STATISTICAL STUDIES ON THE VARIATION OF STAGBEETLES.

BY

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(With 8 figures and 4 tables)

鍬形蟲の變異の統計學的研究

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Quetelet (1871) was the first who worked out the variability of human bodies by the statistical method, and established his law which later enabled Galton and others to recognize the coincidence of the variation curve with the binomial curve. Actual investigations, so far completed, support the law by which the general phases of variation in the organic world are explained. In the year of 1894 Boteson worked on the variation of the stagbeetle (*Xylotrupes gideon*) and, later on that of the earwig (*Forficula auricularia*) and detected the dimorphic curve of frequency of variates. He was followed by a series of investigators on this question including de Vries (1895) on Chrysanthemum, Weldon (1895) on crabfish, Heincke (1897) on herring, Jennings (1911) on Paramaecium, Goldschmidt (1897) on moth and so forth.

As is well known, Bateson distinguishes 'high' and 'low' individuals, applying the terms respectively to large and small sized individuals of the same sex of a species, that he had found by measurement of the horns of Lucanid stagbeetles. The terms refer, however, not only to the horns but also to the body itself, according to its strength. Bateson regrets "no sufficient number of male stagbeetles has yet been received to warrant any statement as to frequency of the various types of male." Now the Lucanid stagbeetles are, however, very common in forest localities in this country.

The stagbeetles occur very abundantly in our university grounds, being represented by two species called respectively *Cladognathus inclinatus*, Motsch; and *Lucanus maculifemoratus*, Motsch. During the last few years (1917–1919), a number of specimens was collected chiefly by Dr. Yoshimaro Tanaka. As is very well known, the male beetles are built very strongly and carry a pair of splendid antlers which are nothing else than vigorous mandibles. The females are furnished with a pair of solid but short jaws. Accordingly, these features of both sexes afford us already an excellent example of sexual dimorphism; but this is not the only difference. Upon further examination we find that there are in these forms other features which show the facts of variation.

Last spring, I had an opportunity to study the above mentioned collection which consists of 1362 males and 1333 females of *Cladognathus* and 320 males and 809 females of *Lucanus*. In specimens, taken at random, measurements and examinations of several facts have been carried out, and we find that the law of 'high' and 'low' individuals quite obviously applies to them. As the *body length* I have taken the extent from the top of the caput to the hind extremity of the sheathwings.

In this place, I wish to express my thanks to Dr. Hatta for his courtesy shown during my present study. I am also very much indebted to Dr. Tanaka who allowed me the free use of the collection.

I. Cladognathus inclinatus, Motsch.

Male.—The development of the mandibles in strength and otherwise, may be said to be proportional to the bodybuild: a large sized 'high' form is built solid and carries, together with strong legs, arched and vigorous antlers with several strong tines (Fig. I, *a–c*), while the small 'low' forms have straight short antlers looking like a pair of scissors with serrated edges, giving a weak appearance (Fig. I, *g*. *h*.) As Fig. I shows, a complete gradation (Fig. I, *a–h*) occurs between the two extreme forms, and a continuous, fluctuating variation is quite obvious in this species (Fig. I, *a–h*).

