Ann. Zool. Fennici 29:39-46
Helsinki 21 April 1992

ISSN 0003-455X

Eye growth in *Choneiulus palmatus* (Němec) and *Nopoiulus kochii* (Gervais) (Diplopoda, Blaniulidae)

Maija Peitsalmi & V. Ilmari Pajunen

Peitsalmi, M., Leveemäki 19, SF-13430 Hämeenlinna, Finland
Pajunen, V. I., Division of Ecology, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland

Received 26 April 1991, accepted 19 February 1992

Developmental stadia of newly moulted individuals of *Choneiulus palmatus* and *Nopoiulus kochii* were determined on the basis of the defence glands. The numbers of ocelli and their relative positions also were determined. The first stadium is eyeless, and one ocellus is present in the 2nd stadium. In later moults 0 or 1 and very rarely 2 new ocelli can be formed. In initial moults the probabilities of different types were constant, but after the 7th stadium the probability of a moult without a new ocellus increased strongly, the maximal number of ocelli observed being nine. In 24% of the 497 and 429 individuals of *C. palmatus* and *N. kochii* studied, respectively, the eyes had different numbers of ocelli, the maximal asymmetry being in *C. palmatus* 2 (8 individuals) and in *N. kochii* 3 (1 individual). The ocular field contains three anterio-posterior rows of possible ocular locations, and new ocelli are added at the anterior border of the eye, usually in locations adjacent to already occupied locations. The first ocelli usually form a single row, then new ocelli are added laterally, and all three rows are usually occupied in older individuals. In *C. palmatus* in 72% of cases growth starts in the ventral row, in 24% in the middle and in 4% in the dorsal row. In *N. kochii* the respective percentages were 45%, 40% and 15%.

1. Introduction

The eye-growth in Blaniulidae appears to be more variable than in other diplopods. Peitsalmi & Pajunen (1991) analyzed the ocular field in *Proteroiulus fuscus* (Am Stein). The number of ocelli and the form of eyes varied considerably, but the growth pattern could be conveniently explained by assuming that the eyes consisted of three anterio-posterior rows of ocular locations. Growth proceeded by addition of new ocelli at the anterior border of the eye, usually in locations adjacent to the already occupied locations. The number of new ocelli formed in a moult were 0, 1, or 2, and the probabilities of the three types were constant throughout preadult growth. Initially the ocelli formed a single line, but later growth was very variable.

In this paper in order to test the general applicability of the earlier results, the analysis is extended to *Choneiulus palmatus* (Němec) and *Nopoiulus kochii* (Gervais).

2. Material and methods

The animals were collected in the vicinity of Tampere (Grid 27°E 682:33) from a domestic compost pile on 24.8.1990.

The animals were kept in a dark room at 10–15°C in jars containing compost material. Newly moulted individuals whose developmental stage could be determined on the basis of defence glands were chosen at intervals of a few days. The animals were preserved in 80% ethanol and studied within 1–2 days. The ocular field of each eye was studied with the aid of a stereomicroscope using 50 × magnification, and the relative position of successive ocelli was noted. In all, 497 individuals of *C. palmatus* and 429 of *N. kochii* were studied.

3. Results

3.1. The number of ocelli and the number of moults

The first postembryonal stadium was eyeless. Eye growth began in the second stadium, in which one ocellus was formed. Growth in later stadia varied, and in 23.9% (*C. palmatus*) and 23.3% (*N. kochii*) of individuals the eyes had different numbers of ocelli. Of individuals with asymmetry in 6.7% (*C. palmatus*) and in 9.0% (*N. kochii*) the difference was two ocelli and in *N. kochii* in one individual the difference was 3 ocelli. When the number of moults and the number of ocelli in an eye was compared (Table 1), it appeared that in early moults usually one ocellus was formed

Table 1. Percentage distribution of ocelli in different stadia; left and right eyes treated separately.

