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NOTES ON LOCUSTS OF ECONOMIC IMPORTANCE, WITH SOME NEW
DATA ON THE PERIODICITY OF LOCUST INVASION.

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The present paper is a part of the results of my revisional work on the group CYRTACANTHACRINI, which includes all the swarming locusts except *Locusta migratoria* (L.), the latter having formed the subject of a previous paper.* The revision itself, being of a purely systematic character and dealing also with a large number of species of no economic interest, is being published elsewhere;† but I thought it might be useful to economic entomologists to give here the principal conclusions arrived at concerning the species of known agricultural importance, especially because this presents an opportunity of discussing some important points in the biology of swarming locusts which would be out of place in the revision itself.

The generic classification of the group has been in a most unsatisfactory state, and I have had to establish a number of new genera, fully described in the revision, where also an illustrated key to the genera is given. This involved the necessity of alterations in the previously used names of almost all economic locusts, while a critical study of the original descriptions, as well as of the majority of existing types, enabled me to establish their correct synonymy; this latter is also given in full in the revision, while here only some of the more important synonyms are included, merely in order to reduce the number of names now in use for the same species.

The paper deals exclusively with the Old World locusts, although I could not avoid discussing one of the South American species closely related to an Old World one.

Schistocerca gregaria (Forsk.) (fig. 1).

Synonyms: *Acridium peregrinum*, Oliv.; *Schistocerca tatarica*, Kirby, Syn. Cat. Orth. (not *Gryllus Locusta tataricus*, L.).

Systematic Notes.—This insect is known to economic entomologists mostly under the name of *Schistocerca peregrina*, Ol. (for which Kirby incorrectly substituted *S. tatarica*), but the name *S. gregaria*, Forsk., has priority.

One of the interesting points in connection with this species is that it is the only Old World representative of the genus, which is widely distributed and represented by a large number of species in South America, penetrating partly also into the Southern United States. One of the South American species, *S. paranensis*, Burm., so closely resembles *S. gregaria* that some authors have considered them to be conspecific and have suggested that *S. gregaria* is of South American origin and migrated across the Atlantic ocean to Africa, where it has found suitable conditions for existence. The suggestion induced me to undertake a comparative study of these two species,‡ and my definite conclusion is that *S. paranensis* is undoubtedly distinct from *S. gregaria* as has been stated by some authors, and especially by Arribalzaga (*Physis*, iv, no. 4, 1918, pp. 49-79). The characters separating these two insects may be briefly summed up as follows:—

1. Face in *paranensis* more reclinate, but perfectly vertical in *gregaria*. Frontal ridge in *gregaria* distinctly constricted at the fastigium, widened above the middle.

* A revision of the genus *Locusta*, L. (= *Pachytylus*, Fieb.), with a new theory as to the periodicity and migrations of locusts.—Bull. Ent. Res., xii, 1921, pp. 135-163.

† Ann. Mag. Nat. Hist., beginning April 1923.

‡ I am greatly obliged to the authorities of the United States National Museum, and Dr. A. N. Caudell for the loan of an extensive series of *S. paranensis* for this purpose.

constricted below it and parallel-sided elsewhere; in *paranensis* not constricted at the fastigium, only slightly and gradually widened downwards, constricted below the ocellum and with the margins distinctly divergent towards the clypeus.

2. Fastigium of vertex in *paranensis* more distinctly sloping, broader and shorter, than in *gregaria*.

3. Pronotum of *gregaria* very strongly constricted in the prozona, decidedly selliform, with the metazona much broader than the prozona, and also broader than long; while in *paranensis* it is simply conical, scarcely constricted, with the metazona only slightly broader than the prozona and not broader than long.

4. Anal field of the clytra in *paranensis* narrower than in *gregaria*.

5. Hind femora in *paranensis* thicker and shorter than in *gregaria*.

6. Mesosternal lobes in *paranensis* with the hind inner angles acute and attenuate, while in *gregaria* the angles are practically straight; the mesosternal interspace, accordingly, is strongly narrowed posteriorly, almost cordiform, in *paranensis*, and only slightly narrowed, with the margins straight, in *gregaria*.

7. Metasternal lobes contiguous in males and narrowly separated in females of *paranensis*, while in *gregaria* they are distinctly separated in males and broadly so in females.

8. Male cerci of *paranensis* more or less emarginate apically; those of *gregaria* obliquely truncate.

9. Male subgenital plate with the lobes acutangular in *gregaria*, and broader, distinctly rounded apically, in *paranensis*.