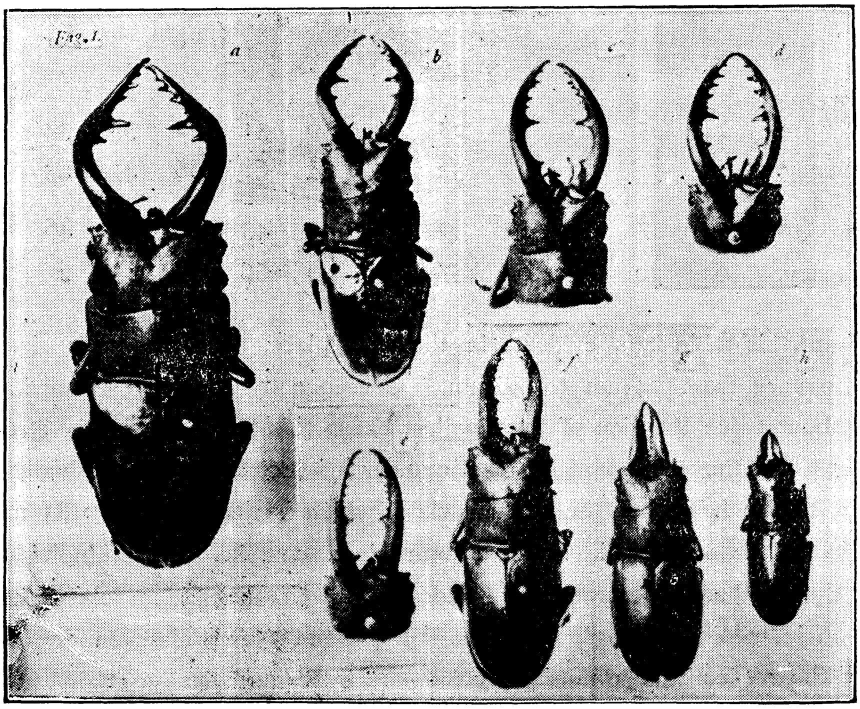

Fig. I. *Cladognathus inclinatus* Motsch. male. View of continuous variation between largest (46mm) *a* and smallest (25mm) *h* variates. *b* (36mm) small form of high tyge, *g* (30mm) large individual of low type, while *c*, *d* (37mm), *e* (35mm) and *f* (34mm) show intermediate forms from high to low. (Natural size).

Examined more precisely, the strength of the antlers together with their curvature is diminished from *a* to *f* (Fig. I) by grades until both mandibles are almost parallel to each other, as seen in *g* and *h*. The tines are also diminished in strength towards the small sized individuals, in which case they are represented merely by the serrated inner edge of the antlers; on the other hand, they get more numerous from the high forms to the low ones (see Fig. I, *a–h*). The variation is indeed, fluctuating; it is, however, not shown by a straight line, but describes a curve, as the following accounts show.

According to the length of the body, which was measured with an exactness of about 1/10 mm, the individuals have been grouped into 23 classes which comprise all those which stand between a given unit and the next one. As the result of these measurements the following table was obtained (Table I).

Table I.

Class. (mm)	24	25	26	27	28	29	30	31	32	33	34	35
Frequency.	2	7	12	35	52	75	**81**	61	66	47	43	52
Class. (mm)	36	37	38	39	40	41	42	43	44	45	46	
Frequency.	62	70	90	104	**137**	124	99	66	60	15	2	

From this table it is evident, in the first place, that the body size is found to vary from 24 mm to 46 mm. Consequently the largest individuals attain about twice the size of the smallest ones; this fact in itself is already striking. In the second place, the number of individuals is gradually increased to the height of the 30 mm class, which is represented by 81 members, while the smallest i. e. the 24 mm class, contains only 2 individuals. Then, the number is decreased by grades to 43 in the 34 mm class, losing about 40 in passing through 3 classes. From the 35 mm class on, the numbers of the respective classes rapidly increase again and finally attain, in the 40 mm class, the climax with 137 individuals. Then, the number falls again by grades as far as the 44 mm class with 62 individuals. In the next class, 45 mm, the number drops very suddenly and still more so in the class of 46 mm, which consists of only 2 of the biggest forms. Taken as a whole, the *prevalent distribution of variates of the 23 classes is met with twice, i. e. at the 30 mm class and at the 40 mm*, the two being separated by a wide gap near the 34 mm class.

I have endeavored to show the results graphically in Fig. 2. The figures on the ordinate show the number of individuals, those on the abscissa giving the body length in millimeters.

A glance at the curve makes it evident that the present species may be assumed to be dimorphic, so far as the majority of individuals is concerned.

In this respect the species is provided with two apices around which the population is crowded: the first apex corresponds to the 30 mm group, while the second falls in the 40 mm class.

