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# Variation in the antepalmate hairs of larvae of the *Anopheles maculipennis* complex (\*)

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The possibility of distinguishing the forms of the *Anopheles maculipennis* complex by the larval chaetotaxy was first pointed out by DE BUCK, SCHOUTE & SWELLENGREBEL (1930). They found that there was a significant difference in the number of branches of the antepalmate hair of the fourth and fifth abdominal segments in the two common Netherlands forms (*atroparvus* and *messeae*). LA FACE (1931) found that there were differences between the various Italian forms in the palmate hair of the second abdominal segment, and this character was later studied by DE BUCK, TORREN & SWELLENGREBEL (1933) in the Netherlands forms. At the suggestion of Dr. L. W. HACKETT, we undertook a study of the larval chaetotaxy of the *maculipennis* forms found in Albania, and this study was subsequently extended to include material from other parts of Europe. We wanted first to find out whether there were differences in larval structure correlated with the observed differences in egg pattern and structure; and second, whether there was geographical variation in larval characters in material of a given egg type from different parts of its range.

The study of larval setal variation in these mosquitoes might be considered to be a rather trivial subject for extensive research; but we believe it to have considerable importance and general interest and we hope, in publishing this paper, to stimulate further work. The study of the ecology of the various *maculipennis* mosquitoes would obviously be greatly facilitated if the larvae could be identified, and since these mosquitoes play varying and still only partially understood roles in the transmission of malaria, the study of their larval ecology is of considerable importance in clarifying the malaria situation in Europe. But even aside from this consideration, which might be classed as «practical», the study of the setal variation of these larvae may be of considerable general biological

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interest. The literature on the morphological and physiological (behavior) differences between the various populations included under the term « *Anopheles maculipennis* » is already enormous, and these mosquitoes are becoming one of the most carefully studied groups of insect « species ». There is considerable basis for hope that a careful evaluation of these studies may throw light on the general problem of the nature of « specific » variation. In such studies characters that can easily be handled quantitatively are of obvious importance (see the recent article by RICHARDS, 1938, and various parts of the book on animal variation by ROBSON & RICHARDS, 1936). The setal variation of these larvae, because of its purely quantitative nature, lends itself readily to statistical handling and mathematical analysis.

#### *Method of Study.*

We have used egg characters as the basic criteria for separating the various *maculipennis* forms; and the material used in this study was in all cases raised from eggs that had been carefully examined. The characters that we considered to be most important for use in separating the egg types have been summarized in a recent paper by BATES & HACKETT (1939). The larvae were in all cases raised in the laboratory — using mud, rain water and breadcrumbs as described by HACKETT & BATES (1939) — so that the possibility of phenotypic variation is excluded.

In most cases larvae from a single batch of eggs were raised and mounted separately, so that variation within and between families could be compared. We have found it most convenient to mount ten larvae on a slide; the larvae on a given slide are then counted from left to right and from top to bottom, so that any particular larva can easily be relocated, in case there is any question about the data. Most of the larvae were mounted either in Euparal or in de Faure's Medium. The latter is probably the more convenient: the larvae are left to clear for twenty-four hours or more (they can be left indefinitely) in a solution made up of 57 grams of chloral hydrate, 37 cc. of distilled water and 6 cc. of acetic acid. They are then mounted in a medium consisting of gum arabic, 39 grams; chloral hydrate, 50 grams; glycerine, 20 cc.; distilled water, 50 cc.; and acetic acid, 5 cc.

When larvae are collected in the field; we find it best whenever possible to bring them into the laboratory alive. We have successfully carried larvae in an automobile for as much as 200 kilometers over very rough roads by putting them in small mason jars which are tightly closed and floated in a bucket half filled with water (the bucket covered with a per-

forated top to prevent the water splashing out), We had great difficulty in bringing larvae alive to the laboratory from a field station only seven kilometers away, before we discovered this method. Larvae collected in alcohol in the field, if transported any distance, are liable to lose many setae unless great care is taken; and we have never had very good results from collecting larvae directly into the de Faure clearing solution in the field - too much water is usually carried into the medium with the larvae.

