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Mapping the ocular field in *Proteroiulus fuscus* (Am Stein) (Diplopoda, Blaniulidae)

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Newly moulted individuals of *Proteroiulus fuscus* were collected by trapping from conifer tree stumps, and their stadia were determined on the basis of defence glands. The number of ocelli and their relative positions also were determined. The first stadium is eyeless. One new ocellus is formed during the 2nd and the 3rd moults, and in later moults the number of new ocelli is 0, 1, or 2, the corresponding probabilities being 0.0167, 0.98 and 0.0033. The distribution of ocelli size classes was in preadults consistent with corresponding trinomial distribution, but in mature individuals the frequency of the dominant size class was lower than expected. In 19% of the 1180 individuals studied the eyes had different numbers of ocelli, the maximal asymmetry being three.

The form of the eyes varies widely. The ocular field appears to contain three anterio-posterior rows of possible locations, and in 76% of the cases, growth starts in the middle row, in 3% in the dorsal, and in 21% in the ventral row. New ocelli are added at the anterior border of the eye, usually in positions adjacent to already occupied locations. The first ocelli usually form a line, then new ocelli are added laterally, with the initial row strongly influencing the direction and form of later additions of ocelli. Successive preadult stadia can be identified on the basis of ocelli number, but in later moults the accuracy gradually decreases.

1. Introduction

In julids and blaniulids the determination of developmental stadium of an individual presents difficulties. The usual methods based on the numbers of segments and legs are unreliable, as after the first postembryonal moults the number of new segments added in a particular moult is variable. Although attempts have been made to establish an optimal decision procedure (Halkka 1958, Brookes 1963), the overlap in numbers of segments, legs, or defence glands restricts the applicability of the methods. Blower & Gabbut (1964) used differences in relative body measurements to distinguish between stadia, but again the overlap is considerable.

Vachon (1947) suggested that in age-determination the regular growth pattern of eyes could be used, and this method was subsequently adopted by Saudray (1952), Sahli (1969), and Blower (1985). This method seems to be suitable in determination of developmental stadia in Julidae, but in some other species difficulties have arisen (Blower 1985).

The growth and form of the ocular field in Blaniulidae has attracted relatively little attention (Hopkin & Blower 1987). This structure is quite variable, and obviously eye-growth should be correlated with other age-related growth. This paper presents results of an attempt to analyse eye-structure in *Proteroiulus fuscus* (Am Stein) using newly moulted individuals whose stadium could be determined on the basis of defence glands (Peitsalmi 1981).

2. Material and methods

The material was collected in the vicinity of Hämeenlinna (grid 27°E 677:37) by trapping (Peitsalmi 1981) specimens in a spruce swamp from 30 decaying conifer tree stumps. The animals were collected weekly in the summer of 1989, and all newly moulted individuals whose developmental stage could be determined on the basis of defence glands were chosen. The animals were preserved in ethanol and usually studied within two days after capture. The ocular field of each eye was studied with the aid of a stereomicroscope using 50 × magnification, and the relative position of successive ocelli noted. In larger individuals, the bending of the ocular rows near the antenna and the larger size of later ocelli caused some difficulty, but sufficient accuracy could be attained by stepwise analysis. The analysis necessitates fresh material, as preserved individuals tend to darken, and distinguishing defence-gland groups becomes difficult. Detailed analysis was carried out with 1064 individuals. In early summer an additional group of 116 individuals was analysed, but minor details regarding the positions of ocelli were not recorded. As the total number of ocelli and the initial eye-growth were reliably known, this additional material was included in initial analysis, but not used in the analysis of detailed eye-growth.

3. Results

3.1. The number of moults and the number of ocelli

The first postembryonal stadium is eyeless. Eye growth begins in the second stadium when one ocellus is formed. In each later moult usually one new ocellus is added to an eye, and the number of ocelli is thus one less than the number of moults. However, sometimes an ocellus does not develop, and sometimes two ocelli appear during a single moult. These types are subsequently referred to as standard moult, null moult, and two-ocelli moult growth patterns, respectively. Due to this variation, the number of moults and the number of ocelli can differ, and the eyes of an individual can have different numbers of ocelli. Of the individuals studied, 951 had the same number of ocelli in both eyes, and in 229 individuals the ocelli numbers differed. This asymmetry amounted in 214 cases to one, in 14 to two, and in one to three ocelli.

