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STUDIES ON THE GROWTH OF *PEDICULUS* (ANOPLURA)

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(With 7 Figures in the Text)

CONTENTS

IN the course of work on populations of lice, some of which has already been reported (Buxton, 1936), I required to know what proportion of the larvae which were found belonged to each of the three instars. Much difficulty has been experienced in defining the points of distinction, and it may be that the results which are here reported will prove valuable to others engaged on similar studies. The work has also some general interest as a study of the growth of an insect of which the metamorphosis is slight; in order to make it more complete in that respect, the scope has been extended to include the adult insect.

HISTORICAL

The anatomy of adult lice began to receive attention many years ago, but it is only rather recently that the structure of the larvae has been examined and figured. Fahrenholz (1912) distinguished the first stage and figured the abdominal chaetotaxy fairly accurately, but he failed to discover that there are two subsequent larval stages. This failure shows that the points of distinction are not very striking, and is perhaps due to the fact that his material was derived from wild populations, because he could not breed his insects. It appears that the first investigator who succeeded in rearing *Pediculus* from egg to adult was Warburton (1910), and it was he who first recorded that there are three larval stages. Shortly after that Patton & Cragg (1913), breeding the insect in Madras, also observed the three stages and figured them. In Hindle's investigations, carried out in 1912 and published in 1919, the three stages were clearly identified and facts about their duration were recorded. Similar observations were made by Sikora (1915), Müller (1915), Hutchinson (1918), and Swellengrebel (1918): Nuttall (1917), in reviewing existing knowledge of the subject, expressed the view that three larval instars were invariable. Sikora and also Müller recorded that a moult occurs within the egg, but this is omitted from the reckoning.

But though it has been established for some time that there are three larval instars, our knowledge of the points of distinction between them remains imperfect, and from the fact that several careful observers failed to distinguish the second and third stages, it may be concluded that the differences are not very great. Patton & Cragg (1913) found that the principal difference was in size: their Plate 69 also shows a progressive increase in the length of thorax and abdomen in comparison with that of the head. The matter was gone into thoroughly by Müller (1915), who published the most complete account which we possess. He figured all three larval stages and gave particular attention to the dorsal chaetotaxy, showing that very definite differences can be discovered between the instars (see below): he also pointed out that the size of the abdomen relative to the head increases in each instar, but that it also grows during an instar. Hase (1915) figured the dorsal and ventral aspects of the first larval stage, but supplied no information about later instars. In his later work the same author (Hase, 1931) published figures of the dorsal view of the three instars, remarking that they could easily be distinguished by the number and position of the setae, without entering into further explanations. An examination of his figures suggests that useful points of distinction might be found in the setae on the dorsal surface of the head and of the abdomen. The dorsum of the first instar has been figured in colour by Keilin & Nuttall (1930), who also give line drawings of all three larval instars (dorsal).

One might summarize the preceding information on the larval instars of *Pediculus* by saying that it is established that there are differences in the proportion of head to thorax and abdomen, but no figures have been published about the range of variation in this respect, and it is not known whether an individual specimen can be referred to its instar by studying measurements and ratios. It is also known that there are considerable differences in chaetotaxy between the instars, but the matter requires further study, and it is not clear whether the differences would be easily appreciated in preserved material or in specimens which have been treated with alkali.

With regard to early instars of other Anoplura, little has been recorded. Enderlein (1905) gave a description of the adult *Polyplax spinulosa* and recorded that the larvae could easily be recognized as those of *Polyplax*, and that they possessed only one pair of setae on each tergite and sternite near the mid-line, except that on the abnormally long second abdominal segment there were two pairs of such setae. It is evident that Enderlein was describing the first larval instar of the insect. Florence (1921) gave a full account of *Haematopinus suis*. She observed that there were three larval instars, and that at each successive moult the thorax and abdomen became larger, relatively to the head: also that at successive moults the chitinous pleural plates became larger. The joint between the tibia and tarsus appeared only at the last moult. It was also recorded that a considerable amount of growth takes place during the course of an instar. In several respects no difference could be found between larvae and adults; for instance, at all stages there were five antennal joints and nine abdominal segments.

Qualitative changes during growth

The material from which these notes were made was a strain isolated from a shirt in London; in size and antennal character the lice presented the characters of *Pediculus humanus corporis*.

Chaetotaxy. Figures published by previous workers suggest that differences exist between the three instars in the chaetotaxy of the dorsal surface of the head. Study of a series of specimens leads me to the conclusion that though differences may be found, they are very slight, and that it would be no easy matter to use them to discriminate between the instars. The figures given by Keilin & Nuttall (1930) are much more accurate than those of Hase (1931).

The figures of Müller (1915), Keilin & Nuttall (1930), and Hase (1931) show that there are differences in the chaetotaxy of the dorsal surface of the abdomen of the three larval instars, but we do not know to what extent the differences vary or whether they can be used with confidence in referring a specimen to its correct instar. I have only given attention to the dorsal side of the abdomen and for the most part to the segments which bear the first and last spiracle, which are believed to be the third and eighth abdominal segments (see below). On the abdominal segments in all instars there are one or two lateral hairs close to the upper edge of the paratergal plate, and there is a row of median hairs across the back. The number of pairs of lateral and median hairs is as follows:

	Segment 3		Segment 8	
Instar	Lateral	Median	Lateral	Median
I	1	1	1	1
II	2	2	2	3
III	2	4–5 (3 rarely)	2	3 and 1 minute

It is easy to distinguish the first instar by the chaetotaxy of the abdomen, of which the setae are few, relatively long, and arranged in longitudinal lines. But it is more difficult to distinguish the second from the third instar, particularly as the third instar is rather variable. In two particulars, however (apart from the number of pairs of setae), these instars are quite distinct. On the third segment and those which follow it the setae in the third instar are never placed in one row, one or more of them being displaced to a position in front of the others; in this respect it will be seen that the louse in its last larval stage shows a tendency to resemble the adult. The second point of distinction is that on the eighth segment of the third instar there is an additional pair of minute setae close to the mid-dorsal line, in line with the other members of the row. These setae, though minute, are easily seen with a 4 mm. objective. A pair of similar but slightly larger additional setae may be observed in a similar position on segment 7. These two points of distinction between instars II and III have not previously been recorded.

