ON A NEW EVOLUTIONARY PHENOMENON: THE SHARP INCREASE OF INTRASPECIFIC VARIATION IN MINIMUM POPULATIONS, AS EVIDENCED BY THE DESERT LOCUST.

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(Plates XV—XVIII.)

(With 4 Plates, 15 Text-figures and 5 Tables.)

Contents.

I.—INTRODUCTION.

(*a*) GENERAL.

The importance of the abundance or otherwise of the population of a species playing a role in the production of variations has been realized since the days of Darwin (1876) who stated that in plants the more abundant species show greater variation, that is to say, a larger number of varieties, than the rarer species. Adlerz (1902), however, was the first author to bring forth clearly an example of the effect of population fluctuation on the production of variations in a species He observed that in the Swedish butterfly, *Polyommatus virgaureae* L., which shows periodic eruptions in numbers, morphological variation is greatly increased during years of mass-abundance than in normal years. Since then, several other such examples have come to light. The theoretical study of the statistical effects of population-size alone, other factors being constant, has been made in recent years by Hagedoorn & Hagedoorn (1921), Dubinin (1931), Wright (1931-1946) and others. From these analyses it is clear that population-size itself is capable of influencing variation-intensity to a considerable extent.

As a result of these observations and analyses, there have been revealed a variety of evolutionary phenomena (which, in the literature, have come to be termed as " Effects ") concerning the effect of population-size on the intensity of the production of variations. Our knowledge of these phenomena is based in some cases on field observations alone, and in others on theoretical analyses alone. The following 4 types of phenomena are hitherto known to exist :—(i) The automatic maintenance (equilibrium) of genetic variability in spite of crossing (the Hardy Effect) ; (ii) the rapid random (automatic) decay of variation-intensity in the total absence of selection pressure (the Hagedoorns Effect) ; (iii) the increase of variation-intensity with high populations (the Adlerz Effect) ; and (iv) the increase of variation-intensity neither in very high nor in very low populations but in populations of intermediate sizes (the Wright-Dubinin Effect).

In the present paper I have described a New Phenomenon or Effect which is characterised by the fact of the *highest* variation-intensity in *minimum* populations and the *lowest* variation-intensity in *maximum* populations. The New Effect has been found from a study of variations in the Desert Locust, *Schistocerca gregaria* (Forskal). This species is subject to periodic mass-outbreaks in comparatively short cycles of about 11 years. The outbreak years are characterised by intensive swarming in enormous numbers and extensive overflow-migrations. In the intervening years the species is confined to restricted permanent breeding areas ; and the seasonal migrations are restricted to this area, there being no overflow-migrations. The swarming and the non-swarming individuals show marked differences in colour, morphology, physiology and behaviour (Uvarov, 1923) and were called the two " phases ", *viz.*, phase *gregaria* and phase *solitaria*. The existence of increased variability in the *solitaria* phase was shown by Roonwal (1936 *et seq.*). In a preliminary account (Roonwal, 1947*d*) I had regarded this increased variation-intensity as an example of the Wright-Dubinin Effect, but later work has shown that it differs markedly from that Effect and is an altogether new phenomenon not hitherto described. I have also critically reviewed the available information on the various phenomena mentioned above, so that the new phenomenon presented here may be viewed against a suitable background.

(*b*) ACKNOWLEDGEMENTS.

It is a pleasure to express my indebtedness to the following gentlemen for the assistance which they kindly rendered in various ways : To Shri Y. Ramachandra Rao, lately Deputy Director, Bureau of Plant Protection and Quarantines, New Delhi, and formerly Locust Research

Entomologist to the Indian Council of Agricultural Research, for supplying valuable information regarding eye-stripe polymorphism in the Desert Locust from his field records and collections ; to Dr. K. R. Nair, Statistician at the Forest Research Institute, Dehra Dun, for assistance in the calculations and for discussing some problems of correlations ; to Brigadier Sir Oliver Wheeler, lately the Surveyor-General of India, New Delhi, for advice regarding suitable map-projections to use and regarding the method of computing land-areas ; and, finally, to Dr. B. P. Uvarov, Director, Anti-Locust Research Centre, London, for providing some information on the distribution of the Desert Locust.

II.—SOME DATA ON THE DESERT LOCUST.

(*a*) GEOGRAPHICAL DISTRIBUTION, ETC., OF DESERT LOCUST.

(Pl. XV.)

(i) *Geographical distribution.*

The geographical distribution of the Desert Locust differs materially in the swarming or *gregaria* phase and the non-swarming or *solitaria* phase. The following are the more important authorities who have contributed records on which our present knowledge of the distribution is based :—Drouet (1861), Walker (1870), Darwin (1876), Uvarov (1923, 1928, 1932), Chopard (1932), Faure (1932), Vayssiére (1933), Predetchensky (1935), Rao (1937, 1945), Waloff (1946*a*, *b*), Roonwal (1950), ' F.A.O.' (1952) and Fortesque-Foulkes (1953).

Phase gregaria.—In the swarming or *gregaria* phase, this locust extends over 3 continents, *viz.*, Europe, Africa and Asia. Each of these continents is invaded to the extent indicated below : ASIA : In Asia it covers the whole of the Western, Middle and S. E. Asia, east (in India) up to Assam and south up to about the level of Madras (Rao, 1945 ; and Roonwal, 1950). Walker (1870) has recorded some specimens from " Ceylon " as being present in the collection of the British Museum (Natural History), London. But Dr. Uvarov (*in litt.*, 10th November, 1947) has informed me that these specimens, which are still present, were almost certainly mislabelled " Ceylon " and were most probably from the mainland of India. There are several records from Nepal and Kashmir. Swarms are recorded north from Afghanistan and Transcaspia (southern U. S. S. R.) to almost the level of the northern tip of the Caspian Sea. The whole of the Western and Middle Asian region (Iran, Iraq, Arabia, Syria, Israel and Turkey) is subject to its invasions. EUROPE : Stray specimens in Southern Europe, evidently migrants from North Africa, have been recorded from Corfu, Noxos, Portugal, and southern England, *vide* Lucas (1920), Uvarov (1923, 1928) and Waloff (1946*b*). AFRICA : The whole of Africa, with the probable exception of the Central Sahara and the tropical rain forests of the Belgian Congo, is subject to its invasions. Swarms are common in Lybia, Algeria, Morocco, French West Africa, Egypt, the Sudan, Eritrea, Ethiopia, Somaliland, Kenya, Uganda, Tanganyika and French Equatorial Africa. Records from South Africa are scanty but specimens in the *gregaria* phase have been recorded as far south as the Cape Province. There are interesting records from the Atlantic islands off the western coast of Africa, *viz.*, from Madeira, Canary, Azores, Cape Verde and Ascension, *vide* Drouet (1861), Walker (1870), Darwin (1876), Chopard (1932), Vayssiére (1933) and Waloff (1946*b*). Scudder (1883) has recorded a swarm that came on board a ship in latitude 25° 28′ N. and longitude 41° 31′ W., *i.e.*, about midway between Africa and America, with the nearest point of land about 1,200 miles off.

Phase solitaria.—The distribution of the *solitaria* or non-swarming phase is restricted to Northern and South (?) Africa and Western Asia up to and including the Indian desert region of Baluchistan, Sind, the Punjab, Rajasthan and Kutch. Thence, the region extends to Iran, Iraq, Arabia, etc., right up to the western coast of Africa, including the Red Sea coast, Eritrea, Somaliland, Egypt, the Sudan, Morocco, French West Africa, Senegal, etc. *Solitaria* phase specimens have also been recorded from South Africa. For further details *vide* Uvarov (1923, 1928, 1932), Faure (1932), Maxwell-Darling (1934-1937), Vayssiére (1936), Rao (1937, 1945) and Roonwal (1946*b*, 1950).

As already pointed out by me (Roonwal, 1949*d*, pp. 167-168), Bodenheimer's (1937) claim of the " Sudano-Deccanian " region (extending from the Sudan in North Africa to the Deccan in peninsular India) as the permanent home of the Desert Locust, is unwarrented in so far as the Deccanian portion is concerned. We know definitely that the permanent home in India is confined to the Western desert regions of Baluchistan, Sind, the Punjab, Rajasthan and Kutch. The locusts reach the Deccan only in very exceptional swarming years and never breed there. The other equally unwarranted claims of Bodenheimer are discussed below.

(ii) *Surface-area of distribution.*

It will be seen from the foregoing account that the area occupied by the Desert Locust in its swarming phase is much more extensive than that occupied in the non-swarming phase, and a quantitative comparison of the two is of considerable interest.

The following method was followed for determining the total area of distribution :—An outline map of the world (Pl. XV) was drawn according to the Re-centred Sinusoidal Projection (Bartholomew) developed from the Sanson-Flamsteed's Equal Area Projection. This projection is area-true for all lands, while distortion is reduced to a minimum. The natural scale on this map was 1 : 100 000,000, which, during reproduction in Pl. XV, was considerably reduced. A scale (in cm.) which was *natural size in the original map* is also given for calculating the degree of reduction from the original during reproduction.

The choice of the map projection to be used was based on the advice of Brigadier Sir Oliver Wheeler, lately the Surveyor-General of India, New Delhi, who wrote (*in litt.*, 12th April, 1945) as follows :—

" 1. The simplest way is to use a map that is drawn on one of the equal-area projections and, as you suggest, count the squares on a piece of squared paper laid over it. This is far quicker than planimeter for an approximation. Planimeter areas have to be cross-checked against blunders and are troublesome. Some equal-area projections commonly used in Atlases are : Bonne's (Modified conical equal-area) ; Sanson's (Sinusoidal equal-area) ; Lambert's Third (Cylindrical equal-area) ; Lambert's Sixth (Zenithal equal area)."

" 2. Mercator's projection should on no account be used *except* by sub-dividing your area into East/West belts, and ascertaining the average scale of each belt. This is easily possible on some world maps by direct reading of a varying (with latitude) scale ; in the absence of such a scale it is necessary to compute the average scale of each belt."

" 3. In the absence of a map on a suitable projection or knowledge of what the projection is, a method that can be applied to *any* projection is to draw (or superimpose) " quadrilaterals" bounded by meridians and parallels and add up the square miles enclosed within each quadrilateral."

" This method is probably more meticulous and troublesome than is necessary for your purposes but if you have to resort to it, we have published tables of the area of ¼° quadrilaterals that are good between 44° N. and 44° S. They do not go to higher latitudes than 44° "

Kellaway (1949, p. 118) has also stated that " for a map of Africa *Sanson-Flamsteed's Projection* is satisfactory for most general purposes " The bulk of my areas lie in Africa.

On this map the distribution of the Desert Locust in the *gregaria* and the *solitaria* phases was carefully plotted and outlined. A transparent squared paper, with ½ centimetre squares drawn in black ink, was then superimposed on the distribution map, and the number of squares in each of the two areas, *viz.*, the *gregaria* and the *solitaria* distribution-areas, were counted off. Due allowance was made for fractions of squares which were suitably added to make up approximations of full squares. In counting the squares only the land-area was, as a rule, taken into account, and not the entire area encircled in the outlines. Thus, the oceanic areas of the Atlantic and the Indian Oceans were omitted. But smaller waters such as the Persian Gulf, the Red Sea, the Mediterranean Sea and the Caspian Sea (which the Desert Locust normally has no great difficulty in crossing, and , as a rule, does cross almost regularly in its periodic migrations) were included in counting. On the scale on which the original map was drawn, 13 linear half-centimetres equalled 4,000 miles. In other words, 13×13 or 169 half-centimetre squares covered an area equal to 4,000×4,000 or 16,000,000 square miles. Therefore, one half-centimetre square represents about 94674·6 square miles. On this basis the following approximate land-areas were obtained :—

(*a*) *Phase gregaria.*

	Square miles.
Europe	[142,012
Africa	11,360,952
Asia	4,970,417
TOTAL	16,473,381
or say	16,500,000

(*b*) *Phase solitaria.*

	Square miles.
North Africa and Asia	8,662,726
South Africa	805,734
TOTAL	9,468,460
or say	9,500,000

It will be seen that the *gregaria* area is about 1·7 times or nearly 1$\frac{2}{3}$ rds the *solitaria* area.

(*b*) POPULATION-DENSITY AND AMPLITUDE AND PERIODICITY OF POPULATION-FLUX IN DESERT LOCUST.

(i) *Relative numbers.*

Having discussed the area of distribution, it is necessary now to obtain some idea on the density of population—a factor which is partly, but not wholly, interlinked with the area of distribution. At the same time, population-density is a factor of great importance in the mechanisms of speciation. Abundant evidence has now been accumulated to show that populations in no species are constant ; they are, on the other hand, in a continuous state of flux. While this broad fact may be taken as well established, it must be said that a more or less precise knowledge on the nature of the flux is limited to but a few species, and here too many important aspects of the flux need fuller investigation. This knowledge mainly concerns 4 aspects, *viz.*, (i) the absolute numbers ; (ii) the periodicity and amplitude of flux ; (iii) the coincidental changes in the morphology, physiology and behaviour of the species undergoing population-flux ; and, finally, (iv) the effect of all these factors on evolutionary processes.

Fortunately, the Desert Locust has proved to be an almost ideal material for the problems stated above. What is more, our knowledge of its population-densities, of the periodicity and amplitude of population-flux, and of the coincidental charges in its morphology, physiology and behaviour, is perhaps more complete than for any other species. There are also other advantages, namely, that (i) the amplitude of flux is very great; and (ii) the periodicity is not immoderately long, one full cycle usually lasting only about 11·1 years on an average (*vide* Roonwal 1950; and Table 1 below).

TABLE 1.—Swarming periods of the Desert Locust in India from 1860 onwards. (*Modified from* Roonwal, 1950.)

Swarming periods.	Non-swarming intervals.	Period for each full cycle.
I. 1860—66 (7 years)	—	—
—	2 yrs.	9 yrs.
II. 1869—73 (5 years)	—	—
—	2 yrs.	7 yrs.
III. 1876—81 (6 years)	—	—
—	7 yrs.	13 yrs.
IV. 1889—98 (10 years)	—	—
—	1 yr.	11 yrs.
V. 1900—07 (8 years)		—
—	4 yrs.	12 yrs.
VI. 1912—19 (8 years)	—	—
—	6 yrs.	14 yrs.
VII. 1926—31 (6 years)	—	—
—	8 yrs.	14 yrs.
VIII. 1940—46 (7 years)	—	—
—	2 yrs.	9 yrs.
IX. 1949—	—	—
AVERAGE : 7·1 years	4 years	11·1 years

Precise knowledge of population-densities and of the amplitude and periodicity of population-flux under natural conditions in the field has been obtained in the last 15 years, largely as a result of long and painstaking investigations by Indian entomologists, particularly Y. Ramachandra Rao and his co-workers, working in the desert regions of Baluchistan, Sind, the Punjab and Rajasthan.

Regarding periodicity, it may be stated that since 1860. there have been nine swarming cycles in India (Table 1), with the swarming periods varying from 5-10 years (average 7·1 years), the non-swarming intervals varying from 1-8 years (average 4 years), and a complete cycle varying from 7-14 years (average 11·1 years).

