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ON STYLOPISATION OF ARAEOPIDS

BY

HÅKAN LINDBERG

WITH 3 TABLES AND 4 PLATES

(From Tvärminne Zootogical Station)

HELSINGFORSIAE 1949

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CONTENTS.

Intro	oduction	5
Ι.		7
	1. Influence of Stylopisation on Development	7
	2. Exterior Morphological Changes due to Stylopisation	11
	The Normal Imago	11
	Dicranotropis Males Parasitised by the Female Elenchus	12
	Dicranotropis Females Parasitised by the Female Elenchus	14
	Dicranotropis Imago Parasitised by the Male Elenchus	16
	Dicranotropis L_V Parasitised by the Male Elenchus	17
II.	Calligypona straminea Stål	18
	1. Influence of Stylopisation on Development	18
	2. Exterior Morphological Changes due to Stylopisation	20
	The Normal Imago	20
	C. straminea Males Parasitised by the Female Elenchus	22
	C. straminea Females Parasitised by the Female Elenchus	22
	C. straminea Imago Parasitised by the Male Elenchus	23
	C. straminea L_V Parasitised by the Male Elenchus	24
III.	Calligypona pellucida Fabr	25
	1. Influence of Stylopisation on Development	25
	2. Exterior Morphological Changes due to Stylopisation	28
	The Normal Imago	28
	C. pellucida Males Parasitised by the Female Elenchus	29
	C. pellucida Females Parasitised by the Female Elenchus	30
	C. pellucida Imago Parasitised by the Male Elenchus	30
IV.	The Parasite	31
V.	Summary	33



Introduction.

In an earlier paper the author dealt with the parasitising of Araeopids of the genus *Chloriona* Fieb. by the Strepsipteron *Elenchus*¹) *chlorionae* Lindb. The stylopisation of these leaf-hoppers reveals certain very constant features which may well be regarded as typical. Normal unparasitised *Chloriona* males — at least in South Finland — are always long-winged, and females nearly always short-winged. Stylopisation by the female *Elenchus* always causes brachyptery in *Chloriona* males, and the females too are brachypterous. As the secondary sexual characters of stylopised leaf-hopper specimens (both males and females) are greatly stunted or do not develop at all, the specimens of both sexes closely resemble each other. The green colour, characteristic of the *Chloriona* species, does not develop in stylopised specimens; the latter are readily distinguished in nature from the similarly shortwinged females thanks to their yellow colour. With regard to the structure of the body, too, leafhoppers (males as well as females) containing *Elenchus* females resemble the normal females.

Chloriona specimens parasitised by *Elenchus* females reach the imago stage. At this the female Strepsipteron pupates and reaches the adult stage. *Elenchus* males pupate in *Chloriona* while the latter is at the last (5th) larval stage. With the emergence of the adult Strepsipteron male from the leaf-hopper larva the larva dies. Strepsipteron males emerge at the same time as the females in the leaf-hopper imagines develop into sexually mature insects. *Chloriona* larvae parasitised by *Elenchus* males are still encountered for some time after the normal occurence of larvae.

Normal *Chloriona* males die after copulation, females after oviposition. Leaf-hopper specimens parasitised by *Elenchus* females do not die until the viviparous L_1 larvae of the Strepsipteron have emerged from the females. Infection by both the male and female Strepsipteron results in a complete castration of the host.

The occasional observations made by the author (1939, 1943) on stylopisation in the other species of the *Araeopidae* family relate primarily to the exterior morphological changes the infection causes in the host. In the species

¹) The author earlier referred this species to the genus *Elenchinus* Pierce, but is now inclined to refer it to the earlier established genus *Elenchus* Curt. (cf. Chapter IV, p. 32).

of the genera Criomorphus Curt., Dicranotropis Fieb. and Calligypona J. Sahlb., studied by the author, largely the same conditions were found as with Chloriona. Contrary to the case with the Hymenoptera, the effect of stylopisation on leaf-hoppers has been but little studied. HAUPT (1916) reports changes in the exterior organs of 4 Araeopid species; subsequently (1933) he gives a short description and reproduces illustrations of 3 stylopised specimens of Calligypona pellucida Fabr. Thanks to the devoted interest of the well-known Strepsipterologist KARL HOFENEDER, some of the important investigations into leaf-hoppers on rice and on their enemies made by ESAKI and HASHIMOTO (1931-34) were translated into German (1940) and so made accessible to a wider circle of scholars. The work of the Japanese researchers provides information on the changes in genitalia caused by parasitic infection. In a work published in 1939, i.e. the same year as the author's thesis on Elenchus chlorionae was published, however, HASSAN reported in greater detail on the effect of stylopisation on the host (the Araeopids Criomorphus williamsi China, Calligypona pellucida Fabr. and C. fairmairei Perris). HASSAN considers not only certain exterior morphological changes but also the reduction of the primary genitalia.

In the Summer of 1945 the author discovered, near Tvärminne Zoological Station in the South of Finland, populations of three Araeopid species highly parasitised by an *Elenchus* species: *Dicranotropis hamata* Boh., *Calligypona straminea* Stål and *C. pellucida* Fabr. Thanks to the rather abundant material provided by these populations it is now possible to compare in a more comprehensive manner the changes created by stylopisation in the *Chloriona* species and in the other species of the *Araeopidae* family.

The habitat of the populations in question was a meadow now out of cultivation, with a plant population dominated by the grasses Aira caespitosa, Poa pratensis and Agrostis vulgaris. In addition, Poa nemoralis, Phleum pratense and Carex leporina grew there. The grass vegetation was in part forced aside by shrubs and tall herbs, such as Urtica dioica, Ranunculus acris, Ribes nigrum, Rubus idaeus, Filipendula ulmaria, Chamaenerium angustifolium, Lythrum salicaria and Galeopsis bifida.

The species *Dicranotropis hamata* as well as *Calligypona flaveola* and *pellucida* very probably live on the grasses dominant in the meadow. As with a number of other Araeopid species, e.g. the *Chloriona* species, these species hibernate during the larval stage. As with the majority of other Araeopids, all three species concerned display wing-dimorphism.

Observations were carried out on the leaf-hopper populations at Tvärminne from July 7 to August 12, 1945. During this period a number of collections were made, partly quantitative, partly qualitative, in order to ascertain the spreading of Strepsipteron infection and the presence of the parasite at the various stages of development of the hosts. The result of the collections of the different species is shown in the tables below. The collections were effected by a pole-net 30 cm in diameter. A quantitative collection comprised 50 sweeps with the net.

When re-visiting the meadow in the next two years (1947, 1949), the change in the composition of the plant population could be followed; the tall herbs gradually completely replaced the previously dominant grasses. Some isolated specimens only of the Araeopids in question could be found, and no widespread infection seems to have existed. However, it seems probable that the earlier strong parasitic infection was the primary cause of the sharp reduction in the number of individuals of the Araeopid populations. The changed character of the vegetation may also have some significance in this respect.

In the paper that follows the separate species of Araeopids will be dealt with individually, and the effect of stylopisation will be considered, partly on the development of the host, and partly on its morphological structure. One chapter is devoted to supplying particulars on the parasite; the final chapter will present a short summary of certain more important results of the author's investigations into stylopisation within the family *Araeopidae*.

I. Dicranotropis hamata Boh.

1. Influence of Stylopisation on Development.

Table 1 shows the composition of the material of *Dicranotropis hamata*, comprising 615 specimens. The quantitative samples are analysed in the table by nrs 1-10. The 10th sample was taken at the close of the imago period of the Dicranotropis, when the number of specimens was very small and was obtained by 4×50 sweeps of the net. For one collection (July 10) the number of sweeps was not counted. At the so-called qualitative collections, not based on a definite number of sweeps, the leaf-hopper specimens were picked alive from the net. These samples, therefore, do not indicate, to the same degree as the quantitative, the proportion between normal and parasitised, macropterous and brachypterous, etc., specimens. As, however, the author sought, in the qualitative samples as well, to collect all the specimens of the leaf-hopper species which constituted the object of the present study, the collections appear on the whole to give a fairly correct picture of the frequency of the specimens of the different species between July 7 and August 12, 1945. Neither during that year nor later has there been an opportunity of effecting similar collections at the beginning and end of the summer on the meadow in question at Tvärminne. Observations in other localities in South Finland,

Table 1.

DICRANOTROPIS HAMATA Boh.

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

			Not	mal		Normal Parasitised by Elenchus Q Parasitised by Elenchus d							ę	asit											
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$3(1 \times 50)$	7.7.		3	1	5	1		2	2						2	1	1			4					22
qual	8.7.	1			3	2	3								1	_				5			-		15
quant	10.7.	7	12	1	39	6	3	10	11			-	2	1	25	5	1	_		9	_				132
qual	11. 7.	1	1	4	9	3		3	5	-	-	4	2	2	6	1				20	-			-	61
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4 (1 \times 50)	18.7.			2	7				1			4	1						-				-		15
$5~(1~\times~50)$	18.7.		2	4	22			2			-	4	5	-	1	-	-	-		13					53
$6 (1 \times 50)$	18. 7.				4							2	3		-		1	-		5	-			-	15
7 (1 \times 50)	18.7.	-	1	6	30		-	1	3			6	14		4					2					67
qual	19. 7.	-	1				-	1		-		3		1	4	-		-		1				-	11
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			2	49		71 98								68					121		-				
							169					-	197												

8

imagines in the latter part of July.

wards the end of

the summer.

