VARIATION AND POST-EMBRYONIC GROWTH IN THE NUMBER OF ANTENNAL SEGMENTS IN THE *PHADKA* GRASSHOPPER (*HIEROGLYPHUS NIGROREPLETUS* BOLIVAR), WITH REMARKS ON THE DESERT LOCUST AND OTHER ACRIDIDAE (INSECTA: ORTHOPTERA).

(With 10 Tables and 2 Text-figures.)

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CONTENTS.

I—INTRODUCTION.

Data on variation and post-embryonic growth in the number of antennal segments in the family Acrididae (locusts and short-horned grasshoppers) are scattered in literature. The earlier data were summarised by Uvarov (1928), but a considerable amount of new and more detailed information has accumulated subsequently.

Here I have presented first, the new data on variation and post-embryonic growth in the number of antennal segments in the *phadká* grasshopper, *Hieroglyphus nigrorepletus* Bolivar, whose egg-pods were obtained by me in June 1950 from the Ajmer State in Rajasthan, and subsequently reared in the Insectary at the Forest Research Institute. A large number of adults and hoppers of all stages were examined. Secondly, I have critically discussed the available data on the Desert Locust, *Schistocerca gregaria* (Forskål), and added some new data on that species. Finally, the available information on the family Acrididae as a whole is summarised and discussed, and some general tentative conclusions arrived at. There is need for more detailed data on this subject, and it is hoped that this may be forthcoming in the future. A general discussion on the growth of the antennal segments in various orders of insects will be found in Imms (1940).

Acknowledgment is made of the assistance received from Mr. Balwant Singh, Research Assistant (I) in the Forest Entomology Branch, in counting the number of antennal segments of *Hieroglyphus nigrorepletus*.

II—ANTENNAE OF *Hieroglyphus nigrorepletus* BOLIVAR.

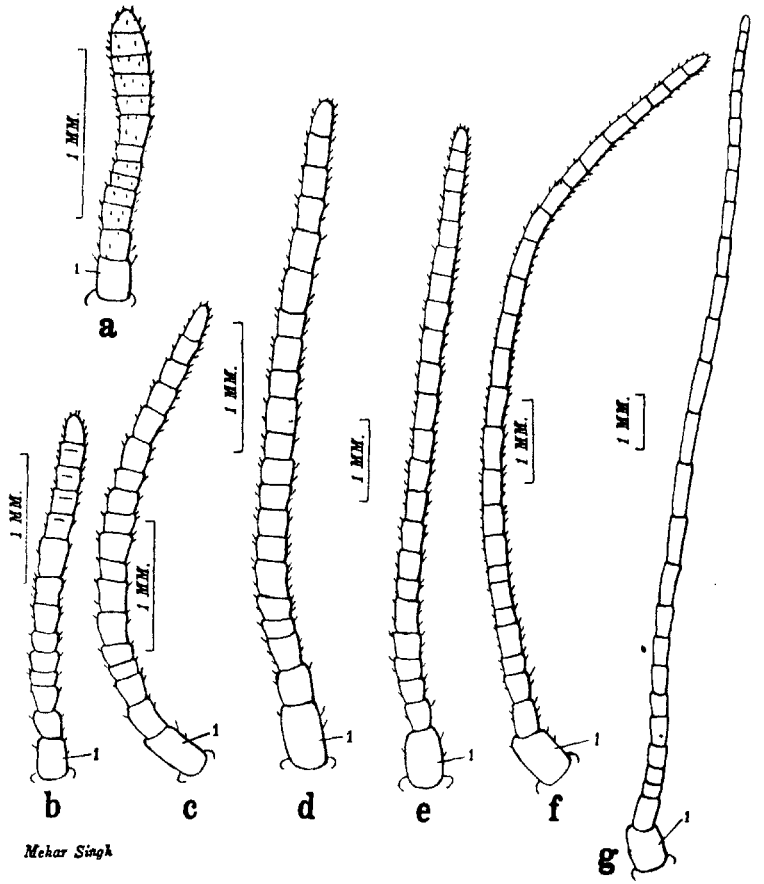
(Text-fig. 1 and Tables 1–3.)

(i) *Post-embryonic growth.*

A careful count of the number of antennal segments was made in all the 6 hopper stages and in the 'fawn type' and 'green type' brachypterous (short-winged)

adults of *Hieroglyphus nigrorepletus* Bol., a maximum of 13 individuals being examined for each stage.* In addition, one example of the rare macropterous (long-winged) adult was also examined. The number in the right and left antennae was counted separately, but no significant differences were found, though the number frequently varies in the same individual. The sexes were analysed separately, but no constant sexual differences were noticeable. The number of antennal segments (Table 1) increases from 13 in the first stage hopper to a maximum of 29 in the seventh or adult stage, the number present in each stage showing a certain amount of variation as discussed below.

In the first and second stages the number is 13 and 14 respectively, though in some individuals of the latter stage the 7th, 8th and 9th segments show some signs



TEXT-FIG. 1.

Hieroglyphus nigrorepletus Bolivar. Antennae of various instars. (*a*) First instar, left antenna of ♂, with 13 segments. (*b*) Second instar, right antenna of ♂, with 14 segments. (*c*) Third instar, left antenna of ♀, with 18 segments. (*d*) Fourth instar, right antenna of ♂, with 21 segments. (*e*) Fifth instar, right antenna of ♀, with 24 segments. (*f*) Sixth instar, left antenna of ♀, with 26 segments. (*g*) Seventh instar (adult), right antenna of brachypterous (short-winged) ♀, with 27 segments.

1, first (basal) segment or scape.

* In this paper the terms 'stage' and 'instar' are used as synonyms.

TABLE 1.

