On Growth Processes in the Antennae of Insects.

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With 1 Text-figure.

CONTENTS.

1. INTRODUCTION.

IT is well known that in many insects with incomplete metamorphosis, and also in the Thysanura among ametabolous forms, increase in the number of the component parts of the antennae takes place during post-embryonic development. Data relating to the growth processes by means of which these additional elements are formed are, however, extremely scanty, and the present communication will serve to draw attention to the subject.

In a previous paper (Imms, 1939) it was shown that the antennae of insects (and of other Arthropoda) are divisible into two types, viz. segmented antennae and annulated antennae. In the first type the antenna is composed of a variable number of segments, each possessing intrinsic musculature. This type of antenna prevails in the Collembola and the Thysanura Entognatha (Campodea, Japyx, &c.). The second type of antenna is composed of a basal segment or scape which carries distally an annulated flagellum. Intrinsic muscles originate within the scape, and are inserted on to the base of the flagellum whose component parts or annuli are devoid of any musculature. It follows, therefore, that the flagellum is only capable of movement as a whole and this is effected by means of intrinsic muscles located within the scape. This type of antenna is found in the Thysanura Ectognatha (Machilis, Lepisma, &c.) and in the whole of the Pterygota. It is, therefore, the characteristic insectan antenna.

The occurrence of segmented antennae throughout the Myriapoda, and in some of the lower groups of Crustacea, points to the conclusion that this type of appendage is the more primitive of the two kinds. It may, furthermore, be reasonably claimed that the annulated type of antenna is a derivative of the segmented appendage. If these contentions are true it will be apparent that the annuli, or separate components of the flagellum, are probably of a different morphological value to the segments or musculated divisions of the more primitive type of antenna. In order to investigate this problem it is necessary to consider any significant growth changes that occur in the antennae, both before and after successive ecdyses, among certain of the lower orders of insects.

2. Growth in Segmented Antennae.

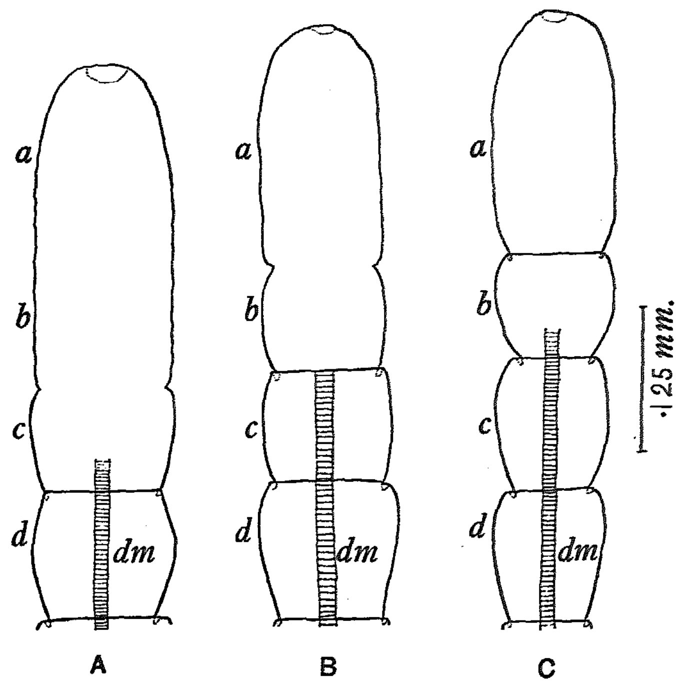
The growth process in segmented antennae has not been previously described, but may be tolerably clearly observed in species of Campodea. Thus, in Campodea lankesteri Silv. progressive stages in this process are represented in Text-fig. 1. It will be seen that the zone of growth is apical or acrogenous, and is consequently restricted to the terminal segment of the antenna. This segment develops a furrow which gradually becomes more pronounced and ultimately demarcates a proximal area or new segment. This latter region gradually increases in size, develops the typical chaetotaxy, and later acquires the intrinsic musculature. Renewed growth of the apical segment results in the demarcation of further new segments and this process goes on during successive instars until the full number of antennal segments is ultimately acquired.[1]

3. Growth Processes in Annulated Antennae.

In the majority of Pterygota in which an increase in the

[1] Regeneration of fractured antennae apparently takes place partly in a similar manner to the process described above.

number of antennal parts occurs during post-embryonic growth, this increase is effected by means of a division of the second



TEXT-FIG. 1.

