A REVISION OF THE GENUS *LOCUSTA*, L. (= *PACHYTYLUS*, FIEB.), WITH A NEW THEORY AS TO THE PERIODICITY AND MIGRATIONS OF LOCUSTS.

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CONTENTS.

I. INTRODUCTORY.

The genus *Locusta*, L. (= *Pachytylus*, Fieb.) includes two of the most destructive swarming locusts of the Old World : the widely distributed *L. migratoria*, L. (with *L. danica*, L., and *L. migratorioides*, Rch. & Frm., as its forms ; see below), and the South African *L. pardalina*, Walk. The literature on the economics, biology and especially on the means of control of these locusts is enormously extensive, but at the same time their systematic arrangement is in considerable confusion, and extremely contradictory opinions as to the mutual relationship of the different so-called species exist among specialists. As a direct consequence of this, the field research and control work of economic entomologists is apt to suffer through the difficulty in getting a particular species properly named,* and thus it is often impossible to make a comparison of the records as to the biology and control of the same species in different countries.

Having had the opportunity of conducting, during the years 1911–14, extensive field research work and control work on *L. migratoria* in the northern Caucasus (Russia), and being a systematist, I could not fail to see at once that only very little progress could be made without a definite solution of the question of the inter-relation between *L. migratoria* and *L. danica*, which latter has been accepted by many authors as a species distinct from *migratoria*, and as conspecific with it, by others. The same question arose before the Turkestan Entomological Station (in Tashkent) as soon as its staff began to work on *L. migratoria*.

Apart from my field work, which involved the study of immense series of living specimens in all stages, I endeavoured to gather all reliable information as to the distribution and local, individual and annual variability of *L. migratoria* and *danica* in different parts of their range, and owing to the support of entomologists and institutions throughout Russia and elsewhere, I managed to concentrate in my hands extremely rich materials from the following sources : Turkestan Entomological Station (V. j. Plotnikov) ; Astrakhan Entomological Station (N. L. Sakharov) ; Natural History Museum in Kherson (J. K. Pachossky) ; Zoological Museum of the Moscow University (Prof. J. Kozhevnikov) ; Caucasian Museum in Tiflis ; Zoological Museum in Berlin. The following persons also contributed very valuable materials and information : Prof. J. Shtchelkanovzev, E. Jatzentkovsky, V. Artsimovicz

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* See, for instance, the interesting paper on the biology and control of the Malayan locust by H. C. Pratt (Bull. No. 27, Dept. Agric. Fed. Malay States, 1915), who states that " many attempts to identify this Malayan locust have been made and correspondence has been entered into with authorites throughout the world, but without success." He has been compelled to call the insect, simply, *Pachytylus* sp.

N. Ikonnikov, V. Boldyrev, L. Moritz, H. C. Pratt (Government Entomologist, Federated Malay States), and many others. Thanks to this generous help, I was able to come to certain conclusions on the question of *migratoria-danica* already in 1915, but the War and other circumstances prevented me from publishing a paper on it   When I arrived in London in 1920 and studied the exotic representatives of the genus *Locusta*, I felt the necessity of revising my previous work and extending its limits so as to include in it all known species and forms of the genus.   This plan proved to be a very productive one, since a far more definite idea as to the inter-relations of different " species " has been thus reached.   A study of the South African *L. pardalina*, Walk., has been also accomplished in the British Museum, but I could not do much with museum material only, and the most effective help in this respect has been rendered me by the Division of Entomology, Pretoria, and especially by Mr. J. C. Faure, who has sent to the Imperial Bureau of Entomology at my request extensive series of specimens, together with most valuable information.

With regard to the biological observations here recorded, it is only thanks to the help rendered me by my assistants, G.Vinokurov, Th. Gliniuk, the late G. Pirkovsky, and others, that I could collect the necessary facts.   My most sincere thanks are due also to all the above-mentioned persons and the heads of institutions who have lent me material and supplied information.

II. ON THE GENERIC NAME *LOCUSTA*, L.

The Linnean genus, *Gryllus Locusta*, includes 20 different species of locusts and grasshoppers, belonging to about as many modern genera.   There is no wonder, therefore, that much controversy arose around the question as to the species to which the Linnean name *Locusta* must be restricted now.   This question becomes still more complicated owing to the fact that Geoffroy (Hist. Ins. i, p. 396, 1762) applied the name *Locusta* quite   erroneously to the   long-horned   katydids   (now called TETTIGONIIDAE, or, wrongly, PHASGONURIDAE), and has been followed in this mistake by all continental European authors, till quite recently.   There is, however, no doubt, that Linné, who adopted the name *Locusta* from the old Roman writers who applied it to swarming locusts, intended it to include those insects and the short-horned grasshoppers generally.   This view was accepted long ago by British authors, and W. E. Leach (Edinburgh Encyclopaedia, ix, pt. 1, p. 120, 1815), though using *Locusta*, Geoffr., for katydids, used at the same time *Gryllus Locusta*, L., for *migratoria*, L., the latter being the only species described by him under this genus, and, therefore, he actually has fixed it as genotype of *Locusta*, L.   A few years later on, Samouelle (Entomologist's Useful Compendium, p. 218, 1819) followed Leach in restricting the genus *Locusta* to *migratoria*, but he calls it wrongly *Locusta*, Leach, not Linné. Stephens in 1829 (Cat. Brit. Ins., i, p. 301, No. 2, sp. 3315) merely repeats Samouelle's interpretation of the genus.   Even if we do not accept the genotype of *Locusta*, L. cited in 1815 by Leach, we shall find a most formal fixation of it in the British Ento-mology of Curtis (iii, pl. 608, August 1836), who in describing *Locusta christii*, Curtis (=*danica*, L.) said positively : " Type of the genus, *Gryllus migratorius*, L." All subsequent works on the same subject are, thus, of no importance, and the generic name *Pachytylus*, Fieber, proposed in 1853 (Lotos, iii, p. 121) for *migratoria* and *danica* is a pure synonym of *Locusta*, L.   The proposal of Rehn (Canadian Ento-mologist, xxxiii, 1901) to restrict the genus *Locusta*, L., to *apricarius*, *viridulus* and *biguttulus*, which are included now in the genera *Stauroderus* and *Omocestus*, as well as that of H. Krauss (Zool. Anz., xxv, 1902, p. 539), who regarded *tatarica*, L., as the genotype of *Locusta*, cannot be accepted in view of Curtis' work, which was overlooked by both these authors.

It is, therefore, in full accordance with what Linné meant by his genus *Gryllus Locusta*, as well as with the formal laws of nomenclature, that *migratoria*, L., must be regarded as the genotype of *Locusta*, L.*

Not less than 16 " species " have been described by different authors as belonging to the genus *Locusta*, L. (= *Pachytylus*, Fieb.). This number, however, has been reduced already by earlier revisers, who synonymised many species; but W. F. Kirby in his Catalogue (Syn. Cat. Orth., iii, 1910, pp. 221–231) still mentioned seven distinct species. My investigations, however, have clearly demonstrated the variability of the species of *Locusta* to an extent far greater than might have been anticipated, and my conclusion, which will be fully proved presently, is that only two species can be distinguished, namely, *migratoria*, L., and *pardalina*, Walk., but the latter differs from *migratoria* in so many important characters that a new genus is described below (p. 162) to include it, which I propose to call *Locustana*, g. n.

III. *Locusta migratoria*, L., and its Forms.

Morphological Characters and Variability of *migratoria* and *danica*.

These two forms, if typical examples are studied, seem to be quite distinct from each other in many morphological characters, and may be regarded, as has been done by most authors, as two independent species. On the other hand, every extensive collection includes specimens of *Locusta* that cannot be identified with certainty with either *migratoria* or *danica*, but seem to represent intermediate forms. This fact induced many authors to regard *migratoria* and *danica* as but extreme individual aberrations of the same species.

In studying this question I tried, first of all, to analyse carefully and impartially† all the external morphological characters of both forms, as given by different authors, studying them on as extensive a series of specimens as possible.

After excluding all characters that at once proved to be too indefinite or simply incidental, the following summary of differences between typical *danica* and *migratoria* has been obtained :—

L. migratoria (fig. 1, C, D, E.)	*L. danica* (fig. 1, A, B.)
Vertex convex, with a median longitudinal keel ; fastigium separated from frontal ridge by an angular transverse keel.	*Vertex* flat, without median keel ; no transverse keel separating fastigium from frontal ridge.
Pronotum relatively shorter and broader in metazona, with a distinct construction before the middle ; fore margin rounded ; hind angle rounded ; median keel low, in profile straight or even concave.	*Pronotum* relatively longer and more compressed laterally, without or with but feeble constriction before the middle; fore margin angulately prominent ; hind angle acute ; median keel high, tectiform, convex in profile.
Elytra‡ relatively longer.	*Elytra* relatively shorter.
Hind femora relatively shorter.	*Hind femora* relatively longer.

* I am much indebted to Mr. J. H. Durrant for the help he has generously given me in the solution of this question.

† I must candidly confess that when starting my work I had only a very modest intention—to find out characters for separating *migratoria* and *danica*, which I assumed beforehand to be distinct specifically. The facts quickly destroyed my preconceived opinion and compelled me to work deductively.

‡ This important and rather striking difference between *migratoria* and *danica* was first noted by the artist of the Zoological Museum in Petrograd, Miss O. M. Somina, who made drawings of both insects for Mr. I. Shevyrev, and the latter drew my attention to it.

A study of long series of both forms showed that the differences in the vertex, as given above, are quite unreliable, since the median keel of the fastigium proved to be absent in one per cent. of the specimens of *migratoria*, as well as in about 7 per cent. of *danica* ; the transverse keel was found in 80 per cent. of *migratoria* and in about 47 per cent. of *danica* ; as for the flatness or convexity of the vertex, it is too indefinite a character to be reliable. The only trustworthy characters are, therefore, the shape of the pronotum and the relative length of the elytra and hind femora. In order to avoid, as far as possible, any subjective judgment, I have expressed these characters in terms of actual measurements. This is quite simple in the case of the elytra and femora, since there exists an inverse proportion between their lengths, and we may simply express the length of the femora as a percentage
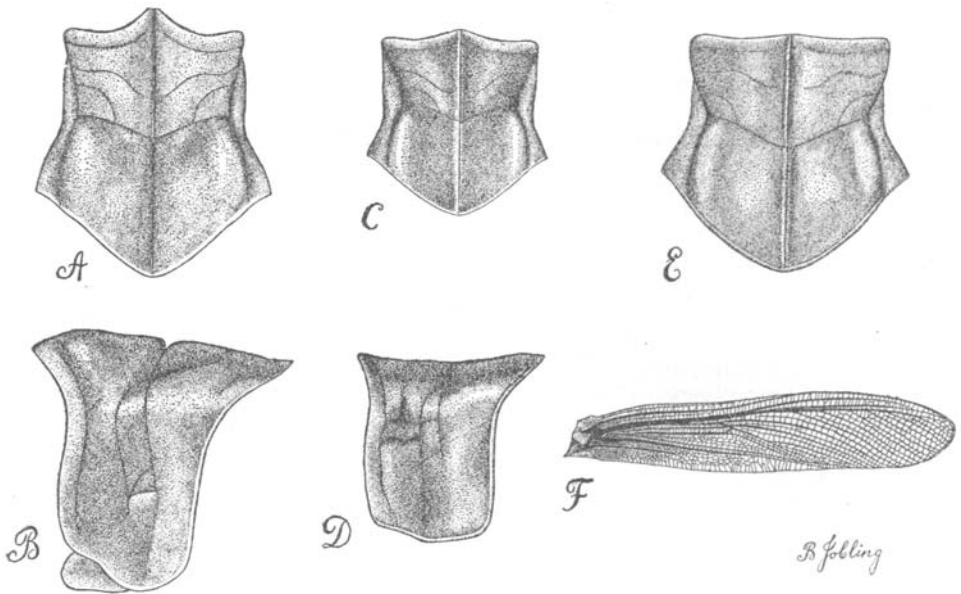

Fig. 1. *Locusta migratoria*, L. : A, B, phase *danica*, L., ♀, Turkestan ; C, D, ph. *migratoria* ♂, progeny of preceding specimen ; E, ph. *migratoria*, typical ♀, Astrakhan ; F, elytron. Elytron natural size, remainder × 3.

of the length of the elytra. As for the shape of the pronotum, numerous measurements have shown that the width of the metazona (measured between the shoulders, *i.e.*, at its widest), if expressed as a percentage of the length of the whole pronotum (along the median keel), gives the best and most reliable impression of the actual shape. The relative height and form of the median keel, which seem to be excluded from consideration by using this proportion, is but a secondary character which depends entirely on the relative length and width of the pronotum. If we imagine that the short and broad pronotum of *migratoria* undergoes a lateral compression, we may expect it to become longer, and its median keel higher and convex, especially in the metazona, which should be most influenced by lateral compression ; there is no doubt, therefore, that the shape of the median keel must be, and actually is, subject to changes correlated with those of the length and width of the whole pronotum.