10. The most important and constant difference in the coloration is the presence in *paranensis* of a more or less distinct pale, dark-edged, fairly broad stripe along the pronotum, which is never present in the common swarming form of *gregaria* (for description of an aberrant, probably non-swarming form, see below); again, the lateral lobes of the pronotum are quite uniformly coloured in *gregaria* (in the swarming form), and with more or less distinct dark and pale fasciae in *paranensis*; the hind tibiae are in the latter red or reddish, and yellow in *gregaria*, except in sexually immature specimens, which are reddish all over; the hind femora of *paranensis* are colorless, but with numerous dark dots along the outer carinae, while in *gregaria* they have, as a rule (but not always), dark bands on the upper side, and no dots on the carinae.

It is not easy to decide whether all these characters are sufficient to justify the specific separation of *gregaria* from *paranensis*, as the extent of variability of the latter still remains unstudied, and some of the specimens before me now show that it is not inconsiderable, and, what is especially noteworthy, the variations may go in the direction of *gregaria*, while the pronotum becomes more strongly constricted, and the frontal ridge and mesosternal interspace show a distinct likeness to those of *gregaria*.

On the other hand, the material of *gregaria* studied shows that the above-mentioned characters of that insect are also not always constant. Amongst the variations found there is one which deserves special attention, because I am convinced that it represents a solitary living phase* of the species. This form agrees perfectly with the description of *Acridium flaviventris*, Burm. (Handb. Entom., ii, p. 631, no. 11, 1838) and I call it, accordingly, *S. gregaria* ph. *flaviventris*, Burm. Its description is as follows (see also fig. 1 B, C):—

Differs from the typical (swarming) phase in the pronotum being much more constricted, and with scattered round callous tubercles (especially in metazona), less widened in metazona, which is about as long as broad (broader than long in *gregaria*) with the hind angle almost straight; median keel well developed also in the prozona,

deeply and broadly cut by the sulci; the upper surface distinctly darkened, with a narrow pale stripe along the median keel; the lateral lobes in the metazona darker than in the prozona, which bears a fairly distinct longitudinal stripe along the middle and another broader one along the lower margin which is pale; mesosternal interspace strongly narrowed posteriorly, with the sides somewhat convex; the hind angles of the mesosternal lobes somewhat attenuate, though less so than in *paranensis*.

This remarkable form is known to me by specimens from the following localities: Kenhardt district, Cape Province, 27.vi.1917, 1♀ (the above redescription is based on this particular specimen); Northern Ceres district, Cape Province, 15.xi.1917, 1♀; Namaqualand, ix.1917, 3♂♂; Rietfontein, Cordonia, Cape Province, 17.iv.1917, 1♀; St. Vincent, Cape Verde Islands, 2♀♀; Ascension Island, 1♀; Red Sea, W. shore of Port Sudan, desert north of railway, 29.ii.1912, 1♀ (G. U. Longstaff); Ain Guettara, north of In-Salah, Central N. Sahara, 12-14.iv.1912, 1♀ (E. Harter); Thebes, Egypt, 1♀; Chaharbar, Persian Gulf, 7.ii.1917, 1♀; Naxos, Greece, 16.iv.1862, 1♀.*

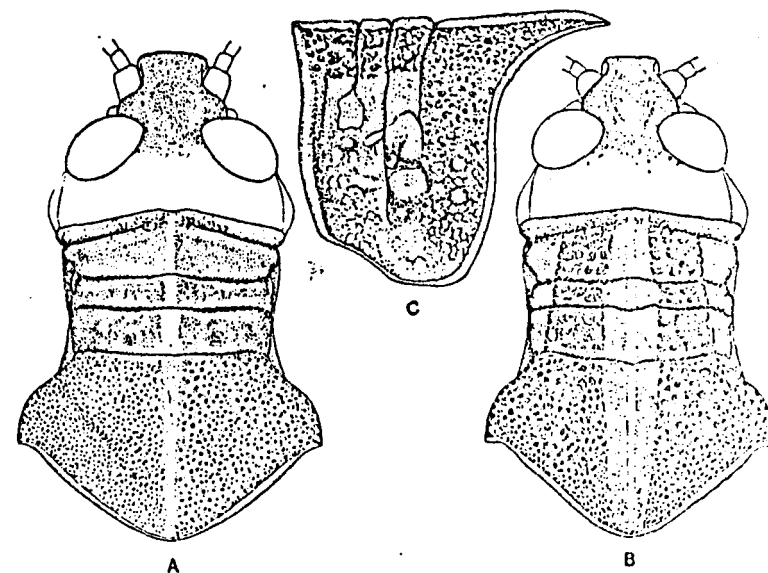


Fig. 1. *Schistocerca gregaria* (Forsk.): A, phase *gregaria*; B, C, phase *flaviventris*, Burm. × 4.

