

Genetic variation of relative growth rates in *Notonecta undulata*

1. THE RELATION OF FEMUR LENGTH TO BODY LENGTH

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1. INTRODUCTION

Students of allometric (or relative) growth attempt to analyse the changes in the body proportions of the growing organism by plotting one dimension (Y) against another (X) on a double logarithmic grid. Often the points so plotted are approximately linear for part or all of the growth period, and the dimensions compared are then said to obey the law of simple allometry, according to the relationship

$$Y = BX^k$$

$$\text{or } y = b + kx$$

where y and x are the logarithms of Y and X , and k and $b = \log B$ are constants (see Reeve & Huxley, 1945; Kavanagh & Richards, 1945).

The most interesting of these constants is the *relative growth coefficient* (k), which measures the ratio of the rates of multiplication of the two dimensions. This coefficient has been given various names in efforts to develop a uniform terminology (see above references), and we shall here refer to it simply as the *growth coefficient*, without danger of ambiguity.

Clark & Hersh (1939) made an interesting study of allometric growth in the water boatman, *Notonecta undulata*. For this purpose they collected data of unusual value in this field, in that young from each of a number of captured wild females were reared individually and measured each instar. The data are therefore of the longitudinal type as defined by Tanner (1962). This makes it possible to examine individual variations in the constants b and k , and to look for evidence of genetic variation in these constants by comparing the variances between and within families. Clark and Hersh did not make any detailed analysis along these lines, though they came to the conclusion that the individuals examined fell into two groups with regard to the growth gradient of the three limbs in relation to body length: in about half the individuals there was an antero-posterior gradient (k highest for the first leg and lowest for the third), while in the remainder k was highest for the middle leg. This conclusion suggests the existence of individual variation which deserves further analysis. Professor L. B. Clark very kindly placed the

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original data at the disposal of one of us (E.C.R.R.), and the first part of a further analysis is presented below. In this paper we shall confine ourselves to the relationship between femur length (the largest segment) in the three legs and body length. Other dimensions, for which the analysis is not yet complete, will be discussed in later papers.

2. MATERIAL

Clark & Hersh (1939) collected eggs from ten wild females and placed them in individual compartments of wire mesh trays which were kept floating in water in a sheltered part of the lake at Minaki, Ontario. Tows from the lake and surrounding ponds were made daily and supplied to the trays. The food, consisting mainly of Ostracods and *Daphnia*, was at all times adequate, and environmental conditions were considered fairly uniform because of the stabilizing effect of the large body of water. The trays were examined daily, and each individual was measured 24 hours after an ecdysis, when it had been narcotized with chloral hydrate or ether, or cooled by adding ice to the water.

The dimensions measured were body length, maximum head and body widths and the lengths of the femur, tibia and tarsus of the three legs, all of which increased with instar number, and distance from synthlipsis to vertex, which decreased as general size increased.

It will be remembered that, as in all Hemiptera, *Notonecta* has incomplete metamorphosis, with five nymphal and one adult instar, making six measurement stages in all. These stages are sufficiently alike for it to be possible to measure the same dimensions on all of them.

Of a total of 231 eggs collected and cultured, 124 survived the first 48 hours and 72 reached the adult stage, so that mortality was rather high. To avoid troublesome complications in the analysis, we have confined ourselves to the 72 animals which completed their growth, making the assumption (which is, perhaps, open to question) that this group, forming 31% of the initial sample of eggs and 58% of those which started their development, is a representative sample of the population. It seems unlikely that whatever selective or randomly operating agencies were responsible for the mortality could have seriously modified the relative growth pattern.

3. METHODS OF STATISTICAL ANALYSIS

In view of the variety of statistical methods which have been used in the study of allometry, something must be said about our own choice of approach. Earlier investigators, if they used any statistical methods at all, calculated the regression of the log, of one dimension on that of another, taken as standard. Clark and Hersh used the Y^2 -weight correction method of Feldstein & Hersh (1935) which adjusts the regression for the assumption that errors are distributed normally before transformation to logs. But, while it may be possible to measure a given dimension with the same arithmetical accuracy over a considerable size range, the factors responsible for growth and therefore for variability at any growth stage must generally act

in a multiplicative way (cf. Hemmingsen, 1934), and Reeve (1940) considered straightforward linear regression on the logarithms of the dimensions to be the appropriate method, and this has also been used by Cock (1963).