The hibernating healthy larvae develop into

or late larval stages, and that young larvae of the new generation appear tohowever, have shown that the Dicranotropis hibernates at certain of the middle

vae were no longer present. All the larvae in existence at that time are parasit-

Table 1 shows that at the beginning of the collections (July 7) healthy lar-

Håkan Lindberg: On Stylopisation of Araecpids

ised by Strepsipteron males. They contain either larvae of Strepsipteron males or puparia. In some of the leaf-hopper larvae the Strepsipteron males have already emerged from the puparium. On studying the table more closely it can be seen that the material comprises a total of 8 *Dicranotropis* larvae in which the Strepsipteron is still at the larval stage (column 13), while Strepsipteron males are still in puparium in 56 larvae (column 14). Empty puparia, from which the Strepsiptera had emerged, were encountered in 119 leaf-hopper larvae (col. 19). The table shows, albeit not distinctly, the evident fact that leaf-hopper larvae with empty puparia are proportionately more numerous in collections effected later (cf. collections July 10, July 16, July 18). A peculiarity to be noted is that a leaf-hopper larva, with an *Elenchus* larva of very retarded development, was encountered as late as August 4.

The circumstances described above regarding the *Dicranotropis* specimens parasitised by Strepsipteron males are fully in accord with those in *Chloriona* species. It will be recalled, however, that among the latter, specimens infected by the *Elenchus* male reach the final larval stage but not — with the exception of a single instance among the several hundred cases studied — the imago stage. As to the *Dicranotropis*, it now appears that specimens parasitised by Strepsipteron males attain the imago stage in a number of cases. The collections comprise a total of 14 such specimens (columns 15, 16, 20), i.e. 7.6 %. It is surprising that all the imago specimens in question are long-winged, a fact that seems more significant against the knowledge that the recently cited exceptional case among the *Chloriona* was also a long-winged specimen (cf. LINDBERG 1939, p. 141). — From the puparia in two of the 14 specimens a Strepsipteron male had emerged (column 20).

On the very first day of collection (July 7) it could be ascertained, thanks to findings of *Dicranotropis* L_v with empty puparia, that adult Strepsipteron males were present. Subsequently (from July 10), *Dicranotropis* specimens, the abdomen containing the Strepsipteron female's cephalothorax, were also encountered, indicating that the latter was at the pupal or imago stage. Judg-

Table 1.

THE MATERIAL OF DICRANOTROPIS HAMATA BOH. FROM TVÄRMINNE 1945 615 specimens.

249 normal specimens (41 macropterous: 10 33, 31 \Im ; 208 brachypterous: 31 33, 177 \Im).

366 parasitised specimens.

169 by Elenchus Q.

71 by El.-Q in larval stage (24 macropt.: 17 중경, 7 QQ; 47 brachypt.: 24 중경, 23 QQ).

98 by El.-Q in pupal or imaginal stage (0 macropt., 98 brachypt: (51 ♂♂, 47 QQ). 197 by Elenchus ♂.

8 by El.-5 in larval stage

68 by El.-3 in pupal stage (56 larvae v, 12 macropt.: 8 33, 4 99; 0 brachypt.)

121 by Elenchus \vec{o} , emerged from puparium (119 larvae v, 2 macropt. $\vec{o}\vec{o}$)

ing by the collections (columns 14—15) the majority of the *Elenchus* males (in 1945) seem to have emerged about the middle of July. By then the sexually mature females are available for pairing, completed in haste during their short life. The *Dicranotropis* larvae parasitised by Strepsipteron males, still present about the end of July — beginning of August, reveal empty puparia.

Let us turn, now, to the leaf-hoppers parasitised by *Elenchus* females (col. 5-12). The specimens of *Dicranotropis* parasitised by female Strepsiptera reach the imago stage. The specimens in question had already reached this stage at the beginning of the collections at Tvärminne. The material of the early days of the collection (July 7-8) contain only leaf-hoppers whose parasites are still at the larval stage. The first leaf-hopper specimens with female puparium (col. 12) were encountered July 10. Characteristic of the latter is the cephalothorax lying on the surface of the host's body, from whose mouth aperture the first larvae emerge. The female imago remains in the puparium, and a close examination is necessary to show whether the puparium contains a pupa or an imago. In the present material leaf-hoppers with parasites at the larval stage (col. 5-8) are in the majority, even in the collections of July 11; later on those with Strepsipteron puparia (col. 9-12) become relatively more and more numerous. About the end of July - beginning of August still, isolated specimens of the former type are present. Throughout the period during which the collections were effected, Dicranotropis imagines with puparia of Strepsipteron females were encountered. The pupal stage of these is likely to be (cf. LINDBERG 1939, p. 92) of short duration, for which reason it can be assumed that the majority of the puparia - of the later collections at least contained adult females.

The table shows that the *Dicranotropis* imagines parasitised by Strepsipteron females live on at least until mid-August (col. 11—12). Non-stylopised *Dicranotropis* are gradually reduced in number, and also die in the middle of August. Leaf-hoppers infected by *Elenchus* males have already disappeared before that. By the end of the summer there are therefore only *Dicranotropis* imagines infected by *Elenchus* females. But along with them there exist already young larvae of the new generation, exposed to attacks by Strepsipteron L_1 , emerging in due course from the special opening of the brood pouch of the female *Elenchus* lying in the leaf-hopper imago. The extended lease of life of the stylopised *Dicranotropis* thus allows infection of the young larvae of the new leaf-hopper generation.

The facts described above regarding the time of appearance of normal and stylopised *Dicranotropis* specimens agree with the conditions obtaining with *Chloriona*, previously discovered by the author. As regards the effect of stylopisation with *Dicranotropis*, an important difference from the conditions with *Chloriona* can be recorded at this early stage. While the stylopised Chloriona specimens, with certain few exceptions¹) are short-winged, a relatively large proportion (14 %) of the stylopised *Dicranotropis* imagines consist of long-winged specimens. A striking fact is that all the long-winged stylopised specimens in the present material are to be found among those in which the female *Elenchus* is still at the larval stage, and amount to a third of the total number (34 %). The leaf-hoppers in which the female Strepsipteron had reached the pupal or imago stage, on the other hand, are all short-winged.

2. Exterior Morphological Changes due to Stylopisation.

The author has earlier (1939) described 3 stylopised imago specimens of *Dicranotropis*, the descriptions being illustrated by drawings of the last abdominal segments. By way of comparison, a drawing of the abdominal apex of the normal male and female imago was also attached.

In the following paper, the author gives first more detailed descriptions, and diagrams of those external organs which may be affected by stylopisation, as they appear in the normal insect, and then descriptions and diagrams of the same structures from stylopised hosts.

The Normal Imago.

The *Dicranotropis* is characterised by the considerable exterior difference in the colour and form of the abdomen between male and female. Both male and female display wing-dimorphism. The macropterous specimens are (in Finland) less frequent than the brachypterous ones. Of the material from Tvärminne 15.8 % of the normal *Dicranotropis* specimens, 24.4 % of the males and 75.6 % of the females are long-winged.

Male (Figs. 1—3): The abdomen is mainly black to greyish black. The first two tergites have a somewhat rough surface and are lighter in colour; the first one is inserted under the posterior margin of the postnotum, the latter under the anterior margin of the third tergite. Medially on the second tergite there is a distinctly delimited, shield-shaped chitinous plate, an organ present in males only. The third to eighth tergites are of approximately the same length — the third, however, distinctly shorter than the others — with more or less parallel anterior and posterior margins, dark in colour, but with weaker and light-coloured median chitins. The 6th and 7th sternites are medially strongly concave. The more dorsally situated 3rd to 6th pleurites are more strongly, the more ventrally situated more weakly chitinised. The 9th abdominal segment is well developed, approximately the length of half the rest

¹) Only 5 instances among the several hundred specimens examined by the author, cf. 1939, p. 141.

of the abdomen, mainly black, medially somewhat lighter in colour, bipartite. Ventrally the long styli are visible. The narrow tips of the styli (Figs. 2—3, pa) are slightly curved and terminate in a somewhat extended part, of the shape of a finch's head, with a short tooth (*»*bill*»*). Inside, at the base, the stylus is furnished with a sharp tooth (za); the outer side of this, similarly to the edge of the stylus, is proximally fine-toothed. Between the basal tooth and the tip there are two small tubercles. The stylus has a number (20—30) of hairs. The connective (s) is bent in an arch. The penis (p), the basal part of which has the shape of a foot, displays numerous sharp backward-turned teeth. In the penis's normal position there is a large tooth on the dorsal side, a fairly large one on the left side, 3 small ones on the right, several small ones in line on the ventral side, and similarly several small ones on the dorsal side of the organ. The 10th abdominal segment ventrally-basally shows a sharp short tooth (z). The 11th segment is very short, light in colour, the 12th longer, oval, dark.

Female (Figs. 4---6): The abdomen of a female is more swollen, broader and lighter in colour than that of the male. Wiht the female too the first two segments are distinctly visible on the dorsal side only, where the tergites insert themselves under the posterior margin of the postnotum and the anterior margin of the 3rd tergite. The 3rd to 8th tergites are more or less extensively marked with dark spots. The anterior and posterior margin and the sides are mainly dark, and medially too there are somewhat darker spots. The 7th and 8th tergites are lighter in colour than the others. Part of the 9th abdominal segment is dark on the upper side. As with the male, the anterior and posterior margins of the tergites are parallel. The posterior margins of the 5th to 9th sternites are medially strongly curved, leaving room for the ovipositor, which is formed by appendages from the 8th and 9th segments. The 3rd to 6th sternites are laterally darker, the 8th sternite with a dark medial bipartite flap. The 10th and 11th segments are light in colour, the 12th dark. The construction of the appendages (the paired gonapophyses of the 8th segment and the median gonapophysis of the 9th) which form the ovipositor, and the lateral gonapophyses of the adjacent protecting 9th segment, are seen in Fig. 6. The gonapophysis (a) of the 8th segment has a fine horizontal-striped tip. The median gonapophysis forms a saw with 35-38 fine teeth. At the tip the teeth are not distinct. The teeth extend roughly half-way down the appendage.

