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Observations on the Variability of Wing Venation in the Honeybees[1)]

By

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(With 4 Text-figures and 2 Tables)

The venation of insects has been adopted since Linné as one of the most useful classificatory criteria. While some characteristics of the venation are so stable that they can be used at the levels of families and other higher categories, others are rather variable among genera, species or even within species. Such grades of relative importance are also seen in the venation of Hymenoptera, particularly of the Superfamily Apoidea or bees (Lantham, 1951) Various bee genera were often erected mainly upon the basis of difference of venation. With respect to the honeybees, their venation is generally stable within the genus *Apis* (s. lat.), but some minor variations exist among races or even individuals. The racial difference of venation has recently been studied by some writers (For instance, Vecchi & Giavarini, 1950, etc.).

In the course of the writers' biometrical comparison of the European and Japanese honeybees (Akahira & Sakagami, 1959), they noticed a considerable variability in the material observed. As far as they are aware, some of such variations have hitherto been relatively unmentioned. But these minor variations are interesting in connection with the study of Zimmermann (1933), who mentioned similar variations in the wild bees and suggested their significance in the study of the mutations in the wild populations.

Material and Methods: The seven samples studied are same of those used in the previous work (Akahira & Sakagami, 1959). Namely, A,B,C,V are respectively workers, normal drones, drones from laying workers and drones from a virgin queen of the mixed Italian honeybee, *Apis mellifera ligustica* Spinola, while X,Y, Z are workers, normal drones and drones from laying workers of the Japanese honeybee, *A. cerana cerana* Fabricius. Each sample lot is made up of 50 individuals. A,B,C are all from a common mother queen, likewise as for X,Y,Z. In studying the specimens, the fore and hind wings were detached at the auxillary sclerites, mounted on slide glasses and observed under microscope usually the right wings alone. Terminology of the wing venation follows that of Lantham (1951).

Results

The wing veins of adults are chitinous tubules hollow except for the terminal

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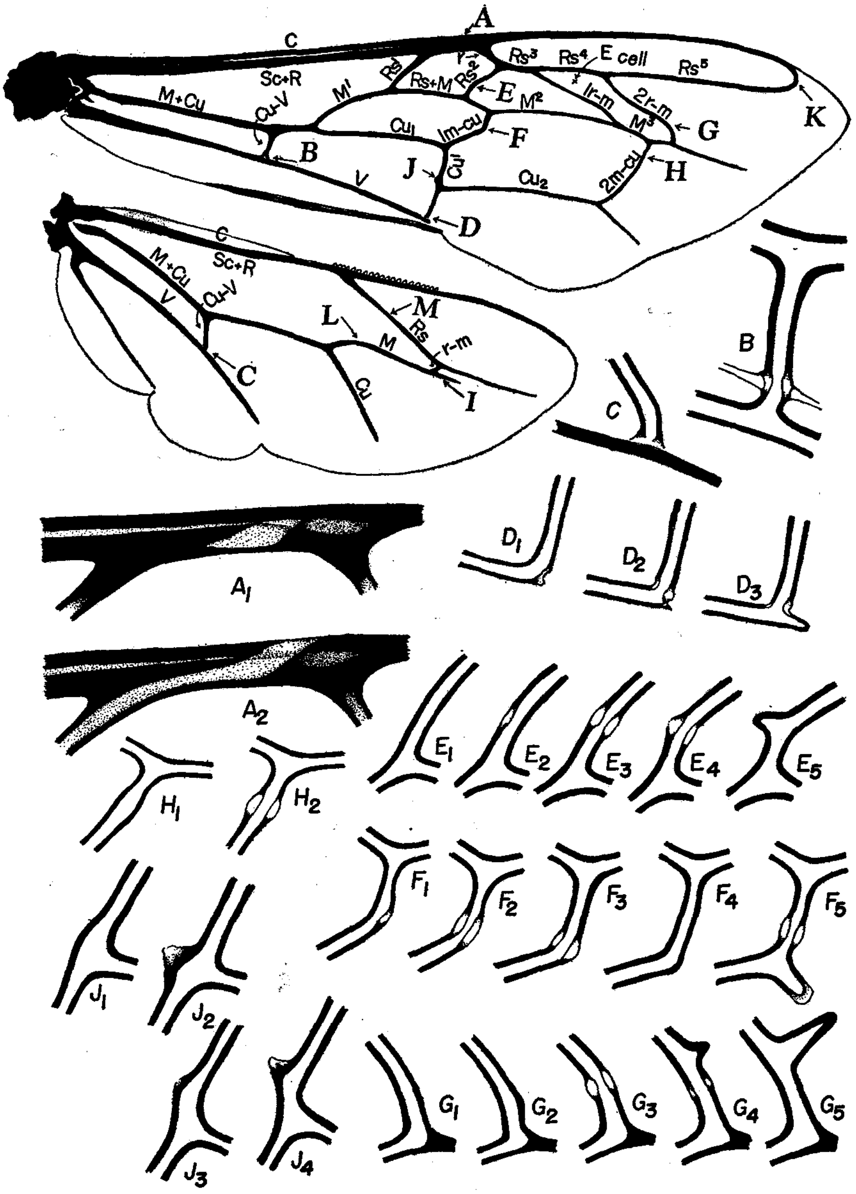

Fig. 1. Schematic representation of venation (above, with symbols of veins and, in larger letters, of positions observed) and various types of anomalies in positions *A*, *B*, *C*, *D*, *E*, *F*, *G*, *H* and *J* (Explanations in text).