On the other hand, Teissier (1948) and Haldane (1950) consider regression analysis unsatisfactory when two dimensions are compared and there is no compelling reason for choosing either one as the independent variate. Teissier proposed the method of minimizing the sum of products of horizontal and vertical deviations of the experimental points from the allometry line, i.e. minimizing the expression

$$\sum \{(y - \bar{y}) - k(x - \bar{x})\} \{(x - \bar{x}) - (y - \bar{y})/k\}$$

which gives the solution $k = \sigma_y/\sigma_x$.

This is the ratio of the regression coefficient of y on x to that of x on y , and surprisingly (as Teissier showed) it has the same sampling variance as the regression coefficient of y on x . The line obtained is the reduced major axis of the correlation surface of (x, y) , and is also the line for which the sum of the perpendicular distances of the observed points is at a minimum when x and y are in standard measure (i.e. each is divided by its standard deviation). Kermack & Haldane (1950) have examined the sampling characteristics of k calculated in this way.

Yates (1950) pointed out that another approach leads naturally to the same formula for calculating k . If γ_x and γ_y are the ratios of the error variance to the true variance of x and of y , and the true law relating y and x is the linear equation (in our terminology)

$$y = b + kx$$

then the estimates of k which are virtually unbiased for large samples are:

$$k' = (1 + \gamma_x) \text{cov}(xy)/\sigma_x^2$$

$$1/k' = (1 + \gamma_y) \text{cov}(xy)/\sigma_y^2$$

If neither error variance can be estimated, but we are prepared to assume that the two ratios of error variance to true variance are equal, i.e. that $\gamma_x = \gamma_y$, we obtain the combined estimate $k' = \sigma_y/\sigma_x$, identical with that of Teissier.

As Kermack and Haldane showed, we may avoid transferring to logs, using the formulae (which assume normal distribution on the log scale)

$$\sigma_x^2 = \log(1 + v_x^2)$$

$$\sigma_y^2 = \log(1 + v_y^2)$$

whence

$$k = \frac{\sigma_y}{\sigma_x} = \left[\frac{\log(1 + v_y^2)}{\log(1 + v_x^2)} \right]^{1/2}$$

where $v_x = \sigma_x/\bar{X}$, $v_y = \sigma_y/\bar{Y}$. If the coefficients of variation on the arithmetic scale are fairly small, we have the even simpler estimate

$$k = v_y/v_x = \bar{X}\sigma_Y/\bar{Y}\sigma_X$$

with standard error $k\sqrt{[(1 - r^2)/n]}$, where r is the correlation coefficient between X and Y , and n is the number of pairs of observations.

This method of approach obviously has many advantages, both theoretically and in making it possible often to estimate k without the labour of transferring the data to logarithms. It has also been developed by Teissier (1955) for the multivariate case, using the methods of factor analysis, so that the allometric inter-relationships of a number of dimensions can be jointly analysed and the relative importance of general and group factors, or influences, acting on each dimension can be estimated.

In the present data there are six instars with large increases in size between each—e.g. body length for a typical individual has the following values: 2.2, 3.1, 4.8, 6.2, 8.5, and 11.8 mm.—and relatively little variation within instars. Evidently the logarithms of these measurements will be far from normally distributed, and the short-cut formulae for k and for the variances on the log scale will give strongly and unevenly biased estimates (as we found to be the case in some preliminary tests). It was, therefore, necessary to transform all the data to logarithms before analysing them.

A full multivariate analysis of the 12 dimensions which increase with instar number, along the lines developed by Teissier (1955), is under consideration; but this requires heavy computational labour, and it seemed advisable to start with a more straightforward analysis of simpler and more easily defined problems. In this paper we shall examine the linearity of the allometric relationship of femur length to body length, and analyse the individual variation in the allometry coefficients for these characters. For this purpose normal regression methods, taking body length as the independent variate, most readily provide the statistical tests we need, and for the present we shall confine ourselves to them. It should be noted, however, that the correlations between pairs of dimensions or their logarithms for the whole growth period are very high, so that k differs little when calculated by the regression method and by Teissier's formula. A similar situation was found by Cock (1963) in his study of the allometric relations of shank length and shank width to body weight in the fowl, k estimated by the two methods being almost identical.