Dicranotropis Males parasitised by the Female Elenchus.

The author has examined 169 *Dicranotropis* imagines parasitised by female Strepsiptera. Of these 71 were still at the larval stage, while 98 had reached the pupal or imago stage. Of the host, 24 specimens were long-winged (17 males, 7 females), and 145 short-winged (75 males, 70 females). A *Dicranotropis* imago containing a female *Elenchus* can be distinguished by its light colour. As the abdomen housing the parasite is swollen the stylopised leaf-hopper very much resembles a normal female (cf. Figs. 5, 7).

The abdomen of the stylopised leaf-hopper male does not reveal the structure characteristic of this sex. The strongly developed 9th segment of the parasitised specimens is small, the exterior genitalia attached to it are greatly shrunk or completely absent (Figs. 7—9). Among the stylopised leaf-hopper males, in the development of their exterior genitalia (the styli, penis and connective) the author distinguishes 4 types.

Type 1 (Fig. 9a, Fig. 10a) comprises specimens with the least reduced organs; they have two distinct, although greatly shrunk styli, of a shape on the whole characteristic of these organs. In addition, there are the rudiments of penis and connective. The former is a swollen, somewhat rounded formation, furnished with a number of small teeth, the latter constitutes a short shaft between the styli and the penis.

With Type 2 as well (Fig. 8, 9b, 10b), rudiments of both styli can be observed, but they are not of the normal shape; in many cases they have fused together. The rudiments of the other copulation organs are greatly shrunk and not distinguishable from each other.

In specimens which the author has referred to Type 3 (Fig. 9c), all that remains is a single tuberculate formation, representing a part of or all the copulation organs. Some specimens have a single, somewhat prolonged part, constituting the rudiment of the styli.

The most reduced type (4) has no remains of copulation organs present at all.

The following table shows the number of the different types and their distribution among the long- and short-winged specimens.

Type 1	f. macr. 1	f. brach. 23	24
2	7	26	33
3	7	20	27
4	2	6	8
	17	75	92

There is, of course, no sharp delimitation between the different types, whereas there is, generally speaking, a correlation with regard to the degree of development of the different copulation organs. The structure of the 9th abdominal segment is to some extent different in the different types. In specimens of Type 1 there is, on the ventral side, a quite distinct depression in which the styli are fixed. In the more reduced types no such depression can be observed.

In *Chloriona* males infected by the female *Elenchus* the author also distinguished 4 types, representing, with regard to copulation organs, specimens

reduced in differing degrees. Generally speaking, the types in *Chloriona* and *Dicranotropis* correspond. With *Chloriona*, a connection could be observed, furthermore, between the degree of development of the styli, the penis and the connective, and the teeth on the abdominal segment. In all stylopised *Dicranotropis* males the 10th segment is a simple ring without an appendage. The 10th segment of the normal male has a tooth (p. 12).

The dark spots on the tergites as well as on the side shields of the sternites differ in extent in the different stylopised specimens. In studying the present material of *Dicranotropis* parasitised by the female *Elenchus* the author has found no general correlation between the degree of development of the exterior and the extent of the dark spots. It is true that the 5 darkest specimens (i.e. those most resembling the normal male) among the stylopised ones proved to belong to Type 1, with least reduced genitalia, but this type comprised quite light-coloured specimens too. Nor was any such connection between colour and the genitalia found to exist in *Chloriona* stylopised by female Strepsiptera.

In Chloriona specimens parasitised by species of the dipterous genus Pipunculus (LINDBERG 1946), the author has, by contrast, found a distinct connection between the colour and the degree of reduction of the genitalia, the degree of development of the chitinous plate on the 2nd tergite and the wings, characteristic of the male. All the stylopised *Dicranotropis* males are completely without the chitinous plate, and as mentioned above, some of them are longwinged, others short-winged. All short-winged specimens have wings of equal length, which is also the case with the long-winged specimens. Such specimens with long wings have a length of wing equal to that of the normal long-winged specimens.

Apart from the light colour and the swollen abdomen, the great shrinking of the 9th abdominal segment and of the copulation organs contributes to a striking similarity between stylopised *Dicranotropis* males and the normal females. Another factor is the recently mentioned absence of the chitinous plate of the 2nd tergite in infected specimens. The stylopised *Chloriona* specimens, in contrast to the normally green females, have a pale yellow colour. In *Dicranotropis* no such difference in colour can be observed, for which reason the similarity between the normal females and the stylopised specimens of this species is more misleading.

Dicranotropis Females parasitised by the Female Elenchus.

Stylopised *Dicranotropis* females show a similarity to the normal female even greater than do the males. Often only by fairly detailed study can it be decided whether a specimen is parasitised or not. If the parasite is at the pupal or imaginal stage, with a visible cephalothorax, stylopisation can naturally be established immediately In all stylopised females studied by the author, the ovipositor with all its individual parts is distinctly shorter than that of the normal females (cf. Figs. 4, 6, 11, 12, 13). The sternites, too, are of a shape different from that in normal specimens. Measurement of the length of the ovipositor from its base to the tip of the median appendage of the 9th segment (by means of a micrometer ocular) gave the following figures: The ovipositor of a normal female is 1.5 mm long, while that of stylopised females varies in length between 0.7—1.3 mm. A breakdown of the specimens into types by varying degrees of reduction is difficult to carry out, due to the very even variation. Specimens with a longer ovipositor, as well as those with a particularly short one, are rare; the commonest length of ovipositor in the present material is 0.8—1.0 mm.

Among the 70 specimens studied, three differed from the others in one particular: they revealed a small rudiment of the median appendages on characteristic of the female *Dicranotropis*, of the 8th sternite (cf. p. 12). These were present in no other specimens. The three specimens in question, furthermore, were distinguished by a relatively long ovipositor (1, 1.2, 1.3 mm, respectively). A correlation in the degree of reduction seems to exist, therefore, between these organs, obviously used in copulation, and the exterior genitalia.

The individual parts of the ovipositor, on the whole, have undergone the same degree of reduction in the stylopised leaf-hoppers. In a number of cases the gonapophyses of the 8th sternite are very weakly chitinised, somewhat shrunk and curved. Some specimens display gonapophyses with crossed tips (Figs. 11, 12). But in the majority of cases the gonapophyses have the shape characteristic of normal specimens, the grooves at the tip are fewer and less conspicuous. The saw-toothed median gonapophysis of the 9th segment of the stylopised specimens is recognisable by its considerably reduced number of teeth. The appendage shown in Fig. 13 (from a specimen with an ovipositor 1 mm in length) has 27 distinct teeth. (Normal females have 35—38 teeth, see p. 12).

A comparison of the structures of the stylopised females of the *Dicrano-tropis* and *Chloriona* genus, reveals the following: The latter displays greater variation in the appearance of the reduced organs. The percentage of specimens with ovipositors completely absent or very greatly shrunk is fairly large. Even the least reduced ovipositors are much shorter than those of the normal female whose ovipositor is 1.7 mm long. The four different types (Types 5–8) of stylopised *Chloriona* females, which the author distinguished mainly on the basis of the reduction of the said organs (LINDBERG 1939, p. 133), show the following ovipositor measurements:

Type 5 no ovipositor

8 approx. 0.45 — approx. 0.6 mm

^{6 0.2—0.4} mm

^{7 0.4-0.45} mm

The above means that the least reduced ovipositors in *Chloriona* are 35.3 % of the normal length.

As mentioned above the ovipositor of the normal female *Dicranotropis* is 1.5 mm long, while its length in the stylopised specimens studied by the author varies between 0.7-1.3 mm. The least reduced ovipositors are therefore 87 % of the normal length.

A further characteristic of the stylopised *Chloriona* females is the structure of the 8th sternite. Normally this consists, both in the *Chloriona* and *Dicranotropis*, of two longish blade-like parts lying extended on both sides of the 9th segment. The blade-like parts of the stylopised specimens are greatly shortened, and in the most reduced specimens they form a continuous median plate(cf. LINDBERG 1939, Fig. 51, p. 132). In every stylopised *Dicranotropis* females studied the 8th sternite retains its division into two longish blade-like parts (Figs. 11—12).

Dicranotropis Imago Parasitised by the Male Elenchus.

As already stated (p. 9), *Chloriona* parasitised by the male *Elenchus* very rarely reach the imago stage. The only known instance was a long-winged female which revealed similar reduction of genitalia as the imagines infected by the female *Elenchus*.

Dicranotropis parasitised by male Strepsiptera that reach the imago stage are considerably more numerous (14 specimens of a total of 189, i.e. 7.5 %), and all such imagines are long-winged. It has been difficult to account for this curious difference of between *Chloriona* and *Dicranotropis*. It is possible that the long-winged specimens develop into imagines earlier than the short-winged, and that their transition into an adult insect in many cases takes place at a time when the male Strepsipteron larva is not yet ready to pupate. The pupation of the Strepsipteron, on the other hand, would have time to take place before the short-winged leaf-hopper develops into an imago. There is no actual observation to support this suggestion that long-winged leaf-hoppers in fact do develop into imagines earlier than the short-winged ones (cf. below p. 34).