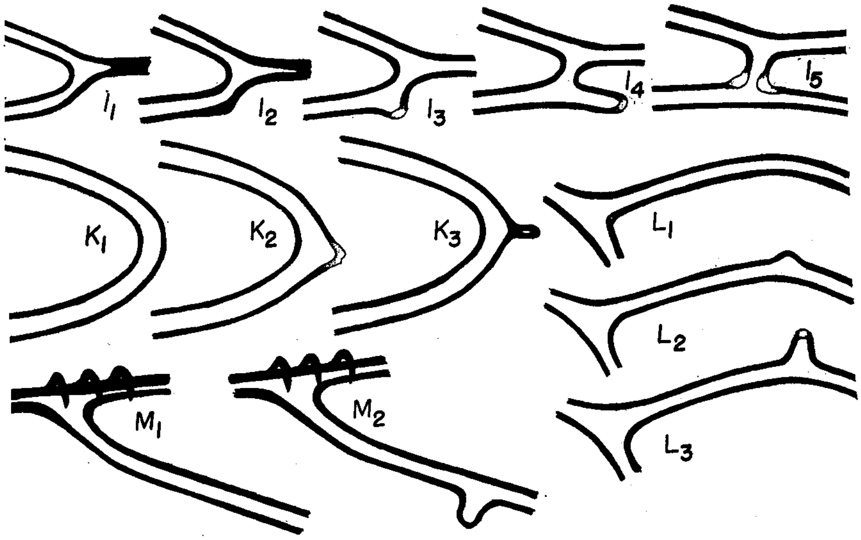

Fig 2. Various types of anomalies in positions *I*, *K*, *L*, and *M*.

parts. Length of each vein and its sections are considerably variable, as well as the angles between two adjoining veins. But the present paper does not deal with such metric characteristics but with the following two qualitative ones: dechitinization and protrusion. Dechitinization (*DC*) means a partial decrease of the chitinous deposition in some particular points of the veins. It shows from a mere pale appearance of the vein to a complete interruption. On the other hand, protrusion (*PR*) is the issue of an excess veinlet from certain positions of veins. The lengths of such veinlet vary according to cases, but usually they are not very long. These two kinds of anomalies appear in relatively fixed positions as described below. Such positions and types of anomalies are shown in Figs. 1 and 2, and the frequencies of each variation in Table 1.

Fore wing

A : Pterostigma caused by the fusion of C and Sc. *Al* : Normally chitinized. A_2 : *DC* at the middle of stigma.

B : Joining point of Cu-V to V.

D : Crossing point of V and Cu^1. D_2 : *DC* on apical side1) alone. D_2 : *DC* on both sides of vein. D_3 : *PR* of V, together with *DC*.

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1) The terms *apical* and *basal* are applied with respect to the basi-apical axis of wings.

Table 1. Frequencies (%) of variations among seven samples*

Species		*Apis mellifera*				*Apis cerana*		
Sexes and Sample marks / Variation		Worker (A)	Normal drone (B)	Drone from laying workers (C)	Drone from a virgin queen (V)	Worker (X)	Normal drone (Y)	Drone from laying workers (Z)
A	1	100	100	100	10	100	100	100
	2				90			
D	1		2			28	94	94
	2	2	76	30	10	62	6	6
	3	98	22	70	90	10		
E	1	88	52	44	22	56	44	72
	2	2	10	6	24	18	12	8
	3	6	6	8		16	32	4
	4	4	26	32	52	6	12	16
	5		6	10	2	4		
F	1	94		4	2			10
	2		92	58	74	86	88	80
	3	6	8	36	14	14	12	10
	4			2				
	5				10			
G	1	90	100	96	74	38	72	60
	2	2		2	22	18	20	20
	3			2	4		4	16
	4	4				28	2	4
	5	4				16	2	
H	1			22	4		2	6
	2	100	100	78	96	100	98	94
I	1	58	60	44	56			
	2	40	20	20	36			
	3	2	18	22				
	4		2	6	4			
	5			8	4	100	100	100
J	1	2	14	24	20			
	2	4	12	22	8			
	3	94	74	50	64	92	84	82
	4			4	8	8	16	18
K	1	66	100	90	36	60	72	42
	2	28		10	58	32	24	42
	3	6			6	8	4	16
L	1	98	84	78	32	100	80	76
	2	2	14	8	38		16	16
	3		2	14	30		4	8
M	1	100	100	92	98	100	96	90
	2			8	2		4	10

* As each sample consisted of 50 individuals, the absolute number may be obtained by halving the values listed.

F : Located on lm-cu near to Rs+M. F_1 : *DC* on apical side alone. F_2 : *DC* on both sides, with gentle curvature of vein. F_3 : *DC* on both sides, with acute flexion of vein. F_4 : Acute flexion of vein without *DC* nor *PR*. R_5 : *DC* on both sides, with external *PR*.

G : Located on 2r-m, near to Rs+M. G_1 : Neither *DC* nor PR. G_2 : Incipient *PR* on apical side. G_3 : *DC* on both sides. G_4 : *DC* on both sides, with distinct *PR* on apical side. G_5 : Prominent *PR* without *DC*.

H : Located on 2m-cu, near to Rs+M. H_1 : Neither *DC* nor *PR*, with slight swelling of tube walls. H_2 : *DC* on both sides.

J : Crossing point of Cu_1 and Cu_2. J_1 : Neither *DC* nor *PR*. J_2 : Slight *PR* on apical side. J_3 : Constriction of vein, neither *DC* nor *PR*.

K : Apex of radial cell. K_1 : Neither *DC* nor *PR*. K_2 : With *DC* and slight *PR*. K_3 : *PR* without *DC*.

Hind wing

C : Joining point of Cu-V to V. Corresponding to *B* in fore wing.

I : Crossing point of r-m and M. I_1 : M without *PR* nor *DC*. I_2 : With rudiment of *PR*, without *DC*. I_3 : Incipient *PR*, without *DC*. I_4 : Distinct *PR* with *DC* at apex. I_5 : Long extension of *PR* with *DC* at crossing point.