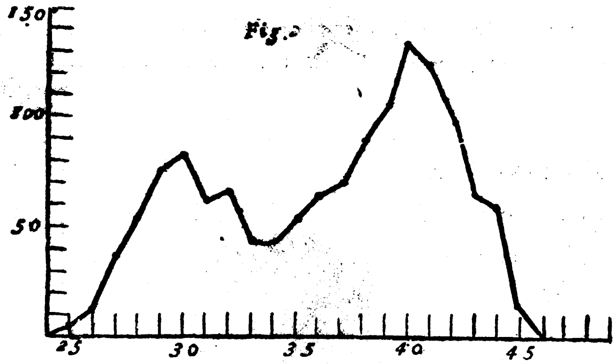

Fig. 2. Curve showing frequeucy of various body lengths of male in *Cladognathus*. Ordinates, numder of individuals; abscissa, body length in mm.

From the curve above given, it is evident that the two apices represent the majority of variates: firstly, it falls on the 30 mm class which exhibits the class of greatest frequency of moderately low individuals, and secondly on the 40 mm class which marks the maximum number of moderately high types, while all the intermediate forms (Fig. I. *b–f*) lie around the sinus, that is 34 mm, which indicates the rarer occurrence; the 37 mm class marks the higher limit beyond which none of the low types are met with, and the 33mm class the lower limit, which is never crossed by any of the high forms.

Female.— In contrast to the male which is armed with powerful antlers the female possesses only a pair of inconspicuous mandibles like forceps. The body size of the female is much inferior to that of the male. The largest female attains at most the body length of 34mm, or a point which reaches hardly the height of the male variates of middle length. It then fluctuates and runs straight to the minimum one of 23mm, so that there can not be drawn a distinct line of demarcation, as shown by a comparison of the two individuals (Fig. 3) standing at the extremities of a row in which 1333 females are serially arranged according to their body length, i.e. magnitude. It is evident that the biggest individual (*a*) is in every respect nothing more than the smallest one (*b*) magnified. More accurate data can be gathered with the same method which consists in the study of the males, in grouping the total population into certain classes according to the body length.

Fig. 3. *Cladognathus inclinatus*, Motsch. female. Surface view, giving 2 extreme variates of population. *a*, largest 34 mm; *b*, smallest 24 mm form. (Natural size).

All 1333 female beetles were grouped according to the units of the scale used in case of the males and we obtained 12 classes as follows (Table 2).

Table 2.

Class (mm)	23	24	25	26	27	28	29	30	31	32	33	34
Frequency	9	19	61	129	187	224	**226**	221	163	68	21	5

From this table (Table 2) we can gather 4 important facts, as the following descriptions show. First, the individuals standing at both the extremities are far inferior to the males in body length, as can be seen at once by comparing table 2 with table 1.[1] Second, the variation in this respect passes over from each unit to the adjacent ones not abruptly as in the males, but fluctuating continuously; accordingly, its range is shorter than in the case of males. Third, there are, in consequence, only 12 classes instead of 23 as in the males. Lastly, the number of individuals in each class increases suddenly towards the high types and then decreases likewise suddenly.

These data can be represented graphically by a curve which is shown in Fig. 4.

The curve starts at first rather slowly and ascends suddenly from 26mm to 28mm; then it slowly attains the mode and descends likewise slowly to 30mm which is at about the same height as 28mm on the opposite limb. From this point to 33mm it descends steeply just as the opposite limb ascends. Then it slides into the high type.

Both limbs of the curve, as is evident from Fig. 4, are nearly symmetrical and the curve is unimodal having an apex at 29 mm. It follows that the mean value of the variates, 28.6mm, nearly coincides with the empirical mode, 29mm, the middle standing class; that is, it is very near to the normal variation curve. The value of the standard deviation $\sqrt{\frac{\Sigma(x^2.f)}{n}}$, where f represents the frequency, x the deviation of any class from the mean, and n the number of variates, is 2.06.

