The number of larval instars in some bark beetle species

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In connection with an investigation of the morphology of the Scandinavian bark beetle larvae, Lekander 1968, the number of laval instars of some species has been determined. As a fairly abundant material of larvae collected at different times during the development is necessary, it has only been possible to investigate the number of instars mainly of the most common species.

The collection of the larvae has been made at different times, either in the laboratory from the same trunk or branch or out in the field in different localities. To avoid a mixture of larvae of different species, material has never been taken from objects attacked by more than one species. At every collection the parental beetles have, if possible, been added to the larval material in order to make a control determination possible on later occasions.

The number of larval instars has been determined by measuring the breadth of the head capsule. At these measurings the capsules have been separated from the bodies, and the greatest breadth has been measured with the aid of a micrometer scale in a microscope with 100 $\times$ enlargement. As a rule about hundred capsules of each species have been measured, but for some species, especially those with a great variation, this number has been considerably increased. Empirically it is quite evident that measuring was easier and the results more accurate if the larvae had first been fixed. "Carl's fixation" consisting of alcohol, formole and acetic acid was used as a fixative.

Hitherto our knowledge of the number of instars in bark beetles has been limited. According to Balachowsky 1949, all bark beetle larvae should have five instars, but as has been shown earlier, Lekander 1959, this is by no means a rule.

Five instars are known from *Chetoptelius vestitus,* Russo 1926, *Hylurgopinus rufipes,* Kaston and Riggs 1937, and *Dendroctonus micans,* Gørn et.alt. 1954. Blackman 1915 has mentioned five instars in *Pityogenes hopkinsi* but as will be shown later, this must be wrong; the right number is probably only three. Finally Bedard 1933 mentioned five instars in *Dendroctonus pseudotsugae,* a figure which he later, 1950, changed to four.

Four instars are known from *Dendroctonus simplex,* Prebble 1935 and *D. pseudotsugae,* Beddard 1950 and Vité and Rudinsky 1957, finally from *Blastophagus piniperda,* Lekander 1959. Hadorn 1933 stated that *Trypodendron lineatum* has four instars, but as will be shown later, this statement may be wrong.

Table 1. *The investigated species divided into subfamilies and tribus.*

subfamily	tribus	species
Scolytinae		Scolytus laevis Chap.
		,, intricatus Ratzb.
Crypturginae		Crypturgus cinereus Hbst.
Ipinae	Polygraphini	Polygraphus poligraphus L.
	Hylesinini	Hylastes brunneus Er.
		Hylurgops palliatus Gyll.
		Blastophagus piniperda L.
		,, minor Hart.
		Leperisinus fraxini Panz.
		Phthorophloeus spinulosus Rey.
	Ipini	Cryphalus abietis Ratzb.
		Ernoporus tiliae Panz.
		Xyleborus cryptographus Ratzb.
		Dryocoetes autographus Ratzb.
		Pityophthorus micrographus L.
		Pityogenes quadridens Hart.
		,, chalcographus L.
		Ips typographus L.
		,, sexdentatus Börn.
		Orthotomicus proximus Eichh.
		,, laricis Fabr.
		,, suturalis Gyll.
	Trypodendrini	Trypodendron lineatum Ol.

Three instars are known from *Pityogenes sparsus* and *Ips pini,* Prebble 1933, *Ips curvidens,* Hierholzer 1954, and *Polygraphus poligraphus,* Lekander 1959.

Finally two instars have been described in *Crypturgus cinereus,* Lekander 1959, *Trypodendron lineatum,* Novák 1960, and *Conophthorus* spec., Herdy and Thomas 1961.

So far as I know this is all that has up till now been published on the number of instars in bark beetles. The relatively small amount of published information shows without doubt that the number varies from species to species, and this investigation has been made in order to clarify, if possible, whether any conformity can be traced. Sufficient material of larvae has been available for 23 species, which are accounted for in table 1 distributed in subfamilies and tribus according to Lekander 1968.