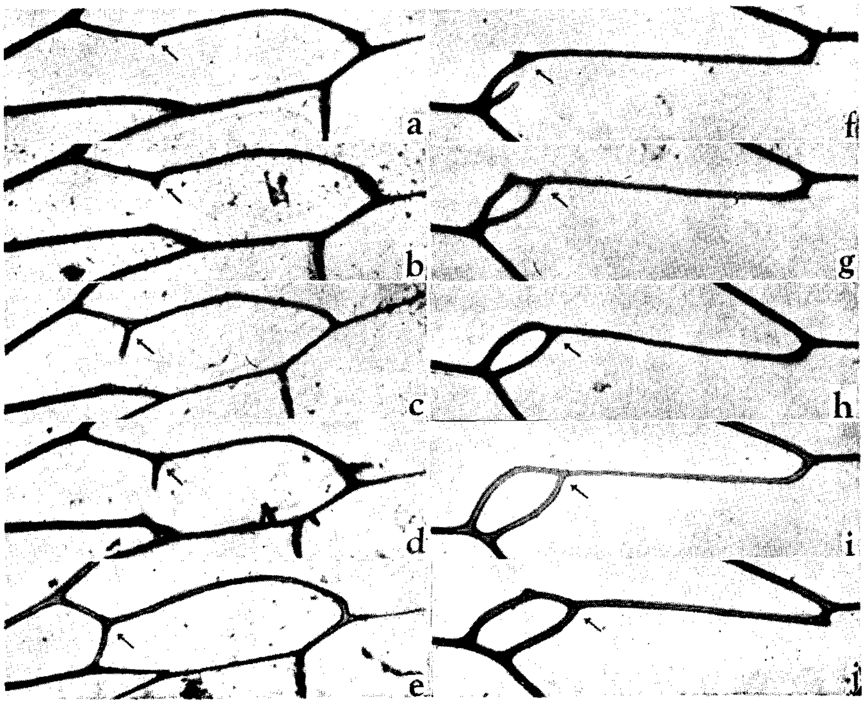

Fig. 3. Formation of secondary cells observed in E cell (left) and *L* (right) in Sample V. (*Cf.* Fig. 1)

The frequencies of these variations markedly differ from case to case. *B* and *C* are provided with *DC* in all samples without exception. A_1 was found only in V but with a remarkable rate. *H*, *L* and *M* are also fairly constant except for the drones from laying workers. The other characteristics showed a considerable variability as follows:

D: There is a distinct tendency of interspecific difference. The Appearance of D_3 was fairly frequent in *A. mellifera* except for normal drones (B), while rather rare in *A. cerana*. Further, the appearance of D_1 is relatively rare in workers in both species. B differed from all other samples by the opposite ratio of D_2 : D_3.

E: This position showed a wide and irregular variation among samples. *PR* seems to be very frequent in drones of *A. mellifera*, but not always in *A. cerana*. The lack of both *PR* and *DC* is highest in A, then in Z!

F: This position, too, is provided with a complex variation mode. *A. mellifera* workers differ from all others by the weaker dechitinization and relatively gentle bending of the vein concerned. The variability is rather prominent in the abnormal drones.

G: Zimmermann (1933) pointed out the issue of *PR* in this position as one of the commonest variations in the bees and other related Aculeata. In the present samples, a distinct *PR* was much frequently observed in the workers and in *A. cerana* than in other samples. Interesting is the higher uniformity of B as to this position. A similar tendency is seen in *K*, too.

I and *J*: These are outstanding for the clear interspecific difference. Especially in *I*, while *A. cerana* always issues a long veinlet, *A. mellifera* seldom has such distinct protrusion, although the rudimentary trend is detected.

Consequently, it may be said that some characteristics clearly differ between species, while others between sexes. Further, it is noticeable that the abnormal drones show a complicated variability in general.

Besides these relatively frequent variations among samples, unusual anomalies were observed in V, which was also characteristic by the exclusive and abundant appearance of A_2: The first case is the division of the 3rd submarginal

Table 2. Formation of secondary wing cells found in Sample V (Types of anomalies a-j are shown in Fig. 3).

	Symbols of individuals in which anomalies were observed (lateral symmetry is shown with italic) (cf. Fig. 3)					Total individual nubmer
	a	b	c	d	e	
Right	*4*, 28, 31, 45	*6*, 38, 44, *4*	13, *33*	19, *29*, *41*	*14*, *43*	14
Left	3, *6*, 17, 27	*4*, *29*, 30	*33*	*14*, *41*, *43*	12	12
	f	g	h	i	j	
Right	3	2, 39	28	26	*30*, *31*	7
Left				*30*, *31*		2

cell of the fore wing (E cell in Fig. 1 above) by the extension of a veinlet from 2r-m. In length such veinlets vary from one to another, but the positions of issue were fairly fixed. Fig. 3, a-e show the gradual steps from incipient protrusion to complete division of the cell. Corresponding to the development of the veinlet, the gradual acuteness of bending of 2r-m and the occasional issue of *PR* from the opposite vein 1r-m were observed as in the figures.

The second case is a similar formation of an abnormal cell near the confluence of M and M+Cu in the hind wing (Fig. 3, f-j). As indicated in the figures by arrows, often a fine *PR* is formed in the direction opposed to the loop finally derived. While the form and situation of M itself are not altered from the normal case in f, M is slightly translocated in other cases, corresponding to the formation of the loop. The points indicated by arrows accord to *L* in Fig. 1. In Table 2, the individuals which developed such two variations are listed as to both wings. Although there is no significant difference regarding the lateral asymmetry of the variations observed in fore and hind wings, the frequencies of both variations show a highly significant diference ($P < .01$). On the other hand, the individuals which possessed the anomalies in both right and left wings were 46.2% and 44.5% in fore and hind wings respectively. These values suggest independent mechanisms governing these two anomalies, but a common mechanism as to their symmetrical appearance.

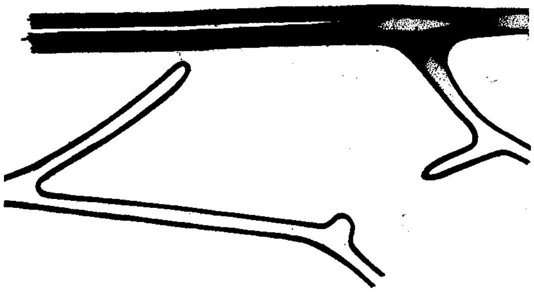

Fig. 4. Partial interruption of veins Rs^1 and Rs^2 found in Sample V.

