Tomuraushi (29) and adjacent areas, from not to conspicuously upheaved. The samples from the underlined localities involve some specimens of P-III or P-II/III (intermediate between P-II and III). The unique specimen from Niinai (32*) is distinctly P-III, but previous information (Ehara 1953, Yasutomi 1954) shows the presence of P-II there.

3) Form P-III (Sapporo form, Fig. 3-III): Elytra slightly expanded at hind edge, with no or minute tubercles, in profile moderately curved with hind edge not bent downward, in posterior view moderately curved.

Distribution: Southwestern part. Localities, 34, 38, 49, 50, 51, 52, 53, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74*, 75*, 76, 77, 78, 79.

The specimens from Kyōgoku (74*) and Wakikata (75*) are somewhat different, elytra are more expanded and vaguely tuberculated, being intermediate with P-II. These localities are shown as P-II/III in Fig. 2 and Appendix, though located amid the P-III area.

P-III': Interestingly the specimens taken from the northernmost area of Hokkaido are similar to P-III, though elytra are slightly more expanded and tuberculated; elytral curvature is moderate but sometimes the summit lies very anteriorly and the curve between summit and apex nearly linear in profile. A slight similarity to P-Ib is also recognized. For the lack of sufficient materials they are tentatively designated here as P-III'.

Distribution: Northernmost part. Localities, 1, 2, 3, 4.

4) Form P-IV (Ohnuma form, Fig. 3-IV): Elytra slightly expanded at hind edge, with no or minute tubercles, in profile sharply curved but not so acute as in P-I, with hind edge not bent downward, in posterior view moderately curved.

Distribution: Southernmost part. Localities, 80, 81, 82, 83, 84.

As mentioned after, this form is similar to Hp inhabiting northern Honshu (cf. also Katakura 1973).

B. Intermediate forms

1) Form P-I/II (Fig. 4-A): Quite variable, but distinguished from P-I by the elytral posterior edge bent downward, while from P-II by elytral characters, such as the degree of expansion and size of tubercles, and body proportion. The separation from P-II is sometimes difficult.

Distribution: Localities, 13, 14, 15, 16, 17, 18, 19, 20, 21.

Distribution of this intermediate form seems restricted at the basin of Teshio River and northern outskirt of Mts. Taisetsuzan. Although no specimen was examined from Bifuka (near Soeushinai, code no. 40), the previous information
Fig. 3. Four basic forms (five types) of *H. pustulosa* in Hokkaido. All females. I, P-I (Sōunkyō form); II, P-II (Typical form); III, P-III (Sapporo form); IV, P-IV (Ohnuma form). shows the presence of this form there (cf. Yasutomi 1954).

2) Form P-II/III (Fig. 4-B): Various intermediate degrees are noticed. At sample level, two types are recognized: A) Homogeneous samples, nearly all specimens are intermediate. B) Heterogeneous samples, mainly consisting of P-I, intermingled with some P-III or P-II/III. The reversed case, the admixture of a few P-II specimens in P-III, was not observed. Classifying heterogeneous samples tentatively in P-II, only homogeneous samples are given below.

Distribution: Localities, 37, 45, 46, 47, 48, 55.

3) Form P-I/III' (Fig. 4-C): Only one sample from Asajino (5) was examined.

Beside the forms mentioned above, all from Hokkaido, some specimens from Honshu were examined. In addition to typical Hp feeding on thistles in natural condition, some questionable forms which feed on potato or *Caulophyllum thalictroides* robustum are distributed in Honshu, though identified morphologically to the former. Aside the questionable forms for the lack of sufficient materials, the specimens of typical Hp from the following localities were examined (number of specimens examined in parentheses):

Lake Ogawara, Aomori Prefecture (6); Sotoyama, Iwate Pref. (8); Lake Tazawa, Akita Pref. (6); Yunodai, Mt. Chōkaisan, Akita Pref. (26); Senakaaburiyama, Kita Aizu, Fukushima Pref. (10); Kuromori, Ohto, Kita Aizu, Fukushima Pref. (3); Kidayama, Monden, Kita Aizu, Fukushima Pref. (1); Mt. Bandaisan, Fukushima Pref. (5); Yunohara spa, Fukushima Pref. (1); Oze, Gunma Pref. (15); Tokura, Gunma Pref. (6); Shimajima, Nagano Pref. (6); Nakafusa, Nagano Pref. (6); Awasuno, Toyama Pref. (10); Serio, Kyoto (9).
Fig. 4. Various intermediate forms of *H. pustulosa* found in Hokkaido. All females. A, P-I/II; B, P-II/III; C, P-I/III'.