Though it would be interesting and useful to give individual dimensions of all the specimens measured, I refrain from doing so in order not to encumber this paper with many pages of figures. I will give, therefore, only a general table of the chief results obtained, which will be enough for our conclusions (see Table I).

TABLE I.

Showing Dimensions of different Phases of L. migratoria, *L.*

	Number of Specimens Examined.				Pronotal Proportion.*				Femoral Proportion.†			
	Total.	migratoria.	danica.	transitional.	Maximum.	Minimum.	Extent of Variation.	Average.	Maximum.	Minimum.	Extent of Variation.	Average.
1. All *migratoria*	171	171	—	—	0·89	0·71	0·18	0·80	0·53	0·40	0·13	0·46
2. All *danica*	166	—	166	—	0·85	0·59	0·26	0·72	0·63	0·43	0·20	0·53
3. Palaearctic *danica*	103	—	103	—	0·84	0·59	0·25	0·72	0·63	0·43	0·20	0·52
4. Extra-Palaearctic *danica* ..	63	—	63	—	0·85	0·66	0·19	0·74	0·60	0·46	0·14	0·55
5. Stavropol province, 1912 ..	25	25	—	—	0·87	0·71	0 16	0·79	0·53	0·42	0·11	0·45
6. do. do. 1913 ..	32	19	8	5	0·87	0·66	0·21	0·77	0·53	0·41	0·12	0·47
7. Valley of R. Kuma, 1913 ..	28	23	4	1	0·87	0·64	0·23	0·78	0·53	0·41	0·12	0·46
8. do. do. 1914 ..	36	25	8	3	0·87	0·65	0·22	0·76	0·54	0·42	0·12	0·48
9. Lac Vshivoye, 1912 ..	11	10	1	—	0·80	0·74	0·06	0·78	0·48	0·41	0·07	0 45
10. do. do. 1913	8	2	4	2	0·80	0·69	0·11	0·75	0·51	0·48	0·03	0·49
11. Konstantinovka, Stavropol prov., 1911	10	—	6	4	0·77	0·68	0·09	0·72	0·55	0·45	0·10	0·50
12. Kalaus, Stavropol prov., 1913..	9	7	—	2	0·89	0·73	0·16	0·79	0·49	0·45	0·04	0·47
13. Valley of R. Terek, 1913 ..	26	22	—	4	0·87	0·76	0·11	0·80	0·50	0·42	0·08	0·46
14. Valley of R. Syr-Darya, 1912..	16	16	—	—	0 89	0·74	0·15	0·80	0·50	0·40	0·10	0·45
15. Mangishlak, Caspian Sea, 1911	10	10	—	—	0 87	0·73	0·14	0·80	0·46	0·43	0·03	0·45
16. Korea, 1900	8	—	8	—	0·78	0·68	0·10	0·73	0·60	0·52	0·08	0·55
17. Smyrna	14	—	14	—	0·84	0·67	0·17	0·75	0·63	0·51	0·12	0·55
18. Azores	20	—	20	—	0·85	0·69	0·16	0·75	0·60	0·52	0·12	0·57
19. Congo	9	—	9	—	0·82	0·68	0·14	0·75	0 59	0·50	0·09	0·54
migratorioides.												
20. S.W. Nyasa	4	—	—	—	0·94	0·83	0·11	0·86	0·46	0·42	0·04	0·44
21. Lagos	5	—	—	—	0·85	0·78	0·07	0·86	0·46	0·42	0·04	0·44

* Relation of the shoulder width to the length of pronotum.
† Relation of the length of hind femur to that of the elytron.

When studying the first two lines of the table we see that individual figures for specimens of both forms are highly variable. Owing to this variability there is no interval between a row of figures for *danica* and that for *migratoria*, which partly overlap each other. This accounts for the fact that a curve representing the variability of the pronotal proportion (fig. 2) in both forms together has only one maximum ; it seems to indicate that, so far as the shape of the pronotum is concerned, there is no possibility of regarding *migratoria* and *danica* as different species, or even as two distinct forms of the same species. The curve of variability of the femoral proportion (fig. 3), on the contrary, has two separate maxima, as if the material studied could be divided into two distinct groups, be these species or units of lower taxonomic value.

As for the average figures for both forms, they are also quite distinct and even not too near each other ; the maxima and minima are also more or less characteristic for each form. It may be noted that *danica* is more variable than *migratoria*, the extent of variation in it amounting to 35 per cent. of the average figure in the case of the pronotal proportion and about 38 per cent. for the femoral ; while the corresponding variations in *migratoria* are only about 29 and 26 per cent. respectively. The next interesting point is that specimens of *danica* from the Palaearctic region are far more variable than those of extra-Palaearctic origin.

All subsequent lines in the table (from the fifth downwards) give figures each for a number of specimens from one locality and taken mostly at the same time, without any selection, and regardless of the forms to which they belonged, in order to obtain an impression as to proportion of both forms and of the extension and direction of variability in each lot separately. We shall have to deal with these lines in more
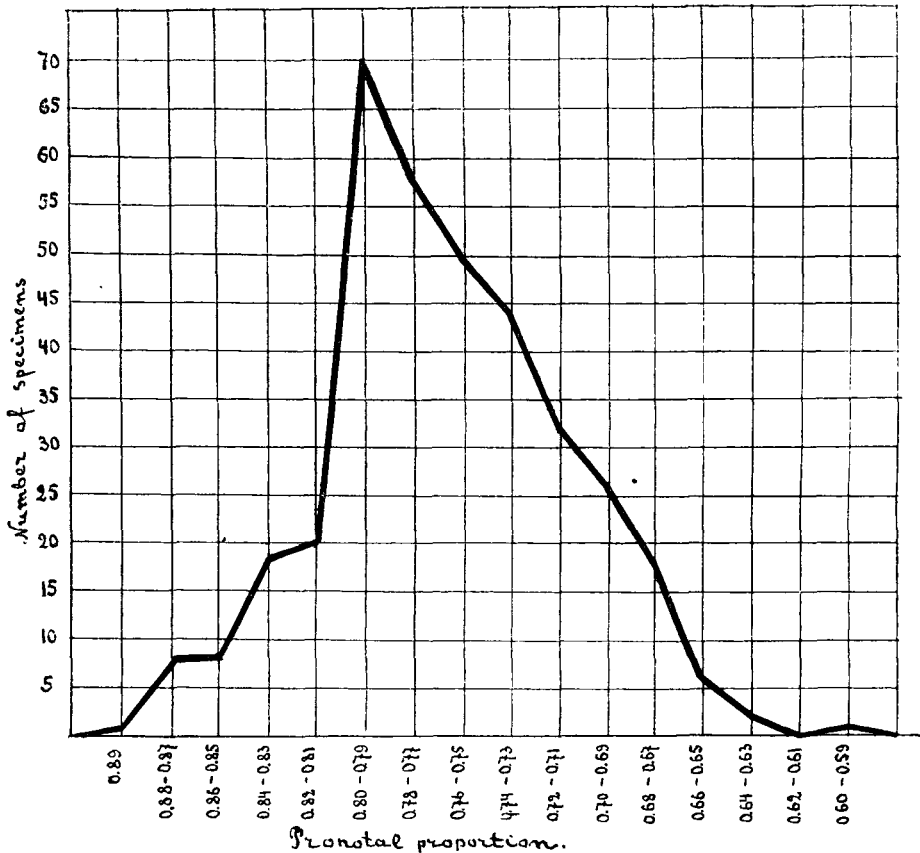

Fig. 2. Diagram showing range of variation in the pronotal proportion in 358 specimens of *Locusta migratoria*, L.

detail afterwards, but it may be noted that the range of variation is rather different not only in series of different origin, but also in lots taken at the same place in two successive years, *i.e.*, from swarms which may be regarded as two successive generations. Examples of this kind will be found in lines 5 and 6, and 7 and 8, of Table I.

If we summarise the results of this attempt at a statistical study of the morphological interrelations between *migratoria* and *danica*, they seem to be rather contradictory,

or, anyway, do not help much towards a definite solution of the question whether these two forms are really distinct or not.
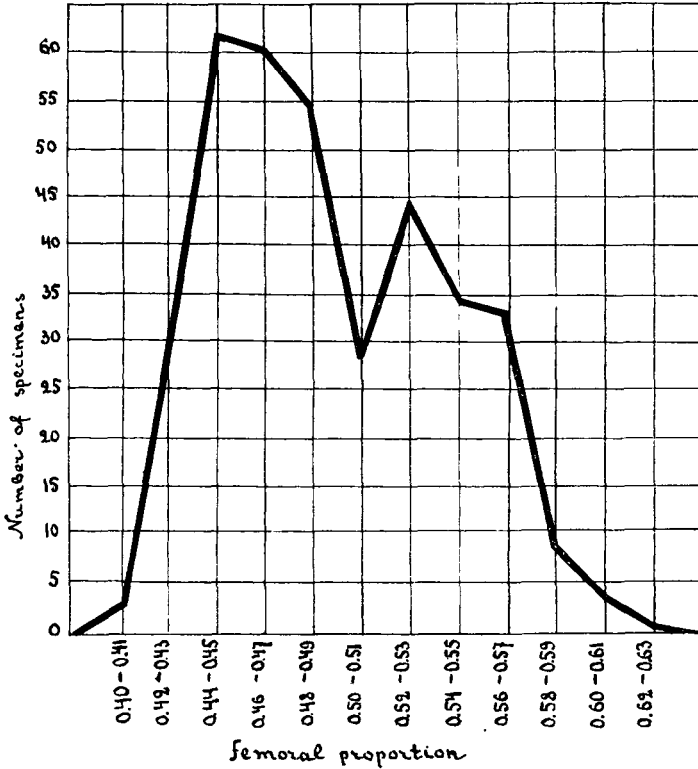

Fig. 3. Diagram showing range of variation of the femoral proportion in 358 specimens of *Locusta migratoria*, L.

Characters drawn from the Genitalia.

The late Dr. N. Adelung, of the Petrograd Zoological Museum, who tried long ago to solve the problem of *migratoria* and *danica*, suggested to me, when I began to work at it, that the anatomy of the genitalia, especially those of the males, might give definite proof of the specific difference of these insects, which he himself believed to be distinct.   He even prepared some rough sketches of the male genitalia of both forms, which, in his opinion, showed that they may be separated without much difficulty by the shape of the penis.   He gave up his work, but handed over to me his sketches and photographs.   After a careful examination of these, and a comparison with several good preparations, I am fully convinced that Dr. Adelung's conclusion is not right ; since the seeming difference between the penis in *migratoria* and *danica* in his preparations (so far as I know, he dissected only one specimen of each form) depends entirely on the fact that he studied the whole genital apparatus without dissecting it, and the somewhat different shapes shown in two of his drawings are merely the result of covering tissues having been more completely removed in one case than in the other.