4. RESULTS

(a) *Linearity on the logarithmic scale*

Clark and Hersh, in their Fig. 3, plotted leg length against body length on a double logarithmic grid, and concluded by visual inspection that the points for each leg tended to lie on a flattened sigmoid curve which approximated to a straight line. We have preferred to work with the femurs, the largest of the leg segments, rather than with total leg length based on the sum of femur, tibia and tarsus lengths. Fig. 1 shows the logarithms of the three femur lengths plotted against that of body length for females, and it will be seen that there is a similar tendency for the points of each femur to lie on a sigmoid curve, to that noticed by Clark and Hersh for the complete legs. A similar tendency is also seen when the corresponding dimensions for males are plotted.

It is of some interest, therefore, to test whether these deviations from linearity are statistically significant, or whether they can be attributed to chance variations.

This test is made in Table 1 for the largest segments—the third femurs—of each sex. The high linear regression variance on the instar means (row 1) indicates that there is a very high correlation between the instar means of femur and body length in each sex. But the residual variance between instars (row 2) is highly significant compared

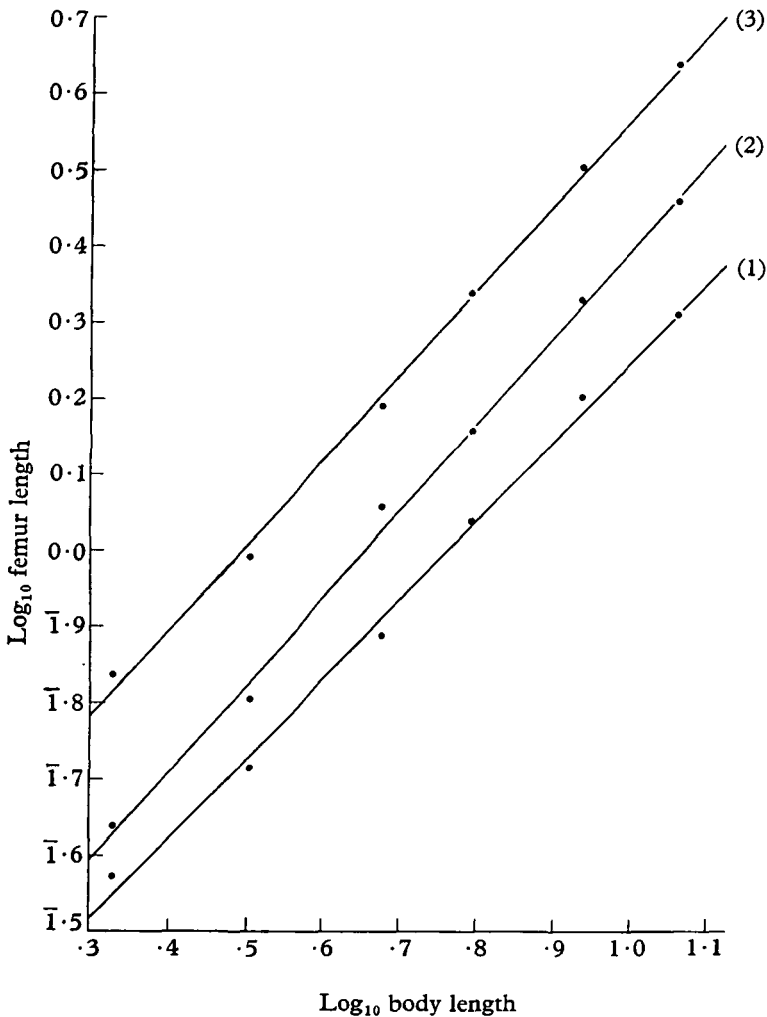


Fig. 1. Allometric plots of femur length against body length on logarithmic scale for females. Each point is based on the mean of 37 measurements. (1), (2) and (3) are the lines for femurs 1, 2 and 3.

with the variance within instars, for each sex, so that there is clearly a significant deviation from linearity on the logarithmic plot. Rows 4 and 5 show that there is an appreciable correlation between the two dimensions within instars.

