

ON GROWTH PROCESSES IN THE DRAGONFLY ANTENNA

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Three types of growth pattern in the odonate antenna are described. These differ from each other in the order in which the unique division (A) of the apical segment, and the 3 successive divisions (B) of the basal segment of the flagellum take place during larval development. These types correspond to higher taxa of the Order, viz (1) the B.B.B.A type is found in the *Coenagrionidae*, *Petaluridae* and *Aeshnidae*; (2) the B.A.B.B type in *Cordulidae* and primitive *Libellulidae*; (3) the B.B.A.B. type in higher forms of *Libellulidae*, with a transitional type between (2) and (3) in some symptetrine species. In this respect the Order can be divided into 2 groups: *Zygoptera-Petaluridae-Aeshnidae* on one hand, *Corduliidae-Libellulidae* on the other.

INTRODUCTION

The antenna of newly hatched odonate larvae is composed of three segments, namely from basal apicalwards, the scape, the pedicel and the flagellum, while that of full grown larvae is composed of seven segments, the scape, the pedicel and five segments of the flagellum, except in the *Calopterygidae*, some *Coenagrionidae*, *Epiophlebiae*, *Petaluridae*, and *Gomphidae*, in which the number of antennal segments is more reduced.

IMMS (1940) stated that in Odonata the antenna grows in such a way that the second annulus (= the basal segment of the flagellum) divides in successive instars, resulting in the production of four new annuli (= three segments of the flagellum), and the final division occurs in the fifth annulus (= the apical segment of the flagellum). He referred to investigations of TILLYARD (1917), BALFOUR-BROWNE (1909) and CALVERT (1934), which are principally concerned with the primitive forms of the Order. However, growth processes, different from Imms' statement, were further reported for several species in different

genera, referable to a number of families (subfamilies) (NEVIN, 1929; MÜNCHBERG, 1938; BICK, 1941, 1951; GARDNER, 1950, 1951a, 1951b, 1953, 1954; KORMONDY, 1959; ANDO & MIYAKAWA, 1969; MIYAKAWA, 1970, 1971; KUMAR, 1972).

The present paper describes growth processes in the antenna of some anisopteran species and reviews data on 33 dragonfly species so far known to the author.

MATERIAL AND METHOD

A number of series of exuviae of cultured larvae were examined and, whenever possible, living larvae were observed. The following species were studied: *Petaluridae*: *Tanypteryx pryeri*; — *Aeshnidae*: *Aeshna juncea*, *A. nigroflava*, *Anaciaeschna martini*, *Anax nigrofasciatus*, *A. parthenope julius*; — *Corduliidae*: *Epithea bimaculata sibirica*, *Somatochlora viridiaenea viridiaenea*, *S. v. atrovirens*; — *Libellulinae*: *Lyriothemis pachygastra*, *Orthetrum japonicum japonicum*, *Libellula quadrimaculata asahinai*; — *Sympetridae*: *Sympetrum speciosum*; — *Trithemiinae*: *Pseudothemis zonata*; — *Pantalinidae*: *Pantala flavescens*.

RESULTS AND DISCUSSION

B.B.B.A TYPE

Figure 1

In *Anax nigrofasciatus*, the first division of the antennal segment occurred at $\frac{1}{3}$ from the base of the flagellum at ecdysis to the third instar, the second division at $\frac{1}{2}$ of the basal segment of the flagellum at ecdysis to the fifth instar, the third division at $\frac{3}{5}$ of the basal segment of the flagellum at ecdysis to the 8th instar, and the fifth (final) division at about $\frac{1}{2}$ of the most apical segment of the flagellum at ecdysis to the ninth instar, thus forming finally a 7-segmented antenna.

In this species, therefore, the segmentation of the antenna occurs through the larval development, in a successive series, in the basal, basal, basal and apical segments of the flagellum. This mode of segmentation will be called B-B-B-A type.

The same mode was observed in *Aeshna juncea*, *A. nigroflava*, *Anaciaeschna martini* and *Anax parthenope julius*.

This type of antennal development was reported by early workers in *Coenagrion pulchellum*, *C. puella*, *Pyrrhosoma nymphula*, *Ischnura elegans* (BALFOUR-BROWNE, 1909) and *Anax junius* (CALVERT, 1934) and was generalized by TILLYARD (1917) and IMMS (1940) for the whole Order.