As for population-densities, it has now been established that in the *solitaria* or non-swarming years densities of adults in the permanent breeding grounds, such as Rajasthan, Sind and Mekran (Baluchistan), never exceed about 1,000-2,000 per square mile, and are usually much less. Until recently, we had no knowledge of the critical densities in the year which inaugurates a new swarming cycle, but the recent work of Misra, Nair & Roonwal (1952) has shown that this figure is not less than about 18,000 adult individuals per square mile ; the increased density inaugurated the recent or 9th cycle which began in 1949 and is now (1953) continuing with vigour. It is of interest to mention here that in the middle of the 1932-1939 non-swarming period of low population, there occurred in July 1935 (as reported by Rao, 1936, and further discussed by Roonwal, 1949*d*) a sudden increase of numbers and the population increased from the *solitaria* figure of about 460 per sq. mile to 13,000 per sq. mile in Mekran and 40,000 per sq. mile in the Sind-Rajputana desert. This ' incursion ', however, fizzled out and no swarming cycle set in ; by December of the same year the new brood showed a population of only about 700 per sq. mile. No precise figures are available of the population-density in swarming years but we may tentatively take it as not less than about 30,000 per sq. mile ; usually, it is certainly much higher. The position as regards population-density may be summed up as follows in a simplified way :—

1. In *solitaria* or non-swarming period	1,000 per sq. mile.
2. In the inaugurating year of a new swarming cycle	20,000 per sq. mile.
3. In the swarming period ..	30,000 and over per sq. mile.

For the hopper stages, I have observed in the swarming years 1940-1946 in the breeding fields in the Rajasthan desert, hopper masses giving maximum densities of about 25,000 per square metre in the freshly hatched first stage hoppers and about 1,050 per square metre in the fifth stage. Singh & Bhatia (1952) have recently recorded somewhat similar maximum densities, *viz.*, 2,840 hoppers per square foot in the first stage and 94 in the fifth stage.

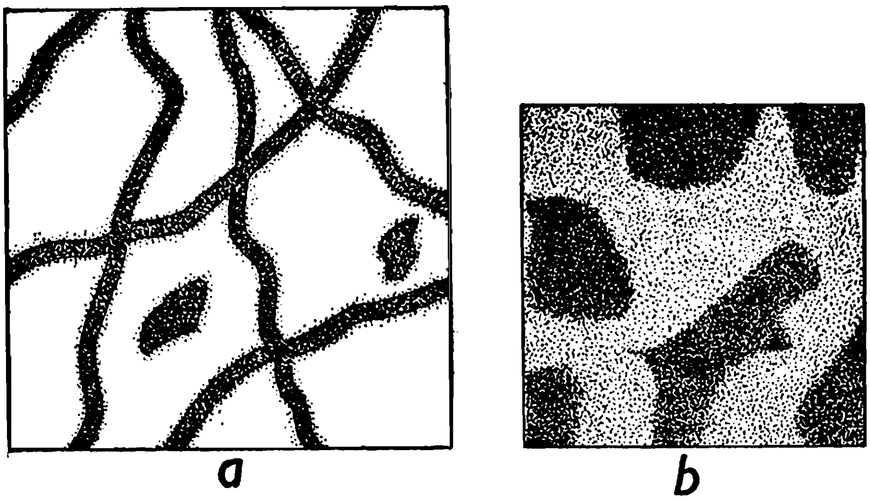
(ii) *Absolute numbers.*

(Text-fig. 1 & Table 2.)

We may now discuss the significance of these population-densities on the absolute numbers of adults present at any one time. *Theoretically,* if we assume that the adults are uniformly distributed in the densities stated above, the total absolute numbers in the area of its entire range of distribution (*vide supra*) would be as follows (Table 2) :—

In the *gregaria* phase period : 495,000,000,000 adults.

In the *solitaria* phase period : 9,500,000,000 adults.



TEXT-FIG. 1.—*Schistocerca gregaria.* Diagrammatic representation of the nature of distribution of population in the *gregaria* (swarming) and the *solitaria* (non-swarming) phase periods. The total surface land-areas occupied during the two periods are shown in their proportionate dimensions ; the *solitaria* area is about 9,500,000 sq. miles and the *gregaria* area about 16,500,000 sq. miles, or 1·7 times larger (*see* text for fuller details). Distribution is more uniform in the *solitaria* period, and comparatively more discontinuous in the *gregaria* period. However, populations in the *gregaria* period are much more concentrated and dense (*ca.* 30,000 or more per sq. mile) than in the *solitaria* period (*ca.* 1,000 or less per sq. mile).

(*a*) Phase *gregaria* period. (*b*) Phase *solitaria* period.

TABLE 2.—Theoretical (calculated) absolute numbers of Desert Locust adults present at any given moment in the entire land-area of its distribution, on the assumption of uniform distribution in the given densities.

Phase.	Total land-area of known distribution (in square miles).	Known approximate densities (per square mile).	Calculated absolute numbers.
(A) Ph. *gregaria*	16,500,000	30,000	495,000,000,000
(B) Ph. *solitaria*	9,500,000	1,000	9,500,000,000
Times increase of A over B	1·7	30	52

Actually, however, these numbers are misleading, since neither in the swarming nor in the non-swarming years is the distribution of population uniform. The distribution is always in ‘ pockets ’ or ‘ islands ’ of varying shapes and dimensions, leaving considerable tracts entirely void. This feature of discontinuity is especially pronounced in the *gregaria* phase, the distribution in the *solitaria* phase being comparatively more uniform (Text-fig. 1). The dimensions of these islands of distribution vary from one to several square miles. They are generally larger in the *solitaria* phase and smaller (more or less confined to individual swarms and the areas where they oviposit) in the *gregaria* phase. This situation results in a certain contradiction, namely, that in the *gregaria* phase the individual ' islands of distribution ' are generally smaller than in the *solitaria* phase, although the total land-area of distribution is much larger (Pl. XV).

The numbers with which, then, we are concerned as that which is dynamically important for interactions in the processes of speciation or production of variations are not the absolute theoretical numbers but the actual densities in small islands of distribution. As already stated, these densities are the lowest (*ca.* 1,000 per sq. mile) in the *solitaria* phase and the highest (*ca.* 30,000 at the least, or nearly 30 times or usually more) in the *gregaria* phase. In discussing their respective effects on the production of variations we shall proceed on the basis of these rough proportions.

III.—DISCUSSION OF KNOWN TYPES OF EVOLUTIONARY PHENOMENA OR " EFFECTS "

(*a*) SOME GENERAL CONSIDERATIONS.

No two individuals of a species are alike. It is this *existence* of variability, howsoever caused, which is the basis of speciation. Since variation first arises in individuals and then spreads to the group, we may say with justification that the progress of speciation ultimately depends upon the behaviour of variability in natural populations. This behaviour, in its turn, depends upon a variety of factors such as genetic differences (mutation rate), geographical and ecological distance (isolation ; migration or cross-breeding rate between different groups, whatever the cause), elimination of variant individuals by ' natural ' and other forms of selection (selection pressure), and, finally, population structure. Briefly, the following are the chief factors at work in speciation :—

1. Mutation pressure.
2. Selection pressure.
3. Migration pressure.
4. Population pressure :
    (*a*) Population size.
    (*b*) Random drift or genetico-automatic processes.

Speciation theoretically implies that a genetically homogeneous population-group, that is, a group in which the balanced gene-frequency in respect of a particular gene *AA* has reached 100 per cent. at level C, first achieves heterogeneity by the introduction of a new allelomorph *aa*, either by crossing or by mutation, and ultimately achieves a new genetic homogeneity at level D. In actual practice, however, in the first place not one but perhaps scores of genes are involved in the origin of a new species. Secondly, complete homogeneity is seldom achieved, except in pure line (clones) and perhaps in extremely small populations of bisexually reproducing forms; there occurs, instead, 'a balanced heterogeneity' which jumps from one peak of stability to another.

The factors leading to genic homogeneity (less variation) or heterogeneity (more variation) are briefly given in Table 3. The state of variability or gene frequencies in a species or population-group is in a continual state of vibration about the equilibrium point in a distribution curve the form of which depends upon the relations between population number and the various pressures indicated above.

TABLE 3.—Factors leading to genic homogeneity or heterogeneity.

FACTORS FOR GENIC HOMOGENEITY	FACTORS FOR GENIC HETEROGENEITY
1. Gene duplication.	1. Gene mutation (u, v).
2. Gene aggregation.	2. Random division of aggregate.
3. Mitosis.	3. Chromosome aberration.
4. Conjugation.	4. Reduction (meiosis).
5. Linkage.	5. Hybridization (m).
6. Population size. (Varying effects reported.)	6. Population size. (Varying effects reported).
7. Environmental or selection pressure (s).	7. Pressure of local environments of subgroups (s_1).
8. Cross-breeding (migration pressure).	8. Individual adaptability.
9. Individual adaptability.	

The relation subsisting between population number (*i.e.*, abundance) on the one hand, and variability on the other, had been realised since a long time on observational grounds (see Darwin, 1876; Adlerz, 1902). Hagedoorn & Hagedoorn (1921) have pointed out the importance of fluctuation in numbers in causing specific uniformity; they, however, believed that the total number of individuals in a species is constant. Elton (1924) has well emphasised the existence of periodic fluctuations in various groups of animals, especially mammals, and has expressed the view that they must be caused by periodic climatic changes acting over wide areas. He further believed that population fluctuation causes uniformity because the whole population re-arises from a few surviving individuals after a period of low numbers; the genotypic constitution tends to become pure. He wrote (p. 159): "In fact there is in many animals a mechanism by which variations in the population are alternately acquired and weeded out or kept as indifferent characters which in turn may become useful at some crisis in the history of the animal at a later date" According to Elton, fluctuation explains many things in evolution, such as: (i) how, by a temporary cessation of the struggle for existence, new and indifferent (non-adaptive) mutations can get a footing and spread; (ii) how some characters are selected periodically; (iii) how species remain on the whole uniform; and (iv) how adaptive fineness may arise without reference to selection and crossing. " There is ", he wrote (p. 160), " so to speak, an entrance examination by natural selection, which weeds out the worst candidates, but the final selection is by lot "

Attempts at theoretical interpretations on mathematical grounds are of recent origin and, for certain types of phenomena, are largely due to the analyses of Chetverikov (1926), Fisher (1930), Haldane (1932); Wright (1931-1946), Dubinin (1931), Dubinin & Romaschoff (1932) and Kolmagorov (1935). Although these analyses are theoretical and refer to one or two types of phenomena only, they have been valuable in providing clarifications which could not be achieved by other means. It now remains to apply similar analylitical techniques to the other types of phenomena discovered in the field by actual biological observations on wild populations. (For a somewhat fuller discussion of the problem, see Roonwal, 1949*b*.)

(*b*) KNOWN TYPES OF EVOLUTIONARY " EFFECTS "

A survey of the published literature shows that four different types of evolutionary phenomena have been recorded in regard to the intensity of the production of variation in relation to population-flux; and a fifth one is presented below in this paper. One of these phenomenon has been conveniently termed in recent literature as the " Wright-Dubinin Effect " and, following this practice, I have termed the other ones also by a similar nomenclature, associating them with the names of their discoverers. These phenomena are as follows :—

1. The Hardy Effect.—Automatic maintenance of genetic variability in spite of crossing.
2. The Hagedoorns Effect.—Rapid random (automatic) decay of variation-intensity in the total absence of selection pressure.
3. The Adlerz Effect.—Increase of variation-intensity with increased abundance (high populations).
4. The Wright-Dubinin Effect.—Increase of variation-intensity in intermediate populations, *i.e.*, populations which are neither too large nor too small.
5. The New Effect (presented here).—Increase of variation-intensity in *minimum* populations.

These effects may now be discussed in some detail (also see Roonwal, 1949*b*).

1. *The Hardy Effect*

Hardy (1908) has demonstrated that genetic variability, once gained by a population, is automatically maintained and is not reduced by crossing. If AA and aa are the new allelomorphs, and their populations are mixed in the proportions q and $1—q$, the second and subsequent generations will show the following structure of gene-frequencies (Hardy's Equilibrium Formula) :—

$$q^2 AA : 2q(1-q) Aa : (1-q)^2 aa,$$

assuming that the numbers are fairly large so as to ensure random mating, that the sexes are evenly distributed among the three varieties (dominant AA, heterozygous Aa and recessive aa), and that all are equally fertile. Proportions will change up to the second generation, but thereafter they will strike an equilibrium and will have no tendency to either increase or decrease. Hardy concluded thus : "In a word there is not the slightest foundation for the idea that a dominant character should show a tendency to spread over a whole population, or that a recessive should tend to die out "

2. *The Hagedoorns Effect*

Hagedoorn & Hagedoorn (1921) visualised the theoretical possibility of a rapid, random (automatic) decay of variability in a stable population in the total absence of mutation and selection pressures. Actual instances are not known. Fisher (1922) has criticised the Hagedoorns Effect and has remarked that such random decay of variance is so extremely slow as to be quite unimportant. He has further pointed out that if k is the rate of decay and n the number of individuals breeding at random, the rate of extinction is $k=\frac{1}{2n_1}$ and it would require $2n$* generations to reduce its variance in the ratio 1 to e† or $1{\cdot}4n$ generations to halve it. When the number of interbreeding individuals in a species is large (say not less than 10,000), it will be seen that the rate of decay of variance is so slow as to be quite negligible. In a later paper Fisher (1930*b*, p. 204) has stated that " random survival, while of great importance in conditioning the fate of an individual mutant gene, is a totally unimportant factor in the balance of forces by which the actual variability of species is determined " He has further stated that this is because, in the total absence of mutation-pressure and selection-pressure, the quantity of variation of an interbreeding group would decrease by random survival at a rate such that the time of relaxation is $2n$ generations (n=number of breeding individuals in each generation). This number is usually very large. The time needed to halve the variance by random extinction of genes in the total absence of mutations is 1·4 times the number of potential parents in each generation (p. 219) ; and the loss of variance due to this cause is very trifling. Thus, the steady random decay of variation as visualized by Hagedoorn & Hagedoorn (1921) will not occur and, in the absence of selection, variability will remain constant but will now evidently depend on the size of the population. If the number of breeding individuals n is small, then the Hagedoorns Effect may become significant.

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* Fisher (1930*b*) later on corrected his original (1922) figure of the " time of relaxation " from $4n$ to $2n$; thus, 2·8 also becomes 1·4.

† Evidently e= gene-extinction.

Hagedoorn & Hagedoorn (1921) have also pointed out the importance of population fluctuation for reducing variations and producing homogeneity. They, however, believed in the constancy of the number of individuals of a species from year to year. By population fluctuation they merely implied migration to new habitats or to the effect of unusual climatic and biological changes, and so on. They also suggested that in spite of the constancy of the total number in a species (which we now know is not the case), only a certain number breed each year out of the surviving population (here again, no evidence is brought forth). This, if true, will have the same effect as fluctuation of population and may, in special cases, be significant. It may be stated that Hagedoorn & Hagedoorn were evidently not aware of the observations of Adlerz (1902) on the effect of population-flux on variation.