It is hardly necessary to describe the abdominal chaetotaxy of the adult. The setae are not only more numerous, but irregularly disposed in several ill-defined transverse rows in both sexes: the irregularity is greater in the females than the males.

Spiracles. In larvae of all instars and in adults the number of functional spiracles is the same, for there is one pair on the thorax and six on the abdomen. Even in larvae of the first instar one may observe that the structure of the spiracle is apparently as elaborate as in the adult, and as air can be seen in the tracheae leading to each spiracle, it is clear that all of them are functional. It is hardly relevant to discuss which abdominal segments carry these six spiracles. I propose to accept the view of Prof. G. F. Ferris, who writes: "According to my way of looking at it the spiracles in the sucking lice are on the third to eighth segments. This is based in part on the assumption that the female genital opening is between the eighth and ninth segments—which is the normal position in most groups of insects—and also taking into consideration the segmentation in such genera as *Hoplopleura* where the presence of definitely developed paratergal plates defines the segments very sharply. In this genus there is what is apparently a small, but very well defined, paratergal plate for the first segment."

Larvae in the first instar differ from others in possessing no paratergal plates, the abdominal spiracles being surrounded by an area of soft cuticle covered with minute rugae. In the second instar, as in the third, the paratergal plates on the third and eighth abdominal segments are regularly defined, as can be seen particularly clearly if one examines a moulted skin.

Antenna. In the antenna in larval instars I–III there are well-defined articulations between the first and second joint, and between the second and the part which follows; this part is itself without articulations, though external constrictions divide it into three portions. The antenna of the larva is therefore 3-jointed. In adults, on the other hand, the antenna is 5-jointed. This difference was correctly described by Landois as long ago as 1864. In *Haematopinus suis* the antenna is 5-jointed even in the first instar (Florence, 1921).

Tibio-tarsal joint. This articulation is clearly marked in all legs and all instars. In this respect *Pediculus* differs from *Haematopinus suis* in which this joint is only developed when the insect becomes adult (see Florence, 1921, text and figures).

Internal. In larvae in the first, but not in later, instars, it is generally possible to see opaque masses, doubtless of excretory material deposited in fat body. In some individuals these masses are much more conspicuous than in

others. They occur in many parts of the insect, frequently in the back of the head, and they are conspicuous in living larvae examined in water, or in specimens mounted in balsam.

Müller (1915) remarks that the diverticula on the front of the midgut often extend into the base of the legs in the first instar, but never in subsequent instars. If one examines living material, uncompressed, it will be found that the phenomenon is very irregular, and not common.

Quantitative changes during growth

Gross measurements

Before proceeding more deeply into the matter, it might be interesting to discover whether the three larval instars could be readily separated by measuring the total length. An opportunity of testing this presented itself when a heavily infested shirt was received from a cleansing station in London. The shirt was divided into small pieces, each of which was searched till it was free of lice; there was therefore no tendency to select the larger insects. The process occupied several days, so that the lice became more and more hungry, and perhaps for that reason shorter. The method was in this respect very crude. Each insect was dropped into spirit and subsequently measured, adults being omitted. The results are presented in Fig. 1, which is based on 1640 larvae. The curve shows three peaks, corresponding to the three larval instars, but it is clear that there was a considerable amount of overlap, and that if one relied on length many larvae could not be assigned to an instar. The measurements for males and females hardly concern us: many males and a few females were shorter than some of the largest larvae of the third instar.

It appears then that it is necessary to go more fully into the matter if reliable points of difference between instars are to be found.

Measurements of parts

The material which was used in the investigations described below was bred for many generations in the laboratory, having been derived originally from a garment from London. The adults present the characters of *Pediculus humanus corporis* in size and the structure of the antennae. All the specimens which were used for purposes of measurement were allowed to feed after emerging from the egg or after moulting. They were then starved for 24 hours at room temperature and killed by hot water, which caused them to die with the legs extended. They were mounted in Canada balsam without pressure.

No attempt was made to preserve or measure freshly moulted specimens, and I have no information about the individual's growth during an instar. All the adult females measured had lived at least 2 days, and their abdominal development appeared to be complete.

All measurements were taken from the mounted material. Considerable difficulty was experienced in finding precise points from which measurements might be taken. There is, for instance, no exact mark at the back of the head, and no sharp line separating thorax from abdomen in larval lice. Eventually the following standard measurements were carried out on all the specimens:

(1) *Length of head* measured from the extreme front of the head, excluding mouthparts, to the base of a V-shaped depression in the front of the thorax