As the number of specimens examined is insufficient, only the similarity with other forms is pointed out. Compiling previous information and my own observation, at least two forms can be morphologically recognized in typical Hp in Honshu.

1) P-H₁ (Honshu form): Similar to P-IV but elytral curvature in profile is more acute and the summit lies more posteriorly. But a considerable variation of elytral curvature is noticed. The unique specimen from Yunohana spa is very
similar to P-I though the summit lying more posteriorly than P-Ia. The specimens from Nakafusa are closely similar to P-III or P-H₂ given below, though the curvature is slightly more acute and the summit lying posteriorly. Previous authors mentioned the form is very similar to P-I except for the difference of leg coloration, the tibia of the former being rather reddish brown while the latter entirely black (Asahina 1952; Ehara 1953, '55). But the coloration of legs is variable, often entirely black. Further the curvature of elytra in posterior view is different, angular in P-I while moderately curved in P-H₁ except for some specimens mentioned above, and the elytral summit lies more posteriorly than P-Ia.

2) P-H₂: Closely similar to P-III though the maculation of prothorax and leg coloration is generally less developed. So far known all questionable forms are similar to this form. The relation of P-H₂ to the questionable forms is discussed by Yasutomi (1973).

The specimens examined here were mostly P-H₁ except for those from Serio, Kyoto, which were P-H₂.

2.2 Variation analysis. For further morphological analysis, some samples, represented by a sufficiently large number of specimens and covering all basic and intermediate forms, were selected (Table 2). These samples are those used in previous studies (Katakura 1973, '74), excluding the specimens with open elytra.

2.2.1. Size and proportion of the body:

Measurements for statistical comparison were undertaken on the following body parts by using ocular micrometer and binocular microscope (scale unit 6.5=1 mm) (Fig. 5-1,
Morphology and Distribution of *H. vigintioctomaculata* Complex

Table 3. Length of three body parts of various samples of *H. pustulosa*. In each sample, mean (x), minimum and maximum values are shown and the standard deviation (SD) is presented in samples with more than 30 individuals.

<table>
<thead>
<tr>
<th>Loc.</th>
<th>Form</th>
<th>L (mm)</th>
<th>W</th>
<th>H</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>x</td>
<td>min.</td>
<td>max.</td>
</tr>
<tr>
<td>UT</td>
<td>I</td>
<td>5.9</td>
<td>5.5</td>
<td>6.3</td>
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<td>ON</td>
<td>I</td>
<td>5.7</td>
<td>5.2</td>
<td>6.3</td>
</tr>
<tr>
<td>SH</td>
<td>II</td>
<td>6.3</td>
<td>5.5</td>
<td>6.9</td>
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<td>KA</td>
<td>II</td>
<td>6.7</td>
<td>6.2</td>
<td>7.4</td>
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<tr>
<td>TO</td>
<td>II</td>
<td>6.4</td>
<td>5.5</td>
<td>7.1</td>
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<td>HI</td>
<td>III</td>
<td>6.5</td>
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<td>5.2</td>
<td>6.5</td>
</tr>
<tr>
<td>YU</td>
<td>II/III</td>
<td>6.4</td>
<td>6.0</td>
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<tr>
<td>TS</td>
<td>II/III</td>
<td>6.5</td>
<td>6.2</td>
<td>6.9</td>
</tr>
<tr>
<td>AS</td>
<td>I/III'</td>
<td>6.4</td>
<td>6.0</td>
<td>6.8</td>
</tr>
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</table>

below): Length of elytron (L), width of epytra (W), length of the perpendicular from the epytral summit to the line connecting apex and base of epytron (H), distance between epytral apex and the junction of the perpendicular from epytral summit with body axis (P). L, W and H in each sample are presented in Table 3, where each sex is given separately. In all characters and samples, females are larger than males, for instance, in HI the sexual difference in L is statistically significant, T=9.98>t_0.05=2.58. Further P-IV (OH) is the largest in all characters in both sexes. Some difference are shown among