Of the present *Dicranotropis* imagines parasitised by the male *Elenchus*, 10 are males and 4 females.

An examination of the males shows that the reduction in them, generally, is not as advanced as that in those parasitised by the females. In the majority of the specimens development of the 9th segment thus is not equally retarded as in the latter, but has retained its characteristic form to a greater degree (Figs. 14, 15). The styli are distinctly developed (Fig. 14), and the colour, on the average, is darker than in those parasitised by the female *Elenchus*. Finally, a rudiment of a plate on the 2nd tergite can be observed and has the shape of two dark angular indentations delimiting a more or less extended, somewhat more strongly chitinised field at the base of the segment. One specimen differs, in its particularly light colour, from the others; this specimen further has a weakly developed 9th segment, very small rudiments of the styli, and the chitinous plate on its 2nd tergite is not visible.

Judging by the 10 specimens, therefore, a relation seems to exist between the structure of the 9th segment and its appendage, and the chitinous plate on the 2nd tergite, and further in the colour of the abdomen. Fig. 14 shows the structure of the 9th segment, Fig. 16b the structure of the 2nd tergite of the least reduced specimen, Figs. 15 and 16a, respectively, the corresponding of the most reduced one.

The 4 female specimens parasitised by male *Elenchus* reveal in this respect a state contrary to that in the *Dicranotropis* males, viz. that the reduction of the genitalia is greater than in those parasitised by female Strepsiptera. The lengths of the ovipositors of the specimens in question are: 0.28 mm, 0.4 (specimen illustrated in Fig. 17), 0.44 and 0.72 mm. Owing to the limited range of the material, the author refrains in this connection from discussing this apparently contrasting relationship.

Dicranotropis L_v Parasitised by the Male Elenchus.

One of the most characteristic features in the stylopisation of *Chloriona* is the detail recorded above (p. 9), that the specimens parasitised by male Strepsiptera do not reach the imago stage but remain at the last larval stage (cf. also p. 16). This is the case, as a rule, with *Dicranotropis* too. Only 7.5 % of the specimens in the present material stylopised by males are imagines (p. 16).

The author examined 165 parasitised L_v of *Dicranotropis*. 92 of these were males and 73 females. The Strepsipteron larva pupates in a position such that its head is directed towards the apex of abdomen of the host, and the operculum projects between the 6th, 7th or 8th tergites, pleurites or sternites. In exceptional cases the operculum projects between the foremost abdominal segments, but only if two pupae are contained in the abdomen.

In stylopised *Chloriona* larvae, at the two final stages (of female larvae) or in the very last stage only (male larvae), there is a reduction in the formation of the rudiments of exterior genitalia. This reduction is at its most distinct in female larvae at the 5th stage, which in normal specimens displays distinct rudiments of all the appendages forming the ovipositor. In stylopised female larvae, only rudiments of the gonapophyses of the 8th segment and the median appendage of the 9th segment could be observed. The reduction of these appendages is markedly different in different specimens, which on this basis may justifially be divided into different categories.

In female *Dicranotropis* larvae at the 5th stage, infected by *Elenchus* males, a reduction of the appendages of the last abdominal segments is also found, and in this case too the rudiments of the gonapophyses of the 8th segment and of the median appendage are also present. As regards the size of the reduced organs, the different specimens vary within very narrow limits, and that do not fall into any clearly distinguishable categories. Fig. 18 shows the normal structure of the appendage in question. In the male larva of *Dicranotropis* the author has found no dissimilarity between stylopised and healthy specimens.

II. Calligypona straminea Stál.

1. Influence of Stylopisation on Development.

Table 2 shows the composition of the material of *Calligypona straminea* collected from the meadow at Tvärminne. The material comprises 273 specimens.

As with *Chloriona* and *Dicranotropis*, *C. straminea* probably hibernates during some of the later larval stages. At the commencement of the collections (July 7, 1945) the normal specimens of the species had already reached the imago stage. Only 4 larvae were collected, all of them infected by male Strepsiptera (columns 14, 19).

The earliest quantitative collections, July 7 to 10, give 23 specimens of normal imagines, 13 imagines containing larvae of female Strepsiptera, and 10 containing puparia of male Strepsiptera. The first *C. straminea* with a male *Elenchus* imago was collected July 11. Among the material found on succeeding days, the number of leaf-hopper specimens containing female imagines of the parasite increased (col. 9–12), while those containing larvae were reduced

Table 2.

THE MATERIAL OF CALLIGYPONA STRAMINEA STÅL FROM TVÄRMINNE 1945.

273 specimens.

113 normal specimens(41 macropterous,: 10 33, 31 99; 72 brachypterous,: 20 33, 52 99). 160 parasitised specimens.

109 by Elenchus Q.

41 by El.- \bigcirc in larval stage (17 macropt.: 11 $\eth \eth$, 6 $\circlearrowright \heartsuit$; 24 brachypt.: 16 $\eth \eth$, 8 $\circlearrowright \circlearrowright$).

68 by El.-Q in larval or imaginal stage (3 macropt.: 0 33, 3 QQ; 65 brachypt.: 29 33, 36 QQ).

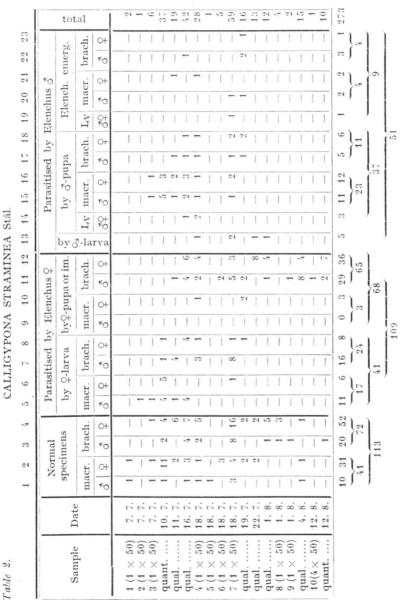
51 by Elenchus 3.

5 by El.-3 in larval stage

37 by El.-3 in pupal stage (3 larvae v, 23 macropt.: 11 33, 12 \bigcirc ; 11 brachypt.: 5 33, 6 \bigcirc).

9 by Elenchus 3, emerged from puparium (1 larva v, 4 macropt.: 2 33, 2 \Im ; 4 brachypt.: 3 33, 1 \Im).

in number (col. 5-8). July 19 the last specimen with female Strepsipteron larva was encountered (col. 8). On that day, but for two specimens, the last leaf-hopper specimens parasitised by the female *Elenchus* were collected. By this time, consequently, in the Summer of 1945, practically all the male Strepsiptera living on straminea had emerged. The leaf-hoppers containing female imagines of the parasite, however, continued to live and, with no reduction



in their number, they were considerably in the majority, towards the end of the imaginal period, over the healthy leaf-hoppers. As shown by the table (columns 1—4), the majority of the latter died early in August.

The circumstances described above, implying an altered ratio between healthy and stylopised leaf-hopper specimens during the imaginal period, are familiar from the descriptions of *Chloriona* and *Dicranotropis*. Stylopisation, therefore, has the same influence on the length of life of *straminea* as of these Araeopids.

An important dissimilarity in the influence of stylopisation on the leafhoppers in question is emphasised in this connection. Earlier in this paper (p. 9) it was intimated that *Chloriona* specimens parasitised by the male *Elenchus* do not reach the imago stage. *Dicranotropis* specimens parasitised by the male Strepsipteron also remain, in the majority of cases ($92.5~\%_0$), at the last larval stage. *C. straminea* reveals a contrary state of affairs: specimens infected by the male *Elenchus* and reaching the imago stage constitute $92.3~\%_0$ in this species. — A possible explanation of this remarkable condition is offered on p. 27.

2. Exterior Morphological Changes due to Stylopisation.

The author has previously studied with the structure of stylopised specimens of a number of *Calligypona* species, and found (1939) changes in the structure of the abdomen in the 4 male specimens of *C. discolor* Boh. examined, and in one male specimen of *C. forcipata* Boh. In a collection (1943) of *C. albostriata* Fieb. $L_{\rm V}$ (six specimens) parasitised by male Strepsiptera, all disclosed changes from the normal. Of the stylopised imagines of this species, the two males available were characterised by a distinct reduction of the genitalia, while three females seemed to show no morphological changes. The latter was the case also with a female specimen of *C. straminea* studied (1939), as well as with a female of *C. pellucida* reproduced in illustration by AHLBERG (1925). It appears therefore that stylopisation differs in its effects upon the different species of the Araeopid genus *Calligypona*. The present investigation, with a more comprehensive material, of two species of this genus, is therefore of particular interest.

The Normal Imago.

Long- and short-winged specimens of *C. straminea* seem to be present in the same proportion among males and females. Sufficient detail is not yet available on the general spreading of the long- and short-winged forms. Judging by the museum specimens available the short-winged form seems to extend further North geographically than the long-winged. Of the present material from Tvärminne (normal imagines) the percentage of long-winged is 36.3, of short-winged, 63.7.

Male (Figs. 19—21): Against the fairly evenly uni-coloured, light yellowish brown surface of the body, the greyish black eyes stand out. An insignificant difference in the shade of colour of the tergum can be noticed between longand short-winged specimens. For instance, the postnotum and the 3rd tergite of the former are somewhat darker, as is the shield on the 2nd tergite. The entire tergum of the latter is uni-coloured, light. While the wings of the long winged specimens protrude over the apex of the abdomen by 1/3 or 1/2 of their length, those of the short-winged specimens extend only to the anterior part of the well developed 9th segment.