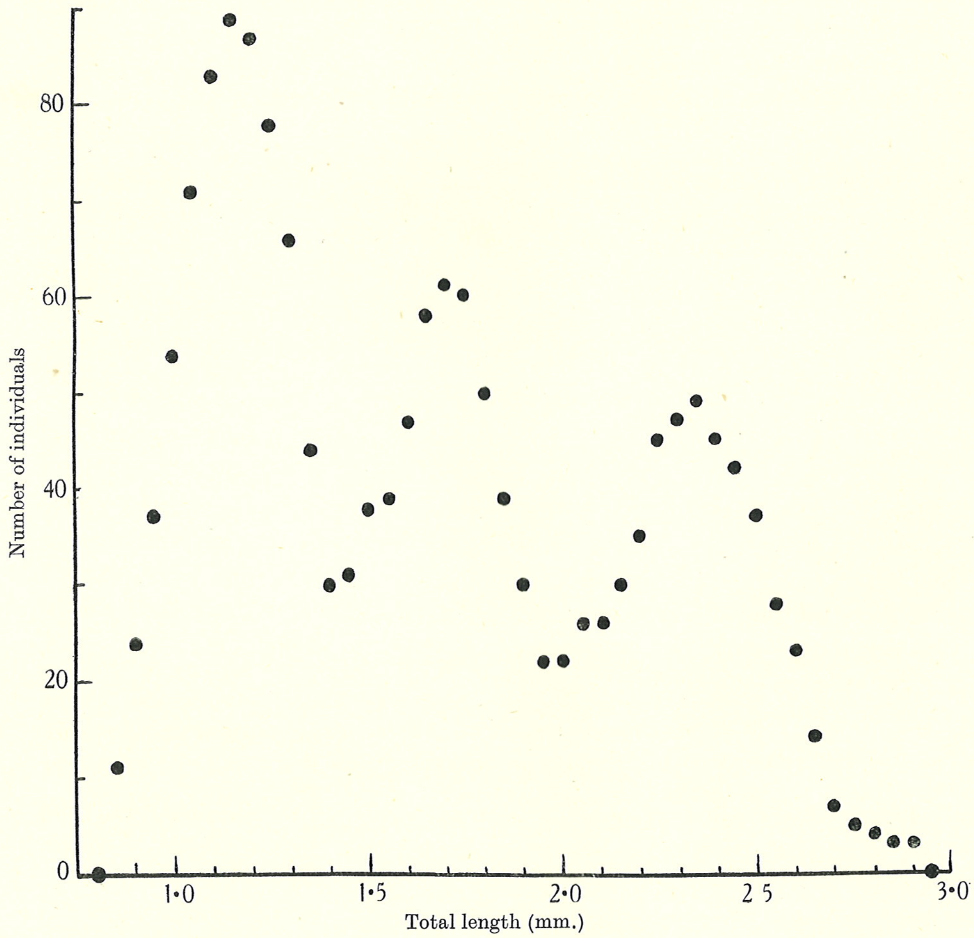

Fig. 1. Showing frequency distribution of total lengths of 1640 larvae of *Pediculus humanus corporis.*

(Fig. 2). The measurement is not a satisfactory one because it depends to some extent on the retraction of the head towards the thorax.

(2) *Breadth of head* at the level of the eyes, including the convexity of the cornea. This is a good measurement, easily carried out between precisely defined points. An occasional specimen cannot be measured as the head is not lying flat.

(3) *Length of thorax and abdomen* measured in the midline from the front of the thorax to the extremity of the abdomen. The measurement in itself is easy to carry out, but is perhaps slightly unnatural in specimens which have been starved for 24 hours because the gut is by that time nearly empty and the abdomen perhaps shorter than it would be immediately after a meal. Moreover, one may suppose that in the females the development of the ovaries may affect the measurement and make a difference between freshly emerged and fully mature insects.

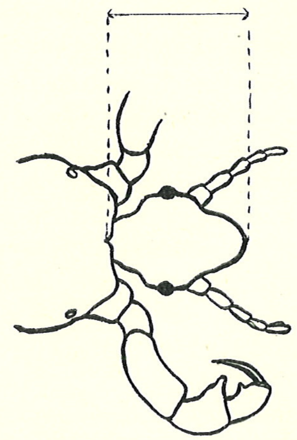

Fig. 2. Outline of head and front of thorax showing the points between which the measurements of "head length" were taken.

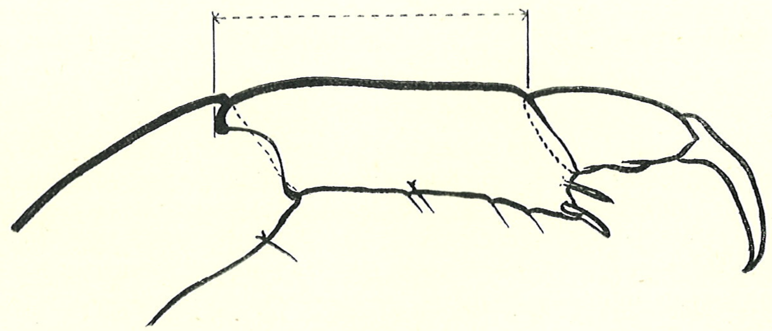

Fig. 3. Outline of part of leg, showing the points between which the measurements for "length of third tibia" were taken.

(4) *Length of tibia* (Fig. 3). The third tibia was selected and the measurement taken along the anterior margin from the base, which is generally covered by the extremity of the femur, to the line separating the tibia from the tarsus, which is easy to discern in all instars. It was clear that the tibia of the first leg should not be selected for measurement owing to the considerable structural differences which develop between male and female; the third was chosen because it was assumed, erroneously, that it would not show secondary sexual characters.

From what has been said it seems that the length of the head and of the thorax and abdomen together are not very satisfactory measurements. The breadth of the head and the length of the tibia are easy to measure, and as the structures are rigid one may assume that the dimensions are not likely to be altered by nutrition, posture, etc.

The measurements obtained are shown in Table I.

Table I. *Giving certain dimensions (mm.) of successive larval instars and adults of* Pediculus humanus corporis

