STRUCTURE AND POSTEMBRYONIC DEVELOPMENT OF FEMALE REPRODUCTIVE ORGANS IN THE DESERT LOCUST, *SCHISTOCERCA GREGARIA*

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(With 4 Tables, 7 Text-figures and 2 Plates)

CONTENTS

I—INTRODUCTION

The structure of the female genitalia and associated structures of Orthopterous insects of the family Acrididae has been studied and discussed by several workers, notably by Fenard (1896-97), Walker (1919-22), Nel (1929), Heberdey (1931), Nelson (1931-34), Vardé (1934), Snodgrass (1931-35), Roonwal (1935-49), Slifer (1940), Qadri (1940), Karandikar (1942), Gupta (1950) and Agarwala (1952-53). The Desert Locust, *Schistocerca gregaria* Forskal (Family Acrididae), has been studied in this respect by Vardé (1934), Roonwal (1935-49), Slifer (1940), Karandikar (1942), Gupta (1950) and Agarwala (1952*b*). Nevertheless, several questions need investigation, and some of these are discussed in the present paper.

II—MATERIAL AND METHODS

Schistocerca gregaria individuals obtained form swarms in India and bred croweded (and consequently in phase *gregaria*) in the laboratory were used. In most cases careful dissections of the abdomen of famales, both in the hopper and adult stages, were made to expose the female reproductive organs. In some cases, especially in the first stage hoppers, the posterior end of the abdomen was cut off, treated with a weak solution of potassium hydroxide in water, stained lightly with alcoholic eosin and mounted flat on a slide. Vertical-longitudinal sections of the first stage female hoppers were cut and examined.

As far as possible, the terminology for the genitalia given by Ander (1956) and Tuxen (1956) has been followed.

III—STRUCTURE OF INTERNAL FEMALE REPRODUCTIVE ORGANS IN ADULT

(Plates 11 and 12 ; Text-figs. 1-6)

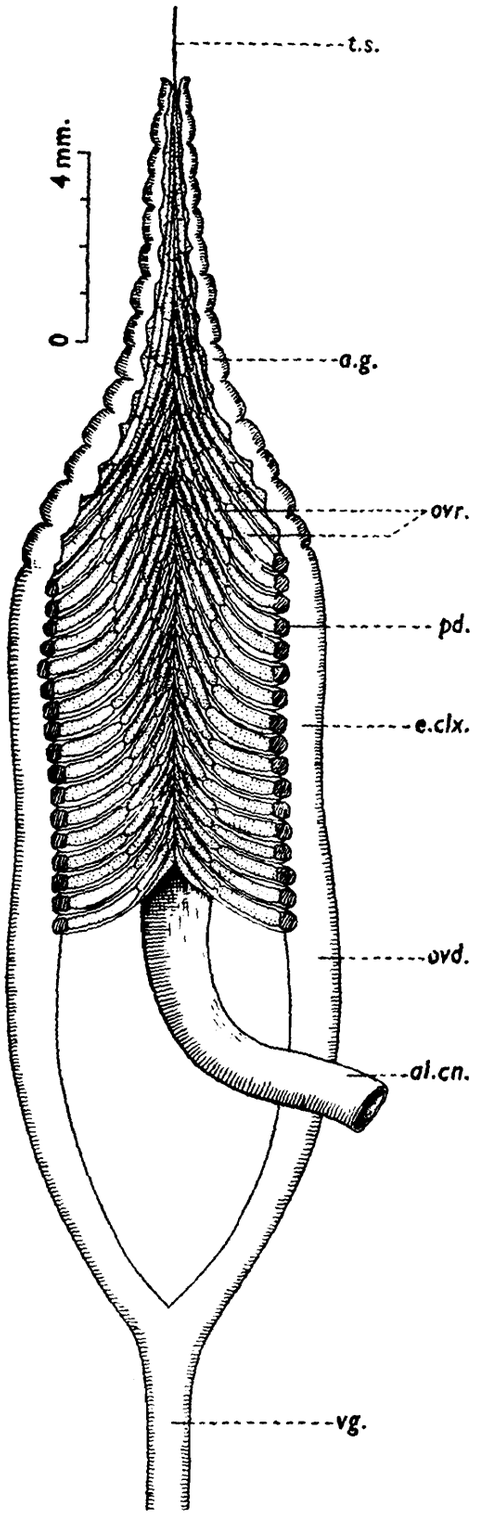
The internal female reproductive organs of *Schistocerca gregaria* consist of the following parts :—

1. The paired ovaries with their ducts.
2. The female accessory glands (*boyau calicial*). Also paired.
3. The spermatheca.