3. *The Adlerz Effect*

Darwin (1876, Chapter 2, pp. 42-43) believed that the more abundant species show greater variation (a large number of varieties) than the rarer ones, but he did not publish any detailed evidence for this belief except saying that he had examined, more or less statistically, a fairly large number of cases among plants. He wrote :

" Alphonse de Candolle and others have shown that plants which have very wide ranges generally present varieties ; and this might have been expected, as they are exposed to diverse physical conditions, and as they come into competition (which, as we shall hereafter see, is an equally or more imporant circumstance) with different sets of organic beings. But my tables further show that, in any limited country, the species which are the most common, that is abound most in individuals, and the species which are most widely diffused within their own country (and this is a different consideration from wide range, and to a certain extent from commonness), oftenest give rise to varieties sufficiently well-marked to have been recorded in botanical works. Hence it is the most flourishing, or, as they may be called, the dominant species,—those which range widely, are the most diffused in their own country, and are the most numerous in individuals,—which oftenest produce well-marked varieties, or, as I consider them, incipient species. And this, perhaps, might have been anticipated ; for, as varieties, in order to become in any degree permanent, necessarily have to struggle with the other inhabitants of the country, the species which are already dominant will be the most likely to yield off-spring, which, though in some slight degree modified, still inherit those advantages that enable their parents to become dominant over their compatriots. In these remarks on predominance, it should be understood that reference is made only to the forms which come into competition with each other, and more especially to the members of the same genus or class having nearly similar habits of life. With respect to the number of individuals or commonness of species, the comparison of course relates only to the members of the same group. One of the higher plants may be said to be dominant if it be numerous in individuals and more widely diffused than the other plants of the same country, which live under nearly the same conditions. A plant of this kind is not the less dominant because some conferva inhabiting the water or some parasitic fungus is infinitely more numerous in individuals, and more widely diffused. But if the conferva or parasitic fungus exceeds its allies in the above respects, it will then be dominant within its own class."

Adlerz (1902) was the first authority to demonstrate clearly the existence of increased variation with the increase of abundance in a species whose population showed periodic fluctuations. His observations, however, appear to have been overlooked. He observed this phenomenon in the Swedish butterfly, *Polyommatus virgaureae* L.* In July 1896 this species greatly increased in numbers in Sweden, and at the same time showed a variety in females which had nowhere been known before. This variety was characterised by the presence of pale blue spots inside the golden-red band on the upper side of the hindwings. The number and clearness of the spots varied greatly. The greater number was 5, and from this to the chief form of the species (with no spots) there were all grades of intermediates. During the following years the numbers declined, and the absolute as well as relative proportion of the said variety became rarer than during the period of mass-increase. In the summer of 1901 again there was mass-increase in the numbers of this species, and again the said variety became more common—more than half the number of captured specimens showed the characters of the new variety.

A similar phenomenon has been subsequently reported by several workers in other species of animals. Thus, Fisher & Ford (1926-1928) found that in several species of Lepidoptera the more abundant species show a greater degree of variation (in depth of pigmentation) than the rarer ones. They also showed that this situation is to be expected even on theoretical (mathematical) grounds, assuming that Mendelian inheritance alone occurs. A similar theoretical conclusion was arrived at earlier by Fisher (1922), *vide infra.*

Fisher (1937*a*) reiterated the same position after statistically studying the egg-size of some British birds, although he was at the same time cautious. He wrote (p. 3): "The theoretical reasons for anticipating a higher variability associated with a numerically larger population are recondite and by no means fully understood. They depend on the balance of selective and mutational agencies, by which the genetic variability of natural populations must be determined. It is because we cannot easily predict this *a priori* that direct empirical knowledge is of importance. In respect of variations conditioned environmentally, there is no reason to suppose that these would be greater or less in a dense than in a sparse population. The same is true of that fraction of the variability which is caused by deleterious mutations. To these all species appear to be exposed." He further wrote (pp. 3-4): "If species of different populations were supplied at the same absolute rate with different neutral mutations, each occurring with extreme rarity, then calculation shows that the number of factors maintained in the heritable variance of the species would be nearly proportional to the logarithm of the population." And again (p. 23): "The excess variability *appears* to be strongly concentrated among the few most numerous

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*Evidently the same as *Chrysophanus virgaureae Linn.* (*family Lycaenidae*).

species of each group, suggesting that evolutionary progress is much more rapid among these than among other species. This important indication may, however, be due to our comparative ignorance of the real relative numbers of the population of the less numerous species."

Ford & Ford (1930) studied the variation in a small colony (of 6-7 miles radius) of the butterfly *Melitaea aurina* Rott. in Great Britain for a period of 49 years (1881-1930). During this period the species fluctuated in numbers as follows: Abundant 1881-1897; less common 1898-1906; uncommon 1907-1912; very rare 1912-1920; increase 1920-1924; abundant 1924-1930. The degree of parasitism was largely responsible for the fluctuation of population. Variation was small in the first and second periods of abundance but very great while the numbers were increasing rapidly. This variation concerned size, shape and colour; also, a high proportion of individuals were deformed in various ways. When the rapid increase of population ceased, the undesirable elements (deformities) practically disappeared, and the species settled down to a comparatively uniform type which, however, was distinct from that prevailing during the first period of abundance. Ford & Ford stated that the lowering of selection-intensity resulted in increased variation and also in increased numbers. In this example two points are worthy of note. First, that the greatest variation occurs while the population is rapidly increasing. Secondly, that the high variation-intensity ceased and was replaced by comparative uniformity when the rapid increase of population stopped and the population presumably settled down at a high but more or less steady level. The cause of the latter decline of variation is not clear.

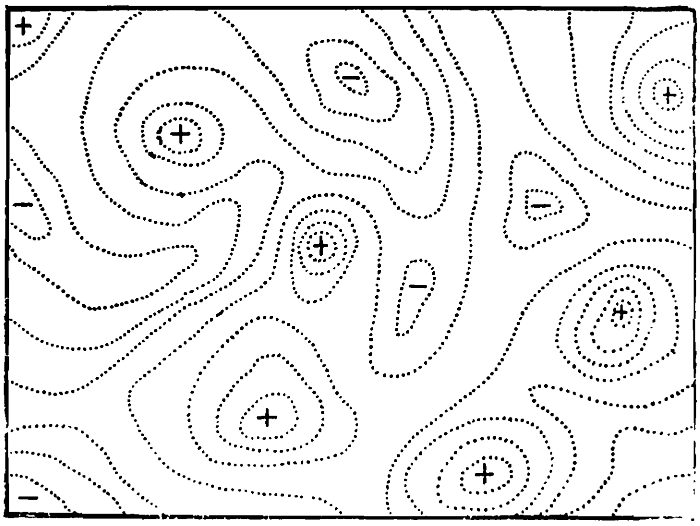
On theoretical grounds, Fisher (1922) stated that increased abundance is accompanied by increased variation. He wrote (p. 324): "In all cases it is worth noting that the rate of mutation required varies as the variance of the species, but diminishes as the number of individuals is increased. Thus a numerous species, with the same frequency of mutation, will maintain a higher variability than will a less numerous species: in connection with this fact we cannot fail to remember the dictum of Charles Darwin, that 'wide ranging, much diffused and common species vary most' (1, chap. ii)." Fisher also gave graphs of distribution of variance in a species under various theoretical conditions.

4. *The Wright-Dubinin Effect*

The important theoretical demonstration that variation (gene-frequencies) may fluctuate merely as a statistical consequence of the 'effective' population-size, all other pressures being constant, we owe largely to the analyses of Chetverikov (1926), Dubinin (1931), Dubinin & Romaschoff (1932), Wright (1931-1946) and Kolmogorov (1935), but more particularly of Dubinin and of Wright. Dubinin termed this process the 'genetico-automatic process', while Wright's term for it was 'random drift' or merely 'drift'. They concluded that speciation occurs most rapidly neither in very large nor in very small populations but in populations of certain intermediate sizes. Great reduction of populalon leads to fixation (of non-adapted genes) and loss of genes;

great increase only to slow change. The most rapid change occurs in a large population which is subdivided into a number of partially isolated groups between which occasional crossing takes place.

In discussing evolution in populations in approximate equilibrium, Wright (1935, p. 257) has considered the " evolutionary processes in populations in which the selective values of different grades of a character depend on the (squares) deviations of the latter, from an optimum. It is assumed that the effects of different genes on the character combine additively (no epistasis) ". Having reached an optimum (in selective variation), there would be no further change and new mutations would now be harmful to start with (*vide* also Fisher, 1930). But if genes have multiple effects, and harmonious adjustment of characters is arrived at, the possibility of numerous optimum " peaks " would arise (Text-fig. 2). Thus, all possible combinations may occur by a trial and error mechanism, and the locus of a population (regarding gene-variations) may be carried across a saddle from one peak to another and prehaps to a higher one. This view contrasts with that of steady progress under natural selection, as developed in its extreme form by Fisher (1930). Haldane (1932) occupies an intermediate position.



TEXT-FIG. 2.—Diagrammatic representation of the field of gene-combinations in two dimensions instead of many thousands. Dotted lines represent contours with respect to adaptiveness. (*After* Wright, 1932.)

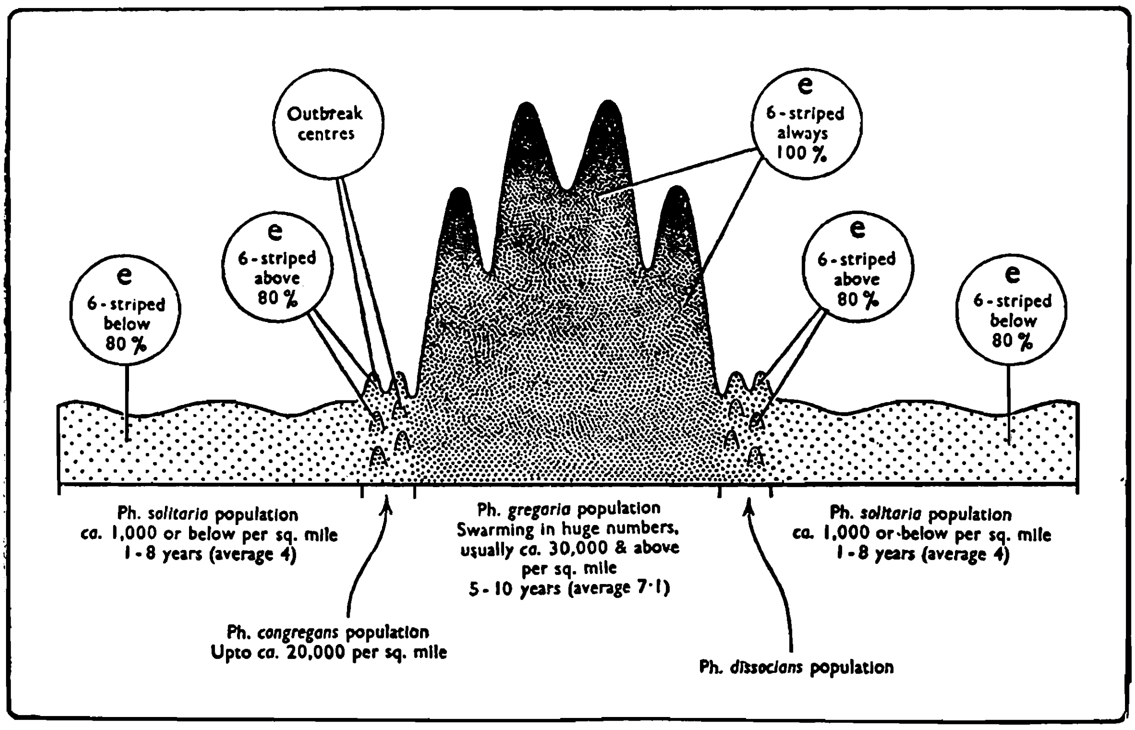
Wright (1935) has shown that the effectiveness of this trial and error mechanism (random drift) of gene-frequencies is normally slow, but is enormously increased if the population is subdivided into many local groups which breed largely within themselves. The distribution of gene-frequencies under random sampling is here determined by the relation between the effective size of the local group and the cross breeding index. " At any time combinations might be reached by chance in particular local groups, with effects of the first order of importance, leading to expansion of such groups (intergroup selection)......................"(p. 265).

These analyses, though important, are theoretical, and actual examples of the Wright-Dubinin Effect are hitherto wanting. As pointed out by me earlier (Roonwal, 1949*b*, pp. 129-130), perhaps the extraordinary degree of speciation in birds and mammals among island forms, particularly in such areas as the island-groups of the East Indies and Australasia, where a species has become divided into a large number of subspecies, one for almost every tiny island in its range of distribution, may be regarded as an example of this Effect. In my earlier accounts (Roonwal, 1947*d*; 1949*b*, p. 130) I had regarded the case of the increased variation in the *solitaria* phase of the Desert Locust, *Schistocerca gregaria*, also as an example of the Wright-Dubinin Effect, but it is now clear that it represents an altogether new and different kind of Effect, described below, which is characterised by increased variation-intensity in *minimum* populations.

IV.—A NEW EVOLUTIONARY PHENOMENON OR " EFFECT ".

(*a*) GENERAL REMARKS.

The data for the New Effect presented here are based on the writer's findings (Roonwal, 1936-1954) in the Desert Locust, *Schistocerca gregaria* (Forskal), of greatly increased variation-intensity in the *solitaria* or non-swarming phase (where the population is the lowest, being of the order of about 1,000 - 2,000 adults, usually much less, per square mile at the maximum), as compared to the *gregaria* or swarming phase (where the population is the highest, being of the order of about 30,000 adults per square mile at the minimum).



TEXT-FIG. 3.—*Schistocerca gregaria.* Diagrammatic representation of the periodic population fluctuation and its relationship to the eye-stripe number. (*Modified from* Roonwal, 1949*a*.) The number of peaks and valleys in the figure has no quantitative significance. The papillae in the region of the *congregans* population (left) represent the " outbreak centres ", while similar papillae in the *dissocians* population (right) represent isolated pockets of high population before the dispersal leading to low population (characteristic of the *solitaria* periods) occurs.

e, " eye-stripe figure " (see Text, p. 31, foot-note, for explanation).

The existence of two extreme phases, the *gregaria* and the *solitaria*, had already been established by Uvarov (1923, 1928) and later on confirmed by Faure (1932) and several other workers.

The *solitaria* and the *gregaria* phase periods alternate (*vide supra*, pp. 7-8 ; and Text-fig. 3). There is also a difference in geographical distribution in the two periods, as shown above. In the *solitaria* period the distribution is more restricted (being about 9,500,000 sq. miles of land-area) than in the *gregaria* period where it is about 16,500,000 sq. miles or nearly 1·7 times as great (Pl. XV).