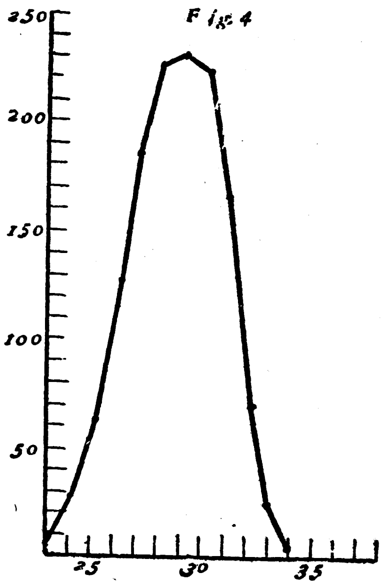

Fig. 4. Diagram showing frequency of body length of female in *Cladognathus*. Figures on axis as previous figure.

The female is, in this respect at least, much more condensed than the other sex and may be taken to be homogenetic, modifying itself in the normal way in which Galton's single variation curve is drawn.

In addition to these facts the mandibles of the females are formed always uniformly like a pair of claws with a fine serrated inner edge; they are neither arched antlers, nor severally tined, nor developed in several strengths according to the size of the body, as in the case of the males.

It follows that the variation in the females is very much narrower in its range than that of the male.

II. **Lucanus maculifemoratus,** Motsch.

Male.—This species was collected also from our university grounds; it is in the habit of living close together with the previous species, althogh it is more rare.

In the male, the big antlers may be said to be uniformly built throughout the whole collection; the most conspicuous feature of this pair of appendages consists in the bifurcation at their terminus. Fig. 5 shows that the antlers are by no means complicated or simplified, according to the body type, i.e. whether the body type is high or low; they are always arched and tined in several ways in the low type (b) as well as in the high type (a), except that the tines of the former are inferior in development to those of the latter.

The only externally noticeable distinction between the two types is found in the caput which in the low type, is truncated on both sides of its hind part, while in the high type this part is not truncated.

Taking the same unit of measurement as in *Cladognathus*, the total 320 male specimens whose body length I measured may be arranged in 23 calsses (Table 3).

Fig. 5. *Lucanus maculifemoratus*, Motsch. Photo of representatives of two extreme variations. *a*, largest 50 mm; *b*, smallest 28mm individual. (Natural size).

Table 3.

Class (mm)	28	29	30	31	32	33	34	35	36	37	38	39
Frequency	1	2	2	10	8	10	10	9	10	18	15	14
Class (mm)	40	41	42	43	44	45	46	47	48	49	50	
Frequency	24	20	22	20	**42**	35	26	12	8	1	1	

From this table we notice, in the first place, that the present species is larger than the male of *Cladognathus* in both the high and low types; in the second place, the variation passes abruptly from one unit to the next one; consequently there are, thirdly, 23 classes as in *Cladognathus*, those at and near the extremities being represented by only a few individuals (see Table 1); and lastly, the numbers of each class are at first irregular in increasing and decreasing. The individuals shows a sudden increase in number from the 43mm class to the 44mm class; thereafter a steady decline takes place down to the 49mm class from which no more are added. The results show that the species in question is more variable than *Cladognathus* and that the maximum frequency is attained at the 44mm class.

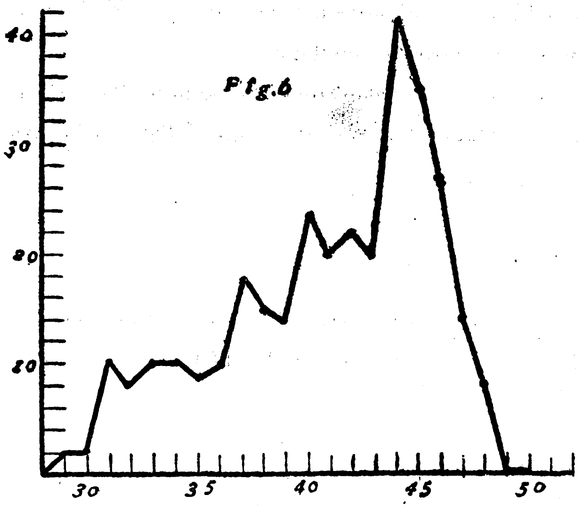

Fig. 6. Curve exhibiting frequency of variates in body length of *Lucanus* male; explanation as in previous figures.