1. *The ovaries and their ducts*

The two ovaries are compact, elongated bodies lying side by side in the cavity of the abdomen above the alimentary canal. In the newly eclosed female they are small, whitish bodies lying in the fourth to sixth abdominal segments and measuring about 7 mm. long and 3 mm. wide. As the female matures, the ovaries increase in size and assume a yellowish colour (due to the presence of yolk in the ripening eggs) until, in a female about to oviposit, the ovaries occupy virtually the whole of the abdomen and also extend into the thorax, are the most conspicuous organs on the dissection of the insect and measure about 26 mm. in lengtn and 11 mm. in width. They are richly supplied with tracheae and on their ventral side they are in intimate connection with fat-bodies.

The ovary of each side is composed of about 40-83 egg-tubes or ovarioles, the total number in the pair varying from about 92-145

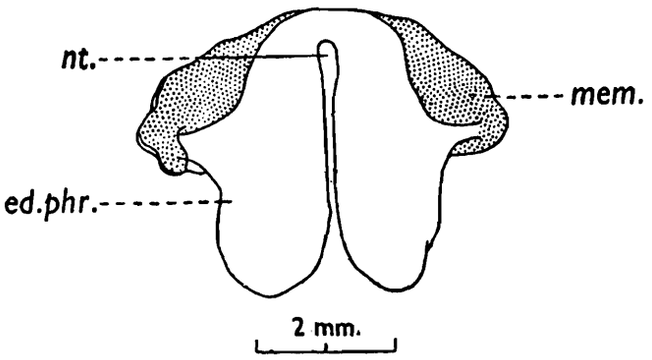


TEXT-FIG. 1.—*Schistocerca gregaria*, adult female. Ovary of a mature individual from a swarm, after egg-laying. Semidiagrammatic.

a.g., female accessory gland (*boyau calicial*) ; *al. cn.*, alimentary canal ; *e.clx.*, egg-calyx ; *ovd.*, paired oviduct ; *ovr.*, ovarioles ; *vg.*, vagina or common oviduct.

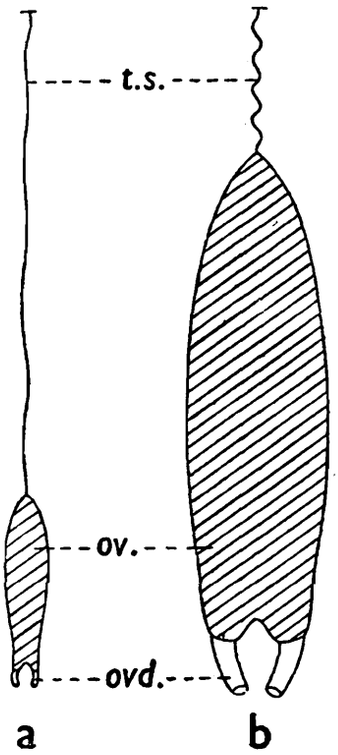
(mean 114·5). The number of ovarioles in an ovary varies in differnt individuals and also in the right and left ovaries of the same individual.

It is rare to find a female with an equal number of ovarioles in the two ovaries. Roonwal (1947), who studied this variation in phase *gregaria* individuals, found 43-83 (mean 57·3) ovarioles in the right ovary and



TEXT-FIG. 2.—*Schistocerca gregaria*, adult female. Second thoracic phragma to show the notch for the passage of the ovarian suspensorium.
ed. phr., endophragma ; *mem.*, membrane ; *nt.*, notch.