The two phases also differ from each other in several other respects. Apart from differences of behaviour (the *gregaria* phase being the swarming phase, the *solitaria* the non-swarming one), there exist some colour differences (especially in the hoppers, see Pl. XVII) and differences in the shape and proportion of the body-parts and the related ratios, particularly the E/F ratios (concerning the elytron-length, E, and the hind-femur-length, F ; see Text-figs. 4 and 5) and ratios connected with the head-width, C (*vide* Roonwal & Misra, 1952 ; Nair, 1952*a*). Other phase differences (Roonwal, 1946*a*) have also been established. Roonwal (1947*a*) has also shown a difference in the distribution of pigment in the cells of the ommatidia of the compound eyes (Pl. XVIII). Other phase differences are illustrated in Pls. XV-XVII and Text-figs. 4-9.

(*b*) INCREASED VARIABILITY IN *solitaria* PHASE OF DESERT LOCUST.

(*i*) *Some variable characters.*

Here, however, we are mainly concerned with the non-phasic type of variations which have been shown to exist in the *solitaria* phase by Roonwal (1936-1952). He showed (Roonwal, 1936) that 2 types of individuals occur in the *solitaria* phase, *viz.*, with 6 and 7 vertical eye-stripes. Later on, several other differences were shown to exist, such as variations in the number of antennal segments, the occurrence of 5- and 8-eye-striped individuals (Text-fig. 6), differences in sex-ratios correlated with the eye-stripe number, differences in the number of moults and the mode of development of the eye-stripes in the 5-, 6-, 7- and 8-striped forms (Roonwal, 1947*a*), and so on. The more important differences as regards increased variation between the *gregaria* and the *solitaria* phases on the one hand, and within the *solitaria* phase as on the other, are briefly mentioned below. For brevity, the words "*gregaria* phase" are abbreviated to "G." and "*solitaria* phase" to "S." :—

(A)—*Morphological Differences* (Pls. XVI-XVIII ; and Text-figs. 4-9.)

1. On the whole, G. less variable than S.

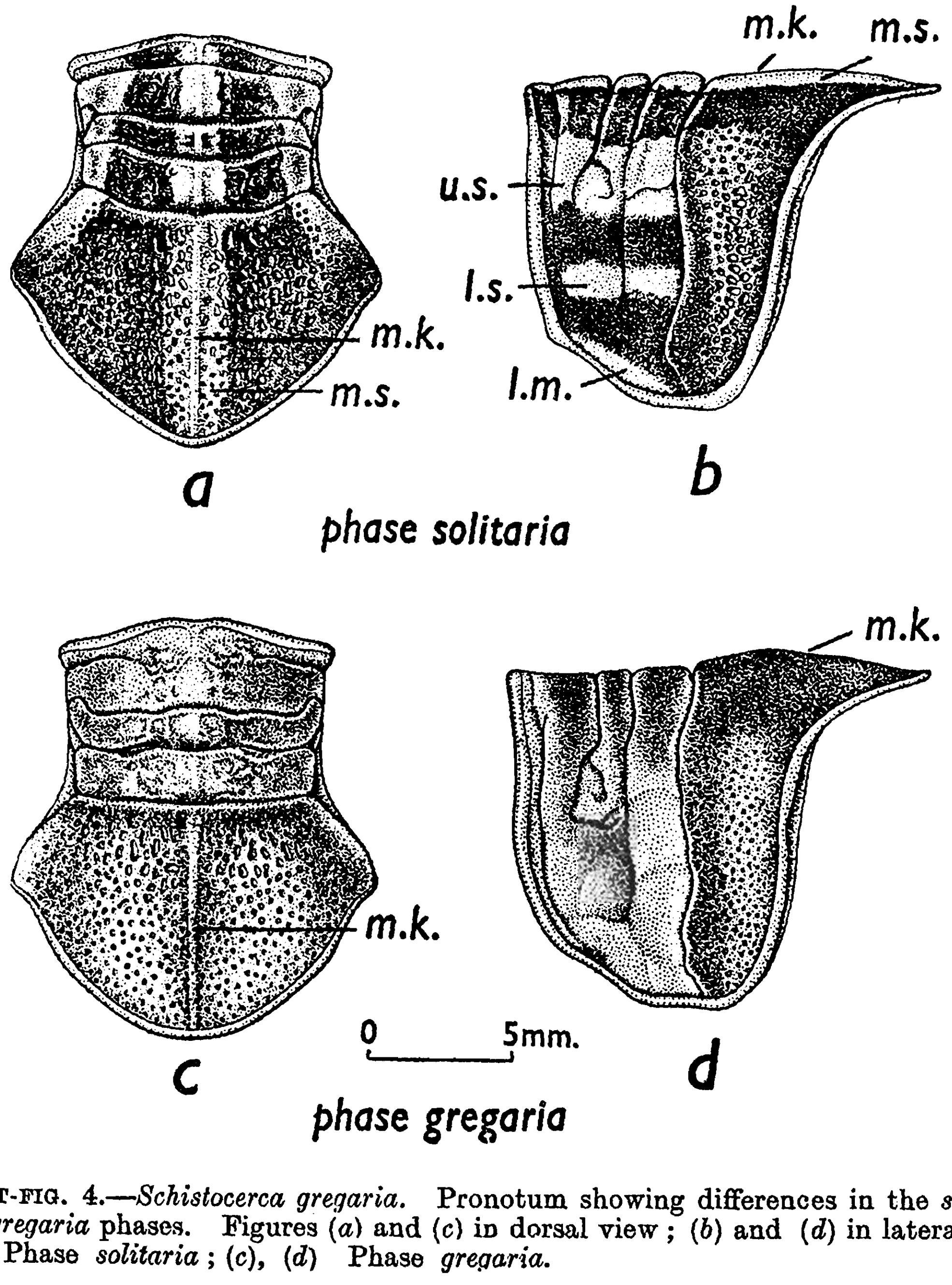
2. G. has 6 eye-stripes only. S. has 5, 6, 7 and 8 eye-stripes, but mostly 6 and 7 (Roonwal, 1936, 1947*a*) (see Text fig. 6).

3. Eye-stripes in G. develop by one type only. In S. there are varying modes of development (Roonwal, 1947*a*).

4. The degree of sexual dimorphism (Text-fig. 7) as expressed by the Sexual Dimorphism Percentage or S. D. P. [(♀/♂—1)×100] in respect of the length of the body-parts is more marked in G. (S. D. P. for

elytron-length or E, 9·76 ; for hind-femur length or F, 8·72) than in S. Within the latter phase, S., the S. D. P. is higher in the 7-eye-striped than in 6-eye-striped forms, thus : 7-striped, for E 20·08, for F 18·33 ; 6-striped, for E 18·04, for F 15·63 (*vide* Roonwal, 1949*c*, 1952*b* ; Roonwal & Nag, 1950, 1951 ; and Roonwal & Misra, 1952).

5. The number of hind-tibial spines in adults show a somewhat greater range of variation in S. than in G. The outer spines vary from 8-12 in S. and 8-10 in G. The inner spines vary from 8-12 in S. and 10-12 in G.



TEXT-FIG. 4.—*Schistocerca gregaria.* Pronotum showing differences in the *solitaria* and the *gregaria* phases. Figures (*a*) and (*c*) in dorsal view ; (*b*) and (*d*) in lateral view ; (*a*), (*b*) Phase *solitaria* ; (*c*), (*d*) Phase *gregaria.*

l.m., lower margin of lateral lobe ; *l.s.*, lower pale horizontal stripe of lateral lobe ; *m.k.*, mid-dorsal keel ; *m.s.*, pale mid-dorsal stripe ; *u.s.*, upper pale horizontal stripe of lateral lobe.

6. The size of the body-parts, *e.g.*, length of elytron, length of hind-femur, width of head, length and width of pronotum, vary far more in the *solitaria* than in the *gregaria* phase, and show, in the former, various groupings which are correlated with the number of eye-stripes (Text-fig. 8)—*vide* Roonwal (1949*c*, 1952*b*), Roonwal & Nag (1950, 1951) and Roonwal & Misra (1952).

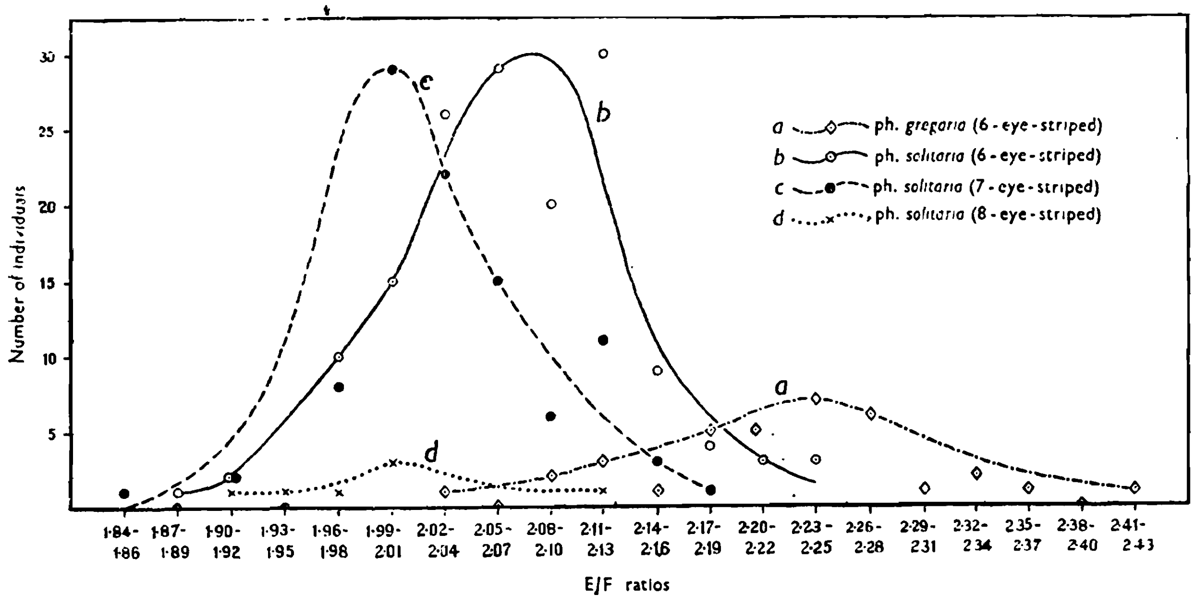
7. Similar increased variations in the *solitaria* phase, as compared to the *gregaria*, occur in respect of the biometrical ratios such as E/F or elytron-length/hind-femur-length (Text-fig. 5)—*vide* Roonwal (1949*c*) Roonwal & Nag (1950, 1951) and Roonwal & Misra (1952).

8. There are 26 antennal segments in the 6-eye-striped G. In S. the number varies from 25-30, as follows (Text-fig. 9): 5-eye-striped 25, 6-striped 26-27, 7-striped 28-29 and 8-striped 30 (*vide* Roonwal, 1952*a*).

(B)—*Other Differences*

1. Usually only 5 moults (excluding the "intermediate moult" in G. and 5-7 in S.)—*vide* Roonwal (1946*a*, 1947*a*).

2. Only one type of hopper (the yellow-black) and one type of adult (pink when immature and yellow when mature) in G. In S. two kinds of hoppers (the "green" type and the "fawn" type), and two kinds of adults (the "blue-grey" type and the "fawn" type)—*vide* Roonwal (1946*b*).



TEXT-FIG. 5.—*Schistocerca gregaria.* Graphs to show the variation in E/F ratios (elytron-length/hind-femur-length) in various types of individuals, *viz.*, phase *gregaria* 6-eye-striped, and phase *solitaria* 6-, 7- and 8-eye-striped. The mean E/F ratio is highest in the phase *gregaria* (6-striped) and lowest in the 8-striped phase *solitaria*. (*Adapted from* Roonwal, 1949*a*, with the addition of data for 8-eye-striped individuals.)

(*ii*) *Periodic variation in eye-stripes during 25 years* (*1926-1950*).

It will be seen from the foregoing account that whereas in the *gregaria* phase individuals there is a narrowing down of variation, in the *solitaria* phase individuals there is a remarkable flowering of variation. In other words, the *gregaria* phase is variation-stable, the *solitaria* phase variation-unstable. This difference is most strikingly demonstrated in the number of eye-stripes. Data for three cycles in India covering a period of 25 years (1926-1950) are now available* and we are thus in

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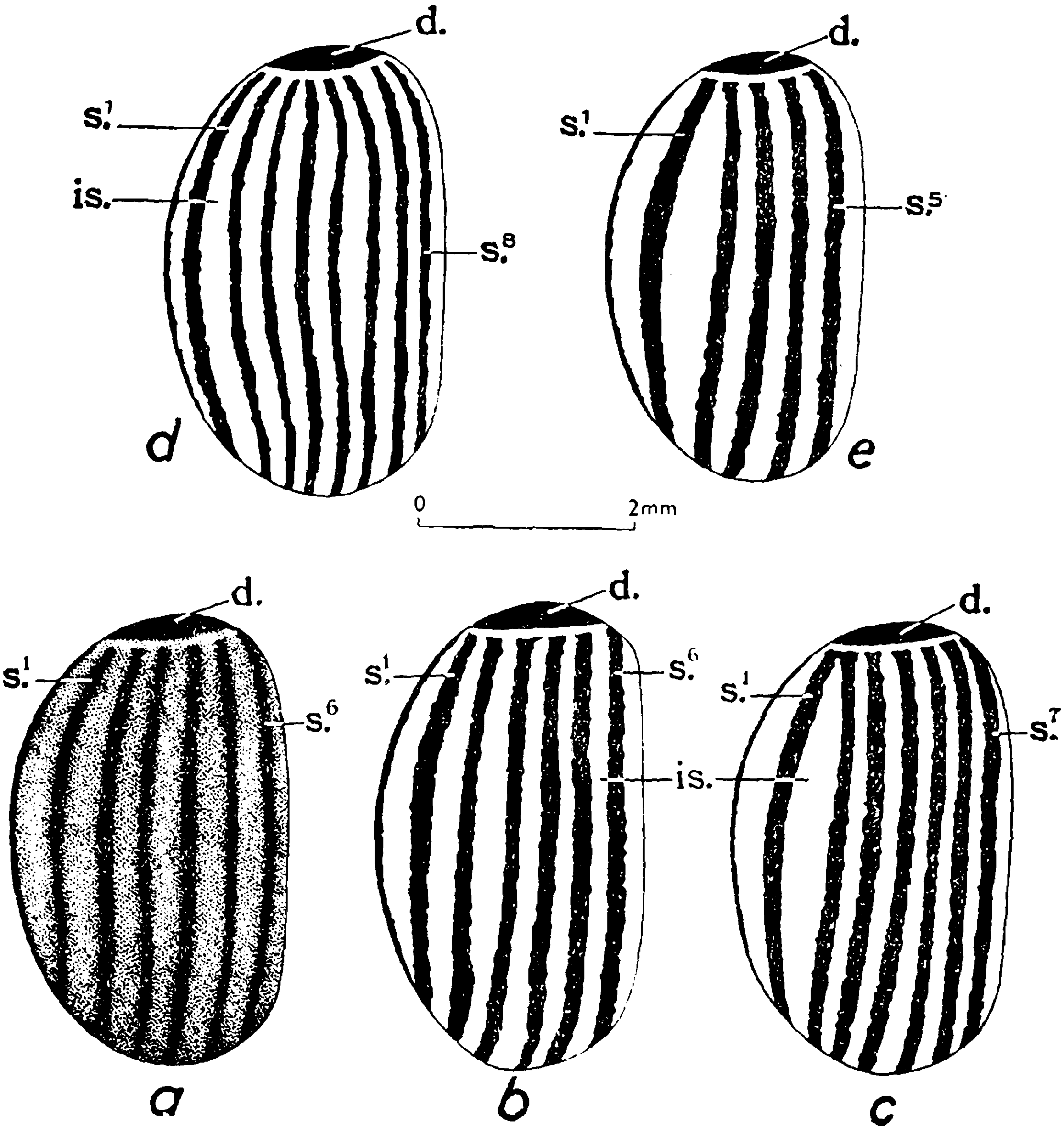
* Data for the earlier years are also available from swarms and has already been made use of (*vide* Roonwal, 1949c) ; these data are, however, comparatively scanty. For a portion of the data for the period 1926-1950 I am indebted to Shri Y. Ramachandra Rao (*in litt.*, 25th April 1947).

a position to observe the periodic appearance and disappearance of this polymorphism simultaneously with the decrease and increase respectively of populations. The following is a brief description of this periodicity of polymorphism :—

1. *Swarming* (*gregaria*) *period 1926-31.*—Except during the last year (1931), all the individuals collected during the 1926-31 swarming cycle were 6-eye-striped. Of the several specimens collected at Pasni (Mekran, Baluchistan coast) in April and May 1931, a good many proved to be of the *solitaria* phase (as judged by E/F ratios and other characters) and one specimen was found to have 7-eye-stripes. Collections made in October 1931 near Pasni also included one or two 7-eye-striped forms.