It is more difficult to see the setae on larvae mounted in Euparal than on those mounted in de Faure's medium, and we used Euparal largely on the theory that the mounts would be more permanent. However, slides made with de Faure's medium over two years ago, with no special precautions such as ringing, seem still to be perfectly good. We have found it to be most convenient to use both transmitted and incident light in examining the larvae; the de Faure mounts are generally perfectly clear with only transmitted light, but the use of incident light as well gives a better perspective.

#### *The Antepalpmate Hairs.*

The antepalpmate hairs of the abdomen of the fourth stage larva (hair n. 2 of MARTINI, 1923) have proved to be the most interesting and the most easily studied of the setae that we have examined. The variation of these hairs may prove to be significant in other Anopheline groups, since DE BUCK, SCHOUTE & SWELLENGREBEL (1930) apparently got the idea of examining them in *maculipennis* from a paper by RUSSELL (1925) reporting differences in these hairs between three American species of *Anopheles*.

TABLE I.

*Antepalpmate hairs of ten species of Anopheles (average for five larvae in each case).*

Segment	<i>super- pictus</i>	<i>marteri</i>	<i>bifur- catus</i>	<i>atro- purvus</i>	<i>labran- chia</i>	<i>typicus</i>	<i>messae</i>	<i>melanoon</i>	<i>subal- pinus</i>	<i>sacha- rovi</i>
I	2.3	4.0	3.6	5.4	6.1	7.5	5.7	6.3	6.6	3.5
II	5.2	5.7	6.1	7.1	7.6	9.5	7.7	11.7	8.5	9.4
III	5.5	5.7	5.2	5.5	7.4	7.7	7.2	11.3	9.5	9.3
IV	1.0	1.3	3.7	2.3	2.9	3.6	4.2	6.6	5.8	8.4
V	1.0	1.1	3.6	2.6	2.9	3.1	3.1	6.8	5.5	6.7
VI	1.0	1.5	3.5	3.4	3.7	4.0	4.9	6.7	5.7	6.1
VII	2.5	5.7	5.8	5.2	5.4	6.1	6.7	7.1	6.3	5.5

Table I gives a summary of the branching of the antepalpmate hairs on the seven abdominal segments of ten Anophelines, three of them out-

side of the *maculipennis* complex. It seems that the abdominal segments fall into four groups as far as the development of this hair is concerned: on the first segment the hair is very small in all of the species that we have examined, and with relatively few branches. Its small size makes its examination difficult, and the counting of the branches somewhat uncertain. On the second and third segments, the hair in all of these larvae is large, well developed, and relatively many-branched. Here the large number of branches makes counting difficult, since it is almost impossible to count the branches on hairs with more than six or seven branches, with any certainty. On the fourth, fifth and sixth segments, the hair is usually strong, and with relatively few branches. In *subalpinus* the variation of the hair on these three segments seems to be precisely the same, but on some of the other forms significant statistical differences can be found between the three segments, even though the general type of hair is the same. On the seventh segment the hair usually has more branches, and it seems to be somewhat more feebly developed than on the segments immediately preceding.

The two segments originally studied by RUSSELL (fourth and fifth) seem also to be the best for separating these *maculipennis* larvae. Little or nothing is gained by the additional study of the sixth segment; from the figures in Table I, it looked as though the hair on this segment might differ significantly in *typicus* and *messeae*, but the study of larger numbers of larvae failed to substantiate this.

#### *Methods of Counting the Branches.*

DE BUCK, SCHOUTE & SWELLENGREBEL (1930) and HACKETT & LEWIS (1935) added one hair from the fourth segment and one from the fifth; whether the branches on one side are counted or whether a cross count is made, does not seem to matter, since the range of variation on the two sides of a given segment is the same. For the purpose of identifying a single larva, it has seemed to us preferable to use the sum of all four hairs, thus minimizing the effect of a single aberant hair; but perhaps this method is not sufficiently more accurate to warrant the additional trouble. Comparison between the means obtained by DE BUCK, SCHOUTE & SWELLENGREBEL and HACKETT & LEWIS and those obtained by our method can easily be made by halving our figures.

