



Title	CLASSIFICATION AND EVOLUTION OF THE PHYTOPHAGOUS LADYBIRDS BELONGING TO HENOSEPILAGHNA VIGINTIOCTOMACULATA COMPLEX (COLEOPTERA, COCCINELLIDAE)
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CLASSIFICATION AND EVOLUTION OF THE PHYTOPHAGOUS LADYBIRDS
BELONGING TO HENOSEPILOACHNA VIGINTIOCTOMACULATA
COMPLEX (COLEOPTERA, COCCINELLIDAE)

By
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A DISSERTATION

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INTRODUCTION

The so-called Henosepilachna vigintioctomaculata complex (henceforth abbreviated to Hv-complex) consists of more than ten "forms" of closely allied phytophagous ladybirds. By its considerable morpho-biological variations this group offers a rare opportunity to analyse the process of speciation. Since the pioneer work by Watanabe and Sakagami (1948), a number of studies have been undertaken on this group from various points of view as cited below. However, the taxonomy of Hv-complex has been quite confused by the lack of sufficient information and accurate documentation on the relations among various forms. The purpose of the present paper is first to make a revision of this biologically interesting but taxonomically troublesome group based on morpho-biological characters and to give their geographic distribution, clarifying sympatric/allopatric relations. This paper also aims to present some tentative interpretations of the evolution of Hv-complex on the background of recent geological history of the Japan Archipelago. Although the system and interpretations proposed in the present paper are still imperfect in many aspects, I believe that such attempts should be made for further evolutionary studies of this fascinating group.

Before going further, the present status of Hv-complex is briefly explained (for the review, cf. Ehara 1955, Koyama 1962, Yasutomi 1966a,b, 1973, 1974a,b, 1977, Sasaji 1971, Katakura 1977, Katakura et al. 1977).

Henosepilachna vigintioctomaculata (Motschulsky) is widely distributed over the cool temperate eastern Asia and is well known as one of the most serious pests of potato (Solanum tuberosum, Solanaceae) in this area. In 1937, Kôno described a curious species, Epilachna pustulosa, based on the specimens from Sorachi and Teshio, Hokkaido, northern Japan. This species was evidently closely related to E. vigintioctomaculata but was both morphologically and biologically distinct from the latter. E. pustulosa had two features not found in E. vigintioctomaculata: the hind margin of elytron was extremely expanded laterally and possessed a distinct tubercle near the base of expansion. Further, pustulosa fed on wild thistles (Cirsium spp., Compositae) in contrast with vigintioctomaculata which fed on the cultivated solanaceous plants. Subsequent studies started by Watanabe and Sakagami (1948) and followed by Ehara (1952, 1953), Yasutomi (1954) and many other Japanese entomologists revealed the sympatric occurrence of pustulosa or the thistle feeder with vigintioctomaculata from diverse localities of Hokkaido and Honshu, two main islands of Japan. But, these studies also revealed that the morphological and biological differences noticed by Kôno (op.cit.) were unstable. The elytral shape was geographically quite

variable in pustulosa and, though less conspicuously, in vigintioctomaculata. Although most sympatric local populations of vigintioctomaculata and pustulosa are easily distinguished by the elytral shape alone as Kôno did, the reliable differences hitherto known between the overall populations of pustulosa and vigintioctomaculata are only of coloration of legs and shape of elytral maculation (cf. Katakura 1974b). Difference in the shape and color of spermatheca was noticed by Ehara (1952, 1953), but this character has not been examined with a sufficient number of populations. As to their food habit difference, many culture tests showed that most local populations of pustulosa could normally grow with potato but vigintioctomaculata could not grow with thistle (cf. Katakura et al. 1977).

The occurrence of the third form feeding on blue cohosh (Caulophyllum robustum, Berberidaceae) was recently confirmed in several localities from the southernmost part of Hokkaido to central Honshu (Fukuda 1970, Yasutomi and Fukuda 1974, Katakura 1976, etc.). This form is sympatric with both vigintioctomaculata and pustulosa. Morphologically, the cohosh feeder is so close to pustulosa that even the characters separating vigintioctomaculata from pustulosa can not be used here. Like the case of sympatric vigintioctomaculata and pustulosa populations, however, the cohosh feeder is separable from the sympatric pustulosa population by its smaller body size and distinct elytral shape as given below. The cohosh feeder also grew with potato but did not

with thistle under laboratory conditions. The relation of the cohosh feeder to pustulosa was more complicated by the discovery of pustulosa, which feeds on both thistle and blue cohosh. At least in the southwestern part of Hokkaido a local form of pustulosa feeds on both thistle and blue cohosh, whereas two forms, respectively feeding on thistle and blue cohosh as host plant, coexist from the southernmost Hokkaido to central Honshu (Katakura 1977).

Moreover, there is another puzzling group called Western Tokyo form (Wt). This form is also a pest of potato and is distributed parapatrically with vigintioctomaculata and pustulosa and allopatrically with the cohosh feeder in the Pacific coastal areas of Honshu. Morphologically Wt is similar to pustulosa, or more to the cohosh feeder when the elytral shape is taken into account. In laboratory Wt preferred blue cohosh and could grow normally with it as well as potato, but some larvae of this form could grow also with thistle (Yasutomi 1976, Watanabe and Suzuki 1965, Hinomizu 1976a).

To summarize, we can now recognize at least three fairly distinct forms (vigintioctomaculata, pustulosa, the cohosh feeder) and one puzzling form (Wt), by the combination of external morphology, food habits and sympatric-allopatric relation. Among them, vigintioctomaculata and pustulosa are phenetically polytypic, each consisting of three and more than seven well characterized local forms.

Taxonomic treatise of this puzzling group has been very confused (cf. Sasaji 1971, Katakura 1974a). Some authors

treated vigintioctomaculata and pustulosa as two distinct species (Watanabe and Suzuki 1965), some regarded them as subspecies of a single species (Yasutomi 1954, 1966a,b, Sasaji 1971, Tsuneki and Kubo 1960) and others as mere infra-specific variations not worthy to be ranked subspecifically (Li and Cook 1961). Taxonomic status of Wt is also confused. Some considered it a member of vigintioctomaculata (Yasutomi 1954, 1966a,b, Tsuneki and Kubo 1960) while others a member of pustulosa (Iwao 1959, Watanabe and Suzuki 1965) or a strain of the cohosh feeder (Yasutomi 1973, 1974a,b) which has secondarily become a crop pest. Some authors avoided the decision on its status (Ehara 1953, Sasaji 1971). No taxonomic treatise has so far done as to the cohosh feeder. In our serial studies on Hv-complex, we have tentatively treated vigintioctomaculata and pustulosa as distinct species, leaving the status of the cohosh feeder and Wt in unsettled (cf. Katakura 1974a).

In the present paper I adopt the following system.

1) Mainly based on the morphological analysis given in the next chapter, Hv-complex is divided into two groups, A and B.

2) Group A includes H. vigintioctomaculata (Motschulsky) alone.

3) Group B involves three subgroups tentatively treated as three distinct species, H. niponica (Lewis), H. pustulosa (Kôno) and H. yasutomii sp. nov. The combination of the former two species is identical to pustulosa in our previous

usage (cf. Katakura 1974a, b) and the third species is equivalent to the cohosh feeder. The distinction of these three species is based on not only morphological features but also on biological features and allopatric-sympatric relation as mentioned in the subsequent chapters.

4) The so-called Wt and two other unsettled populations are indubitably closer to group B and placed within the latter. But their relation to the other members of group B is uncertain. In case of Wt even the affinity to group A is still not precluded.

Since the present system is different from some previous systems including my own, it is synoptically shown in Table 1, together with the names or abbreviations currently used.

A few words are added to the treatment of infraspecific categories. In order to specify the infraspecific local (geographic) variations, two kinds of categories are used below: A) Local forms (forms), infraspecific local variations defined by external morphology, especially by elytral shape; B) local races (races), infraspecific local variations defined by biological properties, especially by food habit. It is still difficult to have a unitary system by combining these two procedures. Groupings by these two procedures do not necessarily coincide with each other. Western Tokyo form stands as an exception. The taxonomic position of the specimens referred to Western Tokyo form is not yet solved, hence they still did not belong to any infraspecific

categories. The name "Western Tokyo populations" may be more suitable. However, the name "Western Tokyo form" is used in this paper for the lasting use of this or similar names by most previous authors.

In the following treatise, species and forms are cited by the abbreviations given in Table 1, except for the citation of full name is necessary.

I. MORPHOLOGY

The external characters and genitalia of H. vigintiocto-
maculata (Motschulsky) fitted to any member of Hv-complex
were described and figured by Dieke (1947, as Epilachna
niponica), and those of some members of Hv-complex were
given by Ehara (1952), Li and Cook (1961) and Sasaji (1971).
The features common to the members of Hv-complex are given
as follows:

Size medium to large. Elytron basically with 14 spots,
spots d-3-b-2 arranged in an arch (Fig. 1), elytral tip
rounded. Abdominal line subcomplete, subterminal, somewhat
rounded or subangulate. Hind margin of visible abdominal
sternite V concave in male (Fig. 2), truncate with a gentle
convexity at middle and mesal depression on about 1/2 of
sternite in female (Fig. 3). Visible abdominal sternite VI
emarginate in male (Fig. 2), split in female (Fig. 3). Male
genitalia (Fig. 7): Median piece of tegmen in profile
strongly bent dorsally near apex and slightly bent backward
just before apex, upperside with pale yellowish setae on
about apical 1/2 and several retrorse teeth, basal knife
edge small. Lateral pieces of tegmen subsqual to the median
piece in length, with apical thorn and pale yellowish setae
on apical 1/3, gently curved down near apex. Apex of siphon
obliquely truncate with a few small teeth at distal side of

ejaculatory opening (Fig. 7'). Female genitalia (Fig. 8): Hemisternite with an inner notch slightly closer to basal than apical end.

Within the genus, this complex is close to some other species of vigintioctopunctata group (Dieke 1947), such as vigintioctopunctata, pusillanima, phillipinensis, reducta, etc., but distinctly differs from these species in the structure of genitalia. At the present, it is difficult to assume which species of vigintioctopunctata group is closest to this complex.

Within the complex, only coloration, especially the melanic tendency, i.e., the shape of elytral maculation, color of legs and color and tint of elytra, have hitherto been used to separate Hv from other members (cf. Ehara 1955, Yasutomi 1966a, Katakura 1974b). Difference in the shape and color of spermatheca between Hv and the thistle feeders (Hp and Hn) was pointed out by Ehara (1952, 1953), but many "forms" including Hy, discovered after Ehara have not so far been studied on this character. Li and Cook (1961) found slight differences in the genitalia of both sexes between Hv and the nominate form of Hp (P-II) but they regarded these differences as mere infraspecific variations. In the present study all these characters were reexamined. As an additional character, Koyama (1962) pointed out a significant difference of state of tuberosity at the inner side of mandibular teeth among Hp, Hv and Wt. This tuberosity was not examined in this study because it was more or less worn off and indistinct

in the individuals collected from the field, especially the post hibernating adults. Through the present study it was confirmed that the characters mentioned above were more or less stable in groups A and B except for the shape of the median lobe of male genitalia reported by Li and Cook (op. cit.). Further, some additional differences to distinguish the two groups were found in antenna, maxillary palpus and male genitalia. The morphological distinction of groups A and B was, therefore, well established by the combination of many, though often subtle characters. On the other hand, distinction of three species within group B is difficult and can be made only by statistical difference of body size and, in each sympatric combination, by the elytral shape. The local forms of each species were defined by their characteristic elytral shapes.

Material and Methods

Morphological comparison was carried out by using 85 samples, which covered most, if not all, of representative members of Hv-complex so far known from Japan, together with some exotic material, all identified with Hv. The number of individuals examined is listed in Appendix at the end of the paper, and the provenance of each sample is mapped in Figs. 10 and 150 with the code numbers given in Appendix. A part of each Japanese sample (in most cases five to ten individuals for each sex, cf. Appendix) and all exotic material were dissected to observe the genitalia and other minute characters.

Morphological analysis was made mainly on these dissected specimens. Most of these dissected specimens were fixed with Kahle's solution at the field and later preserved in 80% alcohol until dissection. Dried specimens including all exotic material were relaxed by boiling prior to dissection. After dissection and subsequent treatment with KOH solution, the antenna, maxillary palpus and genitalia (except tegmen of male) of each specimen were mounted on a slide glass with gum-chroral. The tegmen was dried, mounted on a card board piece and pinned with the specimen. Observations were made under dissecting microscope or optical microscope.

Characters used

The morphological characters used in the following descriptions are briefly explained.

1) Coloration. The following four characters were used. Among them pronotal spots and hind leg coloration were studied only in dissected specimens. Since color characters were suggested to be variable according to thermal condition or humidity (Yasue 1956), laboratory-reared specimens were excluded from the variation analyses.

Pronotal spot: Pronotal maculation of Henosepilachna species was classified into twelve patterns by Dieke (1947) from spotless (pattern A) to entirely black (L). The present study followed his classification system but intermediate states of two successive spot patterns were subdivided. For instance, IJ is the intermediate state of Dieke's I and

J. Fig. 11 shows the sequence of pronotal maculation observed in the present study. C, F, G and typical L of Dieke's patterns were not encountered. Most specimens showed the states between H and KL.

Elytral maculation: Persistent (1~6) and non-persistent (a~h) spots were each numbered according to Dieke (op.cit.) (Fig. 24).

Color and tint of elytra

Hind leg coloration: Hind leg coloration of Hv-complex is quite variable from entirely brown through possession of a black femoral spot to nearly entirely black. Only the variation of femoral color was studied in detail. Femoral color was divided into eight classes according to the size of black spot (Fig. 12). Color variation of trochanter and tibia was ignored because the black part of these segments was reduced more easily than the femoral spot and the three paler classes in the figure (A~C) could not be separated in safety.

2) Structural characters. The following structural characters were examined with the dissected specimens.

Antennal scape (Fig. 4)

First antennal flagellomere (Fig. 4)

Apical segment of maxillary palpus (Fig. 5)

Ninth abdominal tergite (tergite IX, male, Fig. 9): In males of coccinellid beetles the ninth abdominal tergite is a relatively large U-shaped segment (Sasaji 1971) and in Hv-complex fused entirely with ninth abdominal pleurites.

Tenth abdominal tergite (tergite X, male, Fig. 9): The male tenth abdominal tergite of Hv-complex forms an invert flat triangle piece situated at the distal end of abdominal dorsum; well chitinized except for the middle part of frontal margin, with a longitudinal groove medially and with an inner depressed area (inner depression), and the apex with dense long hairs.

Apex of siphon (penis or aedeagus, male, Fig. 7')

Hemisternite (coxite or genital plate, female, Fig. 8)

Spermatheca (receptaculum seminis, female)

3) Metric characters and ratios.

Body size: Although the total body length (the length from head or frontal margin of pronotum to the tip of elytra) and/or the body width are generally used as the indices of body size of beetles, they were not used in the present study by the following reasons: 1) Strongly convex dorsum of Hv-complex makes exact measurement difficult, 2) for Hv-complex these characters seemed not appropriate as indices of body size because of the high variability of elytral shape. Therefore, I adopted the pronotal width (abbreviated PRW), which is easily measurable and far less variable than the elytral shape. Measurement was made for all specimens listed in Appendix, except for those the pronotum of which was broken or apparently aberrant.

Other metric characters and their ratios: In addition to the pronotal width, the following body parts were measured but for the dissected specimens only:

Head width (HDW), the distance between the outermost margins of both eyes.

Interocular distance (IOD), the distance of the narrowest part between both eyes.

Length of tergite X of male (LTT) (Fig. 145)

Width of tergite X of male (WTT) (Fig. 145)

Length of the first antennal flagellomere (LAF) (Fig. 144), the distance between the base and apex of anterior edge.

Width of the first antennal flagellomere (WAF) (Fig. 144), the maximum width between frontal and hind margins.

From these measurements, the ratios IOD/PRW, HDW/PRW, LTT/WTT and WAF/LAF were calculated. Measurement was made directly by ocular micrometer (PRW, IOD, HDW) or made with the figures drawn by the aid of camera-lucida (all others).

In the following descriptions, figures and tables, each Japanese sample is cited by the combination of locality code given in Appendix and abbreviation of species or forms (v: vigintioctomaculata, p: pustulosa, n: niponica, y: yasutomii, w: Western Tokyo form, x: unsettled populations other than Wt). For example, CHp means the sample of Hp from Chihase (sample No. 43) and HAX means the unsettled population from Hakushû, Yamanashi (No. 84), etc. Continental Hv is represented by several samples in the following figures and tables. A sample from Saghalin (No. 86, 38399) is also incorporated. Other continental samples consisting of a fewer individuals and showed similar trend to the representative samples are omitted from the figures and tables.

1. Morphological comparison of two groups of Hv-complex

First the morphological differences between groups A (=Hv) and B (all others) are dealt with. These two groups differ in some color and structural characters.

1.1. Coloration. Generally speaking, group B is darker in color than A of the same locality. This trend was observed on nearly all body parts. It was also noticed in both groups that the northern samples tended darker than the southern counterparts. The following four characters were treated herein: 1) Elytral maculation, 2) tint and color of elytra, 3) pronotal spots and 4) hind leg coloration. The color of spermatheca described later is another useful character for the separation of these two groups.

1.1.1. Elytral maculation. Pattern of elytral maculation is one of the most useful characters for the external distinction of groups A and B. Different phenetic expressions of elytral maculation in these two groups are mainly caused by two elements, the size difference between persistent and non-persistent spots and the difference in the shape and size of some characteristic spots. Persistent spots (1~6) generally well developed and large in size while non-persistent ones (a~h) are variable in size according to individuals or localities. Generally the non-persistent spots are larger and the size difference of persistent and non-persistent

spots is smaller in group B than in A. Shape and size of spots 1, d and 6 are characteristic to each group as follows (also cf. Figs. 13~28):

	Group A	Group B
Spot 1	Subtriangular, right and left spots not fused on suture, or fused at the anterior part but frontal margin of the fused spots biconvexed	More elongate than in group A, two spots generally fused on suture at the anterior half and the frontal margin convexed, if not fused the shape different from that of group A (compare Figs. 14 and 20)
Spot d	Size variable but generally small, not or only partly fused on suture, if rarely entirely fused, fused spots somewhat rectangular, its small size accentuated by surrounding large 1, 3, 5 spots	Well developed, entirely fused on suture, fused spots bell shape or hexagonal in general, subequal to surrounding 1, 3, 5 spots
Spot 6	Large, elongate and curved, its large size intensified by the surrounding smaller spots e, f, g, h; more than twice longer than the largest surrounding spot	Smaller, elliptical, subequal to surrounding e, f, g, h spots or, if larger, less than twice the largest surrounding spot

Some variations were noticed within each group.

1) In V-II and III, spots g and h were generally very small, often minute or evanescent (Fig. 14); spot l generally not fused on suture in V-II while often fused in V-I and III.

2) Among continental samples of Hv, those from Manchuria and Korea, especially the latter, showed reduced elytral maculation; in the extreme case non-persistent spots except small c and very minute f were entirely missing (Fig. 18).

3) Spot d of Hn, particularly of N-II, often small and not fused on suture like group A (Fig. 22).

4) Elytral spot pattern of Wt is quite variable. Most specimens showed the pattern identical to other members of group B but some showed the pattern intermediate between the two groups or nearly identical to group A, namely Hv (Fig. 28). This makes identification of some Wt individuals by external appearance difficult, though the structural characters mentioned later are still useful in such cases.

1.1.2. Color and tint of elytra. It has been noticed by various authors that the color of elytra is more reddish with a stronger luster in group B than in A. Such a tendency is certainly recognized in living individuals except for those just after the emergence. Aged individuals show, however, a deeper color and stronger luster than they were young. Further, the tint fades considerably under preserved condition, so that this character is inadequate for the precise analysis.

1.1.3. Pronotal spots (Table 2). This character have no diagnostic value in sorting two groups by a considerable overlap of variations. But it shows a geographic trend of melanism in Hv-complex, suggesting some inter- and infra-specific differences within each group.

Group A. Color variation is seemingly related to the forms. Most V-I specimens show patterns I, IJ and J while V-II J, JK and K. V-III is intermediate between V-I and V-II, though more similar to the former. In the continental samples the proportion of darker specimens tends to decrease southward. The Korean sample is palest in all the samples examined including group B.

Group B. The pronotal maculation of Hp is most developed of all the samples examined. In Hn, the pronotal maculation is reduced in the order of N-I, N-III and N-II. In Hy the Hokkaido sample (OHy) has fairly well developed spots, while the samples from Honshu have spots smaller than that from Hokkaido. Generally speaking, the spot pattern of Hy is slightly developed than in Hn. All unsettled populations shows the trend similar to N-II.

1.1.4. Hind leg coloration (Table 3). Hind leg coloration shows a trend similar to that of pronotal maculation, but the difference between the two groups is far more distinct. Class C is predominant in Hv except for the Korean sample in which class A is predominant, while classes F, G and H are frequent in the members of group B. Just like the case of pronotal maculation, the northward increase

of darker specimens was observed in both groups. The only difference between two melanic variations is that V-III is intermediate between V-I and V-II, but in the pronotal maculation it is similar to the former while in the leg coloration to the latter.

Since Watanabe and Sakagami (1948), the difference in the leg coloration has been regarded as one of the most reliable characters for the separation of Hv from the other forms. As mentioned above (cf. Table 3), distinction by this character is fairly effective between Hp and Hv but sometimes fails between Hv and the other members of group B due to the overlap of variation ranges.

1.2. Structural characters.

1.2.1. First antennal flagellomere (Figs. 29~63). The shape of flagellomere is one of a few reliable characters for both sexes, nevertheless showing a considerable individual variation.

Group A

Fairly uniform, slender, rod-shaped; uniformly divergent apically, frontal margin nearly straight or very gently curved

Group B

Variable, irregularly club-shaped; more or less swollen apically, frontal margin convex near the apex, sometimes showing aberrant shapes as in Figs. 45 left or 59 middle

No difference was detected on this character between Japanese and continental samples of Hv. Some interspecific variations observed in width/length ratio is mentioned in the next section. This character seems more stable in group A than B. In the latter, Wt is most variable, sometimes showing a condition equivalent to group A which was rare in the other members of B.

1.2.2. Abdominal tergite X of male (Figs. 64~90).

Among the characters adopted in the present study, the shape and structure of male tergite X is reliable for distinction of groups A and B. The differences between the two groups are as follows:

Group A	Group B
Hind margin distinctly angulate or nearly so, both sides sharply curved, widest near the base; margin of inner depression very distinct and often recognized as a dark band at least at the apical half (cf. Fig. 68 middle), contour of the margin V-shaped	Hind margin rounded or flat, rarely biconvex, both sides rounded, often widest a little remote from the base; margin of inner depression generally indistinct, often not detected; even if detected contour of the margin nearly circular

The margin of the inner depression of which presumable cross section is given in Fig. 91, is individually variable in both groups. Further, in group B the margin is relatively distinct in most specimens of the northern samples. Thus

the margin of Hp is generally more distinct than, for example, N-III of Hn or Wt, though no clear line can be drawn among the members of group B. In spite of such variability the condition of the margin of inner depression is of a diagnostic value. Only a few specimens of Hv out of all dissected ones could not be identified by this character alone. Since male tergite X was examined under slightly pressed condition, the margin of the inner depression may be seen differently in natural condition. The contour of male tergite X is also individually variable and of less diagnostic value than the margin of the inner depression. However, the shape as shown in Fig. 64 left, being frequent in group A, was never observed in group B. On the contrary the shape as in Fig. 73 left or 77 middle, being frequent in group B, was never or only exceptionally observed in group A. The shape and structure of all exotic specimens were identical with those of the Japanese material of Hv, but the margin of the inner depression was even stronger than the latter.

1.2.3. Spermatheca (Figs. 92~109). Shape and color of spermatheca were first mentioned by Ehara (1952, 1953) as diagnostic characters in Hv-complex. Some additional items were obtained by the present study.

Group A	Group B
Generally slender, sausage-shaped or slightly swollen apically, sometimes tapering apically; transparent (V-I) or limitedly colored (others)	More or less swollen apically, sometimes apical swollen part distinctly rounded; at least partly colored

Shape is variable individually. Wt and HAx tend to have the distinctly swollen and rounded apex. On the other hand, both groups A and B show the northward increase of the colored area or coloration like in some melanic tendency mentioned earlier. The geographic trend is somewhat different between the two groups.

Group A (Hv). Color variation is closely related with the forms (Table 4).

V-I: Transparent in almost all specimens examined; exceptions are one specimen of SFv, HNv and ASv each and two specimens of KNv, which had pale brown or yellow areas.

V-II: Most specimens have various degrees of brown spots mostly at the apical half. The unique transparent exception is a specimen of CHv. V-III: Intermediate between V-I and V-II; nearly the equal number of transparent and colored individuals are involved. Continental specimens: Generally similar to V-III, though northward increase of colored specimens is suggested.

Group B (Table 5). The northern populations have darker spermatheca than the southern populations, but unlike Hv this geographic trend seems unrelated with species as well as forms.

Hp: Nearly entirely dark brown though tending to become paler basally. Hn and Hy: In both species darker and more widely colored in the northern populations in which the condition is similar to Hp, i.e., the swollen part and the sides are generally dark brown to brown. In the southern

populations coloration is variable from deep brown to yellow and the colored areas vary from nearly entirely to only partly. Unsettled populations: Coloration generally similar to that of southern populations of Hn and Hy. Only INx possessed the relatively darker spermatheca.

Due to the geographic color variation of spermatheca mentioned above, most female specimens of Hv-complex in Japan can be sorted into two groups:

	Hokkaido	Honshu
Group A	Partly yellow to brown	Transparent
Group B	Most parts dark brown	At least partly yellow to dark brown

1.2.4. Other structural differences. In addition to the three characters mentioned above, some other body parts differ between the two groups. Although these body parts clearly show different trend in each group, great overlap of variation ranges between the two groups makes use of these characters for diagnostic purpose difficult. Therefore, only the conditions typical to each group are enumerated (Table 6, Figs. 110~114). Actually many individuals show various degrees of intermediate conditions between the two extremes given in the table.

2. Species and infraspecific variation

Among four species of Hv-complex, Hv can safely be separated from others by many characters mentioned. On the other hand, morphological distinction of three species in group B is made mainly by the difference in the size and body shape. Inter- and infraspecific variations of coloration and some structural characters have been mentioned in the previous section.

2.1. Habitus. External appearance of the members of Hv-complex is quite variable due to local variation in the elytral shape. Based on the shape of elytra, three local forms of Hv, four of Hp and at least three of Hn have so far been recognized in Japan (cf. Katakura 1974b, 1977). Among them at the present only Hy is monotypic. Although the elytral shape itself can not serve as a decisive diagnostic character by conspicuous infraspecific variations, it often performs a useful role for identification of particular individuals. Especially distinction of three species of group B can safely be done by the elytral shape when exact locality and host records are available. First the basic body (elytral) shape is defined, which appears in diverse members of Hv-complex and regarded as the generalized state from which other specialized states have evolved.

Basic body shape (Figs. 115, 125, 134, 138): Body broadly oval and dorsum strongly convex. Both sides of

elytra seen dorsally moderately curved, in lateral and posterior views moderately curved; margin entirely visible from above; without tubercles, lateral expansions, depressions or any other modifications at or near the elytral apex, epipleura gradually tapering apically.

In the following descriptions of forms and species, only the difference from the basic shape is mentioned with some remarks. Samples treated in this study were sorted into forms and given by sample no. at the end of each form.

2.1.1. Group A (=Hv). Maki (1966) recognized two forms of Hv in Japan followed by an additional form by Katakura (1973).

Form V-I (Honshu form): Basic shape. Samples: Nos. 10~33.

Form V-II (Hokkaido form, nominate form): Elytra mildly swollen at the posterior half so that margin invisible and apex slightly projected postward seen from above (Fig. 116), with depressions near apex (Figs. 126, 135), epipleura tapering apically but distinctly narrowed near apex (Fig. 139). Samples: Nos. 3~9.

Form V-III (Rishiri form): Generally identical with basic shape. Sometimes with weak depression near elytral apex and epipleura narrowed near apex. Samples: Nos. 1, 2.

Forms V-I and V-III are similar with each other, nevertheless isolated geographically (cf. Fig. 150, and the next chapter). V-III shows condition intermediate between V-I and V-II in some color characters as mentioned before (Tables 2~

4). All continental specimens (sample nos. 86~111) are of basic elytral shape, i.e., distinguished from V-II by elytral shape.

2.1.2. Group B.

1) H. pustulosa: Three forms of Hp, P-I, P-II and P-III (+ P-III'), were already reported (Katakura 1974b). Admitting P-III' as a separate form, four forms are included here.

P-IV, P-H₁ and P-H₂ (Katakura op.cit.) correspond to H. niponica in this paper.

Form P-I (Sôunkyô form, Figs. 117, 127, 136): Elytra as if shrunk along body axis, in profile very sharply curved and part between summit and apex nearly linear, in posterior view contour mildly angulate. Sample: No. 36.

Katakura (op.cit.) recognized two types: P-Ia, elytral curvature conspicuous with summit postward; P-Ib, elytral curvature less conspicuous with summit forward. The latter being discovered in the northernmost part of the range of P-I might be a form intermediate between P-I and P-III' mentioned later.

Form P-II (Nominate form, Figs. 118, 128, 137): Elytra provided with prominent tubercles, remarkably expanded laterally near and at apex, in profile expanded hind edge bent downward, in posterior view contour somewhat triangular. Elytral curvature in lateral and posterior views variable individually. Elytra generally upheaved along the posterior half of suture in various degrees. Samples: Nos. 35, 37.

Katakura (1974b) reported some P-III like individuals

collected from the same area with P-II. These specimens might be hybrids between P-II and its sympatric counterpart V-II (cf. p. 61). The name "typical form" was used in previous papers for P-II as E. pustulosa was described by this type, but the name might be misleading as far as the shape is concerned.

Form P-III (Sapporo form, Fig. 119): Similar to basic shape. Elytra slightly expanded at hind edge, with no or minute tubercles. Samples: Nos. 39~43.

Specimens having slightly more expanded and tuberculated elytra were collected amid the range of P-III (Katakura 1974b). They were included here as a variation of P-III.

Form P-III' (Wakkanai form, Figs. 120, 129): Elytra expanded laterally at hind edge, with small tubercles, in profile the summit lies very anteriorly and the curve between summit and apex often nearly linear in profile. Sample: No. 34.

By the lack of sufficient material this form was tentatively placed near P-III in Katakura (1974b). Further study revealed that this form was considerably different from P-III by the features mentioned. Hp from Rebun Island (Yasutomi 1974c) belongs to this form.

Four forms of Hp are allopatric with each other (Fig. 151, also cf. p. 39), each separated by a relatively narrow transitional zone. In the transitional zone, the populations showing various degrees of intermediate condition between the two neighbouring forms are discovered (Katakura 1974b).

Such intermediate forms are known between P-III' and P-I, P-I and P-II, and P-II and P-III. Among the material treated in this study MZp (No. 38) is a form intermediate between P-I and P-II.

2) H. niponica: P-IV from Hokkaido and P-H₁ and P-H₂ from Honshu cited as H. pustulosa by Katakura (1974b), as well as any other thistle feeders from Honshu are included. Since geographic variation of the elytral shape of Hn is still not exactly analyzed, the recognition of three forms and the classification of various samples into the forms in the present paper are tentative.

Form N-I (Ohnuma form, Figs. 121, 130, 131): Elytra slightly expanded at hind edge, with no or minute tubercles, in profile sharply curved but not so acute as in P-I. Elytral curvature in profile variable according to locality. Elytral apex in profile projected postward in most Tōhoku populations (Fig. 131). Samples: Nos. 44~46, 48~50.

P-IV and a part of P-H₁ (from Tōhoku district) in Katakura (1974b) are included. UBN (No. 50) may be a form intermediate between N-I and N-II.

Form N-II (Honshu form, nominate form, Figs. 122, 132): Similar to P-I. Elytra slightly expanded at hind edge, with no or minute tubercles, in profile sharply curved and apex projected postward. Samples: Nos. 51, 52, 54~56.

Part of P-H₁ (from central Honshu) in Katakura (1974b) is included.

Form N-III (Ibuki form): Basic shape. Contour of elytra

seen from above slightly variable locally, being more rounded in the western samples (Fig. 123). Samples: Nos. 58~62.

Nearly equal to P-H₂ in Katakura (op.cit.).

Among the samples of Hn examined in this study, three samples, TTn (No. 47), TGn (No. 53) and AMn (No. 57), can not be classified into any of above three forms.

TTn: Nevertheless collected amidst the range of N-I, TTn has a distinct elytral shape (Figs. 124, 133) and easily separable from N-I, rather closely similar to P-III' (Figs. 120, 129); some authors (Yasutomi 1977a, Shinbo 1977) called it "Hachimantai form"; according to Yasutomi (1977b), the distribution range of "Hachimantai form" is restricted to a very narrow area and replaced by N-I through the populations intermediate in elytral shape.