Hieroglyphus nigrorepletus Bol. Counts of the number of antennal segments in the various hopper stages and in the brachypterous (short-winged) adults of 'fawn' and 'green' types.
Abbreviations.—d, damaged; L, left antenna; R, right antenna.

Serial Number.	HOPPER STAGES.																						ADULTS (SHORT-WINGED TYPE EXCEPT WHERE OTHERWISE STATED).								REMARKS.
	1st stage.				2nd stage.				3rd stage.				4th stage.				5th stage.				6th stage.				'Fawn' type.				'Green' type.				
	Male.		Female.		Male.		Female.		Male.		Female.		Male.		Female.		Male.		Female.		Male.		Female.		Male.		Female.		Male.		Female.		
	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	
1	13	13	13	13	14	14	14	14	17	16	20	18	23	23	22	21	25	25	24	23	26	25	23	d	28	29	28	28	27	29	21	29	
2	13	13	13	13	14	14	14	14	20	20	18	18	21	21	21	21	26	d	25	d	27	27	27	26	29	29	28	28	d	29	25	27	
3	13	13	13	13	14	14	14	14	19	18	17	19	21	21	21	16	24	24	24	23	27	24	26	19	28	28	28	28	..	..	28	29	
4	13	13	13	13	14	14	14	14	20	18	18	18	21	21	21	21	d	24	23	23	26	26	28	28	28	28	22	28	..	..	d	28	
5	13	13	13	13	14	14	14	14	20	20	19	18	21	21	21	21	20	23	23	23	26	26	d	16	27	28	20*	28	..	..	27	d	*Apparently damaged, though tip is rounded.
6	13	13	13	13	14	14	14	14	19	19	18	19	23	23	21	21	23	23	23	23	27	27	28	14	28	20*	27	27	..	..	d	27	*Evidently a genuine case of asymmetry.
7	13	13	13	13	14	14	14	14	18	18	18	20	23	23	21	21	23	25	23	d	..	..	23	26	28	27	28	28	..	..	27	d	
8	13	13	13	13	14	14	14	14	19	20	20	19	21	21	23	23	23	24	24	23	..	..	27	27	29	22	28	28	..	..	29	d	
9	13	13	13	13	..	..	14	14	19	19	19	18	21	21	21	22	23	23	25	24	..	..	27	28	29	28	28	28	..	..	..	..	
10	13	13	13	13	..	..	14	14	18	18	19	18	21	21	23	23	24	24	24	24	..	..	27	14	28	28	27	27	..	..	..	..	
11	13	13	13	13	..	..	14	14	..	..	..	..	21	21	22	22	24	23	..	..	..	..	28	28	28	28	27	27	..	..	..	..	
12	13	13	13	13	..	..	..	..	..	..	..	..	20	21	21	21	24	25	..	..	..	..	26	26	29	28	..	..	..	..	..	..	
13	13	13	13	13	..	..	..	..	..	..	..	..	21	21	23	23	24	24	..	..	..	..	..	..	28*	28*	..	..	..	..	..	..	*Macropterous (long-winged) adult.
Range, etc.	13	13	13	13	14	14	14	14	17–20	16–20	17–20	18–20	20–23	21–23	21–23	21 (16)–23	23 (20)–26	23–25	23–25	23–24	26–27	24–26	23–28	14–28	27–29	20–29	20–28	27–28	27	29	21–29	27–29	
	13		13		14		14		16–20		17–20		20–23		21 (rarely 16)–23		23 (rarely 20)–25		23–25		26 (rarely 24, 25)–27		23 (rarely 14, 19)–28		27 (rarely 20–22)–29		27 (rarely 20–22)–28		27–29		27 (rarely 21–25)–29		

of partial division into two segments so as to give the impression of a total of 17 segments. In the third stage the intra-instar variability (*i.e.*, variation between the different individuals of the same instar) is first discernible* and continues in the subsequent instars. The number of segments in the third stage varies from 16–20, but ranges mostly around 18–20. In the fourth stage, the number is usually 21–23 (most commonly 21), but in one female the left antenna had only 16 segments, although the right antenna had 21. In the fifth stage the number is usually 23–25 (most commonly 23), but in one male the right antenna had only 20 segments, although the left one had 23. In the sixth stage the number is usually 26-27, and occasionally as high as 28. At the lower end, numbers as low as 14–19 occasionally occur in the sixth stage on one side of an individual, although the number on the other side of that same individual may be normal; this extreme irregularity appears to be rather more common in females than in males, as the following four counts of females show (see Table 1 for males), the number within brackets being the number on the opposite side of the same individual: 19(26); 16(–); 14(28); 14(27). In the seventh stage (brachypterous adults) the number is commonly 27-28, occasionally 29; rarely, it may be as low as 20–22 on one side, although the number on the opposite side of the same individual is the normal 27-28. In one adult female the number was 20 in the right and 28 in the left, the right antenna showing signs of damage though the tip was rounded. Similarly, in one male the left antenna, which appeared quite normal, had 20 segments, and the right one 28. No significant difference between the 'fawn' and 'green' type adults was noticeable. One macropterous adult male had 28 segments in both the antennae.

Summing up, the post-embryonic growth in the number of antennal segments is as indicated in Table 2 below:

TABLE 2.

Hieroglyphus nigrorepletus Bol. Summary of the post-embryonic growth in the number of antennal segments.

Stage.	I	II	III	IV	V	VI	VII (adult).
Number of antennal segments.	13	14	Usually 18–20. Rarely 16-17.	Usually 21–23 (mostly 21). Rarely as low as 16.	Usually 23–25 (mostly 23). Rarely as low as 20.	Usually 26–27. Rarely as low as 14–19 and as high as 29.	Usually 27–28. Rarely as low as 20–22 and as high as 29.

It will thus be seen that the number of antennal segments alone is not always a safe guide in determining the hopper stage, although it does provide a useful guide when considered with other characters.

