GROWTH IN THE LARVAE OF TENTHREDINIDAE

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From a study of the larvae of some twenty-eight species of Lepidoptera, Dyar (1) concluded that growth, as indicated by the growth of the head in successive instars, follows a regular geometrical progression. Fisher (2), working on *Tortrix pronubana* Hb., applied the findings of Dyar and worked out the growth ratio, which he found to be 1·37. The following table indicates how the growth ratio is arrived at:

Table I. (Fisher, 1924.)

Calculated widths, mm.	Observed widths, mm.
1st instar 0·24	0·22, 0·23, 0·24, 0·24, 0·24, 0·26
2nd instar (0·24 × 1·37) = 0·33	0·30, 0·31, 0·33, 0·33, 0·33
3rd instar (0·33 × 1·37) = 0·45	0·44, 0·46, 0·46, 0·46, 0·48, 0·51, 0·55
4th instar (0·45 × 1·37) = 0·61	0·62, 0·62, 0·62, 0·63, 0·63, 0·65, 0·67
5th instar (0·61 × 1·37) = 0·83	0·82, 0·84, 0·87, 0·88
6th instar (0·83 × 1·37) = 1·13	0·94, 0·97, 1·0, 1·1, 1·1, 1·1, 1·2
7th instar (1·13 × 1·37) = 1·54	1·2, 1·3, 1·4, 1·5, 1·5, 1·5

In the above table the measurements are given in millimetres, and the modes of the observed widths of the head capsules of the first and second larval instars are taken as the basis of calculation. By dividing the mode for the head widths of the second instar larvae by that for the first instar larvae, a figure representing the ratio of increase is found. By further calculation it is possible to estimate the width of the head capsule for any subsequent instar. The close approximation of calculated and observed measurements furnishes the student of life history of Lepidoptera with a means of checking larval ecdysis and development.

Morphologically the larvae of Tenthredinidae bear a close resemblance to those of Lepidoptera, hence it seemed possible that the same general laws with regard to growth might be followed. Material was obtained, therefore, to test the application of Dyar's law for growth in the larvae of Lepidoptera to growth in the larvae of the Tenthredinidae.

METHODS OF STUDY.

Four species of Tenthredinidae were bred in captivity in order to provide the necessary material for an initial study of larval growth. The species were *Pteronus ribesii* Scop., *Pteronus leucotrochus* Htg., and *Pristiphora pallipes* Lep., members of the tribe *Nematini*, and *Ametastegia glabrata* Fall., a member of the widely separated tribe *Selandriini*. The larvae were bred in considerable numbers so that at least ten measurements could be taken for each instar. Measurements were made with a micrometer and are correct to the nearest 0·01 mm.

At the outset it was discovered that whereas in the order Lepidoptera the head capsules, which Fisher (*op. cit.*) has shown to be suitable for measurement, are shed entire, those shed by the larvae of Tenthredinidae are split along the median epicranial suture and along one or both of its lateral arms. This rendered the cast head capsules unsuitable for accurate measurement, and consequently it was necessary to kill larvae in order to obtain the widths of unbroken head capsules.

Since it might not always be desirable to kill larvae in order to obtain head measurements, observations were made to discover if some part of the exuvia other than the complete head presented a measurable unit. Examination of numbers of exuviae showed that the frons was almost invariably intact, and was easily dissected out and mounted for measurement.

The frontal sclerites of successive instars of the four species under investigation were studied in relation to the head widths of their respective instars in order to discover if the relationship between the head and frons was constant. If this proved to be the case, then the head measurements could be calculated from those of the frons. This method would avoid the difficulties which might arise from the destruction of larvae to obtain their head measurements.

A study was also made of the growth of the frons in successive instars. If the growth of the frons was found to be constant, it would appear that the frons could be used as a unit for measuring the growth of the larvae, in place of the head capsule. The use of the frons as a unit for measuring the growth of the larvae of Tenthredinidae would be advantageous, since calculation would be simplified and the destruction of larvae in order to obtain measurements would be avoided.