TGn: Similar to N-III but elytra slightly expanded at hind edge and a little more sharply curved in profile than N-III; further the locality seems distant from the range of N-III; as far as I know TGn is closest to the specimens from Nakafusa, Nagano Pref. (Katakura 1974b).

AMn: Having a condition of elytral shape intermediate between N-II and N-III and collected from the area near the boundary of the two forms, probably representing an intermediate form between N-II and N-III.

3) H. yasutomii: Basic shape.

4) Unsettled populations: Basic shape. Contour of elytra seen from above more rounded in INx than the rest.

Due to this conspicuous variation of elytral shape, the following sympatric combinations can be safely identified:

Rebun Island (V-III/P-III'), Hokkaido except Rebun Island and the southernmost part (V-II/all forms of Hp), southernmost part of Hokkaido (V-II/N-I/Hy), northern and central Honshu (N-I, N-II/Hy).

2.2. Body size and relation of some metric characters

2.2.1. Body size in terms of pronotal width (PRW).

Fig. 140 presents the general trend of body size of the members of Hv-complex in Japan. In the figure the mean value for male specimens of each sample is plotted against that for the female specimens. The value of reared specimens and samples represented by only one individual for either sex are omitted. Evidently females are larger in size than males. Some deviations may have been caused by the sampling errors due to the small number of specimens measured. The body size of each member could be expressed in the descending order as: Hn > Hp ≐ Hv > Wt > Hy. Noticeable variations within each group is mentioned separately below.

Group A (Hv, Fig. 141): Although the size is variable according to samples, the size difference linked with forms is recognized as: V-II > V-III > V-I. All continental samples being externally identical with V-I are smaller than the latter; the south Korean sample is especially small. The northward increase of body size is suggested but V-III is smaller than V-II and the northern and southern samples of

V-I are similar in size.

Group B (Fig. 142): Fig. 142 shows the geographic variation in the members of group B. Localities are arranged from north to southwest. An interesting relation is observed between Hn and Hy. In the southernmost part of Hokkaido to central Honshu where both species are sympatric (cf. p. 41, Figs. 151, 152), their size rarely overlaps, being larger in Hn while smaller in Hy. In the southwestern Honshu where only Hn is known, however, Hn (nearly identical with N-III) becomes considerably smaller. On the other hand, Hp occupying the northern territory of the range of group B shows the size comparable to Hn in the southwestern Honshu though with a marked variation among samples. Summarized, in the northern and southwestern parts of the range of group B where the group is represented by only one species, the body size is medium (Hp and N-III), while in the central part of the range with coexistence of two species of group B body size shifts to larger (N-I and N-II) and smaller (Hy) sides. The cause of this situation reflecting a "character displacement" is uncertain. Although no explanation can be made as to the size variation within Hn, the difference of food plant adopted by each species may be at least partly responsible: Blue cohosh, the host plant of Hy, is a small herb generally lower than ca. 70 cm with a restricted number of small leaves. While thistles, the host plant of Hp and Hn, are giant, often taller than 2 m with very large leaves. Consequently the biomass of a stock of blue cohosh is far

smaller than that of thistle (Hinomizu et al, unpubl.). Further, the density of blue cohosh seems not so high to compensate this biomass difference. The small body size of Hy may be an outcome of adaptation to this food resource limitation. On the other hand, the larval growth of Hp must be completed before the withering of the shoots of adopting thistle species which takes place in early to mid summer. But the larvae of Hn do not suffer such seasonal food shortage because the thistle species adopted by Hn is available throughout the active season as described later.

The size of Hy increases (KHy, OTy) at the southernmost part of its distribution range, but this trend is inconclusive because of the smaller number of specimens examined. The larger size of OTy's males showing the size equivalent to the southwestern samples of Hn must have been overestimated because this value was obtained from only two specimens and the females of the same sample showed a smaller value. Among the unsettled populations Wt occupies the position intermediate between Hn and Hy of their sympatric region. INx is situated amid the size range of Hy. HAx is comparable to the largest Hy or the smallest Wt.

2.2.2. Relation of metric characters. In addition to the pronotal width, the following body parts were measured and their ratios were calculated (cf. pp. 13~14): Interocular distance (IOD), head width (HDW), length (LTT) and width (WTT) of male tergite X, length (LAF) and width (WAF) of the first antennal flagellomere; ratios IOD/PRW, HDW/PRW,

LTT/WTT, WAF/LAF. Fig. 143 shows the frequency distribution of the values of these measurements and ratios for each species, using mean value of each samples (arithometric means for measurements, geometric means for ratios). The following trends are noticed:

1) Three species of group B behave similarly in HDW, IOD, LAF, WTT, HDW/PRW and IOD/PRW. These values vary allomorphically according to size in terms of PRW, but Hp deviated from two other species in WAF and LTT. WAF and LTT values of Hp are relatively larger than those of two other species, resulting in larger values of the ratios WAF/LAF and LTT/WTT. The deviation of Hp in these characters are more clear in Figs. 144 and 145.

2) Hv (group A) having equivalent body size to Hp behaves differently from three species of group B except for WTT; being smaller than Hp in HDW and IOD, subequal to or smaller than Hy in LAF, WAF and LTT and always taking smallest values in the ratios.

3) Wt included in group B is intermediate between Hy and Hp (or Hv) in size but it lies at least in HDW/PRW and IOD/PRW between Hy and Hv instead of Hy and Hp.

Concerning the last point, further examination was made as follows: Relations HDW/PRW and IOD/PRW are given for each sex separately in Figs. 146 and 147, using mean values for each sample. Samples represented by only one individual for each sex are omitted. Generally speaking, two allomorphic trend lines running parallel are observed, one consisting of

three species of group B and another of Hv (group A). Namely, the values of HDW and IOD of Hv are generally smaller than those of three species of group B having equivalent PRW value.. Two unsettled populations (HAX and INx) also lie on the trend line of group B, though male INx slightly deviates toward the Hv-line in IOD/PRW relation. Some inter- and infraspecific variations are recognized in group B. A remarkable deviation from the general trend by the male OTy (designated by an arrow in the figures) is, however, possibly caused by sampling error (cf. Fig. 148). Infraspecific variation is also found in Hv (group A), in which the continental populations show somewhat different trend. Behavior of Wt is noticeable. Some samples of Wt (solid triangles in the figures) being generally smaller in size lie on the trend line of group B while others (open triangles) being larger in size on that of Hv. This trend in Wt is observed in both sexes and both HDW/PRW and IOD/PRW relations. There is a distinct biological difference between the samples of Wt designated respectively by solid and open triangles.

i) Solid triangles represent BOW (sample no. 73), OKw (No. 79), UKw (No. 80), and UIw (females only, sample no. 81), of which BOW, OKw and UIw were collected from wild plants; BOW from Licium chinense, other two from Scopolia japonica. UKw included the individuals collected from Scopolia japonica and those from potato.

ii) Open triangles are KYw (No. 72), KKw (No. 74), NKw

(No. 75), TZw (No. 77) and HIw (No. 82). TZw included the individuals collected from potato and those from Chelidonium japonicum. Four other samples were collected from potato.

Therefore, the two groups of Wt also differ in their food plants, one mainly collected from wild plants and another from potato fields. Figs. 148 and 149 compare the individual variation of Wt with those of Hy, which is considered by Yasutomi (1973) the presumable ancestor of Wt, and V-I, a form of Hv at least partially sympatric with Wt. Obviously the samples of Wt from wild plants lie on the variation trend of Hy while the samples from potato fields on that of V-I. From these facts, it is likely that Wt had originally depended on wild plants and lain on the trend of group B, but some populations had invaded into potato fields and deviated from the general trend of group B toward that of group A. One possible explanation is that the deviation of potato attached Wt was caused by the introgression of some Hv genes into the original populations. This possibility can not be excluded when we consider the now existing mixed populations of Hv and Wt along their distribution limits (cf. the next chapter) and some Hv like features observed in elytral spot pattern and first antennal flagellomere of Wt (cf. pp. 17, 20).

II. GEOGRAPHIC DISTRIBUTION

So far numerous studies have been made to clarify the geographic distribution of Hv-complex in Japan, by Takahashi (1932), Yasue (1963), Koyama (1962), Koyama et al. (1964), Shinbo (1977, 1978), Shinbo and Sakaguchi (1976), Katakura (1974b), Yasutomi (1976) and many other fragmentary or regional records by various authors. Based on these records, information from foreign records, and my own unpublished data, the geographic distribution of the members of Hv-complex is described in this chapter.

1. Group A (Hv, Fig. 150)

Hv is widely distributed over the cool temperate north-eastern Asia, covering the southern part of the Soviet Far East, north China (including Manchuria), Korean Peninsula and Japan. It also occurs in the southwestern part of Saghalin and the westernmost part of Kunashiri (the southern Kuriles). The geographic distribution of Hv in Japan has minutely been studied by many authors, particularly by Takahashi (1932) and Yasue (1963). Local variation was studied by Maki (1966), Ikemoto (1955) and Katakura (1974a, b). In Fig. 150, the northern distribution limit of Hv is drawn based on Stundjuk (1966) (continental Asia and

Saghalin) and Kuwayama (1967) (Kunashiri), while the southern limit in Japan on Yasue (1963) with slight modification.

The southern and western distribution limits in the continent is uncertain. Some authors recorded, however, Hv from diverse localities even south to Burma (Li and Cook 1961, Liu 1963, Pang and Mao 1977). Further, a related form, H. vigintioctomaculata coalescens (Mader), originally described as an aberration of Hv but later treated as subspecies by Dieke, occurs in Szechwan Prov. (south China), Tibet and Nepal (Dieke 1947, Bielawski 1972, Liu 1963). Although these reports show the occurrence of some members of Hv-complex in the southern area, I could not examine any of these specimens. Until closer examination of these ladybirds would be undertaken, I tentatively omit them from the discussion.

As far as the northern territory is concerned, the distribution of Hv is closely related to that of deciduous broad leaved forests and mixed forests composed of deciduous broad leaved trees and conifers, which represent a clear cool temperate element. In Japan, the distribution of Hv approximately coincides with that of Fagus forests in the southern area and the mixed forests in the north. In the far eastern region of Soviet Union, its northern limit is also strongly correlated with the presence of the broad leaved and mixed forests (Ivanova 1962). The southern limit in Japan has often been discussed in relation to the thermal condition. Some isotherms were proposed as indices of the

southern limit of Hv: 14°C isotherm of the mean annual temperature (Takahashi 1932), 21°C isotherm of the summer (May to October) mean temperature (Watanabe 1950) and 14.9°C isotherm of the mean of the highest temperature in November (Shinbo 1978). I here only point out that the southern limit of Hv in Japan approximately coincides with the boundary of warm and cool temperate forests (cf. Hotta 1974).

The distribution ranges of three forms of Hv in and adjacent Japan are:

Form V-I: Northern Honshu and hilly cooler regions of southern Honshu, Shikoku and Kyushu.

Form V-II: Hokkaido except Rishiri and Rebun Islands, southwestern Saghalin and the westernmost part of Kunashiri.

Form V-III: Rishiri and Rebun Islands off the northernmost part of Hokkaido mainland.

Thus the three local forms of Hv are clearly isolated with each other by the geographic barriers, Tsugaru strait (V-I/V-II) and Rishiri strait (V-II/V-III) (cf. Fig. 150). All the specimens from the continental Asia examined in the present study had the basic elytral shape and could not be separable from V-I or V-III (cf. p. 25). As Hv is an important 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 with sudden harvesting, is conceivable. But the regular cultivation of potato started only at the

end of the last century in Japan. The complete disappearance of preexisting local forms during only one hundred years is hardly accepted. Consequently the present distribution pattern of Hv should have been basically unchanged before the dispersal of Hv due to human activities (Katakura 1974b).

2. Group B

All the members of group B have so far been discovered only from Japan. Their distribution range approximately coincides with that of Hv in Japan, but tends to be restricted to the Japan Sea slope, having been never discovered from eastern Hokkaido, Kii Peninsula, and two southern main islands, Shikoku and Kyushu. Koyama (1962) discussed the distribution pattern of the thistle feeders (Hp + Hn) in relation to the maximum depth of snow cover in winter.

2.1. H. pustulosa (Fig. 151). Hp is distributed in Hokkaido except for the eastern and southernmost parts (Katakura 1974b). It is replaced by Hn and Hy in the southernmost part of Hokkaido. Four local forms are recognized (p. 26).

Form P-III': The northernmost part.

Form P-I: Northeastern part.

Form P-II: Central part from north to south.

Form P-III: Southwestern part.

In the areas between two neighbouring forms there are

relatively narrow transitional zone occupied by the intermediate forms. It seems that across these areas one form is replaced by another with a steep morphocline. (Katakura 1974b).

2.2. H. niponica (Fig. 151). Hn is distributed in the southernmost part of Hokkaido (Oshima Peninsula) and Honshu. Recent survey by Shinbo (1974, 1977) extremely enriched our knowledge on the distribution of this species. The distribution ranges of three local forms defined tentatively in the present paper are:

Form N-I: Southernmost part of Hokkaido and northern Honshu (Tôhoku district).

Form N-II: Middle Honshu (Kantô and Chûbu districts).

Form N-III: Western Honshu (Kinki and Chûgoku districts).

As mentioned in chapter I (p. 28), the geographic variation of elytral shape of Hn is not yet exactly known. Although it is still uncertain whether the forms of Hn replace with each other like the forms of Hp or not, fragmentary records show the form replacement similar to Hp. Among the material examined by me, AMn (Fig. 151, B) shows the condition intermediate between N-II and N-III and UBn (Fig. 151, A) between N-I and N-II. Boundary of the forms of Hn in Fig. 151 is arbitrary drawn from such fragmentary data.

2.3. H. yasutomii (Fig. 152). Although the records of

Hy is still scattered, it occurs in the southernmost part of Hokkaido (Oshima, only one locality) and north and central Honshu. Namely, it is widely sympatric with N-I and N-II of Hn. Hy or any cohosh feeder seems not to be distributed in the western Honshu occupied by N-III (pers. comm. by Shinbo, Nakamura). Unlike other species of Hv-complex, Hy is phenetically monotypic. But Hy in Honshu and that in Hokkaido may belong to different races (cf. the next chapter).

2.4. Unsettled populations. The distribution of Wt was recently summarized by Yasutomi (1976), and two other populations were reported by us (Katakura et al. 1978). The approximate position of their distribution are given in Figs. 152 and 153, together with that of Hy. In the Pacific slope of central Honshu, Wt is distributed along the southern limit of Hv. Two other unsettled populations were discovered amid the distribution range of Hv. Recently two populations feeding on Scopolia japonica and a population feeding on both S. japonica and blue cohosh were discovered from central Honshu, also amid the distribution range of Hv (Fig. 153, Hara and Hamaguchi 1979, Shirai pers. comm.). These populations might be Hy or the unsettled populations similar to HAx.

The distribution range of species and forms of group B can not be explained by the now existing climatic and/or geographic conditions. Palaeoecological and geological

knowledge about the history of Japan Archipelago must be required. Some discussion relating to this problem is given in chapter VII.

Between the northern limit of Hn and the southern limit of Hp there is a relatively narrow belt seemingly unoccupied by these two species (Fig. 154). In spite of several surveys, I failed to find any individuals or feeding traces of epilachnid beetles in the leaves of thistles abundantly growing in the area. Although it is always difficult to judge the absence of a given species in an area, the absence of the thistle feeders (Hp and Hn) in this narrow belt is nearly conclusive. Thus the distribution ranges of Hn and Hp are disjunctive, nevertheless being not separated by any geographic or ecological (= food plant) barriers. Unfortunately it is still unknown whether Hy inhabits this belt or not. The presence of the unoccupied belt by the thistle feeders served some basis on my interpretation of the species recognition in group B (see, chapter V).

III. BIOLOGY

1. Life cycle

The annual life span of Hv-complex is simple. They hibernate as adults. Post hibernating adults appear on the host plant in spring, then feed on the host plant, copulate and lay egg masses on the underside of the leaves. Most post hibernating adults die by summer but some enter a second hibernation and again reproduce in the next year (Ivanova 1962, Nakamura pers. comm.). Larvae exclusively feed on the host plants and new adults emerge in mid summer to early fall. New adults enter hibernation by late fall. Hibernacula in Japan is not exactly known but they probably hibernate amid the litter of the forest floor, shrubs and crop fields adjacent to the host plants. We have collected some hibernating adults of Hp at Tomakomai and those of Wt at Yokohama, respectively, from such circumstances. Ivanova (1962) who made an extensive study on the biology of Hv in the Soviet Far East came to the same conclusion. According to her, Hv hibernates under litter of the forests, shrubs and crop fields near the potato fields with the density of 0.1~1.5 individuals per m². It is considered that Hv-complex generally does not form a hibernating aggregation nor make hibernating migration often observed in the carni-

vorous coccinellids (cf. Hodek 1973), though Sakagami (1951) found a rare hibernating aggregation of Hv in Sapporo. Low vagility of the adult beetles has been documented (Iwao 1970, Hinomizu 1976b, Ohgushi unpubl., Kimura unpubl.). In some cases, mean dispersal distance per day was estimated to be lower than 1 m (Ohgushi unpubl., Kimura unpubl.). Hv-complex is generally univoltine. Although some previous authors referred to the bivoltinism of Hv in southwestern Honshu (cf. Takahashi 1932), it might be a misjudgement because the new adults of the southern areas enter aestivation in the summer season (Iwao 1970), and the adults seem as if occur twice in a year. On the other hand, partial bivoltinism of Hv is likely to occur in the northern Honshu in the unusually warm spring (Kurihara, pers. comm.). Physiological mechanism of diapause of Hv (V-I) was studied by Maki et al. (1964) and Maki and Kurihara (1965). The ovaries of new adults degenerated under the conditions shorter than 14~15 hours photoperiods per day. Temperatures above ca. 28°C also evoke ovarian degeneration.

2. Food habits

Beside the morphological variability mentioned above, the diversity in food plants is another important aspect which strongly characterizes Hv-complex. Fourteen species (all thistles combined as Cirsium spp.) belonging to six families have been documented as host plants, i.e., the plants

on which the larvae can complete its growth under natural conditions, of Hv-complex in Japan (Table 8). If edible plants, the plants occasionally fed by adults and/or larvae in nature or laboratory but not utilized as "host plants", are taken into account, the list of the food plants (host plants + edible plants) expands to more than 50 species covering 11 families (cf. Katakura et al. 1977). Table 7 exemplified the food plants of Hv (V-II) and Hp (P-III) confirmed under natural conditions in and near Sapporo, Hokkaido, during 1971~1979. Using these plants (chiefly the host plants), the food habits of various forms of Hv-complex have been examined by many authors. Since most of these studies were compiled by Koyama (1950) and Katakura et al. (1977), the following descriptions and discussions mainly concern the host plants.

2.1. Host plants. Among the members of Hv-complex, Hv and Wt mainly depend on cultivated potato, Hp and Hn on wild thistles and Hy on blue cohosh. Some additional plants are subsidiarily utilized as host plants by nearly every species or forms. Further, there are a few populations depending solely on the plants other than these three kinds of plants. These host plants are enumerated below for each member separately (cf. Table 8).

2.1.1. *H. vigintioctomaculata*. Hv depends on potato in field conditions. Subsidiary host plants in fields are egg plant, tomato, Solanum nigrum, Datura stramonium and possibly

in the southwestern Honshu Lycium chinense, all belonging to Solanaceae (cf. Koyama 1950, 1957, Katakura et al. 1977). Egg plant and tomato are cultivated crops and others are weeds common in and near fields and wastes. In Hokkaido, Schizopepon bryoniaefolius growing in and around forests is frequently utilized by V-II as the host plants (Katakura 1975, Fig. 155). Further, populations of V-II depending on Solanum megacarpum were recently confirmed from two localities (Nopporo near Sapporo, Barato in Ishikari, Katakura unpubl., Fig. 155). On the other hand, records on wild host plants of V-I and V-III are very scarce except for weeds. I have collected adults and eggs of V-I from Solanum maximowiczii at Mt. Hikosan, northern Kyushu (Katakura et al. 1977) and adults from Physalisstrum japonicum at Ômukawa, Yamanashi Pref. (Katakura et al. 1978). These plants might be the wild host plants. Scopolia japonica may or may not be a subsidiary host plant of V-I (cf. later). Ivanova (1962) considered Solanum dulcemara (Solanaceae) and Thladiantha dubia (Cucurbitaceae) the wild host plants of Hv in the Soviet Far East.

2.1.2. H. pustulosa. Hp greatly depends on thistle species (Cirsium spp.), especially on C. kantschaticum or its allies. Creeping thistle (Breca setosa) is often subsidiarily used as the host plant. Among the forms of Hp, P-III shows a high preference for blue cohosh. As far as Sapporo and the vicinity are concerned, P-III commonly utilizes blue cohosh either subsidiarily or as much as

thistle, though hitherto no population depending solely on blue cohosh has been discovered. In the other forms utilization of blue cohosh seems to be very restricted (Hoshikawa, pers. comm.). Hp often invades potato fields and forms mixed populations with Hv (V-II), but the number of such individuals is generally small and the invasion is limited to the fields adjacent to the forest inhabited by Hp. Although the confirmed cases are scarce, completion of the growth by some Hp in potato fields is indubitable (Katakura et al. 1977). On the other hand, some adults of Hp (all so far known cases P-III) are simultaneously discovered with Hv (V-II) on Schizopepon bryoniaefolius growing within their cruising range in forests (Katakura 1975, 1976a). The discovery of P-III on S. bryoniaefolius is however, nearly limited to late summer and fall when thistle and blue cohosh (the main host plants of P-III) are already unavailable by withering (cf. Fig. 156). Perhaps S. bryoniaefolius is not a host plant of Hp. Solanum megacarpum is also sometimes fed by P-III at Nopporo, and the growth of P-III with S. megacarpum was confirmed there (Katakura unpubl., Nakano unpubl.), resulting in the formation of a mixed population of P-III and V-II. This suggests the occasional occurrence of mixed populations of Hv and Hp or of groups A and B even before the human activities have disturbed the natural habitat of these beetles.

2.1.3. *H. niponica*. Hn also greatly depends on thistles though the plant species are different from the species commonly fed by Hp. Cirsium kantschaticum, the main host

plant of Hp, is rather rare in the southernmost part of Hokkaido and absent in Honshu while the thistle species (Cirsium spp.) fed by Hn are absent or rare in Hokkaido except for the southernmost part. Creeping thistle is also used as a subsidiary host plant by N-I in the southernmost part of Hokkaido. Like Hp, Hn often invades the adjacent potato fields and forms mixed populations with Hv (V-II in Oshima, V-I in Honshu). Number of individuals who entered potato fields is sometimes very large. In the extreme case I have collected 32 individuals of Hn together with 83 Hv from a single potato field at Urabandai, Fukushima Pref. Growth of Hn in potato fields was also confirmed. N-III was collected from Scopolia japonica as well as thistles in two localities (Mitokusan, Fig. 10-60, Hoshikawa, pers. comm.; Nakakawachi, Fig. 10-59, Shinbo 1977). S. japonica might be a subsidiary host plant of N-III.

2.1.4. *H. yasutomii*. Hy primarily depends on blue cohosh. In Honshu, it sometimes uses Panax japonicus, too. In Ohnuma, southernmost Hokkaido, Hy does not utilize this plant. Rearing test revealed that Hy in Ohnuma does not complete the growth with Panax japonicus (Katakura 1976b). Therefore, Hy in Hokkaido, though known only by one population, and that in Honshu can be regarded as the different races. A few adults of Hy were collected from Scopolia japonica at Zatôishi, Hirosaki, northern Honshu (Hoshikawa pers. comm.) and the plant may or may not be a subsidiary host plant of the beetle.

2.1.5. Unsettled populations.

Western Tokyo form: Wt is a pest of potato. In the following four cases treated, the beetles concerned were regarded as Wt because they were found amid or adjacent to the distribution range of Wt and phenetically indistinguishable from the latter: Beetles collected from Chelidonium japonicum at Takaozan, Tokyo (TZw, sample No. 77) (cf. Yasutomi 1973); those from Licium chinense at Nokogiriyama, Bôsô (BOW, No. 73); populations feeding on Scopolia japonica at Okutama, Tokyo (OKw, No. 79) and Urayama, Saitama (UKw, No. 80, UIw, No. 81) (cf. Shinbo 1977).

Izumi population (INx): Depending on Chelidonium japonicum.

Ômukawa population (HAX): On Scopolia japonica. Quite recently three additional populations feeding on Scopolia japonica were discovered from Nagano Prefecture, Honshu (cf. Fig. 153) (Hara and Hamaguchi 1979, Shirai pers. comm.). One of these was simultaneously collected from blue cohosh and presumably is Hy. The other two populations might be identical with HAX. No further information about these three populations is available at the present.

Interspecific difference and infraspecific variation of food habits are suggested by the field observations mentioned above. Many rearing tests have been made with various forms of Hv-complex in order to know such food habit difference precisely. Most of these tests used as foods, however, only three kinds of plants, i.e., potato, thistle and blue cohosh.

Since information on the plants other than these three plants is still very poor except for a few cases, only a summary of rearing tests mainly concerning the three kinds of plants is given here (cf. Katakura et al. 1977). An extensive study on the food preference of various populations of Hv-complex made by Hoshikawa will be published elsewhere.

1) Hv can not grow with thistle and blue cohosh.

2) Hp can grow normally with potato as well as blue cohosh.

3) Hn, in general, can grow normally with potato. But failure of the growth or the lower survival by potato are reported in some exceptional cases (Iwao 1959, Koyama and Kobayashi 1957). According to Yasutomi (1974a, b), the survival ratio of Hn with blue cohosh is lower than that with thistle and some populations of Hn can not complete the growth with blue cohosh. Some of these results may involve observational errors and require further confirmation.

4) Hy can grow normally with potato, but not with thistle. Further, Hy from Ohnuma can not complete its growth with Panax japonicus, a subsidiary host plant of Hy in Honshu (Katakura 1976).

5) All unsettled populations can grow normally with blue cohosh (Yasutomi 1974a, b, Katakura et al. 1978). Some larvae of Wt and IN_x could complete its growth with thistle, though small sized adults were obtained (Watanabe and Suzuki 1965, Hinomizu 1976a, Katakura et al. 1978). Adult HAX did not accept thistle though the larval growth

by the plant has not be examined yet. INx and perhaps HAX can grow normally with potato.

The relation of forms and races, two infraspecific categories principally adopted in this study (cf. p. 6), of each species is mentioned here. At the present, only Hy is conclusively divided into two races, Hy in Hokkaido and that in Honshu, by the preference for Panax japonicus. Further, as mentioned above, Hp may be divided into P-III and other forms by the accessibility for blue cohosh, Hn to N-III and others by that for Scopolia japonica, and Hv to V-II and others by Schizopepon bryoniaefolius. Since accurate information about these infraspecific variations is still poor, closer examination of the food habits of various members of Hv-complex is necessary before defining "races" of the species other than Hy. Hoshikawa's results on the food preference of various members of Hv-complex will greatly contribute to clarify the relation of forms and races when published.

2.2. Native host plants. The distribution pattern and form differentiation of Hv indubitably suggest its presence in Japan long before the introduction of potato, the cultivation of which began only about 100 years ago there. The situation around Wt is similar to Hv. It is important, therefore, to clarify their host plants prior to the arrival of potato in Japan. These plants must be essentially native to Japan. Consequently tomato, egg plant and Datura stramo-

nium, all being exotic plants, are excluded from consideration.

Schizopepon bryoniaefolius was reported as one of the native host plants of V-II (Katakura 1975). Solanum megacarpum may be another native host plants of V-II (cf. above). On the other hand, the native host plants of V-I and V-III are uncertain. S. bryoniaefolius seems to be not utilized as a host plant by V-I (pers. comm. by Shinbo, Hozumi; Katakura unpubl.). Scopolia japonica, a native solanaceous plant, is widely distributed in the distribution range of V-I. Nevertheless, all populations so far discovered from this plant belong to group B (N-III at Mitokusan and Nakakawachi, Hy at Zatôishi, unsettled populations at Ômukawa, Okutama and Urayama, and three populations recently discovered from central Honshu), though a few individuals of Hv were simultaneously discovered from Mitokusan, Nakakawachi, Ômukawa, Takamori (Shirai pers. comm.) and Oku-kageyu (Hara and Hamaguchi 1979). Scopolia japonica may be a subsidiary host plant of Hv but should not be the obligatory host plant. The records concerning Solanum maximowiczii, Physalium japonicum and Lycium chinense are still very poor, but true native host plants of V-I might be involved among such native solanaceous plants. Solanum nigrum, which have long been considered the most likely native host plant of Hv (Koyama 1950, 1954, Uchida et al. 1949), is certainly utilized by Hv as the subsidiary host plant in many localities. This plant, is, however, probably a prehistoric naturalized

plant (Maekawa 1943), i.e., an accidental immigrant by the prehistoric human activities. S. nigrum further lacks some ecological properties which enable Hv to use it as the obligatory host plant (Katakura et al. 1977). It is a typical annual weed and can grow only at openlands. By this reason the continuous colonization of S. nigrum seems to be greatly restricted to ecologically unstable sites such as coastal zones and riversides under natural conditions not affected by human interference. Actually, however, Hv is discovered on S. nigrum not growing such places, but in secondary areas such as crop fields and abandoned places.

The native host plants of Wt are also uncertain. From the fact that Wt prefers and grows normally with blue cohosh, Yasutomi (1973, 1976) assumed Wt as Hy which successfully became a pest, though population feeding on blue cohosh has never been discovered within the distribution range of Wt. Among the plants enumerated above as the host plants or suspected ones of Wt, Scopolia japonica and Chelidonium japonicum may be native host plants.

2.3. Food utilization. Different types of food utilization in relation to the phenological sequence of the food plants are observed in Hv-complex. Examination of such biological plasticity may be useful as a clue to considering the evolution of this group. Two cases are described here-with.

1) V-II on Schizopepon bryoniaefolius in forests vs

V-II in potato fields: S. bryoniaefolius offers sufficient food and shelter for V-II throughout its active season. Consequently V-II in forests entirely depends on S. bryoniaefolius alone (Fig. 156, upper, Katakura 1976a). In potato fields, V-II exhibits a different type of food utilization (Fig. 156 middle). Field populations of V-II, as well as those of other forms of Hv and Western Tokyo form, virtually depend their growth on potato though some other plants are occasionally used as subsidiary host plants. Appearance of the beetles in spring may precede the sprouting of potato, which is variable by cultivation practice. Then the post hibernating adults feed several kinds of plants (mainly cultivated crops) until potato becomes available. When potato grew about 10 cm or more, they enter the fields and settle there. In late summer and fall, the newly emerged adults also feed on various plants other than potato due to withering or harvesting of the latter. Therefore the field populations are monophagous or nearly so in the reproductive season and during larval stage while polyphagous in other seasons, especially in fall (Katakura 1976a).

2) P-III vs other forms of Hp: Cirsium kamschaticum, the main host plant of Hp, sprouts soon after thawing. It grows in spring season and blooms in early summer. After blooming and subsequent seeding, withering of the shoot takes place from mid summer. Nearly all shoots wither by late summer whereas the rosettes begin to grow in early summer in some but not all shoots. Rosettes are present

until late fall. In the northern territory of Hp the withering of shoots seemingly offers, in general, no serious problem for Hp because the larvae can complete its growth until the withering and newly emerged adults can utilize abundant rosette leaves, which generally well develop in the areas. On the other hand, for P-III in and around Sapporo, the withering of shoots brings a considerable food shortage in the later growing season or for newly emerged adults, because the amount of rosettes in the area is generally scarce, often virtually unavailable for P-III (Fig. 156 below, Katakura 1976a). Blue cohosh, another important host plant of P-III, covers nearly completely the active season if not seriously infested by the beetles. However, in most cases blue cohosh is entirely eaten by the larvae and new adults and withers until mid summer. Thus the newly emerged adults suffer food shortage in late summer and fall, when they depend on thistle and blue cohosh remained in a very poor condition. Under such circumstance, P-III often feeds on the plants other than host plants, such as S. bryoniaefolius. If the habitat of P-III faces the crop fields, it enters the fields and feeds on various crops like the field population of V-II (cf. Table 7).

Probably most populations of Hv-complex feeding on wild plants depend on only one or two kinds of plants throughout the year, like V-II on S. bryoniaefolius or Hp in the northern areas. In other words, most wild populations of Hv-complex are seemingly mono- or stenophagous. Under

unfavorable conditions, however, the polyphagous nature of the beetles, perhaps mainly of the adults, is unmasked, like P-III or field populations of V-II. Most of edible plants confirmed under natural conditions are just eaten in fall due to such food shortage.

Some comments are added to the phenological correspondence between beetles and the host plants.

1) Unlike Cirsium kamschaticum, the main host plants of Hp, the thistles (Cirsium spp.) fed by Hn offers sufficient food throughout the active season, because their blooming is later than that of C. kamschaticum and the shoots remain available to fall.