As a rule it has not been very difficult to establish the number of instars, as in the majority of species investigated so far, these have been easy to define. In some species, however, it has been impossible to clarify the number of instars, at least with the help of head capsule measurements. The diagrams do not show any clear peaks and are impossible to analyse. This applies to the two *Scolytus*-species investigated, viz. *laevis* and *intricatus* as *Phthorophloeus spinulosus* the diagram of which is seen in fig. 1.

In species with an oblong head capsule, i.e. index more than 1, it has generally been much more difficult to get clear pictures of the different

Table 2. *Number of instars and the mean breadths and standard deviations of the head capsules in some bark beetle species.*

species	instars				
	I	II	III	IV	V
Crypturgus cinereus	0,27	0,33			
Polygraphus poligraphus	0,36 ± 0,021	0,47 ± 0,025	0,59 ± 0,027		
Hylastes brunneus	0,36 ± 0,016	0,51 ± 0,030	0,66 ± 0,033	0,89 ± 0,043	
Hylurgops palliatus	0,38 ± 0,013	0,48 ± 0,017	0,62 ± 0,021	0,77 ± 0,037	
Blastophagus piniperda.	0,47 ± 0,016	0,58 ± 0,023	0,76 ± 0,032	0,99 ± 0,033	
„ minor ...	0,43 ± 0,026	0,54 ± 0,027	0,67 ± 0,037	0,82 ± 0,053	
Dendroctonus micans ..	0,38 ± 0,014	0,53 ± 0,021	0,75 ± 0,037	1,03 ± 0,045	1,36 ± 0,051
Leperisinus fraxini	0,40 ± 0,006	0,53 ± 0,030	0,72 ± 0,053		
Cryphalus abietis	0,25 ± 0,012	0,34 ± 0,013			
Ernoporus tiliae	0,24	0,30 ± 0,010			
Xyleborus cryptographus ♂	0,26	0,32	0,38		
Xyleborus cryptographus ♀	0,27	0,36	0,53		
Dryocoetes autographus.	0,35 ± 0,010	0,53 ± 0,021	0,73 ± 0,030		
Pityopth. micrographus .	0,26 ± 0,008	0,31 ± 0,013	0,37 ± 0,017		
Pityogenes quadridens .	0,35 ± 0,011	0,43 ± 0,012	0,51 ± 0,014		
„ chalcographus	0,32 ± 0,015	0,39 ± 0,011	0,49 ± 0,022		
Ips typographus	0,51 ± 0,015	0,70 ± 0,020	0,92 ± 0,033		
„ sexdentatus	0,68	0,99	1,35		
Orthotomicus proximus .	0,39 ± 0,016	0,51 ± 0,019	0,76 ± 0,034		
„ laricis ...	0,37	0,51	0,74		
„ suturalis .	0,39	0,55	0,76		
Trypodendron lineatum.	0,38	0,63 ± 0,026			

instars. Thus in the *Scolytus* species the index is 1.2 and in *Phthorophloeus* about 1.1. In *Leperisinus fraxini,* on the other hand, it has been possible, with some difficulty, to settle the number of instars in spite of an index varying between 1.1—1.25. Measuring the length of the capsule as combinations of length and breadth is of no use either. The only possibility of establishing the number of instars of these species might be an individual breeding of larvae in vitro as described by Finnegan 1958.

In some species the size of the imagines can vary considerably; in others, on the other hand, this variation is limited. Thus in the *Scolytus*-species this variation is wide, in *S. scolytus* for example the length is reported to vary between 3.5—5.5 mm and in *Phthorophloeus spinulosus* between 1.8—2.5 mm, Spessivtseff 1922. On the other hand *Pityogenes chalcographus,* the head capsule diagram of which is very distinct, varies in length only between 2—2.3 mm, op.c. It is quite natural that in species with wide variation in the length of the imagines there must exist a correspondent variation in the size of the larvae which must result in the diagrams of the breadth of the head capsules being diffuse. In species with low variation in size an opposite relation must exist. Thus the diagrams clearly reflect the ability of the different species to vary in size.