Pteronus ribesii *Scop.*

A study of the development of the larvae of *Pteronus ribesii*, as indicated by measurements of the width of the head in successive instars, suggested that growth was fairly regular during the major portion of the larval life. Complications arose, however, in the later larval stages. In this species the number of ecdyses is influenced by the sex of the subsequent adult, larvae becoming males having five ecdyses and larvae becoming females having six. Observations on several batches of larvae over three seasons indicated that this character was constant. In the ultimate larval instar the larvae of the two sexes approximate each other in size, but those which will become males have passed through four stadia, while those which will become females have passed through five. This variation in the number of instars probably tends to increase the differences in the head measurements for each instar after the first, although it has not been possible to separate the larvae of the two sexes until after the fourth ecdysis.

It is also characteristic of *P. ribesii* that on becoming fully fed the larvae moult and assume an instar in which colour and appearance are different from those of the preceding instars. During this ultimate larval instar no feeding takes place, and a comparison of the head measurements of the penultimate and ultimate larval instars indicate that in the final stadium there is practically no growth. Since the ultimate larval stadium could not be associated with growth, head measurements of the final larval instar are not included in the table below.

In the following table measurements of the head width are given for ten larvae in each of four successive instars. Measurements of the width of the head in the fifth feeding instar, which is peculiar to larvae becoming females, are omitted, since the differences between the greatest head widths of the fourth instar and the smallest head widths of the fifth instar are considerably less than thôse occurring between the extremes of a single instar.

Table II. *Head widths of* Pteronus ribesii (*mm.*).

Instar	Head widths	Average	Growth ratio
1st	0·50, 0·50, 0·51, 0·51, 0·51, 0·52, 0·52, 0·53, 0·53, 0·58	0·52	—
2nd	0·72, 0·73, 0·73, 0·73, 0·73, 0·74, 0·74, 0·75, 0·79, 0·81	0·76	1·43
3rd	1·01, 1·02, 1·02, 1·03, 1·03, 1·06, 1·07, 1·10, 1·11, 1·12	1·06	1·41
4th	1·35, 1·36, 1·36, 1·36, 1·37, 1·42, 1·43, 1·52, 1·53, 1·54	1·42	1·34

Variation in the growth ratio of the head capsules of successive larval instars of *Pteronus ribesii* appears slight. Taking the growth ratio between the head capsules of the first and second instars and the mode of the measured widths of the head capsules of the first instar as the basis of calculation, the calculated widths for the second, third and fourth instars are 0·73 mm., 1·04 mm. and 1·49 mm. respectively. Reference to the above table shows that these calculated widths closely approximate the measured widths of the head capsules of the respective instars.

Pteronus leucotrochus *Htg.*

Pteronus leucotrochus Htg. is closely allied to *Pteronus ribesii*, and has similar developmental irregularities. Larvae which become males have five larval stadia and those becoming females have six, the larvae of the two sexes being approximately the same size in the ultimate larval instar. In this species, however, it seemed possible after close observation to distinguish the larvae which would become females from those which would beçome males, after the third ecdysis. As with *Pteronus ribesii*, head measurements indicated that the ultimate larval stadium was not associated with growth.

In the following table the measurements of the width of the head are given for larvae of *Pteronus leucotrochus* in the four successive instars common to the larvae of both sexes.

Table III. *Head widths of* Pteronus leucotrochus (*mm.*).

Instar	Head widths	Average	Growth ratio
1st	0·51, 0·51, 0·52, 0·52, 0·52, 0·53, 0·53, 0·53, 0·54, 0·55	0·53	—
2nd	0·64, 0·68, 0·70, 0·70, 0·72, 0·72, 0·75, 0·77, 0·77, 0·78	0·72	1·37
3rd	0·99, 0·99, 0·99, 1·01, 1·02, 1·02, 1·04, 1·04, 1·05, 1·07	1·02	1·41
4th	1·31, 1·32, 1·32, 1·32, 1·33, 1·34, 1·34, 1·35, 1·35, 1·36	1·34	1·31

The variation in growth ratio between the successive instars of *Pteronus leucotrochus* is comparatively small. Using as a basis for calculation the growth ratio between the width of the head in the first and second instars and the average width of the head capsule in the first instar, the calculated widths of the subsequent instars are 0·73 mm., 1·00 mm., and 1·37 mm. These calculated widths approximate closely to the measured widths of the respective instars as recorded in the foregoing table.