It will be noted that our figure for German *atroparvus* is remarkably close to that obtained by DE BUCK, SCHOUTE & SWELLENGREBEL for Dutch *atroparvus* (their figure is 5.5, while ours, halved, would be 5.4).

TABLE II.

Total number of branches of the antepalmate hairs of the fourth and fifth abdominal segments of the maculipennis egg types.

Egg type	Region	No. larvae	mean	standard deviation
<i>labranchiae</i>	Italy	132	9.63	1.85
<i>atroparvuz</i>	Germany	154	10.80	1.62
<i>typicus</i>	Albania	146	13.05	1.35
<i>messeae</i>	various	124	14.82	2.40
<i>subalpinus</i>	Albania	122	21.94	2.52
<i>melanoon</i>	Italy	110	24.49	3.30
<i>sacharovi</i>	Albania	100	30.78	4.29

This gives us additional grounds for belief that our *atroparvus* colony, which is descended from the colony kept at the Tropeninstitut in Hamburg, represents a fair sample of the North Sea population. Our figure for *messeae* (based on 50 Albanian larvae, 34 Hungarian larvae, and 15 North German larvae, as will be explained below) is closely similar to the figure obtained by HACKETT & LEWIS for Albanian *messeae* (7.34 to be compared with our 7.41); but it differs considerably from the figure given by DE BUCK, SCHOUTÉ & SWELLENGREBEL (9.1), which was based on a large number of larvae. Our figure for Albanian *subalpinus* (10.97) is also somewhat different from the figure obtained for this same population by HACKETT & LEWIS (12.71).

From the data given in Table II, one could deduce that the *maculipennis* larvae, on the basis of these hairs, fall into three groups: one in which the hair is most frequently two — or three — branched including the first four types, the second with an intermediate number of branches, including *subalpinus* and *melanoon*, and the third including only *sacharovi*, with a large number of branches. It is also apparent, from the standard deviations, that larvae with the larger number of branches are in general more variable. Table III gives the frequency distribution of the data given in Table II.

In the following paragraphs the variation of the antepalmate hairs of these forms is discussed in more detail.

### *Labranchiae*

The larvae used in the study of this type were from our laboratory colony, which is descended from Italian females caught in September, 1937, near Aprilia in the Pontine Marshes. The bimodal frequency distribu-

TABLE III.

Frequency distribution of the total hair count of the maculipennis types.

(The figures for each egg type are percentages of the total number of larvae of that type examined).

Total branches	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39		
<i>labranchiae</i> . . . . .	1	0	5	3	24	16	15	15	27	4																												
<i>atroparvus</i> . . . . .	1	10	12	16	23	30	5	1	1	1																												
<i>typicus</i> . . . . .					1	5	40	25	12	12	3	2																										
<i>messeae</i> . . . . .								2	21	15	10	15	11	12	4	6	2	2																				
<i>subalpinus</i> . . . . .														3	5	9	12	16	19	12	6	11	3	2	2													
<i>melancon</i> . . . . .													1	1	4	2	6	5	8	10	10	11	16	11	5	4	2	2	2									
<i>sacharovi</i> . . . . .															1						1	5	4	7	6	13	4	4	12	6	5	10	10	3	0	6	3	

tion (Table III) may be significant : it seems to reflect a tendency of the larvae to have either two-branched or three-branched hairs, and it may be that two strains are represented in our colony. It is unfortunate that no studies of single families were made in either *labranchiae* or *atroparvus*.

### *Atroparvus.*

The figures for *atroparvus* in Tables II and III are based entirely on material from our German colony. During 1938 we kept five *atroparvus* colonies, based on material from different regions, and the hair counts for these five colonies are given in Tables IV and V. The Portuguese material

TABLE IV.

*Total hair count of atroparvus from different regions.*

Region	No. larvae	mean	St. Deviation
Portugal	41	11.71	1.31
Italy	24	11.71	1.25
Hungary	24	10.88	1.48
Germany	154	10.80	1.62
England	59	9.73	1.71

TABLE V.

*Frequency distribution of the atroparvus hair count by regions.*

(Figures for each country are percentages of the total number of larvae from that country examined).