		Stage 1	Stage 2	Stage 3	♂	♀
	Number examined	20	32	22	103	26
Head length:	Mean	0·336	0·381	0·462	0·513	0·553
	Standard deviation	0·020	0·020	0·021	0·034	0·028
	Coefficient of variation	6·0	5·2	4·6	6·6	5·1
	Maximum	0·369	0·420	0·508	0·560	0·589
	Minimum	0·302	0·341	0·413	0·440	0·471
Head breadth:	Mean	0·281	0·327	0·377	0·437	0·470
	Standard deviation	0·018	0·0126	0·023	0·016	0·014
	Coefficient of variation	6·4	3·9	6·1	3·7	3·0
	Maximum	0·307	0·347	0·444	0·474	0·495
	Minimum	0·253	0·302	0·338	0·389	0·435
Thorax and abdomen length:	Mean	0·931	1·347	1·976	2·176	2·693
	Standard deviation	0·116	0·123	0·107	0·152	0·277
	Coefficient of variation	12·4	9·1	5·4	7·0	10·3
	Maximum	1·120	1·680	2·200	2·48	3·24
	Minimum	0·710	1·140	1·730	1·81	1·90
Total length:	Mean	1·268	1·728	2·438	2·691	3·246
	Standard deviation	0·125	0·141	0·124	0·183	0·296
	Coefficient of variation	9·9	8·2	5·1	6·8	9·1
	Maximum	1·484	2·100	2·660	3·029	3·817
	Minimum	1·052	1·520	2·207	2·256	2·371
Third tibia length:	Mean	0·197	0·270	0·363	0·408	0·377
	Standard deviation	0·010	0·011	0·011	0·020	0·016
	Coefficient of variation	5·1	4·1	3·3	4·9	4·2
	Maximum	0·213	0·289	0·386	0·449	0·405
	Minimum	0·178	0·249	0·333	0·360	0·352

Variability

Consideration of Table I suggests that if one desired to make use of measurements in order to discover the stage to which a particular immature specimen belonged, some difficulty might be encountered. For instance, though the number of specimens measured is not very great, there is occasional overlapping between successive instars, as in the measurements for head length. If more specimens had been examined the amount of overlap might have been greater. In several other instances there is no actual overlapping, but the measurements of the extremes of different instars are very close to one another. For instance, in the figures for the length of thorax and abdomen, the largest individual in the first instar measured 1·120 mm., the smallest in the second 1·140, a difference of under 2 per cent. Similarly, the difference in total length between the largest larva of the second instar and the smallest of the third is only about 5 per cent. On the other hand, if one considers the measurements of the third tibia it will be seen that the difference is greater, even between those individuals of different instars which most nearly approach one another; both between the first and second, and second and third instars, the difference is 15 to 17 per cent. Overlap in size between larvae of the third instar and adults, or between adults of the two sexes, is of little practical importance, for males and females can be so readily distinguished by other characters (Nuttall, 1917). One may, however, observe that in very nearly all measurements the largest third-stage larvae exceed the smallest males and females; between males and females the measurements overlap in nearly every particular.

It is only with unusually large or small individuals that any difficulty occurs, for the mean values for all measurements in successive stages are clearly separate from one another; indeed, the differences between means are so great that any test of significance appears almost superfluous. It might, however, be of interest to apply the customary test for the significance of the difference between means to the figures for head length (in which we have already remarked some overlapping among the extremes in larval instars). Applying this test, it is found that the difference between mean head length in stages 1 and 2 is 0·045 mm. and its standard error 0·0057. The difference is therefore about seven times its standard error, which is to say that it is clearly significant. For the mean head length of stages 2 and 3 the significance is even greater, the difference being about fourteen times its standard error. The difference between males and females in head length is also significant, being about seven times its standard error.

It is not without interest to study the variability stage by stage and measurement by measurement, using for this purpose the coefficient of variation, i.e. the standard deviation expressed as a percentage of the mean (Table I). In doing so one may assume that some of the variability is inherent, but that some of it is due to the difficulty of defining the exact point from which certain of the measurements were taken. As has already been explained, it is more difficult to make a satisfactory measurement of head length than of head breadth; one would therefore expect that the coefficient would be larger in the figure for head length, but this is not so, at least for the larval stages; in the adults, however, head breadth is considerably less variable than head length. It would also be expected that inasmuch as the length of third tibia is easy to measure accurately, the variability in that measurement would be low, but in fact the coefficients of variation in the length of the third tibia are only a little less than those of the length of the head. The length of thorax and abdomen is clearly a very variable character, at least in the first two instars; this may be due to the fact that the abdomen is capable of expansion and that the insects contain different amounts of blood at the time when they are killed. In the adult female there may be much variation due to development of ovaries. The high variability of the total length presumably depends on that of the abdomen, which forms so large a part of it.

It will be seen that there is a general decrease in the coefficients of variation at each successive moult. This decrease is so frequent that one can hardly suppose that it is due to chance, though there are a few exceptions.[1] It seems curious that larvae in the third instar should be *less* variable than the others, for they will shortly moult into adult males and females, which differ considerably from one another. Though there appears to be a tendency for the coefficient of variation to get less in successive larval instars, it is not further reduced in adult males and females.

Changes in proportion during growth

Table I gives the following means in millimetres for head breadth in different stages:

Instar I	Instar II	Instar III	♂	♀
0·281	0·327	0·377	0·437	0·470

If we take the head breadth of the first stage as 100 that of the second is 116·5; similarly, if we take the second stage as 100 that of the third is 115; and taking the third stage as 100 the head breadth of the male is 116, that of the female 124·5. Proceeding similarly with all the means given in Table I one attains the factors for relative growth set out in Table II.

Table II. *Giving the relative growth of parts of* Pediculus humanus corporis. *The figures are based on means given in Table I, and give the percentage increase from stage to stage*

	Stage I to Stage II	Stage II to Stage III	Stage III to ♂	Stage III to ♀
Head length	113·5	121	111	120
Head breadth	116·5	115	116	124·5
Thorax and abdomen length	144·5	146·5	110	136·5
Total length	136	141	110·5	133
Third tibia length	137	134	112	104

Considering first the factors for larvae, two conclusions will be drawn; growth is regular and on a geometrical ratio through larval life (in other words it follows the law first described by Dyar (1890) for caterpillars of Lepidoptera): different parts of the insect grow at very different rates. The table also shows that when insects become adult the increase in the males is less than that in the females in all measurements except the length of the third tibia. In this measurement the male is not only relatively, but absolutely, greater than the female (Table I); in females therefore the relative increase of the third tibia is very little.