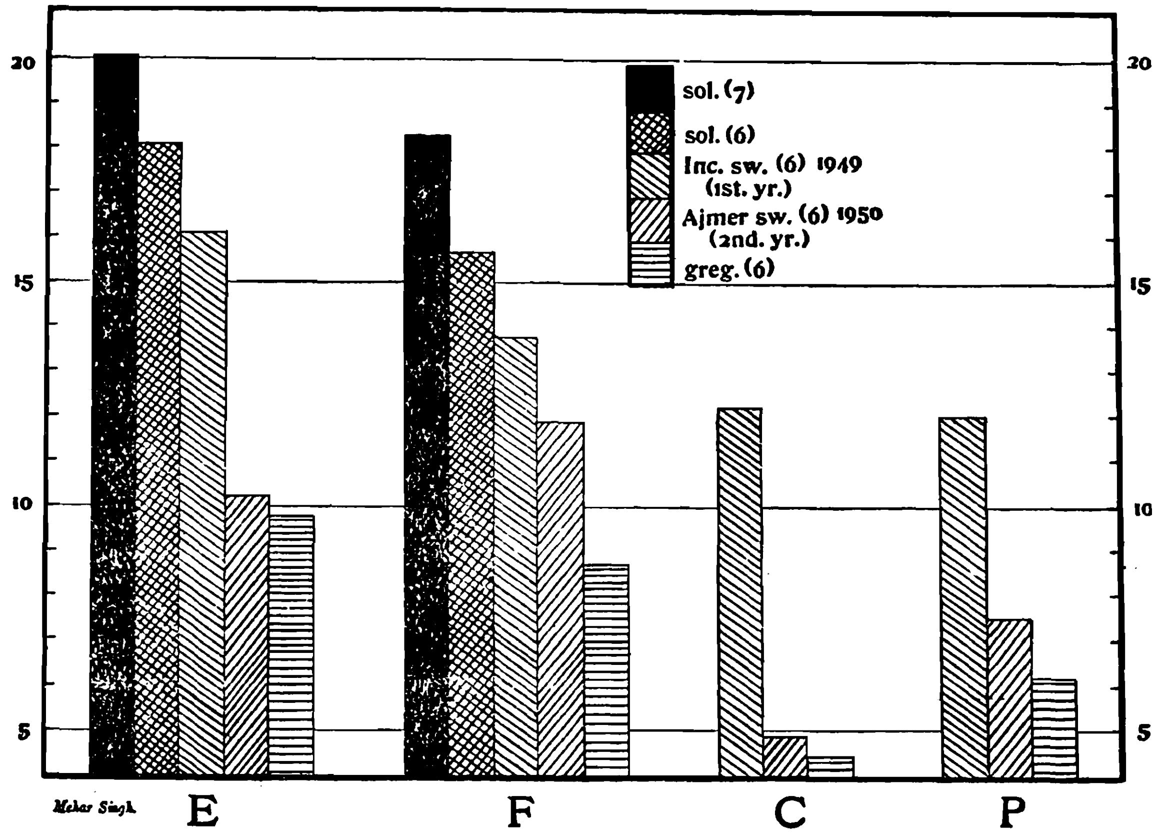


TEXT-FIG. 6.—*Schistocerca gregaria.* Compound eyes of adults in various forms of individuals. (*a*) In *gregaria* or swarming phase, with 6 eye-stripes. (*b*)-(*e*) In *solitaria* or non-swarming phase, with 6, 7, 8 and 5 eye-stripes. In all figures the anterior side is on the right, the posterior one on the left.

d., dorsal spot of eye ; *is.*, interstripe ; *s*1-*s*8, first to eighth eye- stripes, counting from the posterior side.

2. *Non-swarming* (*solitaria*) *period 1932-39.*—As mentioned above, the first indication of the appearance of 7-eye-striped individuals was in the last year of the swarming cycle of 1926-31. During the

solitaria years 1932-39, the relative proportions of the 6- and 7-eye-striped forms varied greatly (*vide* Rao, 1942, and *in litt.*, 1947 ; and Roonwal, 1949*d*)—from about 29-92 per cent in the case of 6-striped forms and, correspondingly, 8-71 per cent in the case of 7-striped ones. The greatest proportion of 6-striped forms was found during the July 1935 incursion of phase *gregaria*-like forms. Again, in 1937 there was a sharp rise in the proportion of 6-striped forms almost to the point of eclipsing the 7-striped ones, but towards the end of the year there was a sharp rise in the number of the latter form. In the peak *solitaria* year, 1936, the proportion of the 7-striped forms was comfortably higher than that of the 6-striped ones. Furthermore, 8-striped forms were first noted in the field in 1936 and most of them were collected during that year, only a few being seen in 1937 and 1938. The proportion of the 8-striped forms, as compared to that of the 6- and 7-striped ones, was always low, not more than about 1 out of every 20 to 50 locusts (Rao, *in litt.*) and the population in these surveys ranged from about 100-2,000 individuals per square mile. Very few 8-striped forms were



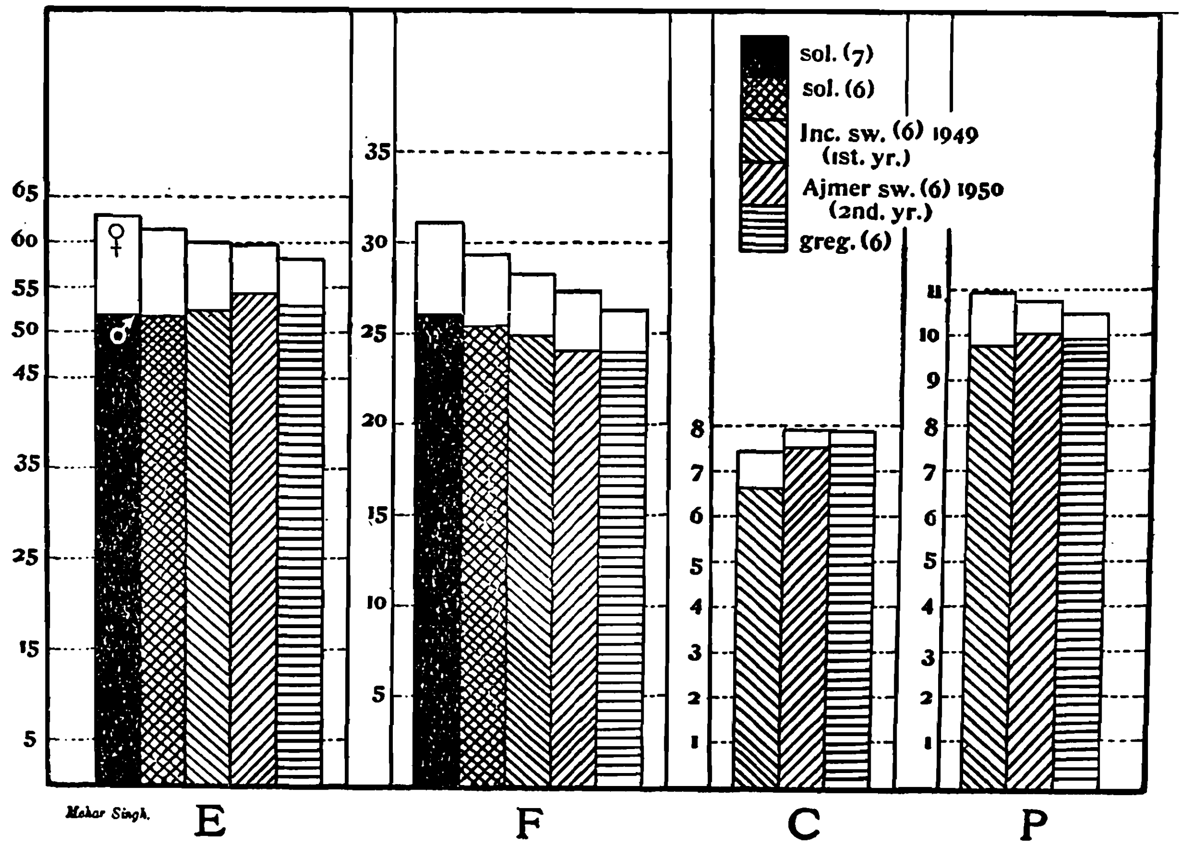
TEXT-FIG. 7.—*Schistocerca gregaria.* Bar diagrams showing the gradient in Sexual Dimorphism Percentage (S. D. P.) in biometric characters, *viz.*, E (length of elytron), F (length of hind-femur), C (width of head at the genal level) and P (length of pronotum at the dorsal keel), ranging from the 7-eye-striped *solitaria* to the 6-eye-striped *gregaria* populations under various conditions of population density and swarming. The polymorphism in the *solitaria* phase is evident, and gradually declines in the extreme *gregaria* phase. (*After* Roonwal & Misra, 1952.)

Ajmer sw. (*6*) *1950* (*2nd yr.*), population from a small swarm at Ajmer in June 1950, *i.e.*, in the 2nd year of the new swarming cycle in India ; *greg.* (*6*), typical extreme phase *gregaria* population (from data of Roonwal, 1949*a* ; and Roonwal & Nag, 1950) ; *inc. sw.* (*6*) *1949* (*1st yr.*), population from a locust concentration at Kakko (Bikaner, Rajasthan) in July 1949, *i.e.*, in the 1st year of a new swarming cycle in India (from data of Misra, 1950) ; *sol.* (*6*), *sol.* (*7*), typical 6-eye-striped and 7-eye-striped *solitaria* populations respectively (from data of Roonwal, 1949*a* ; and Roonwal & Nag, 1951).

found in 1937, and only one in 1938. In 1939, no 8-striped form was found and the proportion of the 6- and 7-striped forms varied as 66-91 : 9-34.

As the 8-eye-striped form represents the extreme development of the *solitaria* period, the following details about the wild forms, kindly supplied by Shri Y. R. Rao (*in litt.*), are of interest :—

(1) 18.ii.1936 : Jasurana (Jaisalmer Dist., Rajasthan) ; ♂ ; E/F 1·99.
(2) 16.vi.1936 : Pholia (Jaisalmer Dist.?, Rajasthan) ; ♂ ; in *solitaria* phase.
(3) 2.ix.1936. Mithra (Bahawalpur State, Punjab) ; ♀ ; E/F 1·97.
(4) 13.ix.1936. Udaramsar (Bikaner Dist., Rajasthan) ; ♂ ; E/F 1·94.
(5) 14.ix.1936. Sardarshahar (Bikaner Dist., Rajasthan) ; ♂ ; E/F 2·08.
(6) 30.ix.1936. Naka Kharrari (Lasbela State, Baluchistan) ; ♀ ; E/F 1·91.
(7) 28.x.1936. Bhagori (Lasbela State, Baluchistan) ; ♀ ; E/F 2·11.
(8) —.ii.1937. Ambagh (Lasbela State, Baluchistan).
(9) 3.x.1937. Girasar (Jaisalmer Dist., Rajasthan) ; ♀ ; E/F 2·00.
(10) 25.vii.1938. Gurrani (near Pasni, Baluchistan coast) ; ♀ ; E/F 1·99.



TEXT-FIG. 8.—*Schistocerca gregaria.* Polymorphic variability in the size of certain body-parts, *viz.*, elytron-length (E), hind-femur-length (F), head-width in genal level (C), and prenatal width at the keel (P), under various conditions of population density from extreme phase *solitaria* (low populations) to extreme phase *gregaria* (high populations). Each bar represents the mean size, in mm., of the body-part in females (higher level) and males (lower level of same bar) under defined population conditions (*see* inset for explanation). The difference between the values in the two sexes is represented by the blank rectangle at the top of each bar. Note the graduality in the fall of values, the male E being exceptional. The graduality in the decline of sexual differences with increasing population density is noticeable. For explanation of abbreviations, *see* Text-fig. 7. (*After* Roonwal & Misra, 1952.)

TABLE 4.—Showing E/F ratios (elytron length/hind-femur length) in the various types of individuals of *Schistocerca gregaria* (Forskal). (Data for the 6- and 7-eye-striped forms are *after* Roonwal, 1949*c* ; and Roonwal & Nag, 1951.)