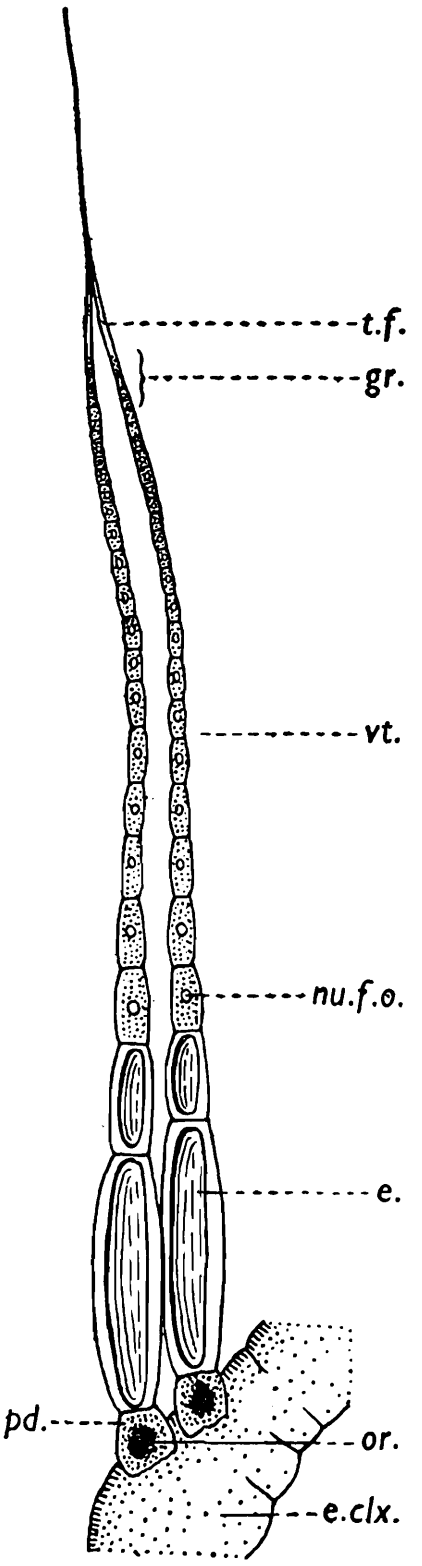
40-81 (mean 57·2) in the left. Thus, while there is no appreciable difference in the mean number of ovarioles in the right and left ovaries, the number in the same individual generally varies, the difference ranging



TEXT-FIG. 3.—*Schistocerca gregaria*, adult female. Diagrammatic representation of the ovary and the ovarian suspensorium, to show the sagging of the latter as the ovary grows in size with maturity.
(*a*) In a young freshly eclosed imago. (*b*) In a female about to lay eggs.
ov., ovary ; *ova.*, paired oviduct ; *t. s.*, terminal suspensorium of ovary

from 0-30 (mean 6·5). According to Roonwal, there is no apparent retotionship between this difference and the total number of overioles in a female.

Each ovariole consists of a single chain of developing eggs, the oldest being situated at its base, *i.e.*, the end which abuts against the egg-calyx.



TEXT-FIG. 4.—*Schistocerca gregaria*, adult female. Two ovarioles from the ovary of a half-mature individual. (*After* Roonwal, 1949.)

e., egg ; *e.clx.*, egg-calyx ; *gr.*, germarium ; *nu. f. o.*, nucleus of *future ova* : *or.*, mass of orange-red pigment ; *pd.*, pedicel or basal follicle ; *t. f.*, terminal filament of ovariole ; *vt.*, vitellarium.

The other eggs of the chain show a progressively decreased development as we move towards the tip of the ovariole until, finally, near the lip