For comparison, it is interesting to note that in the closely allied species *Hieroglyphus banian* Fabr. (where males undergo 6 moults and females 7, in contrast to 6 moults in both the sexes in *H. nigrorepletus*), the post-embryonic increase in the number of antennal segments in the various stages, according to the data of Coleman and Kuhni Kannan (1911),i s from 13 in the first stage in both sexes to 25-26 in the sixth (or penultimate) stage in males and 27-28 in the seventh (or penultimate) stage in females (Table 1). Figures for adults were not given by

* Attention to this phenomenon and to the importance of the third instar in the family Acrididae in general has already been called by Roonwal (1946 ; 1952).

these authors. All the 8 long-winged adults (4 males, 4 females) from Ceylon, that I recently studied, had 29 segments.

(ii) *Variation.*

Variation in the number of antennal segments has to be considered in three respects: (*a*) the occurrence of normal variability as between the different instars (intra-instar variability); (*b*) the occurrence of bilateral asymmetry in the right and left antenna of the same individual; and (*c*) the variation in the increase in the number of segments at each moult.

The normal intra-instar variability has already been considered above to some extent. Regarding the occurrence of bilateral asymmetry, it will be noticed that in the first and second instar hoppers there is complete symmetry, the number in the right and left antennae being 13 in the first and 14 in the second stage in all the individuals examined. The intra-instar difference (Table 1) as well as bilateral asymmetry (Table 3) in the right and left antennae of the same individual are first

TABLE 3.

Hieroglyphus nigrorepletus Bol. Data on bilateral asymmetry (difference between the right and left antenna of the same individual) in the number of antennal segments. (*From* data in Table 1.)

Abbreviation.—T., total.

Stage.	Total number examined.	Number of individuals showing *symmetry* (and % of total).	Number of individuals showing *asymmetry* (and % of total).	Difference in the number of antennal segments in *asymmetrical* individuals.	
				Range.	Frequency distribution of differences. (Figures in brackets indicate frequency.)
I	13	All (100%)	Nil	..	..
II	♂ 8 ♀ 11	All (100%)	Nil	..	..
III	♂ 10	6(60%)	4(40%)	1– 2	1, 1, 1, 2
	♀ 10	2(20%)	8(80%)	1– 2	1, 1, 1, 1, 1, 2, 2, 2
	T.20	8(40%)	12(60%)	1– 2	1(8), 2(4)
IV	♂ 13	12(92·3%)	1(7·7%)	1	1
	♀ 13	10(76·9%)	3(23·1%)	1– 5	1, 1, 5
	T.26	22(84·6%)	4(15·4%)	1– 5	1(3), 5(1)
V	♂ 11	6(54·5%)	5(45·5%)	1– 3	1, 1, 1, 2, 3
	♀ 8	4(50%)	4(50%)	1	1, 1, 1, 1
	T.19	10(52·6%)	9(47·4%)	1– 3	1(7), 2(1) 3(1)
VI	♂ 6	4(66·7%)	2(33·3%)	1– 3	1, 3
	♀ 10	4(40%)	6(60%)	1–14	1, 1, 3, 7, 13, 14
	T.16	8(50%)	8(50%)	1–14	1(3), 3(2), 7(1), 13(1), 14(1)
VII (adult)	♂ 13	5(38·5%)	8(61·5%)	1– 8	1, 1, 1, 1, 1, 2, 7, 8
	♀ 14	9(64·3%)	5(35·7%)	1– 8	1, 2, 6, 8, 8
	T.27	14(51·9%)	13(48·1%)	1– 8	1(6), 2(2), 6(1), 7(1), 8(3)

evident in the third stage (*vide* remarks in foot-note above), and continue thereafter up to the seventh or adult stage. In nearly all the stages from the third to the adult, roughly one-half the number of individuals are symmetrical, and the remainder

asymmetrical. As regards the difference in the number of segments in the right and left antennae of the same individual, this varies from 1–2 in the third stage, 1–14 in the sixth, and 1–8 in the seventh (adult). On the whole, there is a rough tendency for this difference to increase with growth, the range of the difference being rather higher in the older instars. There is also noticeable a slight tendency for this difference to be more marked in females than in males, this feature being especially noticeable in the sixth and seventh stages.

The increase in the number of segments is 1 at the first moult and 2–6 at the second. In subsequent moults the increase in individual isolated hoppers was not followed, so that it is not possible to state the precise increase in number of segments with each moult from individual cases.

III—Antennae of *Schistocerca gregaria* (Forskål).

(Text-fig. 2 and Tables 4–9.)

Variation in the number of antennal segments in *Schistocerca gregaria* will be considered from two aspects, namely: (*i*) variation in the number of segments in the adult and its correlation with the number of eye-stripes, phase-categories and the number of moults; and (*ii*) the post-embryonic growth and variation in the number of segments.

I have here critically discussed the available data, and also added some new facts.

(i) *Variation in the adults.*

Ballard, Mistikawi and Zoheiry (1932) stated that both in the *solitaria* and the *gregaria* phases in *Schistocerca gregaria* the number of antennal segments in individuals undergoing the normal 5-moult (*i.e.*, 6-stage, including the adult) cycle increased from 13 in the first stage to 19 in the second, 21 in the third, 23 in the fourth and 25 in the fifth. No mention was made of their correlation with the variation in the number of eye-stripes which was discovered later (Roonwal, 1936–1947). We now know firstly, that the number of eye-stripes vary from 5 to 8, but are mostly 6 to 7; and secondly, that phase *gregaria* individuals always have 6 eye-stripes whereas phase *solitaria* individuals have either 6 to 7 eye-stripes.

Husain (1937) claimed that 7-eye-striped adults invariably possess 28 antennal segments. He also claimed a correlation of this number with the occurrence of an extra-moult in the 7-eye-striped individuals. Both these claims have not been borne out by subsequent work.