Stadium	Number of ocelli									
	1	2	3	4	5	6	7	8	9	*n*
C. palmatus										
2	100.0									8
3	1.3	97.4	1.3							76
4		15.0	85.0							80
5			9.2	90.8						130
6				10.8	89.2					130
7					15.9	83.3	0.8			126
8					2.6	40.2	56.7	0.5		194
9					0.6	24.1	62.1	13.2		166
10					1.8	5.4	46.4	46.4		56
11						8.3	50.0	41.7		24
12								100.0		4
N. kochii										
2	100.0									4
3	5.3	94.7								38
4		7.9	92.1							114
5			11.7	86.8	1.5					204
6				14.5	85.5					172
7				1.8	17.9	80.3				56
8				1.5	5.9	39.7	52.9			68
9					2.6	21.1	51.3	25.0		76
10				4.0	5.3	13.2	47.4	29.0	1.3	76
11					2.9	14.7	32.4	44.1	5.9	34
12						10.0	40.0	20.0	30.0	10
13							25.0	25.0	50.0	4
14								100.0		2

at each moult (standard moult), but moults in which a new ocellus did not develop (null moult) occurred with low frequency. Four cases in which the ocelli number equalled the stadium number were found. Thus, sometimes two ocelli could be added in a moult (two-ocelli moult). Starting from the eighth moult the frequency of null moult then increased rapidly and in last moults it became the dominant type. The number of ocelli was thus a reliable indicator of stadium only during early development.

The changes in frequencies of different moult types can be analyzed by comparing the stadium-specific frequencies with those obtained by assuming that occurrence probabilities of different moult types are constant and frequencies thus obey a trinomial process (Peitsalmi & Pajunen 1991). Standard moults obviously occurred with high probability ($P > 0.9$) and the data in Table 1 suggest that the probability of a null moult was approximately 40 times of that of two-ocelli moult during early moults. The results using different trial values (Fig. 1) suggested that during early development the probabilities in fact remained constant, the probability of the standard moult being 0.96 in *N. kochii*, and somewhat higher (0.97) in *C. palmatus*. At the eighth moult the probability of the standard moult decreased to the level of 0.65 and dropped during further growth even lower, and the probability of the null moult correspondingly increased. The frequency of two-ocelli moult was always low.

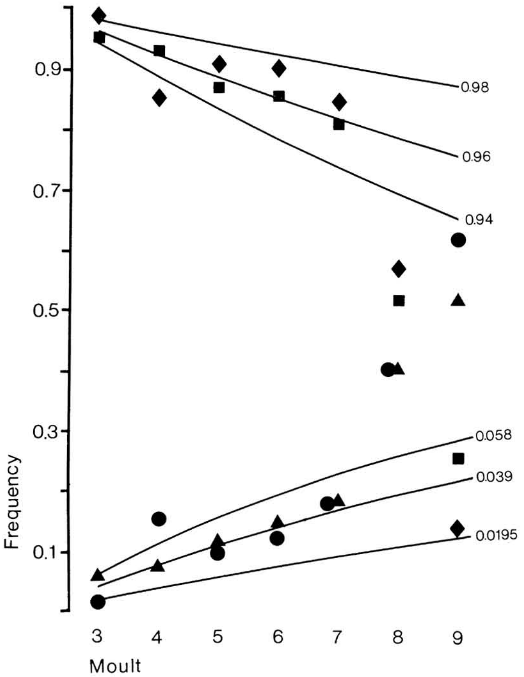

Fig. 1. Increase in number of ocelli in successive moults in the trinomial model. Lines refer to constant probabilities given at the right of lines. — Symbols: diamonds and squares: classes with ocelli number one less than the number of moults; circles and triangles: ocelli number two less than number of moults; diamonds and circles *C. palmatus*; squares and triangles *N. kochii*.