The probable developmental history of different eye types can be reconstructed. If the eyes are symmetrical, but the ocelli number two less than the number of moults, one null moult has occurred in both eyes. An asymmetry of one, with number of moults the same as the greater ocelli number, implies one two-ocelli moult in one eye. When the greater ocelli number is one less than the number of moults, a null moult has occurred in one eye. An asymmetry of two, with the number of moults the same as the greater ocelli number, is the result of a null moult in one and a two-ocelli moult in another eye. More complex scenarios naturally are possible but cannot be identified. The relation between number of moults and number of ocelli is given in Table 1. When a single eye is taken as a unit, there are 67 cases with one two-ocelli moult, one with two successive two-ocelli moults, 255 cases with one null moult, and 14 cases with two null

Table 1. Relation between number of moults, number of ocelli, and absolute difference in numbers of ocelli between right and left eye.

Absolute difference	Number of moults minus maximal number of ocelli				
	−1	0	1	2	3
0		8	902	40	1
1		45	165	4	0
2	1	6	7		
3					1

moults. This suggests that a null moult occurs with a probability four to five times that of a two-ocelli moult. The frequency of asymmetry suggests that the eyes develop independently.

Further analysis is possible by following the changes in successive stadia (see Table 2). The frequency of deviant eye types appears to increase with increasing age.

In analysing eye-growth, a parsimonious null model is to assume that at each moult 0, 1, or 2 new ocelli appear with the fixed probabilities q_0, q_1, and q_2 and that successive moults are independent. After n moults 0, 1, ... $2n$ new ocelli can be formed, and the corresponding probabilities can be obtained by expanding the trinomial $(q_0 + q_1 + q_2)^n$ and summing the terms, leading to similar end results.

In the second and third moults one new ocellus is invariably added, and only from the fourth moult onwards do differences appear. The data in Table 2 suggest that q_1 is relatively large, obviously above 0.90, and q_0 can be approximated as

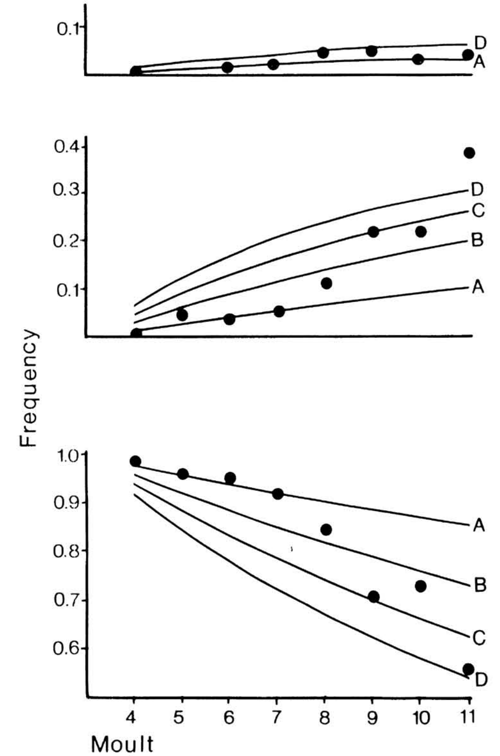

Fig. 1. Increase in number of ocelli in successive moults in the trinomial model. Classes where ocelli number is one less than the of number moults (below), ocelli number two less than the number of moults (middle), ocelli number equal to the number of moults (top). Lines refer to q_1 values 0.98 (A), 0.96 (B), 0.94 (C) and 0.92 (D); q_0 is $5 \times q_2$. Dots show frequencies calculated from data.

Table 2. Percentage distribution of ocelli in different stadia; left and right eyes treated separately. In 2nd stadium one ocellus is invariably present.