Abbreviations.—greg., phase *gregaria* ; *sol.*, phase *solitaria.*

Phase, sex and number of eye-stripes	E/F ratio	
	Range	Mean, with Standard Error
greg. ♂♂ : (6-striped)	2·04—2·30	2·17±0·02
sol. ♂♂ : (6-striped)	1·88—2·23	2·05±0·01
sol. ♂♂ : (7-striped)	1·85—2·13	2·00±0·01
sol. ♂♂ : (8-striped)	1·94—2·08	2·003±0·41
greg. ♀♀ : (6-striped)	2·08—2·43	2·25±0·02
sol. ♀♀ : (6-striped)	1·96—2·25	2·09±0·01
sol. ♀♀ : (7-striped)	1·93—2·17	2·03±0·007
sol. ♀♀ : (8-striped)	1·91—2·11	1·996±0·032

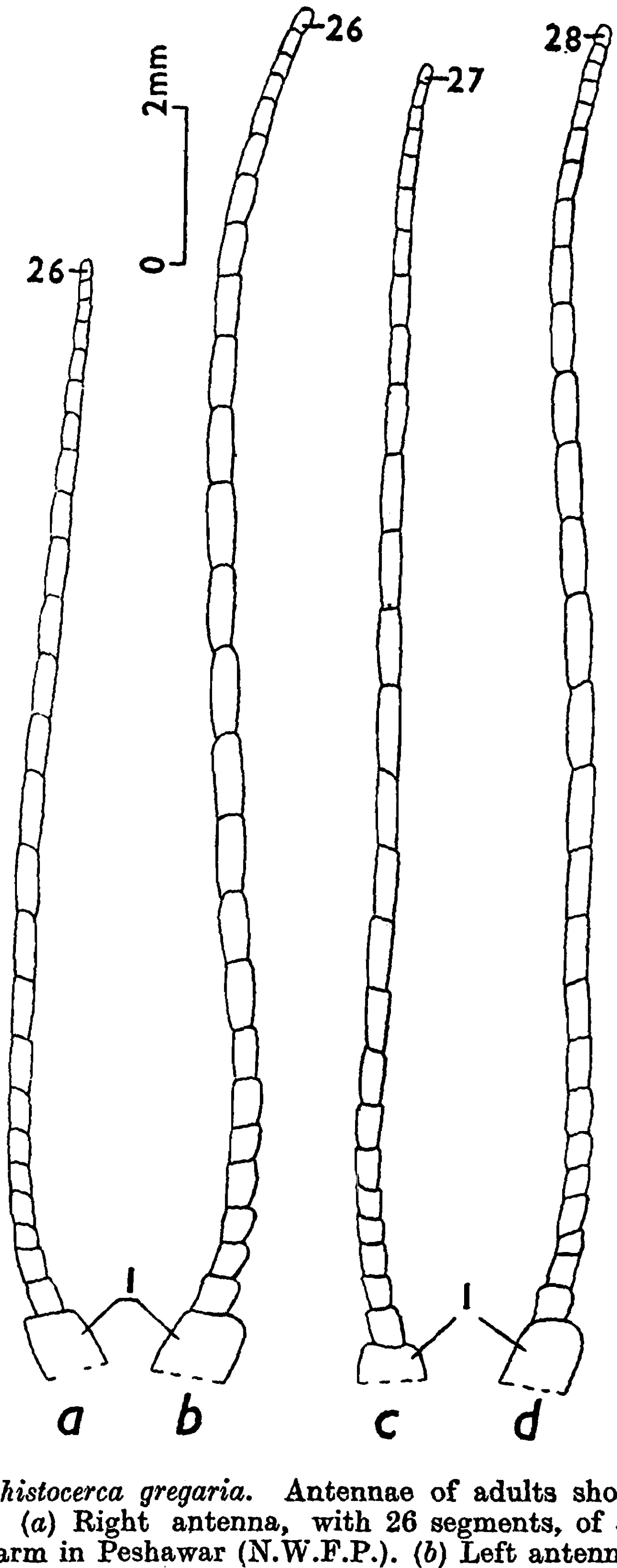
The E/F ratios in the 8-striped forms are the lowest (Table 4) as compared to the other forms determined earlier (Roonwal, 1949*c* ; and Roonwal & Nag, 1951). The combined (male and female) E/F ratios for the *four* types of individuals are as follows (Text-fig. 5) :—(*a*) Phase *gregaria* : 6-striped, 2·22. (*b*) Phase *solitaria* : 6-striped, 2·07 ; 7-striped, 2·02 ; and 8-striped, 1·999.

The sex-ratios also vary in relation to eye-stripe number, as has been shown for the 6- and 7-striped forms (*vide* Roonwal, 1936 ; 1941 ; 1945 ; Nair, 1952*b* and ; Misra, 1953). As in the 7-striped *solitaria* individuals, the proportion of females is higher than males in the 8-striped *solitaria* forms, although the number of available samples of the latter is admittedly small. Of the nine 8-striped individuals collected in the field during 1936-38, 4 were males and 5 females ; and all the five 8-striped individuals bred in the laboratory were females. Thus, we get a ♂ : ♀ ratio of 4 : 10 or 29 per cent ♂ and 71 per cent ♀. The proportion of the sexes in the various types of individuals is roughly as follows :—

(*a*) Phase *gregaria* (6-eye-striped) : ♂ 50 : ♀ 50
(*b*) „ *solitaria* (6- „ „) : ♂ 60 : ♀ 40
„ „ (7- „ „) : ♂ 35 : ♀ 65
„ „ (8- „ „) : ♂ 29 : ♀ 71

3. *Swarming* (*gregaria*) *period 1940-46.*—All the individuals taken from actual swarms had 6-eye-stripes only. However, it was noticed again and again that, both in Baluchistan and Rajasthan, 7-eye-striped forms appeared in the next generation obtained from the *residual* populations left after the departure of the swarms. No 8-striped forms were obtained. The occurrence of 7-striped forms emphasises the fact

that even during swarming years whenever and wherever populations fall, the 7-striped forms begin to appear. Thus, in the winter-spring period, when populations are generally lower than in the summer and autumn periods, there is an appreciable proportion of 7-striped forms, but these forms tend to disappear almost completely in the summer and autumn periods. It must be stated that, on the whole, the 1940-46 cycle was considerably milder than the 1926-31 cycle. It is this mildness of swarm-



TEXT-FIG. 9.—*Schistocerca gregaria.* 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. (*After* Roonwal, 1952*a*.)

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

ing concentrations which, in my opinion, largely accounts for the occurrence of the 7-striped forms throughout the 1940-46 cycle, whereas in the previous cycle no 7-striped forms were found, as seen by an examination of old collections.

The eye-stripe proportions in the various years during the period 1940-46 are given in Table 5.

4. *Non-swarming* (*solitaria*) *period 1947-48.*—During the brief *solitaria* interval between the cessation of the last (1940-46) cycle and the beginning of the present one (1949 to date, *i.e.*, 1953), 7-striped forms were again common, although their proportions varied from generation to generation. No 8-striped forms were reported, although it is not unlikely that they may have occurred in small numbers and their existence overlooked.

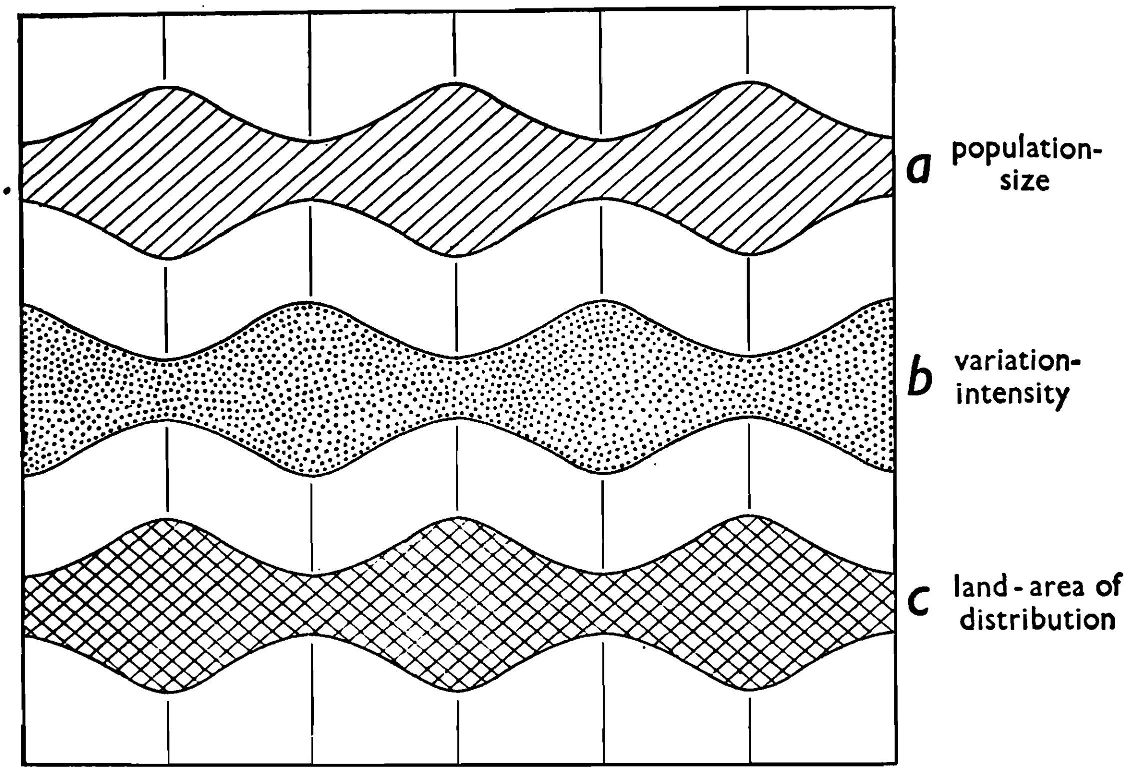
5. *Swarming* (*gregaria*) *period* (*1949 to date,* i.e., *1953*).—The year 1949 saw the occurrence of locust concentrations in the Indian desert regions, the population rising at Kakko (in the Bikaner Distrtict, Rajasthan) from below 1,000 per sq. mile in June to over 18,000 per sq. mile in July (Misra, 1952). By 1950, extensive swarmings had started and it was clear that a new cycle was on. The 5-, 6- and 7-eye-stripe proportions in the Kakko concentration were 0·4 : 94 : 5·6, and for the first time in nature a 5-striped individual was found. A sample from a 1950 swarm gave the 6- and 7-eye-stripe proportions as 93 : 7 (Roonwal & Misra, 1952).

TABLE 5.—Summary of data on the relative proportions of 6- and 7-eye-striped forms in Desert Locust populations in India during the swarming cycle of 1940-1946. (*From* data of Pruthi, 1951.)

Year	Periods and eye-stripe proportions					
	Winter—Spring		Summer		Autumn	
	6	7	6	7	6	7
1940	?	?	67—100	0—33	85—100	0—15
1941	80—100 (mostly 94—100)	0—20 (mostly 0—6)	90—100	0—10	91—100	0—9
1942	64—100	0—36	90—100	0—10	86—100	0—14
1943	77—100	0—23	97—100	0—3	92—100	0—8
1944	92—100	0—8	60—100 (mostly 90—100)	0—40 (mostly 0—10)	47—95	5—53
1945	93—100	0—7	100	0	96—100	0—4
1946	?	?	100 (one sample only)	0	?	?

(*c*) DISCUSSION.

It will now be abundantly clear that eye-stripe polymorphism (and, along with it, polymorphism in several other characters as well) periodically appears and disappears. Similarly, the range of distribution of the species periodically swells and shrinks. In short, the following phenomena are noticeable :—(*i*) The population fluctuates periodically, the ' plague period ' of high numbers corresponding with a considerable increase of range of the species. (*ii*) As regards variation-intensity, the species is comparatively stable during the plague or *gregaria* period but highly polymorphic during the *solitaria* period of *minimum* populations. (*iii*) The phenomenon is periodic and evidently occurs over a wide range (India to Africa) more or less simultaneously. (*iv*) It would appear that the 5-, 7- and 8-striped individuals, which make their appearance during *solitaria* periods, when selection-pressure is low probably owing to reduced numbers, are eliminated, presumably by selection, during the *gregaria* periods of high population and increased selection-pressure, leaving behind only 6-striped individuals.



TEXT-FIG. 10.—*Schistocerca gregaria.* Diagrams to show the periodic relationship between (*a*) population-size, (*b*) variation-intensity and (*c*) global area of distribution

Crossing results (unpublished) show that 5-striped, 6-striped and 7-striped individuals produce both 6- and 7- striped forms in F_1 and F_2 generations. Other results need not be discussed here for the present.

The relationship of the three Phenomena, *viz.*, population-size, variation-intensity and global distribution-range are diagrammatically represented in Text-fig. 10.

This dynamic relationship can also be expressed in another way, thus : Let p represent the small population-size and P the large population-size ; r the reduced global area of the species during the non-swarming (*solitaria*) years and R the increased global area during the swarming (*gregaria*) years ; and, finally, v the reduced variation-intensity (*i.e.*, a variation-stable situation) and V the increased variation-intensity (*i.e.*, a variation-unstable situation) ; then the periodic relationship may be diagrammatically expressed as in Text-fig. 11.

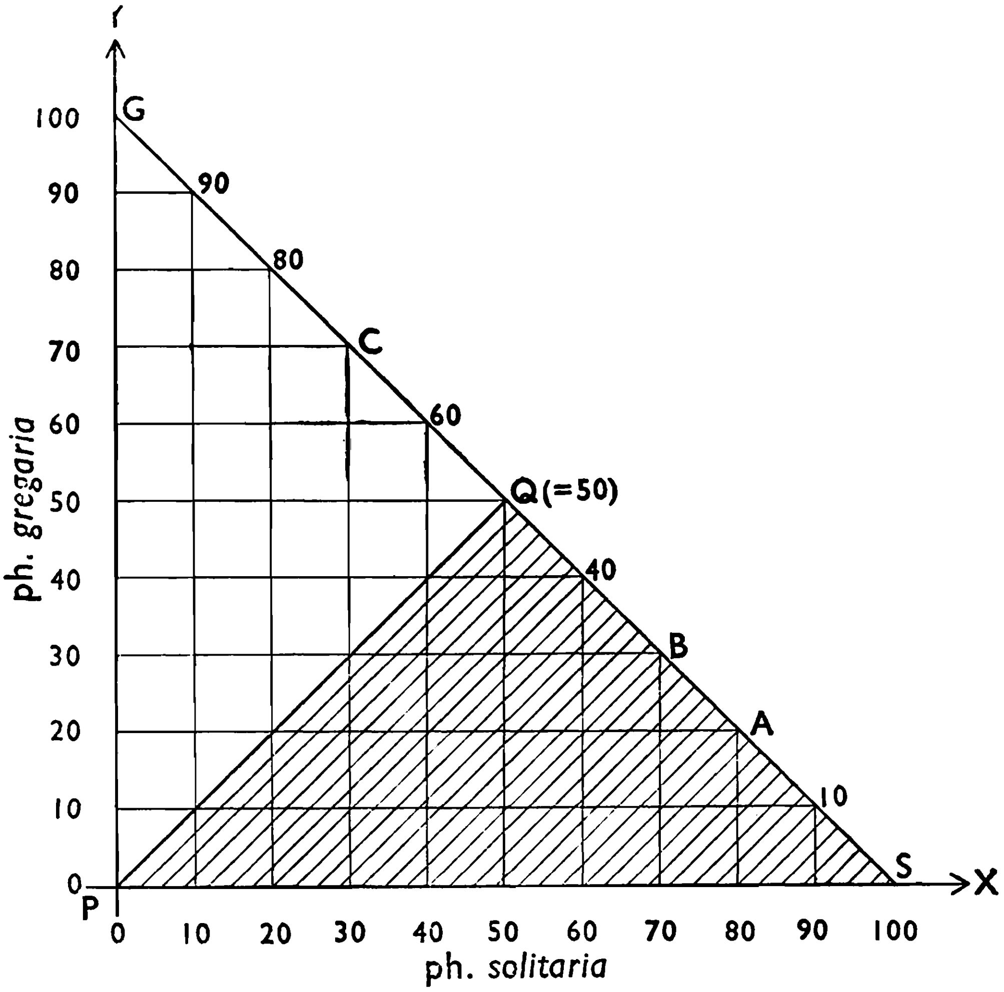
World population of species | $prV \rightarrow PRv \rightarrow prV \rightarrow PRv$. . and so on.