3.2. Details of eye-growth

Comparison of eyes of young and old individuals (Fig. 2) suggested that the eye-growth occurred with successive anterior addition of ocelli and this led often to long single-row pattern. However, additions to lateral directions occurred in larger eyes, and the concept of rectangular ocular field consisting of ventral, middle and dorsal rows (Peitsalmi & Pajunen 1991) was even now applicable. Also, all growth types then postulated: linear, diagonal, lateral, and extended additions could be recognized. Diagonal addition appeared to be the most frequent type in lateral eye-growth, but because many patterns could be attained in several different ways, exact proportions cannot be given. The number of initial linear additions prior to the first diagonally or laterally formed ocellus could be counted (Table 2). The proportions of eyes with 0–4 initial linear additions remain relatively constant in larger eyes. This is consistent with the assumption that the eyes grow at the anterior border.

3.2.1.The inital row

The ocular rows could be accurately determined only when all three rows contained at least one ocellus. Table 3 gives the percentage frequencies of three-row eyes grouped according to the position of the intial row.

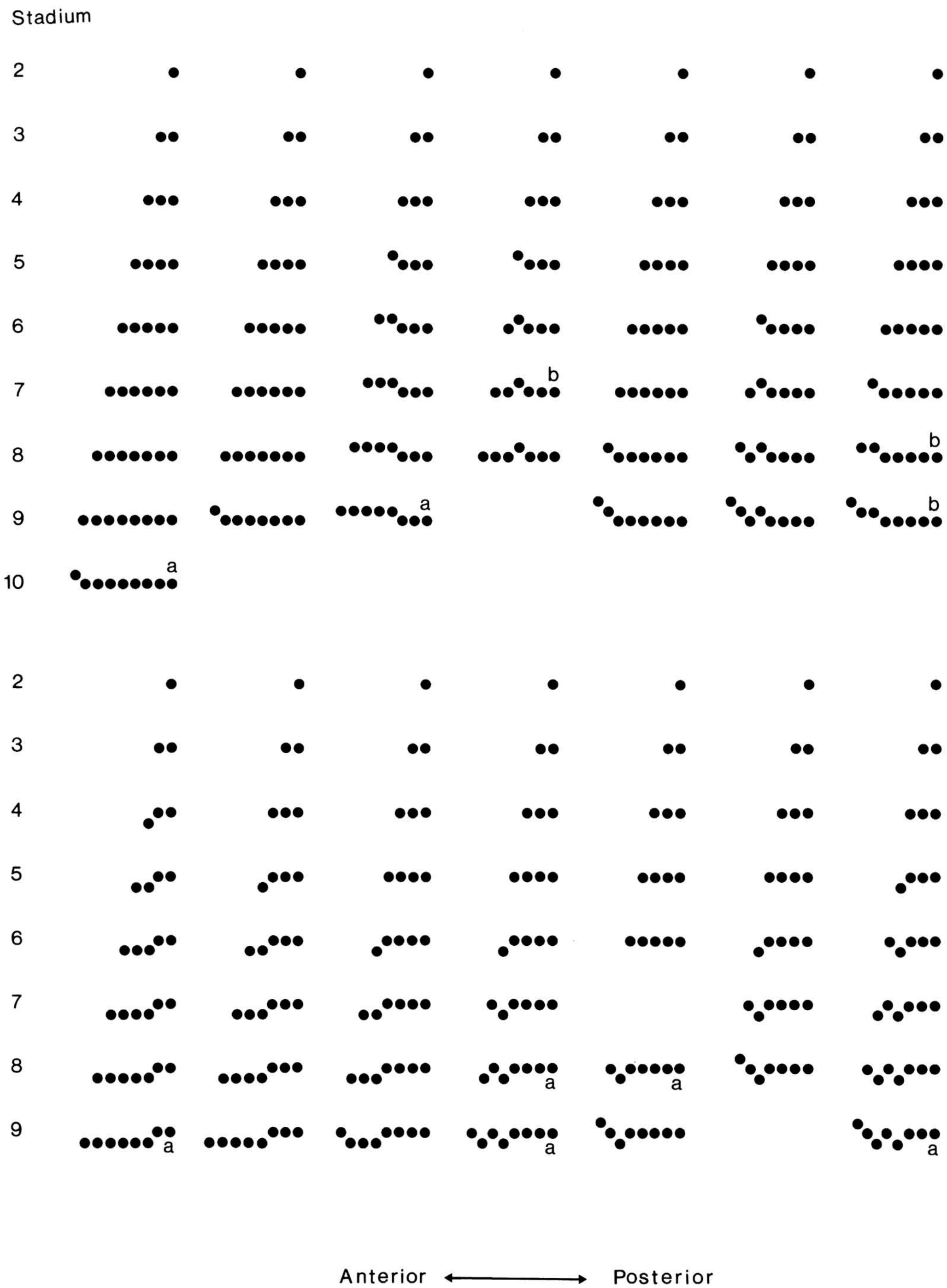

Fig. 2. Representative series of eye growth. Eyes of individuals in later stadia can be derived by assuming anterior addition of a single ocellus. Upper series represent growth in dorsal, lower series growth in ventral direction. Gaps indicate intermediate stages not actually observed. — [a] only in *N. kochii*, [b] only in *C. palmatus*.

Table 2. 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	7	*n*
C. palmatus									
1	100.0								9
2	0.0	100.0							86
3	1.3	24.7	74.0						81
4	15.5	19.7	44.7	34.1					132
5	0.7	14.0	25.2	41.3	18.9				143
6	2.6	9.7	36.8	21.5	13.6	15.8			228
7	0.8	7.5	29.7	9.5	28.6	15.9	8.0		252
8	7.9	7.9	23.8	12.7	11.1	23.9	7.9	4.8	63
n	26	198	329	185	137	91	25	3	994
N. kochii									
1	100.0								6
2	0.0	100.0							45