Stadium	Number of ocelli										
	2	3	4	5	6	7	8	9	10	11	*n*
3	100.0										68
4	0.7	98.6	0.7								138
5		4.1	95.9								196
6			3.1	95.5	1.4						222
7				5.4	92.3	2.1	0.2				516
8					11.2	84.4	4.4				636
9		0.3			1.9	22.2	70.8	4.8			370
10						2.6	22.1	72.7	2.6		154
11							1.9	38.5	55.8	3.8	52

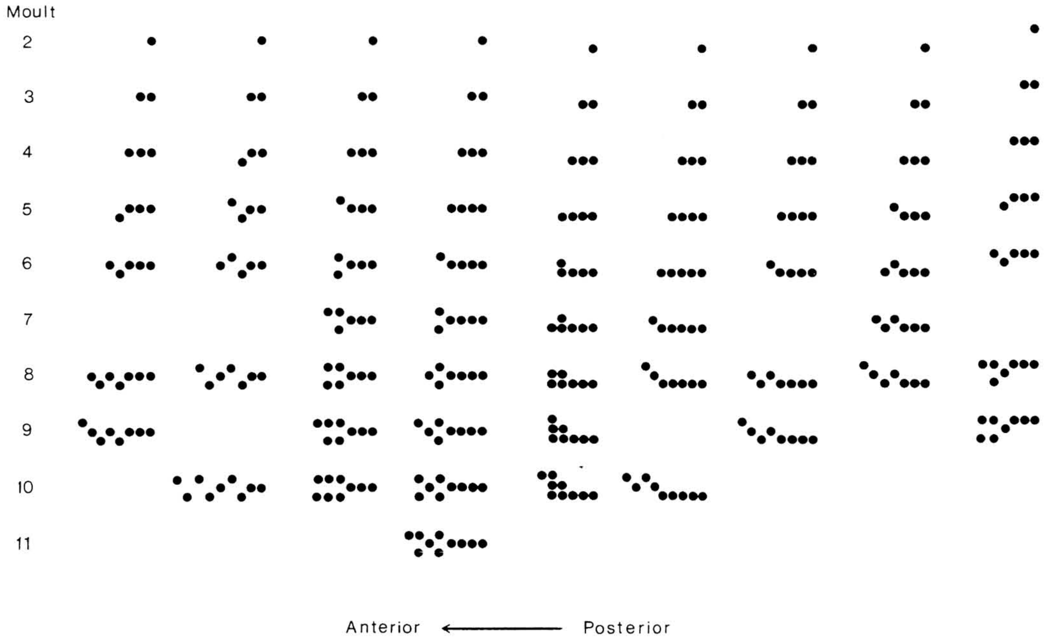

Fig. 2. Some representative series of eye-growth observed in the material. Eyes of individuals in later stadia can be derived by assuming anterior addition of a single ocellus. Gaps indicate intermediate stages not actually recorded.

$5 \times q_2$. The results of calculations using different trial values for q_1 are given in Fig. 1, for ocelli number classes $n-1$, n, and $n+1$. Even when q_1 is large, the frequency of the dominant eye type, in which the number of ocelli is one less than the number of moults, decreases rapidly in older age classes, and the frequency of eyes with ocelli numbering two less than the moult number increases. The assumption $q_0 = 5 \times q_2$ stabilizes the frequency of the eye-type with its ocelli number the same as the molt number to relatively low values. The frequencies of more deviant eye-types are always low. Small changes in the value of q_1 cause appreciable differences in frequencies.

When observed frequencies are compared with theoretical results (Fig. 1), it is apparent that the initial moults agree with the trinomial model with probabilities $q_0 = 0.0167$, $q_1 = 0.98$ and $q_2 = 0.0033$. However, from the 8th moult onwards, the observed values start to diverge from expected frequencies; the probabilities are no longer constant. Assuming that the probabilities now are $q_0 = 0.083$, $q_1 = 0.90$, and $q_2 = 0.017$, the expected percentages of eye-sizes at the following moults are as follows:

Ocelli:	6	7	8	9	10	11
Moult						
8	13.4	83.2	2.7			
9		19.0	75.4	3.8		
10			23.3	68.5	4.7	
11				26.8	62.4	5.4

The values obtained fit the data reasonably well, differences not being significant. We do not maintain that the frequencies used are correct, but they indicate the degree of change. The change is probably connected with the attainment of maturity after the seventh moult.