Rao (1938), and Mukerji and Batra (1938) gave the correlation of antennal segments and eye-stripes in the adults as follows:—5-striped, 25; 6-striped, 26–27; 7-striped, 28–29; and 8-striped, 30.

Rao and Gupta (1939) showed that 6-eye-striped phase *gregaria* individuals (taken from swarms) have 26 segments, while 6-eye-striped phase *solitaria* individuals have 27 segments. I have been able to confirm the first part of this finding. The second part, however, is only partially correct. I have examined a number of phase *solitaria* 6-eye-striped individuals (Table 4) and found in this category individuals with both 26- and 27-segmented antennae, as also found by Rao and Gupta. But a further analysis has shown that *solitaria* individuals with higher E/F ratios (length of elytron/length of hind-femur) tend to have 26 segments, while those with lower E/F ratios have generally 27 segments in the antennae, as is evident from the following summary of the data in Table 4:—

(*a*) *Among males*—

(i) E/F 1·88–2·00.—Out of 15 examples, 1 had 26, and 14 had 27 segments.
(ii) E/F 2·01–2·05.—Out of 12 examples, 7 had 26, and 5 had 27 segments.
(iii) E/F 2·06–2·20.—All the 5 examples examined had 26 segments.

TABLE 4.

Schistocerca gregaria (Forskål). Number of antennal segments in 6-eye-striped phase *solitaria* individuals, taken from Baluchistan in 1936–37 under typical *solitaria* conditions of very low population of usually below 1,000 per square mile. Note correlation with E/F ratio.

Serial No.	Sex.	E/F ratio.	No. of antennal segments.	Serial No.	Sex.	E/F ratio.	No. of antennal segments.
1	♂	1·88	27	26	♂	2·05	26
2	♂	1·88	27	27	♂	2·05	26
3	♂	1·89	27	28	♂	2·06	26
4	♂	1·89	27	29	♂	2·14	26
5	♂	1·89	27	30	♂	2·15	26
6	♂	1·90	27	31	♂	2·17	26
7	♂	1·92	27	32	♂	2·20	26
8	♂	1·92	27				
9	♂	1·96	26	33	♀	1·97	27
10	♂	1·96	27	34	♀	1·97	27
11	♂	1·98	27	35	♀	2·02	27
12	♂	1·99	27	36	♀	2·02	27
13	♂	1·99	27	37	♀	2·05	27
14	♂	1·99	27	38	♀	2·05	26
15	♂	2·00	27	39	♀	2·05	27
16	♂	2·01	26	40	♀	2·09	27
17	♂	2·01	27	41	♀	2·14	27
18	♂	2·01	27	42	♀	2·14	27
19	♂	2·01	26	43	♀	2·14	27
20	♂	2·01	26	44	♀	2·16	26
21	♂	2·02	27	45	♀	2·16	26
22	♂	2·02	26	46	♀	2·17	27
23	♂	2·03	27	47	♀	2·20	26
24	♂	2·04	27	48	♀	2·23	26
25	♂	2·05	26	49	♀	2·24	26

(*b*) *Among females*—

(i) E/F 1·97–2·14.—Out of 11 examples, 1 had 26 segments, and 10 had 27 segments.

(ii) E/F 2·16–2·24.—Out of 6 examples, 5 had 26 segments and 1 had 27 segments.

The correlation between the number of adult antennal segments on the one hand and the number of eye-stripes and phase-category on the other, is briefly summarised in Table 5.

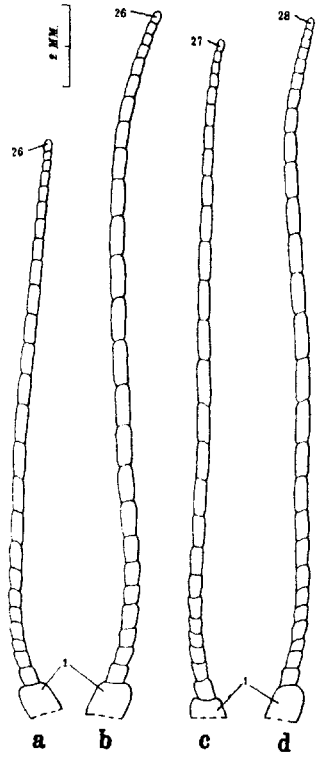
TABLE 5.

Schistocerca gregaria (Forskål). Correlation between the number of adult antennal segments on the one hand, and the number of eye-stripes and phase phase-category on the other.

Number of eye-stripes.	5 (rare).	6	7	8 (rare).
Number of antennal segments.	25	(i) Ph. *greg.*—26. (ii) Ph. *sol.*—26–27. 26 in those with higher E/F ratios and 27 in those with lower ratios.	28–29 (ph. *sol.*)	30
Normal number of moults.	4	5	5–6	6–7

(ii) *Post-embryonic growth.*

Regarding the mode of origin of the difference in the number of segments in the adult, a study of development has shown (Ballard, Mistikawi and Zoheiry, 1932; Rao, 1938; Mukerji and Batra, 1938; and Roonwal, present account) that the number



TEXT-FIGURE 2.

Schistocerca gregaria (Forskål). Antennae of adults showing variation in the number of segments. (*a*) Right antenna, with 26 segments, of a 6-eye-striped, phase *gregaria* ♀ from a swarm in Peshawar (N.W.F.P.). (*b*) Left antenna, with 26 segments, of a 6-eye-striped phase *solitaria* ♀ from Lasbela State, Baluchistan. (*c*) Right antenna, with 27 segments, of a 6-eye-striped phase *solitaria* ♀ from Lasbela State, Baluchistan. (*d*) Left antenna, with 28 segments, of a 7-eye-striped phase *solitaria* ♀ from Baluchistan.