The particular characteristics of this species can also be seen in their exterior genitalia (Figs. 20-21). The cylindrical 9th segment has a fairly round posterior contour. The styli (pa) intruding under its ventral part are comparatively short and narrow; their tip, similar to a small knob on the inner side, is somewhat darker in colour, and slightly bent inward. The connective (s) is roughly of the same length as the styli. The penis (p), also of the length of the styli, has flattened sides and a slightly curved tip. The broad proximal part has a large number of fine teeth. On the ventral contour of the penis there are about 15 teeth. On its ventral surface the 10th segment has two strong protruding teeth (z). In the normal position the tip of the teeth is directed downwards; from a posterior view they are conical. They are darkish in colour and have fine small teeth.

Female (Figs. 22–23): The body is of the same colour as the male, unicoloured, light yellowish brown. The abdomen is thicker, cylindrically conical. The structure of the abdominal segments is in general similar to that of the *Dicranotropis*. There is no equivalent to the median, forked, blade-like part on the posterior margin of the 8th sternite. The ovipositor is more strongly chitinised than the other parts of the abdomen, and rust-brown in colour. Its length (to the tip of the gonapophysis of the 8th segment) is 1 mm. The latter organ (Fig. 23c) is sword-shaped, though not particularly sharp, with less distinct horizontal stripes at the tip. The median gonapophysis of the 9th segment (23a) has approx. 22 blunt and somewhat uneven teeth. The lateral gonapophysis of the 9th segment (23b) is of roughly the same width along its entire length.

The wings of the long-winged specimens extend by roughly a third beyond the apex of the abdomen; with the short-winged, the posterior margin of the wing reaches the posterior half of the 5th tergite or the anterior part of the 6th.

C. straminea Males Parasitised by the Female Elenchus.

The present material includes a total of 56 specimens of male imagines of *straminea* parasitised by the female *Elenchus*. 11 of these are long-winged, the remainder short-winged. All the long-winged male specimens house larvae of the parasite, whereas of the short-winged specimens 16 contain larvae and 29 imagines.

The effect of the stylopisation on the host is restricted to the secondary sexual characters and is analogous to that in *Chloriona* and *Dicranotropis*. However, variations in the degree of reduction body are smaller than with the latter leaf-hoppers. In trying to classify the stylopised specimens by their different types, based on the structure of the copulation organs, the author has limited the number of the types to three. These correspond, largely, to types 1—3 of the *Dicranotropis*. Type 4, characterised by a complete absence of the rudiments of copulation organs, has no equivalent among the *straminea* studied.

The 45 specimens studied are divided into different types as follows:

f. brach. f. macr.	Type 1 3 1	Type 2 9 4	Type 3 23 5
	Total 4	13	28

Type 1 (Fig. 24), with the least reduced organs, has greatly shrunk, but distinctly separated styli. In type 2 (Figs. 25, 27) there is an oblong appendage, forked in certain specimens. In a number of specimens of the first two types a small rudiment of the other copulation organs can be seen (connective and penis). In type 3 (Fig. 26) a single tubercle only remains. The 9th segment of all stylopised males is strongly reduced. Its form, however, varies in the different types; in types 1—2 it is somewhat stronger, and the rudiments of copulation organs lie in a depression bordered by a low elevation, tuberculate on each side of the median line.

The 10th segment, toothed in normal specimens, consists of a single ring in all specimens. All the specimens reveal an absence of the chitinous plate on the 2nd tergite.

Both stylopised and normal specimens of *straminea* are of the same, light yellowish brown colour; stylopised *straminea* — males as well as females — display a striking similarity to normal leaf-hoppers (cf. p. 21). It has not been possible to ascertain any difference between the proportion of long- and short-winged in the different types (cf. Table on p. 22).

C. straminea Females Parasitised by the Female Elenchus.

The material includes 53 female specimens of *straminea* parasitised by *Elenchus* females. 9 of them are long-winged and 44 short-winged. The pecul-

iarity observed in the stylopised females, that long-winged specimens contain only the larvae of *Elenchus*, while the pupae or imagines were all found in short-winged leaf-hoppers, has its equivalent in the females (cf. Table 2, columns 6, 10, and 8, 12, respectively). The majority of the long-winged specimens (6) contain larvae, a smaller number (3) pupae or imagines. The majority of the short-winged (36) contain Strepsipteron pupae or imagines, a few (8) larvae. A glance at the table also shows that the long-winged specimens, with one exception, were obtained during the early period (July 7—16) of collection.

Exterior morphological effects are found, in the females too, in the genitalia only. The difference between the normal females and the infected ones is, however, quite small. All the stylopised females have an ovipositor distinctly shorter than the normal females (1 mm long, cf. Fig. 28); its length varies between 0.7 and 0.35 mm. The proportion between the individual parts of the ovipositor is the same in every instance (Fig. 29). Connected with the weakly developed ovipositor is the changed shape of the ventral segments. In every specimen studied all the appendages are developed, in some they are weakly chitinised and somewhat shrunk. The number of saw-teeth usually found in the gonapophysis of the 9th segment is reduced. A specimen with an ovipositor 0.64 mm in length has 19 teeth (normal specimens have approx. 22), one with an ovipositor of 0.5 mm has 13. The fine horizontal stripes characteristic of the gonapophysis of the 8th segment are also less developed.

In a stylopised female specimen of *straminea* previously studied by the author (cf. p. 20) no difference was found between the length of its ovipositor and that in the normal female. This observation, the correctness of which can no longer be checked as the specimen in question is not available, was made in comparison with stylopised *Chloriona* females having a greatly reduced ovipositor. Possibly a new examination might show that the ovipositor of this particular *straminea* specimen was slightly reduced, as is that of the specimens of the species included in the present investigation.

C. straminea Imago Parasitised by the Male Elenchus.

C. straminea specimens attacked by the male *Elenchus*, in the majority of cases, reach the imago stage. 42 of the 46 specimens in this material containing a Strepsipteron pupa or imago, are imagines. Of these 27 are long-winged (13 males, 14 females) and 15 short-winged (8 males, 7 females). By the time of collection the male *Elenchus* had emerged from the puparium in 8 specimens, while 37 specimens still carried the parasite.

Comparing the proportions of long- and short-winged specimens among normal healthy insects, and those of parasitised specimens it was found that, whereas in normal insects the short-winged form was in a considerable majority, among parasitised specimens the long-winged predominate. The relationships are:

				f.	macr.	f.	brach.
normal				41:	36.3 %	72:	63.7 %
infected	by	female	Elenchus	20:	16.8 %	89:	83.2 %
*	*	male	Elenchus	27:	64.3 %	15:	37.3 %

Somewhat similar proportions, among specimens parasitised by the male *Elenchus* are also noticeable in the other Araeopids studied (cf. p. 16 and p. 34).

Of the present *straminea* imagines parasitised by the male *Elenchus*. 21 are males and 21 females. Changes in the exterior structure due to stylopisation agree with those described in specimens parasitised by females (cf. p. 22-23). Among the males, therefore, it has been possible also in this case to distinguish three types with genitalia reduced in differing degrees. The number of the specimens by types is:

f. brach. f. macr.	Type 1 1 2	Type 2 1 2	Type 3 6 9
	Total 3	3	15

In all female specimens, too, the exterior morphological changes are restricted to the genitalia. The ovipositor of the present specimens has a length varying between 0.6 and 0.35 mm, 0.5 mm being the length of the majority.

C. straminea L_v Parasitised by the Male Elenchus.

Contrary to the case with *Chloriona* and *Dicranotropis*, straminea individuals attacked by the male *Elenchus* — as pointed out above — reach the imago stage. Only 4 (2 males, 2 females) out of 26 specimens (i.e. 8.7 %) from the present material of leaf-hoppers containing an *Elenchus* pupa or imago are larvae (L_V). Similarly to *Dicranotropis* (p. 18), no exterior morphological effect of stylopisation can be found in the male larvae. With female larvae the case seems to differ from the conditions obtaining in *Dicranotropis* and *Chloriona*. Whereas rudiments of the median appendage and the gonapophyses of the 9th segment are found in stylopised female L_V of *Dicranotropis*, and of the gonapophyses and the median appendage only, which obviously represent the gonapophyses of the 8th segment (Fig. 30).

III. Calligypona pellucida Fabr.

1. Influence of Stylopisation on Development.

A study of Table 3, giving the composition of the present material of *Calligypona pellucida*, readily shows that the species is less numerous on the habitat than *Dicranotropis* and *C. straminea*. A total of 88 specimens only is available. At the beginning of the collections (July 7—10) there were, apart from normal specimens, those parasitised by both male and female *Elenchus*. With a single exception (of July 10), all the stylopised specimens contain the parasite at the pupal or imaginal stage. Among *Dicranotropis* the author still found specimens containing Strepsipteron larvae (males and females) 25 (1 male) and 22 (females) days later, respectively, among *C. straminea* 8 days afterwards. This difference between *pellucida* and the other species can possibly be ascribed to the comparative rarity of the former species on the collection site. Regarding *pellucida* too, however, the fact established above is also ascertainable, viz. that leaf-hoppers from which the parasite males had emerged and those containing female imagines are encountered simultaneously.