1) The length of elytron (L) of samples HI and OH, given incorrectly in Katakura (1973) due to the error in calculation, is corrected in the table.
Fig. 5. Body proportions of various forms of *H. pustulosa* in Hokkaido expressed by triangular diagrams. 1) above, sexual difference of body proportion (L, W and H) in sample OH (P-IV); below, body parts measured. 2)~10), above, LWH; below, LHP. 2)~4), variation of body proportions among samples of each form. 5), comparison of body proportions among four basic forms (five types). 6)~10), comparison of body proportions among two basic forms, together with various intermediate ones.

other samples but no significant difference was detected, so that further consideration is not added to.

Nextly the relation of L, W and H (LWH) and L, H and P (LHP) were expressed by triangular diagrams. In this case, the percentage contributions to the sum of characters of a specimen, 100·L, W, H/(L+W+H), or 100·L, H, P/(L+H+P), are plotted in the graph, which thus shows proportions rather than absolute sizes (cf. Mayr 1969). Each triangular graph is scaled in such way as to produce the maximum spread of the points. As the sexual difference is recognized in relative proportions (Fig. 5~1, above), too, the differences in Fig. 5~2~10 are shown by females alone, which are more numerous in most samples (cf. Table 2). Further, the graphs are shown, except for Fig. 5~1, above; 2; basic forms of 10, above, by the means (given by asterisks) and the contours of the maximum spread of the points, ignoring the distribution of each points.

In the graphs LWH represents rather total proportion while LHP that in lateral view. Generally the value of LHP shows a larger spread than those of LWH, in part due to the errors in measurement, for P and H range mostly 20~25 scale units while L and W 40~50.
Morphology and Distribution of H. vigintioctomaculata Complex

3) P-II

4) P-III

5) Four forms combined

6) P-I-II UT-TN-SH
Variation among the samples of each form is shown in Fig. 5-2~4 except P-IV examined by a single sample. The body proportion of P-II and III, especially of the latter, is fairly constant among samples while P-I shows (except L) a conspicuous difference between two samples, which respectively represent two types of P-I mentioned in 2.1; P-Ia (ON) and P-Ib (UT). Difference among four forms (five types) is shown in Fig. 5-5 by using UT (P-Ib), ON (P-Ia), KA (P-II), HI (P-III) and OH (P-IV). Characteristics of each form in LWH and LHP are given separately as follows:

1) LWH: P-I, short L, wide W and high (Ia) or low (Ib) H; P-II, intermediate between P-Ia and III; P-III, long L, narrow W and low H; P-IV, intermediate between P-II and III as a whole, narrow W nearly equal to P-III, intermediate H nearly equal to P-II.

2) LHP: L is nearly equal while H and P are different among forms. H becomes higher and P becomes postward in the order III-Ib-IV-II-Ia.

Summarizing, the elytral proportion of each form is shown as follows: P-Ia, short, wide and high with summit postward; P-Ib, short, wide and relatively low with summit forward; P-II, intermediate between P-Ia and III; P-III, long, narrow and low with summit forward; P-IV, as a whole, intermediate between P-II and III, height and position of summit similar to P-II while width to P-III.

Relation between two basic forms with the intermediates are shown in Fig. 5-6~10, in the following five cases: A, P-I~II, UT-TN-SH, ON-SO-SI-SH, ON-SO-YU-KA; B, P-II~III, KA-TS-HI; C, P-I~III', UT-AS-(HI). In the last case P-III' could not so sufficiently be available that the sample from Hiroshima (P-III) was conveniently used. Although the spread of the specimens in each sample considerably overlaps with other ones, mean values of intermediate forms generally take an intermediate position between those of two corresponding basic forms.

2.2.2. Elytral characters:

From the specimens used for measurements, 30 females were selected at random from each sample for the variation analysis of following four elytral characters. As to the samples with less than 30 individuals all specimens were used for the same purpose. As the preliminary study revealed the absence of sexual difference in these characters, only the females were examined. Each character was divided into 2 to 4 arbitrary classes given below (Fig. 6).