Time $\rightarrow$

TEXT-FIG. 11.—*Schistocerca gregaria.* Chart to show the correlation and periodicity of flux of population-size, global area occupied and variation-intensity. For explanations, *see* text.

We may represent this relationship in yet another way, as in Text-fig. 12. The X-axis represents increasing *solitaria*-ness, and the point S on it represents the extreme state (100 per cent) of *solitaria*-ness. The Y-axis represents increasing *gregaria*-ness, and the point G on it represents the extreme state (100 per cent) of *gregaria*-ness. The lengths of the lines PS and PG are assumed to be equal. The points on the line SG represent the position of *solitaria*-ness or *gregaria*-ness on the *solitaria-gregaria* continuum. The shaded portion represents the variation-unstable population (*i.e.*, one with high variation-intensity), while the unshaded portion represents the variation-stable population (*i.e.*, one with zero variation-intensity). It is assumed for the sake of convenience that : (*i*) in the line PQ dividing the variation-stable area from the variation-unstable area, the point Q lies *midway* between the points S and G on the S-G continuum ; and (*ii*) this line is a straight one, *i.e.*, the rate of fall of variation-intensity remains constant. The extent of distribution of variability in a population at any one point is read off horizontally, *i.e.*, parallel to the X-axis, and thus the amount of variation-intensity present in a population can be read off easily on this diagram. To take a few examples : Point A on the S-G continuum represents 80 per cent *solitaria*-ness (and, correspondingly, 20 per cent *gregaria*-ness) ; in such a population, out of a total of 8 units about 6/8ths or 3/4ths of it is variation-unstable and the remainder variation-stable (with zero variation-intensity). Similarly, point B represents 70 per cent *solitaria*-ness (and 30 per cent *gregaria*-ness) ; in such a population, out of a total of 7 units about 4/7ths of it are variation-unstable, and the remainder variation-stable. Again, point C represents 30 per cent. *solitaria*-ness (and 70 per cent *gregaria*-ness) ; in such a population, with a total of 3 units, all the individuals are variation-stable. These results will, of course, vary with the angle which the line PQ sustains on the X-axis. At point S (of 100 per cent *solitaria*-ness) the entire population is variation-unstable. But, with the point Q being midway on the S-G continuum, the entire population will be variation-stable beyond point Q towards G. In other words, at point Q we get a sudden extinction of variation and the entire population is variation-stable and remains so until point G (100 per cent *gregaria*-ness) is reached.

This idealised condition (of point Q being midway between S and G) need not, and indeed does not, apply to all the variabilities, but varies from character to character. Two examples, which are taken from the data of Roonwal (1945*a*, 1949*c*, *d*), will suffice to illustrate this point. In regard to the character E/F ratio (elytron-length/hind-femur-length) it is known (Roonwal, 1949*c*, p. 161, Text-fig. 1 ; also *vide* Text-fig. 5 above) that it vibrates on the *solitaria-gregaria* continuum in 2 groups or peaks of temporary stability (in the sense of Wright, 1932, *vide* Text-fig. 2 above) as follows :—(*i*) The *solitaria* group with *three* peaks (*i.e.*, with high variability) for the 6- , 7- and 8-eye-striped forms (with possibly a fourth peak for the 5-eye-striped forms). All these peaks are characterised by low ratios. (*ii*) The *gregaria*-group with *one* peak (*i.e.*, with comparatively low variability or, ideally speaking, none) of high E/F ratios. The change from the *solitaria* group of peaks to the *greagaria* group, *i.e.*, from the variation-unstable position to the variation-stable position, takes place *below* the point Q = 50, as is evident from the data of Roonwal (1949*a*, p. 174 ; also *vide* Text-figs. 13 and 14 here). In other words, the sudden change or ' extinction of variation ' referred to above occurs very early or long before the movement of S towards G has gone half-way. Roonwal (1949*a*, p. 174) wrote thus in this connection



TEXT-FIG. 12.—*Schistocerca gregaria.* Idealised diagram to represent the relationship between variation-intensity on the one hand, and the *gregaria* and *solitaria* phases on the other. The shaded area represents the variation-unstable population (*i.e.*, one with great variation-intensity) and the unshaded portion the variation-stable population (*i.e.*, one with no variation), on the assumptions : (*i*) that the dividing line, PQ, between the two areas lies at a point midway on the line S-G which represents the *solitaria-gregaria* continuum ; and (*ii*) that the line PQ is a straight one.

in regard to E/F ratios : " It may be tentatively assumed that the dividing line between *solitaria* and *gregaria* populations is at g*=50. Actually perhaps, this figure may prove to be a little too high, but it may be adopted until more data are available. "

The position regarding the variability in the eye-stripe character is, however, different. The complete or near-complete extinction of variability in this character occurs long after Q = 50. As shown in my " First Hypothesis " (Roonwal, 1945*a* ; *vide* also Nair, 1952*b* for discussion), in a mixed 6- and 7-eye-striped (*i.e.*, variation-unstable) population travelling from S to G, the elimination of the 7-striped forms is very rapid after the proportion of about 70 per cent 6-striped forms is reached. In other words, Q = *ca.* 70. In any case, whatever the position of Q on the S-G continuum, the triangle PQS will be shaded to represent the variation-unstable population showing high variation-intensity, and the triangle PQG will then represent the variation-stable population of zero variation-intensity, the proportions of the two at any one point in a population being read off horizontally, *i.e.*, parallel to the X-axis.

Since in the Desert Locust the determining factor in the degree of variation-intensity is the population density rather than absolute numbers, let us see what are the theoretical possibilities. Let n represent the total number of individuals in an area, s the area occupied, and d the density per unit area. If we further assume that

$$d=\frac{n}{s},$$

then there are 3 theoretical possibilities, A, B, C, as regards the change of d. These, together with the conditions under which they will be realised, are listed below :—

(A)—*d remains constant : This condition will be realised when :*

1. s increases ; and n increases proportionately to s.
2. s decreases ; and n decreases proportionately to s.

(B)—*d increases : This condition will be realised when :*

3. s is constant ; and n increases.
4. s decreases ; and n increases.
5. s decreases ; and n is constant.
6. s increases ; and n increases more rapidly than s.
7 s decreases ; and n decreases less rapidly than s.

(C)—*d decreases : This condition will be realised when :*

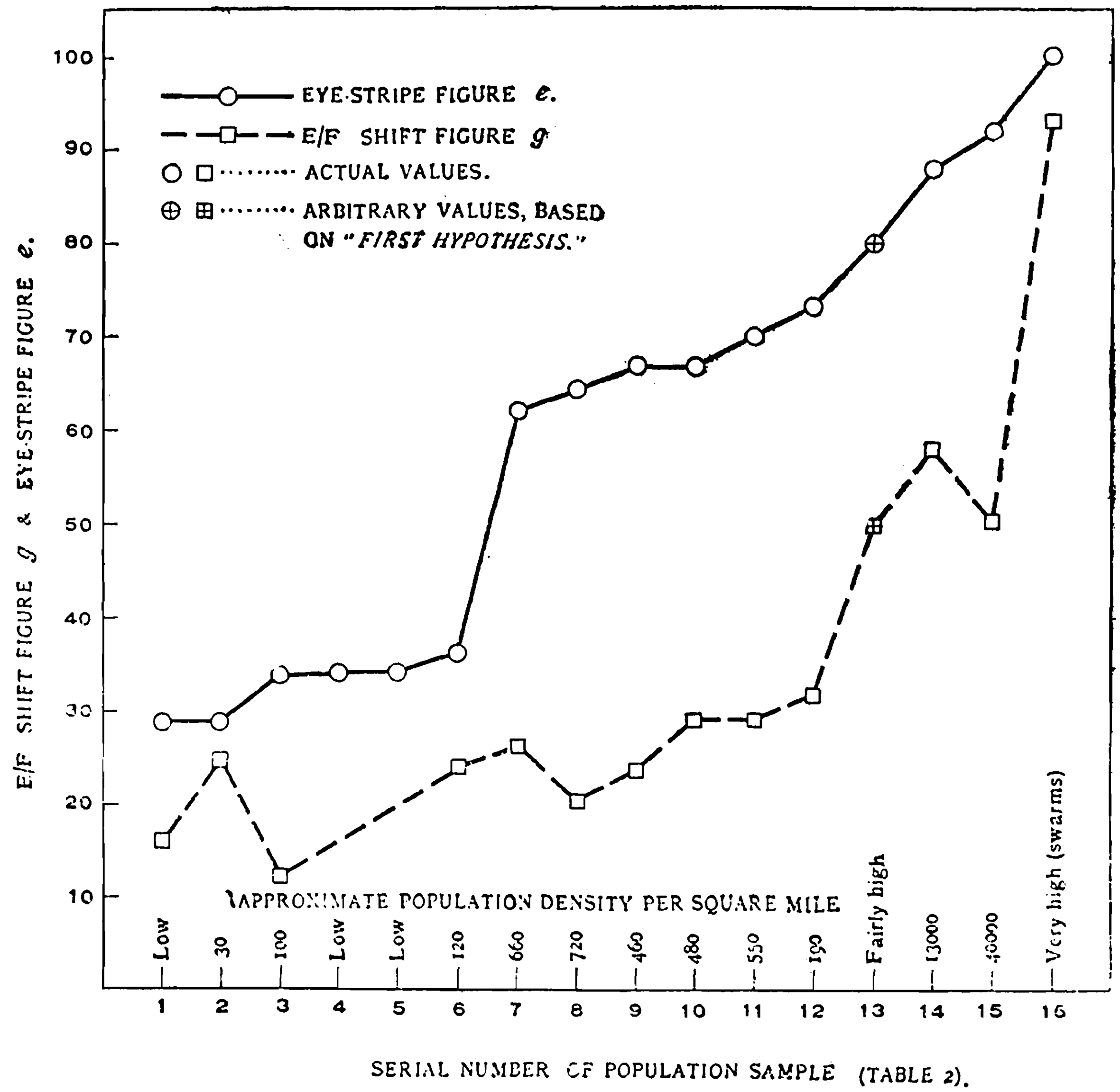
8. s increases ; and n is constant.

---

* The symbol g means the " E/F shift figure " as conceived by Roonwal (1949*d*, p. 171). It means the " shift ", as determined by the E/F ratios, towards *gregaria*-ness in a *solitaria-gregaria* population. Similarly, the symbol e means the " eye-stripe figure " by which is meant the percentage of 6-eye-striped forms in a mixed population of 6- and 7-striped forms (*see* Text-figs. 13 and 14).

9. *s* is contant ; and *n* decreases.
10. *s* increases ; and *n* decreases.
11. *s* decreases ; and *n* decreases more rapidly than *s*.
12. *s* increases ; and *n* increases less rapidly than *s*.

Subject to the correction that the population is not uniformly distributed throughout the range of distribution but is confined to niches or islands, the following situations would seem to occur in the Desert Locust :—In the *solitaria* phase the population density (in the niches in the permanent breeding grounds) is only about 1,000 per sq. mile, whereas in the *gregaria* phase this figure is about 30,000 per sq. mile, or nearly 30 times as great (Table 2). The increase in the area of distribution in the *gregaria* phase is only about 1·7 times that of the *solitaria* phase (*vide supra*, p. 6 & Pl. XV). Thus, the increase of density during the *gregaria* phase takes place by means of situation B(6) mentioned above. And, *vice versa*, during the passage from the *gregaria* to the *solitaria* condition, the situation C(11) evidently comes into play.



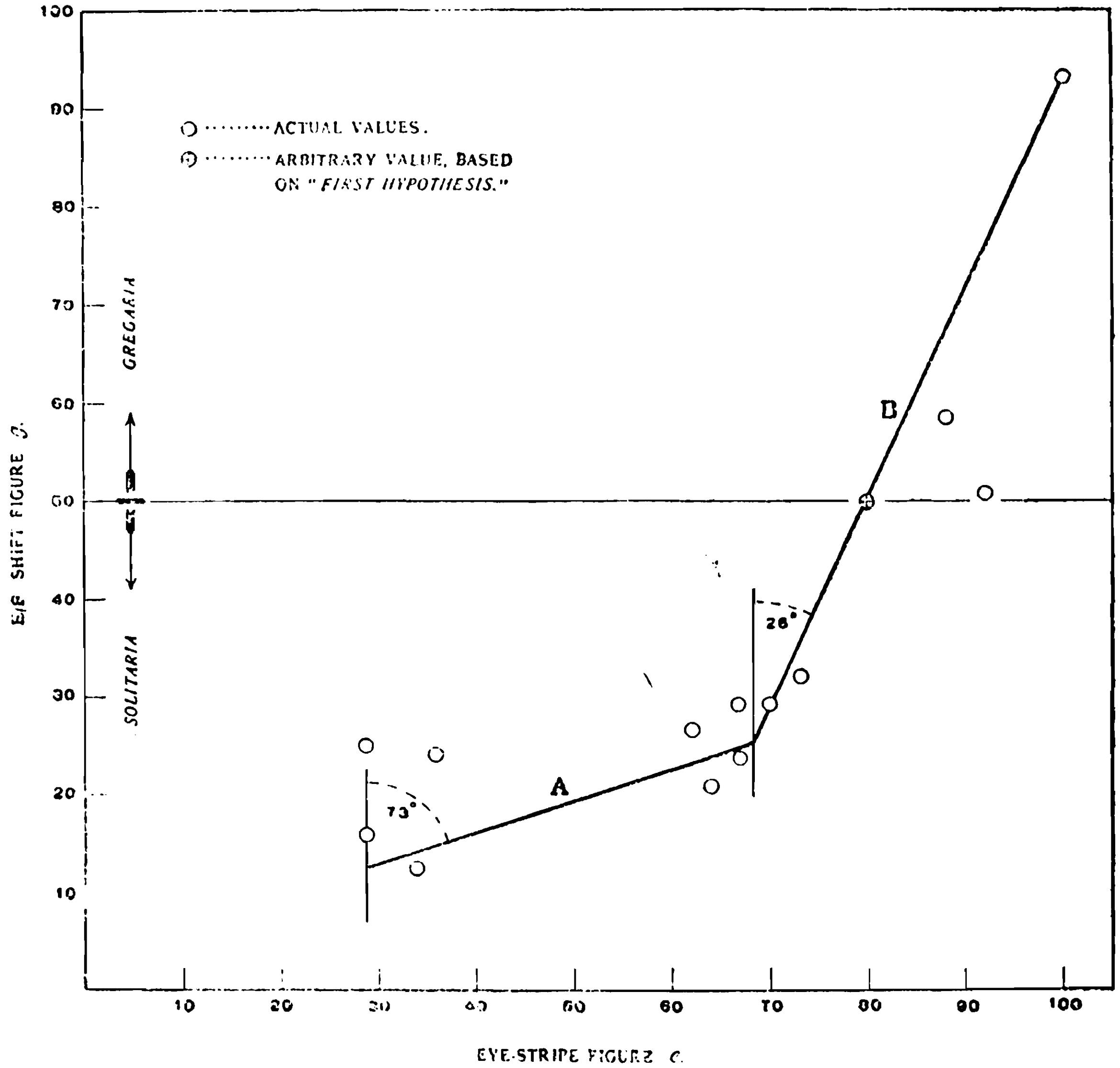
TEXT-FIG. 13.—*Schistocerca gregaria.* Graph showing the correlation between the "E/F shift figure *g*" and the "eye-stripe figure *e*" in several population samples. (*After* Roonwal, 1949*a*.) For further explanations, *see* text, p. 31, foot-note.