2) Hy or the blue cohosh feeder also must suffer food shortage in the later season just like P-III by the severe infestation on the host plant. For Hy in Honshu Panax japonicus may serve as a subsidiary food plant in later season if available. S. bryoniaefolius is also fed by newly emerged adults of Hy at Tsuta, Towada (Yasutomi pers. comm.). On the other hand, the behavior of the newly emerged adults of Hy at Ohnuma, the southern Hokkaido, is uncertain. As mentioned earlier, it does not adopt Panax japonicus as the subsidiary host plant. Further, no edible plants have been discovered from the habitat of this population.

3) The phenology of Scopelia japonica shifts earlier than that of other host plants of Hv-complex. It sprouts in early spring but withers by early summer. Then the populations feeding on this plant must confront severe food

shortage in summer and fall. Examination of ovaries of some specimens suggests that HAx, a Scopolia feeder, is well adapted to this phenology of S. japonica (Katakura et al. 1978). But the food plants of newly emerged adults of the Scopolia feeders are unknown. This shifted phenology of Scopolia japonica may be one of the reasons why Hv (V-I) does not use this plant as the obligatory host plant.

2.4. Remarks on the food habits of Hv-complex. Here the food habits of Hv-complex are summarized with some additional comments.

1) Hv-complex as a whole is quite polyphagous, the host plants of which cover many phylogenetically distant plant species.

2) At the species level, the host plants are, however, restricted and different according to the species of the beetles: Hv= actually a potato feeder, previously solanaceous and/or cucurbitaceous plant feeder, Hp= thistle or thistle and blue cohosh feeder, Hn= thistle feeder, Hy= blue cohosh feeder.

3) In most cases, each population except for those in fields primarily depends on only one kind of plant throughout the year. However, utilization of subsidiary host plants is fairly common.

4) Adult beetles, and perhaps only the adults, can feed on and survive with many plants other than host species when the latter is unavailable. These edible plants belong to

diverse plant families but apparently restricted to only a part of plants growing in and around the habitat of the beetles.

5) Utilization of diverse subsidiary host plants by various populations and plasticity in food utilization clearly show a considerable potential ability of these beetles to overcome the change of food resource.

These facts must be kept in mind when we consider the host shift within Hv-complex, which certainly happened in the past and presumably performed a very important role for the speciation in the group.

Finally the host plants of the common ancestor of Hv-complex are assumed here. The subfamily Epilachninae is unique among Coccinellidae in that all species involved are considered to be phytophagous. Although little is known as to the exact host plants of each species except for the pest species, existing records are sufficient in assuming that the Epilachninae as a whole has a strong connection to solanaceous and cucurbitaceous plants. For example, Schilder and Schilder (1929), who compiled previous records on the food habits of Coccinellidae, concluded that among 24 species of Epilachninae examined, nine species were feeders of solanaceous plants, six of Cucurbitaceae, three of both Solanaceae and Cucurbitaceae, and each two of Graminae, Leguminosae and Malvaceae. Kapur (1950) referred to the food plants of twelve species of Epilachninae: Four species on Solanaceae, three on Cucurbitaceae, each two on Graminae and

Leguminosae and one on Verpenaceae. Gordon (1975) mentioned that 16 American species of Epilachninae were collected from Solanaceae, four from Cucurbitaceae, one or two from Compositae and each one on Aristolochiaceae and Leguminosae. On the other hand, thistle (Compositae), blue cohosh (Berberidaceae), Chelidonium japonicum (Papaveraceae) and Panax japonicus (Araliaceae), all being the host plants of the members of group B, are quite exceptional as the host plants of Epilachninae. Therefore, it is reasonable to regard that the food habit of Hv is a generalized nature of the Epilachninae while those of the most members of group B are derived. Utilization of solanaceous plants by diverse members of Hv-complex as main or subsidiary host plants supports this interpretation.

IV. REPRODUCTIVE ISOLATION

Two species in Hokkaido (Hp and Hv) and western Honshu (Hn and Hv) and three species in the southernmost part of Hokkaido to central Honshu (Hn, Hy and Hv) are sympatric with each other. We can collect two or three species in a same area from different kinds of plants. For example, in the preserved forest at Maruyama, Sapporo, Hokkaido, thistle, blue cohosh and Scizopepon bryoniaefolius often grow side by side, where Hp (P-III) feeds on thistle and blue cohosh while Hv (V-II) on S. bryoniaefolius. At Ohnuma, southernmost Hokkaido, Hy feeds on blue cohosh in the forest, Hn (N-I) on thistle growing mainly along the forest margin and Hv (V-II) on potato at the adjacent field. Similar situations could be seen at Togakushi, Towada, Kiso-Hirasawa and many other localities in the course of collections of the material used in this study (cf. Fig. 10 and Appendix). Thus, their sympatry is, by the definition by Grant (1977), a biotic sympatry but not a neighbouring one. Although the main host plants of these sympatric species are different, their food habit difference is not so enough to isolate them completely under natural conditions. Mixed populations of the thistle feeder (Hp or Hn) and Hv are often observed in the potato fields adjacent the habitat of the thistle feeder. Further, though known only from one locality, a mixed population of

P-III and V-II on Solanum megacarpum was discovered (cf. p. 47, Fig. 155). Hv and Wt form mixed populations in potato fields along their distribution limits. No karyological difference was observed at least between Hp and Hv (Yosida 1948). According to Yasutomi (1954, 1966b), Hp and Hv, as well as Wt and the thistle feeders (Hn, Hp) could successfully produce fertile F_1 hybrids and their F_2 grew normally under laboratory conditions. Takenouchi (1955) observed no cytological anomalies in the meiotic process of the F_1 between some local populations of Hv and Hp. We also obtained F_1 between Hp and Hv (V-I x P-II, V-II x P-III) (Katakura and Nakano 1979), F_1 and F_2 between Hy (Ohnuma) and Hp (P-III, Sapporo), and F_1 between Hv (V-I) and Wt (Katakura unpubl.). Nevertheless, these sympatric species seem to maintain each morphological and biological properties in natural conditions. The hybrid like individuals are very rare even in the mixed populations, though intensive hybrid analysis has not been made yet. Among the material examined by me, one male specimens collected at a potato field in Chipaberi, Rumoi, Hokkaido, is regarded as the hybrid between P-II and V-II. Some P-III like individuals intermingled with P-II previously reported by me (Katakura 1974b) might also be hybrids of P-II and V-II. Hybrid like individuals between V-II and P-III were also collected from Solanum megacarpum at Nopporo with a very low frequency (Nakano, pers. comm.).

These facts suggest that some mechanisms effectively isolate these sympatric forms. Recently we have preliminarily

studied the isolating mechanisms in a sympatric combination of Hv (V-II) and Hp (P-III) (Katakura 1976a, Katakura and Nakano 1979). The results are summarized as follows:

- A) Factors reducing the encounter of Hv (V-II) and Hp (P-III)
1. Phenological difference between V-II and P-III.
 2. Phenological difference between P-III and the host plants of V-II (possibly associated with the post-imaginal conditioning of P-III to its host plants).
 3. Difference of food plant.
- B) Factors reducing the occurrence of hybrids after the casual encounter
4. Incomplete, but positive sexual isolation.
 5. Low hatchability of eggs produced by the heterogamic mating (gametic isolation?).

Some comments are added to these factors:

1) Difference of food habits: P-III mainly depends on thistle and blue cohosh growing in and around forests, while V-II on potato in fields and on Schizopepon bryoniaefolius in forests. P-III can complete its growth with the host plants of V-II, namely potato and S. bryoniaefolius, but V-II can not complete the growth with the host plants of P-III, i.e., thistle and blue cohosh. The entry of V-II into the habitat of P-III is, therefore, nearly completely unsuccessful by the host plant specificity, though the

reversed entry by P-III may be successful.

2) Phenological difference: Two sorts of phenological difference are involved (cf. Fig. 156). First, the appearance of post hibernating adults of P-III is about four weeks earlier than that of V-II in and near Sapporo, though the time of disappearance of the beetles in fall is synchronous. This difference apparently reduces the chance of encounters between V-II and P-III in the earlier season when copulation mainly takes place. Second, phenology of P-III or V-II and their respective host plants well coincide with each other. Consequently, potato and S. bryoniaefolius become available for P-III three or four weeks after the appearance of the latter, while thistle and blue cohosh precede the appearance of V-II. The entry of P-III into the habitat of V-II may be restricted by the phenological difference between P-III and the host plants of V-II. If conditioning to the host plants of P-III is made by P-III before the sprouting of the host plants of V-II as was suggested by Hinomizu (1976a), the role of this isolation is fairly important.

3) Sexual isolation: Sexual isolation of V-II and P-III was studied by means of male multiple choice method. The sexual isolation is not complete, but statistically significant positive choice is observed in either combination (Table 9). Although the actual effect of sexual isolation under various natural conditions is unknown, it certainly decreases the frequency of heterogamic mating at casual encounter.

4) Low hatchability of eggs produced by heterogamic mating (Table 10): In eggs laid by adults not mated before experiment, the hatching ratio was distinctly lower in eggs from heterogamic pairs (mean ca. 4%) than those from homogamic pairs (mean ca. 70% or more), though hatched hybrid larvae could grow normally. The cause of this low hatchability is unknown but presumably the gametic isolation is in operation. Hatching ratio of eggs laid by females mated with heterogamic males in the laboratory but presumably already mated with homogamic males in fields before the experiment were intermediate, though variable, between those of homo- and heterogamic pairs of newly mated adults, but almost all of the obtained offspring were conspecific with the mother. Namely, if a female mated with both homogamic and heterogamic males successively, the produced offspring may be mostly conspecific with the mother and the occurrence of the hybrids may be rare.

From the combination of these factors the rare occurrence of the hybrids in natural conditions is explainable, though any of which alone can not isolate V-II and P-III completely and some other unknown factors may strengthen the isolation.

Existing items of evidence suggest that difference in food habits and phenology probably acts in some degree as the isolating mechanism of other sympatric combination of Hv-complex. On the other hand, we have still little information on the sexual isolation, hatching ratios, and other

possible factors which may act as the isolating mechanisms. These aspects must be one of the most important and fruitful, but so far poorly explored fields of the study of Hv-complex.

V. TAXONOMIC CONSIDERATIONS

As mentioned in a previous chapter, groups A and B are clearly separable by many, though subtle, morphological differences. Obviously they are two distinct taxa within Hv-complex. It must be mentioned, however, that the difference between A and B is far little than the difference among most other species of epilachnid ladybirds. As to group A, it is almost certain that only one species, H. vigintioctomaculata, is involved, judging from geographic distribution, form differentiation, food habits and stable morphological characters. On the other hand, group B is more heterogeneous. This group offers two problems which require further consideration: 1) Splitting of group B into three species, and 2) treatment of unsettled populations. These items are discussed separately below.

1. Recognition of three species in group B

First the conspecificity of the members within each "species" is examined.

Hp: Four local forms of Hp being morphologically very distinct are linked with each other by intermediate forms at the boundary zones (Fig. 151). They might be ranked as subspecies, but apparently belong to a single biological

species. Their variation in morphology and food habits is entirely continuous.

Hn: Geographic variation in the external features of Hn is not exactly known yet. However, the geographic replacement of the forms seems to be similar to that of Hp as far as its tentatively defined three local forms are concerned. The distribution range of N-I is divided into Hokkaido and Honshu by Tsugaru strait but the morphological difference between N-I in the southernmost part of Hokkaido and that in northernmost Honshu is much smaller than the difference between N-I and N-II or N-II and N-III. Some variation of the food habits of Hn seems also to be continuous. These facts support that the populations lumped under the name Hn are regarded to be conspecific.

Hy: Hy is unique among group B by virtual absence of geographic variation in elytral shape. Hy is also split by Tsugaru strait into two isolate populations. Some biological difference is observed between them: Hy in Honshu adopts Panax japonicus as the subsidiary host plant, but Hy in Hokkaido does not. It is reasonable to regard them as infraspecific groups, namely races, of a single species.

Thus it is concluded with sufficient reasons that the members included in Hp are conspecific and, for the lack of negative evidence, that the members of Hn and Hy are each conspecific, regardless the splitting of group B into three species is valid or not.

Hy and Hn keep both biological and morphological

differences despite they are sympatric over a wide range. This strongly suggests that Hy and Hn are reproductively isolated with each other sufficiently. Therefore, group B behaves as one species in the north while two in the south. This group behaves again as one species in the western Honshu due to the absence of the cohosh feeder there. The relation of one northern and two southern species is very complicated. The following three cases are assumed to explain the situation.

Case 1: Actually three biological species are involved.

Case 2: Hy and Hp are conspecific; Hn is another biological species.

Case 3: Hn and Hp are biologically conspecific, Hy is a separate species.

Some characteristics of the three "species" of group B are considered here (Table 11).

1) Disjunctive distribution of Hp and Hn (Fig. 154) is disadvantageous for Case 3. When Hp and Hy are proved to be contiguous in the further study, this favors conclusively Case 2; while when Hp and Hy are disjunctive, the distribution pattern of the three species may favors Case 1.

2) The host plants of Hn and Hy are different with each other. The former mainly depends on thistle while the latter on blue cohosh. Hp (at least P-III) occupies an intermediate position between Hy and Hn in its host plant. However, Hn may be closer to Hp in food habits when the results of rearing tests are taken into account. At least part of Hn

could complete its growth with blue cohosh while Hy could not grow with thistles. Food habits may be advantageous for Case 3.

3) An intermediate body size of Hp can be explained by the food habit difference of the three species (pp. 31~32). It does not exclude any explanations enumerated above.

4) Somewhat deviated WAF and LTT values of Hp (Figs. 144, 145) may favor Case 1.

5) Color difference between Hp and two other species (Tables 2, 3, 5) probably reflects the general trend of geographic color variation in Hv-complex, the northward increase of darker individuals. This tendency does not exclude any other explanations.

6) Body shape of P-III (the southernmost member of Hp) is more similar to Hy than to N-I (the northernmost member of Hn). The smaller individuals of P-III are often difficult to distinguish from Hy. This favors Case 2.

7) Examining variation of some isozymes of Hv-complex, Kuboki (1978) reported that the frequency of an isozymic band named Acph 2 is 0% in Hp (three populations were examined), 25 and 71% in Hy (two populations) and 0 to 86% accompanied with clear northward increase in Hn (eight populations). Then a deep gap is found between Hp and the northern populations of Hn in the frequency of Acph 2. This may be disadvantageous for Case 3.

Thus, Case 1 may be supported by 1) and 4); Case 2 by 1) and 6); Case 3 by 2) while weakened by 1) and 7). None

of these items is conclusive for adoption or rejection of a particular interpretation. Rather, close relationship of the three species of group B seems to arise another possible explanation: Case 4, three species of group B lie on the borderline of good biological species; they are most likely in the process of speciation; Hn and Hy completed reproductive isolation between them but both are not yet fully isolated from Hp.

Anyway, our present knowledge can not decide which interpretation is most likely. Such being the case, the taxonomic solution must inevitably be arbitrary. Two solutions are considered:

S-1: Group B is tentatively regarded as one species with three infraspecific units, Hp, Hn and Hy. In this case, Hp, Hn and Hy can not be treated taxonomically, namely sub-specifically, because such treatise admits polytypic subspecies at one hand (Hn and Hp) and sympatric subspecies at another (Hn and Hy). Three units must bear non-taxonomic names.

S-2: Hn, Hp and Hy are tentatively treated as three separate species.

S-1 leaves many unsolved taxonomic problems and needs further taxonomic revision when the situation is clarified to be one of the cases 1 to 3. On the other hand, S-2 needs the minimum alteration when the situation becomes clear. This is the very reason why S-2 is adopted in this paper. Splitting of group B into three species is thus entirely

tentative, retaining further alterations as follows:

Case 1: Three species, Hp, Hn and Hy.

Case 2: Two species, Hp and Hn; Hy is synonymous with Hp.

Case 3: Two species, Hn and Hy; Hp is synonymous with Hn.

Case 4: Only one species, H. niponica (Lewis), represents group B. Hn, Hp and Hy in this paper will be given appropriate non-taxonomic names. In this case, Hn, Hp and Hy are semispecies of a superspecies H. niponica, or strictly, Hn and Hp, and Hp and Hy behave semispecifically but Hn and Hy behave specifically. This relation of three units may be a special case of circular overlap.

2. Unsettled populations

HAX: HAX is morphologically closely similar to Hy, though somewhat different from the latter in having very swollen but paler spermatheca and conspicuously clavate first antennal flagellomere. Food preference of HAX reported by us (Katakura et al. 1978) is also closely similar to that of Hy (Hoshikawa pers. comm.). HAX may be better treated as a member of Hy and may not be worthy to be treated as a race of Hy. Recently some populations of group B feeding on Scopolia japonica or on both S. japonica and blue cohosh were discovered (Hara and Hamaguchi 1979, Shirai pers. comm., cf. p. 49). Further examination of these populations may

clarify the position of HAx. This population is tentatively separated from Hy by its dependence on S. japonica in wild.

INx: INx is also closely similar to Hy but some noticeable differences are observed between them. Morphologically INx is characterized by relatively slender first antennal flagellomere, relatively darker spermatheca and rounded habitus; and biologically by its host plant, Chelidonium japonicum on which Hy can not complete the growth, and inability to complete its growth with Panax japonicus, a subsidiary host plant of Hy in Honshu (Katakura et al. 1978). In INx is a member of Hy the former certainly represents a distinct race of the latter. On the other hand, the above mentioned biological characteristics of INx are rather similar to Wt. Therefore, it is possible to regard INx as a wild type of Wt, though unlike Wt INx is not a pest of potato (Katakura et al. 1978). Since only one population is available now, further study is needed on the distribution and biology of Chelidonium feeder in order to clarify the relation of INx to Hy as well as Wt.

Wt: Wt is indeed enigmatic. Morphologically Wt is considered as a member of group B by the general appearance. Sometimes, however, Hv like conditions appear in elytral maculation and shape of first antennal flagellomere. In IOD/PRW and HDW/PRW, Wt is divided into two populations, wild and field, of which the former is typically group B while the latter rather resembles Hv (Figs. 146~149). Habitus of Wt is of the basic shape, and similar to Hy, but

body size is somewhat larger than Hy. Wt is a pest of potato. Although its wild host plant is still uncertain, blue cohosh, Scopolia japonica and Chelidonium japonicum are suspected to be such (pp. 49, 53). Wt is similar to INx by its acceptance of Chelidonium japonicum, virtual rejection of Panax japonicus and completion of growth with thistle by some larvae.

Relation to HAx as the Scopolia feeder is also not ignored. Wt is parapatric with Hv with a narrow transitional zone. In this transitional zone Wt and Hv intermingled with each other in various degrees. Such distribution pattern is unique among group B because other members of group B are mostly sympatric with Hv.

As far as the morphological and biological evidence are concerned, Wt is now considered to be closest to INx. The following picture may explain the origin and some morphological deviations of field populations of Wt: Proto-Wt was a member of group B like INx, HAx or wild populations of Wt. Following the cultivation of potato, some populations of proto-Wt invaded the fields and established there as a pest. Hv also became a pest of potato and at some parts of their distribution ranges, Hv and proto-Wt coexisted in the same fields. Occasional breakdown of some ecological isolating factors in the fields resulted in the introgression of Hv genes into proto-Wt resulting in the nowadays field populations of Wt.

To test this assumption, the following items should be studied in detail: Confirmation of the wild host plant(s) of

Wt, especially the survey for the populations depending on blue cohosh, Scopolia japonica and Chelidonium japonicum in and adjacent to the distribution range of Wt is important; degree and extent of isolating mechanisms between Hv and Wt at their sympatric zones. These studies are now in progress in our laboratory.

3. Taxonomic summary

Summarizing previous chapters and above discussion, Hv-complex is taxonomically arranged as follows:

Henosepilachna vigintioctomaculata complex

Group A

H. vigintioctomaculata (Motschulsky)

Group B

H. pustulosa (Kôno)

H. niponica (Lewis)

H. yasutomii sp. nov.

Formae incertae sedis: Western Tokyo form
and two unsettled populations (HAX,
INx)

Interrelationship of the members of Hv-complex is shown in Fig. 157 and the presumable phylogenetic relation in Fig. 158.

Recently Kuboki (1978) discussed the phylogenetic relation of the members of Hv-complex based on the variation

analysis of an isozyme, acid phosphatase. According to him, Hv was distant from other members by some isozymic properties and among the members other than Hv, Hy and Wt (his Hc and Ht, respectively) were most affinitive with each other. My interpretation on the phylogenetic relation agrees with his result in these points. As to Hp and Hn, however, his interpretation involves some ambiguities. He treated Hp and Hn as a single unit (as Hp), nevertheless he found a significant difference between them. If Hp and Hn were treated as separate units in his discussion, the resulting phylogenetic arrangement should be considerably different from that given by him (Kuboki 1978, p. 256, Fig. 6).

VI. DESCRIPTIONS

Remarks

- 1) General features of the members of Hv-complex are given in p. 8.
- 2) Synonymic lists cite only the original description and some important papers.
- 3) Values of measurements and ratios: PRW of all wild bred individuals combined, min.~(range of means of samples)~max., of dissected specimens only the range of means of samples, where arithometric mean for measurement and geometric mean for ratio.
- 4) Collection data are represented by the code numbers of samples given in Appendix, except for those of type specimens.
- 5) Habitus: Only the deviation from the basic shape is pointed out. Detailed descriptions of various forms are already given in pp. 24~30.

Group A

Only one species, Henosepilachna vigintioctomaculata (Motschulsky), is included.

Henosepilachna vigintioctomaculata

(Motschulsky, 1857)

Epilachna vigintioctomaculata Motschulsky, 1857, Etud. Ent. 6: 40 (Japan: Shimoda, Zool. Mus. Moscow Lomonosov state Univ.); Lewis, 1896, Ann. Mag. Nat. Hist. Ser. 6, 17: 24; Mader, 1927, Evidenz.: 35, pl. 1; Bielawski, 1960, Annales Zoologici 18: 2~6.

Henosepilachna vigintioctomaculata, Li and Cook, 1961, Pac. Ins. 3: 48~50 (partim); Sasaji, 1971, Fauna Japonica Coccinellidae: 311~314 (partim).

Epilachna niponica, Dieke, 1947 (nec Lewis, 1896), Smithsonian Misc. Coll. 106: 50~54.

Unique species of group A, separable from the members of group B by elytral spot pattern, leg coloration, shape and structure of male tergite X, shape of first antennal flagellomere, shape and color of spermatheca as given below.

PRW (wild bred total): ♂ 2.71~(3.03~3.59)~3.79mm, ♀ 2.80~(3.17~3.68)~3.91mm. Habitus polytypic with three local forms, V-I, V-II and V-III. V-I and V-III, basic shape; V-II somewhat deviated from basic shape (Figs. 116, 126, 135); three forms also different in size (Fig. 141) and some color characters (Tables 2~4); all continental specimens examined possessing basic shape. Elytral persistent spots larger than non-persistent ones; spot 1 subtriangular, not or only partly fused on suture; spot d small, not or only partly fused on suture; spot 6 large, elongate and curved (Figs. 13~

18). Pronotal pattern A to K, mostly I to J (Table 2, Fig. 11). Hind leg mostly with a black marking on femur; femoral color A to F, most frequently C (Table 3). First antennal flagellomere rod shape and uniformly divergent apically (Figs. 29~40). Male tergite X with hind margin angulate or subangulate; margin of inner depression very distinct (Figs. 64~71). Spermatheca sausage shaped or slightly swollen apically, transparent or partly colored (Figs. 92~97, Table 4). Measurements for dissected specimens: PRW ♂ 3.03~3.59mm, ♀ 3.17~3.73mm; HDW ♂ 1.50~1.70mm, ♀ 1.55~1.76mm; IOD ♂ 0.93~1.07mm, ♀ 0.95~1.11mm; LAF ♂ 169~200 μ , ♀ 170~218 μ ; WAF ♂ 60~70 μ , ♀ 61~72 μ ; WTT (male) 0.67~0.79mm; LTT (male) 0.36~0.44mm; HDW/PRW ♂ 0.46~0.50, ♀ 0.46~0.49; IOD/PRW ♂ 0.28~0.31, ♀ 0.28~0.31; WAF/LAF ♂ 0.32~0.40, ♀ 0.32~0.41; LTT/WTT (male) 0.51~0.63.

Main host plant: Potato (Solanum tuberosum L., Solanaceae). Also on Schizopepon bryoniaefolius Maxim. (Cucurbitaceae) in mainland of Hokkaido.

Distribution: Cool temperate eastern Asia: Amur, Ussuri, North China (including Manchuria), Korean Peninsula, Saghalin, Kunashiri (the southern Kuriles), Japan (Hokkaido, Honshu, Shikoku, Kyushu).

Specimens examined: Many specimens from Japan, Saghalin and continental Asia. Sample Nos., 1~33, 86~111.

Remarks: Examining Motschulsky's type preserved in the Zoological Museum of the Moscow Lomonosov State University, Bielawski (1960) redescribed Epilachna vigintioctomaculata

and designated the lectotype. The lectotype was further examined in detail by Chûjô (1975). According to Chûjô, the lectotype was indubitably Hokkaido form of H. vigintioctomaculata (V-II in this paper). By the courtesy of Prof. Chûjô I also had an opportunity to examine the lectotype and agreed with his interpretation. Problems still remain on the type locality, Shimoda, situated outside the distribution range of H. vigintioctomaculata and far apart from the area occupied by V-II. Chûjô (1975) assumed that the lectotype specimen collected by O. A. Goschkevitch might be collected during his stay in Hakodate situated at the southernmost part of Hokkaido where he visited prior to Shimoda. Dieke's Epilachna niponica is exactly H. vigintioctomaculata s. str. as he supposed himself (Dieke 1947). H. vigintioctomaculata by Li and Cook (1961) and Sasaji (1971) is virtually synonymous with H. vigintioctomaculata complex in this paper.

Group B

Three species and all unsettled populations are included. Separable from H. vigintioctomaculata or group A by the following features common to all members:

Elytral persistent spots in general subequal or slightly larger than non-persistent spots; spot 1 more elongate than in group A, fused on suture; spot d larger, entirely

fused on suture; spot 6 smaller and elliptical (Figs. 19~28). Most part of hind femur generally black (Table 3). First antennal flagellomere clavate, more or less swollen apically (Figs. 41~63). Male tergite X with hind margin rounded or flat; margin of inner depression indistinct (Figs. 72~90). Spermatheca more or less swollen apically, partly or entirely colored (Figs. 98~109, Table 5).

As discussed before, separation of three species in group B was made rather conveniently. Further study may or may not unite H. pustulosa with either H. niponica or H. yasutomii. For the time being, they are treated as distinct species and described below. Unsettled populations already discussed in pp. 71~74 are not treated here.

Henosepilachna pustulosa (Kôno, 1937)

Epilachna pustulosa Kôno, 1937, Ins. Matsumurana 11: 99, fig. 1 (Japan: Hokkaido (Soeushinai, Uriu and Teshio). Ent. Inst. Hokkaido Univ.).

Henosepilachna vigintioctomaculata, Li and Cook, 1961, Pac. Ins. 3: 48~50 (partim); Sasaji, 1971, Fauna Japonica Coccinellidae: 311~314 (partim).

Darkest species of group B. Separable from other members of group B by its darker color, relatively wide first antennal flagellomere and relatively long male tergite X. Allopatric with other members of group B.

PRW (wild bred total): ♂ 2.81~(3.20~3.52)~3.77mm, ♀ 2.80~

(3.36~3.67)~4.03mm. Habitus geographically quite variable with four local forms: P-III', P-I, P-II and P-III. All forms more or less deviated from basic shape (Figs. 117~120, 127, 129, 136, 137). Pronotum nearly entirely black, patterns JK~KL (Table 2). Hind leg black except apical end of femur and tibia; femoral color H (Table 3). First antennal flagellomere wide and distinctly swollen apically (Figs. 41~45, 144). Male tergite X on the average narrower and longer than in other members of group B (Fig. 145); margin of inner depression more distinct than the other members (Figs. 72~75). Spermatheca nearly entirely dark brown (Figs. 98, 99, Table 5). Measurements for dissected specimens: PRW ♂ 3.24~3.51mm, ♀ 3.43~3.65mm; HDW ♂ 1.61~1.73mm, ♀ 1.71~1.79mm; IOD ♂ 1.01~1.09mm, ♀ 1.08~1.17mm; LAF ♂ 174~198 μ , ♀ 194~206 μ ; WAF ♂ 75~82 μ ; ♀ 80~86 μ ; WTT (male) 0.67~0.74mm; LTT (male) 0.43~0.49mm; HDW/PRW ♂ 0.49~0.50, ♀ 0.48~0.50; IOD/PRW ♂ 0.31~0.32, ♀ 0.30~0.32; WAF/LAF ♂ 0.39~0.43, ♀ 0.39~0.44; LTT/WTT (male) 0.61~0.71.

Main host plant: Thistles (Cirsium spp., Compositae). Some populations also fed on blue cohosh (Caulophyllum robustum Maxim., Berberidaceae).

Distribution: Japan (Hokkaido except the southernmost part).

Specimens examined: Sample Nos. 34~43.

Henosepilachna niponica (Lewis, 1896)

Epilachna niponica Lewis, 1896, Ann. Mag. Nat. Hist.

ser. 6, 17: 23~24 (Japan: Nikko and Miyanoshita. British Mus. (Nat. Hist.)) (nec Dieke, 1947).

Henosepilachna vigintioctomaculata, Sasaji, 1971, Fauna Japonica Coccinellidae: 311~314 (partim).

Largest species of group B. Separable from H. pustulosa by its paler color, relatively long first antennal flagellomere and relatively wide male tergite X, from H. yasutomii by its large size and elytral shape, and also by host plant. Allopatric with H. pustulosa, sympatric with H. yasutomii.

PRW (wild bred total): ♂ 2.86~(3.36~3.66)~3.98mm, ♀ 2.92~(3.49~3.83)~4.08mm. Habitus polytypic with at least three forms, N-I, N-II and N-III. N-III with basic shape while other two forms considerably deviated from basic shape (Figs. 121~123, 130 132). Pronotal spot pattern E to KL, mostly I to J (Table 2). Hind leg with color variable but femur black at least medially; femoral color D to H (Table 3). First antennal flagellomere relatively long (Figs. 46~51, 144). Male tergite X on the average wider than H. pustulosa (Fig. 145), margin of inner depression often undetected (Figs. 76~79). Spermatheca partly to nearly entirely dark colored (Figs. 100~102, Table 5). Measurements for dissected specimens: PRW ♂ 3.38~3.80mm, ♀ 3.54~3.94mm; HDW ♂ 1.64~1.81mm, ♀ 1.71~1.87mm; IOD ♂ 1.03~1.14mm, ♀ 1.09~1.21mm; LAF ♂ 191~232 μ , ♀ 196~223 μ ; WAF ♂ 74~82 μ , ♀ 72~86 μ ; WTT (male) 0.71~0.81mm; WTT (male) 0.41~0.48mm; HDW/PRW ♂ 0.48~0.50, ♀ 0.47~0.49; IOD/PRW ♂ 0.30~0.32, ♀ 0.30~0.32; WAF/LAF ♂ 0.34~0.41, ♀ 0.34~0.40; LTT/WTT (male) 0.56~0.64.

Main host plant: Thistles (*Cirsium* spp.).

Distribution: Japan (Honshu and the southernmost part of Hokkaido).

Specimens examined: Sample Nos. 44~62.

Lectotype (Figs. 159~161): Female? Body length 7.8mm, body width 6.7mm, pronotal width 3.7mm. Head medially with a black marking. Pronotal spot pattern typically I, namely with five spots. Scutellum black. Elytra with full 28 spots; spot l fused on suture at anterior two third, spot d entirely fused on suture. Elytra slightly expanded near apex, without tubercles, sharply curved and apex projected postward in profile. Mounted on a cardboard piece of which underside bearing handwritten letters "Nikko" or "Nikk". Labels attached to the specimen are (cf. Fig. 161): SYNTYPE; Japan. G.Lewis. 1920-320.; Nikko; *Epilachna niponica* Lewis (handwritten). Ventral side of this specimen could not be examined. Sex was determined by the condition of visible last abdominal sternite which was seemingly split seen from postward.