The proportionate length of head and body. We may now give particular attention to the relative growth of head and of thorax with abdomen, and to

[1] Larsen (1930) shows that the coefficient of variation of certain (but not all) dimensions of *Notonecta* falls from the first instar to the third or fourth, increasing in the fifth, which is the last larval instar. Spett (1930), working on the grasshopper *Chorthippus*, makes use of the coefficient of variation and of a formula for its standard error. He concludes that the first instar is significantly more variable than the second or third, but that variability rises significantly in the fourth and fifth (the last larval instar). He quotes a Russian paper, which I have not consulted (Zuitin, 1926), showing that *Dixippus* is also highly variable in the first instar.

consequent changes in the ratio of these parts to one another. Change in this ratio is believed to have some practical value in separating the instars, and several authors have already called attention to it in their figures or their text (Patton & Cragg, 1913; Müller, 1915; Keilin & Nuttall, 1930). Working with the original data (not with the means given in Table I), one obtains the following mean ratios, the length of head being counted as unity in each case.

Instar	I	II	III	♂	♀
Ratio	2·77	3·52	4·29	4·24	4·86

The figures show that there is a considerable increase in the (mean) relative length of thorax and abdomen in the three successive larval instars, that the ratio for the male is substantially the same as that for the third instar, and that the ratio for the female is again increased. But whether one could use this ratio for the practical purpose of separating larvae correctly into three instars depends not on the mean values but on the individual scatter about them. All the individual points have been plotted in Fig. 4, a study of which shows that one could successfully refer nearly all the specimens examined to the correct instar, though some difficulty would be experienced in a few cases. As the matter has considerable interest, both practical and theoretical, it appears desirable to publish not only the mean ratios given above, but also statistical information about the consistency of the individual figures about the means; this is given in Table III. It will be seen that there is considerable overlap between extremes.

Table III. *Giving the mean ratio of head length to length of thorax and abdomen (head length* = 1), *and an indication of the consistency of the individual ratios about their means:* Pediculus humanus corporis, *all instars and both sexes*

	Stage I	Stage II	Stage III	♂	♀
Number examined ...	20	32	22	102	26
Mean ratio	2·769	3·520	4·286	4·240	4·863
Standard deviation of ratio	0·279	0·282	0·295	0·281	0·401
Maximum	3·08	4·11	4·78	5·20	5·61
Minimum	2·08	2·95	3·63	3·58	3·88

Fig. 4 and Table III show a considerable degree of inconsistency among the individuals within one instar, and it is perhaps of interest to compare the figures that have been published by previous authors. This I have done by measuring their illustrations and working out the proportion of head length to length of thorax and abdomen. The figures obtained are as follows:

	Patton & Cragg (1913)	Müller (1915)	Keilin & Nuttall (1930)
Instar I	2·29	3·25	2·51 (Pl. IV)
Instar II	3·42	3·78	3·78 (Pl. V, 4)
Instar III	3·67	5·00	3·83 (Pl. V, 5)

From these figures one might warrantably draw the conclusion that though the work was doubtless accurate, some of the authors made their figures from specimens which were far removed from the normal.

The fact that the head of *Pediculus* is relatively large in the first instar was noticed by Hase (1931). He suggested that as lice at all stages must pierce skin and suck blood the length of mouth parts (and consequently to some extent of head) could not be much less in the early instars than in the adult. But surely the phenomenon is one of almost universal occurrence, throughout the animal kingdom. It is generally accepted that it is due to the existence of the growth gradient, and no particular explanation of its occurrence in *Pediculus* appears to be necessary.

Relative growth of several parts. Let us pass to the more general study of the relative growth of several parts of the insect. This is a subject of considerable

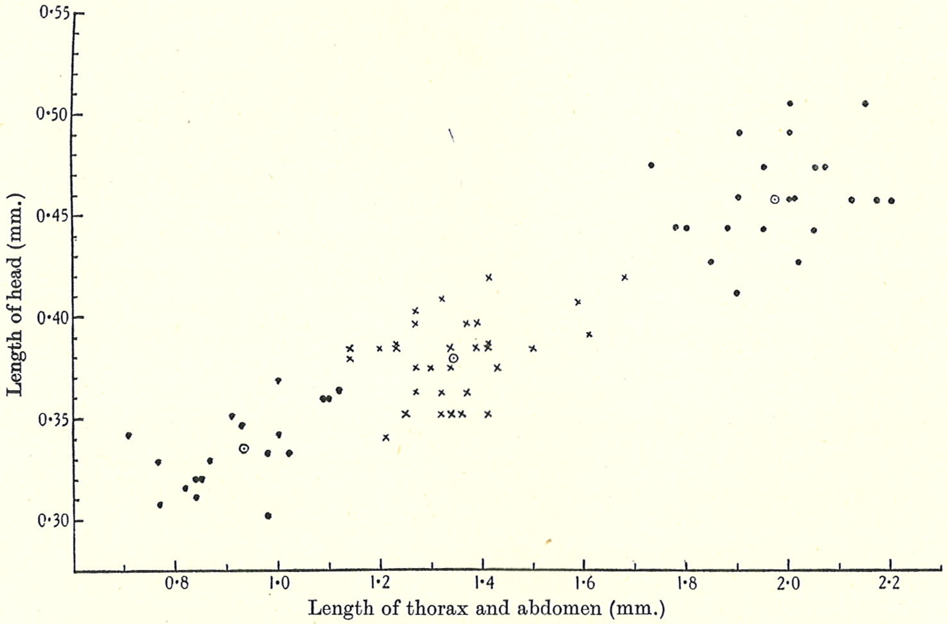

Fig. 4. Showing the relation of length of head to length of thorax and abdomen, in individual larvae of the three instars. The instars are distinguished by different symbols, and the means for each instar are shown by circles. The individual larvae which are shown on this graph are those on which Table I was based.

theoretical interest, and *Pediculus* is in many ways an excellent object for study. It is readily obtainable and easily reared under uniform conditions; it has invariably three larval instars; its metamorphosis is slight and as it is quite apterous, no disturbance of the dimensions of the thorax, owing to development of wing muscles, is to be expected. But in one respect it is not a suitable insect; it would be difficult to study growth in weight, not only because the louse is very small, but because it takes relatively large meals of blood. One must therefore limit oneself to studying growth in linear dimensions.