Total branches :	6	7	8	9	10	11	12	13	14	15	16
Germany			10	12	16	23	30	5	1	1	1
Portugal			2		10	32	39	7	5	5	
Hungary			8		12	30	30	4	4		
Italy				4	12	17	55	4	4	4	
England	3	3	24	15	15	20	17	3			

was received from Dr. R. B. HILL, and is supposedly identical with the material sent to Prof. ROUBAUD and subsequently described by him as *cambournaci* (ROUBAUD & TREILLARD, 1936). The Italian colony was descended from three batches of eggs laid by females collected in a stable near Foggia by Dr. VAN THIEL. From the mosquitoes collected in this stable, 53 batches of *labranchiae*, 3 of *atroparvus* ad 1 of *typicus* were obtained, showing that at least in this locality *atroparvus* and *labranchiae*

are able to live together and retain their identities. The Hungarian colony was based on mosquitoes that were collected in the Nagyhortobagy steppe region. The English material was received from Col. SINTON & Mr. SHUTE, from the colony that they have maintained at Epsom for several years.

These regional samples of *atroparvus* are too restricted to serve as the basis for much generalisation; but one would expect to find some geographical variation in a wide-spread species like *atroparvus* and the differences shown in our tables may well be significant. It is interesting that the Portuguese and Italian populations, from widely separated points on the periphery of the range, show identical means and closely similar ranges of variation. That the English strain should have the fewest branches — should be most similar to the southern *labranchiae* — is curious. But it should be remembered that the Epsom colony is descended from a single female, and shows less variation in general than the English population at large (SHUTE & UNGUREANU, 1938).

### *Typicus.*

The data for *typicus* in Tables II and III are based on a study of five lots of larvae; the composition of these lots is analyzed in Table VI. Four of them (Nos. 255, 328, 371 and 401) represent single families, i. e. larvae raised from one batch of eggs; the other (491) represents several

TABLE VI.

*Frequency distribution of typicus larvae by families.*

Total branches:	10	11	12	13	14	15	16	17	total larvae
Lot 255			2	7	2	11	2	1	25
Lot 328				11	6	2	1	1	21
Lot 371		2	16	5	1	1			25
Lot 401	1	1	11	6	3	3			25
Lot 491		4	17	13	10	2	3	1	50
Total	1	7	57	37	18	18	5	3	146
%	1	5	40	25	12	12	3	2	100

batches of eggs from one locality. It will be noted that except in the case of family 255, the mode is always 12; in other words, the antepalpal hair is normally three-branched. Family 255 is from a locality (Tirana) in which *typicus* is the predominant egg type, with *subalpinus* occurring

relatively rarely, and where we have never found *messeae*; it might possibly be a hybrid, but it seems to us much more likely that it represents a genetic strain of *typicus*. We suspect that all of these *maculipennis* egg types include diverse genetic strains: many larval patterns, for instance, are found in every egg type, and this seems to be a genotypic rather than phenotype variation, since larvae raised from a single batch of eggs resemble each other closely, and larvae from diverse egg batches show great variation even though raised in identical environments.

#### *Messeae.*

We have found this to be the most puzzling of the *maculipennis* egg types: perhaps because of the difficulty of getting sufficient material for study. In Albania we have found *messeae* only in the vicinity of the highland lakes of Ochrida, Malik and Presba (BATES & HACKETT, 1939) — two hundred kilometers from Tirana over very bad roads — so that we have not been able to collect material regularly. When we have the material, we are not always sure of the identification: the eggs of *typicus* in the spring are often very dark, very like normal *messeae* eggs; and in a few cases we have found, from the study of filial eggs of the *atroparvus* cross, that we have misidentified *typicus* as *messeae*. We are sure that *typicus* and *messeae* represent two distinct entities in Albania because: when females are raised in the laboratory under uniform conditions, and crossed with *atroparvus* males, we get two distinct types of F<sub>1</sub> eggs, which correspond to the two egg types found in nature (for description of the distinguishing characters, see BATES & HACKETT, 1939); F<sub>1</sub> eggs of the *typicus* type hatch and produce vigorous, although sterile, adults (BATES 1939), while F<sub>1</sub> eggs of the *messeae* type either fail to hatch or die as first stage larvae; eggs of the *messeae* type, as was noted above, occur only in a single restricted region of Albania, while the *typicus* type is ubiquitous. Thus, while we are sure that *typicus* and *messeae* represent distinct populations in Albania, we are not sure that we can always identify these populations with the means at hand.