The slightly sigmoid tendency of the curves, noticed by Clark and Hersh and visible in Fig. 1, suggests that the deviations from linearity are not due to any simple

mechanism such as one dimension reaching full size earlier, or falling off in growth rate earlier, than the other, which would give a curve convex to one axis instead of a sigmoid curve. Nor is there any obvious tendency for the relative growth rate to change at the last pre-adult instar, as it does for example, in *Maia squinado* (Teissier, 1935). But to test these possibilities further Table 2 shows the effect of fitting a

Table 1. *Regression of log third femur length on log body length*

	Females		Males	
	D.F.	M.S. $\times 10^4$	D.F.	M.S. $\times 10^4$
1. Regression on instar means	1	171,600	1	160,200
2. Residual variance between instars	4	114	4	125
3. Variance within instars	216	0.77	204	1.56
4. Average regression within instars	1	3.8	1	19.6
5. Residual variance within instars	215	0.76	203	1.47

second degree equation to the data of Table 1. The additional variance taken up by the second degree term is not significantly large, and there is no substantial reduction in the residual variance between instars, so that the deviations from linearity clearly cannot be attributed to any simple cause of the type referred to above. While there is no doubt about their statistical significance, these deviations from

Table 2. *Second degree regression of log third femur length on log body length*

	Females		Males	
	D.F.	M.S. $\times 10^4$	D.F.	M.S. $\times 10^4$
Linear regression on instar means	1	171,600	1	160,200
Second degree regression term	1	205	1	137
Residual variance between instars	3	84	3	121
Error variance (residual within instars)	215	0.76	203	1.5

linearity are small in relation to the overall linear trend, and do not preclude us from analysing the individual variation in the growth coefficients. Without the above analysis they might well have been attributed to the effects of chance variation.

(b) *Differences between individuals in the growth coefficient k*

The significant deviations from linearity, though small, make a full regression analysis of the data for individuals difficult, since the error variances would have to be adjusted for the effect of non-linearity. A better method is to calculate the growth coefficients (k) for each individual separately and then to analyse these coefficients for differences between individuals, between sexes and between families. For this purpose it would clearly make very little difference whether we use Teissier's formula or the regression coefficient to calculate k , since one set of estimates would be all slightly higher than the other set. We have used the regression estimates.

The average values of the growth coefficients for each femur are given in Table 3 for both sexes, together with the difference between sexes and its standard error. Females have higher k -values than males, but the trend is the same in both sexes in that the second leg has the highest coefficient of the three, or, in Huxley's (1932) terminology, the growth gradient in the femurs has a high point in the second leg. Clark and Hersh quote rather different values for these coefficients in their Table 3 (femurs 1-3 have k -values 1.066, 1.114 and 1.141 in females and 0.971, 1.060 and 1.104 in males) and they actually find k highest in the third leg. The difference between their estimates and ours probably arises from the fact that they used the Y^2 -weight correction method of Feldstein & Hersh (1935), which gives biased estimates for the reasons mentioned earlier. It is nevertheless surprising that their method alters the shape of the growth gradient, and this fact suggests the possibility of an error in their computations.

Table 3. *Growth coefficients (k) for femur length against body length*

	Females (F)	Males (M)	Difference F—M
Femur 1	1.0403	1.0180	0.0223 \pm 0.0078
Femur 2	1.1418	1.1207	0.0211 \pm 0.0071
Femur 3	1.1188	1.1089	0.0099 \pm 0.0050
Sample size	37	35	

To test for individual variation in the growth gradient among the three femurs, the regression of k on femur number (taken as 1, 2 and 3) has been analysed so as to separate the variances due to differences in slope of the regression lines calculated for each individual (this measures the magnitude of variations in the growth gradient) and the variance due to differences in mean k between individuals, which measures variation in the general level of relative growth of the femurs. Table 3 shows that the regression of k on leg number is not linear, since k_2 is larger than k_1 and k_3 . We can still compare the linear regression coefficients, which will differ from one animal to another if their growth gradients differ, but a correction has to be made to the error variance to remove the effect on it of non-linearity. It should be emphasized that we are here talking about non-linearity in the regression of k on femur number, and not of non-linearity in the regression of log femur length on log body length which was discussed in the previous section.