One might express the information given in Table II in a rather different way, saying that inasmuch as growth from stage to stage is on a geometrical

ratio, and as the factor differs for different parts of the insect, the growth is allometric.[1] One may satisfy oneself that this is approximately true by plotting some measurement of the size of the insect against the size of a part on doubly logarithmic paper. As a standard, one requires some measurement which gives a good expression for the growth of the whole insect, with which the parts may be compared. There is much to be said for using total length as the standard; the only objection to it is that it is the sum of head length and length of thorax and abdomen, neither of which is easy to measure precisely (p. 70), but as the coefficient of variation of total length (p. 72) was not particularly high, it may be accepted as the standard. In Fig. 5 I have done this, plotting the means for

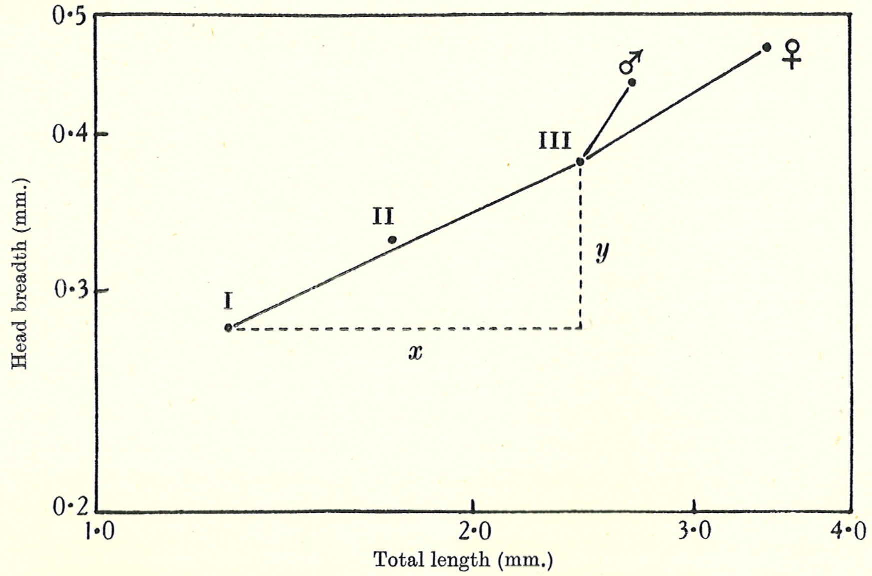

Fig. 5. Showing the relation of means of head breadth and total length on a doubly logarithmic scale (*Pediculus*). The points on the graph relate to the larval instars (I, II, III) and the adults of both sexes. Data derived from Table I. The constant α (for the larval stages) is arrived at by measuring x and y.

total length against head breadth for the three larval instars and males and females. The points for the three larval instars lie very close to a straight line, but not precisely upon one. It is desirable to fit the best straight line to these three points; remembering that the percentage increase of the parts of the insect through larval life is nearly constant (Table II), I have assumed a mean increase for total length of 138·5 per cent and for head breadth 116 per cent. The line shown in the figure, starting from the actual position of the mean of the third instar has therefore been drawn. The position of such a straight line can be expressed by the formula of simple allometric growth, $y = bx^{\alpha}$, where y is the length of part and x of whole, and b and α are constants. It is the value

[1] It appears desirable that this term rather than "dysharmonic" or "heterogonic" should be employed. See Huxley & Teissier (1936).

of constant α which is of most interest, for it determines the slope of the line, in other words the increase of part relative to whole. This constant may be determined directly[1] from the doubly logarithmic graph by measuring dimensions x and y (in ordinary arithmetical units); $\alpha = y/x$. To put the same thing in other words, α is the tangent of the angle which the straight line makes with its x axis. In this way it is found that the value of α for larvae is 0·46. It can be seen from Fig. 5 that the increase of head breadth relative to total length is

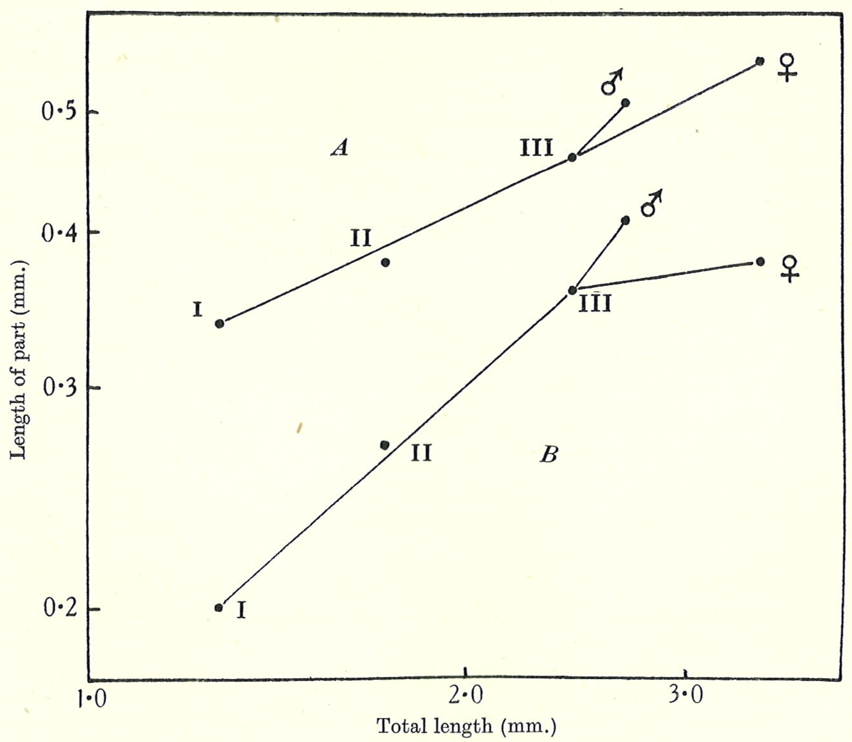

Fig. 6. Showing the relation of mean length of head (*A*), or length of third tibia (*B*) to mean total length (*Pediculus*).

very regular during larval life, but alters abruptly at the last moult, head breadth increasing relatively in both sexes, but especially in the male. The constants for male and female are 1·47 and 0·78.