Remarks: *Epilachna niponica* Lewis had long been considered as a junior synonym of *Henosepilachna vigintioctomaculata* (Motschulsky). Examination of the syntypes revealed, however, that the name *niponica* Lewis can be assigned to certain members of group B. Six syntypes of *Epilachna niponica* Lewis all from Japan are now preserved in the British Museum, Natural History, which consist of three specimens from Nikko, two from Miyanoshta and one from

Junsai Lake (Pope, pers. comm.). Each two specimens from Nikko and Miyanoshita were examined by Chûjô (1968). According to him, two Nikko specimens were Honshu form of the thistle feeder (H. pustulosa in the previous sense and N-II of niponica in the present paper) and two Miyanoshita specimens were Western Tokyo form (Tokyo Seiko form by Chûjô). Dr. Pope of the British Museum, Natural History, kindly gave me an opportunity to examine the remaining two specimens, one from Nikko and another from Junsai Lake, as well as one of the Miyanoshita specimens already examined by Chûjô (op.cit.). The Nikko and Miyanoshita specimens were again identified respectively with Honshu form of the thistle feeder and Western Tokyo form (Figs. 159, 160, 162). On the other hand the specimen from Junsai Lake (Fig. 163) was identified with H. vigintioctomaculata by its general appearance, especially by its elytral maculation. Further, the Junsai Lake specimen is very probably mislabelled because it has a basic elytral shape which is common to vigintioctomaculata form V-I, III, but so far never discovered from the mainland of Hokkaido where Junsai Lake is located. H. vigintioctomaculata from mainland Hokkaido (V-II) is easily separable from others (V-I, V-III and continental specimens) by the elytral shape. In the original description of Epilachna niponica, Lewis (1896) enumerated Nikko and Miyanoshita as the type localities, though the occurrence of the species in additional two localities, Junsai Lake and Fusan in Korea, were referred to, writing "Hab. Nikko and Miyanoshita".

shita. Also found near the Junsai Lake feeding on a species of Physalis, and usually resting on the underside of the leaves. Fusan (Leech)." Then the Junsai Lake specimen should not be regarded as a syntype member of E. niponica simply because it was not collected from the type localities and because some ambiguities as to the provenance. Consequently, the lectotype should be chosen from Nikko and Miyanoshita specimens. Taxonomic position of Western Tokyo form is still uncertain and the lectotype designation of either of Miyanoshita specimen may give further taxonomic troubles. From these reasons I selected a Nikko specimen as the lectotype of E. niponica as designated above. Only two other Nikko specimens examined by Chûjô (1968) should be regarded as the paralectotypes.

Henosepilachna yasutomii sp. nov.

Smallest species of group B. Separable from H. pustulosa by its paler color, relatively narrow first antennal flagellomere and relatively wide male tergite X, from H. niponica by its small size and elytral shape, and also by food plant.

Allopatric with H. pustulosa, sympatric with H. niponica.

PRW (wild bred total): ♂ 2.66~(2.93~3.38)~3.39mm, ♀ 2.75~(3.04~3.34)~3.51mm. Habitus monotypic, basic shape. Pronotal spot pattern HI to KL, mostly IJ to JK (Table 2). Hind leg with color variable but at least femur medially black; femoral color E to H, mostly G and H (Table 3). First

antennal flagellomere relatively narrow (Figs. 52~57, 144). Male tergite X on the average wider than H. pustulosa (Fig. 145), margin of inner depression often undetected (Figs. 80~84). Spermatheca of female partly to nearly entirely dark colored (Figs. 103~105, Table 5). Measurements for dissected specimens: PRW ♂ 2.91~3.38mm, ♀ 3.04~3.34mm; HDW ♂ 1.47~1.61mm, ♀ 1.55~1.67mm; IOD ♂ 0.91~0.95mm, ♀ 0.97~1.06mm; LAF ♂ 156~205 μ , ♀ 172~199 μ ; WAF ♂ 66~76 μ , ♀ 69~75 μ ; WTT (male) 0.59~0.73mm; LTT (male) 0.39~0.45mm; HDW/PRW ♂ 0.48~0.52, ♀ 0.48~0.51; IOD/PRW ♂ 0.28~0.32, ♀ 0.30~0.32; WAF/LAF ♂ 0.36~0.42, ♀ 0.36~0.41; LTT/WTT (male) 0.53~0.65.

Main host plant: Blue cohosh (Caulophyllum robustum Maxim.).

Distribution: Japan (Honshu and the southernmost part of Hokkaido).

Specimens examined: Sample Nos. 63~71 including the following type specimens.

Holotype: Male. Body length 6.7mm, body width 5.5mm, pronotal width 3.1mm. Specimen code, TWy810. Tsuta spa, Towada, Aomori Pref., 10 VI 1976, H. Katakura leg.

Paratypes: 9♂♂10♀♀, same data as holotype; 5♂♂5♀♀, Okusha, Togakushi, Nagano Pref., 18 VI 1976, H. Katakura leg.; 10♂♂10♀♀, Ohnuma, Oshima, S-Hokkaido, 9 VI 1976, H. Katakura leg.

Type depository: Zoological Institute, Hokkaido University.

This species is dedicated to Dr. Kazuo Yasutomi, National Institute of Health, Tokyo, one of the pioneer workers of

"Epilachna problem" and, only the person who has studied this group continuously since as early as 1950.

VII. EVOLUTION OF HV-COMPLEX

1. Chological interpretation

In considering the evolution of Hv-complex, some postulates are adopted: A) By the reason mentioned in p. 24, the common ancestor of Hv-complex had a basic elytral shape. This means that the elytral shape other than basic shape are derived either directly or indirectly from the latter. B) The common ancestor of Hv-complex was a solanaceous, or though less probable, a cucurbitaceous feeder (cf. pp. 58~59). C) Straits functioned as effective geographic barriers against the dispersal of Hv-complex.

Next, some comments of the geology of Japan Archipelago in the middle and late Quaternary is mentioned. Main routes of ice age invasions are Korean strait (Korea/Japan) and northern straits, Tatar (continent/Saghalin), Soya (Saghalin/Hokkaido) and Tsugaru (Hokkaido/Honshu) (cf. Fig. 150). According to Minato (1972), all these straits had closed during the Riss ice age. In the later period of Riss, ca. 170,000 years B.P., Korean, Tsugaru and Soya straits opened. Later, Korean and Tsugaru straits closed twice during early and middle main Würm (respectively 27,000 and 20,000 years B.P.) (Fig. 164). Soya had opened during Riss-Würm interglacial age but had closed during main Würm until its final

formation, ca. 12,000 years B.P. The final formation of Tatar strait which had closed from Riss to Würm took place ca. 7,500 years B.P. On the other hand, Ohshima (1976~1977) criticized Minato's interpretation and assumed the final formation of Tsugaru and Korean straits ca. 140,000 years B.P. Anyhow, the relative importance of these straits functioning as geographic barriers is, Korean \neq Tsugaru $>$ Soya $>$ Tatar $>$ Channels now separating three southern mainlands of Japan (Honshu, Shikoku, Kyushu), as far as the period after the final formation of these straits is concerned.

Three forms of Hv are separated one another by distinct geographic barriers, Tsugaru (V-I/V-II) and Rishiri (V-II/V-III) straits (Fig. 150), suggesting the occurrence of form differentiation after the final formation of these straits. Among the three forms of Hv, V-II alone has apparently deviated from the basic elytral shape. No significant difference was observed among V-I, V-III and continental Hv except for some color characters. This suggests invasion of Hv through the southern route in relatively recent age. If the northern route was adopted by Hv, V-II would be more similar to continental populations of Hv, especially of northern areas, than to V-I. Invasion of Hv via the southern route is supported by another evidence. At the present, the northern distribution limit of Hv still does not reach Tatar strait (Fig. 150). Therefore, the northern route could be used by Hv only when under the climate warmer than, and at the sea level lower than the present, which are unlikely

because the lower sea level during ice age mainly resulted from the increased amount of glacier in cooler age. The recent invasion of Hv suggested by the lack of noticeable morphological difference between V-I and the continental Hv indicates the effective functioning of some barriers between the continent and the Archipelago before the invasion of Hv.

On the other hand, Hp and Hn of group B are polytypic. The boundaries of any two adjacent forms of these species always lie inland (Fig. 151). This implies that the mode of form differentiation was different between groups A and B. Since the distribution ranges of N-I and P-III' are respectively separated by Tsugaru and Rishiri straits, formation of these two forms had to be completed before the final formation of the respective strait. Likewise, the dependence on blue cohosh by Hy and on thistles by Hn must have been completed before the final formation of Tsugaru strait. On the contrary, raiation of Hy with respect to the adoption of Panax japonicus as the subsidiary host plant should have established after the final formation of Tsugaru strait. These items strongly suggest that diversification of group B mainly had taken place before the final formation of these straits. This implies a lasting existence of group B in Japan and hence an earlier colonization of this group in the area. It is conceivable that before invasion of Hv into Japan Archipelago, the invasion routes between the continent and the archipelago had been closed and groups A and B had been distributed in the continent and Japan, respectively.

Such an interpretation further requires to estimate the age when the routes between the continent and the archipelago opened, through which group B or its ancestor arrived Japan.

Thus, the following four stages are postulated in the history of Hv-complex.

Stage 1: Colonization of group B or its ancestor in Japan. Invasion routes between the continent and archipelago had opened.

Stage 2: Group A (or its ancestor) in the continent, group B (or the ancestor) in Japan. Invasion routes had closed.

Stage 3: Invasion of group A into Japan. Invasion routes again opened.

Stage 4: From the final formation of the straits to the present. Invasion routes closed.

When we adopt Minato's interpretation on the history of the Japan Archipelago in the later Quaternary age, stages 1 and 3 are estimated respectively to be Riss (170,000 years B.P.) and main Würm (27,000 and/or 20,000~18,000 years B.P.). On the other hand, when we follow Ohshima's opinion, stage 4 started at ca. 140,000 years B.P., but no clear division corresponding to stages 1 to 3 is given from his interpretation. Mainly adopting Minato's interpretation, further discussion on these stages are given below (cf. Fig. 165):

Stages 1 and 2: Common ancestor of Hv-complex originally distributed in the continent colonized Japan at that time when Japan had formed the eastern edge of the continent

(Fig. 165, 1a). There are two alternative interpretations as to the next step. First, if Minato's interpretation is adopted, the continent, southern Japan and northern Japan were simultaneously separated by the opening of Korean and Tsugaru straits at the beginning of stage 2 (Fig. 165, 1a-1b-2c). Therefore, some morphological features characteristic to all members of group B, particularly those showing derived conditions, should have been established by the end of stage 1 in Japan as the continental margin (Fig. 165, 1b). The clavate antennal flagellomere, rounded or flat hind margin and indistinct margin of inner depression of male tergite X and apically swollen spermatheca of group B might be regarded as derived conditions judging from the variability of these characters in group B. Anyway it is hardly accepted that the states of diagnostic characters in group B are all ancestral. Food habits of group B also may have diverged some degree from the continental stock (e.g., beginning of utilization of thistles as the subsidiary host plant, etc.). Consequently the ancestral stock of group B was probably attained the form or form-race level at the end of stage 1 (Fig. 165, 1b). In stage 1, the archipelago was seemingly connected to the continent with relatively narrow land bridges. Probably the archipelago was more humid and warmer than the continent. The restricted gene flow between the continent and archipelago stocks and different climatic conditions in the two areas might facilitate the divergence of the archipelago stock. At the beginning of stage 2, the archipelago was separated

from the continent by the formation of Korean strait. At the same time, the ancestral stock of group B segregated in two isolates, southern Japan (group B-S) and northern Japan (group B-N) stocks, by the formation of Tsugaru strait (Fig. 165, 1b-2c). On the other hand, if we can postulate that the formation of Korean strait had considerably preceded that of Tsugaru strait, though it lacks any geological evidence, the explanation of the situation is more easy as follows (Fig. 165, 1a-2a-2b-2c): Group B had attained the common derived features during the opening of Korean strait and that of Tsugaru strait (Fig. 165, 2c). This group was later subdivided into groups B-N and B-S by the formation of Tsugaru strait (Fig. 165, 2c). At any rate, after the formation of Tsugaru strait the continental (group A), southern Japan (group B-S) and northern Japan (group B-N) stocks never intermingled throughout stage 2 (Fig. 165, 2c and 2d). Climate fluctuated considerably during this stage, which must have resulted in the periodical change of vegetation. Under such circumstance, the group B-N and mountainous populations of group B-S tended to be isolated to small demes. This should facilitate the form differentiation in group B, especially in northern and mountainous southern areas. Nowadays Japanese flora suggests that wild solanaceous plants (excluding crops and weeds) are adapted to more warmer climate than thistles or blue cohosh in this area. If it is accepted, such fluctuation of environment in ice age also might strengthen shift of food habits from solanaceous feeder to the

feeder of their plants such as thistle or blue cohosh especially in the cooler age. Similar phenomenon might happen in the continent. However, northern or mountain populations isolated in cool age would soon intermingle with the southerly retreated mother populations in the subsequent warm age in the continent. Form differentiation as assumed as to the archipelago stock may be difficult under such circumstance. Speciation of the continental stock (group A) and the archipelago stock (group B) and at least Hn and Hy of group B completed by the end of stage 2 (Fig. 165, 2d).

Stage 3: The continent and the archipelago again fused (Fig. 165, 3). Hv still depended on wild solanaceous plant(s) newly invaded Japan via the southern route. Counter invasion by group B to the continent did not occur or occurred but unsuccessful. The southern stock of group B (group B-S) invaded the southernmost part of Hokkaido (Hn). Hp represents group B-N. As to Hy, two possibilities exist: a) Hy is another member of group B-S invaded with Hn the southernmost part of Hokkaido; or b) Hy is a southern representative of group B-N invaded Honshu in this stage. At the present, it is difficult to decide which interpretation is more likely. However, the following story adopting the second interpretation might be the case: At the end of stage 1 (Fig. 165, 1b) or the earlier stage 2 (Fig. 165, 2b), group B was a facultative or obligatory thistle feeder. Group B was divided into groups B-N and B-S by the opening of Tsugaru strait (Fig. 165, 2c). Imagine that the nature of thistles available

to group B-N and group B-S were somewhat different. Group B-S utilized the thistle whose phenology was similar to those adopted today by Hn. The thistle provided abundant food throughout the active season of group B-S. On the other hand, group B-N utilized the thistle whose phenology was similar to those adopted by Hp. Then the southern population of group B-N tended to suffer food shortage in fall, especially in cooler years, like nowadays P-III (cf. Fig. 156). During stage 2, therefore, the southern population of group B-N gradually increased utilization of blue cohosh as the subsidiary food. The cohosh feeder was thus established by the end of stage 2 in the southernmost part of the distribution range of group B-N. The newly established cohosh feeder, namely Hy, expanded its distribution southward in stage 3. Another possibility that the sympatric speciation of Hy from Hn or vice versa is not probable because Hy and Hn in their sympatric areas are morphologically distinct.

Stage 4: Final formation of Korean and Tsugaru straits again separated the continent, southern Japan and northern Japan (Fig. 165, 4). Racialization of Hv took place. As to Hv, the northern route was still open but Hv could not use this route by the reason mentioned before. The northern population gradually changed from V-I type (basic shape) to V-II type. There are some problems concerning this interpretation: In the northern district, Soya strait separates the distribution range of V-II into Hokkaido and Saghalin, Kunashiri strait isolates V-II in Kunashiri and Rishiri strait

separates V-II and V-III (Fig. 150). This distribution pattern could well be explained if Rishiri strait opened earlier than the other two. However, among these straits Rishiri and Soya are estimated to be opened approximately at the same geological time while Kunashiri strait opened far earlier than the other two. Then the occurrence of V-II in three isolated areas (Hokkaido mainland, Saghalin, Kunashiri) as well as the occurrence of V-III in Rishiri and Rebun Islands needs explanation. Three cases are possible: 1) The northern population of Hv had attained V-II level when Kunashiri strait opened. Subsequent opening of two other straits isolated the populations of V-II in Saghalin and Rishiri-Rebun Islands, too. Later the population in Rishiri and Rebun Islands retrogressed from V-II to V-III. 2) At the final formation of Kunashiri and Soya straits Hv did not reach Kunashiri and Saghalin, respectively. Only the final formation of Rishiri strait isolated Hv in Rishiri and Rebun Islands from that in the mainland of Hokkaido. Northern population of Hv had become V-III level at this moment. The population in the mainland of Hokkaido later became V-II and was introduced in Kunashiri and Saghalin by human activities. 3) At the final formation of these straits, the northern population reached V-III level. After then three populations of Hv isolated in the mainland of Hokkaido, Saghalin and Kunashiri independently attained a similar shape, V-II. Among these three explanations, case 3 is less likely in assuming a parallelism between three local populations.

Case 1 is also unlikely because V-III shows an intermediate condition not only in elytral shape but also in some color characters. Consequently, case 2 is most likely. V-I is distributed on Sado Island off Honshu and V-II in Okushiri Island off the southern Hokkaido. These islands are, however, considered to be never connected to the mainlands, Honshu and Hokkaido respectively, throughout the mid and late Quaternary age. Hv in these islands must have been brought artificially in the recent time, probably accompanied with the agricultural activity as in case of Kunashiri Island or Saghalin, when the above interpretation on invasion and form differentiation of Hv is accepted. Three forms of Hv, as well as the continental stock, independently became pests of potato in the recent age.

2. Biological aspects of evolution of Hv-complex

Finally some biological aspects in the evolution of Hv-complex are mentioned.

In the course of the evolution of Hv-complex, speciation occurred at least twice, i.e., the speciation of groups A and B and that of Hn and Hy. In both cases, the speciation was accompanied by shift of food plants and presumably underwent allopatrically. The evolution of Hv-complex may be said to be characterized by the allopatric speciation accompanied by shift of food plants. My interpretation on

the history of Hv-complex well agrees with the allopatric model of host race formation proposed by Mayr (1963) in explaining frequent occurrence of sympatric host races or sibling host-specific species in insects and other invertebrates.

The role of food plant difference in the sympatric species of Hv-complex is twofold, one is its function as a premating isolating mechanism, and another is that it enables the coexistence of two or three species in the same area. Imagine that group A and group B, as well as Hn and Hy, encountered without food plant difference, namely they all depended on the same plant species. The resulted situation should be quite dissimilar to that we now have. Judging from the present status of V-II and P-III, isolated by a combination of several factors, each alone being incomplete in effect (cf. pp. 62~65), the sympatric species of Hv-complex would not coexist without food habit difference. Therefore, the crucial point in the evolution of Hv-complex is indubitably in the shift of food plants. Unfortunately, the genetics of the shift of food plants is still unknown in the present case, but only some minor genetic change concerning the host selection may be sufficient at the initial stage of speciation. Bush (1969, 1974, 1975) demonstrated that the sympatric host race formation of Rhagoletis species of fruit flies could be accomplished with only a few genetic alterations. If this is true, alteration or expansion of food plants in marginally isolated populations should be

more easy, because under allopatric model of speciation, such as of Mayr, the necessary genetic change for host selection can be more flexible than that in Bush's sympatric model. The host specific sibling species should also arise under allopatric condition with similarly minor genetic change. Karyological similarity of Hp and Hv (Yosida 1948), the normal meiosis of hybrids between Hp and Hv (Takenouchi 1955) and the easy production of hybrids under laboratory conditions in certain members of Hv-complex suggest that rather a small amount of genetic change, instead of a drastic change, appeared in the speciation process of Hv-complex.

Cause of the host shift in Hv-complex might be functional, as was suggested by diverse pattern of food utilization in the present members of Hv-complex (pp. 53~58). Competition, often stressed to explain the niche expansion or niche shift in many species of animals, might strengthen the shift of sympatric members of Hv-complex after the secondary overlap of their distribution ranges, but would not play the leading role in the initiation of the host shift and diversification of food habits in Hv-complex. Probably the periodic climatic change and resulted vegetational change in ice age facilitated the host shift, and hence the speciation, of certain members of Hv-complex.

SUMMARY

1) The so-called Henosepilachna vigintioctomaculata complex was revised based on both morphological and biological evidence and geographic distributional pattern.

2) Morphological analysis of diverse members of H. vigintioctomaculata complex was made by using 85 Japanese and 26 exotic samples, the former covering most, if not all, of remarkable populations of this group so far known from Japan.

3) Previous records on the geographic distribution, biology and some related aspects of the members of H. vigintioctomaculata complex were compiled with additional data.

4) H. vigintioctomaculata complex was divided into two groups, A and B, based on the morphological analysis.

5) Group A involves only one species, H. vigintioctomaculata (Motschulsky) s. str.

6) Mainly based on the biological evidence and geographic distributional pattern, group B was further subdivided into three subgroups which are tentatively treated as three distinct species, H. pustulosa (Kôno), H. niponica (Lewis) and H. yasutomii sp. nov. Group B also includes some populations whose taxonomic position is still unsettled.

7) H. yasutomii sp. nov. was described and the lectotype specimen of H. niponica (Lewis) was designated together with the redescription of H. vigintioctomaculata (Motschulsky)

and H. pustulosa (Kôno).

8) Chorological interpretation on the evolution of H. vigintioctomaculata complex was presented. The Japanese fauna of this group was considered as an outcome of two successive invasions of the continental stock. Members of group B would be descendants of the earlier colonizer which might be established in Japan in the Riss ice age. Group A would be the later colonizer possibly invaded Japan during the maximum Würm ice age.

9) Evolution of H. vigintioctomaculata complex may be characterized by the allopatric speciation accompanied by shift of food habits or host plants which might be resulted from the adaptation to the changing environment during ice ages.

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Jap. Soc. Syst. Zool., Circular, 34: 1~3. (In Japanese)
- 1973. Recent problems on Epilachna vigintiocto-
maculata complex. Kontyû to Shizen (Nature and Insects),
8 (6): 2~8. (In Japanese)
- 1974a. Notes on the Epilachna vigintioctomaculata
complex. Jap. Soc. Syst. Zool., Circular, 47: 1~4.
(In Japanese).
- 1974b. Food habits and its differentiation
(Henosepilachna vigintioctomaculata complex, etc.).
In "The Behavior and Adaptation of Insects" (C. Oshima
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- 1974c. An unrecorded form of the Epilachna
vigintioctomaculata complex (Coleoptera, Coccinellidae)
from Rebun Island, Hokkaido. Kontyû, 42: 231. (In
Japanese)
- 1976. Notes on the geographical distribution
and host preference in the Tokyo West-suburb form of
Epilachna vigintioctomaculata complex. Kontyû, 44: 111~
114. (In Japanese with English summary)
- 1977a. Problems on the Henosepilachna viginti-
octomaculata complex. Kontyû to Shizen (Nature and
Insects), 12 (11): 14~19. (In Japanese)
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morphology of "Hachimantai form" of Henosepilachna
pustulosa. Reported at the 37th Ann. Meet. Ent. Soc.
Jap., Sapporo.

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APPENDIX

Source of material and the number of specimens examined. Data for each sample is basically given by the following order: Code number for samples throughout all material, Locality (locality code): Number of individuals examined ♂/♀ (ditto, dissected), date collected, collected by (HK=H.Katakura), collected from (P=potato, T=thistle, B=blue cohosh). Samples with asterisk are labo-reared, in which the date and plant designate those of immatures or the parents collected on and from.

Japanese material (cf. Fig. 10)

Henosepilachna vigintioctomaculata, 894 ♂♂ 1236 ♀♀ (147 ♂♂ 169 ♀♀)

- 1) Kushu-ko, Rebun Island, Hokkaido (RE): 50/34 (5/5), 2 ix 1976, HK, P.
- 2) Oshidomari, Rishiri Island, Hokkaido (RI): 11/11 (11/11), 3 vii 1978, K.Hoshikawa, P.
- 3) Yûchi, near Wakkanai, Hokkaido (YC): 6/6 (6/6), 4 vii 1978, K.Hoshikawa, P.
- 4) Kitamoshiri, Hokkaido (KM): 31/25 (5/5), 7 ix 1976, Detani et al., P.
- 5) Kami-Shirataki, Hokkaido (KS): 57/62 (5/5), 3 ix 1976, HK, P.
- 6) Chipaberi, near Rumoi, Hokkaido (CP): 59/42 (5/6), 1 ix 1976, H.Fukuda and HK, P.
- 7) Oasa, near Sapporo, Hokkaido (OA): 63/61 (5/6), 30 viii 1976, HK, P.
- 8) Honbetsu, Hokkaido (HB): 28/31 (5/5), viii 1976, K.Jinbu, P.
- 9) Chihase, Shimamaki, Hokkaido (CH): 5/5 (5/5), 28 vi 1978, T.Kimura and HK, Schizopepon bryoniaefolius.

- 10) Shimofûro, in Shimokita, Aomori Pref. (SF): 46/35 (5/5), 12 viii 1976, HK, tomato and egg plant.
- 11) Takizawa-mura near Morioka, Iwate Pref. (TM): 94/157 (5/5), 8 vi 1976, HK et al., P.
- 12) Yunodai, Mt. Chôkaisan, Akita Pref. (YU): 9/20 (5/5), 11 vi 1976, HK, P.
- 13) Zaô spa, Yamagata Pref. (ZA): 13/12 (5/5), 12 vi 1976, HK, P.
- 14) Seki, Sado Island, Niigata Pref. (SA): 7/4 (7/4), 25 vii 1977, T.Shinbo, tomato.
- 15) Kawamata, Oku-Nikko, Tochigi Pref. (KW): 24/33 (0/0), 5 vi 1978, HK et al., P.
- 16) Tsukuda, Akagi-mura, Gumma Pref. (TK): 26/56 (5/5), 16 v 1976, HK, P.
- 17) Musashiranzan, Saitama Pref. (MR): 57/118 (5/5), 11 v 1976, HK, P.
- 18) Hikawa, Tokyo (HW): 1/1 (1/1), 22 vi 1979, HK, P.
- 19)* Kanmuriwa, Urayama, Chichibu, Saitama Pref. (UK): 4/5 (4/5), 23 vi 1979, HK, P.
- 20) Omukawa, Hakushû, Yamanashi Pref. (HA): 40/64 (5/5), 29 v 1977, HK, P.
- 21) Kasio, Oshika, Ina, Nagano Pref. (OS): 28/69 (5/5), 20 vi 1976, K.Miyazawa and HK, P.
- 22) Kiso-Hirasawa, Narakawa-mura, Nagano Pref. (KH): 29/27 (0/0), 22 vi 1976, HK, P.
- 23) Kiso-Fukushima, Nagano Pref. (KF): 28/68 (5/5), 21 vi 1976, HK, P.
- 24) Takamori, Ina, Nagano Pref. (TA): 17/34 (5/5), 19 vi 1976, K.Miyazawa and HK, P.
- 25) Nonomata, Shôkawa, Gifu Pref. (NN): 22/27 (0/0), 23 vi 1976, HK, P.
- 26) Hokunô, Shiratori, Gifu Pref. (HN): 32/89 (5/5), 31 v 1976, HK, P.
- 27) Sakaguchi and Shimoyogo, Yogo, Shiga Pref. (YG): 20/28 (6/6), 6 v 1976, HK et al., P.
- 28) Kurama, Kyoto (KR): 6/14 (0/0), 2 viii 1976, K.Nakamura,

tomato and egg plant.

- 29) Murou, Nara Pref. (MU): 5/6 (5/6), 5 v 1974, T.Shinbo, P.
 30)* Kumano, Mie Pref. (KN): 3/7 (3/7), vi 1974, T.Shinbo, P.
 31) Sanbe spa, Shimane Pref. (SB): 34/52 (5/5), 29 v 1976,
 HK, P.
 32) Mt. Hikosan, Fukuoka Pref. (HS): 35/28 (5/5), 25 v 1976,
 HK, P.
 33) Namino, Aso, Kumamoto Pref. (AS): 4/5 (4/5), viii 1961,
 Y.Yasue, P.

Henosepilachna pustulosa, 273♂♂292♀♀ (57♂♂56♀♀)

- 34) Hama-Yûchi, near Wakkanai, Hokkaido (HY): 37/40 (5/6),
 1 ix 1976, H.Fukuda and HK, T.
 35) KM (cf. No. 4): 26/34 (5/5), 7 ix 1976, Detani et al., T.
 36) KS (cf. No. 5): 56/55 (6/5), 3 ix 1976, HK, T.
 37) CP (cf. No. 6): 60/57 (5/5), 1 ix 1976, H.Fukuda and HK,
 T.
 38) Mizuho, Higashi-Asahigawa, Hokkaido (MZ): 10/10 (10/10),
 14 vii 1978, Sk.Yamane, T.
 39) Nakanosawa, Sapporo, Hokkaido (NW): 7/11 (6/5), 26 vii
 1977, HK, T.
 40) Nopporo, near Sapporo, Hokkaido (NP): 40/41 (5/5), 27~
 28 viii 1976, HK, T.
 41) Tomari, Shakotan, Hokkaido (TR): a) 6/6 (0/0) from T,
 b) 4/5 (0/0) from Arctium lappa, c) 5/6 (0/0) from P,
 9 viii 1976, Sk.Yamane.
 42) Tomakomai, Hokkaido (TO): 8/9 (5/5), 24 viii 1977,
 H.Hinomizu, T.
 43) CH (cf. No. 9): 14/18 (10/10), 28 vi 1978, T.Kimura and
 HK, T.

Henosepilachna niponica, 457♂♂578♀♀ (85♂♂90♀♀)

- 44) Ohnuma, Hokkaido (OH): 39/38 (5/5), 9 vi 1976, HK, T.
 45) Tsuta spa, near Lake Towada, Aomori Pref. (TW): 5/7
 (5/5), 10 vi 1976, HK, T.

- 46) TM (cf. No. 11): 36/43 (5/5), 8 vi 1976, HK et al., T.
 47) Tamagawa, near Lake Tazawa, Akita Pref. (TT): 22/29
 (5/5), 2 vi 1977, T.Matsumura and HK, T.
 48) YU (cf. No. 12): 37/32 (5/5), 11 vi 1976, HK, T.
 49) ZA (cf. No. 13): 35/39 (5/5), 12 vi 1976, HK, T.
 50) Kawakami spa, Ura-Bandai, Fukushima Pref. (UB): 51/72
 (5/5), 13 vi 1976, HK, T.
 51) KW (cf. No. 15): 32/21 (10/10), 5 vi 1978, HK et al., T.
 52) Nangô, Tone, Gumma Pref. (NG): 16/43 (5/5), 14 v 1976,
 HK, T.
 53) Okusha, Togakushi, Nagano Pref. (TG): 2/3 (2/3), 18 vi
 1976, HK, T.
 54) Kurokawa-rindô, near Shimashima, Nagano Pref. (SS):
 44/43 (5/6), 19 vi 1976, HK, T.
 55) OS (cf. No. 21): 34/38 (5/5), 20 vi 1976, K.Miyazawa and
 HK, T.
 56) KH (cf. No. 22): 7/35 (0/0), 22 vi 1976, HK, T.
 57) Amô pass, Kawai-mura, Gifu Pref. (AM): 3/4 (0/0), 29
 viii 1975, Sakaguchi, T.
 58) NN (cf. No. 25): 4/17 (4/5), 23 vi 1976, HK, T.
 59) Nakakawachi, Yogo, Shiga Pref. (NA): a) 11/14 (4/5) from
 T, b) 5/13 (5/5) from Scopolia japonica, 6 v 1976, HK et al.
 60) Mitokusan, Tottori Pref. (MT): 6/5 (0/0), 30 v 1976, HK, T.
 61) Akawase, near Ningyô pass, Okayama Pref. (AK): 22/56
 (5/5), 30 v 1976, HK, T.
 62) Tsuwano, Shimane Pref. (TS): 46/26 (5/6), 28 v 1976, HK, T.

Henosepilachna yasutomii, 76♂♂149♀♀ (49♂♂54♀♀)

- 63) OH (cf. No. 44): 17/31 (10/10), 9 vi 1976, HK, B.
 64) Zatôishi, Hirosaki, Aomori Pref. (HZ): 5/7 (5/5), 23 v
 1977, K.Hoshikawa, B.
 65) TW (cf. No. 45): 18/25 (10/10), 10 vi 1976, HK, B.
 66) a) Kanmata A, Abukuma, Fukushima Pref. (ABa): 10/26 (10/
 10), 8 v 1979, K.Hoshikawa, B.
 b) Kanmata B, Abukuma, Fukushima Pref. (ABb): b-1) 2/2
 (0/0) from B, b-2) 0/2 (0/0) from Panax japonicus,

7 v 1979, K.Hoshikawa.

- 67) Hiranaichi, Abukuma, Fukushima Pref. (AH): 4/2 (0/0),
8 v 1979, K.Hoshikawa, B.
- 68) TG (cf. No. 53): 15/36 (10/10), 18 vi 1976, HK, B.
- 69) SS (cf. No. 54): a) 1/4 (0/0), 19 vi 1976, HK; b) 2/10
(2/5), 17 v 1977, K.Hoshikawa; B.
- 70) KH (cf. Nos. 22 and 56): 0/2 (0/2), 22 vi 1976, HK, B.
- 71) Otaki-mura, Kiso, Nagano Pref. (OT): 2/2 (2/2), 31 vii~
2 viii 1974, K.Hirata, B.