3	0.8	8.6	90.6						129
4	2.4	20.3	22.2	55.1					207
5	1.7	15.2	24.0	19.3	39.8				171
6	5.8	6.7	36.5	10.6	12.5	27.9			104
7	7.9	8.7	32.3	21.2	11.0	7.9			127
8	8.2	14.7	29.5	19.7	11.5	8.2	1.6	6.6	61
9	25.0		25.0	37.5				12.5	8
n	38	151	303	200	102	48	11	5	858

Table 3. Percentage distribution of eyes with initial linear additions in ventral, middle and dorsal positions in different eye-size classes. Number of one- or two-row eyes also given.

Ocelli	Initial row				One or
	ventral	middle	dorsal	*n*	two rows
C. palmatus					
4	100.0	0.0	0.0	11	121
5	88.0	12.0	0.0	25	118
6	63.5	33.8	2.7	74	154
7	71.4	25.0	3.6	112	140
8	70.3	18.9	10.8	37	26
Total	71.8	24.3	3.9	259	559
N. kochii					
4	100.0	0.0	0.0	2	205
5	90.9	9.1	0.0	11	160
6	41.2	52.9	5.9	17	87
7	43.2	38.6	18.2	44	83
8	36.0	48.0	16.0	25	36
9	0.0	40.0	60.0	5	3
Total	45.2	39.4	15.4	104	574

In both species growth usually started in the ventral row. Its clear dominance in eyes with small numbers of ocelli suggested that the three-row pattern was attained more rapidly than in other growth types. The middle row was the next in frequency, being even more common in *N. kochii*. Growth started in the dorsal row always with low frequency.

The distributions of eyes with linear, two-, and three-row patterns are given in Table 4. The frequencies of linear eyes diminished rapidly with continuing growth. One-row eyes were significantly more frequent *N. kochii* in size classes with 3–6 ocelli (χ^2-test, $P < 0.01$) suggesting a lower probability of diagonal and lateral additions in this species.

3.2.2. The two-row pattern

In eyes with two occupied rows the direction of the lateral or diagonal addition could be recorded but the rows could not be identified. A null hypothesis can be based on the frequencies of positions of the initial row in Table 3 and by assuming that in the eyes in which the growth begins in the middle row the second row is occupied at random. In *C. palmatus* we would then

Table 4. Percentage distribution of linear, two-row and three-row arrangements in different eye-size classes.