3.2. Details of eye-growth

3.2.1. Structure of the ocular field

The detailed structure of the eyes in older individuals varies considerably. However, it is easy to recognize comparable patterns in younger and older individuals. Growth patterns such as those given in Fig. 2 suggest that eye-growth occurs by sequential anterior addition of new ocelli, and the earlier pattern remains unaltered. The process can be formally described by assuming that there exists a rectangular ocular field consisting of three rows of potential locations, and only a few of these are actually occupied. In eyes of young individuals the ocelli usually occupy successive locations in a single row. This growth type, in which the new ocellus occupies the next location in the same row as the ocellus formed during the previous moult, is referred to as linear addition. New ocelli can appear also in other rows, but usually in locations adjacent to the last-formed ocellus. The frequently observed oblique pattern is the result of diagonal addition, but the rectangular L-shaped pattern shows that lateral addition is also possible. In eyes containing 8–11 ocelli a gap sometimes occurs between the last ocelli. This growth type, in which the location of the first unused row is left empty, is referred to as extended addition, diagonal or lateral. These different types are presented in Fig. 3.

The actual steps leading to a particular complex eye structure cannot usually be identified, and in fact most eye types encountered can be constructed solely by repeated linear and diagonal additions. The relative frequencies of different types cannot thus be determined, but the number of initial linear additions can indeed be counted. Table 3 gives the number of linear steps prior to the first necessary diagonal addition, grouped according to number of ocelli.

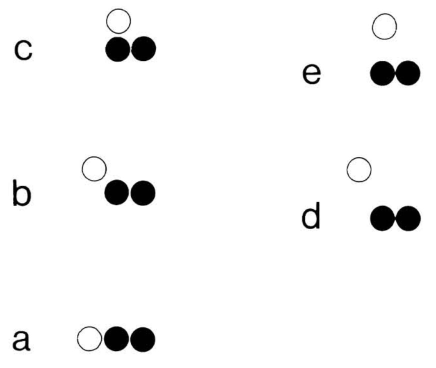

Fig. 3. Presumed steps of eye-growth. a) linear addition, b) diagonal addition, c) lateral addition, d) extended diagonal addition, e) extended lateral addition.

The results show that with increasing number of ocelli the frequency of linear additions rapidly stabilizes. As the proportion of eyes with 0–3 initial linear additions remains practically constant in larger eyes, the assumption that eyes grow at the anterior border seems to be true.

3.2.2. The initial row

The position of the initial row can only be determined in cases where all three rows contain at least one ocellus. Table 4 gives the percentage

Table 3. Percentage distribution of minimum number of initial linear additions in eyes of different size-classes.

Ocelli	Minimum number of linear additions							
	0	1	2	3	4	5	6	*n*
2	2.9	97.1						69
3	2.8	34.4	62.8					145
4	3.6	15.8	51.5	29.1				196
5	0.8	21.3	37.1	26.2	14.6			240
6	0.7	22.8	31.9	29.3	11.7	3.6		557
7	0.5	13.9	50.2	19.7	13.6	1.9	0.2	634
8	0.9	12.9	52.8	29.4	3.4	0.6		326
9	2.6	9.9	53.9	24.4	7.2	2.0		152
10		21.6	27.0	45.9	5.4			37
11		25.0	25.0	50.0				4
n	28	480	1044	560	210	37	1	2360

frequencies of eyes grouped according to the position of the inital row.

In the majority of cases growth starts in the middle row. A ventral position for the initial row is relatively frequent in smaller size classes; apparently the three-row pattern is attained more rapidly than in other types. The frequency of the dorsal row growth-pattern is always low.

Linear arrangement of ocelli was found in 272 cases of the total of 2360 eyes, the distribution of ocelli number being as follows:

Ocelli	2	3	4	5	6	7
Number	67	92	57	35	20	1
Frequency	0.99	0.63	0.29	0.16	0.04	0.002

As expected, the probability of extended linear addition decreases rapidly with continuing growth.

3.2.3. The two-row pattern

When growth begins in the middle row, the first diagonal or lateral addition leading to the two-row pattern can occur either ventrally or dorsally, but in other rows the direction of additon is obvious. Cases in which extended additions had apparently occurred were occasionally detected, but precise evaluation was difficult, and they are not treated separately. In eyes with a two-row pattern there were 613 dorsal and 256 ventral additions, relative frequencies being 0.71 and 0.30, respectively. Using the average frequencies for different rows given in Table 4, and assuming that when the initial row is the middle position, dorsal and ventral additions occur with equal probability, we would expect 356 dorsal and 513 ventral additions (frequencies 0.41 and 0.59, respectively). Growth in the middle row thus obviously produces more dorsal additions, the frequencies being about 0.65 for dorsal and 0.35 for ventral ones.