The methods of computation are shown for females in Table 4. Since the term for non-linearity (row 2) is equally represented in the variances of rows 3, 4 and 5, it does not contribute to rows 6 and 7, but it must be subtracted from row 5 to give the adjusted error term of row 8.

Table 5 gives the results of applying this analysis to both sexes, and also includes the variances due to the average linear regression of k on leg number and the average deviation from linearity.

There is in both sexes a significant linear regression of k on leg number, indicating the existence of a gradient in growth coefficients along the body, while the significant

term for non-linearity shows that the gradient is not a linear one—its highest point is, as Table 3 indicated, in the second leg. There are significant differences between animals in mean k , but there is no sign of differences in slope of the regression lines. This means that there are differences between animals in the mean level of relative growth rate of the limbs, but no significant variation in the shape of the growth gradient. On the basis of this analysis it is clearly impossible to accept the conclusion of Clark and Hersh that the growth gradient varied between animals, about half of them having k highest in the first leg and the rest having k highest in the second leg. Their conclusion seems to have been based on inspection of the k values, calculated by the Y^2 -weight formula, without any statistical test.

Table 4. *Regression of k on leg number : computation in females*

Row	D.F.	S.S.* × 10 ⁴
1. Linear regression	1	1138
2. Deviation from linearity	1	957
Residual variance on fitting		
3. Single line	109	1877
4. Parallel lines	73	1360
5. Separate lines	37	1216
6. Differences in mean k (3 - 4)	36	518
7. Differences in slope (4 - 5)	36	143
8. Adjusted error (5 - 2)	36	259

* S.S. = Sum of Squares.

Table 5. *Regression of k on leg number : completed analysis*

	Females		Males	
	D.F.	M.S. × 10 ⁴	D.F.	M.S. × 10 ⁴
Linear regression	1	1138**	1	1448**
Deviation from linearity	1	957**	1	766**
Differences in mean k	36	14.4	34	15.7**
Differences in slope	36	3.98	34	3.84
Adjusted error	36	7.20	34	3.74

** Variance ratio significant at 1% level. Row 3 is tested against the average of rows 4 and 5.

The variation in mean k between individuals suggests the action of genes which influence the general growth rate of the limbs in relation to that of body length, and their effects should be reflected in differences between families. There were nine families containing at least one animal of each sex raised to maturity and measured each instar, and the data on these families can be analysed to show the variance between sexes, between families, and within sex and family, in mean value of k for the three femurs. The number of animals in each family, the mean k for each sex, and the sums and differences of these means, are given in Table 6.

The resulting analysis of variance of k is shown in Table 7. Since the subclass numbers vary, the sums and differences are weighted by a weighting factor inversely proportional to their variances, calculated in the usual way, i.e. for each family $w = n_f n_m / (n_f + n_m)$, where n_f and n_m are the numbers of females and males in the family. Then the weighted variance of S gives the variance between families and the weighted variance of D gives the interaction variance between sex and family, while $[(\text{sum of } wD)^2 / (\text{sum of } w)]$ gives the variance between sexes. The error variance is taken as the variance in mean k within sexes and families.

Table 6. *Numbers of progeny and mean k for each family in both sexes*

Family no.	Female progeny		Male progeny		S = $k_f + k_m$	D = $k_f - k_m$
	n_f	k_f	n_m	k_m		
1	3	1.1119	3	1.1009	2.2128	0.0110
2	3	1.1334	2	1.0962	2.2296	0.0372
3	2	1.0956	7	1.0780	2.1736	0.0176
4	3	1.0675	1	1.0480	2.1155	0.0195
5	6	1.1031	5	1.0858	2.1889	0.0173
6	8	1.1001	6	1.0826	2.1827	0.0175
7	1	1.0623	3	1.0514	2.1137	0.0109
8	2	1.1029	3	1.1121	2.2150	-0.0092
9	9	1.0996	5	1.0771	2.1767	0.0225

Notes: n and k are number of progeny and mean k for the three femurs averaged over the progeny of each family.