The above data are expressed diagramatically in Fig. 6.

From its start to the 43mm class, the curve describes a zigzag line and then ascends steeply to the 44mm class, from which it descends nearly vertically, forming a very acute angle with its two limbs; then at the end it follows a horizontal course (Fig. 6). The curve is, however, unimodal. In this unimorphic curve the mode is at 44mm and the mean at 41mm; the median magnitude, 39mm, is, therefore, distant from the mean. I dare to assume, nevertheless, that the *Lucanus* male is on the way to dimorphism similar to that which is obvious in the male of *Cladognathus*.

Female.—The female variates of *Lucanus* are as simple as those of *Cladognathus*; the individuals of the low type can not be distinguished from those of the high type except by the much inferior body length in the former, which is a little more than half of the latter (Fig. 7). It is remarkable that the caput is truncated from both sides at its hind part, just

Fig. 7. *Lucanus maculifemoratus*, Motsch. female. View representing highest *a* (39mm), and lowest *b* (25mm) individuals. (Natural size).

as in the males of the low type (compare Fig. 7 with Fig. 5); the females look more gentle than the males, because the anterior side margin of the caput is round, instead of angular as in the case of the latter.

Concerning the body length, for the measurement of which 809 females were employed, the specimens are classified into 15 groups (Table 4), using the same units as in the foregoing cases.

Table 4.

Class (mm)	25	26	27	28	29	30	31	32	33	34	35	36
Frequency	2	3	7	20	36	60	86	121	**175**	124	94	56
Class (mm)	37	38	39									
Frequency	18	16	1									

Excepting the maximum and minimum length, in which the present species surpasses the last one, the variation resembles in every respect that in the females of *Cladognathus*. The highest and the lowest individuals are inferior in body length to the males. So far as the boby length is concerned, the variation passes not abruptly from one class to the next one, but fluctuates continuously. Accordingly its range is not so wide as in the males, and the classes are limited to 15, while the males are grouped into 23. The number of individuals in the respective classes increases at first slowly, then very suddenly towards the long types i.e. the 33mm class; finally it decreases likewise suddenly, until at the end it is gradual again.

The statements given on the females of *Cladognathus* are, therefore, also valid in this case. There are, however, two points by which the two species diverge from each other. First, the females of *Lucanus* comprise 15 classes, while those of *Cladognathus* are divided into only 12 classes. The second point of divergence, which is very important, consists in the fact that the individuals of *Lucanus* are added very abruptly to its maximum and decrease likewise abruptly, so that the multiplication attains directly the highest point; whereas in the case of *Cladognathus* both the increased and the decreased number in some classes near the maximum is only slightly diminished. These divergencies are shown more clearly in the curve which follows (Fig. 8).

The curve given from the data above illustrated (Fig. 8.), affords us an excellent example of the unimodal type which is nearly symmetrical on both sides of the mode, 33mm; the mean is 32.7mm and the median 33mm. Thus the theoretical mode coincides almost completely with that of the curve, so that it stands very near the normal curve.

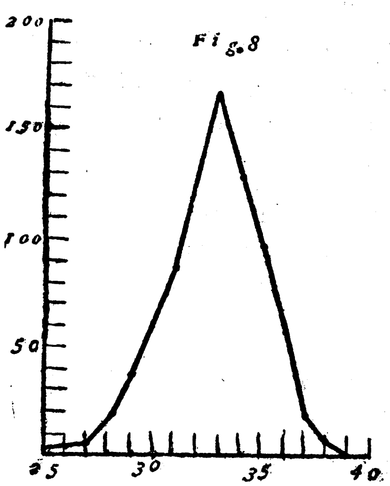

Fig. 8. Curve showing frequency of various grades of body length of females in *Lucanus*. Figures on axis represent units and numbers as before.