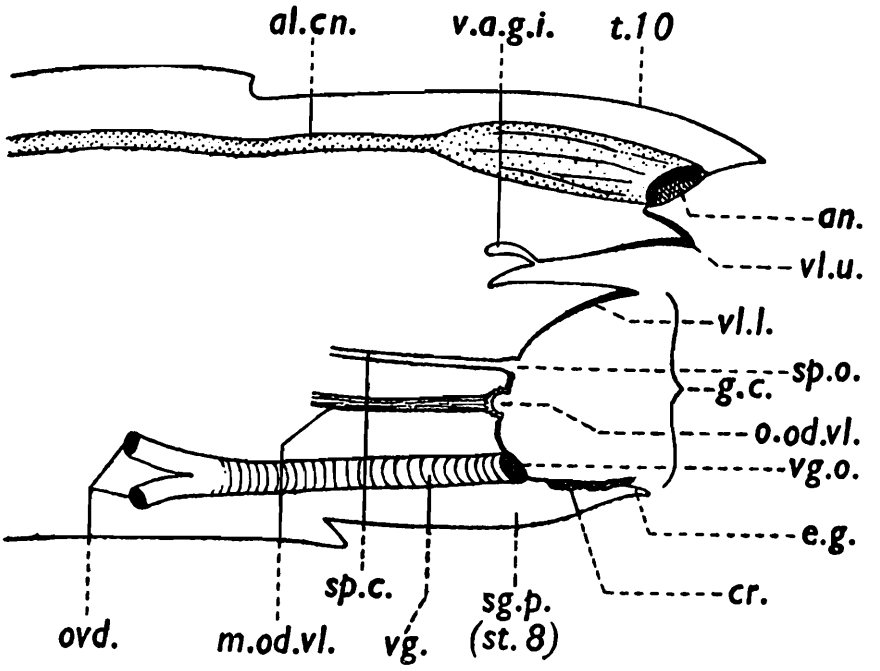
itself they merge into a mass of undifferentiated cells which constitute the *germarium* (*gr.*), the part of the ovariole with differentiated eggs being called the *vitellarium* (*vt.*). At the base of each ovariole, lying between the basal egg-follicle and the egg-calyx, there is a small *basal chamber* or *pedicel* (*pd.*). This chamber often (sometimes in all ovarioles in a female) contains (Text-fig. 4) a granular mass of orange-red pigment (Roonwal, 1945, 1949). Each egg is contained in an ovarian follicle formed by a "dipping in" of the follicular cells surrounding the egg in that region.

The apex of the ovariole is continued forward into a *terminal filament* (*t.f.*), which is a slender thread-like prolongation of the peritoneal layer of the wall of the ovariole, and obliquely meets a common *ovarian suspensorium* which supports all the ovarioles of both the ovaries. It is convenient to distinguish two regions in the ovarian suspensorium, *viz.*, (i) a *median suspensorium* (*m.s.*) where the terminal filaments of the various ovarioles join it, and (ii) a *terminal suspensorium* (*t.s.*) which is merely an anterior prolongation of the former. The terminal suspensorium is attached to the body-wall of the mesonotum just in front of the second thoracic phragma (the phragma between the meso- and metathorax) which has a notch in its body through which the suspensourium passes (Text-fig. 2). The ovarian suspensorium is thin but strong. Its terminal portion, which is about 14 mm. long, is longitudinally folded along a median line and is somewhat V-shaped in transverse section. When the ovary is young and small the terminal suspensorium is taut, but as the ovary matures and increases in size the tension on the suspensorium decreases, and in a ripe female the suspensorium sags considerably (Text-fig. 3).

The ovarioles are of the panoistic type, *i.e.*, they do not possess any special nutritive cells, each egg storing up its own nutriment. Consequently, the ripe egg is large and full of yolk. Freshly laid eggs are about 5·1-8·0 mm. long and about 0·9-1·6 mm. in maximum diameter. With the growth of the embryo they absorb water from the outside and increase in size to about 8·1-9·6 mm. in length and 1·5-2·9 mm. in width (*vide* Roonwal, 1954*b*). Although most of the ovarioles in a ripening ovary are at about the same stage of development, there are others which, due perhaps to want of space, are considerably underdeveloped, and between these two extremes all grades of development are met with. Therefore, the number of ova deposited by a female at any one oviposition may not correspond to the number of ovarioles present and may, in fact, be fewer.

The ovarioles of each side open into a common canalicular chamber, the *egg-calyx* (*e.clx.*). In a female about to oviposit, all the ripe eggs descend into the egg-calyx of its side, having migrated there form their respective ovarioles. Each egg-clayx leads posteriorly into a short (*ca.* 7-9 mm. long) oviduct, which passes beneath the apodeme of the subgenital plate (8th abdominal sternum). It then bends inwards to unite, below the alimentary canal and in the level of the anterior margin of the subgenital plate, with its fellow of the opposite side to form the *common oviduct* or *vagina* (*vg.*). The latter is a short duct, about 3-4 mm. long, and opens to the exterior near the posterior margin of the subgenital plate.