The third and final case is the partial interruption of Rs^1 and Rs^2 in the fore wings (Fig. 4). Although only two examples were obtained, the probable occurrence of a factor which tends to evoke such interruption is noticeable.

Discussion

All variations detected by the present writers can be classifed into the following three types.

Type I: With DC: $A_{1,2}$, B, C, D_{1-3}, E_{2-4}, $F_{1,3;5}$, $G_{3,4}$, H_2, I_{3-5}, J_{2-3}, K_2, L_3.
Type II; With PR: D_3, $E_{4,5}$, $F_{4,5}$, $G_{4,5}$, I_{2-5}, $K_{2,3}$, $L_{2,3}$, M_2.
Type III: Without DC nor PR: E_1, G_1, I_1, J_1, K_1, L_1, M_1.

The variations including both DC and PR are D_3, F_5, G_4, I_{3-5}, K_2 and L_3. Among them, a common causal mechanism is conceivable in $I_{3,4}$ K_2 and L_3 where DC occurs just at the points of the issuing of PR. In other instances, however, the common causal mechanism is also probable but evidence is still insufficient to prove it. Although the direct causal mechanism of such anomalies must be sought by means of observatins during metamorphosis, it may indubitably be connected with the weak deposition of chitin during the post pupal stages, in which the rudiments of venation are still plastic. It is interesting that both dechitinization and protrusion are usually prominent on the apical sides of the veins, suggesting the stronger pressure acting in this direction.

The constancy of the positions where the anomalies appear is remarkable. Maa and Shao (1947) discovered similar variations in both *Apis cerana* Fabricius (of the populations of South China, mainly of Fukien, consisted of 1507 worker specimens observed) and *A. indica skorikovi* Maa (of the population of Darjeeling, consisted of 75 workers observed)[1]. The frequently observed anomalies in their material were in the following order: K_{2-3} (= B, C in their definition, ca. 15.8 %) > G_{2-3} (= G, H, I in their definition, ca. 12.4 %) > those in 1r-m (ca. 5.4 %) > F_{1-2} (=J in their definition, ca. 4.34%) > H_2 (=K in their definition, ca. 0.03 %)> those in 2m-cu (0.03 %) in the South Chinese populations, and F_{1-2} (Ca. 30.5 %)> G_{2-5} (Ca. 16.9 %) > those in 1r-m (Ca. 14.7 %) > those in 2 m-cu (Ca. 12.8 %) in the population of Darjeeling. On the other hand, there are found in writers' own material, as far as those variations described by Maa and Shao alone are considered, K_{2-3} (34%) and G_{2-5} (10%) in *A. mellifera*, and K_{2-2} (40 %) and G_{2-5} (31 %) in *A. cerana*.

The higher rate in the appearance of the appendiculate radial cell (K_{2-3} except for the population of Darjeeling) and the protrusion from 2r-m (G_{2-5}) is common to all samples. On the other hand, the appearance of abnormal 1r-m was very frequent in the South Chinese populations, while it was almost never found in others. The anomalies of 1r-m were very frequent in the material studied by the Chinese writers, but never in the writers' own. Further, Maa and Shao did not refer to the variations found in J and E, perhaps due to the lack or scarcity of anomalies in these positions, nevertheless such were rather frequent in the writers' observations. Unfortunately, the writers' samples of workers were taken from only one colony in both species; it cannot be determined whether such differences are of the ture racial or specific type, unless further comparisons among many colonies are carried out.

Higher appearance of variations in G is interesting, because this position

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[1] Later this subspecies (nom. nud.) was regarded as identical to *A. cerana* Fab. (Maa, 1953).

was already suggested by Adolph (1880, according to Zimmermann, 1933) as one of the most variable points in the venation of bees and other Aculeata, found in the majority of the well-known genera such as *Anthophora, Apis, Bombus, Eucera, Nomada, Dufourea, Andrena, Halictus, Colletes, Sphecodes, Megachile, Osmia, Anthidium, Heriades*, and further in *Vespa, Odynerus*, Scoliidae, Mutillidae). The other positions of high variability shown by Zimmermann are 1r-m, 1m-cu, and 2m-cu, which are partially proved in the present study, or in Maa and Shao (1947) in the honeybees, too. Further, the formation of a secondary wing cell found in sample V is also reported by Zimmermann in *Bombus muscorum*.

As to the sexual difference in the frequencies of variations, Maa and Shao reported that the anomalies are very infrequent in the drones. This does not always correspond to the writers' results. As shown in Table 1, the relative frequencies vary from sample to sample in a fairly complicated manner. Such sexual difference of variations was analysed with various wild bees and its significance in detecting the recessive mutations was discussed by Zimmermann (1933). Owing to the peculiar sex determination in higher Hymenoptera, the males of this group are always haploid, being deviod of the father. Therefore, if a recessive mutation $A \rightarrow a$ occurred in one particular character, the genetic make-up of the offspring may be either 1) $(Aa+AA)$♀ and $(A+a)$♂ in the case of $Aa \times A$, or 2) $(Aa+aa)$♀ and $(A+a)$♂ in $Aa \times a$. The ratio of the phenotypic appearance of the recessive genoptye a in males may remain of the same magnitude in both cases, but may vary in females according to the ratio a/A, which may affect the female's chance to mate with the recessive male. If a/A is sufficiently small, the phenotypic appearance of a may be larger in males than in females. Inversely, such sexual difference may serve as a useful index to suggest the occurrence of a recessive mutation without experimental analysis. Comparing various specimens of wild bees, Zimmermann found such sexual difference in several wing characteristics including G and H mentioned in the present paper, and suggested their mutative nature. In the present sutdy, such sexual difference was relatively rare except for L in both species, and F in *A. mellifera*, although the range of variability were in general wider in drones than in workers.