A) Size of tubercle. 0, absent; 1, faint or very small; 2, prominent: B) Degree of expansion of the hind edge. 1, not expanded; 2, slightly expanded; 3, considerably expanded; 4, extremely expanded: C) Degree of depression at expansion. 0, absent; 1, slightly depressed; 2, remarkably depressed: D) Direction of elytral edge in profile. 1, not bent downward; 2, bent downward at least near the suture of elytra.

Percentage ratios of individuals exhibiting each class are shown in Fig. 7. As the description of each form is already given in 2.1, only the summary of the results is given here:
Fig. 6. Elytral characters of *H. pseudulosa* in Hokkaido. A, size of tubercles; B, degree of expansion; C, degree of depression at the expanded part; D, direction of hind edge. Further explanations in text.

1) Characters A and B are most developed in P-II, while opposite in P-I (both Ia and Ib), and slightly more developed in P-III and IV than in P-I.

2) Character D shows diametrically opposed condition between P-I, III, IV, I/III' and P-II, I/II, II/III.

3) Character C is intermediate between A+B and D.

4) Three basic forms are linked with intermediate forms, but the linkage is virtually absent in P-I~I/II and P-II/III~III as to character D, and relatively weak in P-I/II~II in character C.

5) The heterogeneity within the basic form is generally low except P-II and III in character B, while conspicuous in intermediate form P-I/II except character D.

6) Consequently, these four characters, especially A and B, are positively correlated for each other.

7) Qualitatively each form is expressed by the following formula, which designated the degree of each character in the order ABCD.

   I: 0101. II: 2(3~4)(1~2)2. III: (0~1)(1~2)01. IV: (0~1)2(0~1)1. I/II: (1~2)(1~3)(0~2)2. II/III: (1~2)(2~3)(0~1)2. I/III': (0~1)(1~2)01.

The relation between these characters and proportions mentioned in **2.2.1** is given in Fig. 8.
In the figure mean relative length of elytron is shown in ordinate, and the value of index of elytral characters in abscissa. The relative length of elytron is given by $100 \cdot \frac{L}{(L+W+H)}$. While elytral index as follows: The typical condition in P-I is designated as 0, and in P-II as 2. The intermediate conditions are given by the value 1 when three classes are distinguished, and 0.67 and 1.33 for four classes. Discarding character C, which is quite variable in P-II, the values mentioned in A, B, C are summed up for each specimen, and the frequency distribution of this elytral index is plotted for each sample.

Both basic and intermediate forms exhibit fairly stable morphological condition among the specimens of each sample, showing the morphological stability of local populations, though intermediate forms are more variable. Further, the body proportion and elytral characters are positively correlated for each other. For instance, in P-I/II, the samples close to P-II in proportion behave similarly in elytral characters, too. Comparing the geographical position of the samples (cf. Fig. 2), it is noticed that basic forms occupy relatively large areas, while the intermediate ones narrow transitional belts, which indicate the relatively steep gradient of clinal change.

In the previous paper (Katakura 1974) the anomaly tendency of elytral maculation was reported on the samples of Hp used in the present study. The northward increase of the frequency of anomalous individuals was noticed in Hp in Hokkaido. The frequency of anomalies was low in P-III and IV while P-I and
II showed the conspicuous difference of the frequency among samples, i.e. the samples collected from southern localities showed the low frequency while those from northern ones, the opposite trend. Further P-I/II also showed a trend similar to P-I and II, though less conspicuously than in the latter. Therefore, the clear correlation between form differentiation and frequency of anomalies of elytral maculation is not detected in Hp in Hokkaido. The mechanisms governing such anomalies are still unknown, but thermal condition at pupal stage is suspected because Yasue (1956) reported the increased anomalies in the pupae kept under cool condition (15°C) in another Henosepilachna species, H. sparsa (Herbst).

3. Forms of Hv

Hv is less variable than Hp in morphological characters. From the elytral structure, three forms have been recorded within Japan: Hokkaido (Maki 1954), Honshu (Maki op. cit.) and Rishiri (Katakura 1973) forms. The relation between Honshu and Hokkaido forms was discussed by Maki (1966). Based upon the previous information and my own observations, the characteristics of these forms
Morphology and Distribution of *H. vigintioctomaculata* Complex

Fig. 9. Distribution of *H. vigintioctomaculata* in Hokkaido. Abbreviations of Provinces and code numbers of localities in Appendix. Open circle, V-II; solid circle, V-III.

are described below. The distribution in Hokkaido is shown in Fig. 9, using code numbers given in Appendix.