My studies show, on the contrary, that the male genitalia of *danica* and *migratoria,* which are composed of several very complicated pieces (see fig. 7, A, B, C, D), are rather constant in the shape of the different parts, and though slight variations do occur, these are in no way connected with the external differences, and afford no reliable criterion for separating the two forms.

Colour Characters in Adults and Larvae.

In regard to the general coloration, as well as the pattern of the different parts, adults of both *danica* and *migratoria* are rather variable, and no definite colour characters can be given for separating them. Generally speaking, however, the extent of the colour variability in *migratoria* is far less than in *danica*, and there is a well-marked tendency in the former to a paler general coloration and less defined markings ; especially noteworthy is the fact that the hind tibiae in *migratoria* are never red, save quite exceptionally.

The coloration of *danica* is generally far more variable, with the evident prevalence of bright green forms ; dark brown, even almost black forms occur also not infrequently, while the pattern is very variable but always well pronounced. The hind tibiae in *danica* are very often red, but this character is far from being constant, since often quite typical specimens have the hind tibiae pale or greenish.

While, as above stated, the coloration of the adults is of but very little use for separating the two forms, it is quite otherwise in the case of larval stages, in which there is a very striking difference. In fact, it is almost impossible to find any definite type of coloration of the larvae of *danica*, which vary enormously ; uniformly green forms are most common, but fawn, grey, brown, and even black ones may be met with together. Quite the opposite is the case in *migratoria*, in which each larval stage exhibits quite constant colour characters. Their coloration presents a combination of black and orange-red (or yellow), the earlier stages being almost entirely black, while orange, or yellow, appears first in the third stage, extending gradually after each subsequent moult.* There is, of course, a certain variability in the shade of the colours, but as a rule larvae of *migratoria* of the same stage are all practically identically coloured ; and it is important to note that this type of coloration never occurs in the larvae of *danica* in spite of the wide range of variation in the latter.

Sexual Dimorphism.

There is a well-pronounced sexual dimorphism of the general dimensions in *danica*, the males (adults) being distinctly smaller than the females ; average figures of the length of the body, elytra, etc., for males differ from corresponding figures for females by about 20 per cent. of the latter, so that one may separate the sexes by the size only, provided that the specimens are all taken at the same place and time. As for the proportions between the dimensions of the different parts of the body, they are not connected with the absolute dimensions and remain the same in both sexes.

In *migratoria* no such apparent difference in size between the sexes is observed, the males being on the average smaller than the females by only some 4 per cent. of the figures for the latter ; and males of larger size are indistinguishable from females so far as the dimensions are concerned. Since the absolute dimensions in both *migratoria* and *danica,* especially in the latter, are rather variable, they are of very little value for separating these forms.

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* I do not propose to give a detailed description of the larval stages of *migratoria*, since this has been done more than once by different authors ; very good descriptions and fairly good coloured figures have been given by H. C. Pratt (Dept. of Agric. Feder. Malay States, Bull. No. 24, 1915).

Another case of sexual dimorphism is observed in the adults of *migratoria* during the period of copulation and concerns the general coloration.* The males gradually assume a bright yellowish general coloration, most pronounced on the pronotum, while the females become more dull coloured, the pronotum turning to dark brown. These changes doubtless depend on some physiological processes connected with the maturation of the sex products. As for *danica*, it is not yet known whether it exhibits any change of coloration during adult life.

Biology.

While *danica* seems to have no marked preference for any particular type of locality for its permanent habitation, except vast waterless tracts and forests, *migratoria*, on the contrary, has strictly defined permanent breeding grounds. In Russia, where much attention has been paid by entomologists to the biology of *migratoria*, its breeding grounds are all confined to the basins of the Caspian and Aral Seas and of Lake Balkhash, and more definitely to the deltas of the rivers discharging into them, namely, the Volga, Ural, Kuma, Terek, Arax, Syr-Darya, Amu-Darya, Ili, etc. These deltas, as a rule, extend over vast areas irrigated by numberless channels which change their course almost every year, some of them forming temporary pools and small lakes. The shores of these channels and even the beds of the shallower ones, as well as all the less elevated portions of land separating the channels from each other, are covered with a dense growth of the gigantic cane, or reed grass (*Phragmites communis*, Trin.), sometimes 10–15 feet high, which form almost impenetrable jungles extending over hundreds of square miles. These reed-beds, however, are not uninterrupted, since many of the islands between the channels are more elevated above the level of the water than is suitable for the growth of the reeds, which require a very damp soil. The soil of such islands mostly contains a large proportion of sand, and a peculiar flora of low, not very dense, mesophilous and xerophilous grasses covers them. It is in such localities that *migratoria* lays its eggs, as a rule,† while its larval swarms wander all over the valley, penetrating through the reed-beds, and even swimming across the streams. The leaves of the reeds, which contain a very large percentage of silica, represent the most preferred food of the larvae. The climatic conditions in these reed-beds are very peculiar and differ very much from those prevailing in the adjoining steppes and deserts ; since the waters of the river are there spread over a vast surface, the evaporation is very extensive, and the damp, hot air amidst the reeds at midday vividly recalls the tropics.

All the sufficiently investigated breeding grounds of *migratoria* in Russia are of the character described, and nowhere except in these grounds does this insect live and breed permanently. Naturally the locusts are not always equally numerous in the breeding regions, and in the years of minimum development only a few swarms or even but single individuals may be found ; during the next few years their number increases, the swarms become more and more dense, and a maximum is in this way attained.

The newly-hatched larvae collect in small groups, each of which is, as a rule, formed by larvae hatched from one egg-mass. These groups soon begin to move irregularly to and fro ; if two groups meet they form one larger group and in this way larval swarms are formed, and their movements become more and more regular. Most authors regard want of food as the direct cause of these movements, but this explanation is entirely wrong, at least so far as concerns *Locusta migratoria* and

* This fact was first observed by my assistant, Mr. Th. Gliniuk, in 1912, in Stavropol province, and was recorded by me in the paper : " The Fight against Locusts in the Government of Stavropol in the years 1907–1912," St. Petersburg, 1913 (in Russian).

† The matter is really more complicated than this, since the selection of spots for oviposition is usually closely connected with the more minute character of the soil and vegetation.

Dociostaurus maroccanus, Thunbg., both of which I have studied for several years. It is true that when the vegetation is very rich, the rapidity and extent of movement of larval swarms is less than in the case of a sparse vegetation, but larvae *will* move, however densely overgrown with their most favourable food-plants the place may be. Moreover, in both the species referred to, the larvae do not feed during movement, save in some exceptional cases, as, for instance, when a swarm has previously wandered for a long time over barren ground and then comes across a field of corn or other rich vegetation. My observations, though far from being complete, leave no doubt that a factor of utmost importance in the movement of larval swarms is temperature, and the following outline of the daily regime of a swarm will help to explain this.

It is a well-known fact that larval swarms do not move at all during the night, which they pass on plants in a semi-comatose state, caused doubtless by the low temperature. The first rays of the rising sun bring the larvae back to active life, and they begin at once to feed. The hotter the temperature grows, the more active become the insects, and soon they one by one jump or crawl down to the ground, where they continue to move about, now crawling, now jumping, as if feeling uneasy. Each larva in doing so disturbs its fellows, which leads to still more rapid general movement ; this is at first entirely irregular, but sooner or later, through mutual influence, a common direction of movement is found and the swarm begins its day's march. So far as our observations in the Northern Caucasus go, the average temperature causing the first movements of the larvae lies near 13–15° C. In ordinary circumstances, *i.e.*, provided the sun shines all day and no unusual changes of weather occur, swarms keep moving the whole day, and as a rule do not feed when they move.* In the afternoon, when the temperature begins to fall, the velocity of the movement decreases until, in the evening, the swarm stops ; it is very interesting to note that this evening cessation of movement occurs when the temperature is again near 13–15° C. One by one the larvae crawl up plants and begin to take their evening meal. There is no doubt that swarms do not choose their resting places, but simply stop where they are overtaken by the critical temperature. I have seen many swarms which have stopped for the night at entirely barren spots just after they have crossed a strip with abundant vegetation, or only a few yards before reaching it.

Such is the behaviour of larval swarms of *migratoria* under ordinary conditions of weather, and all my observations lead me to the definite conclusion that their movement has nothing to do with hunger and depends entirely on thermotropism (probably negative), and on another, as yet little known, tropism which is displayed by the tendency of each larva to repeat the movements of its nearest fellows and to move in the same direction as they do.†

The behaviour of larval swarms under abnormal conditions of weather lends further support to this conclusion. If the day is colder than usual and the temperature does not rise above 15° C., the swarm remains and feeds all day where it spent the night. If the temperature falls during a normally hot day, the swarm stops long before its usual time. Especially interesting and instructive is the following example : if a swarm is moving at the temperature in sunshine not much above the critical point and the sun is temporarily hidden behind a cloud, so that the temperature falls below that point, the swarm stops, or in any case its movement

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* I intentionally avoid discussing here the question of the direction of movements and its causes, since it is very complicated, and besides, it has no direct connection with the chief problem we are now investigating ; one point, however, is worth mentioning : that the direction of movement has, as a rule, nothing to do with the looking for food, since, for one thing, larvae do not feed during the day, and they often move from fertile spots into entirely barren places.

† This kind of tropism is not uncommon among other insects, and even vertebrates ; a herd of cattle will afford excellent examples of it.

becomes slower and less defined ; as soon as the cloud has passed and the sun shines again, the swarms starts its march afresh ; even small clouds hiding the sun just for a few minutes produce the same effect.

There is likewise an upper limit of temperature that causes the cessation of movement ; and on very hot, close days swarms often stop their march during midday ; in that case, however, the larvae do not climb plants to feed but collect in close clusters under the plants, evidently hiding from the direct rays of the sun. This being a more rare phenomenon, I have no precise data as to the exact temperature at which it occurs, but anyhow it gives additional support to my theory that the movements of larval swarms depend primarily on thermotropism.*

After the final moult the wanderings of swarms on foot naturally cease, though when the majority of a swarm is in the last larval stage and only single individuals become winged, the latter may often be seen crawling and jumping with the swarm.

A few days after the last moult, newly-winged insects are incapable of long flight, their elytra and wings being not yet hard enough. This period is passed by swarms in the same spot, devouring vast quantities of food, and it is a very favourable (and also the last) opportunity for their destruction by spraying.

When locusts are fit for flight, single individuals begin to take wing and fly for a short distance, often circling above the still sitting swarm. Whenever a locust flies near enough to another that is at rest, the latter is disturbed and often takes wing and flies in the same direction ; this is again a manifestation of the same tropism which causes the movement of larval swarms. The larger the number of individuals with fully developed wings, the more often do they take these short flights, and the more other locusts join them, disturbing yet others when circling above the swarm. It is easy to understand that this must necessarily result, sooner or later, in the whole swarm taking wing. During the first movements no definite direction of flight is apparent, but since each individual tries to follow its nearest fellow, a common direction of flight must necessarily result. During the first few days these flights are rather irregular, and swarms do not assume a definite direction, but simply circle above their breeding grounds. If two swarms meet, they mix together, and so the swarm gradually grows larger and larger. The larger the swarms grow, the more regular and the longer become their flights, and at last the time comes when they assume a definite direction, and the insects take leave of their breeding region altogether ; then only few scattered swarms remain where just a day or two before locusts were numberless. In fact this emigration from the breeding regions is often so complete that only single individuals are left behind, and those prove to be nearly all parasitised by the larvae of Sarcophagid flies, or by red mites (*Trombidium*).

What is the cause of this emigration ? The generally accepted theory is that locusts migrate from want of food. I have already proved that this is not the case in the larval swarms, and as for flyers, the very idea of locusts being compelled to emigrate from breeding regions by the lack of food could never occur to anyone who has seen these vasts areas overgrown with luxurious vegetation of a kind most acceptable to locusts. In fact, swarms always leave behind them immense feeding grounds and emigrate sometimes to almost vegetationless deserts, which, as a rule, adjoin the permanent breeding areas of *migratoria*.