This observation suggests either 1) the variability caused not only by the genetic, but also by the non-genetic factors, or 2) the wide distribution of the recessive mutations if considered according to Zimmermann, and further, 3) the more complicated nature of the genetic mechanism governing the phenotypic appearance, affected by the occurrence of dominant mutations or much complicated alleles. Such complicated mechanism is assumed from the comparisons between normal and abnormal drones in both species. It is remarkable that the frequency of anomalies varied between them of the same strain (except for V). At present, it cannot adequately be explained whether such difference was caused by the development of mutative changes, or by the effects of environmental factors. The third possible explanation, the occurrence of biparental males in the normal drones seems to be less plausible, because such diploid males proved in *Habrobracon* were not obtained in the experiments conducted by Mackensen (1951),

Consequently, the origin of various anomalies found in the honeybees must be sought in further studies. However, it is probable, that some anomalies such as found in *G*, *H* and *E* are of mutative origin, as suggested by Zimmermann. He pointed out that some of such supposed mutations might be fixed during the course of evolution and serve as taxonomic criteria. In certain bee genera such as *Nomada*, *Halictus* and *Andrena*, subgenera have been often erected based upon such wing *anomalies*. Perhaps, a similar mechanism may be expected for the extension of the vein M in the hind wings beyond the conjunction with r-m, which has been used as one of the most useful morphological characteristics to distinguish the European and Asian honeybees (Cf. Tokuda, 1924, Maa, 1953, Akahira & Sakagami, 1959), and in a lesser degree, for *J* and D, which also varied according to species in the present study.

Summary

Some observations were made on the variability in the dechitinization and protrusion of veinlets in the wing venation of the honey-bees, both European and Japanese forms. The frequencies of variations are diverse among characteristics, species and sexes. But there are certain regularities in the relative abundance of some anomalies. Further considerations were given as to the origin and significance of such anomalies.

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The wing veins of adults are chitinous tubules hollow except for the terminal

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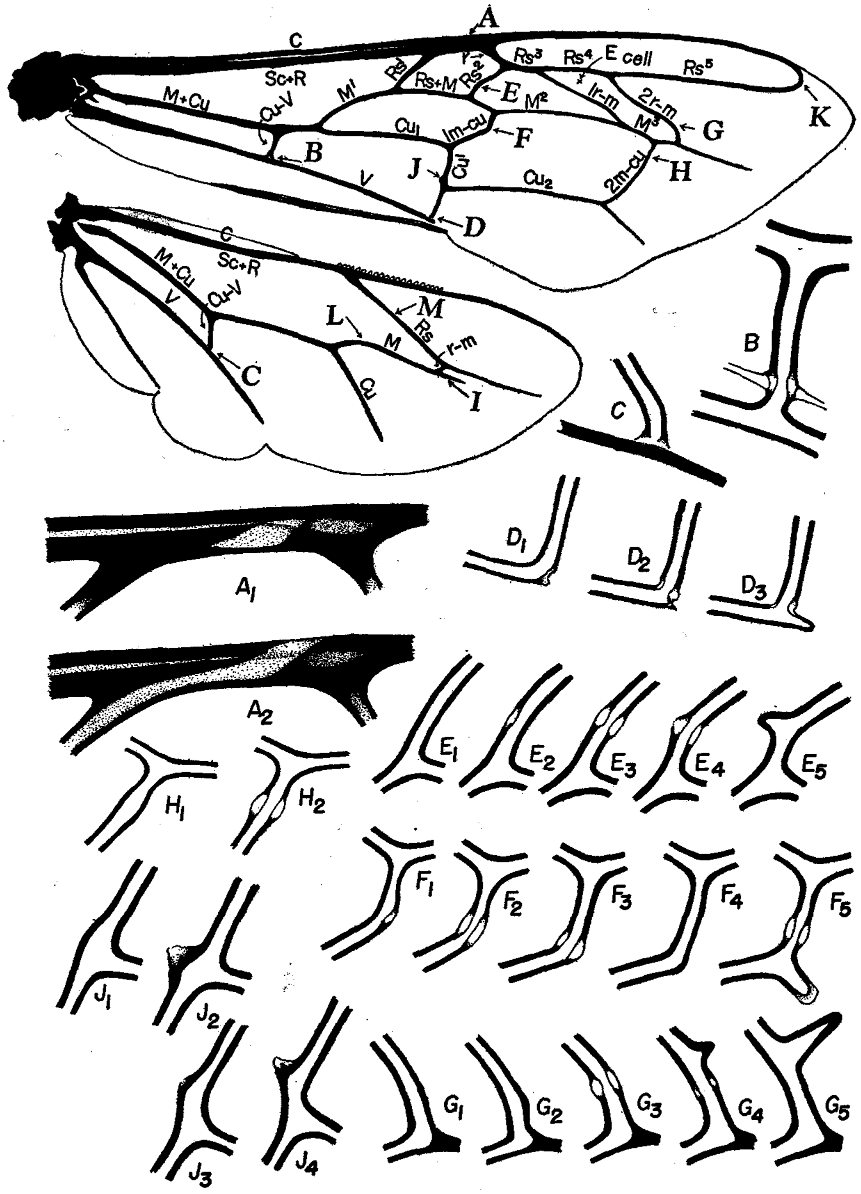