Unsettled populations, 226~~88~~363~~99~~ (101~~88~~108~~99~~)

Western Tokyo form

- 72) Kazusa-Kameyama, Bôsô, Chiba Pref. (KY): 8/6 (8/6), 12 v
1976, K.Yasutomi, probably from P.
- 73) Nokogiriyama, Bôsô, Chiba Pref. (BO): 15/31 (11/14), 15
and 20 iv 1978, HK, Lycium chinense.
- 74) Kaneko, Iruma, Saitama Pref. (KK): 40/72 (10/10), 10 v
1976, HK, P.
- 75) Nakayama, Yokohama, Kanagawa Pref. (NK): 52/91 (10/12),
26 iv 1976, HK, P.
- 76) Jûniso, Kamakura, Kanagawa Pref. (JK): 12/28 (0/0), 28
iv 1976, HK, P.
- 77) Takaozan, Tokyo (TZ): a) 19/25 (10/10) from P, b) 5/5
(5/5) from Chelidonium japonicum; 7 vi 1978, HK.
- 78)* HW (cf. No. 18): 1/3 (1/3), 22 vi 1979, HK, P.
- 79) Kurasawa-dani, Okutama, Tokyo (OK): a) 2/0 (2/0), 16 v
1971, T.Shinbo; b) 1/1 (1/1) and c)* 1/3 (1/3), 22 vi
1979, HK; all from Scopolia japonica.
- 80) UK (cf. No. 19): a)* 2/2 (2/2), 4 v 1973, T.Shinbo,
Scopolia japonica; b)* 1/1 (1/1) from Scopolia japonica
and c)* 2/1 (2/1) from P, 23 vi 1979, HK.
- 81)* 340 m alt. near Isukuda, Urayama, Saitama Pref. (UI):
1/3 (1/3), 23 vi 1979, HK, Scopolia japonica.
- 82) Hiraoka, Tenryû-mura, Nagano Pref. (HI): 25/37 (11/10),
21 vi 1976, HK, P.

Other unsettled populations

- 83) Izumi, Nikko, Tochigi Pref. (IN): a) 4/5 (0/0), 27 v 1977, HK; b) 0/2 (0/0), 20 vi 1977, K.Hoshikawa; c) 4/3 (4/3), 6 vi 1978, HK; d)* 5/5 (5/5) reared with B and e)* 5/4 (5/4) reared with P, 27 v 1977, HK; Chelidonium japonicum.
- 84) HA (cf. No. 20): a) 20/30 (10/10), 29 v 1977, b) 0/5 (0/5), 17 iv 1978; HK, Scopolia japonica.
- 85) KF (cf. No. 23): 1/0 (1/0), 21 vi 1976, HK, P (this individual is probably H. yasutomii).

Foreign material (cf. Fig. 150, all dissected)

All identified with H. vigintioctomaculata.

Saghalin

- 86) G. Nevel'sk, Zapad. pobep.: 3/3, 10 vi 1972, Konokov.

Soviet continental Far East (248850??)

- 87) Amurskaja obl. Arharinsk., R-N:S.Chornoberezovka, poima r. Arharay: 4/16, 14 vi 1976, V.N.Kuznetsov, P.
- 88) Habar. Kraj, Pole Tioe: 0/1, 7 vii 1968, Rochomskaja.
- 89) Primorsky Kraj, P. Ternej: 0/2, 20 ix 1971, V.N.Kuznetsov.
- 90) Primorsky Kraj, Shktovesky, P.Peishula: 2/3, 2 vii 1971, V.N.Kuznetsov.
- 91) Promorsky Kraj, Shikotovskiy: 0/1, 25 vii 1971, V.N.Kuznetsov, P.
- 92) Primorsky Kraj, Shkotovek, R-N:Peishula: a) 0/1, 18 v 1972, b) 2/2, 17 viii 1972, c) 3/2, 10 ix 1972; V.N.Kuznetsov.
- 93) Primorsky Kraj, Ussurijsk. Zapovednik: 0/1, 30 v 1975, V.N.Kuznetsov.
- 94) Primorsky Kraj, Ussurijsky Kraj, Selo Berisovka: 9/19, 7 vii 1975, V.N.Kuznetsov, P.

- 95) Primorsky Kraj, Hasansky, R-N: Zapovednik Kedrovaja pad:
4/2, 30 viii 1971, V.N.Kuznetsov.

North and northeastern China (25882199)

- 96) Chûhô, Manchuria: 15/15, 2 ix 1944, Y.Mori.
97) Tíehling, Manchuria: 1/0, 18 vi 1936, R.Kimishima.
98) Wenchüansze, Manchoukuo: 1/1, 17 viii 1940, S.Matsumura.
99) Pingtingshan, Manchoukuo: 1/0, 18 viii 1940, S.Matsumura.
100) Changchiakou: 2/2, 1 ix 1941, H.Yuasa, egg plant.
101) Changchiakou: 1/0, 18 viii 1942, C.Watanabe.
102) Taiyüan: 2/2, 14 ix 1941, H.Yuasa, P.
103) Shalingtzü(?): 2/1, 11 viii 1941.

Korea (33884399)

- 104) Genzan (=Wonsan): 0/1, 2 viii 1919, E.Gallois.
105) Sainei (=Jaeryyong): 0/1, vii 1934, K.Kin.
106) "Chôju-san": 0/1, 23 vii 1934.
107) Seoul: 3/2, 1 ix 1918, E.Gallois.
108) Koyong-A, Kyonggi-do (near Seoul): 15/16, 10 vii 1968,
K.Li, Solanum nigrum.
109) Koyong-B, Kyonggi-do (near Seoul): 15/20, 14 vii 1968,
K.Li, P.
110) Mt. Sorak (Sulak-san?), 500 m alt.: 0/1, 5 vi 1972,
S.Teranuma.
111) Chôsen: 0/1, Muramatsu.

Table 1. Synopsis of the system adopted and those used by previous authors.

Present system ¹⁾ (abbrev.)	Sasaji (1971)	Yasutomi (1974a, 1977a) ²⁾	Katakura (1974b)
1. <u>vigintioctomaculata</u> (Motschulsky) (Hv)	Group C	Onijyūyahoshi	<u>vigintioctomaculata</u>
Honshu form (V-I)	Race C ₂	Honshu f.	V-I
Hokkaido f. (V-II)	Race C ₁	Hokkaido f.	V-II
Rishiri f. (V-III)	_____	_____	V-III
2. <u>pustulosa</u> (Kōno) (Hp)	Group A	Kobuōniijyūyahoshi	<u>pustulosa</u>
Wakkanai f. (P-III')	_____	Dōhoku f.	P-III'
Sōunkyō f. (P-I)	Race A ₂	Sōunkyō f.	P-I
Nōminate f. (P-II)	Race A ₁	Typical f.	P-II
Sapporo f. (P-III)	Race A ₄	Sapporo f.	P-III
3. <u>niponica</u> (Lewis) (Hn)	_____	Ohnuma f.	P-IV + P-H ₁ part
Ohnuma f. (N-I)	_____	Honshu f.	P-H ₁ part
Honshu f. (N-II)	Race A ₃	Ibuki-Tsuwano f.	P-H ₂
Ibuki f. (N-III)	_____		
4. <u>yasutomii</u> sp. nov. (Hy)	_____	Towada form or the cohosh feeder	the cohosh feeder ⁴⁾
5. Unsettled populations			
Western Tokyo form (Wt)	Group B	Tokyo West suburbs form	Western Tokyo form
Omukawa population (HAX) ³⁾	_____	_____	_____
Izumi population (INX) ³⁾	_____	_____	_____

1) 1: group A, 2-5: group B in the present study (nec Sasaji).

2) Yasutomi (1974) was modified by his 1977's paper.

3) Recently discovered (Katakura et al. 1978).

4) Not included in Katakura (1974b) but listed in Katakura (1977).

Table 2. Variation of pronotal spot pattern. Classes of pattern follows Dieke (1947). Both sexes combined. Reared specimens are omitted. Continental samples: Amur=No.87, Ussuri=No.94, Manchuria=No.96, Korea=Nos.108 + 109. A sample from Saghalin (No.86) is included in V-II.

Group, species and form	No. of individuals examined	(paler)			Classes					(darker)		
		H	HI	I	IJ	J	JK	K	KL			
A. Hv												
V-III	32			5	5	14	8					
V-II	82			1	1	22	25	33				
V-I	174			62	59	50	3					
Amur	20			11	4	5						
Ussuri	28	1		14	3	10						
Manchuria	30	1	3	15	8	3						
Korea	66	47	8	11								
B. Hp												
	113						31	67	15			
Hn												
N-I	70			15	10	22	19	4				
N-II	56	4	6	29	8	2	2	4	1			
N-III	50	1	7	13	13	11	5					
Hy												
OH	20					1	9	6	4			
TW+HZ	30		3	5	4	13	3	2				
Others	53			7	13	18	11	4				
Unsettled												
Wt	132	2	4	91	23	8	4					
HAx	25	5	1	11	6	2						
INx	7				6	1						

Table 3. Color variation of hind femur. Grade as in Fig. 12. Both sexes combined. Continental samples as in Table 2. A sample from Saghalin (No. 86) is included in V-II.

Group, species and form	No. of individuals examined	(paler)			Classes			(darker)		
		A	B	C	D	E	F	G	H	
A. Hv										
V-III	32			19	8	3	2			
V-II	82			37	20	14	11			
V-I	174		1	145	19	8	1			
Amur	20			13	3	4				
Ussuri	28		6	16	4	3	2			
Manchuria	30	3	6	19	2					
Korea	66	31	24	11						
B. Hp										
	113									113
Hn										
N-I	70				1	1	18	24	26	
N-II	56				3	4	34	12	3	
N-III	50						28	20	2	
Hy										
OH	20							2	18	
TW+HZ	30						5	21	4	
Others	51					3	9	36	3	
Unsettled										
Wt	132				4	5	88	35		
HAX	25				1	3	12	8	1	
INx	7						7			

Table 4. Color variation of spermatheca of Hv (group A).
 Reared specimens included. Continental samples as in Table
 2. V-II involves a Saghalin sample (No. 86).

Form	No. of specimens examined	Transparent	Pigmented
V-III	16	9	7
V-II	39	1	38
V-I	89	84	5
Amur	16	4	12
Ussuri	18	6	12
Manchuria	15	8	7
Korea	30	15	15

Table 5. Color variation of spermatheca of group B. No transparent specimen was detected. Reared specimens included.

Species and form	No. of specimens examined	At most apical half of swollen part colored	Intermediate	At least swollen part entirely, and part of the base colored
Hp	56	0	3	53
Hn				
N-I	35	1	21	13
N-II	28	4	18	6
N-III	26	6	15	5
Hy				
OH+TW+HZ	25	0	9	16
Others	29	8	19	2
Unsettled				
Wt	77	19	48	10
HAX	15	5	10	0
INx	12	0	5	7

Table 6. Morphological differences between groups A and B in some body parts.

Characters	Conditions typical to	
	Group A	Group B
1) Antennal scape (Fig. 110)	Frontal margin rather sharply curved and swollen forward	Frontal margin moderately curved
2) Terminal segment of macillary palpus (Fig. 111)	Inner edge distinctly angulate	Inner edge rounded
3) Male tergite IX (Fig. 112)	Contour of frontal margin V-shaped medially paler	Contour of frontal margin U-shaped, medially dark colored and sometimes irregularly pigmented
4) Apex of siphon (Fig. 113)	Semi-parallel sided and tip more projected	Slightly swollen and tip less projected
5) Hemisternite (Fig. 114)	Widest medially, inner notch narrow and distinct	Widest posteriorly, inner notch shallow and indistinct

Table 7. Food plants of Hv (V-II) and Hp (P-III) confirmed under natural conditions in and near Sapporo during 1971~1979 (modified from Katakura et al. 1977 with additional records). +: edible plant, ++: host plant.

Plant family	Plant species	Hv (V-II)	Hp (P-III)
Chenopodiaceae	<u>Spinacia oleracea</u> L. (spinach)		+
Berberidaceae	<u>Caulophyllum robustum</u> Maxim. (blue cohosh)		++
Cruciferae	<u>Brassica campestris</u> L. (chinese cabbage)	+	+
Leguminosae	<u>Glycine max</u> Meer. (soy bean)	+	
	<u>Phaseolus coccineus</u> L. (scarlet bean)	+	
	<u>Vigna Catiang</u> Endl. var. <u>sinensis</u> King (yard long bean)	+	
Buxaceae	<u>Pachysandra terminalis</u> Sieb. et Zucc.		+
Araliaceae	<u>Kalopanax pictus</u> (Thunb.) Nakai (Sennoki)		+
Solanaceae	<u>Physalisstrum japonicum</u> (Franc. et Savat.) Honda	+	
	<u>Solanum nigrum</u> L. (black nightshade)	++?	+
	<u>S. megacarpum</u> Koidz.	++	++
	<u>S. tuberosum</u> L. (potato)	++	++?
	<u>S. melongena</u> L. (egg plant)	+	+
	<u>Lycopersicon esculentum</u> Mill. (tomato)	+	+
	<u>Capsium annuum</u> L. (green pepper)	+	+
	<u>Datura stramonium</u> L. var. <u>chalybea</u> Koch.	+	
Cucurbitaceae	<u>Schizonepon bryoniaefolius</u> Maxim.	++	+
	<u>Citrullus vulgaris</u> Schrad. (water melon)	+	
	<u>Cucumis sativus</u> L. (cucumber)	+	+
	<u>C. Melo</u> L. (melon)	+	
	<u>Cucurbita Pepo</u> L. (pumpkin)	+	
Compositae	<u>Cirsium</u> spp. (thistles)		++
	<u>Breca setosa</u> (Bieb.) Kitam.	+	++
	<u>Arctium Lappa</u> L. (great burdock)	+	+

Table 8. Confirmed or presumable host plants of the members of Hv-complex in Japan. +++: main host plant, +: subsidiary host plant, ?: suspected. Further explanations in text.

Plant family and species	Hv	Hp	Hn	Hγ	Unsettled
Berberidaceae					
<u>Caulophyllum robustum</u>		+++P-III		+++	?
Papaveraceae					
<u>Chelidonium japonicum</u>					+++INx +TZw
Araliaceae					
<u>Panax japonicus</u>				+Honshu	
Solanaceae					
<u>Lycium chinense</u>	+V-I				BOw
<u>Scopolia japonica</u>	V-I?		N-III?	HZy?	+++HAX Wt
<u>Physalisstrum japonicum</u>	V-I?				
<u>Solanum tuberosum</u>	+++	+	+		++Wt
<u>S. melongena</u>	+				
<u>S. nigrum</u>	+				
<u>S. megacarpum</u>	+++V-II	+P-III			
<u>S. maximowiczii</u>	V-I?				
<u>Lycopersicon esculentum</u>	+				
<u>Datura stramonium</u>	+				
Cucurbitaceae					
<u>Schizopepon bryoniaefolius</u>	+++V-II				
Compositae					
<u>Cirsium</u> spp.		+++	+++		
<u>Breca setosa</u>		+	+N-I		

Table 9. Results of crossing experiment by means of male multiple choice method between a sympatric combination of Hv-complex, Hv (V-II) and Hp (P-III) (Katakura and Nakano 1979).

Combination and crosses	Mating behavior observed			Actual mating ³⁾		First trial by male ³⁾		
	HO ²⁾	HT	HO+HT	HO	HT	HO	HT	
V _{II} ♂/V _{II} ♀ P _{III} ♀	HA ¹⁾	12	8	5	13	8	14	11
	NA	12	2	1	9	3	13**	2
	Total	24	10	6	22	11	27*	13
P _{III} ♂/V _{II} ♀ P _{III} ♀	HA	14	3	8	10	5	18*	7
	NA	7	3	5	10	5	11	4
	Total	21	6	13	20	10	29**	11

1) HA: post hibernating adult, NA: newly emerged adult.

2) HO: homogamic, HT: heterogamic.

3) * and **: the difference between HO and HT is statistically significant at 5% and 1% levels, respectively.

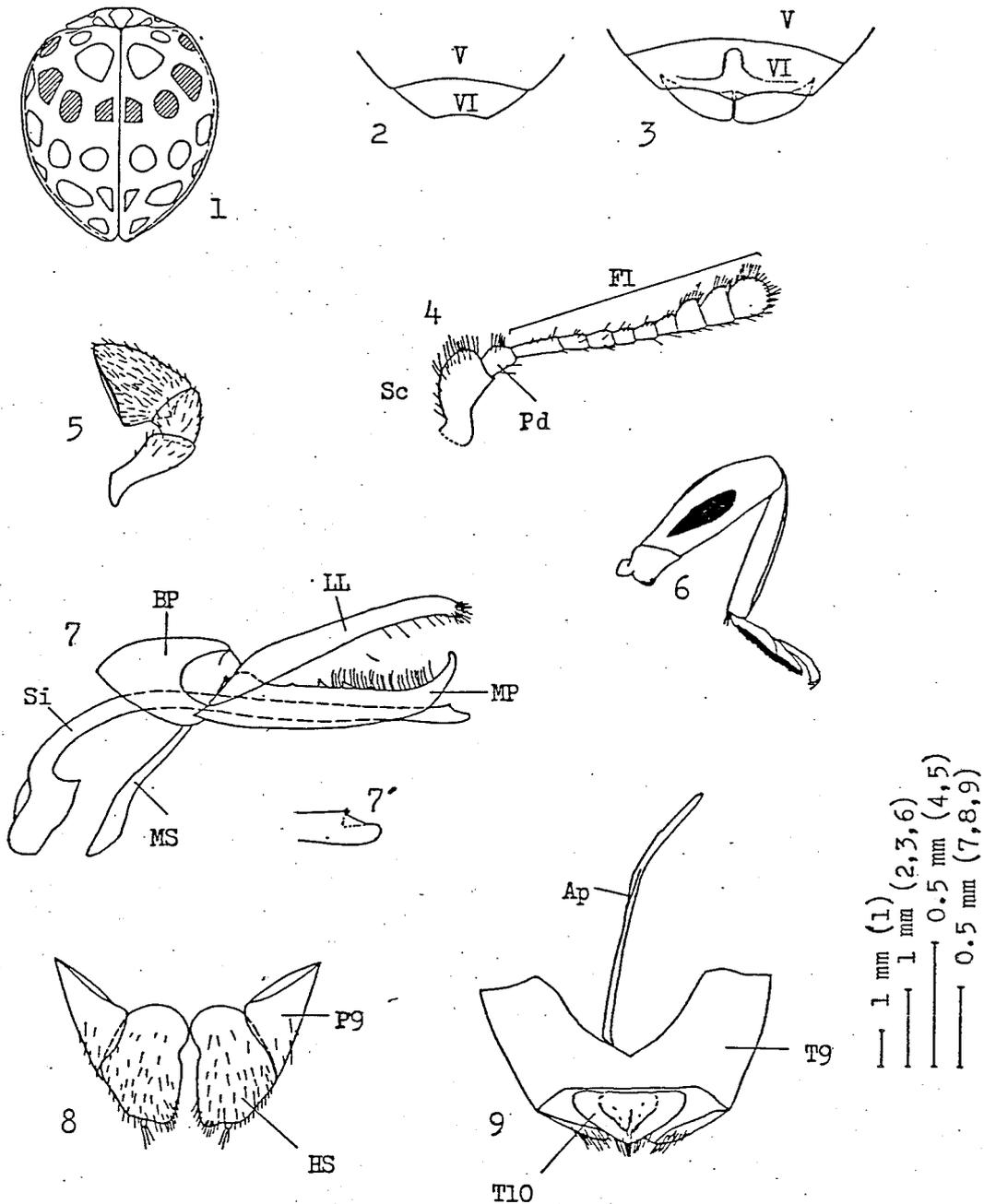
Table 10. Hatching ratios of eggs by homogamic pairs of NA (newly emerged adult), heterogamic pairs of NA and heterogamic pairs of HA (post hibernating adult) between V-II and P-III (Katakura and Nakano 1979).

Combination	No. of pairs examined	Average no. of eggs examined for each pair	Hatching ratio (%)		
			mean	min.	max.
Homogamic					
V _{II} ♂ x V _{II} ♀, NA	9	303	71.6	56.4	85.2
P _{III} ♂ x P _{III} ♀, NA	10	83	74.2	56.9	85.7
Heterogamic					
V _{II} ♂ x P _{III} ♀, NA	7	135	4.0	0	17.1
P _{III} ♂ x V _{II} ♀, NA	10	263	4.0	0	35.1
V _{II} ♂ x P _{III} ♀, HA	4	38	26.3	4.2	55.5
P _{III} ♂ x V _{II} ♀, HA	11	192	31.6	1.1	70.8

Table 11. Comparison of some characteristics of three species of group B

Items	<u>H. niponica</u>	<u>H. pustulosa</u>	<u>H. yasutomii</u>
Distribution	Sympatric with Hy, allopatric with Hp	Allopatric with both Hn and Hy	Sympatric with Hn allopatric with Hp
Main host plant	Thistle	Thistle (excl. P-III), thistle and blue cohosh (P-III)	Blue cohosh
Body size	Large (N-I, II), medium (N-III)	Medium	Small
WAF, LTT values	<u>H. pustulosa</u> deviated from other two		
Color	Paler	Darker	Paler
Habitus	<u>H. pustulosa</u> (P-III) is more similar to <u>H. yasutomii</u> than <u>H. niponica</u> (N-I)		
Frequency of Aaph 2*	0~86% with clear northward increase	0%	25~71%

* Kuboki (1978)



Figs. 1~9. Explanation of some characters in Hv-complex. All drawn based on H. vigintioctomaculata (Motschulsky), form V-I. 1, dorsal view (elytral spots, d-3-b-2 are hatched); 2 and 3, fifth and sixth visible abdominal sternites of male and female; 4, left antenna seen dorsally; 5, left maxillary palpus seen dorsally; 6, left hind leg; 7, male genitalia; 8, female genitalia; 9, genital segments of male. BP, tegmen, basal piece; LL, do, lateral lobe; MP, do, median piece; MS, do, median strut; Si, siphon; P9, pleurite of abdominal segment 9; HS, hemisternite; T-9 and 10, ninth and tenth abdominal tergites; Ap, apophysis of ninth abdominal segment; Sc, scape; Pd, pedicel; Fl, flagella.

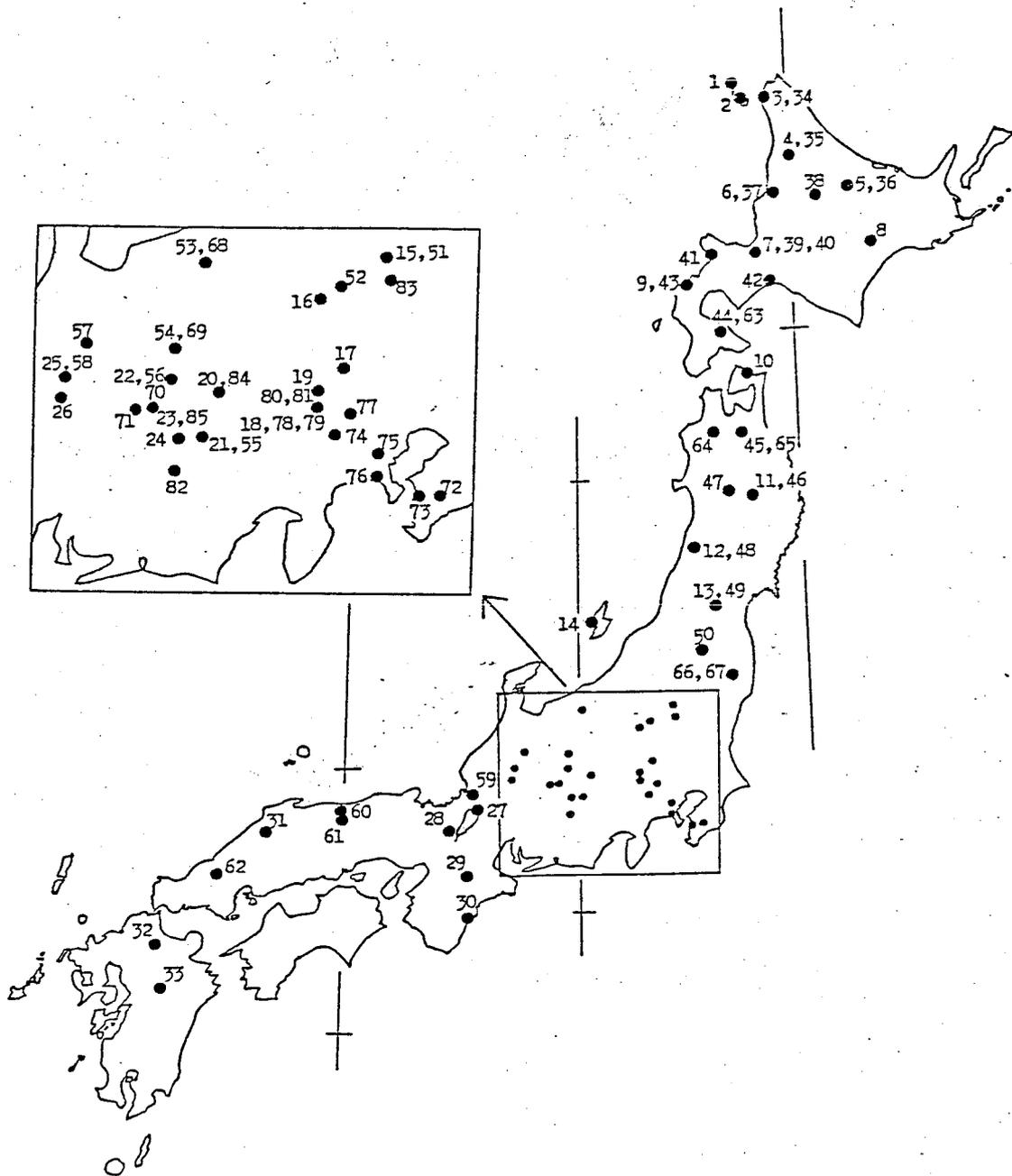


Fig. 10. Provenance of Japanese samples of Hv-complex used for morphological studies. Each sample is shown by the code number given in Appendix.

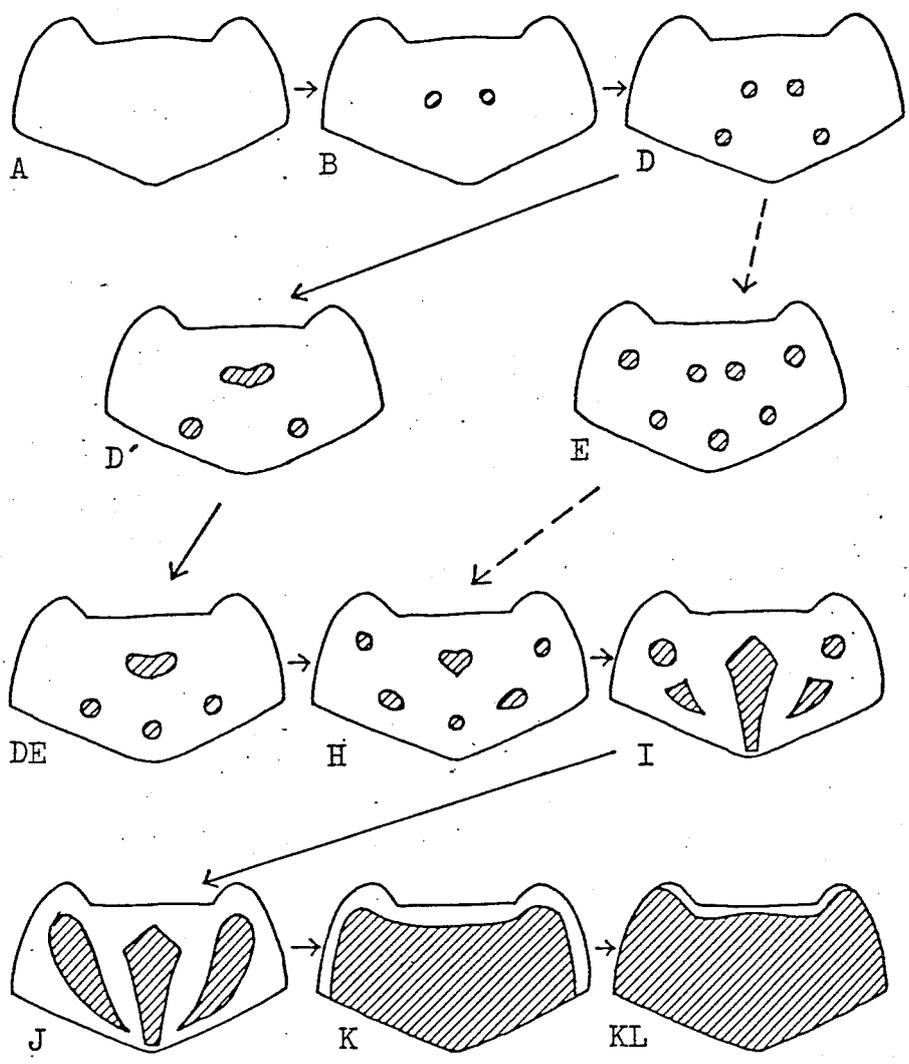


Fig. 11. Variation of the pronotal pattern in Hv-complex.