Table 7. *Analysis of variance in mean k for femurs 1-3 against body length*

	D.F.	M.S. $\times 10^4$	Interpretation
Between sexes (S)	1	144	
Between families (F)	8	51.2**	V(E) + 20.5 V(F)
Interaction: S \times F	8	5.6	
Error (within S and F)	54	10.1	V(E)

Notes: ** significant at 1% level

V(E) = Error Variance

V(F) = Component of variance between families

The difference between the sexes is significant, as we saw by another test earlier, but there is no evidence of interaction between sex and family—the interaction variance is, in fact, low compared with the error variance. The variance between families is, on the other hand, clearly significant, and this must be put down to genetic variation in the mean level of k in the three legs, since all the individuals in the test were reared together under the same conditions and it is very difficult to see how any environmental differences between families having such an effect could have arisen.

On the assumption that each family are the progeny of a single male as well as of a single female, we can estimate the heritability of mean k , to obtain a rough measure of the proportion of the phenotypic variance of this index which is attributable to genetic causes. The 'Interpretation' column of Table 7 gives the expected values of the between-family and error variances on simple assumptions. The factor 20.5 in the former is a measure of the mean number of femurs per family, appropriate to the method of calculating the variance between families. It is calculated from the formula:

$$\text{Mean no. of femurs per family} = 12 \left(\frac{\sum w - \frac{\sum w^2}{N}}{N-1} \right)$$

where N is the number of families, w is as defined above, and the factor 3 in 12 is there because the Mean Squares are given on the basis of an individual femur. $V(E)$ could, in fact, be subdivided into $V(a) + 3V(b)$, where $V(a)$ is the variance of an individual femur within legs, sexes and families, and $V(b)$ is the interaction term between femur number and individual within sexes and families.

The heritability of mean k is calculated as follows:

$$V(F) = 2.01$$

$$V(E) = 10.12$$

$$\text{Heritability \%} = 200 V(F) / [V(F) + V(E)] = 33\%$$

This suggests that about one-third of the phenotypic variance in mean k for the three femurs against body length is the result of genetical variation. This figure, it should be noted, will be an underestimate if the relationship between members of a family is less than that of full sibs—i.e. if more than one male has contributed to any of these families.

5. DISCUSSION

Leg growth in *Notonecta* presents a rather typical picture of the kind of allometric growth that has been found in numerous studies of insects and crustacea (Huxley, 1932; Teissier, 1935; Reeve & Huxley, 1945) but few of these appear to have been previously investigated in detail with the help of statistical methods, and very little attention has been paid to the question of genetical variation in the allometry coefficients. The double logarithmic graphs published by Clark and Hersh suggest to the eye that relative growth of the legs gives a close approximation to simple allometry, with possibly some deviation in the direction of a sigmoid curve. Our fuller analysis shows that there are, in fact, significant deviations from simple allometry (or linearity on the double log plot), and that these are not eliminated by fitting a second degree curve. The causes of these sigmoid deviations from linearity are quite obscure, but they may possibly indicate that the allometry equation does not give an adequate representation of the course of relative growth. The deviations are, however, relatively small and certainly not large enough to make it meaningless to fit linear regression equations to each individual and compare their slopes, the

only difficulty being that the deviations from linearity will, in any normal regression analysis, swell the error variance and reduce the apparent significance of tests in which this is used. This difficulty has been avoided by calculating the growth coefficient k separately for each individual and analysing the variation in these k values.

The k -values of a series of bilateral appendages, or other serial parts such as segment widths of the crustacean abdomen or successive segments of a single leg, often differ in an ordered way, and there is then said to be a *growth-gradient* (Huxley, 1932). The physiological basis of such gradients is quite unknown, but they usually show a decline in k antero-posteriorly, suggesting a connection with the order of development of the segments (the law of antero-posterior development). The primary gradient may, however, be modified by the presence of a secondary sexual character with a high growth ratio. Teissier (1935) found that the walking legs of male *Maia squinado* go through three successive stages of simple allometry, of which only the last shows a growth gradient (a typical antero-posterior one). During this phase the chela in males is growing at its most rapid rate, so the late appearance of a growth gradient in males seems to be a secondary sexual phenomenon associated with the doubtless hormonally induced high growth ratio of the male chela during the last moult, which introduces sexual maturity. During the earlier growth of males and throughout the growth of females, the k values of the four walking legs are virtually identical, so that no primary growth gradient appears to exist here.