This form shows an extremely interesting tendency of *S. gregaria* to vary in the direction of *S. paranensis*, displaying at the same time certain characters of its own.

The distinctions of *flaviventris* from the common swarming phase (which should be called ph. *gregaria*) are very striking, but there occur some clearly transitional forms between them; thus, a male in the British Museum, from Zanzibar, agrees perfectly in the shape of the pronotum with the typical *gregaria*, while its coloration is that of *flaviventris*, and the sculpture is intermediate between the two forms: another specimen, a female from Hadramaut, Arabia, has the pronotum shaped and sculptured as in *flaviventris*, but quite uniformly coloured. The possibility of regarding *flaviventris* as a geographical race (subspecies) of *gregaria* is out of the question, since

* There is in the British Museum one more male of this form, labelled "Matuku, 21.7.71, brought home by the "Challenger" Expedition, but the occurrence of the species in that locality (Fiji Islands) seems to me highly improbable, and this is probably a case of mislabelling.

* The term introduced by me in the paper on *Locusta* (l.c.).

the two forms seem to have practically the same distribution. These considerations lead to the only possible conclusion, namely, that *gregaria* and *flaviventris* represent two different phases of one dimorphic species, exactly as is the case with *Locusta migratoria* and *Locustana pardalina* (Uvarov, l.c.). There is no doubt that *gregaria* is the swarming phase of the species, as the specimens actually taken from swarms invariably belong to it, but there is also no doubt in my mind that *flaviventris* represents the solitary phase. This suggestion is based, primarily, on the comparative scarcity of *flaviventris* in collections, where it is almost always represented by single specimens from each particular locality, never bearing a label that they have been taken from a swarm, while labels of that kind are not unusual on specimens of *gregaria*. It is, however, not only on these, partly negative, proofs that my interpretation of *flaviventris* is founded, as I have before me the definite evidence of Dr. E. Hartert relating to a female of *flaviventris* taken by him in the Sahara, and stating that "there were no swarms of locusts in Northern Sahara in 1912 and the specimen I got at Ain Guettara was not out of a swarm hut single." This interesting observation confirms my point of view in a most decisive manner, though direct observations on the transformation of one phase into another are needed. I hope, however, that these lines will attract the attention of field entomologists to the problem.

Geographical Distribution.—*S. gregaria* is an essentially African species, extending also into south-western Asia (as far north as Transcaspi*) and as far east as Kashmir, whence there is one specimen in the British Museum, unfortunately without more precise locality), and into Southern Europe (Corfu, Naxos, Portugal), but its distribution in Africa, and especially its permanent breeding regions, are yet very inadequately known. It is well known as a swarming locust in Algeria, Tunisia, Morocco, Egypt (in the latter oily occasionally), Sudan, East Africa and Senegal, while it seems to be absent from the whole belt of tropical forests, but reappears again in South Africa, whence both phases are known to me by specimens (Johannesburg, Capetown and other localities in the Cape Province whence *ph. flaviventris* is recorded; see above), as well as from the literature (numerous records are given by H. Karny in Zool. Anthropol. Forschungsreise in W. und Centr. Südafrika, etc., iv, Lief. 1, 1910, p. 65), though the records of its occurrence there as a swarming locust are lacking, which, however, may be due simply to its confusion with the superficially similar *Nomadacris septemfasciata*, Serv. (see below). Karny, in the paper quoted above, expressed the opinion that the South African area of distribution of the species is not connected with the North African one, and he asserts even that the latter does not extend farther southwards than Senegal and the Red Sea. The erroneousness of this assertion is shown by the well-known work of Vosseler (Die Wanderheuschrecken in Usambara, Ber. über Land- und Forstwirtschaft in D.-Ostafrika, ii, 1905, p. 6), which was published five years before Karny's paper, as well as by numerous East and West African localities given by La Baume (Die Afrikanischen Wanderheuschrecken, Beih. z. Tropenpflanzer, Bd. si, no. 2, 1910, p. 115). It is true that there are yet no records from Portuguese East Africa, Nyasaland and Rhodesia, but this may be attributed partly to the confusion of swarms of this species with those of *N. septemfasciata*, and partly to specimens of the solitary phase being, probably, very wary and difficult to catch.†