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* The habits of the larval swarms of *migratoria* are well known to those concerned with locust control in Russia, and as the insects are now almost exclusively destroyed by spraying with arsenical insecticides, which are of use only when the actual food of the larvae is poisoned before feeding, no spraying is done during day, when swarms are in movement. The daily work is usually divided into two periods, and spraying is done in the early morning, before the larvae begin to go down from the plants, and in the evening ; the evening work begins before the swarms stop for the night, since it is always easy to reckon where a certain swarm will stop, and the spraying is continued till it is quite dark ; this evening spraying is the more effective. In cool weather, when swarms do not move, work goes on all day continuously.

Still more unacceptable becomes the theory of emigration being caused by lack of food, if we turn our attention to certain physiological changes which locusts undergo during the period of emigration. When dissecting individuals taken from emigrating swarms, it will be found that by far the greater portion of the inner cavity of the body is occupied by air-sacs, described long ago by American ento-mologists in the Rocky Mountain locust, and occurring doubtless in all other migrating species of locusts. These air-sacs are only temporary organs, reaching their highest development at the period of emigration and disappearing towards the end of that period, when the developing reproductive organs take their place. During the emigration, however, the air-sacs are enormously large and all the other internal organs are much compressed, including the stomach, thus rendering the insect almost incapable of taking food, at any rate in large quantities. This assumption, based upon anatomical facts, is supported also by field observations ; for, in fact, the emigrating swarms, when they stop their flight, do not feed much, though incidentally they may cause great damage by merely cutting the stems of cultivated plants.

Further anatomical researches reveal also the fact that the fat-body is more developed in insects just before and at the beginning of emigration, and is almost exhausted towards the end of it ; probably locusts during this period live essentially on the food reserves in the fat-body, being unable to take much vegetable nourish-ment and consequently scarcity or even lack of food has nothing to do with the emigration.

A Russian entomologist, K. N. Rossikov, called attention to another possible explanation of the emigration of *migratoria* from its breeding grounds. He believed it to be an immediate result of the activity of the parasites of the adult locusts, *i.e.*, Sarcophagid larvae and red mites ; he believed that the parasitised individuals become restless and try to get rid of their parasites by flight. If this were so, the result would be that only parasitised individuals would emigrate and all the non-parasitised would remain behind in the breeding grounds, though actually just the opposite is observed. This theory, therefore, is as groundless as the previous one.

One more theory is that emigration might be regarded as a tendency of the species to avoid overpopulation of a breeding region and to find new suitable breeding grounds. As for the possibility of overpopulation of breeding regions of *migratoria*, this idea is simply absurd, since these regions are vast enough to harbour many hundred times more locust swarms than there are in years of maximal development.

To investigate the presumption that swarms are emigrating to look for new breeding grounds we must see what is the fate of swarms after they have left their permanent breeding regions.

As far as is known at present, a swarm of emigrating locusts usually covers a very long distance at one flight ; if sometimes it settles down on its way (and this is often caused by unfavourable conditions of weather), it soon resumes its flight again. I will not discuss here the question of the direction of the flight and its probable causes, since but very little is known about it. One fact, however, is firmly established and is of great importance for our immediate purpose : it is that in the majority of cases the swarms maintain throughout the same more or less defined direction which they assumed when starting ; of course, a strong wind or other incidental circumstances may to a certain extent alter this direction.

This straight flight, aimless and causeless as it seems, does not last long, though a swarm may cover during it very long distances, the velocity of flight being far greater than might be expected.

Sooner or later, the regularity of the flight seems to be lost ; swarms begin now to settle down, then take wing again and circle about ; they begin also to eat more, since their air-sacs have grown smaller and the fat-body is also exhausted. I believe,

therefore, that the cessation of flight is caused entirely by these two purely physiological phenomena, and it is obvious that no possibility exists for swarms to look for suitable new breeding grounds ; they merely settle down wherever they are compelled to do so by their physiological condition, quite irrespective of the character of the locality. This may occur accidentally near some suitable spot, and there is also the probability that the swarm would find one during the irregular circular flights which take place at the end of the emigration and precede pairing and oviposition ; but the extent of these flights is rather limited and this probability is correspondingly small. Theoretically it is far more probable that the cessation of emigration would become necessary in a locality quite unlike the normal breeding grounds.

A typical and very convincing example of this kind was observed in Stavropol province in the autumn of 1912, when numerous large swarms of *migratoria* emigrating from the breeding area at the mouth of the river Terek invaded that province. One or two of these swarms settled down in the lower portion of the valley of the river Kuma, which is itself a breeding region of the same locust, but was in that particular year free from the local swarms ; the Terek swarms con- sequently found there most favourable conditions and oviposition took place in the normal manner. Practically all the other invading swarms stopped their flight in the steppe adjoining the middle course of the Kuma, some of them on the very border of the valley. Now this part of the valley presents some very suitable breeding grounds, which have often played an important part as the source of invasions in Stavropol province. Several of the swarms visited these grounds more than once during their circular flights, which are often supposed to serve the purpose of finding suitable places for oviposition. Ultimately, however, only a small number of scattered locusts oviposited there, while all the swarms deposited their egg-masses in the dry steppe, where the conditions of soil and vegetation are entirely different from those in normal breeding grounds. It is especially interesting to note that some of the eggs were laid on a portion of the steppe sloping towards the valley of the river, *i.e.*, in the closest proximity to the above-mentioned suitable area.

This latter fact and a study of the general conditions under which oviposition took place clearly show that nothing in the least like a conscious (or instinctive— the exact word does not matter in this case) choice of suitable places by swarms can be assumed. There is, however, one exception : when a swarm settles down for oviposition, and the females, after several attempts to penetrate the soil, find it too hard, they become restless, take wing again, and after a few rounds settle down at another spot. Thus we must conclude that oviposition takes place whenever the majority of females are ready for it, and quite irrespective of the suitability of the conditions for the next generation, provided that oviposition is physically possible.

In conclusion, the theory that emigration has as its aim the finding of new breeding places is also groundless, and there is at present no possibility of explaining the emigration by any causes except physiological ones : the development of the air-sacs compels the insects to fly, and this impulse is strengthened by their gregarious- ness, that is by some kind of tropism which makes each individual keep close to its fellows and follow their movements. Later on we shall see what is the biological meaning of the emigration.

Such is, briefly, the life-cycle of *migratoria*. The biology of the larvae and adults of *danica* is only very insufficiently known,* but what is known shows that their behaviour is entirely different from that of *migratoria*. The chief biological feature of the latter in both larval and adult stages—gregariousness—is quite absent in *danica*. This is especially striking in the larvae ; if a wandering swarm of *migratoria*

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* This is directly due to the fact that most entomologists have regarded *danica* as distinct from *migratoria* and as being an entirely harmless species, so that the study of its habits has been neglected.

larvae comes across a solitary specimen of the same form, the latter immediately joins the movement, but when a larva of *danica* is overtaken by a swarm of *migratoria*, it tries to escape by leaps as quickly as it can. At the same time, the larvae of *danica* seem to possess thermotropism of the same kind as that exhibited by *migratoria*, their time of feeding being restricted to the evening and early morning, while during the day they are probably also on the move, though I have no reliable observations on this point. As for the adults of *danica*, the only point of their biology that we know for certain is that they do not form swarms and hardly migrate at all ; a study of their behaviour, as well as of their anatomy (air-sacs) is of the greatest importance for the solution of the whole problem.

Some very interesting indications of further biological differences between *danica* and *migratoria* have been obtained at the Turkestan Entomological Station by V. Plotnikov in his breeding experiments.* This entomologist obtained from typical individuals of *danica*, kept in the laboratory, a second generation of larvae in only 16–30 days after oviposition, instead of in the following spring as is usually the case with *migratoria*. In one particular experiment even three generations were bred in one year. That this unusually short period of hatching was not due to the unnatural conditions of the experiment is shown by the fact that eggs laid in the same laboratory by individuals of *migratoria* did not hatch before the following spring. Dissections of eggs showed that the development of the embryo begins in eggs of both *migratoria* and *danica* shortly after oviposition ; but in the case of *migratoria*, when the embryo reaches a rather advanced stage, development is suspended for several months, corresponding to the period of hibernation, though in the laboratory there is no change in the conditions to account for this. At the same time and under exactly the same conditions, the embryos in eggs of *danica* develop without any interruption. These experiments suggest an explanation of the fact that, while the larval stages of *migratoria* may be found only in spring and the beginning of summer and the adults during the summer and autumn, there is no such strict regularity about the occurrence of the stages in *danica*, though many eggs of this form probably hibernate as well.

Field Observations on the Transformation of *migratoria* into *danica*.

During the great invasion of locust swarms which occurred in the Stavropol province in the autumn of 1912 (see p. 147), I used the opportunity for studying, from the systematist's standpoint, as large a series of specimens as possible. All the insects collected, which were taken from the swarms without any selection and amounted to many hundreds, proved to be quite typical *migratoria*. Nothing in the least like *danica* was observed in field, either by myself or by my assistants, whom I had previously instructed to look out for all aberrant forms and who knew *danica* perfectly well ; the number of individuals thus studied without collecting them is difficult to estimate, but it doubtless amounted to many thousands. I believe, therefore, that I am right in assuming that the swarms consisted purely of *migratoria*, and that *danica*, or even intermediate forms, were entirely absent. The measurements of the specimens from those swarms are given in the fifth line of Table I (p. 139), and the following conclusions may be drawn from them : the specimens are rather uniform, the extent of their variability $(0 \cdot 16)$ being less than the average for *migratoria* $(0 \cdot 18$—see line 1) ; the average figures for the pronotal $(0 \cdot 79)$ and the femoral $(0 \cdot 45)$ proportions are extremely near to the average for *migratoria* $(0 \cdot 80$ and $0 \cdot 46$, respectively). The colour characters, though not very reliable, were very constant, which is not the case in *danica*. If we consider also that the locusts kept in close swarms which had no tendency to disperse, we must conclude that the swarms were formed exclusively by typical individuals of *migratoria*.

According to the routine of the control work adopted in Russia, all the swarms were closely watched during their wanderings by the trained staff, and all the spots where oviposition took place were marked out and also noted on the maps. Owing to this procedure there was no doubt that in the following spring we had to conduct the destruction work against the immediate progeny of those swarms. As soon as the larvae in 1913 reached their third stage, when differences between *migratoria* and *danica* are more apparent than in the earlier stages, it became evident that although the bulk of the larval swarms consisted of *migratoria*, there were many individuals which were certainly *danica*, these being different in coloration and showing a tendency to desert the swarms. In spite of the intensive control measures, several small swarms escaped destruction and attained their final moult ; these adult specimens proved to be rather different from those of their parental swarms (see line 6 of the table, p. 139). A rather large admixture of typical *danica* was very obvious, but still more numerous were specimens of an intermediate character which could not be identified either with *danica* or with *migratoria* ; the bulk of the insects, however, might have been referred to *migratoria*, but showed an obvious inclination towards *danica*, in fact they had the pronotum more compressed laterally, the median keel more raised, the elytra longer and the femora relatively shorter, than in the specimens from the parental swarms ; their coloration was also more variable. The proportions are especially instructive when compared with those for the swarms of 1912 ; in studying these figures one may see that the extent of variation was far larger than in 1912, and the average figures also changed in the direction of *danica*. The swarms were not so dense as in 1912, and the individual insects showed obviously less developed gregarious habits ; numerous single individuals of *danica* were scattered all over the steppe, without any connection with the swarms ; the latter did not undertake any migrations and gradually dispersed.

Similar, though less striking examples are given in lines 7 and 8, 9 and 10 of the table, in compiling which precautions were also taken to obtain the series most likely to represent two successive generations. Unfortunately, I could not secure reliable examples of more than two such generations from one spot.