The part which the migration or crossing factor might play in controlling variation-intensity in the Desert Locust is not well understood.

But in so far as the larger migratory movements are concerned, *viz.*, the seasonal migrations, they are similar in the *gregaria* and the *solitaria* phases. There is a free exchange of population between the large geographical areas concerned, as the N. African populations migrate seasonally to Arabia, and populations from the latter region migrate seasonally to Iran and India. The reverse movements occur with equal regularity. Thus, we may assume with justification that a thorough mixing up of these populations over vast areas occurs regularly in both phases, with this difference that in the *gregaria* phase the usual bounds of the permanent breeding grounds are erupted and migrations occur over greater distances and areas.

The exact mode of the periodic population-increase itself is not understood, although a number of explanations have been put forward (*vide* Roonwal, 1949*a*, for discussion). How misleading some of these explanations can be when they are not rigidly checked against facts will be evident from the comparatively recent attempt of Bodenheimer (1937). This author has attempted to explain periodicity on the basis of a difference in the number of annual generations between the migration and the non-migration periods, potential increase, environmental resistance, and so on. His account, however, contains so many errors and unfounded assumptions that is not surprising that he has completely confused the issues. It will suffice to point out a few of his errors. First, his purely imaginary scheme for the building up of Desert Locust outbreaks runs in the following sequence : Population ebb ; preparatory years (2-6 generations) ; prodromal years (1-3 generations) ; eruption (2-10 generations); crisis (1-2 generations) ; and population ebb (a few to many generations). Bodenheimer has left unexplained the precise meaning of the terms 'preparatory', 'prodromal', 'eruption' and 'crisis' But even if we were to give an approximate meaning to these terms, there is in fact not the slighest factual evidence for the sequence of events mentioned above. All that can be distinguished are the plague or mass-outbreak years (usually showing some sort of a peak) with very high population (of about 30,000 or more adults per sq. mile in swarms), and the non-plague years with a very low but fluctuating population (of not over about 1,000—2,000 non-swarming adults per sq. mile). However, in the year preceding the start of full-scale swarming, it is now evident that there are certain initial concentrations of population up to about 20,000 per sq. mile for a generation, as was recently found in Kakko in Bikaner District, Rajasthan, in 1949 by Misra (1952). The number of generations assigned by Bodenheimer to each one of his imaginary periods has, of course, no basis in fact.

Secondly, Bodenheimer has claimed that all the species of locusts, such as those of the genera *Schistocerca*, *Locusta*, *Calliptamus* and *Dociostaurus*, which migrate extensively are able to develop more than one annual generation in their *gregaria* phase, while the *solitaria* phase has only one generation. This claim certainly does not hold true for the Desert Locust, *Schistocerca gregaria*, which in the *solitaria* phase has 2-3 annual generations (theoretically perhaps 4), and in the *gregaria* phase 3-4 (theoretically perhaps 5), as shown below. The existence of 2-3 annual generations (depending on the area) in the *solitaria* phase in nature in western India has been demonstrated by Rao (1942) who concluded that theoretically " there is the possibility of four successive generations following one another in the course of the year, though ordinarily not more than three broods can be expected " (p. 242). It should be stated, however, that in places like Pasni (Mekran Coast, Baluchistan), which is an area of scanty winter rains and no summer rains at all, there is normally only one annual generation, *viz.*, in winter. In the *gregaria* phase, in South-Western Asia, Fortescue-Foulkes (1953, pp. 12-14) has concluded that there may be as many as 2, or sometimes even 3, monsoon generations in India. He has distinguished 3 major seasonal breeding areas in S. W Asia as follows :—(*i*) Only one breeding season a year—" monsoon " breeding (Sind, central and southern Rajasthan, Cutch, Saurashtra, N. Bombay). (*ii*) Two breeding seasons a year—" winter-early spring " and " main-spring " breeding seasons (S. Iran). (*iii*) Three breeding seasons a year—" monsoon ", " winter-early spring " and " main spring " breeding seasons (N. Pakistan; and the Punjab and Uttar Pradesh in North India). Fortescue-Foulkes concluded (p. 17) that " it is thus theoretically possible for five successive generations to be produced during the year in South-Western Asia, an



TEXT-FIG. 14.—*Schistocerca gregaria.* Graph obtained when the " eye-stripe figure *e* " is plotted as a function of the " E/F shift-figure *g* ". (*After* Roonwal, 1949*a*.) For further explanations, *see* text, p. 31, foot-note.

estimate which corresponds with the maximum number of generations which might be produced by swarms migrating between North-East Africa and Middle East (Davies 1952). The production of all five generations, however, depends not only on suitable climatic conditions but also on the continuity of swarm displacements between the seasonal breeding zones, and can only be established by a more detailed study of particular breeding seasons and years." It may be mentioned in this connection that under favourable conditions of temperature and soil moisture under laboratory conditions, Husain & Ahmad (1936) have obtained as many as 8 successive generations per year at 40° C., about 7 at 36° C. and 5 at 30° C. in the incubator. I have observed during the years 1935-38 in the *solitaria* phase in Pasni (Mekran Coast, Baluchistan) that whereas in nature there is only one annual breeding in December-February coinciding with the winter rains, in cages under semi-natural conditions with moist soil and an abundance of fresh food, breeding was continuous and about 2½ annual generations were obtained ; it is hardly necessary to mention that in summer one generation was over in about 2-3 months, whereas in winter, owing to low temperatures, the period of development was considerably prolonged.

Thirdly, the accuracy of Bodenheimer's claim of the " Sudano-Deccanian " region as being the permanent home of the Desert Locust, has already been refuted above (see p. 4) in so far as the Deccan and the adjoining regions in India are concerned. Fourthly, his statement that the mortality of adults in the so-called imaginal diapause is certainly very greeat cannot be substantiated. There is no diapause in any stage in the Desert Locust ; only, during the winter months (November to February) as compared to the hotter months, the rate of development is very much slowed down and the life-duration, especially of the adults, considerably prolonged as a result of low temperatures. Fifthly, there is no evidence to support Bodenheimer's assertion that mortality is greater in the winter than in the summer months.

Finally, a word may be said about the mutual relationships of the various types of evolutionary Effects or phenomena discussed above, ranging from the Hardy Effect to the New Effect described here. It is difficult to believe that all these Effects, which are in appearance distinct from one another, are completely independent and are caused by totally different mechanisms. Rather, it would seem that the mechanism which brings them into play is fundamentally the same, and that the various Effects are merely different phases or expressions of that mechanism.

A further question which arises is whether the types of polymorphism which periodically arise and are swamped away as in the Desert Locust, can be of any significance in the actual process of speciation. In other words, will these variations ever become stable and thus produce separable specific populations. It is difficult to answer this question, but we have no reason to believe that the variations discussed here are utterly transitory and of no speciation-value.

V.—EVOLUTION OF VARIOUS TYPES IN DESERT LOCUST.

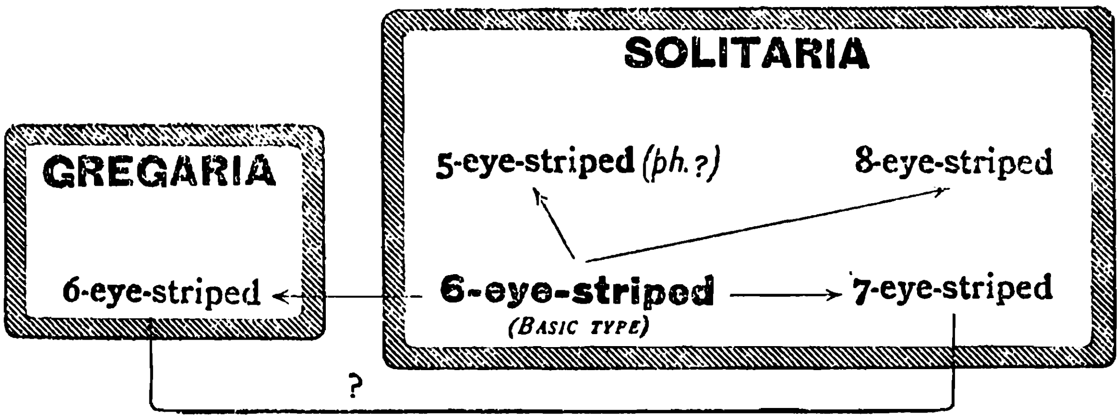
(Text-figure 15.)

Having considered the various forms that exist in the Desert Locust, it would be appropriate to discuss their evolution. The following types have so far been recognized :—

Group (A).—Phase *gregaria* type (6-eye-striped).

Group (B).—Phase *solitaria* types (5- , 6- , 7- and 8-eye-striped types). Two further types have also been recognised, *viz.*, the "blue-grey type " and the " fawn type " (Roonwal, 1945*b*; 1946*b*); the former is more common (91 %) than the latter (9%), and in both types 6- and 7-eye-striped individuals occur.

Leaving aside these 2 colour-types in the phase *solitaria* group, the evolution of the various forms of *Schistocerca gregaria* would appear to be as follows (Text-fig. 15) :—



TEXT-FIG. 15.—*Schistocerca gregaria.* Diagram to show the evolution of the various polymorphic forms.

The 6-eye-striped *solitaria* must be regarded as the *basic type*, since it is the most common and the most stable type. Under certain conditions, it produces or evolves into 2 different groups, *viz.*, (*i*) the *gregaria* phase group in which only 6-eye-striped forms occur ; and (*ii*) the *solitaria* phase group in which, in addition to the 6-striped forms, forms with 5, 7, and 8 eye-stripes occur. It would seem that all these different forms arise directly from the ' basic type ' (6-eye-striped *solitaria*). This conclusion is supported by preliminary results of the crossing experiments briefly mentioned above (p. 28). The position of the 5-striped forms is not quite clear. Misra (1952) has reported the first and only example of a 5-striped form taken wild in 1949 which was the first year of a new swarming cycle ; previous records are all from breeding cages. Tentatively, I am inclined to place the 5-striped forms with the *solitaria* group and as having evolved from the ' basic type ' (6-striped *solitaria*) rather than from the 6-striped *gregaria*.

VI.—SUMMARY.

1. A number of different evolutionary phenomena or " Effects " are known to exist in regard to the influence of population-structure on the processes of speciation or production of variations. Here I have brought forth evidence, based on the Desert Locust, for the existence of a new type of phenomenon.

2. New data on the land-area occupied by the Desert Locust, *Schistocerca gregaria* (Forskal), are given with the aid of a world map drawn on an " equal-area " projection. This area is about 16,500,000 sq. miles in the swarming (phase *gregaria*) periods and about 9,500,000 sq. miles in the non-swarming (phase *solitaria*) periods, or in the ratio 1·7 : 1.

3. The density of population and the amplitude and periodicity of population-flux in the Desert Locust are discussed. The population density is about 1,000—2,000 per sq. mile or less in the *solitaria* phase and about 30,000 per sq. mile or more in the *gregaria* phase. The periodicity of plague cycles varies thus : 5-10 years (average 7.1) in the swarming years ; 1-8 years (average 4) in the non-swarming years ; and 7-14 years (average 11·1) for the complete cycles.

4. A critical review in given of the known types of phenomena or " Effects " concerning the production of variations in relation to population density and other characteristics. The various phenomena are : (*i*) the Hardy Effect ; (*ii*) the Hagedoorns Effects ; (*iii*) the Adlerz Effect ; and (*iv*) the Wright-Dubinin Effect.

5. (*a*) A new phenomenon or " Effect ", as evidenced by the case of the Desert Locust, is described. This Effect consists in the fact that intraspecific variability (polymorphism) is sharply increased during the non-swarming or phase *solitaria* periods of *minimum* populations, and almost completely obliterated during the swarming or phase *gregaria* periods of *maximum* populations. The *gregaria* phase is variation-stable and the *solitaria* phase variation-unstable.

(*b*) The periodic appearance and extinction of these polymorphic variations are traced over a period of 25 years (1926-50) during which the phenomenon was observed in 3 swarming periods and 2 non-swarming periods.

(*c*) Some new data on the characteristics of the 8-eye-striped individuals are provided. Their E/F ratio is the lowest among the phase *solitaria* group of individuals, being lower than in the 6-and 7-striped *solitaria* forms. They also have the highst proportion of females, the ♂ : ♀ ratio being 29 : 71.

(*d*) The various factors which lead to the increase or decrease of population density are discussed theoretically.

6. The evolution of the various types of polymorphic forms in the Desert Locust is traced. The 6-eye-striped phase *solitaria* form is considered as the *basic type* from which the other types are believed to have been derived directly in two directions : (*i*) the '*gregaria* phase group' with a single type (6-eye-striped) ; and (*ii*) the '*solitaria* phase group' with 5- , 6-, 7- and 8-eye-striped types. The exact position of the 5-eye-striped type is rather problematical owing to want of sufficient data.

VII. REFERENCES.

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

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VIII.—EXPLANATION OF PLATES XV—XVIII

LETTERING

b., basement membrane.
c. c., crystalline cone.
c. g., cerebral ganglia.
cr., cornea.
cr. c., corneagen cells.
cr. i., inner layer of cornea.
cr. o., outer layer of cornea.
e. op., epiopticon.
fn., fenestra or hole in basement membrane.
n. c., nerve cells.
n. c. s., sheath of nerve cells.
n. f., nerve fibres.
nu. c. c., nuclei of crystalline cone (Semper's nuclei).
nu. p., nuclei of primary pigment cells.
nu. r. d., distal nuclei of retinular or visual cells.
nu. r. p., proximal nuclei of retinular or visual cells.
nu. s., nuclei of secondary pigment cells.
om., ommatidia.
op., opticon.
op. n., optic nerve.
p., primary pigment cells.
p. op., periopticon.
pr. n. f., post-retinular nerve fibres.
pr. p. l., post-retinular pigment layer.
r., retinula.
r. c., retinular or visual cells.
r. n. f., retinular nerve fibres
rh., rhabdom.
rp., reddish brown pigment granules.
s., secondary pigment cells.
t. d., distal or small tracheae.
t. p., proximal or large tracheae.
y. p., dirty-yellow pigment granules.