1) Form V-I (Honshu form, Fig. 10-I): Elytra not expanded at the posterior half so that margin visible from above (Fig. 11, A-1), without depression near apex, epipleura gradually tapering apically (Fig. 11, C-1).

Distribution: Northern Honshu and hilly regions of southern Honshu, Shikoku and Kyūshū.

2) Form V-II (Hokkaido form, Fig. 10-II): Elytra expanded at the posterior half so that hind part of margin invisible and elytral apex slightly projecting (Fig. 11, A-2), with depression near apex (Fig. 11, B), epipleura tapering apically but distinctly narrowed near apex (Fig. 11, C-2).

Distribution: Hokkaido except Rishiri and Rebun Islands.

3) Form V-III (Rishiri form, Fig. 10-III): Elytra not expanded so that margin visible from above, with or without depression near apex, epipleura gradually tapering but sometimes distinctly narrowed near apex.
Fig. 10. Three forms of *H. vigintioctomaculata* found in Japan. I, V-I (Honshu form); II, V-II (Hokkaido form); III, V-III (Rishiri form).

Fig. 11. Morphological diagnostic characters between the forms of *H. vigintioctomaculata*: A, dorsal view; B, posterior view; C, epipleuron.
Distribution: Rishiri and Rebun Islands.

This form is morphologically closely similar to V-I. The anomaly tendency of elytral maculation is also similar to the latter (Katakura 1974). But the slight depression and distinctly narrowed epipleuron near apex of elytra, which are sometimes recognized in V-III, are hard to recognize in V-I tentatively examined by me.

The specimens from Saghalien (only one specimen) and Kunashiri (southern Kuriles) examined by me are of typical V-II. Maki (1966) studied the morphology and biology of V-I and II with the samples collected from various localities of Honshu and Hokkaido. According to him, each form does not show detected local difference while two forms are definitely different, geographically isolated by the Tsugaru Channel. Further, most larvae of V-II can not pass safely the hot season of Honshu under which the larvae of V-I grows normally. Thus he regarded them as geographical races, worth to be ranked subspecifically. Moreover he mentioned that V-I is common to the specimens from northern China in morphological characters, and probably the same to those from Korea and Manchuria reported respectively by Nakayama (1939) and Kawabe (1947). He also assumed the occurrence of V-II in southern Saghalien and Kuriles, based upon previous information on the distribution (Uchida and Watanabe 1946) and anomaly tendency of elytral maculation (Kurisaki 1942). His assumption as to V-II was verified by the occurrence of V-II in Saghalien and Kunashiri. But the discovery of V-III suggests a situation more complicated. Moreover, the specimens from Manchuria, southern Korea, Ussuri and southwestern Japan tentatively examined by me resemble V-I, but show some subtle differences in body size or elytral features as reported elsewhere.

4. Comparison of the distribution of Hv and Hp

Hv is widely distributed over the northeastern temperate Asia, covering China, Manchuria, Japan, Korea and Siberia (Dieke 1947, Uchida and Watanabe 1946). On the other hand, Hp has been recorded only from Japan. In Japan, two species are sympatric, both mainly confined to central and northern areas, though Hv is recorded from much more localities, apparently in part due to its damage to important crop plants. The distribution of Hp in Hokkaido and of Hv in Hokkaido and adjacent areas is summarized as follows:

Hp: So far never recorded from the adjacent islands and eastern areas of Hokkaido. I also failed to discover Hp from these areas. Therefore, it is possible that Hp is not or only sparsely distributed there. Four basic forms in Hokkaido are separately distributed in five areas: Northernmost part (P-III'), northeastern part (P-I), central part (P-II), southwestern part (P-III) and southernmost part (P-IV). Further, Hp inhabiting northern Honshu is very similar to P-IV nevertheless separated by the Tsugaru Channel from the latter. The presence of forms similar to P-III in isolated areas (southwestern part and northernmost part, cf.
Fig. 2) may be interpreted either as the outcome of parallel evolution or as relics after formation of other forms. The latter assumption is more likely, because: 1) Judging from the morphological features prevailing in Epilachninae (cf. Dieke 1947, Li and Cook 1961) the characters possessed by P-I, II and IV, that is the conspicuous curvature of elytra in profile or expansion and tuberculation of elytra, are regarded as differentiated conditions. Consequently P-III is regarded as resembling the ancestral state. 2) The areas occupied by intermediate forms form relatively narrow belts and no intermediate form is found between P-III and IV (Fig. 2). This distribution pattern may be explained by the evolution of various forms from the ancestral form under rather isolated condition and later increase of the range with resulting hybridization in relatively recent time.

The factor limiting or having limited the distribution of each form is unknown. Synthetic studies combining geological, geographical and biological information must be carried out to solve the problem.

A third possibility, the establishment of P-II/III from a dispersal stock is theoretically possible, especially in Kyōgoku (code no. 74) and Wakikata (75). But the dispersal ability of Hp and Hv seems not so strong as in some other coccinellid species making hibernating aggregation (Harmonia axyridis, etc.), though no precise study has been made on their dispersal ability.

Hv: Hv is distributed all over Hokkaido including adjacent islands, and also in Kuriles (Kunashiri) and Sāghalien. Three forms are morphologically recognized and at least in and near Hokkaido, each form is definitely isolated by geographical barriers, V-I and II by the Tsugaru Channel and V-II and III by the Strait of Rishiri. As Hv is a pest of crop plants, especially of potato, a secondary mixture of once established local populations by the human interference, that is the homogenization of populations by incessant small scale dispersals due to extensive cultivation followed by sudden harvesting, is conceivable. But the cultivation of potato, as well as other crop plants, started only at the end of the last century in Hokkaido. The disappearance of pre-existing local forms, even if such would be established as in Hp, during only one hundred years is hardly accepted.

Above mentioned differences on the distribution of both species with their forms indicate that the form differentiation occurred independently in Hp and Hv by different process and/or different periods.

Naturally the classification of forms of Hp and the discussion on the distribution of Hv and Hp presented in this study are still of preliminary nature. Further researches may increase or decrease the number of forms and breeding experiments may clarify the genetic structure of these phenotypic groups. Another aspect to be resolved is a closer comparative study on the population of Hp inhabiting Honshu, and those of Hv in the continental Asia. The first problem is especially important by the recent discoveries of some additional forms or intermediate forms in Hokkaido and the presence of forms similar to P-III and P-IV (P-H₂ and P-H₃, respectively) in Honshu as described in 2.2 in the present paper.
Morphology and Distribution of H. vigintioctomaculata Complex

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Summary

The morphology and distribution of various forms of H. vigintioctomaculata (Motschulsky) and H. pustulosa (Kôno) inhabiting Hokkaido and adjacent areas were studied.

1) Four basic forms are morphologically recognized in H. pustulosa in Hokkaido (previous usage in parentheses): P-I (Sônkyô), P-II (Typical), P-III (Sapporo) and P-IV (Ohnuma). Further, various intermediate forms are recognized as P-I/II, P-II/III and P-I/III'. H. pustulosa has so far never been discovered from eastern Hokkaido and adjacent islands. Its distribution range in Hokkaido is divided into five areas by the distribution of the forms: northernmost (P-III'), northeastern (P-I), central part from north to south (P-II), southwestern (P-III) and southernmost (P-IV). The presence of forms closely similar to P-III in isolated areas (P-III, southeastern Hokkaido; P-III', northernmost part) may be interpreted as relics after the formation of other forms from previously widespread P-III. Basic forms are principally allopatrically distributed, linked with various intermediates occupying narrow transitional belts.

2) Three forms of H. vigintioctomaculata are recognized in Hokkaido and the adjacent areas: V-I (Honshu), V-II (Hokkaido) and V-III (Rishiri form, from Rishiri and Rebun Islands). These forms are definitely isolated by geographical barriers, V-I and II by the Tsugaru Channel and V-II and III by the Straight of Rishiri.

3) Different pattern of distribution in the forms of H. pustulosa and H. vigintioctomaculata suggests the form differentiation independently occurred in two species by the different process and/or at different periods.