By the calculation of the value of $\sqrt{\frac{\Sigma(x^2 . f)}{n}}$ the standard deviation was obtained as 2.14.

Comparing this curve with that of the females of *Cladognathus*, we see that here the apical angle is very acute instead of being an obtuse angle as in the case of *Cladognathus*. The conclusion is, therefore, justified that the variation in the females of *Lucanus* fluctuates normally between the two extremities, 25mm and 39mm.

Bateson (1894) was the first who made out in his study of stagbeetles of *Xylotrupes*, and earwigs, the existence of two apices in the frequency of variation. Bateson's case is based upon the length of the horns of 342 male beetles and the length of the forceps of 583 male earwigs. In the present investigation, we took the body length as the chief factor, because the specimens are abundant enough to ascertain the curve which Bateson made out otherwise. Our curve is, like his, *dimorphic* in *Cladognathus* at least.

In the dimorphic curve which de Vries (1895) gave for *Chrysanthemum segetum*, the author ascribes its two apices to the influence of the mixed factors of two different species, assuming the first maximum to be caused by the plants with 13 radial petals and the second by those of 21. In the course of his experiments with culture selections, from plants with dimorphic curve, he produced two plants which have 13 and 21 petals as their single modes respectively. This assumption is confirmed by Heincke (1898) from a study of herring and by Jennings (1911) in the culture of Paramaecium.

The statistic demonstration of the dimorphic curve, which was carried out by Weldon (1894) on crabfish (*Carcinus maenas*), has been verified by Gigard (1894) employing the same material; he states that the curve derived from the small individuals is caused by parasites.

According to Goldschmidt (1913), who stated on the wings of a moth, *Lymantria mobacha*, the inferior apex of the dimorphic curve comes from the small type moulted always from small pupae which in their turn come from poorly nourished caterpillars.

Besides de Vries, the three last named authors assume the dimorphic curve to be caused by environmental factors. Bateson denies external circumstances which drive the animal into the dimorphic condition, inasmuch as the high and low forms are living close together under one and the same stone. The results of the present investigation are, therefore, in this respect in agreement with those of Bateson. It follows that the dimorphic condition of a species living under the same environmental circumstances is an inborn character.

From the results of the present investigation of *Cladognathus*, the following assertions are justified:— The female is less variable than the male. Concerning the *body length*, the latter is *dimorphic* while the female is, on the contrary, *unimodal*. The *mandibles*, or antlers of the male exhibit modifications which may be said to be almost endless, until they are reduced to those of the low types which are nothing more than a pair of forceps; accordingly the male in this respect, closely resembles the female which is provided with merely a pair of claw-like jaws. The resemblance goes not unfrequently so far that a male and a female, which are about equal in body size, may not at a glance be distinguished from each other when they are put into an insect box, containing many others. Thence, I dare to assume that the primary form of the species was represented by the female, from which the male form was derived by the variation acting on it in producing the complicated antlers from the claw-like mandibles. In fact the antlers are undergoing still further modifications.

For this assertion, the results obtained from *Lucanus* afford still stronger evidence. The variation is more striking also in the male than in the female; but it is less pronounced, compared with *Cladognathus*, inasmuch as here the *dimorphic condition* of the body length is not yet obvious enough, although a tendency thereto cannot be denied. What concerns the female, the variation is still simpler; it represents a *typical unimodal* type. The female shows, a striking characteristic which consists in the truncated posterior side margins of the caput. This morphological characteristic is visible again in the low-typed males (Fig. 5, *b*) and grows weaker towards the high-typed ones, until it is totally lost in the highest (Fig. 5, *a*). Notwithstanding the antlers which differ widely from the claw-like mandibles of the female, the female has this criterion referred to in common with the low-typed male. This characteristic, then, must once have been, I think, one of the conspicuous species characters. Here we are, therefore, also forced to assume that the female represents the primary type, whence the male type has been derived.