Quite interesting are the records of this species from some of the Atlantic Islands—namely, the Verde, Grand Canary and Ascension (British Museum)—which can only be explained as a result of migrations of swarms from the African mainland. That migrations of this species may be and are extensive enough to enable it to reach even an island as remote as Ascension cannot be doubted, since there are in the British Museum two specimens of the *ph. gregaria* taken as far as 500 miles

from land, and Scudder has recorded a swarm that came on board a ship in lat. 25° 28' north, long 41° 33' west, i.e., about midway between Africa and America, with the nearest point of land 1,200 miles off (Psyché, ii, 1883, p. 124). This latter fact caused Scudder to explain the first appearance of the species in the Old World as a result of direct migration across the ocean from South America, since he thought that the species occurred in the latter country as well. In my opinion, however, the presence of *S. gregaria* in the New World has never been positively proved, as old records are unreliable and apply to *S. paranensis* (and possibly some other American species), while some specimens in the South American material from the U.S. National Museum, which are similar in general appearance to *gregaria*, are in fact different from it exactly in the characters separating the latter from *paranensis*. As for true *gregaria*, the British Museum collection contains two specimens labelled as being of South American origin; one of them is the type of *Acridium sellatum*, Walker, and reputed to be brought by Charles Darwin from Montevideo, but is not labelled in Darwin's own hand, as all his other insects are; another specimen is labelled "Berbice," but neither collector nor the date of collection are known, which makes this record also quite unreliable. I am inclined to think, therefore, that there is no true *gregaria* in South America, but this can be definitely settled only by American entomologists working on the spot. This opinion does not directly contradict Scudder's conclusion, which is also generally accepted, that *S. gregaria* is of South American origin, since it is the only Old World representative of a genus consisting of many New World species.

Bionomics.—I am not going to dwell here on the individual life-history of *S. gregaria*, which is already comparatively well known owing to the investigations of Künckel d'Herculis* and of Vosseler,† though many important points, especially those concerning the physiology, still require elucidation. My intention is only to discuss briefly some points of the species-life of this locust in connection with its swarming habits.

In the first place I should like to draw attention to Vosseler's conclusion (l.c., p. 339) that the migration either of larval or of adult swarms has nothing whatever to do with the want of food, which agrees perfectly with what I have stated for *L. migratoria*. Another often repeated explanation of the causes of migration of adult swarms—that they are looking for new suitable breeding-grounds—is also most emphatically denied by Vosseler for *S. gregaria*, again in complete accordance with my observations on *L. migratoria*. Künckel d'Herculis (l.c.) has already observed, and Vosseler has studied more thoroughly, the extremely interesting colour changes in the individuals forming migratory swarms; these changes are in *S. gregaria* far more pronounced than in *L. migratoria*, but it is highly probable that they are due to the same causes, and I believe that they are in direct physiological connection with the processes of the maturation of the sexual products, and of the development and reduction of the fat-body; further researches in this direction are, however, necessary.

Unfortunately, the annual life-cycle of *S. gregaria* is yet very incompletely known, and practically nothing at all has ever been done to study its permanent breeding-grounds; in fact, it is not known even whether there are any definite conditions necessary for its permanent breeding. This makes a study of the periodicity of this species impossible on the basis of existing records, but the occurrence of two different phases of the species suggests a promising line of investigation; it is obvious that the clue to the solution of the problem of periodicity lies in a thorough study of the conditions of existence of both phases, and of the changes in those conditions necessary to produce a transformation of one phase into the other. This will necessitate investigations not only during the years of mass invasions, but also, if not much

* An accidentally stray specimen has been recorded by me from that country.—Horae Soc. Entom. 1912, no. 3, 1912, p. 31.

† I am inclined to attribute to this latter cause the comparative scarcity of the solitary phase

* Invasions des acridiens, vulgo sauterelles, en Algérie. Algier. 1893-1905.

† Die Wanderheuschrecken in Usambara im Jahre 1903-1904, zugleich ein Beitrag zu ihrer Biologie.—Ber. Land- u. Forstwirt. in D.-O.-Afrika, ii, 6, 1905.

more thoroughly, in the years of minimum occurrence, when the solitary phase is more likely to be found. Observations of this kind have been conducted by German entomologists in East Africa, but have not been published in full; a short note by Morstätt,* however, states definitely that the periodicity of locusts in German East Africa was due not to invasions from outside, as is too often suggested without any serious evidence, but to periodical increased multiplication of local insects, living usually scattered on dry grass-lands (solitary phase?). This author is inclined to attribute the periodical increases in the number of locusts, leading to the formation of swarms (as a result of transformation into the swarming phase?) to abnormally dry years; future students of *S. gregaria* should pay attention to the influence of moisture and temperature on the development of this locust.