A closer study of the standard error of the breadth of the head capsules clearly shows that this error is far greater in larvae belonging to the tribus

Table 3. *The ratio between the head capsule breadths in two consecutive instars in some bark beetle species.*

species	II/I	III/II	IV/III	V/IV	m
Crypturgus cinereus	1.22				1,22
Polygraphus poligraphus	1,30	1,26			1.28
Hylastes brunneus	1,42	1,29	1,35		1,35
Hylurgops palliatus	1,28	1,29	1,24		1,27
Blastophagus piniperda	1,22	1,32	1,29		1,27
Blastophagus minor	1,24	1,25	1,23		1,24
Dendroctonus micans	1,39	1,41	1,37	1,32	1,33
Dendroctonus simplex	1,34	1,35	1,34		1,34
Leperisinus fraxini	1,31	1,35			1,33
Cryphalus abietis	1,36				1,36
Ernoporus tiliae	1,25				1,25
Xyleborus cryptographus ♂	1,23	1,17			1,20
Xyleborus cryptographus ♀	1,28	1,48			1,38
Dryocoetes autographus	1,44	1,42			1,43
Pityophthorus micrographus	1,20	1,20			1,20
Pityokteines sparsus	1,35	1,31			1,33
Pityogenes quadridens	1,25	1,19			1,22
Pityogenes chalcographus	1,22	1,25			1,24
Ips typographus	1,39	1,31			1,35
Ips sexdentatus	1,45	1,36			1,40
Ips pini	1,36	1,36			1,36
Orthotomicus suturalis	1,42	1,38			1,40
Orthotomicus proximus	1,34	1,40			1,37
Orthotomicus laricis	1,38	1,44			1,41
Average increasing factor	1,32	1,32	1,30	1,32	1,32

Hylesinini than in those belonging to the tribus *Ipini,* table 2. This fact is also quite evident from the diagrams, fig. 1 and 2. These are in the different larval instars of *Hylesinini* as a rule broad and indistinct, unlike *Ipini,* where they are more concentrated and clearly delimited from each other.

There is an interesting difference also as regards the number of instars; in *Hylesinini* the number varies between three and five, in *Ipini* the number in the majority of species is three, although two instars can also occur. Judging from available facts in these two tribus, there seems to exist two fundamentally different types of development. In the first mentioned tribus the fully-developed stage of the larvae is reached by a varying number of instars depending on the size of the species. In the latter tribus, irrespective of the size of the species, the last instar is reached in the majority of species by a constant number of instars. In spite of this the relation between the breadth of the head capsules from one instar to the next, the increase factor, is practically identical in the two tribes, viz. about 1.3, tab. 3. What is the reason for this? A close study of the diagrams, fig. 1 and 2 as table 2 shows that in the different Hylesinin species the head capsule breadth in the first instar varies within relatively narrow limits. Thus the average breadth in the first instar is in e.g. *Leperisinus fraxini* (3 instars) 0.40 mm, *Hylurgops palliatus* (4 instars) 0.38 mm and in *Dendroctonus micans*

Table 4. *The ratio between the head capsule breadths in last and first instars as the number of instars in some bark beetle larvae. (Ipini underlined)*