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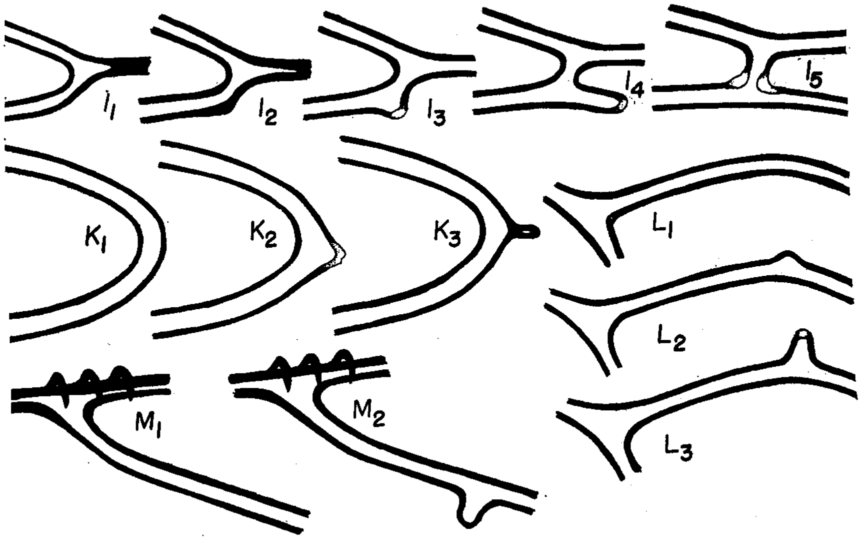

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	4	4	26	32	52	6	12	16
	5		6	10	2	4		
F	1	94		4	2			10
	2		92	58	74	86	88	80
	3	6	8	36	14	14	12	10
	4			2				
	5				10			
G	1	90	100	96	74	38	72	60
	2	2		2	22	18	20	20
	3			2	4		4	16
	4	4				28	2	4
	5	4				16	2	
H	1			22	4		2	6
	2	100	100	78	96	100	98	94
I	1	58	60	44	56			
	2	40	20	20	36			
	3	2	18	22				
	4		2	6	4			
	5			8	4	100	100	100
J	1	2	14	24	20			
	2	4	12	22	8			
	3	94	74	50	64	92	84	82
	4			4	8	8	16	18
K	1	66	100	90	36	60	72	42
	2	28		10	58	32	24	42
	3	6			6	8	4	16
L	1	98	84	78	32	100	80	76
	2	2	14	8	38		16	16
	3		2	14	30		4	8
M	1	100	100	92	98	100	96	90
	2			8	2		4	10

* As each sample consisted of 50 individuals, the absolute number may be obtained by halving the values listed.

F : Located on lm-cu near to Rs+M. F_1 : *DC* on apical side alone. F_2 : *DC* on both sides, with gentle curvature of vein. F_3 : *DC* on both sides, with acute flexion of vein. F_4 : Acute flexion of vein without *DC* nor *PR*. R_5 : *DC* on both sides, with external *PR*.

G : Located on 2r-m, near to Rs+M. G_1 : Neither *DC* nor PR. G_2 : Incipient *PR* on apical side. G_3 : *DC* on both sides. G_4 : *DC* on both sides, with distinct *PR* on apical side. G_5 : Prominent *PR* without *DC*.

H : Located on 2m-cu, near to Rs+M. H_1 : Neither *DC* nor *PR*, with slight swelling of tube walls. H_2 : *DC* on both sides.

J : Crossing point of Cu_1 and Cu_2. J_1 : Neither *DC* nor *PR*. J_2 : Slight *PR* on apical side. J_3 : Constriction of vein, neither *DC* nor *PR*.

K : Apex of radial cell. K_1 : Neither *DC* nor *PR*. K_2 : With *DC* and slight *PR*. K_3 : *PR* without *DC*.

Hind wing

C : Joining point of Cu-V to V. Corresponding to *B* in fore wing.

I : Crossing point of r-m and M. I_1 : M without *PR* nor *DC*. I_2 : With rudiment of *PR*, without *DC*. I_3 : Incipient *PR*, without *DC*. I_4 : Distinct *PR* with *DC* at apex. I_5 : Long extension of *PR* with *DC* at crossing point.

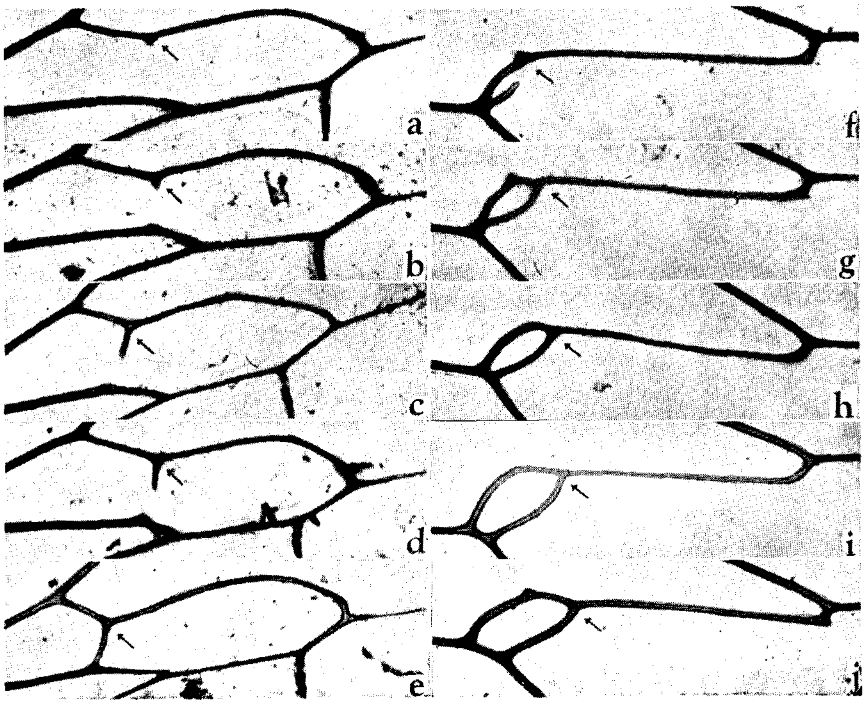

Fig. 3. Formation of secondary cells observed in E cell (left) and *L* (right) in Sample V. (*Cf.* Fig. 1)

The frequencies of these variations markedly differ from case to case. *B* and *C* are provided with *DC* in all samples without exception. A_1 was found only in V but with a remarkable rate. *H*, *L* and *M* are also fairly constant except for the drones from laying workers. The other characteristics showed a considerable variability as follows:

D: There is a distinct tendency of interspecific difference. The Appearance of D_3 was fairly frequent in *A. mellifera* except for normal drones (B), while rather rare in *A. cerana*. Further, the appearance of D_1 is relatively rare in workers in both species. B differed from all other samples by the opposite ratio of $D_2 : D_3$.