The data from our *messeae* hair counts are summarized in Table VII. Lots 400, 403 and 408 represent single families from Lake Malik in Albania; lot 504 is a single family from the Nagyhortobagy steppe of Hungary; lot 527 is from several batches of eggs collected at Bad Nauheim in Germany, and sent to us by Dr. Fritz WEYER. It is unfortunate that we got so few larvae from the Bad Nauheim eggs: the mean of these fifteen larvae is 16.87 (standard deviation  $\pm 2.16$ ) which is much clo-

ser to the figure given by de BUCK, SCHOUTE & SWELLENGREBEL, for the Dutch form (9.1), or doubled for comparison, 18.2) than is our general average for *messeae* (14.82). Albanian *messeae* is from the periphery of the range of the form, and probably here, as in *atroparvus*, there is geographical variation; the fact that our hybridization experiments (BATES,

TABLE VII.

*Frequency distribution of messeae larvae by families and regions.*

Total branches :	11	12	13	14	15	16	17	18	19	20	21	total larvae
Lot 400 (Albania)		7	2	4	4	4	2	1			1	25
Lot 403 »		1	3	4	6	2	6		2		1	25
Lot 408 »	1	13	6	4			1					25
Lot 504 (Hungary)	1	5	5	1	7	6	3	2	4			34
Lot 527 (Germany)			2		2	2	3	2	2	2		15
Total	2	26	18	13	19	14	15	5	8	2	2	124
%	2	21	15	10	15	11	12	4	6	2	2	100

1939) gave exactly the same results as those obtained by DE BUCK, SCHOUTE & SWELLENGREBEL, however, leads us to believe that our Albanian form is specifically identical with the Dutch form.

It will be noted that of the three Albanian families listed in Table VII, lot n. 408 shows exactly the same distribution as the *typicus* families in Table VI, while the other two families show a larger number of branches than would be expected in *typicus*; we are, however, reasonably sure of the identification of lot 408, since the eggs were collected in June, when differences between the forms are usually clear.

#### *Subalpinus* and *melanooon*

The figures for both of these egg types are based on mixed lots of larvae: the *subalpinus* from various localities in Albania, and the *melanooon* from two separate collections at Fondi, Italy, half way between Rome and Naples. Four families of *subalpinus* larvae were studied separately, but none showed any striking deviations from the species average.

The figures for larval hairs do not give much support for the theory that these two egg types represent genetically independent populations. The differences between them seem to be of the same order of magnitude as the regional differences found in *atroparvus*.

### *Sacharovi*

The antepalmate hairs of this type have so many branches that it is difficult to count them with any accuracy, and we have limited our study to 100 larvae, composed of four separate families. We prepared many more slides, with the object of counting enough larvae to get a more regular curve for the frequency distribution of this species, but we decided that the results would hardly justify the labor involved.

### *Hybrid Larvae*

One of the most interesting aspects of the variation of these antepalmate hairs is the intermediate condition of hybrid larvae. In a previous paper (BATES & HACKETT, 1939, fig. 3) we published a graph of the frequency distribution of single hairs in *atroparvus*, *subalpinus* and *atroparvus* × *subalpinus* F<sub>1</sub> the hybrid being almost precisely intermediate between the parents. The same thing is shown by the frequency distribution of the total hair count for this case and for a hybrid between *atroparvus* and *melanoon*, which is given in Table VIII.

Nine larvae of the F<sub>1</sub> hybrid of *atroparvus* × *sacharovi* had the following hair counts :

total branches :	13	14	15	16	17	18	19	20	21
number of larvae :	1	1		2		1	3		1

The range of *atroparvus* (Table III) is from 7 to 16, and of *sacharovi* from 19 to 39.