Breeding Experiments by V. Plotnikov.

Though field observations like those described above are of great value, they have the disadvantage of not affording absolute proof, and the only way to obtain this is by breeding experiments. Such experiments have been undertaken by my friend V. Plotnikov, in Tashkent, and, though conducted on a very moderate scale, have yielded some most interesting and valuable results. Since all the actual specimens from these experiments were given to me by V. Plotnikov, and are before me now, I am able to give a little more detailed account of the results than were recorded in his original communication.

In the summer of 1913 several specimens of both sexes of very typical *danica* were isolated in cages, in which copulation and oviposition took place ; the eggs hatched without hibernation, as is not uncommon with *danica*, but so far as we know never occurs in *migratoria*. The description of the larvae and adults bred from them is given by V. Plotnikov, as follows :—

" The larvae had in the first stage a dark grey coloration, and not black as in *migratoria*. In later stages they acquired various colorations—uniformly green, dark grey or brownish—but a number of them had the typical colouring of *migratoria*, namely, a general reddish brown colour (sometimes greenish), with velvety black stripes (broad or narrow) along the sides of the pronotal keel and black stripes on the sides of the abdomen. The adults presented no characters typical of *danica* ; the profile of the pronotal keel was usually straight, sometimes even concave. The males were, however, smaller than the females."

After studying the specimens, I can only confirm Plotnikov's statement that while the parents are all very typical *danica*, save that not all of them have the hind tibiae red (which character is not quite constant in that form), their direct offspring are on the contrary all well-defined *migratoria*, though a few of them have the tibiae red, as is sometimes the case in this form. One of the parents and one of the off-spring are figured above (fig. 1, A, B, C, & D).

Another experiment is described by V. Plotnikov, as follows :—

" In 1914 I bred from egg-masses sent from Amu-Darya district* *P. migratorius*, and from egg-masses deposited by these insects I bred in the spring of 1915 again *migratorius*. On the 19th June I found in the soil of the breeding cage, where these individuals (now mature) used to live, five egg-masses, which I transplanted carefully into the soil of another cage ; there, on the 6th August, *i.e.*, more than 48 days after the oviposition, a single larva hatched, a female of dark grey coloration ; the rest of eggs in the egg-masses remained with an half-developed (hibernating) embryo. When in its second stage, this larva acquired a green coloration, which it retained till the fifth (final) stage. The profile of its pronotal keel was convex. . . . The adult insect retained the convex keel of the pronotum ; its body was green, the elytra light brown, and its hind tibiae turned red."

This specimen is before me now, and I can only confirm V. Plotnikov's opinion that it represents the most typical *danica*. As for its actual parents they possess all the essential characters of *migratoria* very well defined, and no one could hesitate to identify them with that form. Unfortunately the experiments were discontinued upon Plotnikov's joining the army.

V. Plotnikov's conclusion from his experiments is as follows : " . . . it is impossible to separate *P. migratorius* and *P. danicus* by any characters ; characters of *danicus* (including its capacity to produce a second generation) are expressed in the latter species more strongly. It is possible to suppose that this species is now in the process of splitting off from the primitive species, *P. migratorius*."

My own conclusions differ somewhat from this, but I shall come to them later on. All that I shall point out now is that these experiments prove finally the possibility of the actual breeding of *migratoria* from *danica* and *vice versa* ; my field observations on the same subject give evidence that it may occur not under laboratory conditions only, but in nature as well. On the other hand, we must not forget the numerous differences between them, especially the biological ones, which prevent us from regarding *danica* as a mere synonym of *migratoria*. It is evident that they must be regarded as two different forms of the same species without, in the meantime, any more precise definition of their systematic value.

Locusta migratorioides, Rch. & Frm.

This insect was described from specimens from Abyssinia ; later on, Saussure and other authors recorded it from many tropical localities. In its morphological features it is very much like *migratoria*, while its difference from *danica* is far more marked than in the latter. From *migratoria* it differs only in the following characters :—The pronotum (fig. 4) is still more constricted before the middle ; its median keel very low, often concave in profile ; fore margin almost straight ; hind margin very widely rounded ; the shoulder width almost equal to the length of the pronotum, the average pronotal proportion being 0·86, while it is 0·80 in *migratoria* ; the elytra relatively longer and the hind femora shorter, which results in the femoral proportion being on the average 0·44, as against 0·46 in *migratoria* (see Table I, lines 20 & 21).

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* A permanent breeding region of *L. migratoria.*—B.U.

It is quite obvious from this definition that *migratorioides* presents no new features as compared with *migratoria*, but it seems to be in all the chief characters merely a further modification of *migratoria* in the direction opposite to *danica*. Unfortunately the material of *migratorioides* now at my disposal is rather scanty, and the extent of its variability remains uncertain. Still, there is in the British Museum one female taken at Sarkwalla, Northern Territories, Gold Coast, 4–7.xi.1915 (*Dr. J. J. Simpson*), which is in all respects intermediate between *migratoria* and *migratorioides*.
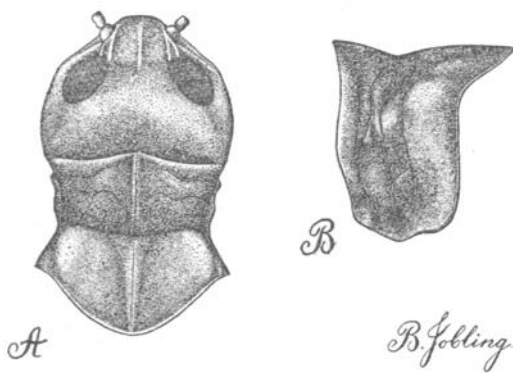

Fig. 4. *Locusta migratoria*, ph. *migratorioides*, Rch. & Frm., ♂ from Lagos : A, head and pronotum from above ; B, pronotum, side view (× 3).

The study of the male genitalia of *migratorioides* reveals no difference whatever from the structure observed in *danica* and *migratoria* (fig. 7).

As for the coloration of the larval stages, we have a good description of them given by H. C. Pratt (*l.c.*) and from it, as well as from the study of the actual specimens sent by Mr. Pratt to me in 1913, I was unable to find any reliable difference between them and the larvae of *migratoria*.

On the other hand, Mr. Pratt says in his paper that the coloration of the larvae is not very constant and the green individuals occur alongside with the typically coloured ones. The figures of the green and black adults given in his paper (*l.c.*, pl. XIV) certainly represent *danica*. This is, then, an indication that the same inter-relation exists between *migratorioides* and *danica* as has been proved positively for *migratoria* and *danica*. A confirmation of the same fact I received not long ago, when several specimens of locusts were sent from North Borneo to the Imperial Bureau of Entomology for identification. They all proved to be *migratorioides*, but as the lot was rather small, the Bureau asked for more material, and after several months a new collection arrived, with a note that the specimens were taken singly at the same spot as the swarms from which the first lot had been collected, and represented the actual offspring of those swarms. All specimens in this second lot are quite typical *danica*.

One more example of the transformation of *migratorioides* into *danica* I have found in Dr. La Baume's paper on the African locusts.* In a reference to Dr. L. Sander's book† he discusses an invasion of locusts which took place at Misahöhe, Togo, in December 1893, while in March 1894 new larval swarms appeared at the same locality, which Dr. Sander believed to be the direct progeny of the December swarms.

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* Die Afrikanischen Wanderheuschrecken.—Beih. zum Tropenpflanzer, xi, No. 2, 1910, p. 82, footnote 22.

† Die Wanderheuschrecken und ihre Bekämpfung in unseren Afrikanischen Kolonien. Berlin, 1902.

These latter consisted, as Dr. La Baume stated after a study of the specimens, of *migratorioides*, while the March swarms, again according to his determination, were composed of *danica*, which leads him to the conclusion that they could not possibly be the direct progeny of the December swarms. I believe, however, that Dr. Sander (who simply did not distinguish *migratorioides* from *danica*) was right, and that the December swarms of *migratorioides* actually produced the March swarms of *danica*.

All these facts, of course, do not furnish us with absolute proof of the transformation of *migratorioides* into *danica* ; but since such a transformation is firmly established for *migratoria* and *danica*, I feel justified in assuming it to be true in this case also.

Geographical Distribution.

Of the three forms here dealt with, *danica* has the most extensive range ; in fact, it is found throughout the whole of the Eastern hemisphere, except the coldest regions beyond 60° northern and southern latitude, very high mountains* and vast waterless deserts. As for the Western hemisphere, though many books state that *danica* occurs in America, I know of no reliable evidence to this effect, and am fully convinced that all the older records are due to mistakes, either in labelling the specimens or in their identification.** Thus, F. Walker described *Pachytylus brasiliensis*, which is conspecific with *danica*, from a specimen in an unlabelled collection which included insects not from Brazil only, but from other parts of the world also, and the mistake in locality in this case is beyond doubt.

A form with such an enormous area of distribution may be expected to present some geographical variations, and in fact, apart from the individual variability which, as I have already stated, is very great in *danica*, some more constant variations, probably connected with geographical conditions, are also observed. Thus Australian and New Zealand specimens are rather small on the average, with a comparatively short pronotum and the wings slightly infumate ; they have been described by Saussure as a distinct species, *Pachytylus australis*, Sauss. As, however, no one has yet studied extensive series of individuals of Australian origin, the constancy of these characters is not proved ; on the other hand, specimens of the same kind occur incidentally in other localities as well, and their distinctions from the typical *danica* do not exceed the average extent of observed individual variability. Again, as I have already pointed out (p. 139), there is a slight difference between the individuals of *danica* from the Palaearctic region and those of tropical origin, which also may depend on geographical conditions ; but in this case likewise more extensive investigations are wanted.

The area of distribution of *migratorioides*, though not so extensive as that of *danica*, still occupies the greater part of the latter, in fact the whole of it except the Palaearctic region.

The latter region is the home of *migratoria*, which is however common in its south-eastern parts only (especially in the basin of the Black, Caspian and Aral Seas and that of Lake Balkhash), where its permanent breeding grounds are, while its emigrating swarms penetrate much farther north and westwards, sometimes as far as Finland and England. On the other hand, single individuals, which agree in all their morphological characters with *migratoria*, occur far beyond the Palaearctic region as well. Thus, Brunner v. Wattenwyl recorded† *migratoria* from the Malay Archipelago (Batjan and Borneo). I have myself seen a quite typical specimen of

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* I have recorded (Revue Russe d'Entom., xiv, 1914, p. 232) this form from the Pamir upland as high up as 11,000 ft. above sea-level ; there is in the British Museum a couple of specimens taken at Giangtse, Tibet, at an altitude of 13,000 ft.

** Dr. J. Rehn, of Philadelphia, informed me recently that he is of the same opinion.

† Abh. Senkenberg. Naturf. Ges., xxiv, pp. 194, 196.

migratoria sent from Southern Celebes by Dr. Roepke to the Imperial Bureau of Entomology, which had the following note attached : " A Locustid from S. Celebes (Pangka djene) appearing there in small swarms and causing damage to the natives' plantations, such as rice, corn, etc."

The Theory of Phases.

Though the above recorded facts by no means exhaust the points to be considered in connection with the problem of the interrelations of *migratoria, danica* and *migratorioides*, they yet permit us to make an attempt to find out the best explanation at present possible. The following theory seems to me to agree in a rather satisfactory manner with all the facts known at present, though some modifications of it may prove to be unavoidable when new data are available.

As a starting point, I take it as positively proved that the three forms cannot be separated specifically and that they represent taxonomic units of lower grade than the species, which must be called, according to the law of priority, *L. migratoria*, L. They are, however, quite distinct from each other, though connected by transitional forms.