1, first (basal) segment or scape; 26, 27, 28, twenty-sixth, twenty-seventh and twenty-eighth segments.

of antennal segments increases with each moult, the number in the first stage always being 13. Since extra-moulting is also *one* of the methods of the addition of extra eye-stripes (*vide* Roonwal, 1947), a certain degree of correlation between the increased number of eye-stripes and that of the antennal segments will be evident. On the other hand, individuals with the same number of eye-stripes, *viz.*, 6, may have a varying number of antennal segments, the number being partly correlated with phase-category but *not* to the number of moults, since 6-eye-striped individuals have, normally, 5 moults in *both* the *solitaria* and the *gregaria* phases. The statement of Mukerji and Batra (1938), that 'since the number of eye-stripes

have been found to correspond with the number of instars, and as the latter, in turn, bears a relationship with the number of antennal segments of each stage, it follows that the three factors are organically connected with one another', is only partially true, for the correlations claimed by these authors in respect of eye-stripes and moulting are only partial, as has already been shown by Roonwal (1947).

A study of post-embryonic development has shown that irrespective of the kind of adults produced in respect of eye-stripes and phase-category, *two* types of individuals are produced in the third instar hopper, one with 20 and another with 21 antennal segments. Thereafter, in eight 6-eye-striped examples studied, the course of subsequent development was common and 2 segments were added at each moult, thus resulting in 26- and 27-segmented adults (Table 6).

TABLE 6

Schistocerca gregaria (Forskål). Course of development of the antennal segments in 6-eye-striped individuals (all with 5-moults).

Stage.	I	II	III	IV	V	VI (adult)
Number of eye-stripes.	1	2	3	4	5	6
Number of antennal segments.	13	19	20 21	22 23	24 25	26 27

The origin of the initial difference in the third stage is obscure, but it is not due to an extra-moult. It may be mentioned that this is yet another example of the peculiarity and extraordinary importance of the third instar (*vide* Roonwal 1940; 1952; and present paper, foot-note on p. 219 above). Nor is the difference in the number of moults *alone* the cause of the difference in the number of segments in the individuals with a varying number of eye-stripes as contended by Mukerji and Batra (1938), though moulting certainly is *one* of the factors which leads to the addition of segments. The number of segments is also partly correlated with phase-category in the 6-eye-striped individuals. The problem needs further enquiry.

IV—DISCUSSION AND GENERAL CONCLUSIONS.

(Tables 7–10.)

A study of the available data on variation in the number of antennal segments and their post-embryonic growth in the Acrididae shows that these features are distinguished by the following general characteristics:—

(i) The number of segments in the adult varies, with the species, from 17–30; variation within the species is confined to narrow limits not exceeding 1–2 as a rule.

The lowest adult numbers occur in *Poecilocerus pictus** (18) and in *Colemania sphenarioides* (17–19), and occasionally in *Hieroglyphus nigrorepletus* (as low as

* Four adults from India were examined by me and gave the following counts (R, right; L, left antenna):—♂ (R, 18; L, 18), ♂ (R, 18); ♀ (R, 18); ♀ (R, 18; L, 18).

20–22, though the usual number is 27–28). The highest numbers occur in *Hieroglyphus banian* (29), *H. nigrorepletus* (27–29), and a few (8-eye-striped) individuals of *Schistocerca gregaria* (30). Variation within a species is usually within narrow limits of 1–2; but in a few cases somewhat wider limits of variation are met with, as in *Hieroglyphus nigrorepletus* (1–9), the adult number in this species being 27–29, rarely as low as 20; and in *Schistocerca gregaria* (1–5), the adult number being 26–28, rarely 25–30.

(ii) During post-embryonic growth there is an increase * (by 1 or more segments at each moult) in the number of segments from an initially low figure in the first instar.

(iii) Generally speaking, since the number of segments increase with each moult, extra-moulting individuals (*i.e.*, individuals which undergo more moults than is normal for the species) tend to have more segments in the adult than the normal-moulting individuals; conversely, under-moulting individuals have fewer segments.

Thus, in *Melanoplus bivittatus* and *Schistocerca gregaria* the extra-moulting and under-moulting individuals have, generally, more and fewer segments respectively than the normal ones. On the other hand, in *Hieroglyphus banian* and *Colemania sphenarioides* the extra-moulting individuals have the same number of segments as the normal ones (Tables 1, 7 and 8).

(iv) The initial number of segments in the first instar hopper varies with the species from 8–14 (Tables 7 and 8).

This number is generally constant for the species, and variation within the species is uncommon. In a few cases, however, the number has been shown to be inconstant. Thus, in *Locusta migratoria* Linn. it varies from 13–14, and other numbers are also encountered rarely. In *Melanoplus mexicanus* Sauss. (=*M. atlantis* Ril.) it is 12, but in *M. spretus* (which is the supposed gregarious phase of *M. mexicanus*), it is 12–13. The number is lowest in *Poecilocerus pictus* and *Colemania sphenarioides*, in both of which it is 8, and highest in species of *Locusta*, *Schistocerca*, etc. (13–14).

(v) The number of segments in the adult is correlated to a certain extent, but not absolutely, with the initial number in the first instar, the adult number being generally higher in species with the higher initial number (Tables 7 and 8).

Thus, in *Poecilocerus* and *Colemania* the initial number is 8 and the final (adult) number 17–19; in *Phoetaliotes*, *Camnula* and *Dissosteira*, the initial number is 11, and the final number 23–24; in some species of *Melanoplus* the initial number is 12, and the final number 23–26; finally, in the remainder (*e.g.*, *Hieroglyphus*, *Schistocerca*, *Locusta*, etc.) the initial number is 13 (rarely 14), and the final number usually 26–29 and occasionally as low as 20–22 (some individuals of *Hieroglyphus nigrorepletus*) and as high as 29 (some individuals of *H. nigrorepletus*) and 30 (some individuals of *Schistocerca gregaria*).