E: This position showed a wide and irregular variation among samples. *PR* seems to be very frequent in drones of *A. mellifera*, but not always in *A. cerana*. The lack of both *PR* and *DC* is highest in A, then in Z!

F: This position, too, is provided with a complex variation mode. *A. mellifera* workers differ from all others by the weaker dechitinization and relatively gentle bending of the vein concerned. The variability is rather prominent in the abnormal drones.

G: Zimmermann (1933) pointed out the issue of *PR* in this position as one of the commonest variations in the bees and other related Aculeata. In the present samples, a distinct *PR* was much frequently observed in the workers and in *A. cerana* than in other samples. Interesting is the higher uniformity of B as to this position. A similar tendency is seen in *K*, too.

I and *J*: These are outstanding for the clear interspecific difference. Especially in *I*, while *A. cerana* always issues a long veinlet, *A. mellifera* seldom has such distinct protrusion, although the rudimentary trend is detected.

Consequently, it may be said that some characteristics clearly differ between species, while others between sexes. Further, it is noticeable that the abnormal drones show a complicated variability in general.

Besides these relatively frequent variations among samples, unusual anomalies were observed in V, which was also characteristic by the exclusive and abundant appearance of A_2: The first case is the division of the 3rd submarginal

Table 2. Formation of secondary wing cells found in Sample V (Types of anomalies a-j are shown in Fig. 3).

	Symbols of individuals in which anomalies were observed (lateral symmetry is shown with italic) (cf. Fig. 3)					Total individual nubmer
	a	b	c	d	e	
Right	*4*, 28, 31, 45	*6*, 38, 44, *4*	13, *33*	19, *29*, *41*	*14*, *43*	14
Left	3, *6*, 17, 27	*4*, *29*, 30	*33*	*14*, *41*, *43*	12	12
	f	g	h	i	j	
Right	3	2, 39	28	26	*30*, *31*	7
Left				*30*, *31*		2

cell of the fore wing (E cell in Fig. 1 above) by the extension of a veinlet from 2r-m. In length such veinlets vary from one to another, but the positions of issue were fairly fixed. Fig. 3, a-e show the gradual steps from incipient protrusion to complete division of the cell. Corresponding to the development of the veinlet, the gradual acuteness of bending of 2r-m and the occasional issue of *PR* from the opposite vein 1r-m were observed as in the figures.

The second case is a similar formation of an abnormal cell near the confluence of M and M+Cu in the hind wing (Fig. 3, f-j). As indicated in the figures by arrows, often a fine *PR* is formed in the direction opposed to the loop finally derived. While the form and situation of M itself are not altered from the normal case in f, M is slightly translocated in other cases, corresponding to the formation of the loop. The points indicated by arrows accord to *L* in Fig. 1. In Table 2, the individuals which developed such two variations are listed as to both wings. Although there is no significant difference regarding the lateral asymmetry of the variations observed in fore and hind wings, the frequencies of both variations show a highly significant diference ($P < .01$). On the other hand, the individuals which possessed the anomalies in both right and left wings were 46.2% and 44.5% in fore and hind wings respectively. These values suggest independent mechanisms governing these two anomalies, but a common mechanism as to their symmetrical appearance.

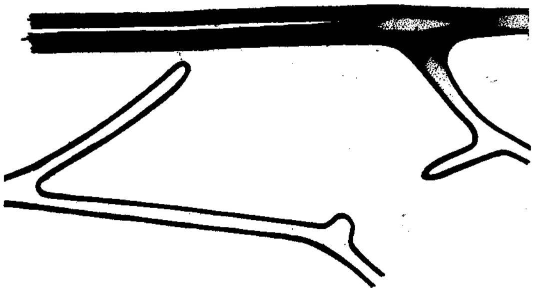

Fig. 4. Partial interruption of veins Rs^1 and Rs^2 found in Sample V.

The third and final case is the partial interruption of Rs^1 and Rs^2 in the fore wings (Fig. 4). Although only two examples were obtained, the probable occurrence of a factor which tends to evoke such interruption is noticeable.

Discussion

All variations detected by the present writers can be classifed into the following three types.

Type I: With DC: $A_{1,2}$, B, C, D_{1-3}, E_{2-4}, $F_{1,3;5}$, $G_{3,4}$, H_2, I_{3-5}, J_{2-3}, K_2, L_3.
Type II; With PR: D_3, $E_{4,5}$, $F_{4,5}$, $G_{4,5}$, I_{2-5}, $K_{2,3}$, $L_{2,3}$, M_2.
Type III: Without DC nor PR: E_1, G_1, I_1, J_1, K_1, L_1, M_1.

The variations including both DC and PR are D_3, F_5, G_4, I_{3-5}, K_2 and L_3. Among them, a common causal mechanism is conceivable in $I_{3,4}$ K_2 and L_3 where DC occurs just at the points of the issuing of PR. In other instances, however, the common causal mechanism is also probable but evidence is still insufficient to prove it. Although the direct causal mechanism of such anomalies must be sought by means of observatins during metamorphosis, it may indubitably be connected with the weak deposition of chitin during the post pupal stages, in which the rudiments of venation are still plastic. It is interesting that both dechitinization and protrusion are usually prominent on the apical sides of the veins, suggesting the stronger pressure acting in this direction.