Pristiphora pallipes *Lep.*

In contrast to *Pteronus ribesii* and *P. leucotrochus*, development appears regular throughout the larval life of *Pristiphora pallipes* Lep. In the various stocks which have been collected and reared during five seasons no males have appeared. The species is parthenogenetically thelytokous, therefore all the larvae available for measurement have been females and the number of ecdyses has been constant. In *P. pallipes* the larvae do not moult on becoming fully fed, but immediately construct a cocoon and become pupae without passing through a definite prepupal instar disassociated from feeding and growth, as occurs in *Pteronus ribesii* and *P. leucotrochus*.

The number of larval stadia for larvae of *Pristiphora pallipes* which become females appears to be four, and measurements of the width of the head capsule in all the larval instars are given in the following table.

Table IV. *Head widths of* Pristiphora pallipes (*mm.*).

Instar	Head widths	Average	Growth ratio
1st	0·44, 0·46, 0·46, 0·47, 0·48, 0·48, 0·48, 0·50, 0·50, 0·51	0·48	—
2nd	0·56, 0·61, 0·62, 0·66, 0·66, 0·68, 0·70, 0·71, 0·71, 0·72	0·66	1·37
3rd	0·84, 0·89, 0·92, 0·93, 0·93, 0·93, 0·94, 0·96, 0·97, 0·97	0·93	1·40
4th	1·11, 1·17, 1·19, 1·19, 1·21, 1·21, 1·22, 1·25, 1·29, 1·29	1·21	1·30

The measurements of the head capsules of the larval instars of *Pristiphora pallipes* show greater variation than those of *Pteronus ribesii* and *P. leucotrochus*, but the growth ratio between the average head widths of the successive instars is fairly constant. Using the growth ratio between the average head widths of the first and second instar larvae and the average width of the head capsule in the first instar as a basis for calculation, the calculated widths of the head capsules in the second, third and fourth instars are 0·66 mm., 0·90 mm., and 1·23 mm. respectively. These calculated measurements are well within the range of the actual measurements for the particular instars given in the preceding table.

Ametastegia glabrata *Fall.*

The larvae of *Ametastegia glabrata* used in this investigation were reared parthenogenetically in the laboratory and, as the species is arrhenotokous, were therefore males. In this species the sex of the subsequent adult influences the number of larval instars, larvae which become females having six larval instars and larvae which become males having only five. In the parthenogenetically produced larvae the number of larval instars was constant. As in *Pteronus ribesii* and *Pteronus leucotrochus*, the larvae moult on becoming fully fed and enter into a prepupal stadium during which no food is taken. This ultimate instar is not associated with increase in size in the larvae.

In the table below the measurements are given of the widths of the head capsule in the four successive feeding instars which are common to the larvae of both sexes.

Table V. *Head widths of* Ametastegia glabrata (*mm.*).

Instar	Head widths	Average	Growth ratio
1st	0·37, 0·37, 0·38, 0·38, 0·38, 0·38, 0·39, 0·40, 0·41, 0·41	0·39	—
2nd	0·53, 0·53, 0·53, 0·54, 0·54, 0·54, 0·54, 0·55, 0·55, 0·56	0·54	1·38
3rd	0·72, 0·75, 0·77, 0·77, 0·77, 0·78, 0·78, 0·79, 0·79, 0·80	0·77	1·42
4th	1·03, 1·03, 1·04, 1·04, 1·04, 1·04, 1·06, 1·06, 1·06, 1·07	1·05	1·38

The growth ratio between the widths of the head in the four successive feeding stadia common to the larvae of both sexes of *Ametastegia glabrata* shows a striking uniformity. Calculating the head widths of the subsequent instars, using the average width of the head capsule of the first instar and the growth ratio between the head capsules of the first and second instars as a basis, gives the following: second instar 0·54 mm., third instar 0·75 mm. and fourth instar 1·04 mm. These calculated widths closely approximate the measured widths recorded in the above table.

ON THE USE OF THE FRONS IN MEASURING GROWTH IN THE LARVAE OF TENTHREDINIDAE.