species	ratio between last and first instars	number of instars	author
Crypturgus cinereus	1,22	2	
Ernoporus tiliae	1,25	2	
Cryphalus abietis	1,36	2	
Conophthorus spec.	1,39	2	Herdy & Thomas 1961
Pityogenes quadridens	1,40	3	
Pityophthorus micrographus	1,45	3	
Xyleborus cryptographus ♂	1,45	3	
Pityogenes chalcographus	1,52	3	
Polygraphus poligraphus	1,64	3	
Trypodendron lineatum	1,65	2? 4?	Hadorn 1933, Novák 1960
Leperisinus fraxini	1,77	3	
Pityokteines sparsus	1,77	3	Prebble 1933
Ips typographus	1,81	3	
Orthotomicus proximus	1,87	3	
Xyleborus cryptographus ♀	1,90	3	
Orthotomicus suturalis	1,97	3	
Orthotomicus laricis	1,99	3	
Ips sexdentatus	2,00	3	
Dryocoetes autographus	2,05	3	
Ips curvidens	2,08	3	Hierholzer 1954
Blastophagus minor	1,91	4	
Hylurgops palliatus	2,01	4	
Blastophagus piniperda	2,09	4	
Dendroctonus simplex	2,41	4	Prebble 1933
Hylastes brunneus	2,47	4	
Dendroctonus pseudotsugae	2,64	4	Vité & Rudinsky 1957
Chaetoptelius vestitus	2,65	5	Russo 1926
Hylurgopinus rufipes	2,87	5	Kaston & Riggs 1937
Dendroctonus micans	3,58	5	Gøhrn et.alt. 1954
Pityogenes hopkinsi	1,74	5	Blackman 1915

(5 instars) 0.38 mm. Thus in these species the newly hatched larvae are practically of the same size, but to become fully-grown they have to pass a varying number of instars. In *Ipini,* on the other hand, the newly hatched larvae vary considerably in size from one species to another. Thus the head capsule breadth in the first instar is in e.g. *Pityophthorus micrographus* 0.26 mm, *Dryocoetes autographus* 0.35, *Ips typographus* 0.51 and *Ips sexdentatus* finally 0.68. All these species have three instars. In this tribus the necessary size of the larvae will be obtained not through a varying number of instars but through a different size in the larvae from the beginning.

Unfortunately little information exists as to the size of the eggs. Measurements of my own are available only from 12 species, and from this limited material it is impossible to decide whether the eggs of the *Ipini* vary more in size then those of the *Hylesinini*.

Concerning the other tribus within the subfamily *Ipinae, Polygraphini* represented by *Polygraphus poligraphus* has three instars with a wide variation breadth, conf. Lekander 1959. The head capsule breadth in the first instar is 0.36 mm, which agrees fairly well with the common Hylesinin scheme.

Among the proper Hylesinins only *Blastophagus minor* needs to be mentioned. As is well known this species is always associated with blue stain fungi which are transplanted into the wood in connection with the construction of the galleries. When the larvae hatch they gnaw fully normal tunnels between bark and wood as the fungus has probably not had enough time to develop. Later on the larvae usual bore their way into the sapwood where they remain until pupation. Probably this boring into the wood takes place when the fungus has reached such a degree of development that the larvae can feed on it entirely. In two cases the larval material has been divided into larvae which had bored into the wood and larvae which were still living between bark and wood. In one case, fig. 1: a, the larval material was taken from a pine with favourable conditions for the development of the fungus; in the second case, fig. 1: b, from a tree with unfavourable conditions.

In the first case it is quite evident that the two first larval instars developed between bark and wood and the majority of the two last instars in the wood. In the second case the two first and the majority of the third instars developed under bark, and the last one in about the same degree under bark and in wood. Evidently the development and to some degree also the size of the larvae depends to a great extent on the developmental conditions of the fungus. Perhaps this explains why the diagram of a great number of larvae from different trees shows relatively distinctly two first instars, which develop without fungus diet, and on the other hand two last instars with a considerable variation owing to the varying degree of the supply of fungus food.

The conditions in the tribus *Trypodendrini,* in this investigation represented by *Trypodendron lineatum,* are to some degree difficult to interpret. Hadorn 1933 in his comprehensive investigation of the biology etc. of this species has stated that the larvae have four instars. He established that the dimensions of the head capsule were almost unchanged during the larval development. The increase was exceedingly small and could only be settled with the help of the microscope. To get an idea of the number of instars he put a dot of Indian ink on a newly hatched larva. When the dot had vanished by an ecdysis a new one was applied and so he could establish three ecdyses, viz. four instars. Novák 1960, who has also made a thorough study of this bark beetle, has by measuring the head capsule breadth and the length of the mandibles been able to establish only two instars. The breadth of the capsule in the first instar varied between 0.36 and 0.48 mm and in the second one between 0.54 and 0.72. My own measurements, comprising only 68 specimens also show two instars, fig. 2. The first one varies between 0.37 and 0.45 mm, the second between 0.58 and 0.69; figures which correspond quite well with Novák's. When measuring the head capsule breadths it is evident