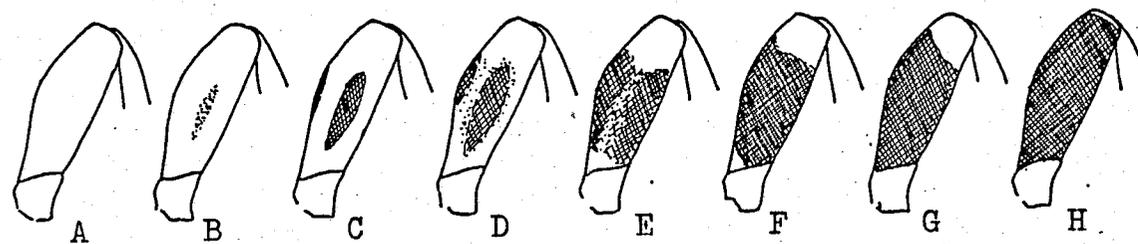
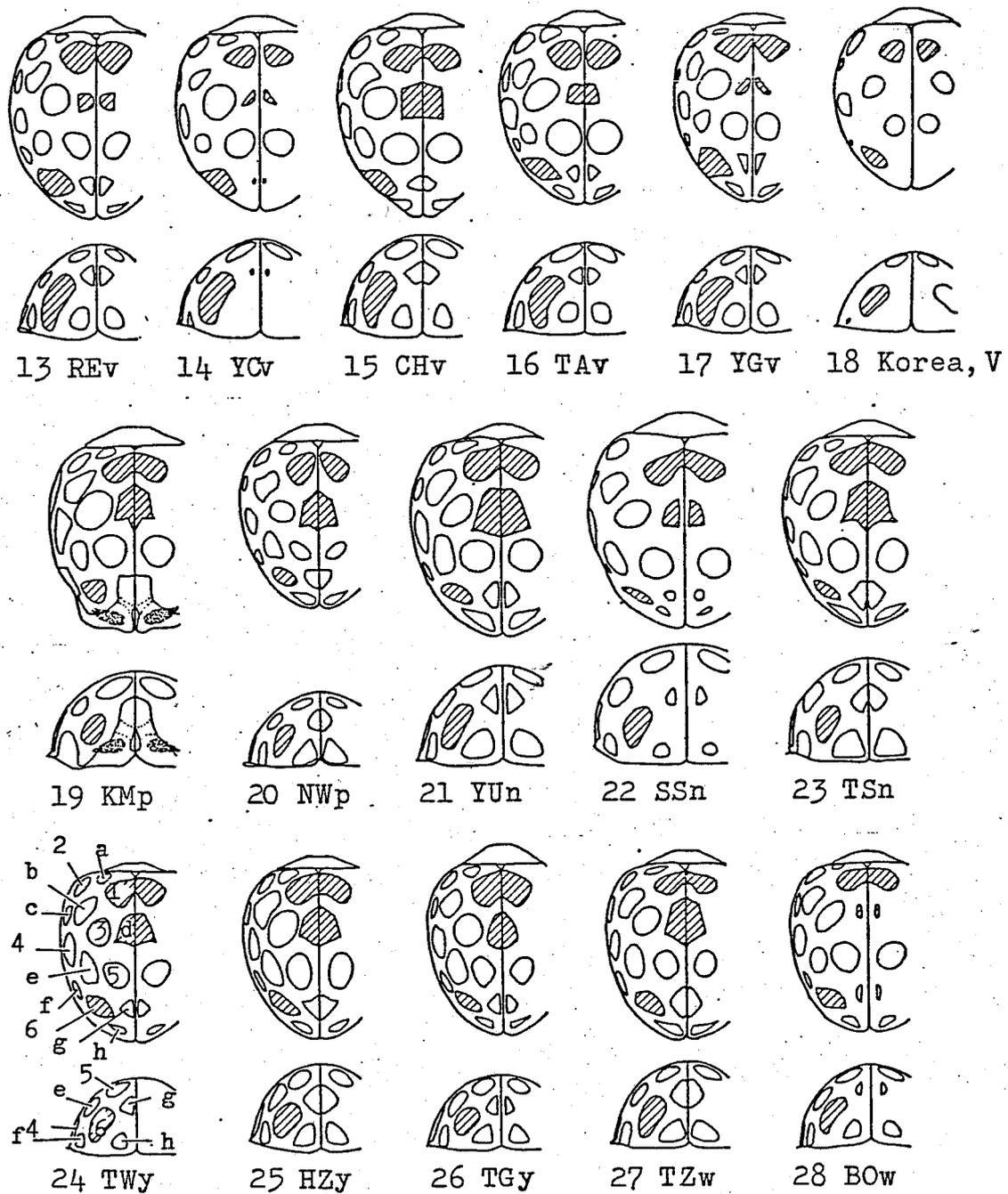
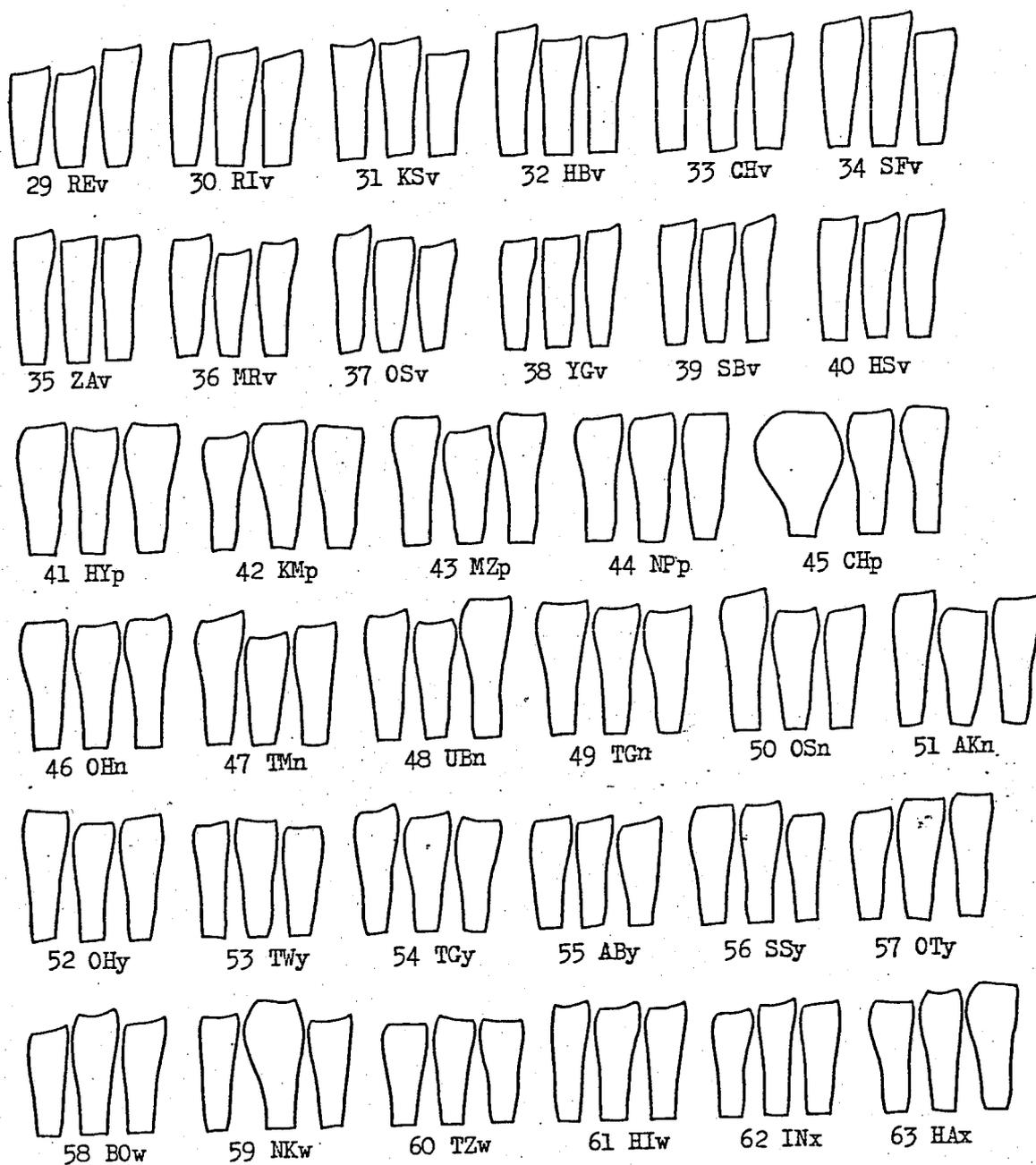


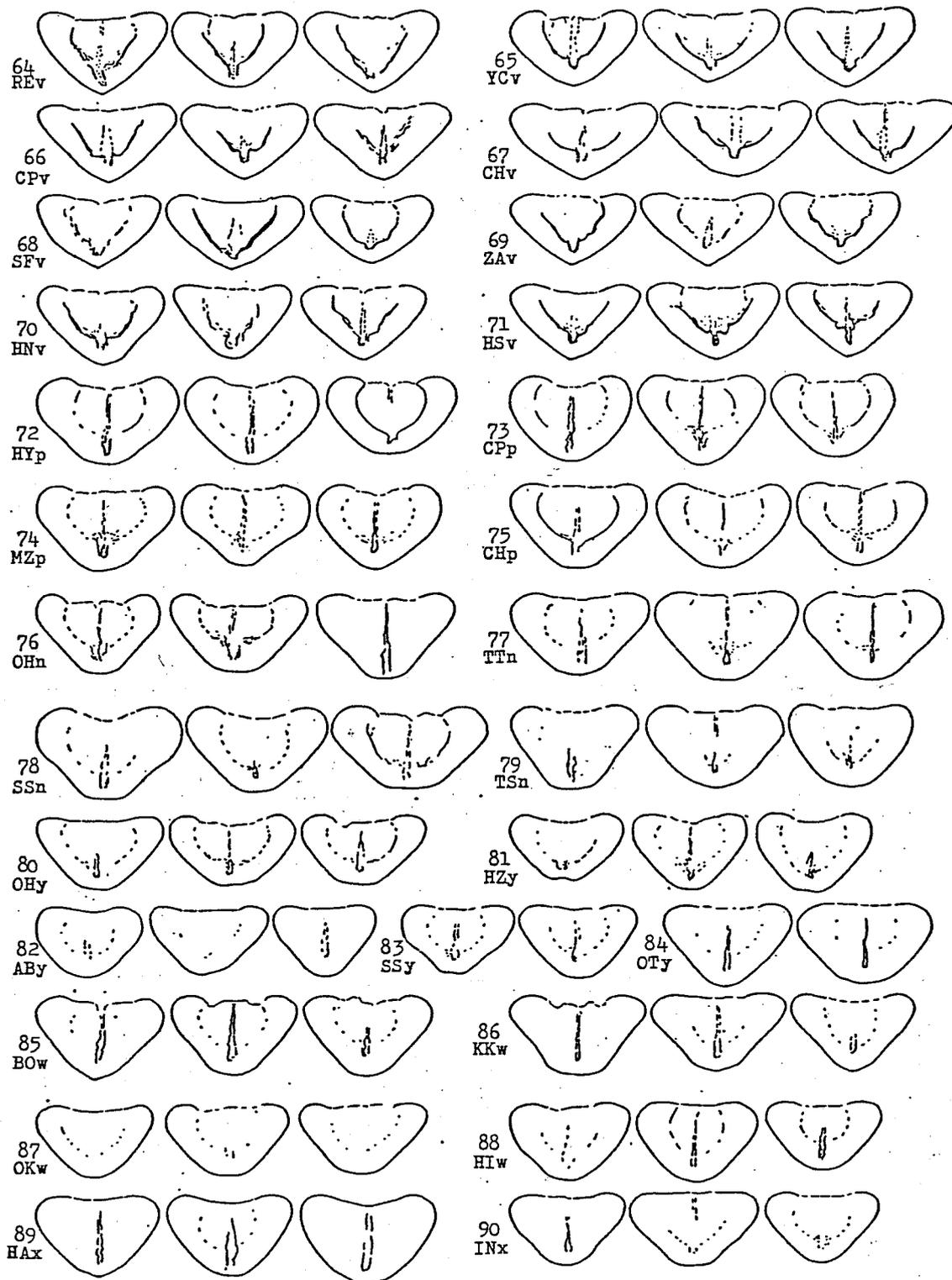
Fig. 12. Classification of color patterns of hind femur.



Figs. 13~28. Elytral maculation of Hv-complex showing individual variation and difference between groups A and B. Spots 1, d, 6 are hatched. 13~18, Hv; 19~20, Hp; 21~23, Hn; 24~26, Hy; 27, 28, Wt.



Figs. 29~63. First antennal flagellomere. Dorsal view; frontal margin, right. 29~40, Hv; 41~45, Hp; 46~51, Hn; 52~57, Hy; 58~63, unsettled populations.



Figs. 64~90. Tergite X of males: Pressed condition.
 64~71, Hv; 72~75, Hp; 76~79, Hn; 80~84, Hy; 85~90,
 unsettled populations.

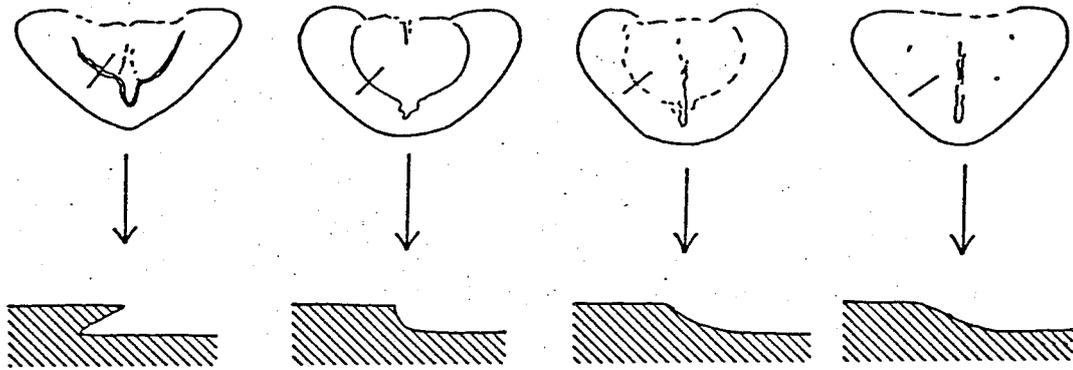
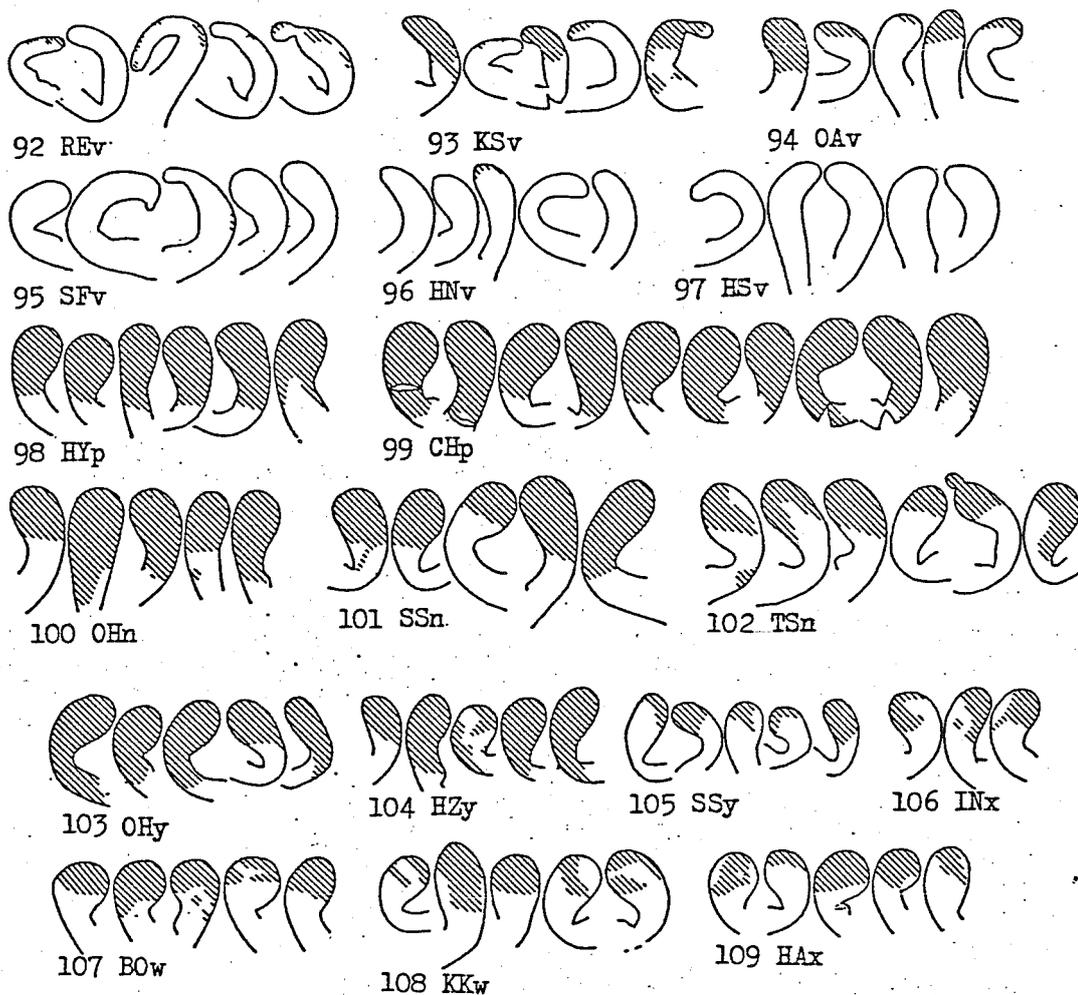
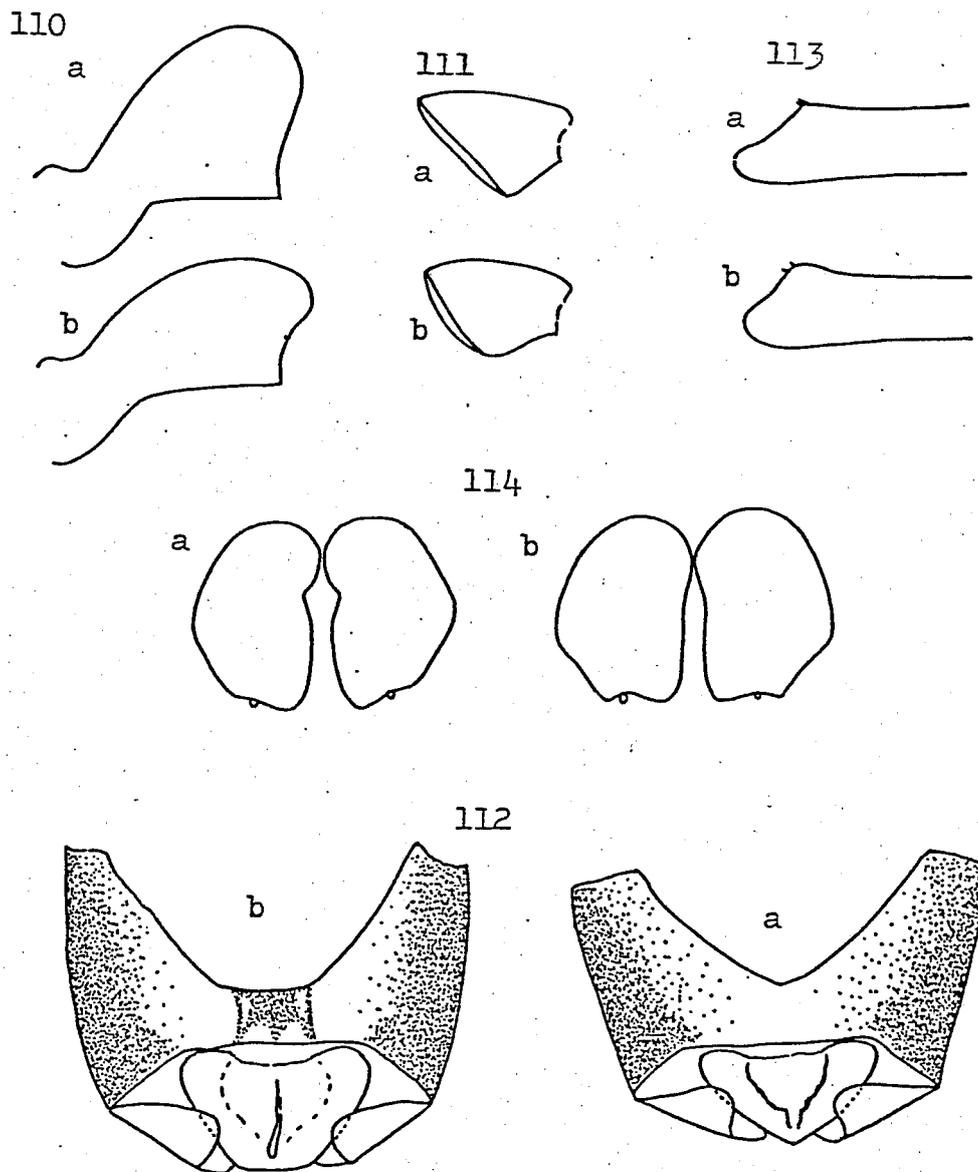


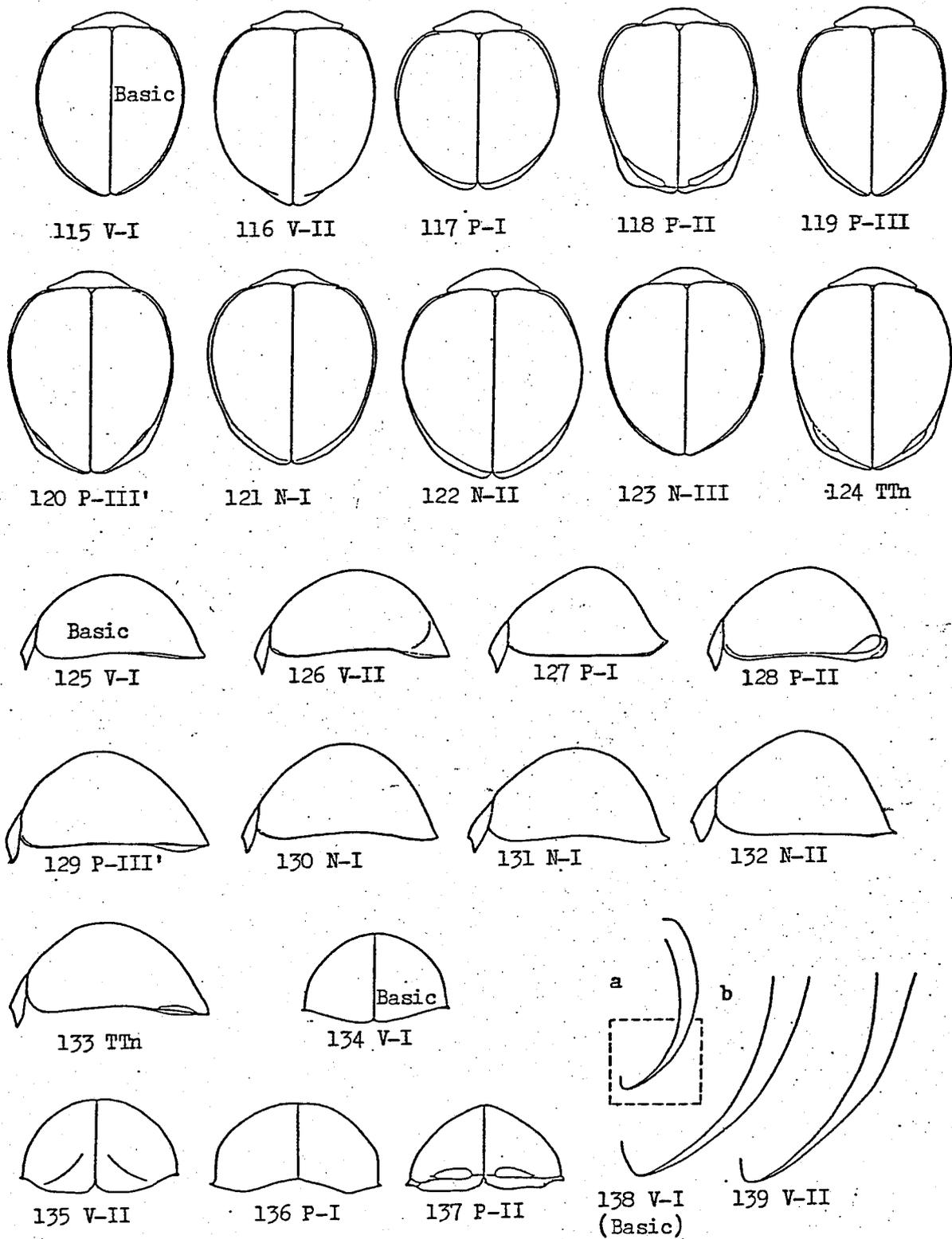
Fig. 91. Presumable cross-section of the margin of inner depression of male tergite X.



Figs. 92~109. Spermatheca. Slightly pressed condition.
 92~97, Hv; 98, 99, Hp; 100~102, Hn; 103~105, Hy; 106~
 109, unsettled populations. Pigmented area hatched.



Figs. 110~114. Morphological differences between groups A and B of Hv-complex in some body parts (cf. Table 6). 110: Antennal scape. 111: Apical segment of maxillary palpus. 112: Male abdominal tergites IX and X. 113: Siphon apex (lateral view). 114: Hemisternites of female. a and b: Condition typical to groups A and B, respectively.



Figs. 115~139. Variation in the elytral shape. 115~124, dorsal view; 125~133, lateral view; 134~137, posterior view; 138 and 139, epipleuron. Basic shape (represented by V-I), 115, 125, 134, 138; V-II, 116, 126, 135, 139; P-I, 117, 127, 136; P-II, 118, 128, 137; P-III, 119; P-III', 120, 129; N-I, 121, 130, 131; N-II, 122, 132; N-III, 123; TTn, 124, 133.

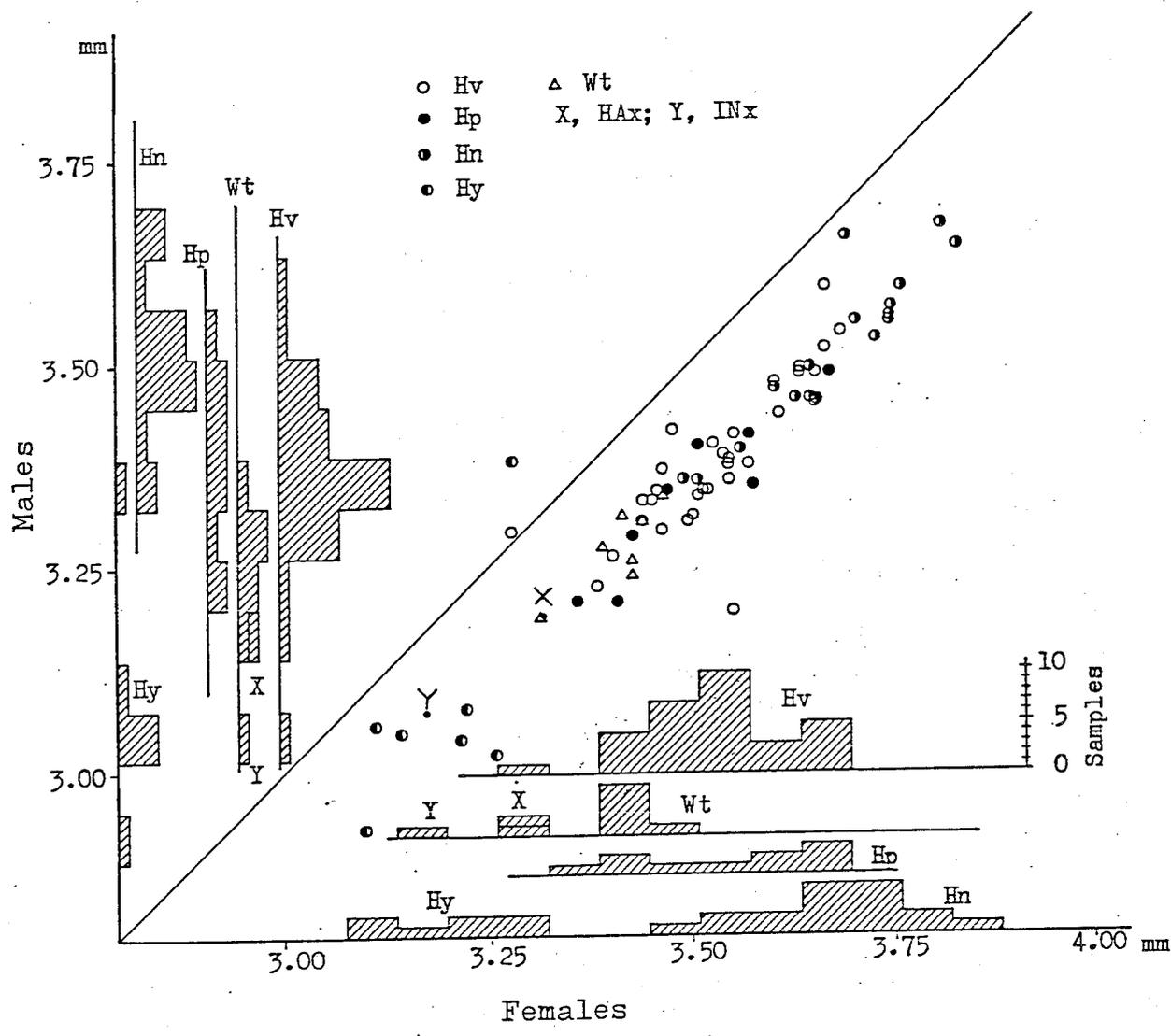


Fig. 140. Body size by pronotal width (PRW) of the members of Hv-complex.

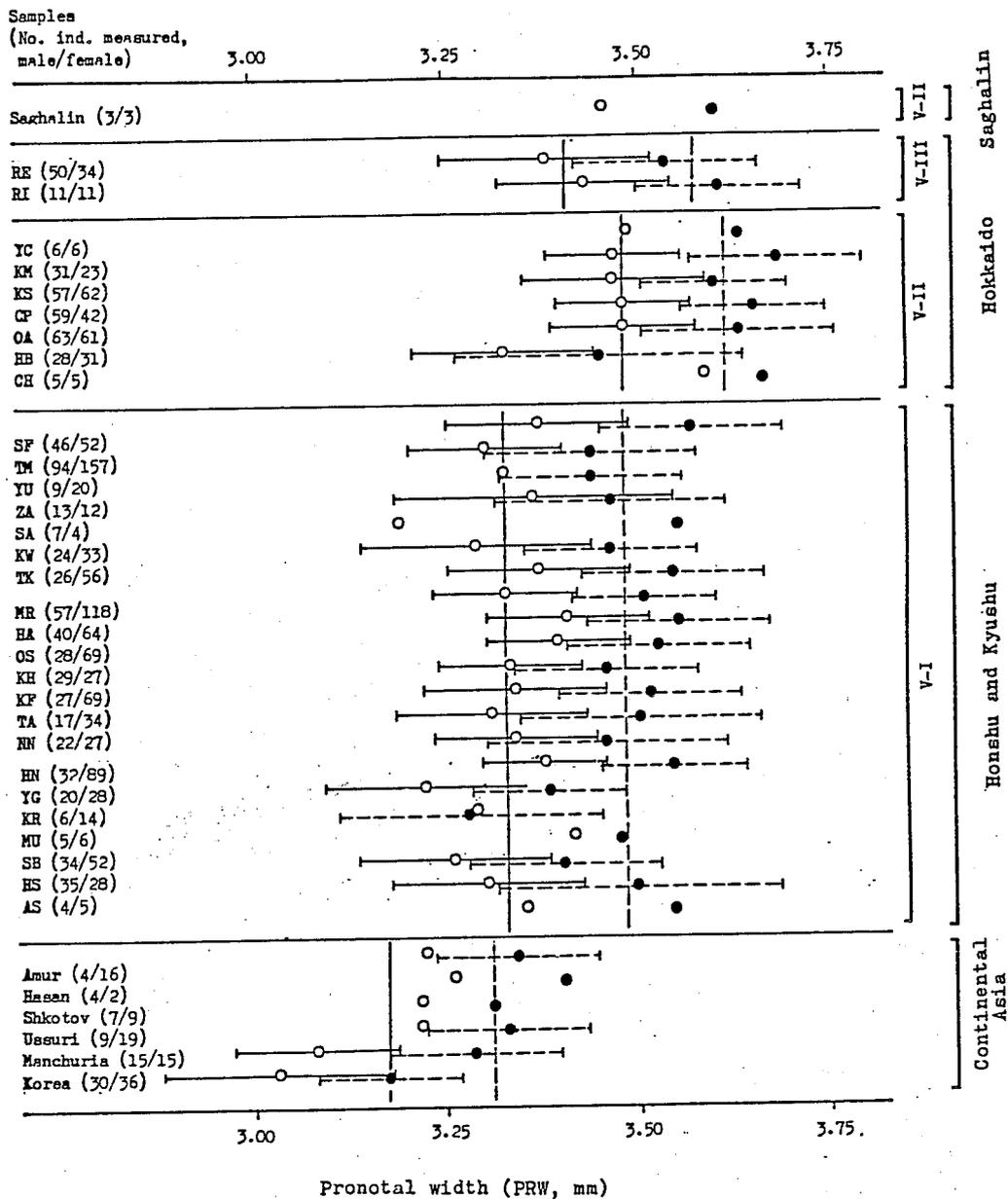


Fig. 141. Body size variation in Hv (group A) in terms of pronotal width (PRW). Both Japanese and continental samples are approximately arranged from north (upper) to south (below). Each sample is represented by mean (open circle= male, closed circle= female). The range of LSD (solid line= male, broken= female) is given to the samples with more than eleven individuals. Averages of means for each form are shown by vertical lines (solid= male, broken= female). Exotic samples: Saghalin= No. 86, Amur= No. 87, Ussuri= No. 94, Shkotov= Nos. 90~92, Hasan= No. 95, Manchuria= No. 96, Korea= Nos. 108, 109.

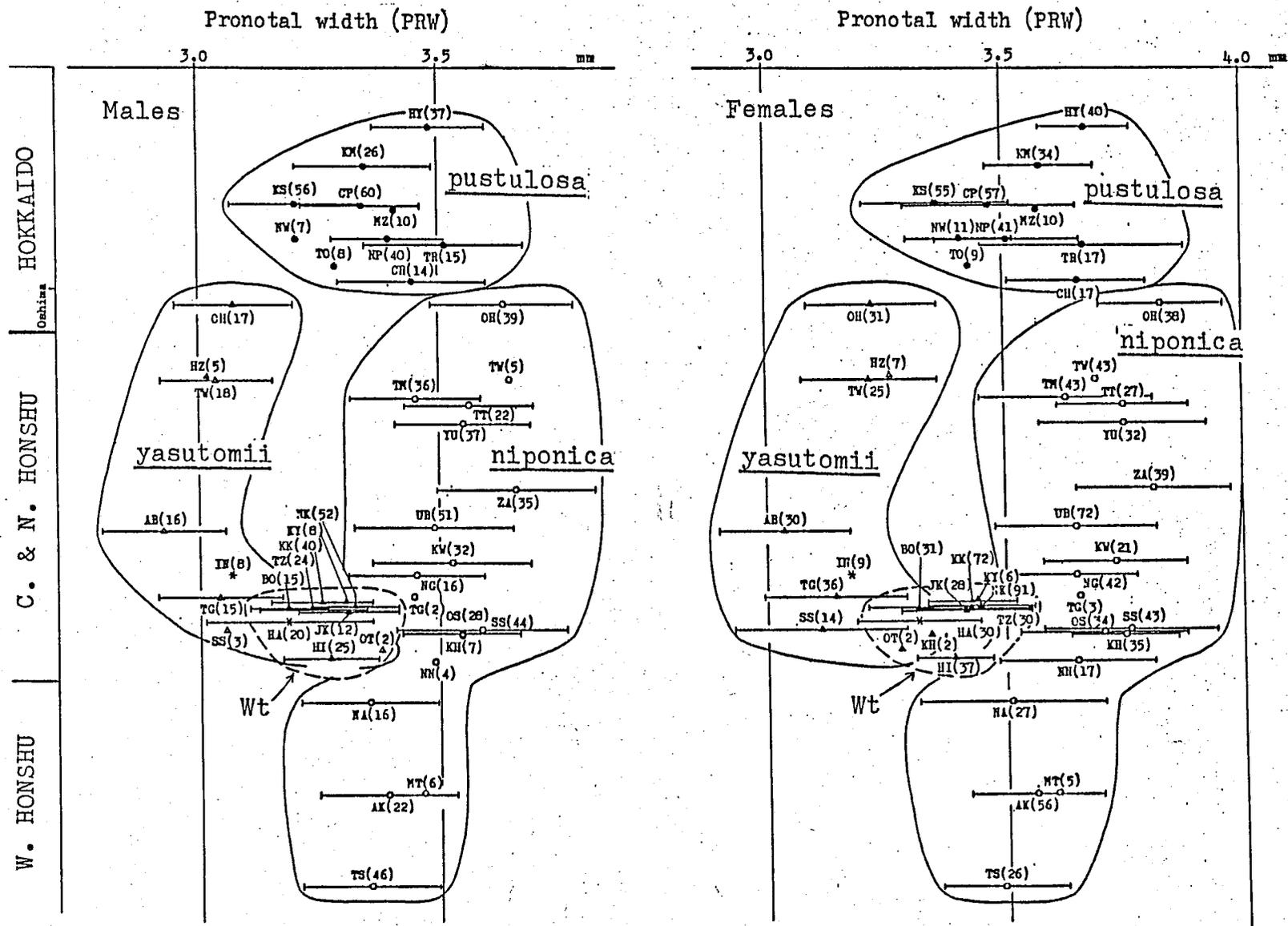


Fig. 142. Geographic variation of body size in the members of group B. Each sample, shown by locality code given in Appendix (number of specimens measured), is represented by mean with LSD.