Furthermore, Table 3 shows distinctly that leaf-hoppers containing *Elenchus* males survice the emergence of the parasite, and that such leaf-hopper specimens, carrying empty puparia, during the later phase of the period of collection, exceed in number the leaf-hoppers containing *Elenchus* male puparia. The longest length of life, however, occurs in leaf-hoppers containing female Strepsiptera. After July 11 only 4 normal *pellucida* were encountered, against 29 parasitised. During July 7—11 the proportion of normal to parasitised specimens was 16: 39.

The long- and short-winged forms of *C. pellucida* are equally widely spread throughout Finland, but the long-winged seem to be more common. Among the material from Tvärminne all unparasitised specimens are long-winged, while among the infected 51 are long (75 %) and 17 short-winged (25 %). The limited extent of the material permits of no definite deduction as to stylopisation causing increased brachyptery, though such seems to be the case. If this is so we would have certain analogous conditions to those with *Chloriona*, where stylopisation, as is known, regularly caused brachyptery in the host.

A point emerging distinctly, in spite of the limited material, is the larger relative number of macropterous specimens present among leaf-hoppers infected by male Strepsiptera. The proportions are:

					f.	macr.	f.	brach.
Infected	by	the	male	Elenchus	42	(84 %)	8	(16%)
9	34	33	female	Elenchus	9	(50 %)	9	(50 %)

C. pellucida, therefore, conforms in this respect with Chloriona, Dicranotropis (p. 16) and C. straminea (p. 24). Reference to the possible explanation of this condition is made on page 16, Attention must be drawn at the same time, to the fact, that, when exceptionally the male *Elenchus*, emerges from an imago (in leaf-hoppers, Chloriona, Dicranotropis, in which the male parasite as a rule emerges from L_{v}), the imago specimen is always long-winged. Spec-

imens of leaf-hopper species parasitised by the male *Elenchus* in which the developed male parasite mainly emerges from imagines, are on the other hand in a large number of cases short-winged (*C. straminea, C. pellucida*).

In addition, in connection with the Table, the author wishes to point out that no larva of *pellucida* containing male Strepsipteron in the pupal or the imaginal stages were found. Specimens infected by male Strepsipteron larvae are not included in the material. There is, thus, a considerable dissimilarity among the Araeopids studied by the author, in view of the stage of development which the host has reached at the time of emergence of the male Strepsipteron. The following table can be compiled:

	e	Elenchus emerged from L_V		nchus ed from
Chloriona Dicranotropis	∞ 175	(approx. 100 %) (92.5 %)	1	(7.5 %)
C. straminea C. pellucida	3	101	42 50	(93.3 %) (100 %)

With regard to the stage of development of the host at the time the male *Elenchinus* emerges, the two *Calligypona* species thus show great mutual conformity, while *Dicranotropis* reveals a greater similarity with *Chloriona*. An explanation of these dissimilarities might be that the different species complete their development at varying rates, or during somewhat differing periods. The *Calligypona* species, as a rule, reach their imago stage when male Strepsiptera pupate, while the majority of *Chloriona* and *Dicranotropis* speciesness are still, then, in their last larval stage.

That it is characteristic of *Calligypona* species that specimens parasitised by male Strepsiptera reach the imago stage by the time the parasite emerges, is shown by earlier observations as well. AHLBERG (1935) reproduces a picture of a long-winged female of *C. pellucida* containing a male *Elenchinus*. Three *C. discolor* Boh. examined by the author (1939) and parasitised by male Strepsiptera, were imagines, as was a specimen of *C. albostriata* infected by

Table 3.

THE MATERIAL OF CALLIGYPONA PELLUCIDA FABR. FROM TVÄRMINNE 1945.

88 specimens.

20 normal specimens (all macropterous,: 8 33, 12 우우).

68 parasitised specimens.

18 by Elenchus ♀.

1 by El.-Q in larval stage (macropt. d).

17 by El.-♀ in pupal or imaginal stage (9 brachypterous,: 4 ♂♂, 5 ♀♀).

50 parasitised by Elenchus &.

0 by El.-3 in larval stage.

20 by El.-3 in pupal stage (17 macropt.: 8 33, 9 QQ; 3 brachypt.: 2 33, 1 Q). 30 by Elenchus 3, emerged from puparium (25 macropt.: 9 33, 16 QQ; 5 brach-5 QQ).

no larvae parasitised by Elenchus-J.

both male and female Strepsipteron, also described by the author (1943). HAUPT (1916), on the other hand, bred a male Strepsipteron — which he defined as *Elenchus walkeri* Curt., — from an *Achorotile albosignata* Dhlb. larva.

2. Exterior Morphological Changes due to Stylopisation.

The Normal Imago.

C. pellucida belongs to a group of related species differing from one another mainly in the dissimilarities in structure of their male genitalia. Both males and females are fairly varied in colour, a considerable difference obtaining between the light-coloured short-winged and the dark-coloured long-winged forms.

Male (Figs. 31-33): The wings of the macropterous form are transparent and extend by 1/3 beyond the apex of the abdomen; both thorax and abdomen are dark. The 1st and 2nd tergites, however, are mainly light in colour, the shield on the 2nd tergite dark. The 9th abdominal segment, stronger than the other segments, is roughly of the same length as the 7th and 8th together. The posterior margins of the 5th and 6th sternite are concave. The 4th to 6th sternites have more strongly chitinised lateral shields, the 7th and 8th a single shield. Ventrally, the 9th segment is equal in length to the 7th and 8th sternite together. The posterior margin of the 9th segment is concave, both dorsally and ventrally. The 10th to 12th segments extend into the concavity on the dorsal side; the styli (pa) protrude from the ventral concavity. They taper towards the tip, are somewhat twisted, and form an angle of approx. 150° with each other. The connective (c) is roughly of the same length as the styli. The proximal part of the penis (p) is broad, the distal somewhat narrower; the penis is bent and has a few small hooks. The ventral part of the 10th segment has an anteriorly-directed appendage (z) of hook-like shape, situated immediately behind the distal part of the penis.

The tegmina of the short-winged form almost extend to the apex of the abdomen, are brownish yellow in colour and not completely transparent.

Female (Figs. 34—35): The transparent wings of the long-winged female also extend slightly beyond the apex of the abdomen. The body is light or dark brown in colour. Both tergites and sternites are fairly strongly chitinised. The most central parts of the 7th and 8th tergites are more weakly chitinised. The posterior margins of the 7th and 8th sternites are decidedly inwardcurved; the more strongly chitinised parts of the sternites form lateral shields. The ovipositor is dark, the »bed» of the same light, with weak shading in the neighbourhood of the ovipositor. The 10th segment in part, the 12th in its entirety, is dark in colour. The structure of the three appendages is seen in Fig. 34. The median gonapophysis of the 9th segment has approx. 30 teeth.

C. pellucida Males Parasitised by the Female Elenchus.

The present material includes 6 *pellucida* male specimens parasitised by female Strepsiptera. Only one specimen — long-winged — contains the parasite at the larval stage; of the leaf-hoppers containing the parasite at the pupal or imaginal stage, two are long- and three short-winged. The proportion is entirely different from that in *Dicranotropis* and *straminea*, in which there are no macropterous specimens with the pupa or imago of the parasite among the material. The following table gives a comparison between the three species in question in this respect. The number of macropterous *pellucida* parasitised by the female *Elenchus* pupa or imago is particularly striking.

Males		parasite at	f. macr. at pupal	f. bra at larval	
		larval stage	or	stage	or
			imaginal stag	e :	imaginal stage
	Dicranotropis	17		24	51
	C. straminea	11		16	29
	C. pellucida	1	2		4

Females

Incomparison, a corresponding table for *pellucida* females is given below:

	parasite at larval stage	or	at larval stage		
Dicranotropis C. straminea C. pellucida	7 6	3	23 8	47 36 5	

The table of the females shows close conformity with that of the males, except that among *straminea* three long-winged specimens (as against 36 short-winged ones) contain *Elenchus* at the pupal or imaginal stage.

The morphological changes caused by stylopisation relate to the host's colouring and structure of its secondary sexual organs. The stylopised males — long- as well as short-winged — are considerably lighter than the normal ones. The tergites, as well as the lateral shields on the sternites, are weakly chitinised; in a couple of specimens there is only a weak shading anteriorly on the tergites. The shield on the 2nd tergite, characteristic of the male, is not developed; in its place there are two, somewhat more strongly chitinised spots, of the shape of a comma, at the base of the tergite. In the darker specimens the small spots of comma-like shape are more distinctly outlined.

The 9th abdominal segment is but weakly developed, ventrally oval, caudally concave, leaving room for the 10th segment. Medially-caudally the segment has a more or less shallow depression from which the greatly reduced penis protrudes. Apart from the penis, the styli of all the specimens studied are in the form of two small tuberculate formations. There is a difference also in the overall size of the 9th segment. Measured ventrally its length varies between 0.2 and 0.4 mm (cf. Fig. 35a—c). The author found no correlation between the degree of reduction of the genitalia and the extent of dark coloured area, or the structure of the tergite shield. On the basis of the limited material available the author has not established types characterised by the extent of the reduction of the organs. It is important to note that the specimen with the least developed 9th segment and the least developed. genitalia was parasitised by both male and female *Elenchus* (cf. below).

C. pellucida Females Parasitised by the Female Elenchus.

The material includes 12 *pellucida* females infected by the female *Elenchus*. Half of them are macropterous, half brachypterous.