Ocelli	1	2	3	4	5	6	7	8	9
C. palmatus									
1-row	100.0	100.0	75.3	34.1	18.8	15.8	7.9	4.8	
2-row			24.7	57.6	63.6	51.7	47.6	36.5	
3-row				8.3	17.5	32.5	44.5	58.7	
n	9	86	81	132	143	228	252	63	
N. kochii									
1-row	100.0	100.0	90.7	55.1	39.8	27.9	7.9	6.6	
2-row			9.3	43.9	53.8	55.8	57.5	52.4	37.5
3-row				1.0	6.4	16.3	34.6	41.0	62.5
n	6	45	129	207	171	104	127	61	8

Table 5. Distribution of minimum number of initial linear additions in different eye-size classes in eyes with two ocelli rows, all grouped according to the direction of the second row.

Ocelli		Minimum number of linear additions								Total	Mean ± *SE*
		0	1	2	3	4	5	6	7		
C. palmatus											
Dorsal	3	1	16							17	0.94 ± 0.06
	4	1	5	57						63	1.89 ± 0.05
	5	1	7	4	56					68	2.69 ± 0.09
	6		6	13	3	31				53	3.11 ± 0.16
	7		1	6	4	4	40			55	4.38 ± 0.15
	8	2	3	1	2			5		13	3.15 ± 0.70
										Total 269	
Ventral	3		3							3	1.00
	4	1	10	2						13	1.08 ± 0.14
	5		10	10	3					23	1.70 ± 0.15
	6	2	12	45	6					65	1.85 ± 0.08
	7	1	5	52	6	1				65	2.02 ± 0.07
	8			6	2	1	1			10	2.70 ± 0.34
										Total 179	
N. kochii											
Dorsal	3		3							3	1.00
	4	3	10	35						48	1.67 ± 0.09
	5	2	6	8	30					46	2.44 ± 0.13
	6	4	2	3	1	13				23	2.74 ± 0.34
	7	2		3	5	1	14			25	3.80 ± 0.32
	8	3	3					1		7	1.29 ± 0.81
	9	1							1	2	3.50 ± 3.50
										Total 154	
Ventral	3	1	8							9	0.89 ± 0.11
	4	2	30	11						43	1.21 ± 0.08
	5		19	24	3					46	1.65 ± 0.09
	6	2	4	26	3					35	1.86 ± 0.11
	7	1	8	26	10	3				48	2.13 ± 0.12
	8		3	9	11	2				25	2.48 ± 0.17
	9	1								1	0.00
										Total 207	

expect additions in the dorsal direction in 84%, and in *N. kochii* in 65% of the cases. The actual respective values were 60% and 43%. In both species the null hypothesis seemed not to be true (Table 5, χ^2-test, $P < 0.001$ in both species). Diagonal and lateral additions in the middle row appeared to be mostly in the ventral direction. Thus, dorsal additions usually indicated a ventral initial row. In two-row eyes of this type the two-row pattern seemed to be attained later, after a greater number of initial linear additions.

3.2.3. The three-row pattern

The analysis of the three-row pattern (Table 6) confirmed that when growth started in the middle row, the addition leading to a two-row pattern usually occurred in both species in the ventral direction. In most cases the ocellus leading to the three-row pattern was formed by diagonal addition, and this part of the growth sequence could be accurately traced. In only one eye (in *C. palmatus*) were two ocelli formed in the vicinity of

Table 6. *C. palmatus* and *N. kochii*, distribution of minimum number of initial linear additions in different eye-size classes in eyes with three ocelli rows grouped according to initial row. For the middle row direction of first diagonal or lateral addition given. In addition, in *C. palmatus* one 7-ocelli eye with initial row of 5 ocelli and an ocellus both ventrally and dorsally adjacent to centrally formed ocellus found but not included.