The present results from the study of the two species of stagbeetles interest us so far as they are concerned with variation, in the fact that they parallel each other, and as to the degree of variation, in the fact that both the forms are divergent from each other. It is obvious that *Lucanus* is in this respect inferior to *Cladognathus;* hence the course of variation in the latter can, to some extent, be deduced in that of the former. For instance, the obtuse-angled curve in the females of *Cladognathus* must have been an acute-angled one as in the case of the same sex of *Lucanus;* likewise the zigzag-lined curve in the males of the latter shows, without doubt, a tendency to pass over later into the dimorphic curve of the former. This multifarious variety of forms, which both the species of stagbeetles exhibit, forces us to assume that the beetles in question are in character quite variable. It is this variability, I think, that caused the beetles to exhibit sexual dimorphism.

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摘　要

のこぎりくわがた及び**みやまくわがた**の雌雄に就き先づ前頭より翅蓋の先端に至る體長を測定し、これを基準としてその變異を統計學上より研究せり。

のこぎりくわがたの雄1362を檢するに、大腮の發達程度により所謂鋸齒型の小形種と鍬形型の大形種(附圖 1. h 及 a)とを區別し得れど、兩形種の間には中間形種ありて、(附圖 1. c, d, e 及 f) 體長 24mm――46mm の一連續的變異なる事を示す。但し中間形種を表はす 34mm の個體數は比較的少數なり。從つて頻度曲線は双頂曲線なり。然るに雌に於ては 1333の統計に依れば、變異幅員は著しく制限され 23mm――34mm なり。而して最大頻度は中間形 29mm にありてその兩極端に於ける個體の形質の差も著しからず(附圖 3.)。即ち完全なる連續的彷徨變異にして、29mm に於て單頂を表はす規準曲線に近き頻度曲線を畫く。而してその標準偏差は 2.06 なり。

みやまくわがたの雄は前種の雄より大形にしてその變異は 28mm――50mm の連續的變異なり。大腮は前種の如く大小形種に於てその差、顯著ならざるも、前頭部の横隆は形狀の發育程度著しく異る(附圖 5)。320個體の示す頻度曲線は單頂にして 44mm に最大數を有す。故にその頂點は著しく大形種の極點に偏側し前種の雄の如き双頂曲線に分化する傾向を示す。

雌は809にして前種と等しく雄に比し變異幅員は著しく極限せられ 25mm――39mm の彷徨變異にして 33mm に單頂を有する規準曲線に近き頻度を示す。その標準偏差は 2.14 なるを以つて前種の雌に比し頂點の急坂なる事を示す。

上記の双頂曲線の原因は Bateson の**かぶとむし**及び**はさみむし**の例と同樣に雄の內在性に由るものにして、異種屬の混在或は外界の影響等に原因するものに非ず。

くわがたむしに於ては雄は雌に比し變異性著しく大なり。而して**のこぎりくわがた**の最小形の雄は同形の雌に近似し大腮の發育程度も大差なし。**みやまくわがた**に於ても同樣にして最小形の雄の頭部の横隆は雌のものと形狀等し、而も雌は何れも標準變異を示す。故に雌形は此等種屬の原形にして雄形はこれより變化發達せしものと解し得。體長に據る變異に於ては兩種は共通點を有し、只**みやまくわがた**は前種に比し稍々變異の分化程度低きに留る。**のこぎりくわがた**の雌は他種の雌の如く嘗ては急坂頂點の曲線を示し、**みやまくわがた**の雄は遂には双頂曲線を示すに至る事想像するに難からず。何れの**くわがたむし**も著しく變異性に富む事明白にして斯る變異性に基きその雌雄二形は分化さるゝに至りしならん。