The antennae of petalurids usually consist of six segments in the final instar,

whereas those of *Tachopteryx thoreyi* are 7-segmented (NEEDHAM & WESTFALL, 1955). In *Tanypteryx pryeri*, the number of antennal segments increases from three to six during larval development, exclusively by divisions of the basal segment of the flagellum as reported previously (ANDO & MIYAKAWA, 1969).

A similar growth pattern of 6-segmented antennae was reported for *Coenagrion hastulatum* (GARDNER, 1954), and for *Erythromma najas* and *Enallagma cyathigerum* (BALFOUR-BROWNE, 1909). Consequently, in these species the growth type of the antenna is indicated as the B.B.B.O type. This is apparently a variation of the B.B.B.A type, owing to the lacking of the final division in the apical segment of the flagellum.

B.A.B.B TYPE

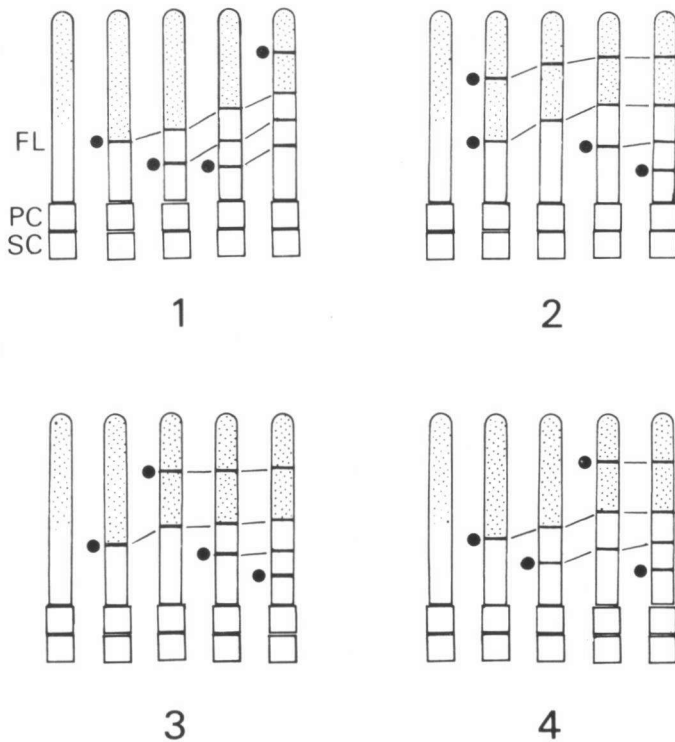
Figures 2-3

In *Epitheca bimaculata sibirica*, the first segmentation of the antenna occurred at two points in the flagellum at ecdysis to the third instar, thus simultaneously forming three segments of the flagellum. Then, two successive divisions occurred exclusively at the basal segment of the flagellum at ecdysis to the sixth and to the eighth instar (Fig. 2). Therefore, this will be named B:A.B.B type, a variation of the B.A.B.B type as described below.

In *Somatochlora v. viridiaenea* and *S. v. atrovirens*, the first division of the antennal segments took place at a basal portion of the flagellum at ecdysis to the third or to the fourth instar, the second division at a median portion of the apical segment at ecdysis to the fourth or to the fifth instar, the third division at the basal segment at ecdysis to the seventh or to the eighth instar, as reported in a previous paper (MIYAKAWA, 1971). This mode of growth pattern is the B.A.B.B type.

In *Libellula quadrimaculata asahinai*, the first division of the antennae appeared at $\frac{1}{3}$ from the base of the flagellum at ecdysis to the third instar, the second division at $\frac{1}{2}$ of the apical segment at ecdysis to the fourth instar, the third division at a median but slightly apical portion of the basal segment at ecdysis to the fifth instar, and the fourth (final) division at $\frac{1}{2}$ of the basal segment of the flagellum at ecdysis to the eighth instar (Fig. 3), thus showing the B.A.B.B type.

Similar processes were observed in *Orthetrum j. japonicum*, and were reported for *Libellula depressa* (GARDNER, 1953) and in *Sympetrum fonscolombei* (GARDNER, 1951).



Figs. 1-4. Diagram illustrating the four growth types of odonate antennae. (Black circles indicate the newly formed joint; FL – flagellum, PC – pedicel, SC – scape): (1) *Anax nigrofasciatus* (B.B.B.A type); – (2) *Epietheca bimaculata sibirica* (B:A.B.B type); – (3) *Libellula quadrimaculata asahinai* (B.A.B.B type); – (4) *Pseudothemis zonata* (B.B.A.B type).