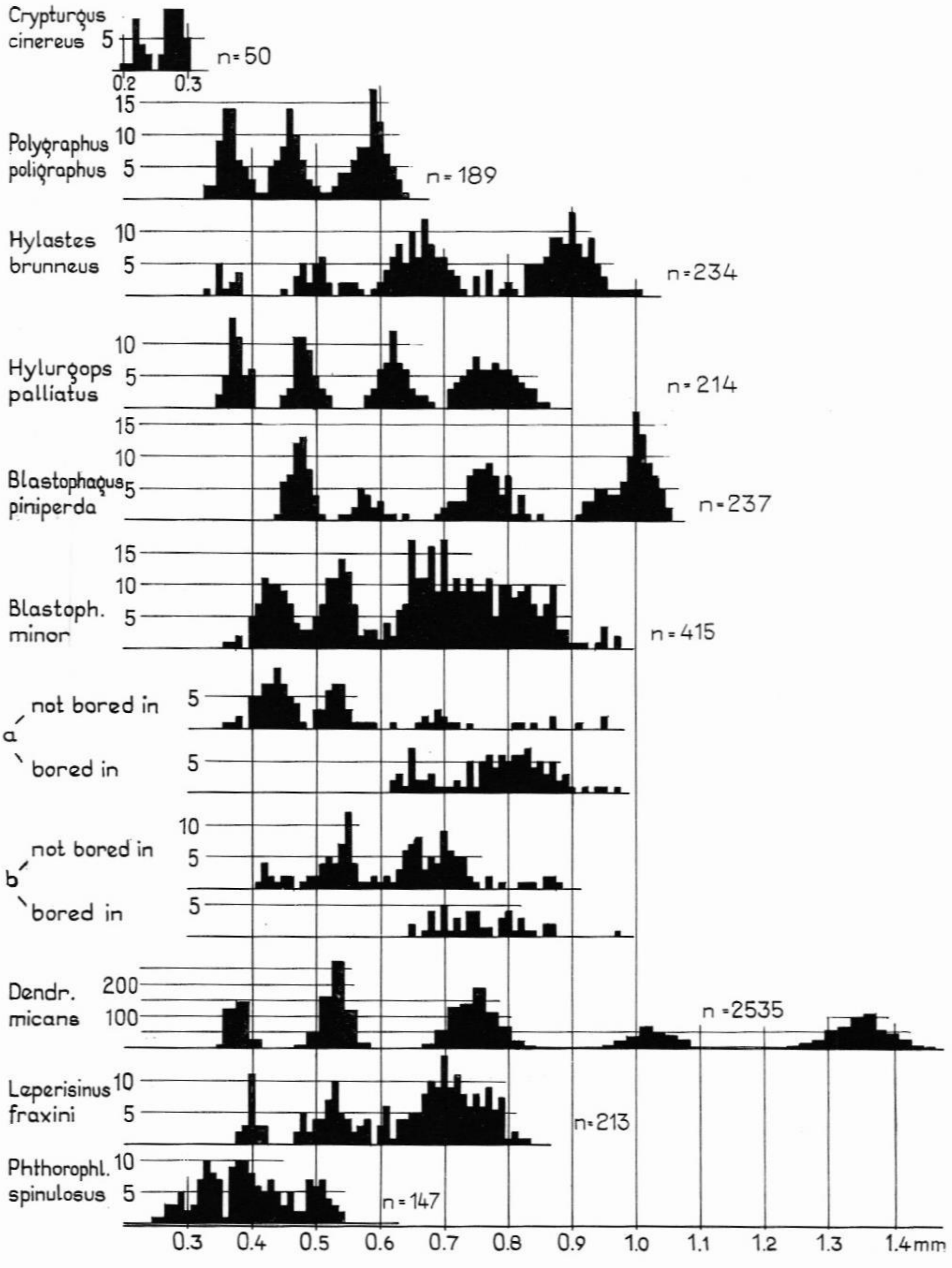

Fig. 1. Diagrams of the head capsule breadths in some mainly Hylesinin larvae.