The average number of minimum linear additions for different size classes of eyes with two ocelli rows are given in Table 5. With growing ocelli number the number of additions naturally increases but stabilizes when eye-size reaches 6–8 ocelli. In eyes characterized by dorsal additions (initial growth in the ventral or middle row), the values are consistently larger, the differences being in most groups highly significant. In a considerable number of cases the initial row has one ocellus less than the total ocelli number, whereas in eyes with a ventral addition, the initial row is much shorter than could be expected on the basis of ocelli number. The mechanism causing the difference is probably as follows: After the first dorsal addition the next addition often occurs in the still empty ventral row, leading to a three-row pattern, but after ventral addition subsequent additions occur in the already occupied rows, retaining the two-row pattern. This process also explains the preponderance of the ventral-row pattern in small eye-size classes in Table 4.

Table 4. Percentage distribution of eyes with initial linear additions in dorsal, middle and ventral positions in different eye-size classes. Number of one- or two-row eyes is also given.

Ocelli	Initial row				Ocelli in less
	Ventral	Middle	Dorsal	*n*	than three rows
2					69
3		100.0		2	143
4	71.4	28.6		14	182
5	47.6	52.4		63	177
6	31.4	66.1	2.5	239	318
7	20.7	76.2	3.1	415	219
8	10.4	86.9	2.7	259	67
9	13.6	80.6	5.8	139	13
10	5.7	91.4	2.9	35	2
11		100.0		4	
Total	21.3	75.7	3.0	1170	1190

3.2.4. The three-row pattern

The analysis can be extended to eyes with three rows. When the initial growth occurs in the middle row, and diagonal or lateral additions occur in the vicinity of the same central ocellus in opposite directions, the direction of the first diagonal or lateral addition cannot be determined. Such cases are thus treated as an additional group. The numbers and frequencies of different types were as follows:

Second row:	Ventral	Middle	Dorsal	Ventral/ dorsal
Inital row				
Ventral	–	231	12	
Middle	261	–	30	423
Dorsal	2	32	–	
Ventral	–	0.95	0.05	
Middle	0.37	–	0.04	0.59
Dorsal	0.06	0.94	–	

Both in ventral and and dorsal growth-patterns, extended additions occur with low frequency. In the middle-row pattern, dorsal additions are more rare than expected on the basis of the two-row pattern. Instead, the pattern in which both lateral positions are occupied is common. Obviously the dorsal addition is almost inevitably followed by a further addition to the ventral row at the same position. If the second row is formed ventrally, the dorsal row is usually occupied only after additional ocelli are added in the rows already occupied.

The distribution of minumum linear additions follows the pattern established in two-row eyes (Table 6). When growth begins in the ventral row, diagonal or lateral additions necessarily are in the dorsal direction. As in two-row dorsal addition, initial linear growth is characterized by rows of up to five ocelli. In the majority of cases the dorsal row is occupied immediately after the middle row. When growth begins in other rows, a three-ocelli pattern in the initial row is the dominant group. Five-ocelli inital rows occur in the middle-row pattern, but only with low frequency. The differences are significant.

Now the major lines of eye-growth can be summarized. In 75% of the cases growth starts in the middle row. Of these, 65% begin diagonal or lateral growth dorsally, usually after three ocelli are formed in a line. Then a new ocellus is formed opposite in the ventral row. Later the growth is more variable.

If the first diagonal or lateral addition occurs ventrally, the two-row pattern is retained during

Table 5. Distribution of minimum number of initial linear additions in different eye-size classes in eyes with two ocelli rows.

Ocelli		Minimum number linear additions 0	1	2	3	4	5		Total	Mean ± *SE*
Dorsal	2	1							1	
	3	1	49						50	0.98 ± 0.02
	4	1	9	100					110	1.90 ± 0.03
	5		3	43	63				109	2.55 ± 0.05
	6	1	16	30	77	65			189	3.00 ± 0.07
	7		12	30	27	33	11		113	3.01 ± 0.11
	8	1	8	18	7	2			36	3.03 ± 0.14
	9		1	2	2				5	2.20 ± 0.37
								Total	613	
Ventral	3	1							1	
	4	1	2						3	0.67 ± 0.33
	5		26	6					32	1.19 ± 0.07
	6		40	62	1				103	1.62 ± 0.05
	7		9	64	17				90	2.09 ± 0.06
	8		2	12	6				20	2.20 ± 0.14
	9			2	3				5	2.60 ± 0.25
	10			2					2	
								Total	256	

some additions, and the three-row pattern is established when a large ocelli number is attained.