Antennal growth in Campodea: A, B, and C progressive stages. In A, the demarcation of segment *b* from the apical segment *a* is not yet evident: segment *c* is clearly indicated while segment *d* is nearly fully grown. In B, segment *b* has become marked off from the apical segment *a*, segment *c* is nearly fully grown, and segment *d* has attained its full dimensions. In C, segment *b* is nearly fully grown while segments *c* and *d* are complete. The median dorsal longitudinal muscle (*dm.*) has been drawn under polarized light.

annulus. A very full account of this method of antennal growth was given by Fuller (1920) who investigated twelve species (belonging to ten genera) of South African termites. In the abstract the process is simple and represents the development of new elements between annuli III and IV. The new elements are ordinarily added two by two, the distal one being always longer and in a more advanced condition than the proximal. In some antennae, according to Fuller, the addition appears to be one by one, but this is only because the proximal number of a pair is more delayed in its development than usually happens. All multiplication of antennal parts ceases with, or soon after, the third ecdysis.

In the first instar of the Acrididae, or short-horned grasshoppers, the antennae usually consist of thirteen component parts—a basal segment or scape, followed by twelve annuli. In the imago the number of these parts ranges from about eighteen up to twenty-eight. The latter figure, according to Uvarov (1928), appears to be the maximum found in this family. The

TABLE 1.

I	II	III	IV	V	A	I′
13	17	20	22	24	25	13
12	16	19	21	23	24	12
11	15	18	20	22	23	11
10	14	17	19	21	22	10
9	13	16	18	20	21	9
8	12	15	17	19	20	8
	11	14	16	18	19	
7	10	13	15	17	18	7
	9	12	14	16	17	
6	8	11	13	15	16	6
	7	10	12	14	15	
5	6	9	11	13	14	5
		8	10	12	13	
4	5	7	9	11	12	4
		6	8	10	11	
	4	5	7	9	10	
			6	8	9	
3		4	5	7	8	
				6	7	
	3		4	5	6	3
		3		4	5	
			3		4	
				3	3	
2	2	2	2	2	2	2
1	1	1	1	1	1	1

Showing the increase in number of antennal 'segments' at each instar in the locust Dociostaurus maroccanus. From Paoli. A, adult; I and I′, first instar: II–V, second to fifth instars. 1 is the basal segment.

addition of annuli takes place by the simple division of certain of the original components. This process has been best studied by Paoli (1937) in the locust Dociostaurus maroccanus and it will be seen on referring to Table I that, by the successive division of the second annulus, in each instar up to the imago, eight annuli are produced. There appears to be some variability as to the origin of each of the remaining annuli. According to Paoli only the original fifth, sixth, seventh annuli of the first instar subdivide whereas in Chopard's Fig. 26 it will be seen that each annulus up to the seventh undergoes subdivision. In Locusta migratoria migratorioides Takahasi (1925) describes a similar method of increase of the antennal parts; in the first instar each of the annuli from the second to the seventh undergoes division into two components. The multiplication of parts in the subsequent instars is confined to second and third or second to fourth annuli. In the Phasmidae a very similar process takes place except that, according to Ling Roth (1917), who investigated Carausius morosus, each 'segment' from the fourth to the tenth, or last, undergoes subdivision. Ling Roth's numeration is not strictly accurate, his fourth 'segment' being, in fact, the third. This latter part, which is the second annulus of the present nomenclature, divides into ten distinct annuli by the time the last ecdysis has taken place. The repeated division of the second annulus is in accordance with what happens in other Orthoptera. Thus, in Periplaneta Bugnion (1921) states that at the time of eclosion from the egg the antenna consists of 47 'articles': in the imago the number is about 170 and this augmentation is brought about by the successive division of the third 'article' (or second annulus). According to Chopard (1938) it also obtains in the families Gryllidae and Tettigoniidae.

Among the Mantidae Bugnion (1921 *a*) states that in Empusa egena Charp. growth similarly takes place by means of the repeated division of the third 'segment' (second annulus) and also by the secondary division of some of the newly formed elements. The fifteen terminal annuli, which exist from the time of eclosion from the egg, never undergo division.

Qadri (1938) has contributed some observations on antennal growth in Blatta orientalis. He describes the process as one of the simultaneous separation of two 'joints' from the third 'joint' (second annulus). This process of multiplication goes on until the fourth instar, and no further additions to the number of antennal joints were observed in nymphs in the fifth and sixth instars. In the males, however, one or two pairs of new annuli are differentiated from the second annulus prior to the final ecdysis into the adult. The second annulus in the male is consequently shorter than the corresponding part in the female. A similar process of antennal growth from a formative region in the second annulus has been observed by the same author in Lepisma saccharina and Petrobius maritimus among Thysanura; in Ephemera vulgata and in the Plecopteron Nemoura variegata.