The special drawback to the use of the head capsule as a unit for measuring growth in the larvae of Tenthredinidae has already been referred to. The possibility of using the frons as a unit for measuring growth seemed feasible, and therefore a study was made of the ratio of the frons to the head in the larval instars and the growth ratio of the frons in successive instars, using the larvae of the four species of Tenthredinidae in which growth was being observed.

Table VI. *Width of the frons in* Pteronus ribesii (*mm.*).

Instar	Width of frons	Average	Growth ratio
1st	0·23, 0·23, 0·24, 0·24, 0·24, 0·25, 0·25, 0·25, 0·26, 0·27	0·25	—
2nd	0·30, 0·31, 0·31, 0·31, 0·31, 0·31, 0·32, 0·32, 0·32, 0·32, 0·32, 0·32, 0·32, 0·32	0·32	1·28
3rd	0·40, 0·40, 0·41, 0·41, 0·41, 0·41, 0·41, 0·41, 0·42, 0·42, 0·42, 0·43, 0·43, 0·43	0·42	1·31
4th	0·50, 0·50, 0·50, 0·51, 0·52, 0·52, 0·52, 0·52, 0·52, 0·53, 0·53, 0·53, 0·54, 0·54	0·52	1·23

The variation in growth ratio in the successive instars is slight. Using the average width of the frons in the first instar and the growth ratio between the first and second frons widths, the calculated widths of the frons in the subsequent instars are 0·32 mm., 0·42 mm. and 0·54 mm. Reference to the table shows that these approximate to the measured widths of the frons in the respective instars.

Ratio of frons width to head width in Pteronus ribesii.

1st instar	25 : 52	= 0·48
2nd ,,	32 : 76	= 0·42
3rd ,,	42 : 106	= 0·39
4th ,,	52 : 142	= 0·36

From these figures it would appear that the ratio between the width of the frons and that of the head is not constant during the larval instars. Although the variation is comparatively slight, the ratio shows a steady decrease as larval development proceeds. This indicates that in *Pteronus ribesii* the width of the frons could not be used as a basis for the calculation of the width of the head.

Similar measurements were made of the frons of the larvae of *Pteronus leucotrochus*.

Table VII. *Width of the frons in* Pteronus leucotrochus (*mm.*).

Instar	Width of frons	Average	Growth ratio
1st	0·25, 0·25, 0·25, 0·26, 0·26, 0·27, 0·27, 0·27, 0·27, 0·27	0·26	—
2nd	0·34, 0·34, 0·34, 0·35, 0·35, 0·35, 0·36, 0·36, 0·36, 0·36	0·35	1·34
3rd	0·44, 0·44, 0·44, 0·44, 0·45, 0·45, 0·45, 0·45, 0·46, 0·47	0·45	1·28
4th	0·58, 0·58, 0·59, 0·60, 0·60, 0·60, 0·60, 0·60, 0·60, 0·61	0·60	1·33

Variations in the growth ratio of the frons in successive larval instars of *Pteronus leucotrochus* are slight. The calculated widths of the frons for the second, third and fourth instars are 0·35 mm., 0·47 mm., and 0·63 mm. respectively. These approximate fairly closely to the measurements given for the instars.

Ratio of frons width to head width in Pteronus leucotrochus.

1st instar	26 : 53	= 0·49
2nd ,,	35 : 72	= 0·47
3rd ,,	45 : 102	= 0·44
4th ,,	60 : 134	= 0·44

The ratio of the width of the frons and that of the head shows only slight variations in successive instars of the larvae of *Pteronus leucotrochus*. The tendency for the ratio to decrease during larval development is much less marked in *P. ribesii*.

Measurements of *Pristiphora pallipes* are given in Table VIII.

The growth ratio of the frons appears less constant in successive instars of *Pristiphora pallipes* than in *Pteronus ribesii* and *P. leucotrochus*. The calculated widths of the frons for the second, third and fourth instars are 0·32, 0·42 and 0·56 mm. respectively. For the second and third instars the calculated widths of the frons agree approximately with the measured widths given in the table. In the fourth instar, however, the calculated width slightly exceeds the greatest measured width of frons for that instar.