It was mentioned above (p. 28) that the normal female is relatively light in colour. As regards colour, the stylopised specimens are no different from the normal. It is only in regard to the length of the ovipositor and, in connection with this, the shape of a number of sternites that the parasitised differ from the normal. Fig. 34 gives a ventral view of the abdominal segment of a normal female, Fig. 36 that of an parasitised specimen with an unusually short ovipositor. The ovipositor of the normal female is 0.9 mm, that of the parasitised varies between 0.35 and 0.53 mm. Among the present material 2 specimens have an ovipositor roughly 0.35—0.4 mm in length, and 10 specimens one approx. 0.45—0.53 mm long. The size of the concavities on the 5th to 8th sternites is related to the length of the ovipositor. The saw-teeth characteristic of the median gonapophysis of the 9th segment, in the parasitised specimens, vary in number between 6 (fig. 36) and 25. (In normal specimens the number is 30, p. 28).

Among the parasitised *pellucida* females are three specimens containing both the male and female *Elenchus*. An interesting fact about these specimens is that their ovipositor is more reduced than that of the other parasitised specimens (cf. above).

C. pellucida Imago Parasitised by the Male Elenchus.

The present material contains 50 *pellucida* specimens parasitised by the male *Elenchus* (19 males, 31 females). The long-winged specimens total 42, the short-winged 8. The majority (6) of the latter are females.

The morphological changes caused by stylopisation by males are similar to those caused by females. The size of the 9th segment of the males, as well as the abdominal appendages, vary within the same limits in each category of parasitised specimens. The same applies to the female genitalia. Nor can any stronger reduction of the organs be observed in the fairly numerous specimens of stylopised *pellucida* with several parasites (5 specimens with 2, 3 with 3 *Elenchus* males).

IV. The Parasite.

The author has bred male Strepsiptera from *Dicranotropis* and *Calligypona* straminea. All the specimens bred are clearly of one species. No male Strepsipteron was bred from *C. pellucida*, but it is assumed that the same species also parasitises this Araeopid.

The taxonomic definition of the present species of Strepsiptera has caused great difficulty, and still cannot be considered as established. This also seems to be the case with the taxonomic position of several species of the family Elenchidae described previously (cf. ULRICH 1927).

On the basis of male specimens from different parts of Europe the following species have been described (cf. ULRICH l.c. and HOFENEDER 1942—1943):

Elenchus (Stylops) tenuicornis Kirby 1815. — Host: Calligypona (Liburnia) sp., probably brevipennis Boh. — England.

Elenchus walkeri Curtis 1829. — Host: Calligypona (Liburnia) sp. — England.

Pseudelenchus carpathicus A. Ogloblin 1925. — Host: Dicranotropis divergens Kbm. — Russia.

Elenchinus delphacophilus Ahlberg 1925. — Host: Calligypona (Delphax) pellucida Fabr. — Sweden.

Elenchinus chlorionae Lindberg 1939. — Host: Chloriona glaucescens Fieb. and C. smaragdula Stål — Finland.

On the basis of female specimens certain *Elenchus* species have also been described. Åpart from the host species, certain characteristics of the cephalo-thorax have also been employed to characterise the species.

Elenchus dubius A. Ogloblin 1926. — Host: Calligypona (Liburnia) sp. — Bohemia.

Elenchus forcipatus A. Ogloblin 1926. — Host: Calligypona (Liburnia) forcipata Boh. — Bohemia.

Elenchus lugubrinus A. Ogloblin 1926. — Host: Calligypona (Liburnia) lugubrina Boh. — Habitat unknown.

OGLOBLIN (1925) established the genus *Pseudelenchus* with the new species *carpathicus*. The genus was characterised by its 4-jointed antennae. The genera previously established within the family *Elenchidae* had been believed to possess 5-jointed antennae. ULRICH (1.c.) found, in a male Strepsipteron emerged from *Chloriona glaucescens*, five antenna joints too. He emphasises that in cases in which a microscopic study has been carried out, *Elenchus* males have proved to have 4-jointed antennae; the branching-off from these is a process of the 3rd joint. Nor did the author (1939) distinguish more than 4 joints in the antennae of *chlorionae* established by him. That the number of the antenna joints has been recorded differently may be due to the fact that

specimens preserved in different ways look very different. On dried specimens, the process from the antennae really appears to form a separate joint.

On the basis of the above it seems probable that all the species so far established in our continent belong to the genus *Elenchus* Curt., characterised by 4-jointed antennae of similar structure. No structural differences seems to exist that would justify a distinction between the genera *Elenchus* and *Elenchinus* Pierce 1918. *Pseudelenchus* too falls within the genus *Elenchus*. Similar conclusions have been reached by BOHART (1941) in revising the taxonomy of North-American Strepsiptera; he refers all the genera attributed to the family Elenchidae to the original genus *Elenchus* Curt.

It is difficult to pronounce on the justification for differentiating the various species. It is certain, however, that the assumption, postulated above all by PIERCE (e.g. 1909), that every host species has a particular parasite species, is incorrect. The leaf-hoppers (several species of *Calligypona*, two *Chloriona* species, two *Dicranotropis* species, three *Criomorphus* species), known in Europe as hosts of Strepsiptera of the genus *Elenchus*, are so similar in their way of life and structure that their parasites may well belong to one species.

A certain difference in size seems to exist between the different *Elenchus* males described. A length of body of 1.5 mm has been recorded for *tenuicornis*, *delphacophilus* and *carpathicus*; of 1-1.2 mm for *walkeri*, and of 1.6 mm for *chlorionae*. The difference in length can be accounted for by the fact that measurements have been taken from specimens preserved in different ways. Variations in the size of body may also be due to a tendency to race formation in connection with adaptation to parasitism in different hosts.

Based on the very insignificant dissimilarities found (1939), the author has maintained the distinction between his *chlorionae* and AHLBERG's *delphacophilus*, although he now considers it probable that the two species are identical. The *Elenchus* species emerged from Araeopids treated in this paper are definitely referred to *delphacophilus*. However, this determination, as stated above, is preliminary. Two *Elenchus* males sent to the author by the Deutsches Entomologisches Institut (»Ostpreussen, Trasnitz, im Grase, leg. H. von Oettingen»), he has also referred to the same species. Although the name *delphacophilus* is employed, it must be pointed out that OGLOBLIN's species (*Pseudelenchus*) *carpathicus*, described the same year (1925) as *delphacophilus*, also belongs to the same species. Should it appear that all Araeopid parasites within a more extensive area belong to one and the same species, this should bear the name *E. tenuicornis* Kirby. HASSAN assumes that all *Elenchids* living on Araeopids belong to the same species. He also calls the species he studied, *tenuicornis* Kirby.

The Elenchus females found parasitising on Dicranotropis hamata, Calligypona straminea, and C. pellucida at Tvärminne, conform with the E. chlo*rionae* female. It is also considered possible that female Strepsiptera found on other Araeopids, in spite of the dissimilarities mentioned in the descriptions, may belong to the same species.

V. Summary.

In the areas covered by these entomological studies, Araeopids, to a greater extent than other leaf-hoppers, seem to be attacked by Strepsiptera. Apart from isolated stylopised specimens of different species, the author encountered, at Tvärminne in South Finland, infected populations of *Chloriona glaucescens* Fieb. and *C. smaragdula* Stål, of *Dicranotropis hamata* Boh. and *Calligypona straminea* Stål and *C. pellucida* Fabr. In the Canary Isles the author found, in January 1949, a population of *Calligypona striatella* Fall. parasitised by Strepsiptera.

From those cases where the parasite is identifiable it is evident that the Araeopids are attacked by species of the Strepsipteron genus *Elenchus* Curt. or other genera attributed to the family *Elenchidae* (HOFENEDER 1941—1943, cf. also p. 32).

It seems that the life-cycle — in South Finland — of Strepsiptera living on Araeopids with the same life-cycle as the *Chloriona* species (i.e. hibernation at larval stage), is similar to that of *Elenchus chlorionae* Lindb. living on these leaf-hoppers (cf. LINDBERG 1939). The effect the stylopisation has on the development of the host is also likely to be roughly the same. As with *Chloriona*, the length of life of the parasitised leaf-hoppers exceeds that of the healthy. In all known cases the female Strepsipteron reaches its imaginal stage in the adult leaf-hopper. It thus exists as an imago from the beginning of July for about a month. During this period it is fertilised and gives birth to the viviparous larvae. After the birth of the Strepsipteron larvae the host dies.

There are considerables differences between the life histories of different Strepsiptera. Male *Elenchus chlorionae* larvae regularly pupate and emerge as imagines from the last larval stage of the host (*Chloriona*). When the host is *Dicranotropis*, the male *Elenchus* usually emerges as an imago from L_v , but sometimes the *Dicranotropis* completes its metamorphosis before the parasite emerges. With *Calligypona* species as host, on the other hand, conditions are different. In *C. pellucida*, for example, no case was found of a larva housing a Strepsipteron puparium. In *C. straminea*, as an exception, the imago parasite emerged from the host, in the last larval stage, though more usually emergence was delayed until the host had completed its metamorphosis. In all species examined the male *Elenchus* emerges from the imago during the first fortnight in July, and the host survives the emergence of the parasite by some time.

It can be stated of all the species studied that stylopisation causes complete castration of the host. The primary genitalia in stylopised *Chloriona* were

found to be greatly reduced; all the specimens of every species studied reveal changes in the structure of the secondary sexual organs. The reduction of these organs varies within fairly wide limits, in such a way however, that in a number of species it is relatively strong, in others less. The greatest variations in reduction are shown by the *Chloriona* species. Among stylopised female imagines there are specimens with a very well developed ovipositor, and specimens with no ovipositor at all. Among the males these are specimens with weakly developed but still distinct genitalia, along with specimens in which the genitalia are completely absent. The most strongly reduced males and females reveal great similarity with each other (cf. LINDBERG 1939, p. 133).