In *Notonecta* the situation is quite different. The onset of sexual maturity at the last moult does not have any noticeable effect on the relative growth rates, and there is from the first instar a sharp gradient in size of the legs, reflected in all their segments, as Table 8 shows for the femurs. The relative sizes of the three femurs do not change very much during growth, while each is increasing in length 6-7 times. In the adult femurs 1 and 2 are about $\frac{1}{2}$ and $\frac{2}{3}$ as long as femur 3.

Table 8. *Relative femur lengths in Notonecta females*

	Length as % of third femur length			Actual length of third femur
	Femur 1	2	3	
First instar	54	63	100	0.68 mm.
Adult instar	47	66	100	4.35 mm.

This size gradient, and the fact that it remains much the same from the first instar onwards, are evidently the result of the adaptive enlargement of the third legs as specialized swimming organs, an adaptation which is as essential in the first nymphal stage as in the adult. It is obviously established during embryonic growth preceding the first instar. A slight modification occurs in the size gradient during subsequent growth, as is indicated by the differences between the k -values of the three femurs shown in Table 3. This 'growth gradient' in k causes a small decrease in the relative size of the first femur and a small increase in that of the second femur, compared with the third. This pattern of k -values is not what one would expect if

there were either a primary antero-posterior gradient in k unmodified by the adaptation of the third legs for swimming, of a similar gradient modified by an increased growth rate of the third legs.

Our analysis of the k -values shows that there is significant variation between animals in the mean relative growth rate of the three femurs, and that part of this is genetically determined. On the other hand, no significant individual variation was found in the shape of the growth gradient—i.e. in the relative magnitudes of k for the three femurs. In other words, such individual variation as has been found, whether of environmental or genetic origin, causes correlated variations in k for the three legs together but no independent variation in k for particular legs. A similar situation has been found for the variation in hair number on the abdominal sternites of *Drosophila melanogaster*, since in wild stocks genetical variation is present which causes correlated changes in hair count of all the segments, but not independent changes on particular segments (Reeve & Robertson, 1954).

Individual variation in the growth ratio, k , may turn out to be a common feature of allometric growth when it is looked for. As a recent example, Cock (1963) found clearly significant variation in k for shank length against body weight in two breed crosses of the fowl, during the period of simple allometry from 2–10 weeks of age. Moreover, the fact that the two crosses differed in mean k makes it obvious that genetic variation in this index was present. An essentially analogous situation is found in the relation of various dimensions in *Drosophila subobscura*, where we are only able to study size allometry of individuals of the same growth stage, or allomorphosis. Robertson (1962) found that selection to change the ratio of wing to thorax length caused leg length to change in the same direction as relative wing length, while Misra & Reeve (1964), from a study of clines in body dimensions of populations of *D. subobscura* and *D. robusta*, found evidence of two groups of genes acting independently, the first group affecting general body size and so causing correlated changes in head and thorax size and probably all other dimensions roughly in proportion, and the second group affecting wing and leg size only.

SUMMARY

This paper presents the first part of a further analysis of data collected many years ago by Clark and Hersh on allometric growth in *Notonecta undulata*, the water boatman. The data consist of measurements of a number of dimensions, taken each instar, on 72 individuals reared separately from egg to adult. These individuals were the progeny of nine wild females, so that a rough estimate can be made of the magnitude of genetic effects by comparing the variances within and between families. The paper examines the allometric relationship between femur length of the three legs and body length.

The statistical problems in this type of analysis are discussed. There are significant deviations from linearity when the six points for femur length are plotted against body length on a double log graph, but these are small compared with the overall linear trend. The growth coefficients (k) are calculated for the three femurs against body length for each individual, and are analysed for differences between

femurs, between sexes and between and within families. This analysis shows that there are significant differences between the three femurs in growth coefficient, but the growth gradient, or pattern of k values between the three femurs does not vary significantly from one individual to another. On the other hand, mean k for the three femurs shows significant individual variation and also a significant variation between families. From this it appears that about one third of the phenotypic variance in mean relative growth rate of the femurs is due to genetic effects.

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