Table VIII. *Width of frons in* Pristiphora pallipes (*mm.*).

Instar	Width of frons	Average	Growth ratio
1st	0·21, 0·22, 0·22, 0·22, 0·22, 0·23, 0·23, 0·24, 0·24, 0·24, 0·25, 0·25, 0·28	0·24	—
2nd	0·30, 0·30, 0·30, 0·32, 0·32, 0·32, 0·32, 0·32, 0·33, 0·33, 0·33, 0·33, 0·34	0·32	1·33
3rd	0·38, 0·38, 0·40, 0·40, 0·40, 0·41, 0·41, 0·41, 0·41, 0·42, 0·42, 0·43, 0·43	0·41	1·28
4th	0·47, 0·50, 0·50, 0·51, 0·51, 0·51, 0·51, 0·51, 0·52, 0·52, 0·52, 0·52, 0·52	0·51	1·24

Ratio of frons width to head width in Pristiphora pallipes.

1st instar	23 : 48	= 0·48
2nd ,,	32 : 66	= 0·48
3rd ,,	41 : 93	= 0·44
4th ,,	51 : 121	= 0·42

The ratio between the width of the frons and that of the head is fairly constant in the successive instars of *Pristiphora pallipes*, but, as with *Pteronus ribesii* and *P. leucotrochus*, there is a slight decrease in the frons-head ratio during larval development.

In the following table the widths of the frons in successive instars of *Ametastegia glabrata* are recorded.

Table IX. *Width of frons in* Ametastegia glabrata (*mm.*).

Instar	Width of frons	Average	Growth ratio
1st	0·20, 0·20, 0·21, 0·21, 0·21, 0·21, 0·21, 0·21, 0·22, 0·22	0·21	—
2nd	0·27, 0·27, 0·28, 0·28, 0·28, 0·29, 0·29, 0·29, 0·30, 0·30	0·29	1·35
3rd	0·37, 0·38, 0·38, 0·38, 0·39, 0·39, 0·39, 0·39, 0·39, 0·40	0·39	1·34
4th	0·45, 0·46, 0·47, 0·48, 0·50, 0·50, 0·50, 0·51, 0·52, 0·52	0·49	1·25

The growth ratio of the frons in successive instars of *Ametastegia glabrata* is fairly constant. The calculated widths of the frons for the second, third and fourth instars are 0·28 mm., 0·38 mm. and 0·51 mm. respectively. These calculated widths closely approximate to the actual measurements of the frons in the various instars, given in the table above.

Ratio of frons width and head width in Ametastegia glabrata.

1st instar	21 : 39	= 0·53
2nd ,,	29 : 54	= 0·53
3rd ,,	39 : 77	= 0·50
4th ,,	49 : 105	= 0·46

The frons-head ratio varies only slightly in the larval instars of *Ametastegia glabrata*. The tendency for the ratio to decrease during the course of larval development, already noted in other species, is again apparent. It is interesting to note that in this species, which belongs to the tribe *Selandriini*, the frons occupies a greater proportion of the head than in the species of *Nematini* which have been examined.

GENERAL DISCUSSION.

From a study of growth in the larvae of four species of Tenthredinidae: *Pteronus ribesii* Scop., *Pteronus leucotrochus* Htg. and *Pristiphora pallipes* Lep. (tribe *Nematini*), and *Ametastegia glabrata* Fall. (tribe *Selandriini*), it would appear that Dyar's Law for the growth of the larvae of Lepidoptera can be applied to some phases of the development of the larvae of Tenthredinidae. The foregoing data show that increase in the width of the head capsule follows a geometrical progression during successive larval instars associated with feeding and growth.

In confirmation of this conclusion it is interesting to examine some figures published by Middleton (with Rohwer (3)) in America. Dealing with *Cladius isomerus* Norton, Middleton recorded head measurements for the successive larval stadia of both sexes and these measurements are given in the following table together with calculated ratios of growth and expected widths of the heads of instars 2 to 5.

Table X. *Head widths of* Cladius isomerus (*mm.*).