B.B.A.B TYPE

Figure 4

In *Sympetrum speciosum*, the first division of the antennae occurred at $\frac{1}{3}$ from the base of the basal segment of the flagellum at ecdysis to the third instar, the second division at $\frac{3}{5}$ of the basal segment at ecdysis to the fifth instar, the third division at about $\frac{1}{3}$ of the apical segment at ecdysis to the sixth or the seventh instar and the fourth (final) division at $\frac{3}{5}$ of the basal segment of the flagellum at ecdysis to the eighth instar.

A similar situation was found in *Pseudothemis zonata* (Fig. 4) and *Pantala flavescens*.

This mode of antennal growth process will be called B.B.A.B type.

GARDNER (1951b), studying the life-history of *Sympetrum danae*, found that in the second division the number of flagellar segments increases from two to four at ecdysis to the fifth (according to his count, the sixth) instar, due to the simultaneous divisions of the basal and apical segments. This mode of antennal growth pattern may be indicated as the B.A:B.B type or B.B.A.B type, a transitional type between B.A.B.B type and B.B.A.B type. KINOSHITA & OBI (1931) reported a similar situation in *S. frequens*. The same is possibly true for *S. sanguineum* (GARDNER, 1950), *S. pedemontanum* (MÜNCHBERG, 1938) and *S. vicinum* (NEVIN, 1929).

BICK (1941, 1951) clearly mentioned that in *Erythemis simplicicollis* and *Tramea lacerata* the third division of the antenna takes place in the apical segment, whereas the first, the second and the fourth division occur in the basal segment of the flagellum, thus showing the B.B.A.B type.

POSSIBLE OTHER TYPES

Recently KUMAR (1972) studied the life-history of *Trithemis festiva*. The final division of the antennal segment of this species occurred in the last segment of the flagellum. On the other hand, his figures 7 and 9 suggest that the second division of the antenna took place in the apical segment of the 2-segmented flagellum, thus representing the B.A.B.A type. This, however, would be an exceptional type, since no other case of the apical segment of the antenna dividing twice has ever been brought on record in dragonflies.

KORMONDY (1959) examined the life-history of several *Tetragoneuria* species. In *T. cynosura* the earliest divisions of the antenna occurred at two points in the flagellum at ecdysis to the third instar, forming three segments in total, the second division in an intercalary segment of the flagellum at ecdysis to the sixth instar, and the third division at the most apical segment of the flagellum at ecdysis to the eighth instar. This description agrees well with the situation in *E. bimaculata sibirica* in the earliest divisions of the antenna, but it disagrees in the two successive divisions. Since no other case of an intercalary segment of the flagellum participating in the production of new segments has ever been reported in dragonflies, we believe that the species probably has the same pattern as *E. bimaculata sibirica*.

CONCLUDING REMARKS

The growth patterns in the odonate antenna, so far quoted, are listed in Table I.

It is likely that generally in the Order the most basal segment of the flagellum of the antenna possesses a growth center to produce three new segments successively through postembryonic development as was stated by IMMS (1940).