Anacridium aegyptium (L.).

Synonyms: *Acridium aegyptium*, L.; *Orthacanthacris aegyptia*, L.

The economic importance of this well-known Mediterranean species is almost negligible, as it never swarms and occurs always in single, scattered specimens, but it is an occasional pest of leaves of cotton plants in Turkestan, Transcaucasia, the Punjab and Egypt; more serious injury has been recorded to young tobacco plants in Dalmatia and Italy.†

Valanga nigricornis melanocornis (Serv.).

Synonyms: *Acridium melanocorne*, Serv.; *Acridium consanguineum*, Serv.; *Cyrtacanthacris melanocornis*, auct.; *Orthacanthacris melanocornis*, auct.

Systematic Notes.—My study of this genus (*l.c.*), which ranges from Australia to Indo-Malaya, showed that some of the species are widely spread over the numerous islands and represented by a corresponding number of geographical races. Thus, the Javanese *Acridium melanocorne* is only a subspecies of *A. nigricorne*, Burm., which occurs in Malacca.

Bionomics.—A detailed account of this insect has been published by Roepke,‡ who studied it in Java, where it is a serious occasional pest of various wild and cultivated plants, particularly of *Castilloa*, bread-fruit, *Ficus*, *Hevea*, coconut palms and maize. It is not a swarming species, since it does not display any social and migratory instincts even when it appears in large numbers.

It is not impossible that other subspecies of *V. nigricornis*, Burm., may prove to be of economic importance in other parts of Indo-Malaya.

Palanga succincta (L.).

Synonyms: *Acridium succinctum*, L.; *Cyrtacanthacris succincta*, L.; *Orthacanthacris succincta*, L.; *Acridium assectator*, F.-W., etc.

Systematic Notes.—This insect, known to Indian entomologists as the "Bombay Locust," is readily recognisable by the straight, laterally compressed prosternal tubercle, the rose-coloured base of the wings, and by the pale elytra with but few grey marks.

Geographical Distribution.—The species is distributed all over southern and south-eastern Asia and the Malay Archipelago (Sumatra, Borneo, Nias), but its exact range is as yet very inadequately known. According to Bainbrigge Fletcher§ it "occurs throughout the plains of India and Ceylon," but a more exact definition of its area is wanting.

* Die Ursachen der Heuschreckenplagen in Ostafrika.—Kosmos, 1921, No. 3.

† Grasses. Landbuch der Pflanzenkrankheiten, iii, p. 132.

‡ Die Heuschreckenplagen.—Teysmannia, xxvi, 1915, pp. 115-124; 337-358;

§ Journ. Biol. Entom. Meeting at Pusa, i, 1920, p. 310.

Austracris guttulosa (Walk.).

Synonym: *Cyrtacanthacris guttulosa*, Walk.

This species and *A. basalis*, Walk. (= *A. plagiata*, Walk.) have been recorded by Jarvis† as being classed as sugar-cane pests in the Brisbane collection of economic insects in the Agricultural Department, but he has not yet been able to confirm this view, and the specific identification also is not reliable.

Austracris basalis (Walk.).

Synonyms: *Cyrtacanthacris basalis*, Walk.; *C. plagiata*, Walk.

The short description which Jarvis (*l.c.*) gives of the insect which he calls *Cyrtacanthacris* (?) *proxima* applies to *A. basalis* better than to any other known species, and I believe it to be the same.‡

Nomadacris septemfasciata (Serv.).

Synonyms: *Acridium septemfasciatum*, Serv.; *Cyrtacanthacris fascifera*, Walk.; *C. purpurifera*, Walk.; *C. subsellata*, Walk.; *Acridium sanctae-mariae*, Finot; *A. coangustatum*, Luc.

Systematic Notes.—The outstanding feature of this insect, which (if it be examined with due attention) makes a mistake in its identification quite impossible, is the reticulation of the basal half of the elytra, which is finer and denser than in any other locust of that size; the cellules between the veinlets are correspondingly minute.

* The Bombay Locust (*Acridium succinctum*, Linn.)—Mem. Dept. Agr. India, Entom. Ser., i, 1, 1906.

† Notes on Insects damaging Sugar-cane in Queensland.—Bureau Sug. Expt. Sta., Queensland, Entom., Bull. No. 3, 1916, p. 22.