Among the Odonata the antenna, in the first instar nymph, consists of a scape and two annuli; while in the last nymphal instar the number of annuli is usually six and more rarely five. According to Tillyard (1917) the second annulus divides in successive instars, resulting in the production of four new annuli. In those forms wherein six annuli are developed, and they are the majority, this condition is brought about by the division of the fifth annulus into two components. This statement of Tillyard's is confirmed by the observations of Calvert (1934) on the development of the nymphal instars of the dragonfly Anax junius, and of those of Balfour-Browne (1909) on nymphs of Coenagrion and other genera.

Among Hemiptera, in the Coccid Trionymus sacchari Uichanco and Villaneuva (1932) state that the third antennal 'segment' in the first, second, and third instars of female nymphs, which bear '6-segmented' antennae, is apparently in a transitional state and divides in the fourth and later instars, ultimately giving rise to the maximum number of 'segments' in the adult. Whether the female adult has seven or eight 'segments' in the antennae depends upon the resulting number of daughter 'segments' produced from this earlier third 'segment'. Dr. H. C. James informs me that an examination of females of Pseudococcus longispinus, which have only four instars, supports the foregoing opinion in that the full number of 'segments' appears to be acquired by the division of the third 'segment'.

In the mayfly Chloeon dimidiatum Lubbock (1864) found that new antennal parts are formed by the division of the original third 'segment'. Ide (1935) states that in Stenonema canadense and other mayflies new parts do not arise in the manner described by Lubbock, but by a differentiation of 'segments' from the proximal end of the 'unsegmented flagellum'. The new elements, he states, are formed distally to those added in the previous instars. While the 'flagellum' of Ide and the 'third segment' of Lubbock are names for the same original antennal part it seems possible that the actual process of antennal growth differs somewhat among different members of the Ephemeroptera.

4. Discussion.

It will be evident from the foregoing remarks that when new component parts are added in the case of annulated antennae they are formed by the division of the 'third segment' or second annulus. This process has been recorded in the majority of the so-called exopterygote orders of insects. On the other hand, in the Acrididae and Phasmidae, among Orthoptera, all the remaining annuli may also undergo subdivision. In some Odonata the fifth annulus may also divide into two components. In all cases, however, the first annulus, or pedicel, never undergoes subdivision. It is, therefore, possible that this component is to be regarded as homologous with a segment of the segmented type of antenna which has lost its intrinsic musculature. Whatever the proper morphological status of the pedicel may be it is noteworthy that in insects with annulated antennae it has become the seat of the peculiar proprioceptive organ known as Johnston's organ. There appears to be, indeed, a positive correlation between the presence of Johnston's organ in annulated antennae and its absence in segmented antennae. Thus, I find that it is absent in Campodea, Japyx, and Heterojapyx among the Thysanura Entognatha and in all Collembola. On the other hand, it is present in practically all the Pterygota and, according to Eggers (1928), in the Thysanura Ectognatha also—a fact which may perhaps ultimately lead the way to solving the problematic functions of this organ. It would seem that, in some manner or other, it may be concerned with the perception of forces which exercise strain or tension on the antennal flagellum, which is only movable by means of basal muscles. This type of antenna, whose component parts have no means of individual adjustment to any external forces of displacement, is in sharp contrast with segmented antennae where each segment is individually movable by means of intrinsic muscles.

In the case of segmented antennae the addition of new components would be difficult to achieve by the methods of growth just described owing to the presence of their intrinsic muscles. On the other hand, the process of acrogenous growth referred to in Campodea results in the gradual acquisition of new segments together with their intrinsic musculature.

5. Conclusions.

The addition of new components in the segmented type of insect antenna, as shown in Campodea, is by means of acrogenous growth. The apical segment develops a furrow which, becoming more pronounced, demarcates a proximal area or new segment. Continued growth of this kind results in the formation of further new segments until the full number is ultimately acquired. The intrinsic muscles of the new segments are acquired as each segment becomes formed.

New components in the annulated type of insect antenna are formed by the division of the second annulus or so-called 'third segment' from the base. In certain of the Orthoptera and Odonata some, or all, of the remaining annuli also divide and thus give rise to additional annuli.

There is a positive correlation between the presence of Johnston's organ in the pedicel of annulated antennae and its absence in segmented antennae. This fact suggests that it is, in some way or other, concerned with the perception of forces or stimuli affecting the antennal flagellum as a whole.

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