References


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Morphology and Distribution of H. vigintioctomaculata Complex


Appendix

Localities and number of specimens examined.

1) Abbreviations for provinces and code numbers of localities are shown in parentheses. 2) The localities without code numbers are those suburb districts of the preceding localities. 3) Gothic numerals given in each locality show the number of the specimens examined. 4) Roman numerals given in each locality of *H. pustulosa* show the form of the specimens.

**H. pustulosa**

**Slvya (SO):** Wakkanai (1) III' 17; KamiYuchi (2), near Wakkanai III' 12; Kabutonuma (3), near Wakkanai III' 4; Koishi (4) III' 3; Assajo (5) I/III' 51; Hamatonbetsu (6) I 13; ShimoTonbetsu (7) I 1; Shimohorobetsu (8) I 15; Utanobori (9) I 13.

**Abashiri (AB):** NakaOkoppe (10) I 9; Omneyu (11), near Rabeshibe I 51; Oketo (12) I 3.

**Kamikawa (KA):** TeshioNakagawa (13) I/II 143; KamiOtoineppu (14) I/II 405; Shiokari (15) I/II 114; Antaroma (16) I/II 30; Kamikawa (17) I/II 3; Sounkyo (18) I/II 120; Aizankei (19) I/II 31; Yukomanbetsu (20) I/II 120; Tenninkyo (21) I/II 71; Shirogane spa (22) 1I 2; Kamuikoton (23) II 268.

**Rumoi (RU):** Shosanbetsu (24) II 68.

**Tokachi (TO):** Kawakami (25), Rikubetsu (26) III' 15; Horoka (27) II 4; Nukabira (28) II 6; Tomuraushi (29) II 491; Nipesotsu (30) II 8; TokachiChikubetsu (31) II 10; Niina (32) III' 1; Shintoku (33) II 4.

**Hidaka (HD):** Nioi (34), near Biratori III' 1; Upstream of Nukabira River (35) II 6; Upstream of Saru River (36) II 3; Monbetsu (37) II/III 7; Mt. Apoidake (38) III' 1.

**Sorachi (SO):** Moshiro (39) II 69; Soeushinai (40) II 116; Shokanbetsu (41) II 27; Penkepetan River (42) II 18; Ojiraruka River II 2; Ashibetsu (43) II 8; Mt. Yuibaridake (44) II 7; Onsenbashi, Yubari II/III 4; Tsugitate (46), near Yubari II/III 123; Kakuta (47) II/III 20.

**Iburi (IB):** Horonai (48), Azuma II/III 5; Shiraai (49) III' 4; Muroran (50) III' 1; Toya (51) III 40; Nakajima (52), Lake Toya III 156; Toyoura (53) III' 1.

**Ishikari (IS):** Hamamasu (54) II 1; Atsuta (55) II/III 18; Ebetsu (56) III' 1; Nopporo (57) III' 192; Atsubetsu III' 1; Hiroshima (58) III 126; Tsukisamu (59) III 20; Hoshioki (60), near Teine III' 1; Mt. Teine (61) III' 2; Sapporo (62), including adjacent areas III 309; Mt. Kamuidake III' 1; Misumai (63) III' 77; Jyozankei (64) III' 78; Mt. Muine (65) III' 9; Ashibetsu Falls (66) III 31; Mt. Soranumadake (67) III' 48; Mt. Izaridake (68) III' 2; Okotan (69), Lake Shakotsu III' 2; Eniwa valley (70) III' 81; Chitose-Shikotsu (71) III' 8.

--- 1) The specimens labelled 'Kawakami' distinctly belonging to type P-Ia are preserved in Entomological Institute, Hokkaido University. This locality is here tentatively designated as Kawakami, Rikubetsu.
H. Katakura

Shiribeshi (SH): Hariusu (72) III 2; Asari (73) III 2; Kyōgoku (74) II/III 17; Wakikata (75), near Kyōgoku II/III 1; Kawakami (76), Kimobetsu III 1; Makkari (77) III 3; Niimi spa (78) III 16; Shimamaki (79), including Harauta and Chihase River III 19.