The intermediate condition of these hybrids would seem to rule out the possibility of the hair branching being controlled by a single gene (since the F<sub>1</sub> does not show segregation), and furnishes one more bit of evidence that the *maculipennis* egg types (or at least some of them) represent « real species », i. e., independent and genetically diverse natural populations.

### *Other Setal Characters*

We have found considerable difficulty in studying the character of the palmate hair of the second abdominal segment, described by LA FACE (1931), since every intergrade between « branched » and « palmate » seems to occur. Certainly there appear to be statistical differences between the various forms in the development of this hair, but we have not been

TABLE VIII.

Frequency distribution of total hair count of hybrid larvae.

Total branches	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>atroparvus</i> (154 larvae) . .	1	10	12	16	23	30	5	1	1	1																
<i>atroparvus</i> × <i>subalpinus</i> (25 larvae)					4	8	12	26	12	8	4	16														
<i>atroparvus</i> × <i>melancon</i> (21 larvae)					9	14	9	0	24	29	5	5	5	5												
<i>subalpinus</i> (122 larvae) . .										3	5	9	12	16	19	12	6	11	3	2	2					
<i>melancon</i> (110 larvae) . . .									1	1	4	2	6	5	8	10	10	11	16	11	5	4	2	2	2	2

able to devise any very practicable and objective method of measuring these differences. Such studies as we have made support the conclusion given by HACKETT & MISSIROLI (1935, p. 56).

We made a special study of the abdominal hairs of *sacharovi* and *subalpinus*, forms which can be distinguished even as adults. We found no consistent difference at all in the setae of the under side. On the upper side, the antepalmate hair of the first segment seems usually to be fewer branched in *sacharovi* than in *subalpinus*: but the difference is average, not absolute. Hair no. 3 (MARTINI, 1923) of the first segment, usually unbranched, is sometimes bifurcate in *sacharovi*: in one family (20 larvae) 75 % had this hair branched; in another family (20 larvae) 20 % had the hair branched; while in two other families (33 larvae) the hair was always simple. A general survey of the other abdominal setae failed to reveal any character that might serve for absolute differentiation between *subalpinus* and *sacharovi*.

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#### SUMMARY

Variation in the branching of the antepalpmate hairs in the *maculipennis* larvae seems to be correlated with egg type, and to a lesser extent with genetic strains (families) and geographical region. *Atroparvus* and *labranchiae* seem to be closely related, as do *typicus* and southern *messeae*. The differences between *subalpinus* and *melanoon* seem to be of the same order as the geographical differences found in *atroparvus*. *Sacharovi* in larval characters, as in characters of the egg and adult, seems to stand by itself. Over most of Albania and Greece, where only *typicus*, *subalpinus* and *sacharovi* are found, it should be possible to identify larvae from a given breeding place with reasonable accuracy. The setal characters of hybrids are intermediate, additional evidence that the parental forms represent genetically diverse natural populations.

#### RIASSUNTO

Nel gruppo *Anopheles maculipennis* i caratteri delle uova possono mettersi in correlazione con le variazioni delle setole palmate inserite nel 4° e 5° segmento addominale delle larve al 4° stadio. Sotto questo riguardo si notano alcune differenze inerenti alle zone geografiche ed ai ceppi. Altri caratteri chetotassici delle larve sono poco definiti.

Dalla chetotassi larvale l'*atroparvus* e il *labranchiae* risultano più affini tra di loro, anziché col *typicus* e col *messeae*. Le differenze tra il *subalpinus* e il *melanoon* sembrano dello stesso ordine di quelle accertate tra gli *atroparvus* di varie provenienze. Quanto al *sacharovi*, la chetotassi larvale depono per un biotipo a sè, e ciò corrisponde ai caratteri delle uova e degli adulti. Nella maggior parte dell'Albania e della Grecia, ove si repertano solo *typicus*, *subalpinus* e *sacharovi*, sembra possibile differenziare le larve con abbastanza sicurezza in base alla chetotassi.

Negli ibridi le setole hanno forme intermedie tra quelle dei biotipi e ciò avvalorla la concezione che questi rappresentino geneticamente dei gruppi naturali autonomi.

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