(vi) Generally speaking, in a species the intra-instar variation (*i.e.*, variation between the different individuals of the same instar) first appears commonly in the third instar but sometimes also in the second (as in *Poecilocerus*, *Locusta* and *Dociostaurus*) (Table 7). Rarely, it is evident in the very first instar, as in *Melanoplus spretus* and in *Locusta migratoria migratoria*. Once it has made its appearance, the intra-instar variation is continued in the subsequent instars, though not in a regular way.

(vii) The increase in the number of segments with each moult in a species is generally constant (within narrow limits of variation), but varies from moult to moult, the number added generally, but not always, decreasing in the later moults as compared to the earlier (Tables 9 and 10).

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* For a general discussion on several orders of insects, see Imms (1940).

TABLE 7.

Number of antennal segments in each stage of a normal post-embryonic development in some Acrididae. *Abbreviation.*—Ad., adult.

* Species in which the number of antennal segments varies in extra- and under-moulting cases are given in Table 8, and are marked here with an asterisk.

Species. [Number of normal moults are given in square brackets.]	Morphological stage (in Roman numerals) and the number of antennal segments.								Source.
	I	II	III	IV	V	VI	VII	VIII	
1. *Patanga succincta* [7] ..	?	?	16	21	22	23	?	26 (Ad.)	Lefroy (1906), for hoppers; Roonwal (present account) for adult (1 ♂ only).
2. *Hieroglyphus banian*									
♂♂ [6]	13	16	19–20	21–22	24–25	25–26	29(Ad.)	..	Coleman and Kuhni Kannan (1911) (figures for ♀♀ are probable); and Roonwal, (present account) for adults.
♀♀ [7]	13	16	19–20	21–22	24–25	25–26	27–28	29 (Ad.)	
3. *Hieroglyphus nigrorepletus* [6]	13	14	18–20 Rarely 16–7.	Usually 21–23 (mostly 21). Rarely as low as 16.	Usually 23–25 (mostly 23). Rarely as low as 20.	Usually 26–27. Rarely as low as 14–19, and as high as 29.	Usually 27–28. Rarely as low as 20–22, and as high as 29. (Ad.)	..	Roonwal (present account).
4. *Poecilocerus pictus* [6] ..	8	8(?) –9	10–11	12–14	15	15–16	18(Ad.)	..	Pruthi and Nigam (1939) for hoppers; Roonwal (present account) for adults (2♂, 2♀).
5. *Melanoplus differentialis* [6]	12	16	18	20	23	25	26(Ad.)	..	Shotwell (1941).
6. **Melanoplus mexicanus* Sauss.									
(=*M. atlantis* Ril.) [5]	12	15	18	20	22	?(Ad.)	..	..	Shotwell (1930; 1941).
Ditto [5]	12	15	17–18	21	23–24	?(Ad.)	..	..	Uvarov (1928, p. 295).
7. *Melanoplus spretus* (supposed gregarious phase of *M. mexicanus*) [5] ..	12–13	17	20–22	24–25	26	?(Ad.)	..	..	Partly from Uvarov (1928, p. 45).
8. **Melanoplus bivittatus* [5].	13	17	19	20	22	24(Ad.)	..	..	Shotwell(1941).

9.	*Melanoplus femur-rubrum* [5]	12	16	18	20	22	24–26 (Ad.)	..	..	Shotwell (1941) for hoppers and adults; Roonwal (present account) for adults (1 ♀, 26 segments).
10.	*Melanoplus packardii* [5] ..	12	16	19	20	21	24(Ad.)	..	..	Shotwell (1941).
11.	*Melanoplus gladstoni* [5] ..	12	15	18	20	21	23(Ad.)	..	..	Shotwell (1941).
12.	*Phoetaliotes nebrascensis* [5]	11	15	18	20	23	23(Ad.)	..	..	Shotwell (1941).
13.	*Camnula pellucida* [5] ..	11	12	17	18	20	23(Ad.)	..	..	Shotwell (1941).
14.	*Dissosteira carolina* [5] ..	11	14	18	20	23	24(Ad.)	..	..	Shotwell (1941).
15.	**Colemania sphenarioides* ..	8	9–10	10–12	13–15	15–17	17–19 (Ad.)	..	..	Coleman (1911).
16.	*Locusta [migratoria] migratoria* [5].	13–14	15–19	20–21	22–23	24–25	?(Ad.)	..	..	Lebedeva, 1925 (from Uvarov, 1928, p. 45).
17.	*Locusta [migratoria] migratorioides* [5].	13	19	21	22	24–25	?(Ad.)	..	..	Uvarov (1928, p. 45).
18.	*Calliptamus italicus.*									
	♂ ♂ [5]	13	16	18–20	21–22	23–24	?(Ad.)	..		Uvarov (1928, pp. 282–283).
	♀ ♀ [6]	13	17	20–22	22–23	23–24	?	?(Ad.)	..	
19.	**Schistocerca gregaria*, 6-eye-striped. [5]	13	19	20–21	23	25	26–27 (Ad.)	..	..	Rao (1938); Mukerji and Batra (1938); Roonwal (present account).
20.	*Schistocerca paranensis* [5]	13	17	20–22	24–25	26	?(Ad.)	..	..	Uvarov (1928, p. 265).
21.	*Schistocerca americana* (supposed solitary phase of *S. paranensis*) [5]. ..	13	17	20–22	25	26	?(Ad.)	..	..	Uvarov (1928, p. 45).
22.	*Schistocerca* sp. (swarming in British Guiana, South America) [6]. ..	14	17	20	22	24	26	?(Ad.)	..	Cleare (in Bodkin and Cleare, 1919).
23.	*Dociostaurus maroccanus* [5]	13	15–17	17–20	21–22	23–24	?(Ad.)	..	..	Sviridenko (1925, from Uvarov, 1928).
	Ditto .. [5]	13	17	20	22	24	25	..	..	Paoli (1937, from Imms, 1940)
	Ditto .. [5]	13	16	20 (rarely 18).	22 (rarely 21).	24	25	..	..	Jannone (1939).