‡ There should be other true swarming locusts in Australia, but exact records are lacking.

ounded or angular as in other locusts. Oblique
 (as seen in number) on the elytra and the almost obliterated
 pronotum furnish further distinguishing characters. The rose
 on the hind wings, which caused this species to be called "Red Locust"*
 south Africa, is not a constant character, and it is very likely that it may change
 during the individual life (probably in connection with the development of the sexual
 products).

The species is very constant in its structural characters, save in one—the shape of
 the pronotum, and in that respect two different forms of the species may be distin-
 guished. In one form the pronotum is comparatively shorter and has a distinct
 constriction before its middle: this is the more common (and also the typical) form,
 and all the specimens taken from swarms, seen by me, belong here. Another form,
 described by Lucas as *Acridium coangustatum* from Réunion and later on by Finot
 as *A. sanctae-mariae* from Madagascar, and known to me also by a few examples from
 different localities in Africa, differs from the typical form in the pronotum being
 relatively more elongate and without a constriction, but simply narrowed anteriorly.
 As this type of difference is characteristic for the swarming and solitary phases of
 some other locusts in which the phases are actually known (*Locusta migratoria*, *Locus-
 tana pardalina*, *Schistocerca gregaria*), I venture to suggest that *coangustata* is but a
 solitary phase of *septemfasciata*; this suggestion, of course, needs confirmation, but
 it may be useful to draw the attention of future students of this species to it.

Geographical Distribution.—The exact distribution of this locust is not yet
 sufficiently known. It inhabits South Africa, extending in the west as far as the
 lower Congo (Luki, Leopoldville, Kinchassa), while in the east the most northern
 localities known to me are: Lake No, at the junction of Batir-el-Cazal and Bahr-el-
 Djebel in the Sudan, and Zegi-Tsana, Abyssinia. The species occurs also in Mada-
 gascar, Réunion and the Comoro Islands; it seems that from the islands only the
 form *coangustata* is known. Further localities for the latter are: Luki, Mayumbe, on
 the lower Congo; Valley of Muza, basin of lower Zambezi; Luangwa Valley, North-
 eastern Rhodesia; Uganda; Mount Chirinda, Southern Rhodesia; Pretoria.

Bionomics.—Although the species is known as an occasionally very serious pest of
 different crops, our knowledge of its bionomics is very unsatisfactory. Thus, its breed-
 ing conditions have never been studied, and even the annual life-cycle is not definitely
 established. It seems, however, that in the latter respect *N. septemfasciata* belongs
 to the same group as *Patanga succincta*, i.e., it passes a very long period (winter
 months) of its adult life in a sexually immature state, which is the cause of a corres-
 pondingly long period of migrations. At the same time, it also does not swarm so
 regularly as *Schistocerca gregaria* or *Locustana pardalina*, and in this respect again
 agrees with *Patanga succincta*. Thorough studies of this species, prolonged over
 several years, covering not only mass invasions but the periods of minimum occurrence
 as well, when the solitary phase may be expected, should yield results of practical
 importance.

Cyrtacanthacris tatarica (L.).

Synonyms: *Acridium ranaceum*, Stoll; *A. aeruginosum*, Burm. et auct. (Stoll); (not *Schistocerca tatarica*, Kirby, see above).

The species enjoys an unusually wide distribution, being common all over Africa
 (south of the Sahara), Madagascar, Seychelles, Ceylon and India, reaching as far
 east as Siam.

According to Bainbrigge Fletcher* *C. tatarica* "occurs throughout the plains
 India on almost all crops, but is usually found in small numbers only. It is a main
 pest of cotton and other crops." There are no records of this species being introduced
 in Africa.

Chondracris rosea (De Geer).

Synonyms: *Gryllus flavicornis*, F.; *Acridium flavicornis*, F.; *A. melanocornis*
 Lefroy† (nec Serv.).

This large, solitary-living species, easily recognisable by its uniformly green
 coloration and rose wings, has been recorded by van Deventer‡ amongst other main
 and occasional pests of sugar-cane in the Dutch East Indies, where it occurs as a
 race *Ch. rosea brunneri*, Uvar.

* Proc. Third Entom. Meeting at Pusa, i, 1920, p. 310.

† Mem. Dept. Agric. India, i, no. 1, p. 53, pl. xii, fig. 3; Indian Insect Life, p. 74, fig. 19.

‡ De dierlijke vijanden van het suikerriet en hunne parasieten, 1912, p. 279.