Oshima (OS): Ohnuma (80) IV 157; Ohnuma bokuju (81) IV 52; Hakodate-Kakkumi (82) IV 31; Masukawa (83), Hakodate IV 1; Fukushima (84) IV 1.

H. vigintioctomaculata

Shoya (SO): Wakkanaï (1) 3; Koishi (2) 13; HamaTonbetsu (3) 2; Rishiri Is. (4) 150; Rebun Is. (5) 105.

Abashiri (AB): Ohmu (6) 2; NakaOkoppe (7) 41; Engaru (8) 22; Koshimizu (9) 12; Oketo (10) 23.

Kamikawa (KA): TeshioNakagawa (11) 1; KamiOtoineppu (12) 131; Otoineppu (13) 16; Nishisato (14), Bifuka 29; Aibetsu (15) 3; NakaAibetsu (16) 3; Antaroma (17) 5; Ōsunkō (18) 5; Shirogane spa (19) 3; Mt. Tokachidake (20) 11; Mt. Furandake (21) 1; Furano (22) 1; Kamuikotan (23) 21.


Kushiro (KU): Akan (26) 21; Akkeshi (27) 7; KamiOboró (28), near Shibecha 25; Shirarutoroshitoro (29), Shimamaki 23; Takkobu (31), Kushiro 2; Otanoshige (32), Kushiro 6; Shoro (33), near Shiranuka 2; KamiCharo (34) 21.

Rumoi (RU): Touri Is. (35) 1.

Tokachi (TO): Ashoro (36) 21; Nukabira (37) 4; Tomuraushi (38) 61; Nipesotsu (39) 1; Niina (40), near Shintoku 1; Shintoku (41) 11; Shikai (42) 46; Memuro (43) 2; Obihiru (44) 37; Atsunai (45), near Uraboro 8.

Hidaka (HD): Noi (46), near Biratori 1; Biratori (47) 2; Monbetsu (48) 91; Nii-kappu (49) 16; Urakawa (50) 61; Mt. Apoidake (51) 6; Shoya (52) 1.

Sorachi (SO): Soeushinai (53) 26; Penkepetan River (54) 7; Kokuryō (55) 4; Bibai (56) 270; Iwamizawa (57) 4; Onsenbashi (58), Yūbari 3; Umaoiyama (59) 2.

Iwuri (IB): Horonai (60), Azuma 3; Oiwa (61), Yūfutsu 64; Shadai (62), near Shiraoi 1; Lake Kuttara (63) 1; Murotan (64) 15; Toyoura (65) 4.

Ishikari (IS): Hamamasu (66) 239; Atsuta (67) 3; Ebetsu (68) 81; Nopporo (69) 18; Hiroshimo (70) 124; Hoshioki (71), near Teine 149; Mt. Teine (72) 2; Sapporo (73), including adjacent areas 227; Misumai (74) 2; Jyōzankei (75) 47; Asiribetsu Falls (76) 1.

Shiribeshi (SH): Suigenechi (77), Otaru 1; Kyōgoku (78) 18; Wakikata (79), near Kyōgoku 2; Makkari (80) 1; Iwanai (81) 1; Harauta (82), Shimamaki 103.

Hiyama (HI): Okushiri Is. (83) 232; Otobe (84) 3; Esashi (85) 19; Kaminokuni (86) 1.

Oshima (OS): Kaminoyu (87), Yakumo 1; Nigorikawa (88), Mori 1; Mori (89) 27; Ohnuma (90) 1; Isoya (91), Kayabe 1; Ohfune (92), Kayabe 4; Kakkumi (93), Kayabe 1; Esan (94), Shirikishinai 16; Shirikishinai (95) 10; Toi (96), near Hakodate 1; Narukawa (97), Nanane 7; Akanuma (98), Kameda 6; Akagawa, Kameda 28; Nakamichi (99), Kameda 2; Hakodate (100) 43; Niyama (101), Ohno 5; Ohno (102) 38; Ippongi (103), Ohno 1; Garō (104), Kamisato 1; Kamaya (105), Kikonai 1; Satsukari, Kikonai 7; Kikonai (107) 1; Uriya (108); Kikonai 2; Fukushima (109) 5.

Kunashiri (Kurile): Kotankeshi 31.

Saghalien: Tarandormi 1.