TABLE 8.

Number of antennal segments added at each moult in species of Acrididae undergoing extra-moulting and under-moulting.
(For normal moulting, see Table 7.)

Abbreviations.—Ad., adult stage; n., normal number of moults; e.m., extra-moult; u.m., under-moult; A, B, normal- and extra-stage respectively of a morphological instar or stage.*

Serial No. from Table 7.	Species. [Number of moults is given in square brackets.]	Morphological (not chronological) stage* (in Roman numerals) and the number of antennal segments.								Source; and remarks.
		I	II	III		IV		V	VI	
				A	B	A	B			
6	*Melanoplus mexicanus Sauss.* (= *M. atlantis* Ril.) [n., 5]. 1 e.m. [6].	12	15	18	19	22		23	? (Ad.)	Shotwell (1930, 1941).
8	*Melanoplus bivittatus* [n., 5]. 1 e.m. [6]	13	17	19	22	23		24	26(Ad.)	Shotwell (1930, 1941).
15	*Colemania sphenarioides* [n., 5]. 1 e.m. [6]	8	9–10	10–12	13–15	15–17		17–18	17–19 (Ad.)	Coleman (1911). Probable figures.
19	*Schistocerca gregaria* [n., 5]. 1 u.m. [4]	13	19	20–21		23		25 (Ad.)	..	Rao (1938); Mukerji and Batra (1938); Roonwal (present account).
	1 e.m. [6]	13	19	20–21	22–23	25		26–27	28–29 (Ad.)	
	2 e.m. [7]	13	19	20–21	22–23	25	27	28	30 (Ad.)	

* The 'morphological stage' is to be distinguished from the 'chronological stage' (*vide* discussion in Roonwal, 1946, pp. 79–81).

TABLE 9.

Number of antennal segments added at each moult in some Acrididae. (*From* data in Tables 1, 7 and 6.)

Species. [Number of moults indicated in square brackets.]	Number of antennal segments added at each moult (between consecutive instars I–VIII).						
	1st moult (I & II)	2nd moult (II & III)	3rd moult (III & IV)	4th moult (IV & V)	5th moult (V & VI)	6th moult (VI & VII)	7th moult (VII & VIII)
1. *Patanga succincta* [7]	..	..	5	1	1	..	..
2. *Hieroglyphus banian* (*a*) [♂6] ..	3	3–4	?	?	?	3–4	..
(*b*) [♀7] ..	3	3–4	?	?	?	?	1–2
3. *Hieroglyphus nigrorepletus* [6] ..	1	2–6	?	?	?	?	..
4. *Poecilocerus pictus* [6]	1	?	?	1–3	0–1	2–3	..
5. *Melanoplus differentialis* [6] ..	4	2	2	3	2	1	..
6. *Melanoplus mexicanus* Sauss. (=*M. atlantis* Ril.) (*a*) [5] ..	3	2–3	2–4(?)	2–3(?)	?	..	..
(*b*) [6] ..	3	3	1	3	1	?	..
7. *Melanoplus spretus* (supposed gregarious phase of *M. mexicanus*) [5] ..	4–5	3–5	?	1–2	?	..	..
8. *Melanoplus bivittatus* (*a*) [5] ..	4	2	1	2	2	..	..
(*b*) [6] ..	4	2	3	1	1	2	..
9. *Melanoplus femur-rubrum* [5] ..	4	2	2	2	2–4	..	..
10. *Melanoplus packardii* [5]	4	3	1	1	3	..	..
11. *Melanoplus gladstoni* [5]	3	3	2	1	2	..	..
12. *Phoetaliotes nebrascensis* [5]	4	3	2	3	0	..	..
13. *Camnula pellucida* [5]	1	5	1	2	3	..	..
14. *Dissosteira carolina* [6]	3	4	2	3	1	..	..
15. *Colemania sphenarioides* (*a*) [5] ..	1–2	?	?	?	?	..	..
(*b*) [6] ..	1–2	?	?	?	?	..	..
16. *Locusta* [*migratoria*] *migratoria* [5] ..	?	?	?	?	?	..	..
17. *Locusta migratoria migratorioides* [5] ..	6	2	1	2–3	?	..	..
18. *Calliptamus italicus* (*a*) [♂5] ..	3	2–4	?	?	?	..	..
(*b*) [♀6] ..	4	3–5	?	?	?	?	..
19. *Schistocerca gregaria*							
(*a*) 5-eye-striped [4]	6	1–2	2–3	2	..	..	..
(*b*) 6- ,, [5]	6	1–2	2	2	2	..	..
(*c*) 7- ,, [5]	?	?	?	?	?	..	..
(*d*) 7- ,, [6]	6	1–2	?	2–3	1–2	?	..
(*e*) 8- ,, [7]	6	1–2	?	2–3	2	1	2
20. *Schistocerca paranensis* [5]	4	3–5	?	1–2	?	..	..
21. *Schistocerca americana* (supposed solitary phase of *S. paranensis*) [5] ..	4	3–5	3–5	1	?	..	..
22. *Schistocerca* sp. (swarming in British Guiana, South America) [6] ..	3	3	2	2	2	..	..
23. *Dociostaurus maroccanus* [5] .. (From Jannone, 1939).	3	4 (rarely 2)	*ca.* 2	2	2	..	..

TABLE 10.