The constancy of the positions where the anomalies appear is remarkable. Maa and Shao (1947) discovered similar variations in both *Apis cerana* Fabricius (of the populations of South China, mainly of Fukien, consisted of 1507 worker specimens observed) and *A. indica skorikovi* Maa (of the population of Darjeeling, consisted of 75 workers observed)[1]. The frequently observed anomalies in their material were in the following order: K_{2-3} (= B, C in their definition, ca. 15.8 %) > G_{2-3} (= G, H, I in their definition, ca. 12.4 %) > those in 1r-m (ca. 5.4 %) > F_{1-2} (=J in their definition, ca. 4.34%) > H_2 (=K in their definition, ca. 0.03 %)> those in 2m-cu (0.03 %) in the South Chinese populations, and F_{1-2} (Ca. 30.5 %)> G_{2-5} (Ca. 16.9 %) > those in 1r-m (Ca. 14.7 %) > those in 2 m-cu (Ca. 12.8 %) in the population of Darjeeling. On the other hand, there are found in writers' own material, as far as those variations described by Maa and Shao alone are considered, K_{2-3} (34%) and G_{2-5} (10%) in *A. mellifera*, and K_{2-2} (40 %) and G_{2-5} (31 %) in *A. cerana*.

The higher rate in the appearance of the appendiculate radial cell (K_{2-3} except for the population of Darjeeling) and the protrusion from 2r-m (G_{2-5}) is common to all samples. On the other hand, the appearance of abnormal 1r-m was very frequent in the South Chinese populations, while it was almost never found in others. The anomalies of 1r-m were very frequent in the material studied by the Chinese writers, but never in the writers' own. Further, Maa and Shao did not refer to the variations found in J and E, perhaps due to the lack or scarcity of anomalies in these positions, nevertheless such were rather frequent in the writers' observations. Unfortunately, the writers' samples of workers were taken from only one colony in both species; it cannot be determined whether such differences are of the ture racial or specific type, unless further comparisons among many colonies are carried out.

Higher appearance of variations in G is interesting, because this position

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[1] Later this subspecies (nom. nud.) was regarded as identical to *A. cerana* Fab. (Maa, 1953).

was already suggested by Adolph (1880, according to Zimmermann, 1933) as one of the most variable points in the venation of bees and other Aculeata, found in the majority of the well-known genera such as *Anthophora, Apis, Bombus, Eucera, Nomada, Dufourea, Andrena, Halictus, Colletes, Sphecodes, Megachile, Osmia, Anthidium, Heriades*, and further in *Vespa, Odynerus*, Scoliidae, Mutillidae). The other positions of high variability shown by Zimmermann are 1r-m, 1m-cu, and 2m-cu, which are partially proved in the present study, or in Maa and Shao (1947) in the honeybees, too. Further, the formation of a secondary wing cell found in sample V is also reported by Zimmermann in *Bombus muscorum*.

As to the sexual difference in the frequencies of variations, Maa and Shao reported that the anomalies are very infrequent in the drones. This does not always correspond to the writers' results. As shown in Table 1, the relative frequencies vary from sample to sample in a fairly complicated manner. Such sexual difference of variations was analysed with various wild bees and its significance in detecting the recessive mutations was discussed by Zimmermann (1933). Owing to the peculiar sex determination in higher Hymenoptera, the males of this group are always haploid, being deviod of the father. Therefore, if a recessive mutation $A \rightarrow a$ occurred in one particular character, the genetic make-up of the offspring may be either 1) $(Aa+AA)$♀ and $(A+a)$♂ in the case of $Aa \times A$, or 2) $(Aa+aa)$♀ and $(A+a)$♂ in $Aa \times a$. The ratio of the phenotypic appearance of the recessive genoptye a in males may remain of the same magnitude in both cases, but may vary in females according to the ratio a/A, which may affect the female's chance to mate with the recessive male. If a/A is sufficiently small, the phenotypic appearance of a may be larger in males than in females. Inversely, such sexual difference may serve as a useful index to suggest the occurrence of a recessive mutation without experimental analysis. Comparing various specimens of wild bees, Zimmermann found such sexual difference in several wing characteristics including G and H mentioned in the present paper, and suggested their mutative nature. In the present sutdy, such sexual difference was relatively rare except for L in both species, and F in *A. mellifera*, although the range of variability were in general wider in drones than in workers.

This observation suggests either 1) the variability caused not only by the genetic, but also by the non-genetic factors, or 2) the wide distribution of the recessive mutations if considered according to Zimmermann, and further, 3) the more complicated nature of the genetic mechanism governing the phenotypic appearance, affected by the occurrence of dominant mutations or much complicated alleles. Such complicated mechanism is assumed from the comparisons between normal and abnormal drones in both species. It is remarkable that the frequency of anomalies varied between them of the same strain (except for V). At present, it cannot adequately be explained whether such difference was caused by the development of mutative changes, or by the effects of environmental factors. The third possible explanation, the occurrence of biparental males in the normal drones seems to be less plausible, because such diploid males proved in *Habrobracon* were not obtained in the experiments conducted by Mackensen (1951),

Consequently, the origin of various anomalies found in the honeybees must be sought in further studies. However, it is probable, that some anomalies such as found in *G*, *H* and *E* are of mutative origin, as suggested by Zimmermann. He pointed out that some of such supposed mutations might be fixed during the course of evolution and serve as taxonomic criteria. In certain bee genera such as *Nomada*, *Halictus* and *Andrena*, subgenera have been often erected based upon such wing *anomalies*. Perhaps, a similar mechanism may be expected for the extension of the vein M in the hind wings beyond the conjunction with r-m, which has been used as one of the most useful morphological characteristics to distinguish the European and Asian honeybees (Cf. Tokuda, 1924, Maa, 1953, Akahira & Sakagami, 1959), and in a lesser degree, for *J* and D, which also varied according to species in the present study.

Summary

Some observations were made on the variability in the dechitinization and protrusion of veinlets in the wing venation of the honey-bees, both European and Japanese forms. The frequencies of variations are diverse among characteristics, species and sexes. But there are certain regularities in the relative abundance of some anomalies. Further considerations were given as to the origin and significance of such anomalies.

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