Such intermediate forms were not found in other species, but all stylopised specimens of these species have distinct male or female characteristics; the females e.g. have always a more or less developed ovipositor. The stylopised specimens (including males), however, have a somewhat appearance because of the weaker development in pigmentation generally strong in males, and of the swelling of the abdomen containing the parasite (cf. also HASSAN 1939). In no other species has any equivalent been found to the condition obtaining in *Chloriona* — that a colour characteristic of the normal leaf-hopper (for *Chloriona*, green) has not developed in the stylopised specimen.

Morphological changes can also be observed in the rudiments of the exterior genitalia of the last stage host larva.

One of the most characteristic features of the stylopisation of *Chloriona* is the brachyptery of the host regularly caused by the infection. This constant feature in *Chloriona* is not present in the other Araeopids studied. The following table, an extract from Tables 1—3, giving the number of the male and female imagines parasitised by female and male *Elenchus* illustrates these facts.

		otropis				llucida
	f.macr.	f.brach.	f.macr.	f.brach.	t.macr.	f.brach.
Males parasitised by female Elenchus Females parasitised by	17	75	11	45	3 .	4
female Elenchus	7	70	9	44	6	5
Males parasitised by male Elenchus	10		13	8	17	2
Females parasitised by male Elenchus	y 4		14	7	25	6
Total	38	145	47	104	51	17
	(21.4%)	(78.6%)	(31.1%)	(68.9%)	(75%)	(25%)
Normal males	10	31	10	20	8	
Normales females	31	177	31	52	12	
Total	41	208	41	72	20	
	(15.8%)	(84.2%)	(36.3%)	(63.7%)	(100%)	

As is shown by a comparison of the percentages of long- and short-winged among the infected and the normal, no increase in brachyptery can be established due to Strepsipteron infection within the *Dicranotropis* and *C. straminea* populations. The case may be different with *C. pellucida* (see p. 27).

As mentioned above, it is particularly striking that among species which are commonly parasitised by *Elenchus*, where the host reaches the imago stage before the emergence of the parasite, these host imagines are either exclusively long-winged (*Dicranotropis* and *Chloriona*) or include a majority of long-winged specimens (*C. straminea*, *C. pellucida*).

The question of the extent to which an infection by Strepsiptera is fatal to a population of leaf-hoppers, has been discussed (cf. LINDBERG 1939, p. 155). As mentioned in the introductory note to this paper (p. 7), it seems probable that populations of *Dicranotropis hamata*, *Calligypona straminea*, and *C. pellucida* attacked in 1945 by *Elenchus* disappeared owing to the extremely widespread attacks by Strepsiptera.

If the practical difficulties can be overcome, great economic value may be derived from the use of Strepsiptera in combating infestations by leaf-hoppers pests. The collection and transference of leaf-hoppers containing Strepsipteron females from an area of high incidence of parasites to an area where the leaf-hopper attack is heavy might well prove practical, and would expose the leaf-hopper pest population to attack by the numerous L_1 Strepsiptera larvae. The fairly wide range of host-selection in Strepsiptera would increase the practical value of this, since it would make possible control over a range of related species.

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EXPLANATION OF THE PLATES.

Plate I. Dicranotropis hamata Boh. — 1. Abdomen of normal male, dorsal view. — 2. The same, ventral view. — 3. Genitalia of normal male. — 4. Abdomen of normal female, ventral view. — 5. The same, dorsal view. — 6. Genitalia of normal female: a gonapophysis of 8th abdominal segment, b median appendage of 9th segment, lateral view, c the same, ventral view, d gonapophysis of the 9th segment. — 7. Abdomen of stylopised male (parasitised by *Elenchus* male), dorsal view, type 3. — 8. The same, type 2. — 9. Apex of Abdomen of stylopised male, ventral view: a type 1, b type 2, c type 3.

p penis, pa paramer, s connective, z teeth on the 10th segment, za teeth on the paramers, 2-12 abdominal segments.

Plate II. Dicranotropis hamata Boh. — 10. Genitalia of stylopised male (parasitised by *Elenchus* female), ventral view. — 11. Abdomen of stylopised female, ventral view. — 12. The same, less reduced type. — 13. Genitalia of stylopised female: a median appendage of 9th segment, b gonapophysis of 8th segment. — 14. Abdomen of stylopised male (parasitised by *Elenchus* male), ventral view, less reduced type. — 15. The same, the most reduced type. — 16. Postnotum and 1st—3rd tergites of stylopised male: a the most reduced type, b less reduced type. — 17. Abdomen of stylopised female, ventral view. — 18. Apex of abdomen of stylopised larvay (parasitised by *Elenchus* male), ventral view. ppenis, pa paramer, c connective.

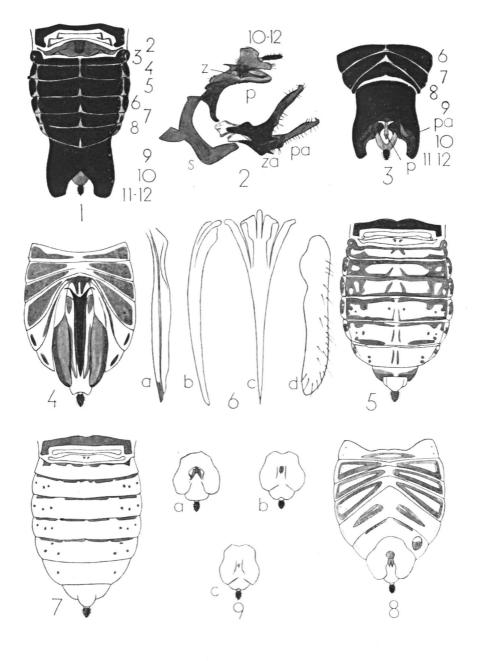
Plate III. Calligypona straminea Stål. — 19. Abdomen of normal male, dorsal view. — 20. The same, ventral view, — 21. Genitalia of normal male. — 22. Abdomen of normal female, ventral view. — 23. Genitalia of normal female: a median appendage of 9th segment, b gonapophysis of 9th segment, c the same of 8th segment. — 24. Apex of abdomen of stylopised male, ventral view, type 1. — 25. The same, type 2. — 26. The same, type 3. — 27. Apex of abdomen of stylopised male, ventral view. — 29. Genitalia of stylopised female: a median appendage of 9th segment, b gonapophysis of 9th segment, c the same of 8th segment. — 28. Abdomen of stylopised female, ventral view. — 29. Genitalia of stylopised female: a median appendage of 9th segment, b gonapophysis of 9th segment, c the same of 8th segment. — 30. Apex of abdomen of stylopised larva (parasitised by *Elenchus* male), ventral view.

p penis, pa paramer, s connective, z teeth on the 10th segment, 7-12 abdominal segments.

Plate IV. Calligypona pellucida Fabr. — 31. Abdomen of normal male, dorsal view. — 32. The same, ventral view. — 33. Genitalia of normal male. — 34. Abdomen of normal female, ventral view. — 35. Genitalia of normal female: a median appendage of 9th segment, b gonapophysis of 8th segment, c the same of 9th segment. — 36. Abdomen of stylopised female, ventral view. — 37. Apex of the abdomen of stylopised male. — 38. The same, more reduced type. — 39. The same, the most reduced type. — 40. Median appendage of 9th segment of stylopised female.

p penis, pa paramer, c connective, z teeth on the 10th segment, 5-9 abdominal segments.

Plate I.





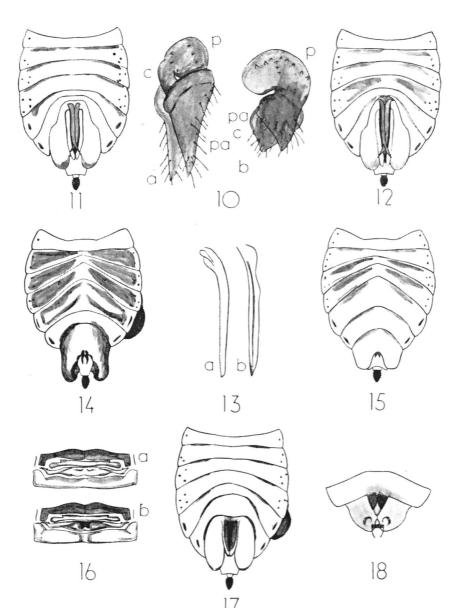


Plate III.

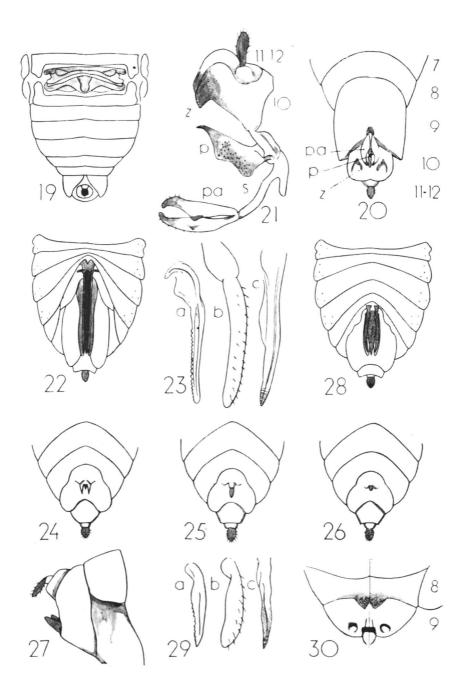


Plate IV.