What term, then, should be applied to them ? They are certainly not mere individual aberrations—as they are often assumed to be by other authors—since they are rather constant in their average morphological characters and still more so in their biology ; nor can we call them subspecies, *i.e.*, geographical races, as they are found together in the same locality ; nor are they seasonal forms, since the transformation of one of them into the other has evidently nothing to do with season. The only more or less suitable term for them is " morpha," in the sense proposed by A. P. Semenov-Tjan-Shansky,* who proposed to apply this name to such forms of a species that present a direct result of the immediate external influences on the individual insect during its development, and which therefore do not appear in succeeding generations if the original influence ceases. Under this definition come seasonal forms, which may be obtained by the artificial application to developing individuals of certain factors causing their appearance under natural conditions ; the forms resulting from feeding larvae by some special food, etc. The same term may be applied, according to the personal opinion of A. P. Semenov-Tian-Shansky, expressed in his letters to me, to the case of the *Locusta* forms. It seems to me, however, that the term " morpha " is rather vague, and moreover we are yet far from knowing whether the transformation of one form into the other is due to some immediate external influence or to some yet unknown internal cause ; I think, therefore, that the term " phase " (Latin *phasa* ; abbreviation—*ph.*) suggested to me by Dr. G. A. K. Marshall is more appropriate, and its meaning will be made clear in the course of the explanation of my theory.

There is no doubt in my mind that *migratorioides* is the oldest form of the species, since its morphological and colour characters are far more constant in comparison with the more plastic *migratoria*, to say nothing of the extremely variable *danica*. The permanent breeding regions of *migratorioides* have never yet been investigated ; the only description of breeding places of this form in the Malay States given by H. C. Pratt (*l.c.*, pp. 6–7) must obviously be referred not to the permanent breeding grounds, but merely to the places where the oviposition of emigrated swarms took place. All we know at present concerning the permanent breeding areas of *migratorioides* is based on the records of the occurrence of its swarms ; and these data enable us to state that the best conditions for the development of this form seem to be present in tropical countries with a rather damp and hot climate, but undoubtedly not in forests. Since, on the other hand, these breeding grounds seem to be yet undiscovered, we may presume that they are also not in open, grassy land,

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* Die taxonomischen Grenzen der Art und ihrer Unterabteilungen. Berlin, 1910.

which is easily accessible and mostly cultivated or, anyhow, populated.   I believe, therefore, that permanent breeding grounds of *migratorioides* are to be looked for somewhere deep in the impenetrable jungles, overgrown with high grasses, reeds, and such-like vegetation ; but even if I am mistaken in this supposition, it would not affect my theory, which is based on the indubitable fact that the permanent breeding of *migratorioides* is possible only in localities with certain natural conditions, whatever those conditions may actually be.

Another well-known fact is that the development of *migratorioides* in its breeding grounds does not go on always at the same rate, but that it is subject to a periodical rise and fall, though the exact cause of the increase of locusts is entirely unknown. When the increase is at its height, large swarms are formed, and their emigration follows.   Such emigrated swarms settle down and oviposit whenever they are compelled to do so by purely physiological causes, and their progeny undergoes a transformation into the solitary-living phase—*danica*.   The very plastic, easily adaptable, and in all respects more progressive *danica* must play an important part in the extension of the range of the species, gradually but steadily populating new regions.   Being a product of a mutation arising partly from some unknown internal cause and partly from outer (probably climatic) influences, *danica* is naturally subject to sudden displays of atavism, which results in the transformation into the ancestral phase *migratorioides*.   We do not know yet whether this phenomenon can occur spontaneously as a result of some internal physiological factor, but there is no doubt that it is much favoured and often probably caused by the oviposition of *danica* taking place under conditions like those of the permanent breeding grounds of *migratorioides*.   The gregariousness of the *migratorioides* phase is, of course, one of the causes of a rapid increase in the number of individuals and swarms, and soon— in the course of a few generations—the size of the swarms reaches the maximal point, which is followed by emigration.   In this way the dispersion of the species goes on alternately by the gradual spreading of the *danica* phase and by the periodical extensive emigrations of *migratorioides*.   As a result, the species is now distributed all over the Eastern hemisphere ; but, as we know, the distribution of *migratorioides* is limited to tropical regions only, while *danica* goes over to the Palaearctic region as well, where the swarming phase of the species is represented by *migratoria*.   This latter fact might be satisfactorily explained by the impossibility of finding in the Palaearctic region the natural conditions exactly like those of the tropical breeding grounds of *migratorioides*, chiefly in regard to a combination of heat and dampness. The above-described (p. 143) reed-beds of *Phragmites* in the south-eastern part of the Palaearctic region represent in all respects the nearest possible approach to tropical conditions.   This statement is strongly supported by the fact that the fauna of these reed-beds includes two more Acridians of an undoubtedly tropical origin ; these are *Gelastorrhinus sagitta*, Uvar., and *Oxya turanica*, Uvar., both described* from the valley of the Amu-Darya, in Transcaspia, and the former found also on the River Kura, in Transcaucasia.   Though very peculiar, and in the summer recalling the tropics, the climatic conditions of these reed-beds are, of course, not tropical, and their effect on the progeny of *danica* breeding there is not the same as in the tropical breeding grounds of *migratorioides* : the reverse transformation of *danica* into a swarming phase does not reach the phase of *migratorioides*, but stops half-way at the *migratoria*-phase.   This seeems to indicate that the transformation is due primarily to the direct influence of external conditions, its extent being proportional to changes in the latter, but only precise laboratory investigations can help to clear up this complicated problem.   It is interesting to recall here that individuals of *migratoria* incidentally occur in tropical countries also (see p. 152), and we may presume that their appearance is due to some abnormal conditions of the development.

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* Horae Soc. Entom. Ross, xl, No. 3, 1912.

Little is known yet as to what happens in the breeding grounds after the emigration,* except that the number of locusts drops suddenly to a minimum. I presume that scattered swarms of the gregarious phase, as well as the progeny of individuals of the solitary phase, cause the gradual increase in the number of swarming individuals, and after a few years a new emigration occurs.

Thus, the periodicity of locust invasions is caused entirely by the wonderful phenomenon of the transformation of a swarming locust into a solitary, harmless grasshopper. Of course, the outline here sketched is necessarily rough, and the actual proceedings are far more complicated, but the theory seems to me to be the best possible in the circumstances.

The biological result of these phenomena is that the maintenance and dispersion of the species is ensured in all circumstances : the swarming phases enable the species to extend at one stroke its area of distribution to distant regions, and its dispersion to the remotest islands is undoubtedly due to emigrating swarms ; on the other hand, the well protected and easily adaptable solitary phase secures a strong footing in the countries thus reached, and under favourable conditions gives rise to new emigrants ; the results achieved show that such an arrangement has been extremely useful to the species. Even the most radical changes in the natural conditions of the permanent breeding regions would result not in the extermination of the species, but only in its transformation into the more adaptable *danica* phase.

An example of that kind occurred in Southern Russia. Though the now existing permanent breeding regions are restricted, as I have described above (p. 143), to the valleys of the rivers discharging into the Caspian and Aral Seas and Lake Balkhash, the deltas of rivers emptying into the Black Sea (*i.e.*, Kuban, Don, Dnieper, Danube, etc.) also harboured not very long ago—up to the end of the eighties of the last century—some permanent breeding grounds of *migratoria*. At present, however, only the lower valley of the Danube is still a breeding region, while the valleys of the other rivers of the basin of the Black Sea no longer serve that purpose. This is easily explained by the fact that the valleys of the Don, Kuban and Dnieper were during the end of the last century more or less cultivated or, at any rate, their natural conditions were entirely changed by the persistent grazing of herds of cattle. As a direct result of this the possibility of the transformation of the solitary phase into the swarming one exists there no longer, and though the transformation takes place incidentally, single specimens of *migratoria* being not uncommon, their numbers do not increase, nor are swarms ever found.

The theory of phases suggests the theoretical possibility of the control of *migratoria* by some measures directed not against the insect itself, but against certain natural conditions existing in breeding regions which are the direct cause of the development of the swarming phase. The above-quoted example in South Russia shows that even comparatively slight cultivation of breeding regions leads to the desired changes ; but the conditions necessary for the breeding of the swarming phase have not been exactly studied, nor are the direction and extent of such changes known. The first step, therefore, should be the most careful investigation of all existing, as well as extinct, breeding regions, together with parallel breeding experiments under laboratory conditions ; on the basis of results thus gained a system of theoretically useful and practically possible measures for the conversion of breeding regions may be outlined.

IV. LOCUSTANA PARDALINA, WALK., AND ITS PHASES.

My personal knowledge of this locust is limited to the study of preserved specimens, especially of a large series sent to the Imperial Bureau of Entomology by Mr. J. C. Faure,

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* The direct cause of this ignorance is that injurious insects, and locusts especially, are studied only in the years of maximum development, and nobody cares about them in the minimum years, when the clue to the whole locust problem is most likely to be found.

of the Division of Entomology, Pretoria.   Before proceeding to my own observations on the morphology of the species, I will quote an extract from a letter from Mr. Faure, dated 14th October 1920, which includes some very important and interesting information on the question of the phases of *L. pardalina*.

" My personal experience with the species began in the summer of 1914–15, when scattered swarms began to appear shortly after the break-up of a prolonged and very severe drought.   Voetgangers (*i.e.*, nymphs) of all stages and flyers occurred together in loose swarms, and it was practically impossible to destroy them by the usual method of poisoning.   The swarms did not move in the usual compact formation, nor did they camp for the night in dense clusters.   Many of the adults were strikingly undersized, and a large percentage of both adults and voetgangers were abnormally coloured.   Only in swarms that approached the normal in density did the typical orange and black colour of the voetgangers begin to show up.

" Although I did not realize the fact at the time, I was witnessing the transition from the grasshopper to the swarm phase.   Towards the winter, that is in May and June 1915, the flyers began to move about in fairly definite loose swarms, and they laid their eggs in compact deposits, with the result that large swarms of typical swarm · voetgangers hatched the following spring.   We received no reports that winter of swarms of flyers coming into the Union from the Kalahari or anywhere else, and the outbreak in the period September to December 1915 was very severe in the area in which the scattered locusts had been observed the previous summer.

" It was quite evident, therefore, that the invasion of September-December 1915 had arisen from locusts bred up within the borders of the Union.   Formerly the Kalahari Desert had been thought to be the chief source of our invasions of *Locusta pardalina*.   Now we are convinced that large outbreaks can and do arise within our borders without the help of swarms coming in from the Kalahari.   In the past, huge swarms have undoubtedly come into the Union from the Kalahari, and no doubt history may repeat itself in the future.   But we no longer regard the Kalahari as a sort of permanent breeding ground, and are now inclined to believe that it will ordinarily only develop into a breeding ground if we allow swarms of flyers to escape into it from the Union.

" In 1917 I again saw scattered locusts from February to April, and another severe outbreak of voetgangers occurred the following spring and summer.   In a general way it was a repetition of what had occurred in 1915, and realizing what was going on, I was better able to make observations.

" *Locusta pardalina* does not merely occur in scattered swarms and in compact swarms—it also lives as a grasshopper, *i.e.*, single specimens have often been collected miles away from the nearest swarm and in seasons when no swarms have been known to exist anywhere in the country.   I have good reasons for believing that the species is probably never entirely absent from certain parts of the Union.   During the past five years I have often searched for specimens during the intervals between the occurrence of swarms, and in practically every case I have succeeded in capturing two or three at least in say an hour's walk on the veld.   Of course one should not expect to find them late in the winter or during a bad drought.

" The specimens captured singly almost always have the colours of the grasshopper phase, and they are as a rule a good deal smaller than swarm forms.   Further, I have frequently taken last-stage nymphs and newly-fledged adults living the life of single grasshoppers.   Although I have not been able to make a careful study of the specific characters of these single living forms, I am quite satisfied in my own mind that they are identical with the swarm forms.   Again, these single forms may occur in the district or on the farm on which swarms are present, and I have on several occasions seen a few individuals with abnormal colours amongst a swarm

of typical swarm-form voetgangers. The only conclusion I could come to was that these stray forms have been picked up by the swarm. I have also found grasshopper-phase adults in a swarm of swarm-phase flyers, and have seen a very small green-marked male in copulation with a large typical female.