Frequency of the number of antennal segments added at each moult in the Acrididae. (*From* Tables 1, 7, 8 and 9.)

No. of antennal segments added. →	Range.	Frequency.							Total number of species (and kinds regarding moulting) for which data are available.
		0	1	2	3	4	5	6	
1st moult ..	1–6	0	5	4	10	10	1	4	29
2nd moult ..	1–5	0	5	14	14	10	5	0	26
3rd moult ..	1–5	0	6	9	5	2	2	0	18
4th moult ..	1–3	0	8	14	9	0	0	0	23
5th moult ..	0–3	1	7	9	2	0	0	0	17
6th moult ..	1–4	0	2	2	3	2	0	0	4
7th moult ..	1–2	0	1	2	0	0	0	0	2

The increase at each moult may vary from 0–6 segments. From a study of the available data for the Acrididae (Table 10) it is seen that the number of segments added at each moult of the successive chronological moults is as follows:—

First moult: 1–6, mostly 3–4.
Second moult: 1–5, mostly 2–3.
Third moult: 1–5, mostly 2.
Fourth moult: 1–3, mostly 2.
Fifth moult: 0–3, mostly 1–2.
Sixth moult: 1–4, mostly 1 (4 cases only).
Seventh moult: 1–2 (2 cases only).

It will be seen that there is a tendency for the number of segments added at each moult to decrease with the successive chronological moults.

(viii) The increase in the number of segments at each moult does not appear to be correlated either with the initial or the final number of segments in that species, nor with the number of moults undergone during post-embryonic growth.

Thus, with the same initial number of segments in the first instar and the same number of moults in species of *Hieroglyphus* and *Melanoplus* (Table 7), the final number of segments may still vary.

(ix) Bilateral asymmetry may occur in some individuals of the older instars in a species, the remaining individuals of that instar being symmetrical. The degree of asymmetry roughly tends to increase with age, being greater in the older instars; it may also be rather more common in females than in males, especially in the older instars.

Thus, in *Hieroglyphus nigrorepletus* (Tables 1 and 3), from the third instar onward, roughly one-half the number of individuals are asymmetrical; the difference in the right and left antenna is 1–2 segments in the third stage, and is as high as 1–14 in the sixth. (For a fuller discussion of this species, *vide supra*.)

(x) In species where eye-stripe variation occurs, the number of antennal segments generally shows a positive correlation with the number of eye-stripes.

Thus, in *Schistocerca gregaria* where the number of eye-stripes varies from 5–8 (Roonwal, 1936, 1947), the 5-eye-striped (4 moult) individuals have 25 segments, the 6-eye-striped (5 moult) ones 26–27 segments, the 7-eye-striped (5–6 moult) ones 28–29 segments, and the 8-eye-striped (6–7 moult) ones 30 segments (Table 5–8). It may be added that the eye-stripe variation in this species is only partially connected with the number of moults (Roonwal, 1947).

(xi) The number of segments is also correlated with the phase-category where the phase-type of variation (see Uvarov, 1928) occurs. Phase *gregaria* individuals generally have fewer segments than phase *solitaria* ones.

Thus, in *Schistocerca gregaria* the 6-eye-striped individuals have 26 segments in phase *gregaria* and 26–27 segments in phase *solitaria* (Rao and Gupta, 1939), though both categories normally undergo only 5 moults. Among the phase *solitaria* 6-eye-striped individuals, there is noticeable, as shown above, a correlation between the E/F ratios and the number of antennal segments. Individuals with higher E/F ratios tend to have 26 segments, and those with lower ratios 27 segments. This feature is interesting in as much as phase *gregaria* individuals have the highest E/F ratios and, correspondingly, only 26 antennal segments. In other words, even in the phase *solitaria* individuals the number of segments tends to decrease as we move from the extreme *solitaria* towards the *gregaria* end of the series. In *Dociostaurus maroccarrus*, however, according to Jannone (1939, p. 416), there are 26 adult segments in all the phase-categories.

Finally, it should be emphasised that there is need for more data both regarding the number of segments in the adults and the manner of post-embryonic growth. A word regarding the technique of counting is necessary. Counting can be done in either dry or spirit specimens, and is best done in strong incident light (from an electric lamp or directly from the sun) and under a magnification of about 15 to 20 times. Transparent permanent mounts on slides are not particularly helpful. Occasionally, a segment appears to be divided into two by means of a faint transverse suture; such cases should be carefully examined to decide whether the division is real or otherwise.

V—Summary.

During post-embryonic growth in the *phadkā* grasshopper, *Hieroglyphus nigrorepletus* Bolivar, the number of antennal segments increase from 13 in the first stage to a maximum of 29 in the seventh stage or adult. The number of segments in each stage are as follows:—I, 13; II, 14; III, usually 18–20, rarely 16–17; IV, usually 21–23 (mostly 21), rarely as low as 16; V, usually 23–25 (mostly 23), rarely as low as 20; VI, usually 26–27, rarely as low as 14–19, and as high as 29; VII (adult), usually 27–28, rarely as low as 20–22, and as high as 29.

2. The characteristics of post-embryonic growth, intra-instar and intra-individual (bilateral asymmetry) in *Hieroglyphus nigrorepletus* are elucidated.

3. The post-embryonic growth in the number of antennal segments in the Desert Locust, *Schistocerca gregaria* (Forskål) is critically discussed, and some new data added. A correlation between the number of segments and the E/F ratios is shown to exist in 6-eye-striped phase *solitaria* individuals, those with higher ratios having 26 segments and those with lower ratios 26–27 segments.

4. Available data on the family Acrididae on the number of antennal segments and their variation and post-embryonic growth are summarised and discussed. Based on this data, a set of general characteristics is formulated.

VI—References.

(* Those not seen in original are marked with an asterisk.)

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