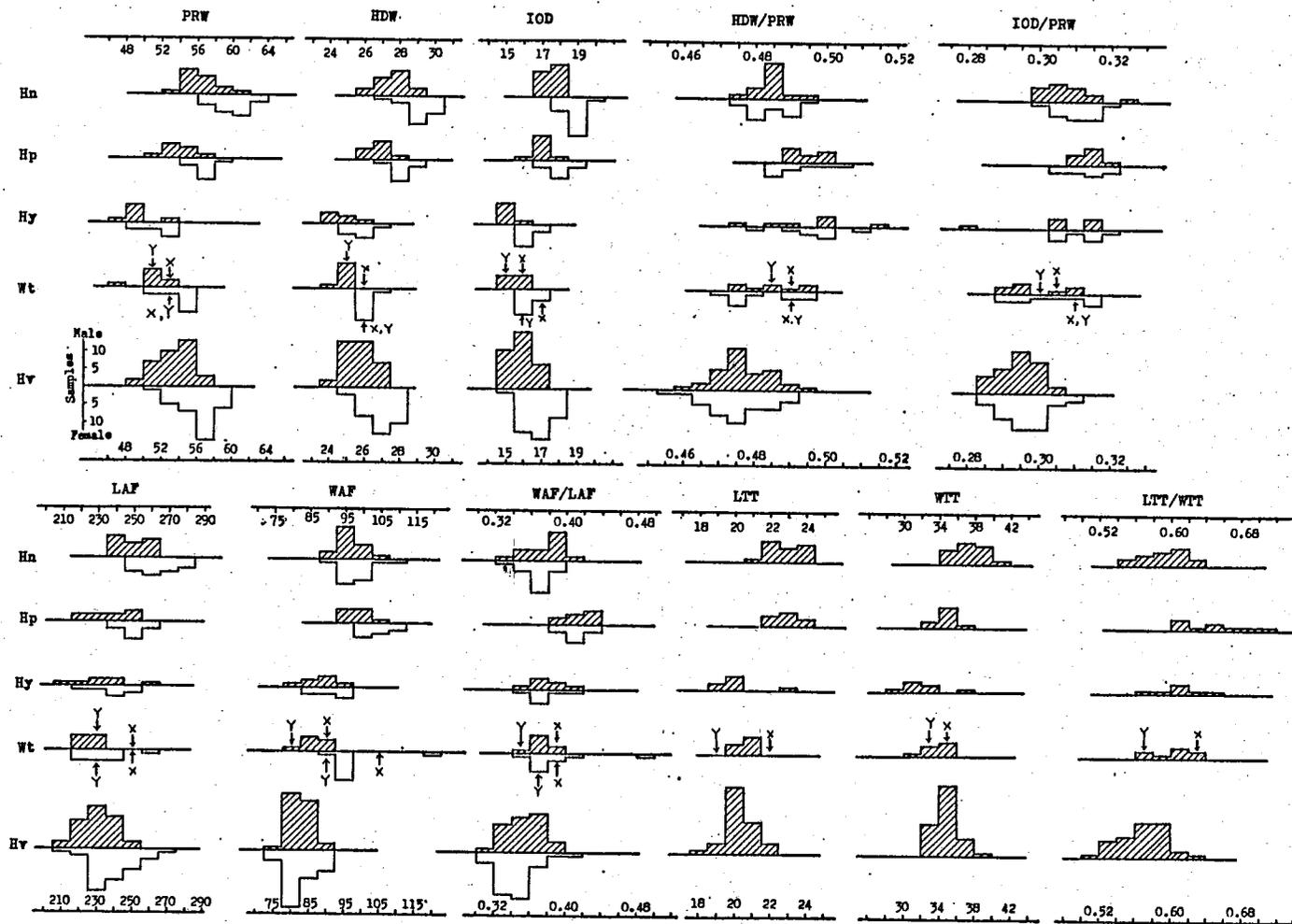


Fig. 143. Frequency distributions of the values of measurements and ratios for the members of Hv-complex. Scale units for PRW, HDW and IOD, 16.1= 1 mm; for LAF and WAF, 125= 0.1 mm; for WTT and LTT, 50= 1 mm. X=HAX, Y=INx.

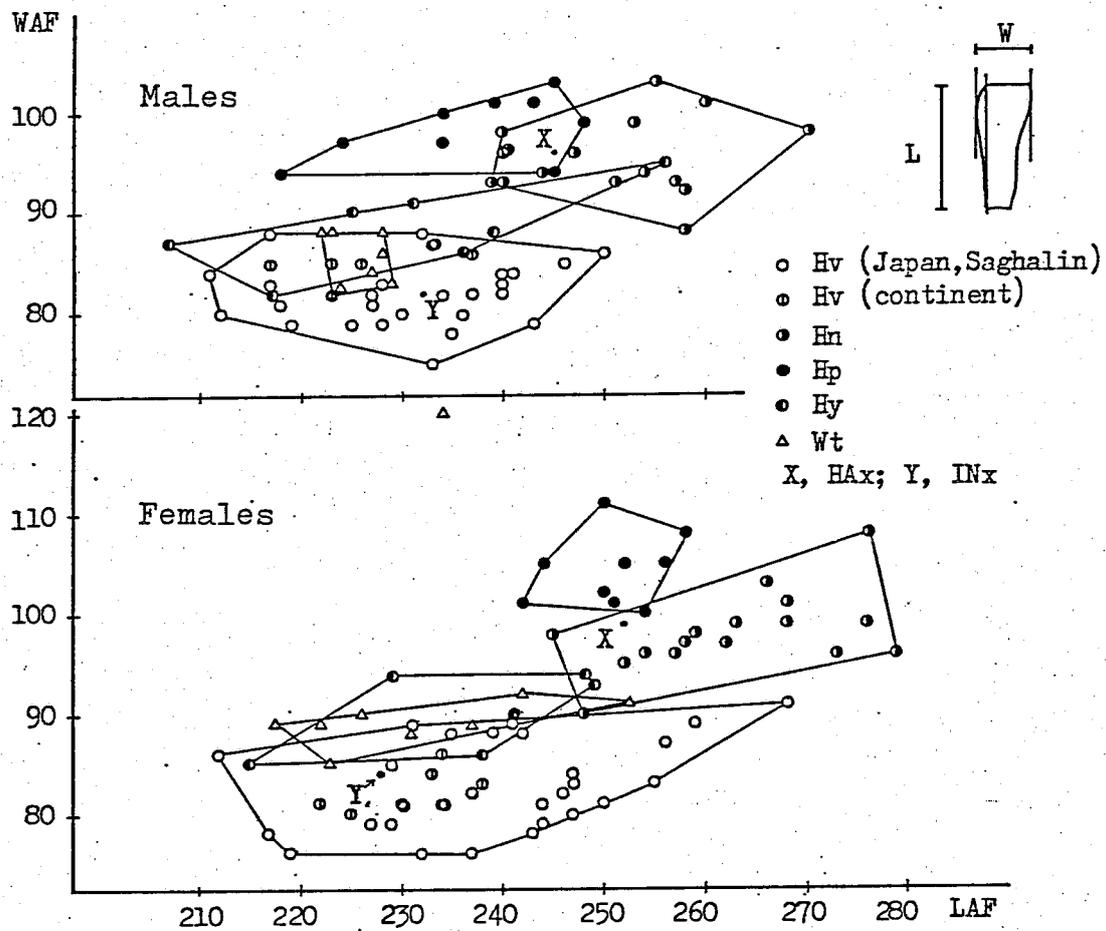


Fig. 144. Relation of length (LAF) and width (WAF) of first antennal flagellomere. 125 scales= 0.1 mm.

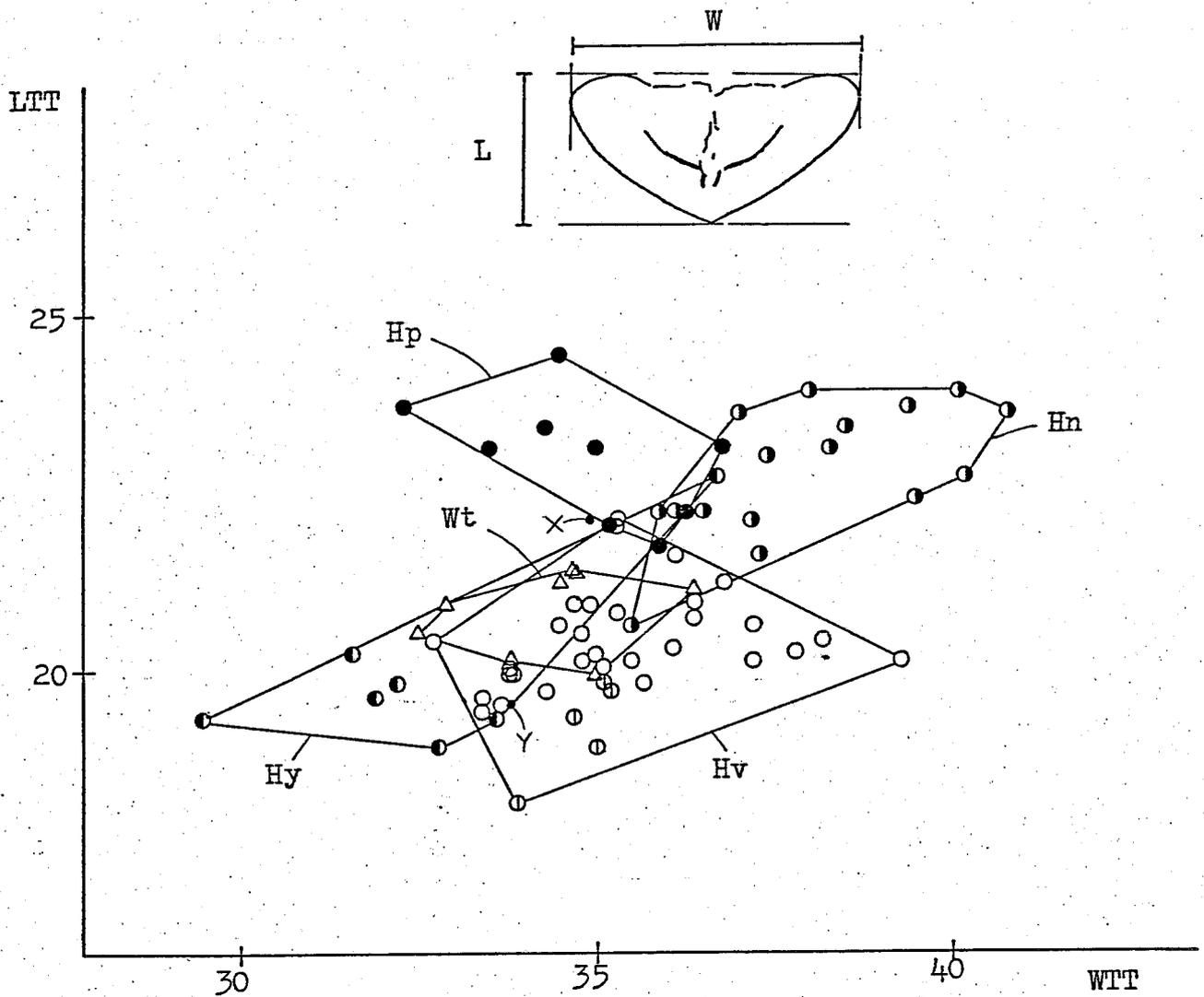


Fig. 145. Relation of width (WTT) and length (LTT) of male tergite X. Symbols as in Fig. 144. Scale 50=1 mm.

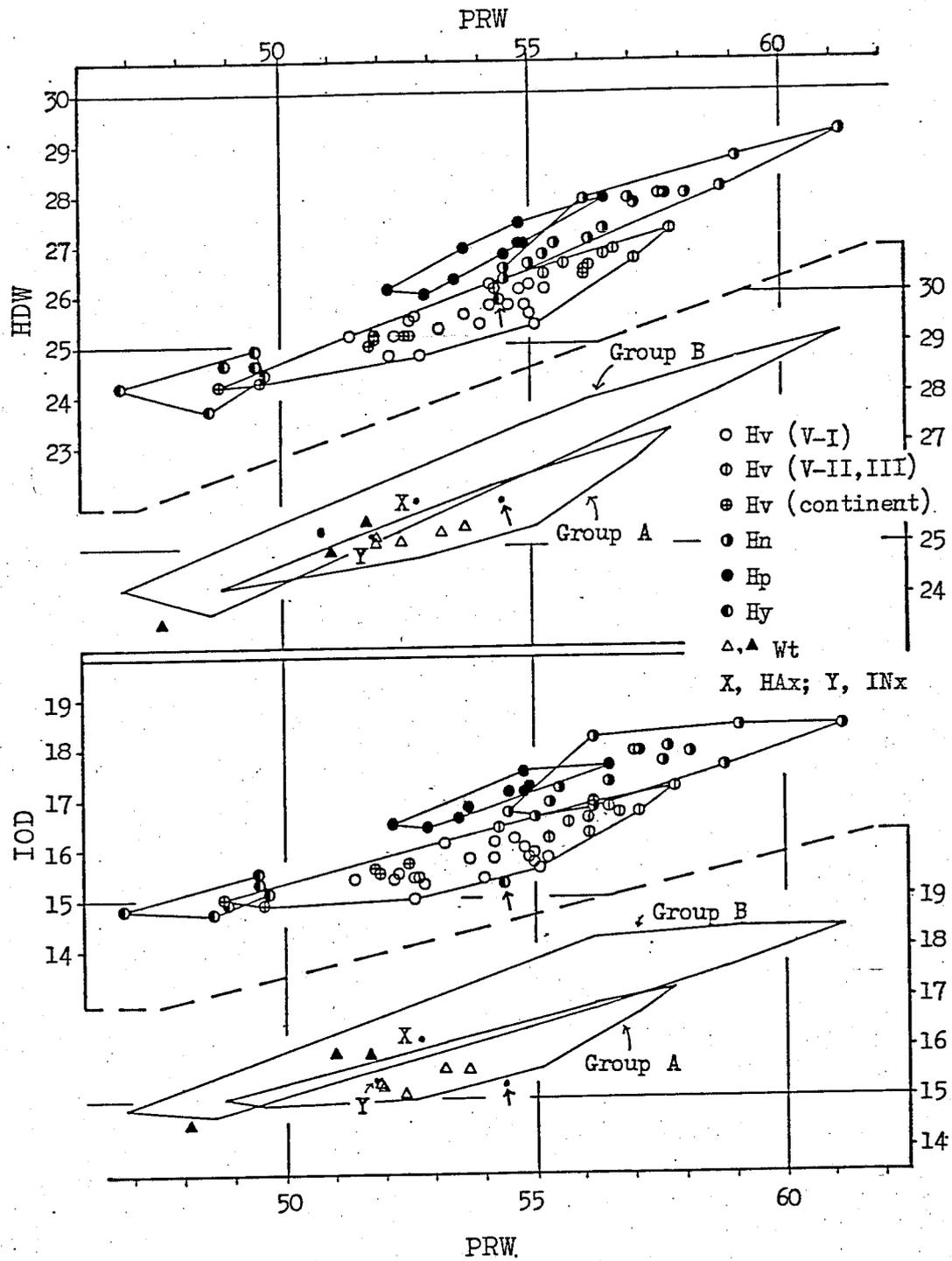


Fig. 146. Relation of head width (HDW, upper) and interocular distance (IOD, below) to pronotal width (PRW). Males. Each dot represents the mean value of each sample.

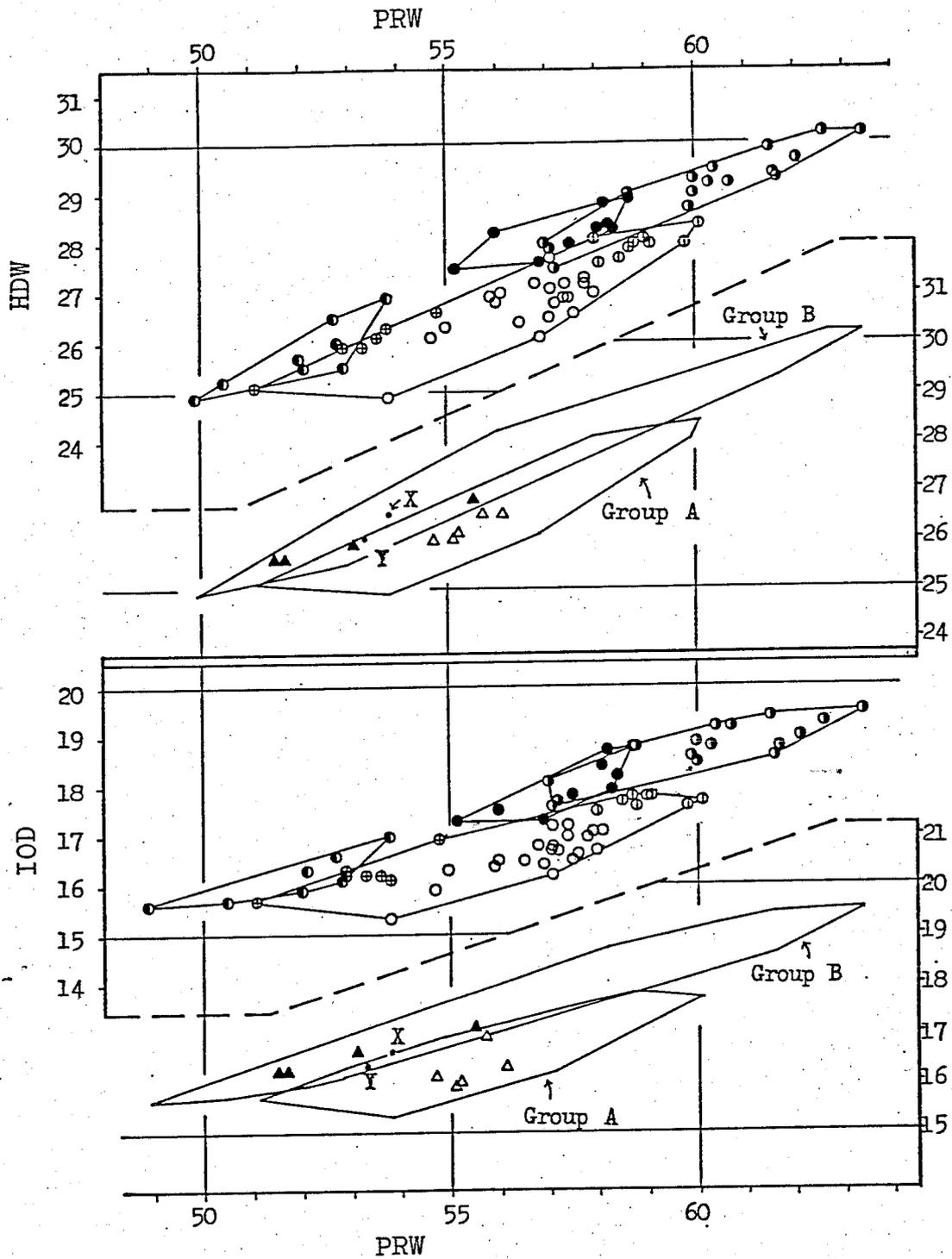


Fig. 147. Relation of head width (HDW, upper) and interocular distance (IOD, below) to pronotal width (PRW). Females. Other explanations as in Fig. 146.

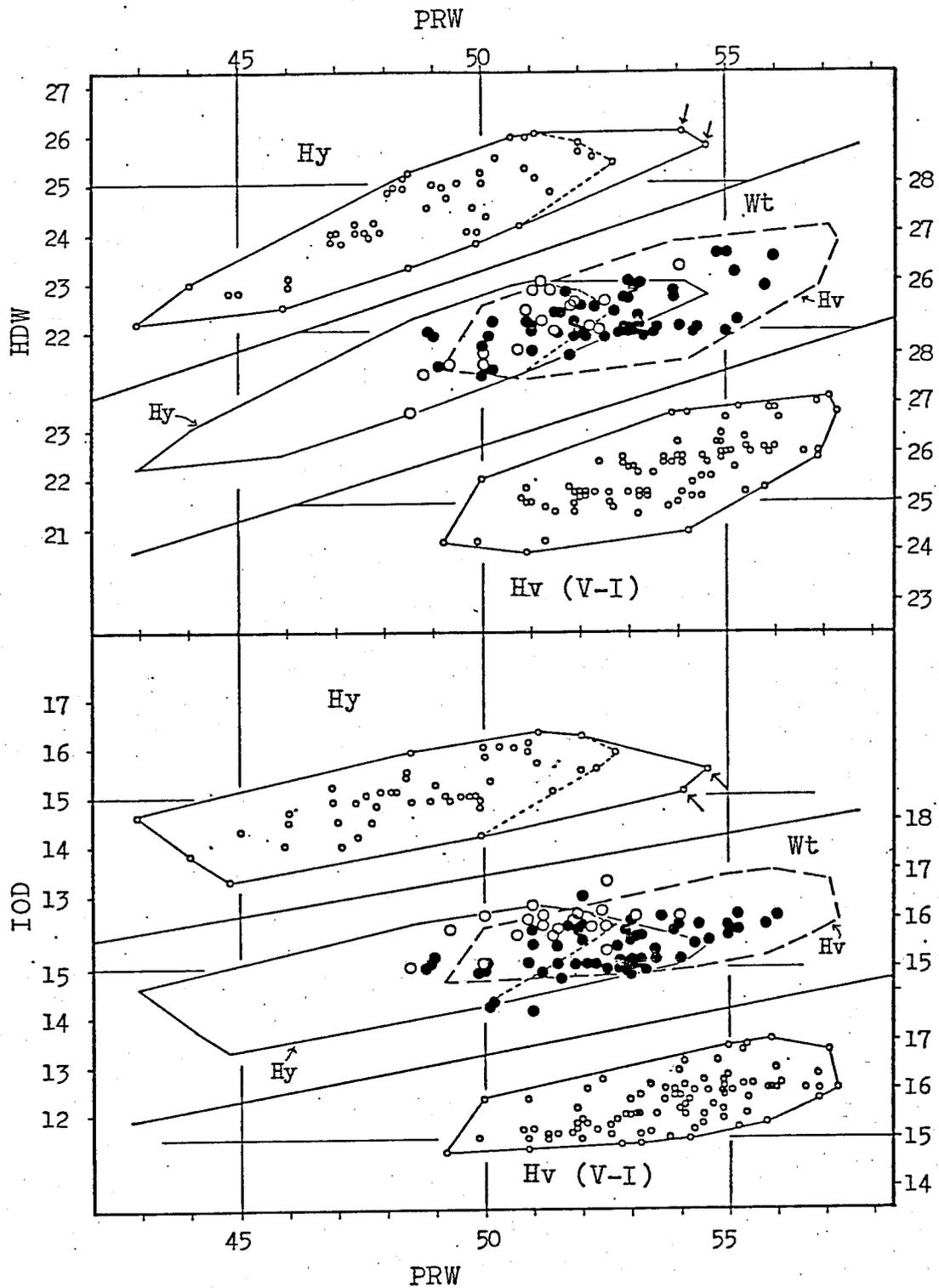


Fig. 148. Relation of head width (HDW, upper) and interocular distance (IOD, below) to pronotal width (PRW) showing individual variation of Hy (arrows indicates OTy's males), Hv (V-I) and Wt (open circle, from wild plants; solid circle, from potato fields). Males.

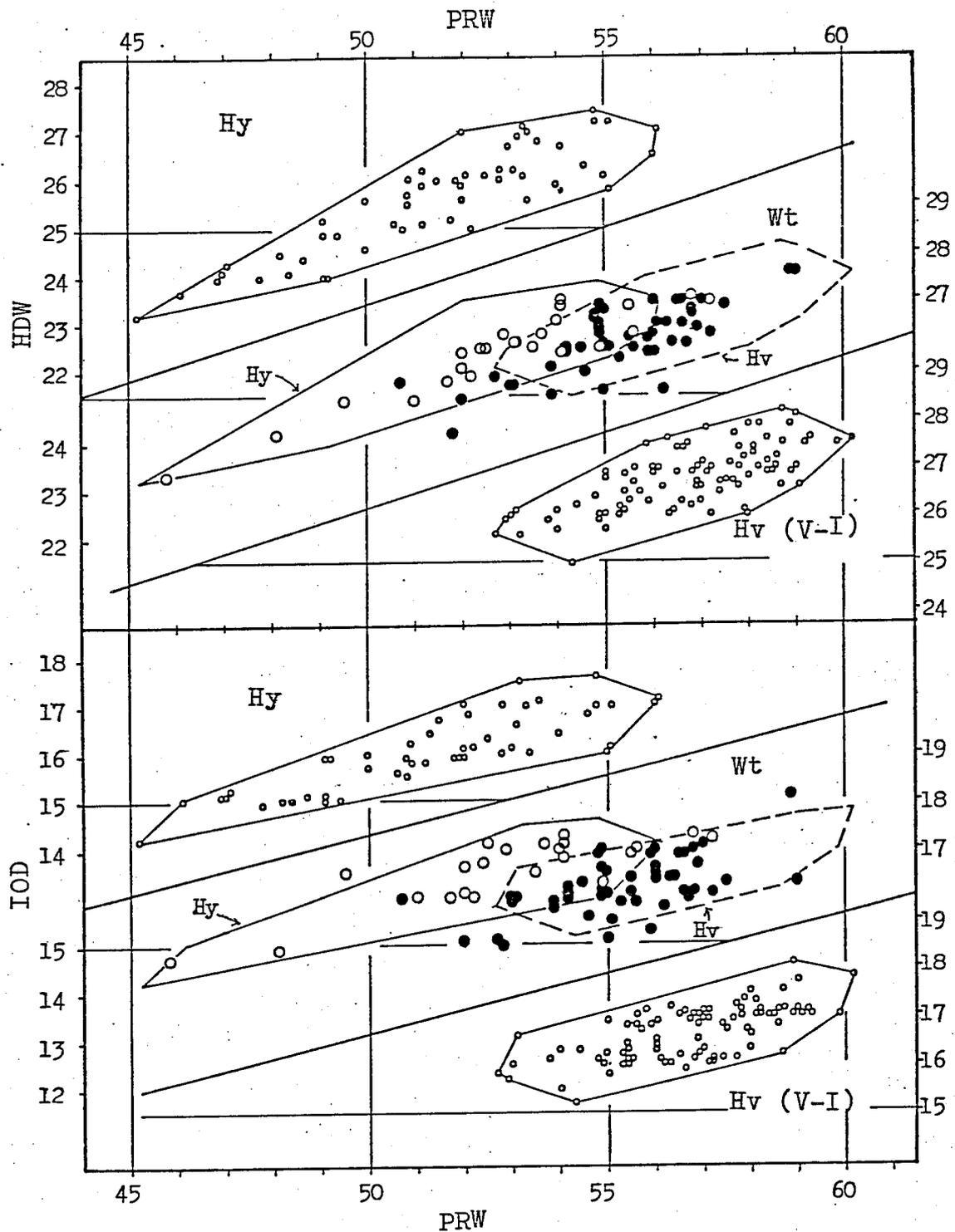


Fig. 149. Relation of head width (HDW, upper) and interocular distance (IOD, below) to pronotal width showing individual variation of Hy, Hv (V-I) and Wt (open circle, from wild plant; solid circle, from potato fields). Females. Further explanations in text.

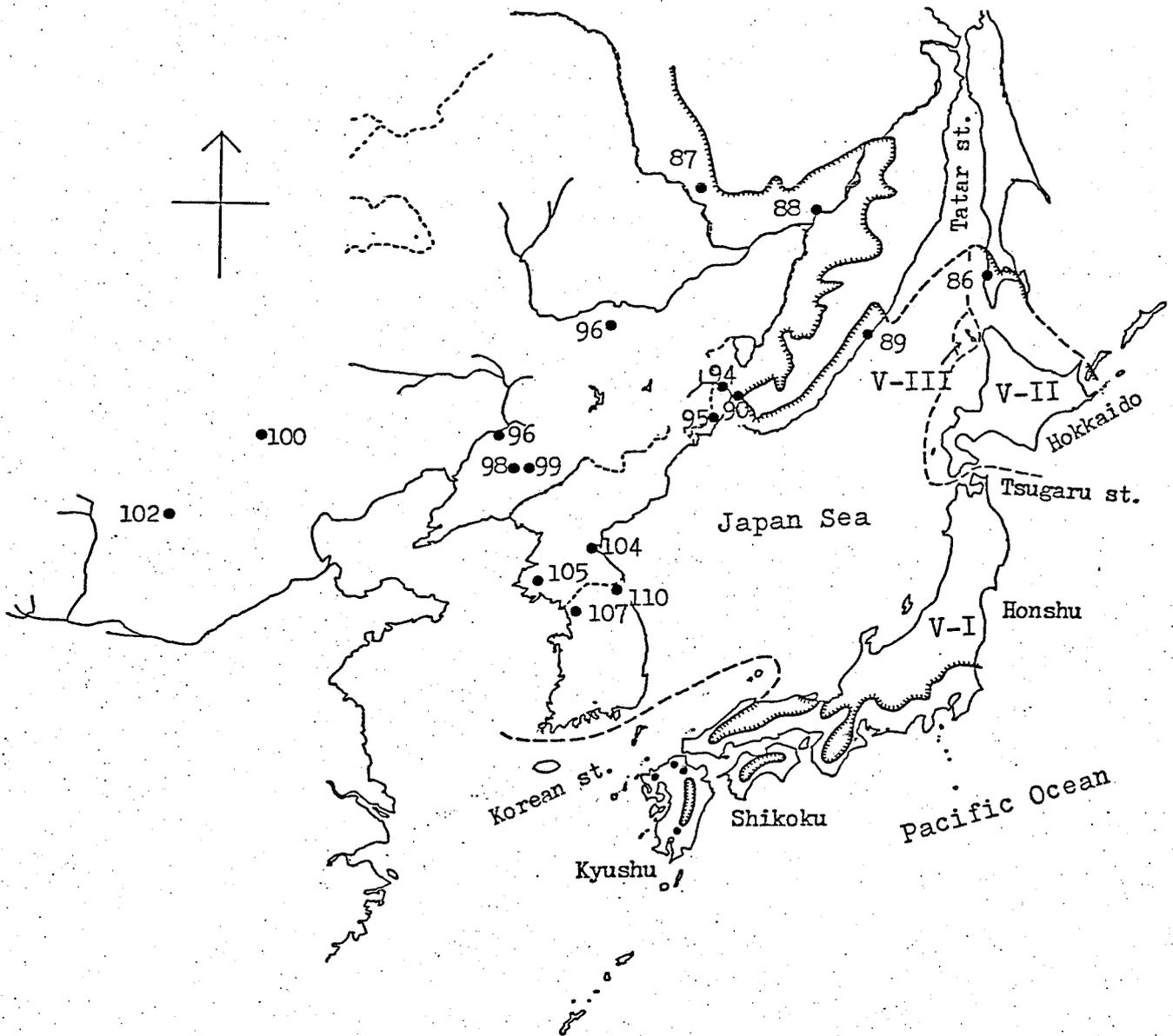
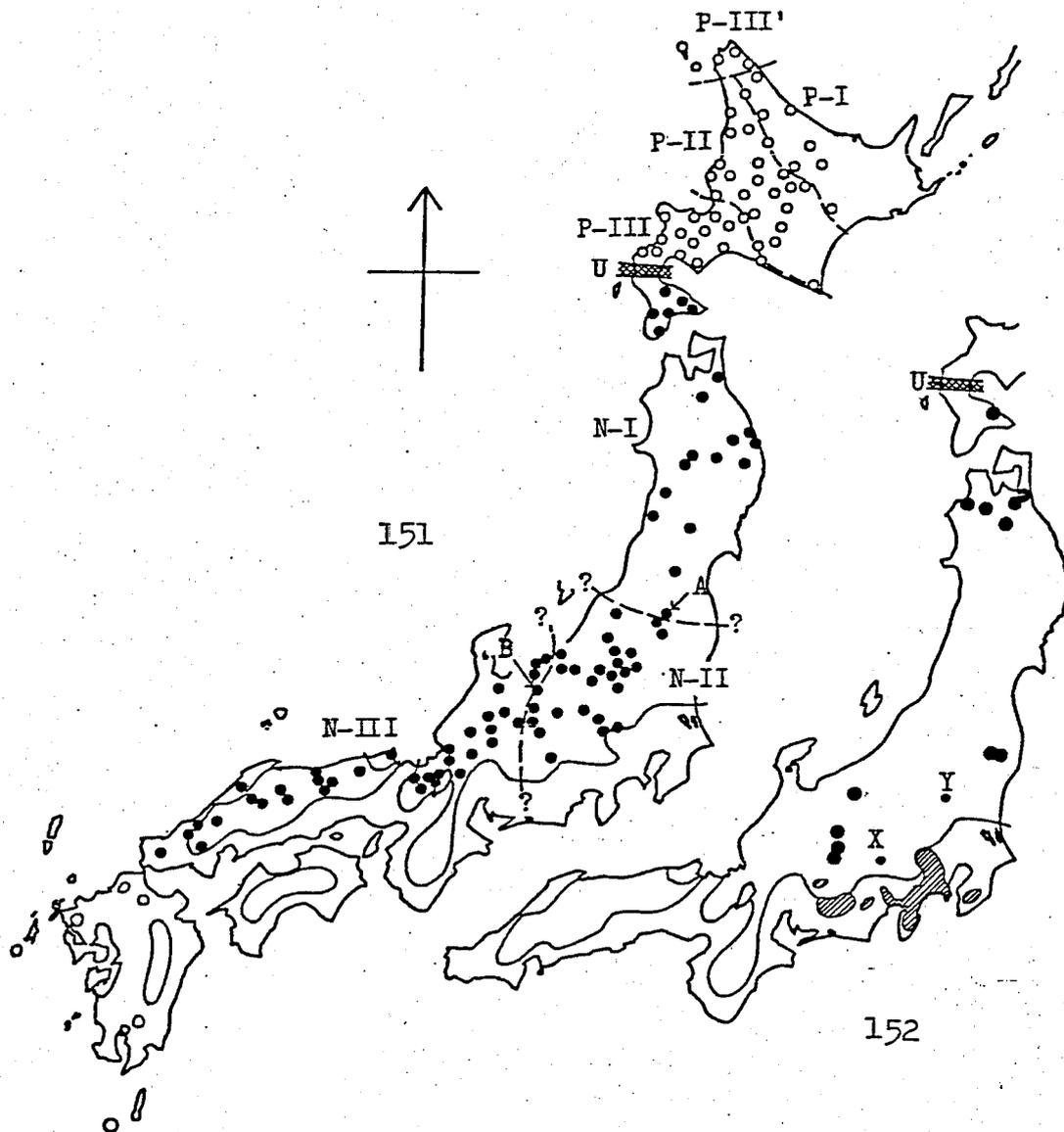


Fig. 150. Geographic distribution of H. vigintioctomaculata (group A). Provenance of some exotic material used for the morphological analysis is shown by the code numbers given in Appendix. Further explanations in text.