Table I
Growth processes in the odonate antenna

Species	Instar No. ¹ just after formation of new segment				No. of final instar	References
	from the basal segment of the flagellum		from the apical segment			
Coenagrionidae						
<i>Coenagrion hastulatum</i> (Charp.)	2	3	5		10	GARDNER, 1954*
<i>C. puella</i> (Linn.)	3	3	5	10	10-13	BALFOUR-BROWNE, 1909
<i>C. pulchellum</i> (Vander L.)	2	3	5	10	10-13	BALFOUR-BROWNE, 1909
<i>Enallagma cyathigerum</i> (Charp.)	2	3	5		10-12	BALFOUR-BROWNE, 1909
<i>Erythromma najas</i> (Hans.)	2	3	5		10-14	BALFOUR-BROWNE, 1909
<i>Ischnura elegans</i> (Vander L.)	2	3	5	10	12	BALFOUR-BROWNE, 1909
<i>Pyrrhosoma nymphula</i> (Sulz.)	2	3	5	10	11-12	BALFOUR-BROWNE, 1909
Petaluridae						
<i>Tanypteryx pryeri</i> (Selys)	3	5	8		14	ANDO & MIYAKAWA, 1969
Aeshnidae						
<i>Aeschna juncea</i> (Linn.)	2	5-7	8	9-10	13	present paper
<i>A. nigroflava</i> (Martin)	2-3	4	5-6	7-8	13	present paper
<i>Anaciaeschna martini</i> (Selys)	2-3	4	7	9	?	present paper
<i>Anax junius</i> (Drury)	2	5	8	9	13	CALVERT, 1934
<i>A. nigrofasciatus</i> Oguma	3	5	8	9	13	present paper
<i>A. parthenope julius</i> Brauer	3	5	7	10	12	present paper
Corduliidae						
<i>Epitheca bimaculata sibirica</i> (Selys)	3	5-6	7-8	3	12?	present paper
<i>E. cynosura</i> (Say)	3	6?	9?	3	12	KORMONDY, 1959
<i>Somatochlora viridiaenea</i> <i>viridiaenea</i> (Uhler)	3-4	5-6	7-8	4-5	12	MIYAKAWA, 1971
<i>S. v. atrovirens</i> (Selys)	3-4	5-6	7-8	4-5	12	MIYAKAWA, 1971
Libellulidae						
Libellulinae						
<i>Libellula depressa</i> Linn.	3-4	5-6	7-8	4-5	12-13	GARDNER, 1953*
<i>L. quadrimaculata asahinai</i> Schmidt	3	5	8	4	?	present paper
<i>Lyriothemis pachygastra</i> (Selys)	3	5	7	4	10-11	MIYAKAWA, 1970
<i>Orithetrum japonicum japonicum</i> (Uhler)	3	5	8	4	?	present paper
Sympetrinae						
<i>Erythemis simplicicollis</i> (Say)	3	6	9	8	13	BICK, 1941
<i>Sympetrum danae</i> (Sulz.)	3	5	7	5	10	GARDNER, 1951b*
<i>S. fonscolombei</i> (Selys)	3	5	7	4	11	GARDNER, 1951a*
<i>S. frequens</i> (Selys)	3	5	7	5	10	KINOSHITA & OBI, 1931
<i>S. pedemontanum</i> (Allioni)	2	3	6	5	10	MÜNCHBERG, 1938
<i>S. sanguineum</i> (Müll.)	2	3	6	4	9	GARDNER, 1950*
<i>S. speciosum</i> (Oguma)	3	5	8	6-7	10	present paper
<i>S. vicinum</i> (Hagen)	3-4	5	7	5-6	11	NEVIN, 1929
Tritheminae						
<i>Pseudothemis zonata</i> (Burm.)	3	5	8	7	12	present paper
<i>Trithemis festiva</i> (Ramb.)	2	4	6?	3	10	KUMAR, 1972*
Pantaliinae						
<i>Pantala flavescens</i> (Fabr.)	3	5	6-7	6	?	present paper
<i>Tramea lacerata</i> (Hagen)	3	4	6	5	10	BICK, 1951

¹ Instar number does not include the prolarval stage.

* Prolarva counted as first instar.

Another growth or division center exists in the most apical segment of the antennal flagellum and the center once makes its division into two new parts. The difference of the growth patterns in the antenna of Odonata depends on the time of operation of the growth center in the apical segment, relative to that of the growth center in the basal segment of the flagellum.

In Zygoptera, the apical growth center operates later than the basal growth center in the postembryonic development. The same is true for primitive Anisoptera, *Petaluridae* and *Aeshnidae* (B.B.B.A type). In some cases the apical growth center does not operate until the end of the larval period (B.B.B.O type).

On the other hand, representatives of the *Corduliidae* show a different pattern. The apical growth center is active and operates at a very early stage of larval development simultaneously with or a little later than the first operation of the basal growth center, and prior to its second operation (B.A.B.B type). The primitive *Libellulidae* likewise show this pattern of development.

The higher *Libellulidae* possess a type somewhat different from the above. In these, the apical growth center operates later than the second operation of the basal growth center of the flagellum, but prior to its third operation (B.B.A.B type). However, the difference between the B.A.B.B and the B.B.A.B types seems phylogenetically to be not essential, since in the genus *Sympetrum* the two types occur along with a transitional type.

It could be concluded, therefore, that there are three main types of growth pattern in the odonate antenna so far known, and these are brought into two groups, the one for the Zygoptera-*Petaluridae*-*Aeshnidae*-group, in which the division of the apical segment occurs late in the larval development or is lacking, the other for the *Corduliidae*-*Libellulidae*-group, in which the division of the apical segment occurs early and prior to the final division of the basal segment of the flagellum. This conclusion is in agreement with the genealogical tree constructed by FRASER (1957). So far as I know, data for *Cordulegasteridae* and *Synthemistidae* are lacking, but it is likely that they show very interesting and important growth patterns of the antenna.

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