Ocelli	*C. palmatus*								*N. kochii*							
row	0	1	2	3	4	5	Total	Mean ± *SE*	0	1	2	3	4	5	Total	Mean ± *SE*
Ventral																
4		11					11	1.00		2					2	1.00
5			22				22	2.00	1		9				10	1.80 ± 0.20
6	1	4	2	40			47	2.72 ± 0.10				7			7	3.00
7	1	6	6		67		80	3.58 ± 0.12	7		2		10		19	2.32 ± 0.44
8	2	1	5	2	2	14	26	3.65 ± 0.34	2		1	1		5	9	3.33 ± 0.73
						Total	186							Total	47	
Dorsal																
6	2						2	0.00		1					1	1.00
7			4				4	2.00			7	1			8	2.13 ± 0.13
8		1	3				4	1.75 ± 0.25		1	3				4	1.75 ± 0.25
9												3			3	3.00
						Total	10							Total	16	
Middle ventral																
5		2					2	1.00		1					1	1.00
6	1		23				24	1.92 ± 0.08			9				9	2.00
7		6	7	14			27	2.30 ± 0.16		3	2	11			16	2.50 ± 0.20
8	1			2	4		7	3.14 ± 0.55		2	5		5		12	2.67 ± 0.36
9											1				1	2.00
						Total	60							Total	39	
Middle dorsal																
5		1					1	1.00								
6			1				1	2.00								
7											1				1	2.00
8																
9											1				1	2.00
						Total	2							Total	2	

the same central ocellus in opposite directions. When the initial growth occurred in the ventral or dorsal row, the three row pattern was in 83% (*C. palmatus*) and 73% (*N. kochii*) of the cases established in two successive additions starting from the linear row. When the initial row was the middle row, in 62% (*C. palmatus*) and 66% (*N. kochii*) of cases the three-row pattern was attained after three successive diagonal additions: the first diagonally (again usually in a ventral direction), the second again in the middle row and the third diagonally in the last unoccupied row. In other cases varying numbers of additions retaining the two-row pattern occurred prior to the addition in the third row. The differences in the growth pattern between the middle and lateral rows seemed to explain the dominance of the ventral row pattern in small eye-size classes (4–5 ocelli) shown in Table 3 and the long initial linear growth in two- and three-row eyes with a ventral initial row.

4. Discussion

The material contained 35 (*C. palmatus*) and 24 (*N. kochii*) individuals with an unusually extended caudal part. The new defence-gland group was difficult to count or was not visible, but the new ocellus at least in one eye was already formed. Apparently eye-growth precedes the formation of defence glands. It is thus possible that individuals at the later stages of an ongoing moult can be mistaken as having a two-ocelli moult. In 57% and 54% of individuals with an extended caudal part,the eyes had different numbers of ocelli; twice the frequency in the entire material. This suggests that the formation of new ocelli is not strictly synchronized.

The tendency toward linear eye growth in *C. palmatus* and *N. kochii* has been noted earlier. Blower (1955) used the linear arrangement of ocelli as a diagnostic character separating these species from *P. fuscus*. Later Hopkin & Blower (1987) described in both species several individuals which have "displaced" ocelli in the middle of the ocular row. Our data indicated that two- and three-row patterns are a normal feature in these species.

In all three blaniulid species hitherto studied, the same basic pattern of eye growth was present. In early moults one new ocellus was added in 95–98% of cases, in the remaining cases a null moult occured with clearly greater frequency than did a two-ocelli moult. Later, presumably with the attainment of maturity, the frequency of standard moults decreased rapidly. Many minor details were similar. Thus, growth started in the ventral row with high frequency, and this often led more rapidly to a two- and three-row structure. Initial growth in the dorsal row was always rare. Growth in the middle row seemed to lead to a more variable growth pattern. The main species-specific differences appeared in the frequency of growth in the middle row.

In *P. fuscus* the initial growth usually starts in the middle row, and this at least partly explains the more variable growth pattern. On the other hand, material used by Peitsalmi & Pajunen (1991) contains only a few large individuals, the largest individuals being in the 11th stadium. However, no termination of eye-growth could be observed in large individuals.

Acknowledgements. We wish to thank Dr. Henrik Enghoff for identification of the species and for comments on the manuscript, and Dr. Carolyn Norris for revision of the English text.

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