" These single forms of *L. pardalina* can readily be distinguished in the field from our other veld grasshoppers (1) by the fact that they have milky-white glistening underwings, and (2) by their peculiar manner of flight. They almost always soar upwards and then dip and swerve before settling down.

" From the swarm-phase the grasshopper-phase of *L. pardalina* differs chiefly in size and in colour. As regards colour, the single forms are remarkable for their great variability, and it would be quite an undertaking to describe in detail all the shades of colour they exhibit. Usually there is a striking protective resemblance. Where there is plenty of green grass both voetgangers and flyers may be almost entirely green, or at least partly green. Where the veld is only sparsely covered with grass and bushes, they resemble the colour of the soil more or less. In parts of the Karroo, notably Beaufort West and Prince Albert, there are patches of gravelly soil varying from slaty-blue to almost black. In 1917 I was greatly surprised to find a very striking tendency amongst the scattered veotgangers to vary in colour from place to place more or less in accordance with the colour of the soil. When the progeny of these scattered locusts appeared on the same farms in swarms six months later there was no trace of such a protective resemblance ; they all wore the King's regulation swarm uniform !

" As far as size goes, the single-living forms are generally considerably smaller than the swarm forms. This is especially true of the males. Some of the males are so small that one can scarcely believe that they belong to the same species as the swarm males.

" When it occurs in large swarms *L. pardalina* scatters far and wide over the central plateau of South Africa, but its natural home is in the semi-arid parts of the country. It does not like the eastern Orange Free State, for instance, where there is a fairly good rainfall and a rather dense growth of grass. Its favourable breeding grounds are districts like those in the south-western corner of the Free State where the rainfall is slight and the veld consists of short grass mixed with short Karroo bush (*Pentzia*). In looking for scattered brown locusts I have got the habit of going to spots in the veld where there is an outcrop of white limestone in the red sand."

These valuable observations of Mr. Faure's leave no doubt that *L. pardalina* has, like *L. migratoria*, two different phases, which differ in morphology and coloiation, but more profoundly in the biology. Especially striking is it that there is a sort of parallelism in the variation from the swarming to the solitary phase in both these species, as will be presently evident. My study of extensive series of both phases of *pardalina* sent by Mr. Faure, with a careful designation of the conditions under which each particular lot was collected (*i.e.*, whether from swarms or singly), enables me to state the following differences between them.

The difference in the shape of the pronotum is well marked, though less striking than that between *migratoria* (or *migratorioides*) and *danica*. The pronotum of the swarming phase of *pardalina* (fig. 5, A & B) is more constricted before the middle, with the fore margin feebly prominent, the hind angle distinctly rounded, and the median keel slightly lower, and deeper cut by transverse sulci than in the solitary phase (fig. 5, D & E) ; but it is hardly possible to express these differences in figures, as I have done for the phases of *migratoria*, in which they are far more pronounced.

It is possible, however, to apply the method of proportions to another character— that of the relative lengths of the elytra and hind femora. As in *migratoria*, the elytra of the swarming phase of *pardalina* are relatively longer and the hind femora

shorter than in the solitary phase.   The femoral proportion (*i.e.*, the length of hind femora expressed as a percentage of the length of the elytra) in the swarming phase averages 0·44, with a maximum of 0·47, and a minimum of 0·41 ; the average proportion for the solitary phase is 0·46, with 0·50 maximum and 0·41 minimum.

While the elytra of *migratoria* and *danica* do not differ except in the relative length, there exists a well-marked difference in the shape and venation of the elytra in the two phases of *pardalina*.   Those of the swarming phase (fig. 5, C) are broader, with the fore margin more convex and the apex obliquely rounded, while the solitary phase (fig. 5, F) has the elytra narrower, with the margins almost straight and parallel and the apex obliquely truncate.   The most striking difference, however, is in the venation : the discoidal field in the swarming phase is much broader, and its false vein distinctly curved and much thicker than in the solitary phase, in which this field is rather narrow, parallel-sided, and with the false vein only slightly thickened and almost, or even quite, straight.   Naturally all these characters are subject to variation, and forms in all respects intermediate occur.
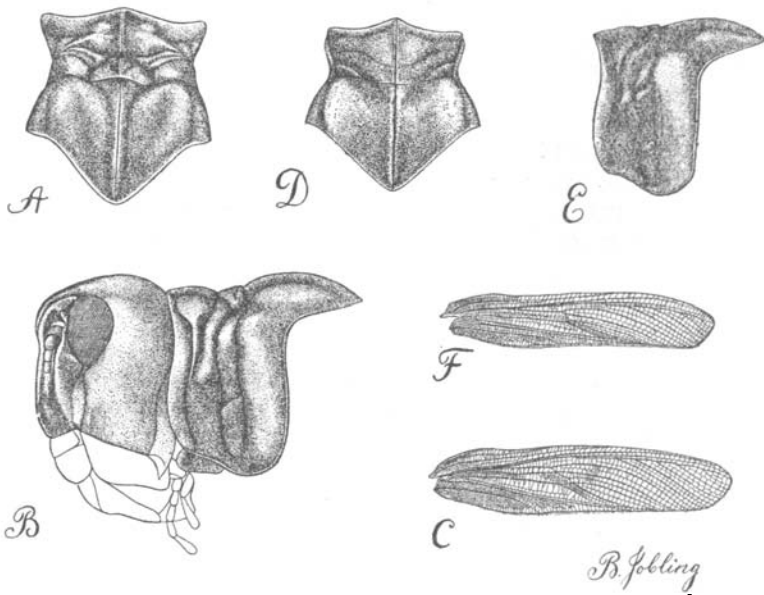

Fig. 5. *Locustana pardalina*, Walk.: A, B, C, phase *pardalina* ; D, E, F, phase *solitaria*, Uvar., nov.; C and F, natural size, remainder × 3.

The difference in the absolute dimensions between the two phases of *pardalina*, noted by Mr. Faure, is a phenomenon not observed in *migratoria*, but in the South African species it is well marked, the average length of the body of the swarming phase being 41 mm., while in the solitary phase it is only 34 mm., and occasional specimens occur even as small as but 24 mm.   The individual variability in size is in the solitary phase very extensive, but the swarming phase is rather constant in this respect ; this is also the case in the phases of *migratoria*.   Again, sexual dimorphism is as well marked in the solitary phase of *pardalina* as it is in *danica*, the average length of the body being 32 mm. in the males and 36 mm. in the females, while the difference in the size of dwarf males, attaining about 22–24 mm., and the largest females with a length of nearly 45 mm. is very striking.   The males of the swarming phase are scarcely smaller than the females, which agrees with the relative size of the sexes in typical *migratoria* or *migratorioides*.

The extremely variable and decidedly protective general coloration of the solitary phase of *pardalina* in all stages of post-embryonic development, noted by Mr. Faure, exactly corresponds with the coloration of *danica*. The larvae of the swarming phase of *pardalina* present an astonishing likeness to those of *migratoria* and *migratoiroides*, the coloration presenting the same combination of orange and black.* The adults of the swarming form are rather uniformly coloured, and some bright yellow specimens in the series sent from Pretoria lead me to the suggestion that at the time of mating a general change of coloration may occur, as it does in *migratoria* (see p. 143). In the coloration of the most aberrant individuals of the solitary phase, one particular feature is noteworthy : the presence of a more or less pronounced pale or white oblique cross on the pronotum, which design is very characteristic of the species of the closely related genus *Oedaleus*.

An examination of the male genitalia revealed no difference whatever between the two phases of *pardalina*, but this was only to be anticipated.

The above-quoted conclusions of Mr. J. C. Faure concerning the transformation of the solitary phase into the swarming one, at which he arrived quite independently of my work on *migratoria*, give a very strong support to the theory of phases as a direct cause of the periodicity. His observations are especially interesting because they concern the period of the transition from the solitary to the swarming phase, on which my investigations of *migratoria* have given very few facts. It seems that in
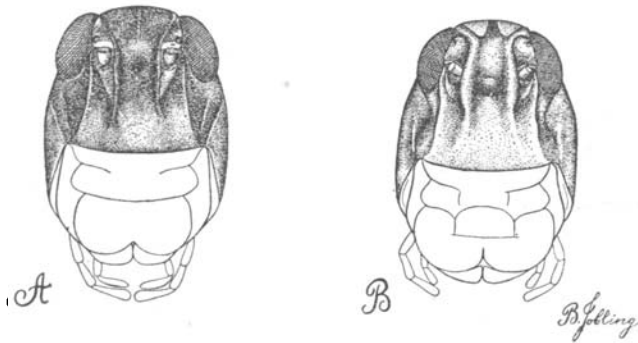

Fig. 6. Front view of head of : A, *Locusta migratoria* ph. *danica*, L. ; B, *Locustana pardalina* ph. *pardalina*, Walk. (× 4).

pardalina the transformation of solitary individuals into the swarming phase takes more than one generation, but the actual causes of the transformation are in this case also obscure, as they are in *migratoria*. Data as to the migrations of the flyers and the fate of migrating swarms of *pardalina* are yet lacking, and further investigations of this problem, closely connected with the careful study of all conditions of breeding grounds, are extremely important from the point of view of locust control in South Africa.

V. SYSTEMATIC PART.

Key to the Genera Locusta, L., and Locustana, g. n.

1 (2) Frontal ridge not widened at the median ocellus (fig. 6, A). Pronotum (fig. 1, A, B, C, D, E) with the typical transverse furrow cutting the median keel about its middle ; furrows in the prozona feeble. Mesosternal lobes only a

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* It is extremely interesting to note here that the larvae of most swarming and migratory locusts (*Schistocerca peregrina*, Ol., *Dociostaurus maroccanus*, Thb., etc.) present the same general type of coloration in black and reddish, or yellow, forming a very striking design. This phenomenon is well worth further investigation.

little longer than broad. Elytra (fig. 1, F) not less than five to six times as long as their maximal width ; hind radial vein diverging from the middle radial only slightly and close to the bifurcation of the former ; discoidal area much shorter than half the elytra ; inter-ulnar area about half as broad again as the discoidal area, rather densely areolated, with areolets more than three deep, without a regular false vein. Hind femora narrow, more than four times as long as their maximal width ; their upper margin more or less distinctly serrate ; upper carina of the externo-median area straight. ♂ : supra-anal plate (fig. 7, A) triangular, its surface practically flat ; cerci (fig. 7, A) short, rounded, conical ; subgenital plate with apex obtusely conical ; penis (fig. 7, B) very large, strongly recurved apically. ♀ (fig. 7, E) : subgenital plate with lateral margins straight ; apex truncate ; lower valves of ovipositor with basal part distinctly longer than broad, with an obtuse lateral tooth in the apical part ..   ..   ¡ ..   *Locusta*, L.
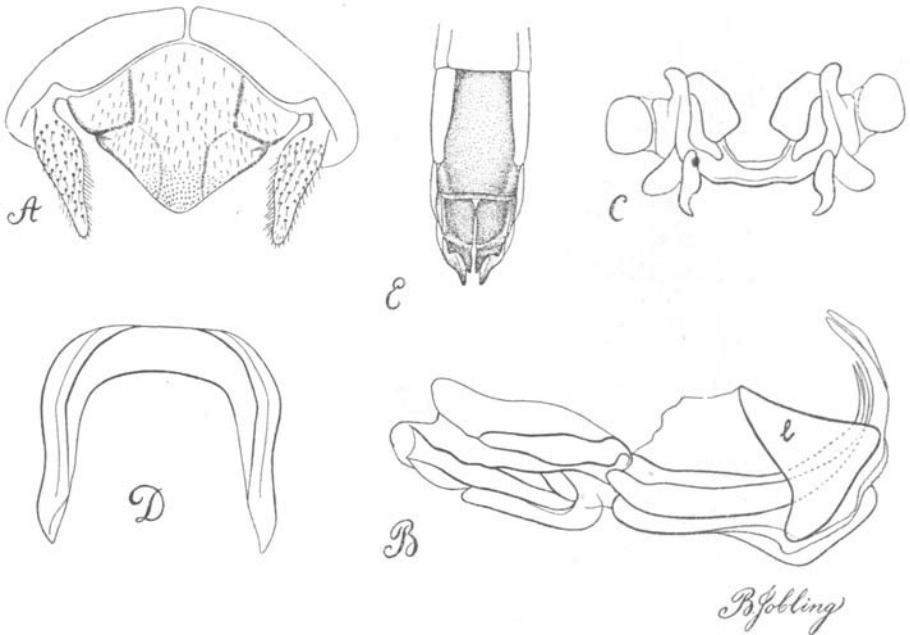Genotype : *Gryllus Locusta migratoria*, L.