that only two instars can be established. If Hadorn's observations are right the species should have instars which do not manifest themselves in any growth whatever of the head capsules or mandibles. It is true that this species has a different biology as compared with the majority of the other bark beetle larvae as they nourish themselves exclusively on ambrosia fungi. A morphological investigation of the larvae has shown that the head capsule must be regarded as faintly developed and is in some respects degenerated, Lekander 1968, for which reason it is possible that special conditions may prevail in this species. If, however, the larva has only two instars, the increase coefficient is about 1.60; this is abnormally high and much higher than has been established in other bark beetle species. Four instars, however, give an increasing factor of only 1.18, which on the other hand is a little low. With a rate of 1.6 between the first and last instar (se below) three instars would be the most natural. However, none of the investigations performed indicate this number, so for the present it is only possible to establish that this species diverges from other bark beetles as in so many other respects.

Among other subfamilies sensu Lekander op.c. one species of *Crypturginae* has been investigated, viz. *Crypturgus cinereus*. This species has quite clearly two instars only, see fig. 1. I will later deal with the subfamily *Scolytinae* in another connection.

When estimating the probable number of instars in a bark beetle species the ratio between the head capsule breadth in the last and first instars is of good help, table 4. In this table the species are arranged according to the number of instars, and species with the same number of instars have in their turn been arranged according to the ratio between the last and first instars; finally the species belonging to the tribus *Ipini* are underlined. From the table it is quite evident that a certain regularity exists between the number of instars and the ratio figures. If the head capsule breadths of the first and last instars are known it is possible with the help of the table to estimate the number of instars with a relatively high degree of probability.

In the table also Blackman's 1915 statement about the number of instars of *Pityogenes hopkinsi* which should be five has been included. The ratio between the last and first instars is, however, only 1.74, which shows that the number of instars has probably been miscalculated. Without doubt, this species has only three instars, as is the case with the other investigated *Pityogenes* species.

As has already been pointed out, it has been impossible to determine the number of instars of *Phthorophloeus spinulosus* by means of head capsule measurements. It is probable, however, that the first instar has a breadth of about 0.27 mm and the last one of about 0.49. The ratio between these numbers is 1.8, which indicates that the number of instars is probably three. The same impossibility has existed when determining the number of instars of *Scolytus intricatus* and *laevis*. The breadth of the head capsule is in the first instar of *intricatus* about 0.46 mm and in the last one about 0.96, which gives a ratio of 2.08. In *laevis* the corresponding figures are about 0.50 mm and 1.04 respectively, which also gives a ratio of 2.08. According to table 3 these species probably have four instars.