In Fig. 6, curve *A* deals similarly with the relation of head length to total length. This does not differ very greatly from what is shown in Fig. 5; the change at maturity is less, but in the same direction in both males and females; this can be seen by inspecting the figure, or from the values of constant α given in Table IV.

[1] Determination by measuring from a graph, particularly from one on doubly logarithmic paper, is admittedly not very precise. I feel that it is justified because the measurements themselves show so much scatter (Table I) that no great precision in after-treatment could give a very accurate value for the constant.

Table IV. *Values of constant α for relative growth of certain parts compared with total length as standard,* Pediculus humanus corporis

Part	Standard	Larval instars	♂	♀
Head breadth	Total length	0·46	1·47	0·78
Head length	,,	0·51	1·06	0·62
Third tibia	,,	0·93	1·20	0·12

Curve *B*, Fig. 6, gives the relative growth of third tibia and total length. It will be seen that the line expressing the growth of the three larval instars is nearly at an angle of 45° with the axes of the graph, so that constant α is close to unity (0·92). In this case there is an approach to "isometric growth", the special case in which the growth rates of the part and the whole are equal. The graph shows also that the growth of the third tibia is nearly isometric with total length for the male, but for the female the allometry is very pronounced and negative ($\alpha = 0{\cdot}12$).

It is not necessary to discuss the allometric growth of insects in general, for the subject has recently been dealt with fully by Huxley (1932). His book furnishes many examples, especially among the Crustacea, of growth which is regularly allometric up to maturity, at which time sexual differentiation produces a relative increase (or decrease) in the growth of the part studied. In the present paper I propose to limit myself to those insects in which the metamorphosis is not complete, and to give particular attention to the differentiation of the sexes. Much the most complete body of fact available is that published by Spett (1930), on the grasshopper *Chorthippus*. The same author's later papers (1934, 1935), of which the text is in Russian, contain a mass of valuable material. In *Chorthippus* there are invariably four larval instars, and the sexes may be separated even in the first instar. It is therefore possible to define the gradual development of differences between males and females throughout larval life, a thing which has probably not been done with any other insect. Spett made eight measurements on each insect and had adequate material of all instars of both sexes. His figures show that in any particular measurement a difference exists between the means of males and females, even in the first instar; this difference would not be regarded as significant when considered by itself, as it is about as great as its probable error; but in subsequent instars the significance increases, and in adults the difference between male and female for each dimension is between ten and twenty times its probable error. I have endeavoured to make use of the information given by Spett (1930) and to discuss allometric growth and differentiation in the sexes of *Chorthippus*. In doing this it is difficult to decide what measurement to use as standard. Measurements of total length are not given (doubtless because the abdomen is so soft and capable of expansion). Neither hind femur nor prothorax appear to be suitable as standards, for if one plots certain other organs (e.g. elytron) against either of them, one obtains complex curves. It is not clear whether the complexity of the curves is due to choice of unsuitable standard, or whether it is comparable to the diminishing allometry which is reported by

Dawes & Huxley (1934). If anyone wishes to go further into the matter he might be well advised to use the data on the grasshopper *Dociostaurus* (Spett, 1934), for here weighings as well as linear measurements are available; it seems evident that total weight would be the best of all standards to which to refer the parts.

Differentiation of sex at the last moult, much as in *Pediculus*, has been recorded by other authors. If one takes the figures given by Bodenheimer (1929) for *Schistocerca* and plots body length against weight, it can be shown that in the female there is a great relative increase of weight at the last moult, observable in the newly emerged female before the ovaries have completely developed. In this sex, therefore, the increase of body length against weight is only allometric during the larval stages. But the growth of hind femur plotted against body length is regularly allometric for all instars, and both sexes of adult.[1] The work of Severin & Severin (1911) on the stick insect, *Diapheromera*, shows that the growth of front femur relative to head and body is regularly allometric through the larval instars and in the female, but in the male the front femur is actually longer, and the head and body actually shorter than in the female. In this sex, therefore, there is a break in the curve for growth of males observable in the last larval instars and in the adult (Fig. 7). Kirkpatrick's (1923) figures for the bug *Oxycarenus* show allometric growth of rostrum and total length, through all larval stages; in the adult male there is a slight relative decrease in the length of the rostrum.

It would probably be correct to sum the matter up by saying that the beginning of sexual differentiation in the insects may be first observed at the last moult, or in any instar previous to that moult. It is often due to a relatively slight modification in a differential growth ratio which has been uniform in the earlier instars.

For studies such as these one would wish to have information on the increase of several linear dimensions and of weight for all instars and both sexes; moreover, the data must be submitted to proper statistical treatment, for the reader requires to know at least the number of individuals measured and the value of the mean and standard deviation. It would also be useful to know whether the specimens were bred or caught in nature. So far as I am aware no set of figures meets all these needs except those published by Spett (1934) on the grasshopper *Dociostaurus*. His data for many other Orthoptera are extremely full and valuable, but do not include weight. Much of the material which is quoted in current literature is indeed hardly appropriate, the investigations having been undertaken for some quite different purpose. For instance, several writers quote figures published by Balfour-Browne (1909) on the development of Agrionids. This author was working out the life history under conditions of great difficulty, and it is clear from his paper that the temperature at which he reared his insects and the conditions of nutrition

[1] On p. 516 of this author's paper the length of hind femur of female is given as 15·5 mm. The context seems to show that this is a misprint for 25·5 mm.