Instar	Middleton's observed widths		Growth ratio (average for both sexes)	Calculated widths
1st	0·4	0·4	—	—
2nd	0·5	0·5	1·25	0·5
3rd	0·6	0·67	1·27	0·62
4th	0·8	0·8	1·26	0·79
5th	1·0	1·1	1·31	0·98

Here it is seen that the growth ratio between the head widths of the four instars concerned are fairly uniform and the calculated widths obtained by using the growth ratio of the first two instars as a basis for calculation show a very close approximation to Middleton's observed widths.

The regular rate of growth in the larvae of Tenthredinidae is interfered with in the later stages by the development of sex differentiation, a complication which does not appear to have been observed by Dyar and Fisher in their work on the larvae of Lepidoptera, and also by the occurrence in some species of a prepupal instar which does not appear to be associated with growth.

In the species under observation in which the two sexes were present: *Pteronus ribesii*, *P. leucotrochus* and *A. glabrata*, the females had one larval ecdysis more than the males, yet in the ultimate larval instar the sexes could not be separated on measurements.

Measurements of the width of the head in the fourth and fifth larval instars of *Pteronus ribesii* are given below.

	Millimetres
4th instar (both sexes)	1·35, 1·36, 1·36, 1·36, 1·37, 1·42, 1·43, 1·52, 1·53, 1·54
5th instar (females only)	1·60, 1·60, 1·61, 1·64, 1·65, 1·70, 1·83, 1·99

From these measurements it will be seen that the width of the head is greater in the fifth instar than in the fourth, but there is no definite line of demarcation. The difference between the largest head capsules of the fourth instar and the smallest of the fifth instar is much less than the difference between extremes for any instar. Measurements of the width of the head in larvae of the fourth and fifth instars of *Pteronus leucotrochus* and *Ametastegia glabrata* revealed a similar irregularity of development owing to the influence of sex differentiation in the later larval stages.

In the species *Pteronus ribesii*, *P. leucotrochus* and *Ametastegia glabrata* the larvae moulted on becoming fully fed, and entered an ultimate larval stage during which no feeding took place. Examination of the head capsules of this prepupal stage showed that practically no growth had occurred. The following are the measurements of the head widths of the fifth and sixth instar larvae of *Pteronus ribesii*.

	Millimetres
5th instar (females only)	1·60, 1·60, 1·64, 1·61, 1·65, 1·70, 1·83, 1·99
6th instar (females only)	1·73, 1·73, 1·74, 1·74, 1·75, 1·75, 1·99, 2·03

These measurements show that although the average width of the sixth instar capsules is slightly greater than those of the fifth instar, measurements of individual head capsules showed considerable overlapping, some of the head capsules of the fifth instar being larger than some of the sixth. Similar conditions occurred in *P. leucotrochus* and *A. glabrata*.

The study of the width of the frons in successive larval instars of the same species of Tenthredinidae revealed similar conditions with regard to the growth of the larvae. During the greater part of the larval life the increase in the width of the frons followed a fairly regular geometrical progression, but in the later stages growth was irregular. As with the width of the head capsules, the irregular development was owing to the influence of sex differentiation and the occurrence of a prepupal instar in which practically no growth takes place.

CONCLUSION.

In the species of Tenthredinidae so far studied growth and development appear more complicated than in the larvae of Lepidoptera. In the initial stages growth, as indicated by the width of the head or the width of the frons in successive instars, follows a fairly regular geometrical progression. In the later instars, the influence of sex differentiation and the occurrence in some species of a prepupal stadium, disassociated from growth, renders larval growth irregular.

Since growth does not follow a regular geometrical progression throughout the larval life, Dyar's Law for growth in the larvae of Lepidoptera has only a limited application to growth in the larvae of Tenthredinidae. The present study of growth in four species of Tenthredinidae suggests that Dyar's Law can be used satisfactorily to check the number of ecdyses during that part of the larval life directly associated with feeding and increase in size.

Observations on the increase in width of the head and the frons in successive larval instars indicate that either may be used as a unit for measuring growth in Tenthredinidae. The characteristic splitting of the head capsule at ecdysis renders it more convenient to use the width of the frons as the unit for measuring growth in Tenthredinid larvae.

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