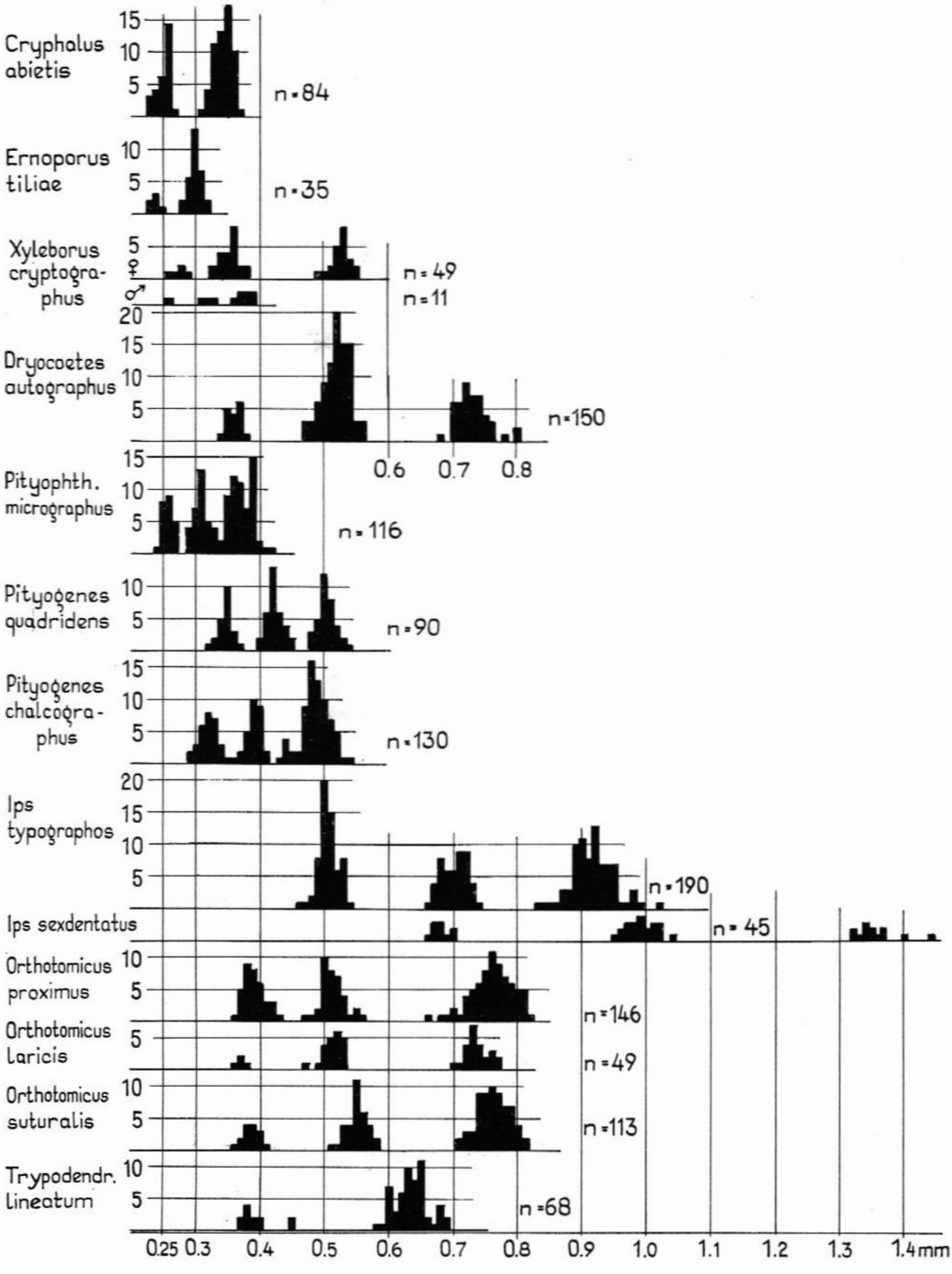

Fig. 2. Diagrams of the head capsule breadths in some Ipin larvae.

Even though a relatively small number of bark beetle larvae has been investigated regarding their number of instars, this table can probably be used as a basis for estimating the number of instars and when controlling whether the results obtained can be regarded as probable or not.

The results and views dealt with above can be summarized as follows:

1. The number of instars in bark beetle larvae varies, from two to five.
2. In tribus *Hylesinini* the number is three, four or five.
3. In tribus *Ipini* predominantly the number is three. Some small species have two only.
4. The variation of the size of the larvae in the first instar is in *Hylesinini* essentially smaller than in *Ipinini.*
5. In *Hylesinini* the larvae will become full-grown through a varying number of instars depending on the size of the species, in *Ipini* on the other hand because of the varying sizes of the larvae in the first instar.
6. With the help of the ratio between the head capsule breadths in the last and the first instars it is possible to estimate the number of instars with some degree of probability.

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