Figs. 151 and 152. Geographic distribution of the members of group B. 151: Hp (open circle) and Hn (solid circle). Broken lines show the approximate position of boundaries of forms. Contour line in southwestern part is the southern distribution limit of Hv. A: Urabandai, B: Amô pass. U: unoccupied zone by the thistle feeders. 152: Hy (solid circle) and unsettled populations, X=HAX, Y=INx, hatched=Wt.

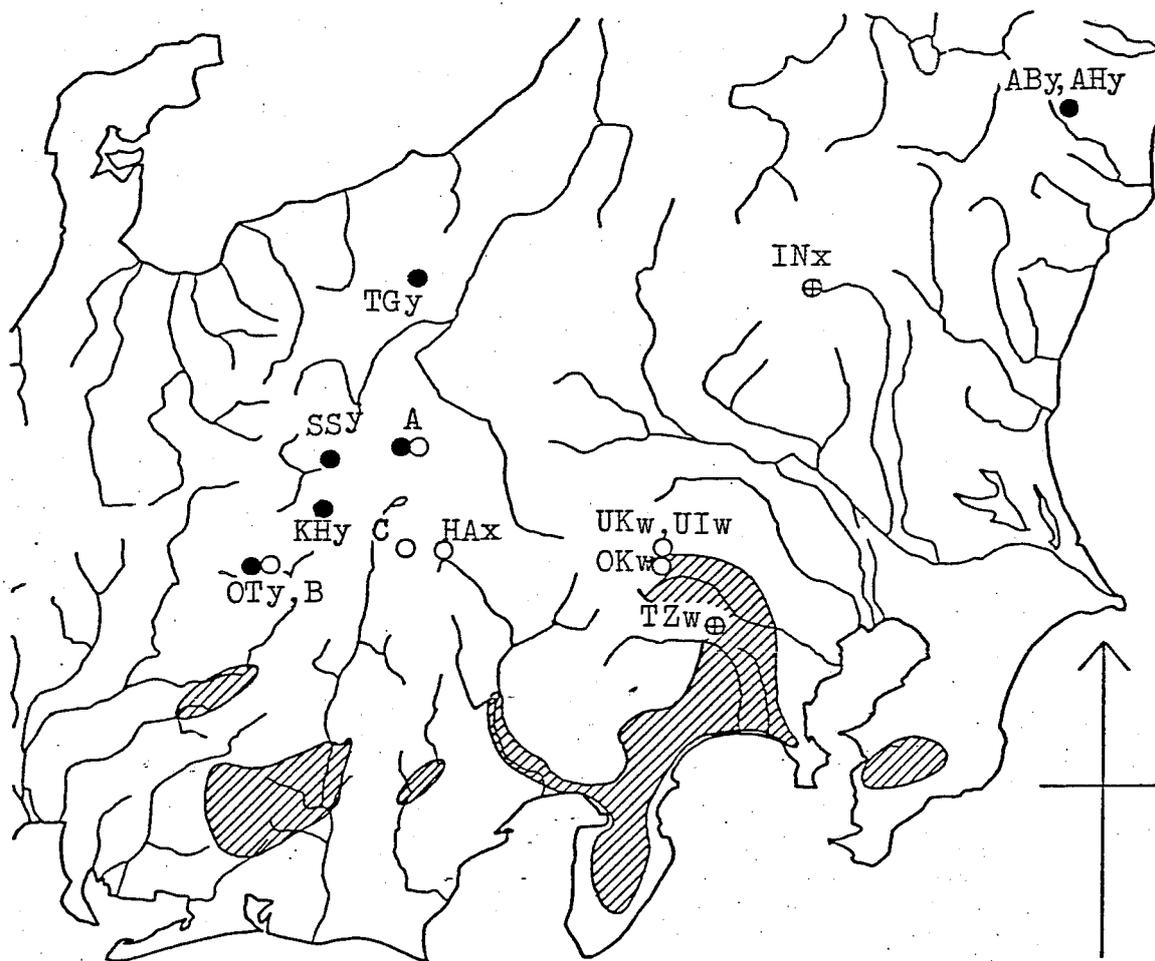


Fig. 153. Distribution of the unsettled populations and *H. yasutomii* in middle Honshu. ●: population feeding on blue cohosh, ○: on *Scopolia japonica*, ⊕: on *Chelidonium japonicum*. Hatched area: Distribution of Wt (Yasutomi 1976). A and B: Okukageyu and Otaki, respectively (Hara and Hamaguchi 1979), C: Takamori (Shirai pers. comm.). Further explanations in text.

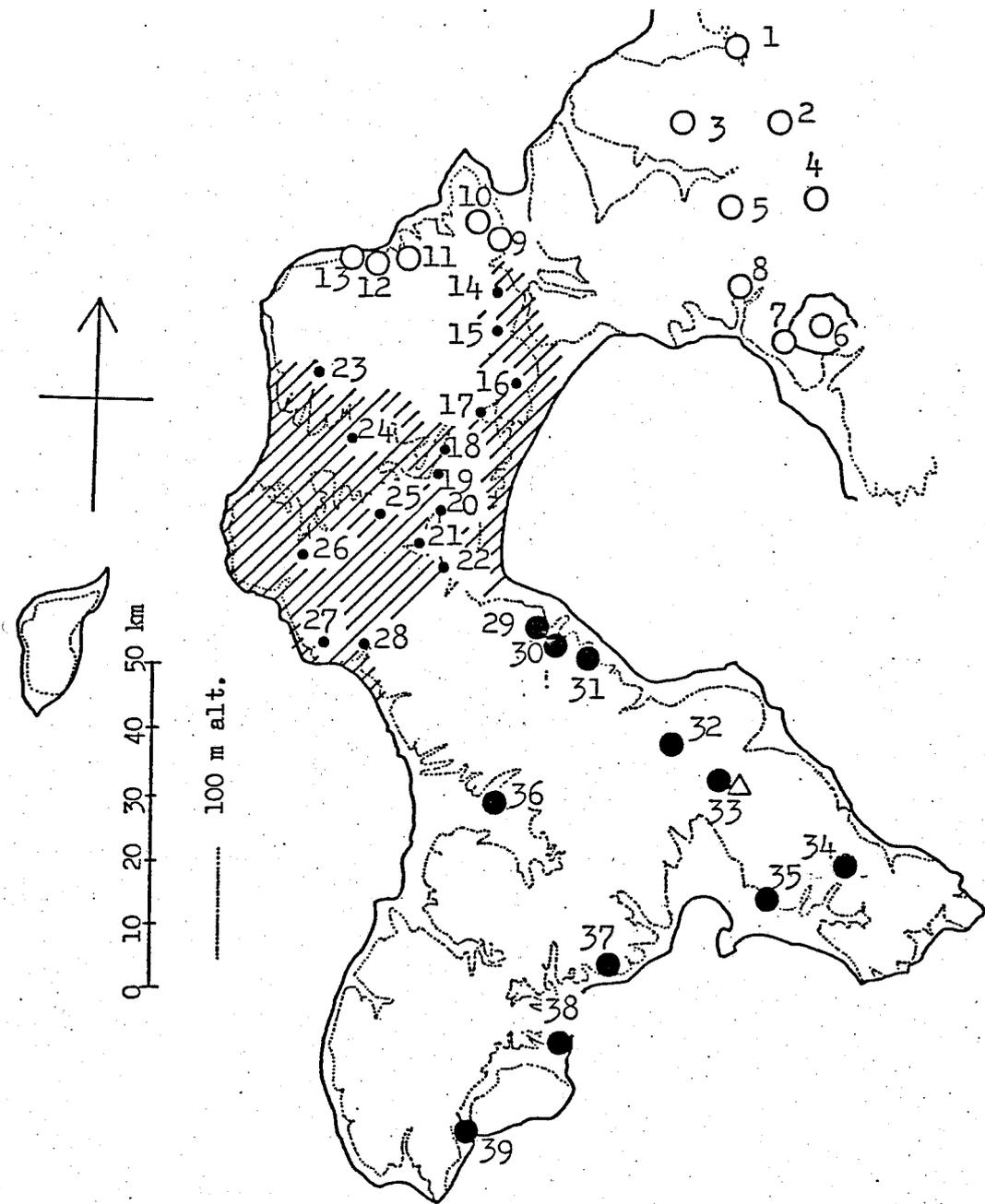


Fig. 154. Distribution of Hp (open circle) and that of Hn (solid circle) in the southernmost part of Hokkaido, showing an unoccupied zone (hatched area) by the thistle feeders. Triangle: Hy. Localities: 1 Kozawa, 2 Mt. Yôtei, 3 Niimi spa, 4 Makkari, 5 near Konbu, 6 Nakajima (Lake Tôya), 7 Tôya, 8 Toyoura, 9 and 10 Nakanokawa, 11 Tomari, 12 Chihase, 13 Harauta, 14 Kurokawa Rindô, 15 Futamata, 16 Riv. Monbetsu, 17 Inaho, 18 Hanaishi, 19 Nakawato-Shibunnai, 20 Tomisaki, 21 KamiYakumo, 22 Namarikawa, 23 Riv. Makomanai, 24 Imagane, 25 Imagane-Yakumo, 26 Nigorikawa, 27 Kannai, 28 Keni'chi, 29 Nodaoui, 30 Ginkonyu, 31 Nigorigawa, 32 Ohnuma Bokuzyô, 33 Ohnuma, 34 Kakkumi, 35 Masukawa, 36 Assabu, 37 Izumisawa, 38 Shiriuchi, 39 OshimaFukushima.

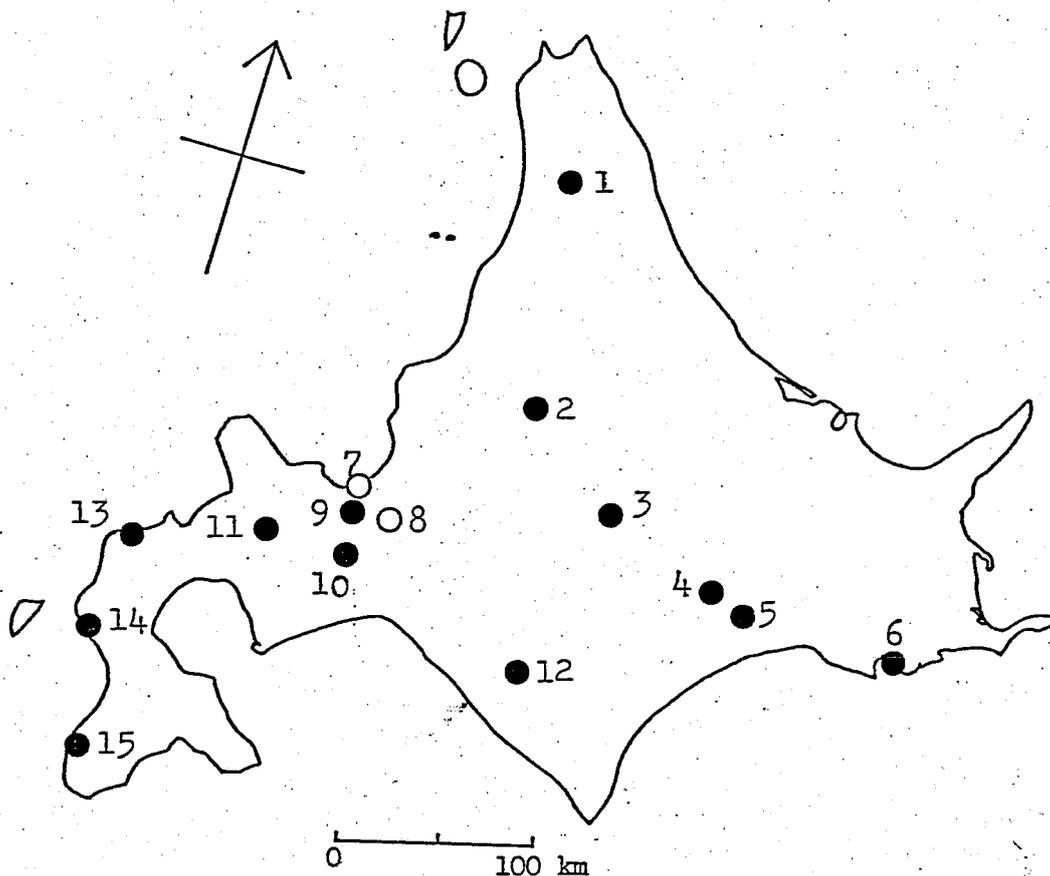


Fig. 155. Distribution of Hv (V-II) feeding on Schizopepon bryoniaefolius (closed circle) and on Solanum megacarpum (open circle). Localities: 1, Pankenai; 2, Kamuikotan; 3, Chikkabetsu; 4, Honbetsu; 5, Kami-Charo; 6, Akkeshi; 7, Barato; 8, Nopporo; 9, in and near Sapporo (Maruyama, Kobetsuzawa, Moiwayama, Nakanosawa, Tsunejizawa, Heiwa-no-taki, Hakkenzan, Kamuidake, Hôheikyo, Usubetsu); 10, Kôryû mine; 11, Mt. Yôtei; 12, Koiboku near Shizunai; 13, Chihase and Tomari (Shimamaki); 14, Kaitorima; 15, Ishizaki.

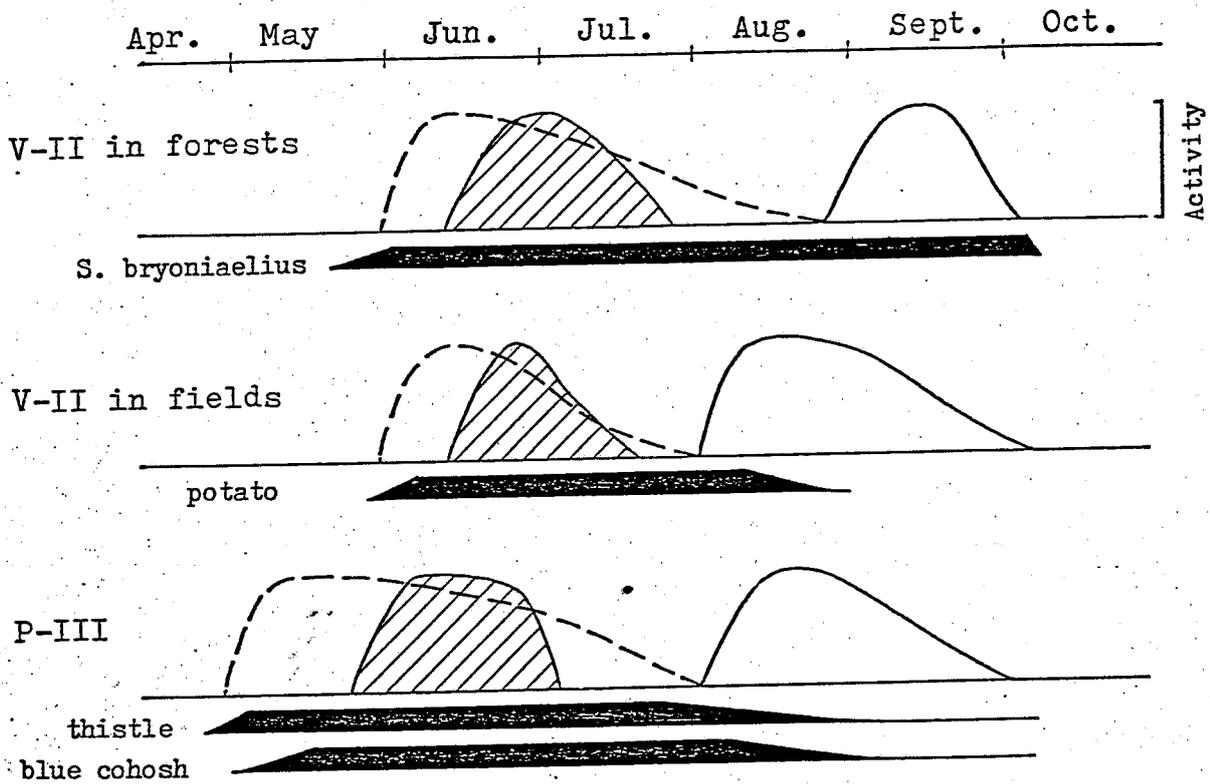


Fig. 156. Schematic life cycle trends of Hv (V-II) and Hp (P-III) and their host plants in and near Sapporo. Thick broken line: post hibernating adults. Thick line: newly emerged adults. Hatching: oviposition period.

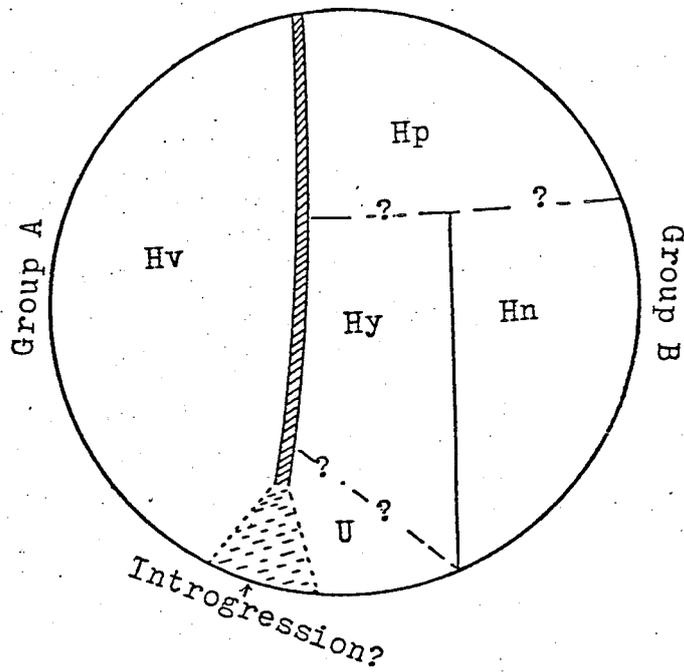


Fig. 157. Interrelationship of the members of Hv-complex. U: unsettled populations.

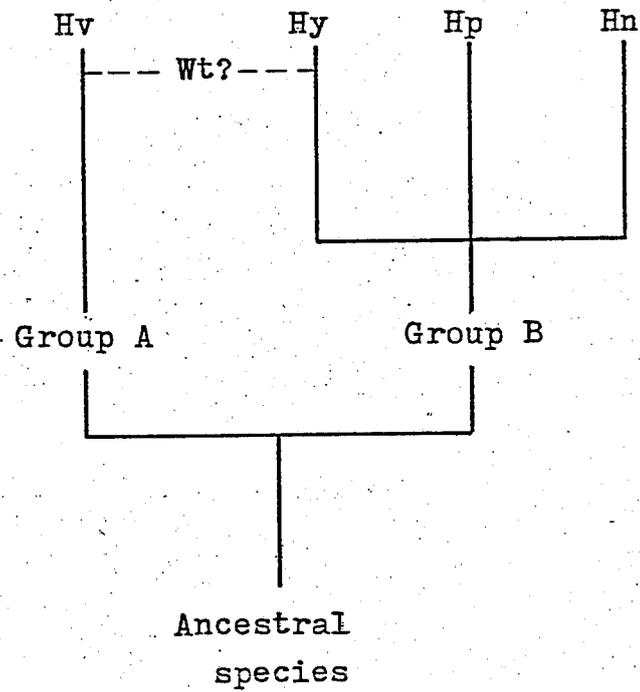
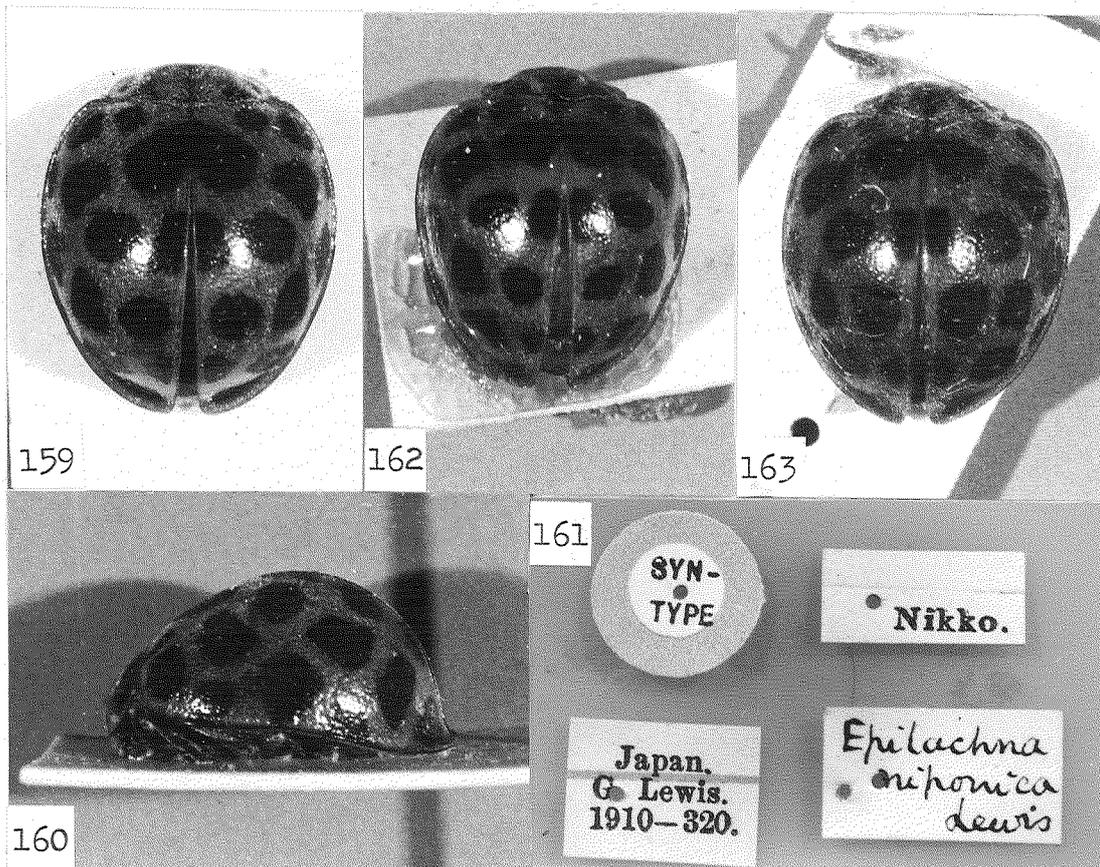


Fig. 158. Presumable phylogenetic relation of the members of Hv-complex.



Figs. 159~163. Syntype specimens of Epilachna niponica Lewis. 159~161: Nikko specimen and the labels attached to it. 162: Miyanoshiba specimen. 163: Junsai Lake specimen. Further explanations in text.

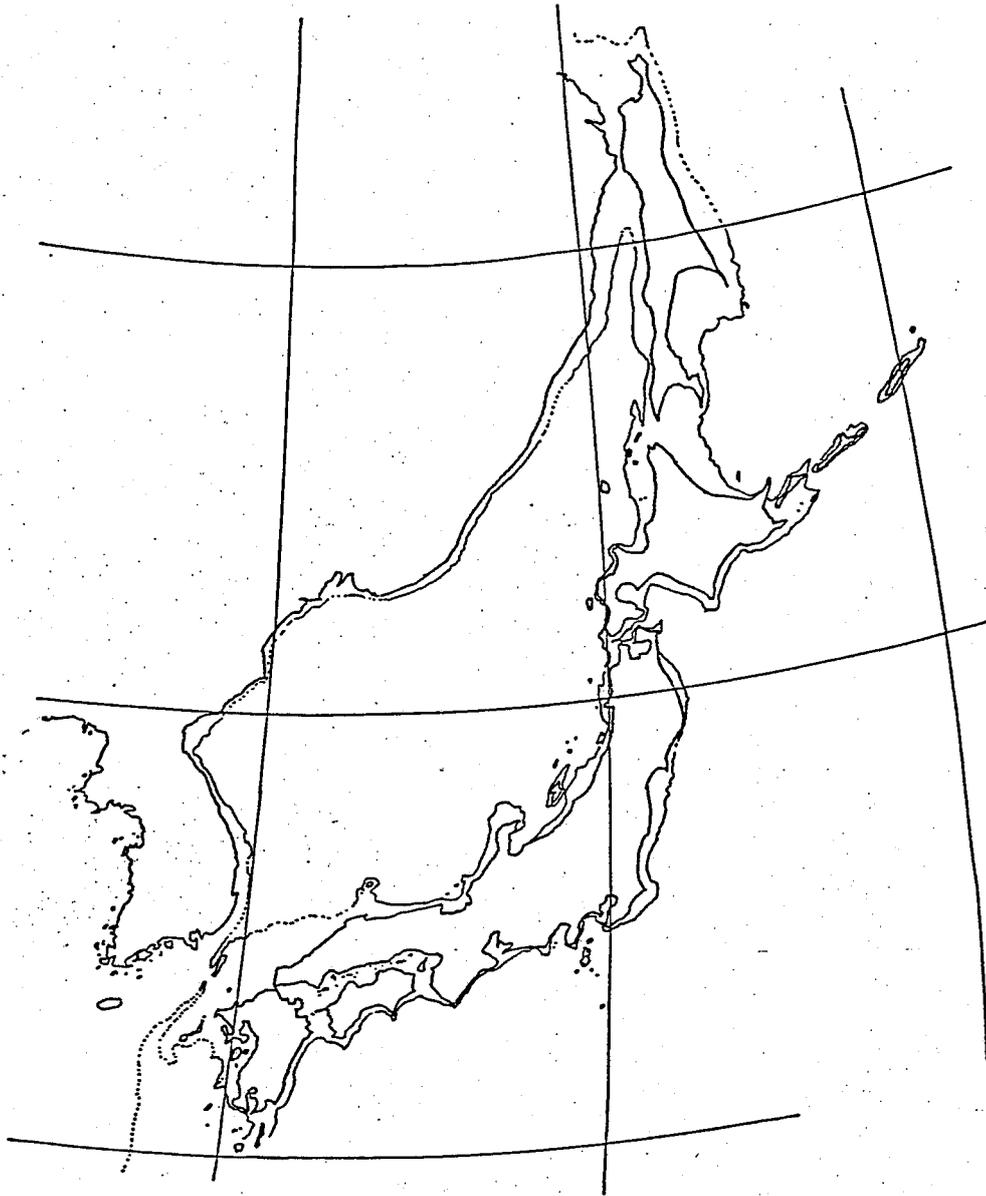


Fig. 164. The shore line around Japan in the mid main Würm ice age (after Minato 1972).

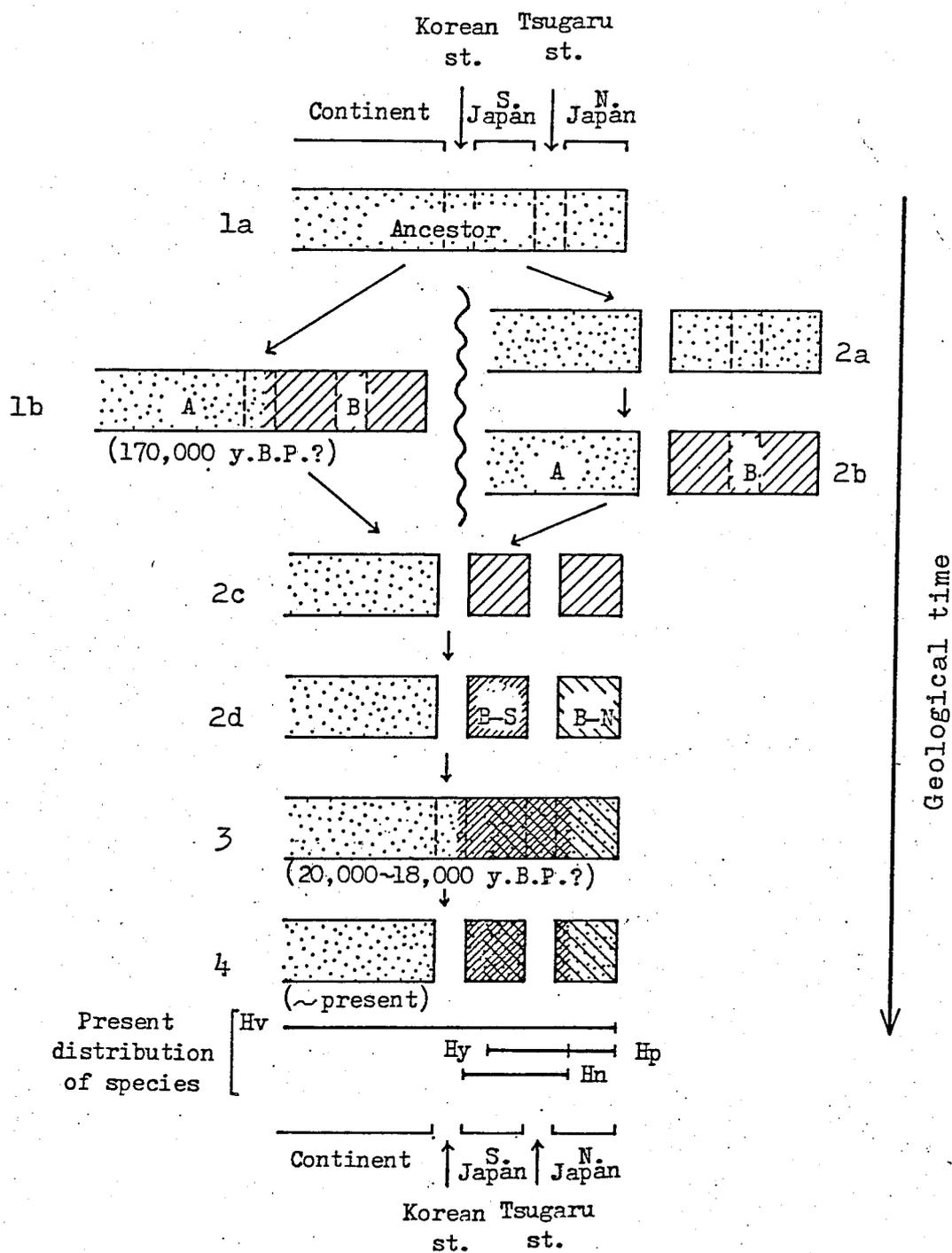


Fig. 165. Diagrammatic view of the evolution of Hv-complex. Two alternative interpretations (1a-1b-2c vs 1a-2a-2b-2c) are mentioned. Dotted: Common ancestor (1a and 2a), or group A (others). Hatched: Group B. In 2d to 4, light hatching shows group B-N (Hp and Hy) and heavy hatching, group B-S (Hn). Here Hy is tentatively regarded as the southernmost representative of group B-N invaded southern Japan in stage 3. Estimation of ages given to 1b and 3 based on Minato (1972). Further explanations in text.