varied greatly. Surely then, his facts are unsuitable for use in a severely statistical discussion. The work of Calvert (1929) on certain dragonflies is open to the same objection: the author showed great skill in working out a difficult life history, but his material should not be quoted as a contribution to biometry. Calvert took fifty eggs of *Nannothemis*, but only three of the larvae survived beyond the 2 mm. stage, and of another genus, *Anax*, only one larva was reared; presumably therefore the conditions were unfavourable. But in

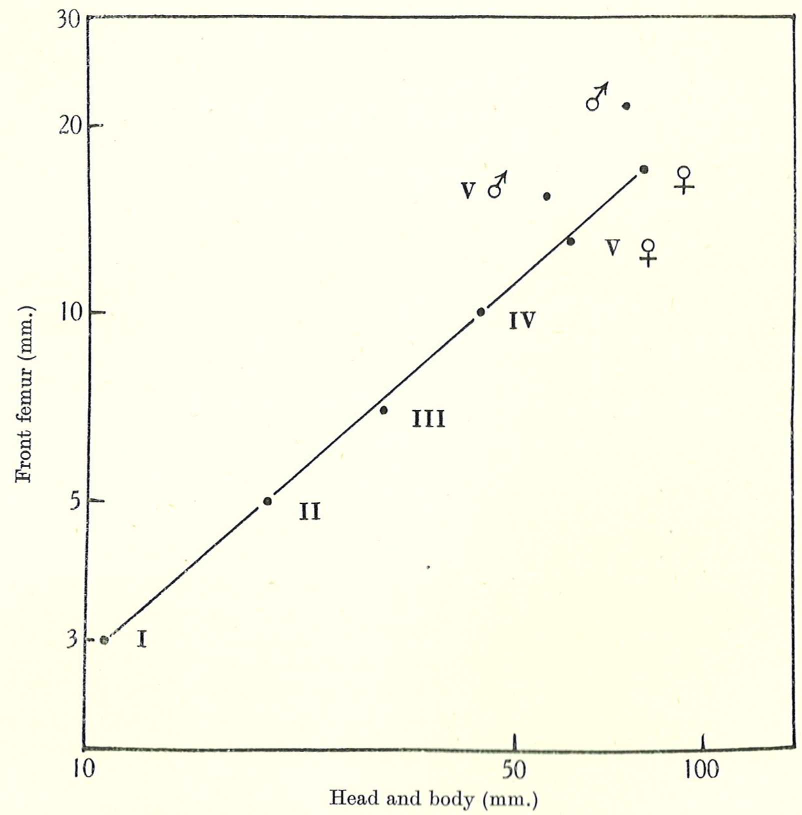

Fig. 7. Showing the relation of length of front femur to length of head and body in Phasmid (*Diapheromera*) (Severin & Severin, 1911).

spite of this Calvert discusses the different growth rates of the genera and even compares his observations on the one surviving larva of *Anax* with Donaldson's great body of figures on the growth of the rat.

It would be substantially true to say that the growth of the louse, and indeed of Arthropods in general, is allometric (Huxley, 1932): in *Pediculus*, as in many other organisms, relatively small differences between the sexes, only observable at the last moult, make a slight complication. That in itself surely renders it difficult to sustain the view first put forward by Przibram & Megušar (1912) for *Sphodromantis*, and more recently applied by Bodenheimer (1933, and previous papers) to insects in general. It will be remembered that the view of these authors is that the weight of an insect doubles and its linear dimensions are increased by 1·26 at each moult. But if the major proportions of a creature alter greatly during the course of growth, is it possible that the increase in length and also in weight could follow so simple a law? This objection to the view of Bodenheimer and the earlier views appears to be valid, whether one accepts or rejects the hypothetical "latent divisions" by aid of which it may be possible to bring the observed figures into line with theory. There are a number of other reasons for refusing to accept the view that weight doubles and length increases by 1·26: some of them are summarized by Spett (1934).

Summary

1. The paper discusses the points of difference between the three larval instars in *Pediculus* and the changes in proportion which take place during growth, not only during larval life but also at the final moult.

2. It is easy to separate larvae of the first instar from others, more difficult to distinguish those in the second and third instars. The principal points of difference are as follows:

First instar. Setae on dorsum of abdomen, few, long and in longitudinal lines: one median pair on most segments. Paratergal plates (carrying spiracle) absent. Mean measurements as in Table I, the best point of distinction between instars being in length of third tibia, which is 0·197 mm. in first instar. Ratio of head to thorax and abdomen about 1:2·8.

Second instar. Setae of dorsum of abdomen in one transverse row, containing 2–3 pairs of setae. Paratergal plates present (as also in third instar). Mean length of third tibia, 0·270 mm. Ratio of head to thorax and abdomen about 1 : 3·5.

Third instar. Setae on dorsum of abdomen, not in one row, but somewhat irregular: a pair of minute supplementary setae, on seventh and eighth segments, close to midline. Mean length of third tibia, 0·363 mm. Ratio of head to thorax and abdomen about 1 : 4·3.

3. During larval life the dimensions of all parts increased as geometrical progressions (Dyar's law), but the rate of increase is different in different parts of the body, so that the proportions, for instance, of head to thorax and abdomen alter with growth; in other words, growth is allometric or heterogonic. But when the insect attains maturity the measurements of several of the parts depart significantly from the geometrical progression which has prevailed during larval life. In most parts of the body the increase at maturity is greater in females than males (no point of distinction having been observed in larvae in the preceding instars); but in the length of the third tibia the increase in the female is much less than in the male. Among other insects in which metamorphosis is slight there are several in which the rate of growth of parts alters at the last moult and becomes different in the two sexes; in some indeed the difference develops much earlier than the last moult. Probably, therefore, it would be true to say that regular allometric growth is generally disturbed by the development of secondary sexual characters.

It is a pleasure to acknowledge help received from Dr J. S. Huxley.

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