Fig. 7. Genitalia of *Locusta migratoria*, L.: A, male supra-anal plate and cerci from above ; B, penis and lower genital valves (*e*) in profile ; C, epiphallus ; D, upper bridge of genital valves ; E, end of female abdomen from beneath. (E × 3, remainder × 12).

2 (1) Frontal ridge distinctly widened at the median ocellus (fig. 6, B). Pronotum (fig. 5, A, B, D, E), with the typical transverse furrow cutting the median keel distinctly before the middle ; furrows in the prozona deep. Meso-sternal lobes distinctly longer than broad. Elytra (fig. 5, C, F) not more than four to five times as long as broad ; hind radial vein strongly diverging from the middle radial long before its bifurcation ; discoidal area almost as long as half the elytra ; inter-ulnar area about as broad as the discoidal, sparsely areolated with two rows of areolets, separated by a false vein. Hind femora broad, less than four times as long as their maximal width ; their upper margin not serrate ; upper carina of the externo-median area convex.   ♂ : supra-anal plate (fig. 8, A) trapezoidal, with the apex prominent in the middle, irregularly denticulate, its surface with chitinous tubercles ;

cerci (fig. 8, A) rather large, compressed laterally ; subgenital plate with the apex slightly widened ; penis (fig. 8, B) very short, with short acute apex.   ♀ (fig. 8, E) : subgenital plate with lateral margins slightly convex ; apex rounded, with a median projection and bisinuate laterally ; lower valves of ovipositor with the basal part about as long as broad, the apical part unarmed laterally   ..   ..   *Locustana*, g. n.

Genotype : *Pachytylus pardalinus*, Walk.

This key shows only the most striking differences between the two genera ; other distinctive characters, especially those observed in the male genitalia, may be easily understood by a comparison of the figures (figs. 7 and 8).
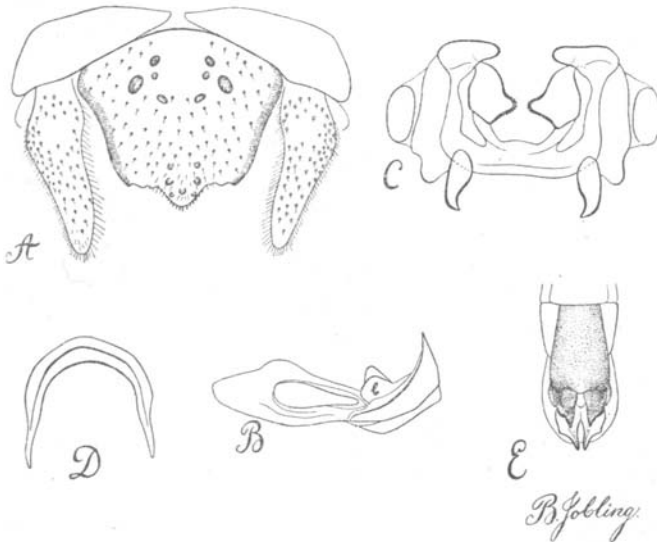

Fig. 8. Genitalia of *Locustana pardalina*, Walk. : A, male supra-anal plate and cerci from above ; B, penis and lower genital valves (*e*) in profile ; C, epiphallus ; D, upper bridge of genital valves ; E, end of female abdomen from beneath. (E × 3, remainder × 12).

A full description of the new genus *Locustana* is given below.

Key to the Phases of Locusta migratoria, *L*.* (figs. 1 & 4).

1 (2) Pronotum distinctly compressed laterally, but feebly constricted before the middle ; median keel high, tectiform, convex in profile ; the fore margin angulately prominent ; the hind angle acute.   Hind femora (on the average) longer than half the elytra.   Hind tibiae often red.   Larvae of variable coloration, but never black and red (or black and yellow).   Both larvae and adults occur singly or in very loose swarms   ..   .. ph. *danica*, L.

2 (1) Pronotum only feebly compressed laterally, but distinctly constricted before the middle ; median keel low, neither tectiform, nor convex in profile ; fore margin not prominent ; hind angle not acute.   Hind femora (on the average) shorter than half the elytra.   Hind tibiae only exceptionally red.   Larvae of a constant black and red (or black and yellow) coloration.   Both larvae and adults occur in dense swarms.

* It is quite obvious that the exact determination of the phases is possible only in the case of typical specimens and not of intermediate examples ; the most reliable results can be obtained only from examination of large series.

3 (4) Pronotum with the median keel straight in profile ; hind margin rotundato-
           angulate   ..   .. ph. *migratoria*, L.
4 (3) Pronotum with the median keel concave in profile ; hind margin widely
           rounded   ..   .. ph. *migratorioides*, Rch. & Frm.

Synonymic Notes.

The synonymy of *L. migratoria* ph. *migratoria*, L., and *L. migratoria* ph. *danica*, L.,
is quite correctly given by W. F. Kirby in his Catalogue (iii, pp. 229, 230), apart from
the fact that he distinguishes them as two different species, and I think it unnecessary
to repeat it here.   To the synonyms of *danica*, however, must be added *Pachytylus
australis*, Sauss. (Prodr. Oedip., pp. 119, 120, no. 5, 1884), but not *Locusta australis*,
Froggatt (Agric. Gaz., N.S. Wales, xiv, p. 110, 1903), which represents *Gastrimargus
musicus*, F., as has already been stated by Prof. Y. Sjöstedt (Ark. Zool., xii, no. 20,
p. 11, 1920).

Pachytylus capito, Sauss. (Prodr. Oedip., pp. 119, 120, no. 4, 1884) is undoubtedly
identical with *L. migratoria* ph. *migratorioides* (Rch. & Frm.).

Pachytylus minor, Sauss. (Abh. Senck. Naturf. Ges., xxi, p. 631, 1899) belongs to the
genus *Piernoscirta*, as I am able to state from an examination of good photographs
of the type specimen most obligingly taken for me by Dr. J. Carl, of the Geneva
Museum.

The only remaining species of *Locusta* in Kirby's Catalogue is *L. pardalina*
Walk., conspecific with *sulcicollis*, Stål, and *capensis*, Sauss., which is here made
the type of the new genus *Locustana*, m.

A Description of the Genus *Locustana*, nov. (figs. 5, 6 B & 8).

Antennae distinctly compressed dorso-ventrally.   Frontal ridge in profile straight
or feebly concave, distinctly widened and impressed around the median ocellus,
flat elsewhere, with the margins very obtuse, disappearing just below the ocellus.
Fastigium of the vertex slightly sloping, forming a straight widely rounded angle
with the frontal ridge, flat, distinctly longer than broad, with the margins distinctly
raised, convex, with the median keel always developed ; the distance between the
eyes slightly less than twice as broad as the frontal ridge between the bases of the
antennae.   Eyes oval, with the fore margin almost straight ; their width in the
broadest part, which is in the middle, is equal to about half their maximal height.
Pronotum with the prozona constricted, deeply furrowed, convex between the
furrows ; the typical furrow cuts the median keel distinctly behind the middle ;
median keel moderately elevated ; lateral lobes with the hind angle widely rounded.
Mesosternal lobes distinctly broader than long, their inner angles widely rounded ;
mesosternal interspace subquadrate in the female and slightly longer than broad in
the male.   Elytra hyaline throughout, except the basal parts of the marginal and
basal areas, which are coriaceous ; rather broad and short, not more than four to
five times as long as their maximal width ; apex oblique ; hind radial vein strongly
diverging from the middle radial long before its bifurcation (halfway between the
base and the bifurcation) ; discoidal area almost as long as half the elytra, with a
sinuate or straight false vein ; inter-ulnar area about as broad as the discoidal, or
scarcely broader, sparsely areolated, with two rows of the areolets separated by a
rather regular false vein ; axillar vein free, in most cases reaching the hind margin.
Wings rather short, not more than twice as long as their greatest width.   Hind
femora rather broad—less than four times as long as their maximal width ; upper
keel not serrate ; upper carina of the externo-median area distinctly convex.

♂.—Supra-anal plate, with strongly chitinized margins, trapezoidal, distinctly
longer than the basal width ; its surface distinctly concave, with several small chitinous
tubercles in the basal half, forming a trapezium ; outer margins nearly straight ;

apex triangularly prominent, irregularly denticulate ; hind angles obtusely rounded. Cerci rather large, strongly compressed laterally. Subgenital plate subconical, with the apex attenuate and slightly widened. Penis* short, widely and obliquely truncate posteriorly, with the apex triangular, sharp ; upper genital valves large, united with the penis : lower valves small, lying close to the sides of the penis and covering about half of it laterally, with obtuse upper projections ; they are connected with each other above the penis by a bow-shaped transverse bridge emitting forwards two long, apically narrowed, lateral branches ; epiphallus large, with the two upper apophyses obtusely rounded and projecting inwardly and with lower sharply pointed, beak-shaped teeth, with the inner lobes rounded and minutely and obtusely serrate near the lower angles.

♀.—Supra-anal plate obtusely triangular. Subgenital plate much longer than broad, widened posteriorly, with the lateral margins slightly convex ; apex rounded, bisinuate, with a small projection in the middle. Upper valves of the ovipositor with short, strongly recurved, rather obtuse apices and not very sharp margins. Lower valves with the basal part about as long as broad ; apical part without lateral teeth, with widely rounded lateral angles ; apices feebly decurved, short, acute.

Genotype : *Pachytylus pardalinus*, Walk.

Key to the Phases of Locustana pardalina, *Walk.*† (fig. 5).

1 (2) The average size smaller ; the males much smaller than the females. Pronotum more compressed laterally between the shoulders, but less constricted before the middle ; median keel more raised, not lower in prozona than in metazona ; fore margin more or less projecting in the middle ; hind angle sharp. Elytra shorter and narrower, with the margins almost straight and parallel, with the apex obliquely truncate ; discoidal area narrower, parallel-sided, with the false vein straight and not incrassate. Coloration of larvae, as well as that of the adults, very variable, but the larvae are never coloured black and red. Both larvae and adults occur singly and in loose swarms.   ..   ..   ph. *solitaria*, n. ph.

2 (1) The average size larger ; the males only a little smaller than females. Pronotum not compressed laterally between the shoulders, but strongly constricted before the middle ; median keel less raised, in prozona distinctly lower than in the metazona ; fore margin straight ; hind angle rounded. Elytra broader and also longer, with the margins convex, and the apex obliquely rounded ; discoidal area broader, with the sides sinuate, and the false vein distinctly incrassate and sinuate. Coloration of the larvae uniformly black and red. Both larvae and adults occur in dense swarms
ph. *pardalina*, Walk.

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* The terminology of the parts of the genitalia adopted here is that of L. Chopard (Recherches sur la conformation et le dévelopment des derniers segments abdominaux chez les Orthoptères.—Thèses présentées a la Faculté de Sciences de Paris ; Série A, No. 847, 1920).

† See the footnote on page 161.