If growth begins in the ventral row, linear growth tends to last longer. The three-row pattern is established in two successive additions.

Table 6. Distribution of minimum number of initial linear additions in different eye-size classes in eyes with three ocelli rows.

Ocelli row		Minimum number linear additions 0	1	2	3	4	5	Total	Mean ± SE
Ventral	4	1	9					10	0.90 ± 0.10
	5	1	4	25				30	1.80 ± 0.09
	6	3	10	14	47			74	2.41 ± 0.10
	7	2	6	24	9	44		85	3.04 ± 0.12
	8	1	2	11	7	2	1	24	2.51 ± 0.22
	9	2	3	4	3	5	1	18	2.70 ± 0.35
	10		1	1				2	1.50
								Total 243	
Dorsal	6		5	1				6	1.17 ± 0.17
	7		3	10				13	1.77 ± 0.12
	8		1	6				7	1.86 ± 0.14
	9		1	6	1			8	2.00 ± 0.19
								Total 34	
Middle ventral	5		6	1				7	1.14 ± 0.14
	6		27	43				70	1.61 ± 0.06
	7		22	58	29			109	2.06 ± 0.06
	8		5	26	15	3		49	2.33 ± 0.11
	9		2	11	9			22	2.32 ± 0.14
	10			2	1			3	2.33 ± 0.33
	11			1				1	
								Total 261	
Middle dorsal	6		1					1	
	7		4	8	1			13	1.77 ± 0.17
	8		1	8	1			10	2.00 ± 0.15
	9		1	3		1		5	2.20 ± 0.49
	11				1			1	
								Total 30	
Middle dorsal/ventral	3	2						2	
	4	2	1					3	0.33 ± 0.33
	5		11	14				25	1.56 ± 0.10
	6		22	24	32			78	2.13 ± 0.09
	7		19	88	35	3		145	2.15 ± 0.05
	8		14	68	31	3		116	2.20 ± 0.06
	9		3	26	11	1		41	2.24 ± 0.10
	10		2	3	6	1		12	3.50 ± 0.26
	11		1					1	
								Total 423	

4. Discussion

In Julidae one new ocellus or an ocular row is added in the eye at each moult starting from the second postembryonal moult (Vachon 1947, Saudray 1952, Sahli 1955, 1956). According to Blower (1985), in *Julus scandinavicus* Latzel, a new ocular row is added at each moult, but the number of ocelli decreases with age. The number of rows is thus a relatively secure method of stage-determination, provided that the successive rows are correctly distinguished.

In Blaniulidae, interpretation of the growth pattern of eyes is more difficult. According to Blower (1985) the ocelli form an anterio – posterior row or fill a triangular field. Hopkin & Blower (1987) note that in *Choneiulus palmatus* (Němec) and *Nopoiulus kochii* (Gervais) the ocelli form a single row with occasional "displaced" ocelli, and in *P. fuscus* additional ocelli were found distally above the ocular row. The common opinion seems to be that starting from the second postembryonic moult, one new ocellus is formed at each moult, but the fact that left and right eyes can have different numbers of ocelli is well known (Hopkin & Blower 1987).

The present results show that in *P. fuscus* the eyes of an individual develop independently, and that starting from the 4th moult there is a small probability of a null moult or a two-ocelli moult. A simple trinomial model describes the preadult moults adequately. At maturity the probability of deviant moults increases appreciably. In young individuals ocelli number is thus a reliable indicator of stadium, at least for individuals having the same number of ocelli in both eyes. If the ocelli numbers differ by one, the larger ocelli number should be used, and if they differ by two then the intermediate value should be chosen. After maturation, however, the method is less accurate.

When the concept of three ocular rows and diagonal and lateral additions is adopted, the wide variation of blaniulid eye structure is easy to understand, and there is no need to postulate abnormal positions of ocelli. In young individuals one- and two-row types are dominant, and usually the second row lies dorsal to the initial row. This type was recognized as the "very acute triangular field" by Blower (1985), who does not comment on the possibility of a three-row pattern. In our material, however, 66% of the individuals exhibit a three-row eye pattern. Our data refer to a single local population, and it is possible that eye-growth shows considerable interpopulation variation.

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