The posterior end of the subgenital plate (morphologically the 8th but actually the 7th sternum) is reflected over itself on the dorsal side (Text-fig. 5). This reflected area has a median-dorsal, chitinous, ridge-like fold which is prolonged posteriorly to form a hollow so-called *egg-guide* (*e.g.*). The vaginal opening lies at the base of the ridge just dorsal to the anterior margin of this deflection. The opening, therefore, lies in a discrete space, the *genital cavity* (*g.c.*), whose floor is formed by the chintinised deflection of the subgenital plate, the anterior wall by a vertical membrane (described below), and the roof by the bases of the lower (ventral) ovipositor valvulae. The posterior end of the genital cavity is functionally closed when the female is ovipositing, since the sub-genital plate is closely pressed against the bases of the lower valvulae—the eggs come out first at the slit between the lower valvulae and finally at the slit between the upper ovipositor valvulae. The reflected portion of the subgenital plate bears, on its inner side, a pair of frilled, crescentic and strongly chitinised areas (*cr.*) of problematic function.

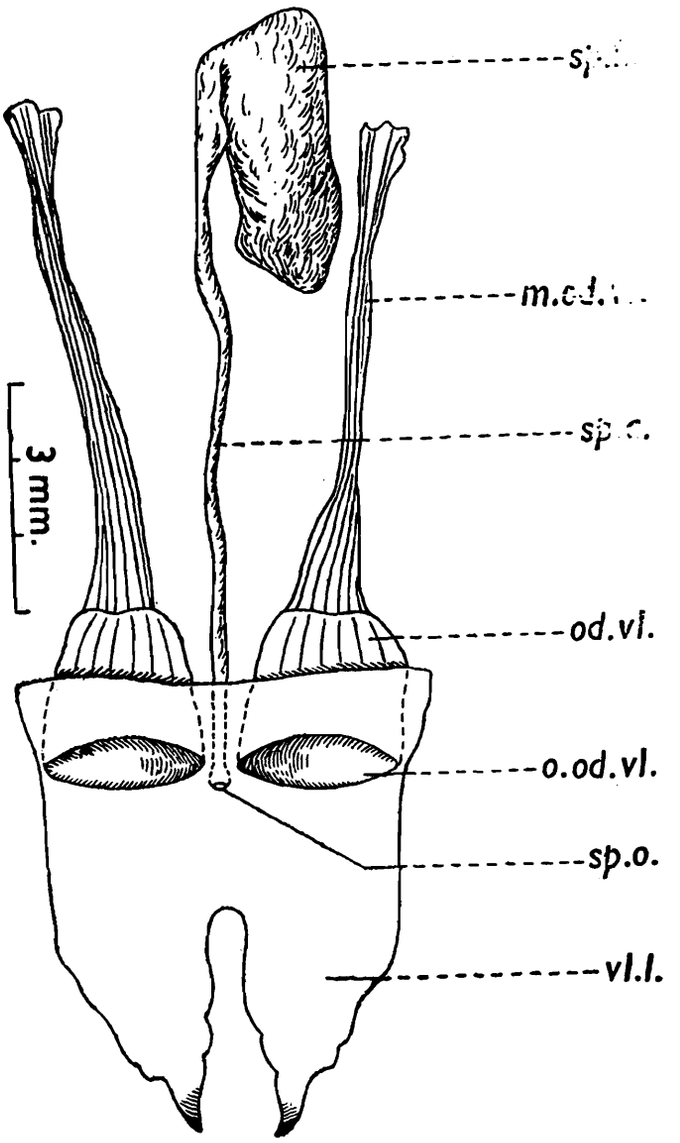


TEXT-FIG. 5.—*Schistocerca gregaria*, adult female. Longitudinal-vertical section of the posterior end of the abdomen, to show the relative position of the opening of the female reproductive organs and associated structures. Diagrammatic.

al. cn., alimentary canal ; *an.*, anal opening ; *cr.*, crescentic chitinized areas on reflected portion of subgenital plate ; *g. c.*, genital cavity ; *m. od. vl.*, muscles of oviductary vesicle ; *o. od. vl.*, opening of oviductory vesicle ; *ovd.*, paired oviduct ; *sg. p.*, subgenital plate ; *sp. c.* spermathecal canal ; *sp. o.*, spermathecal opening ; *st. 8.*, eight sternum of abdomen ; *t. 10.*, tenth tergum of abdomen ; *v. a. g. i.*, vestigeal accessory genital invagination ; *vg.*, vagina or common oviduct ; *vg. o.*, vaginal opening ; *vl. l.*, lower (ventral or anterior) valvulae of ovipositior ; *vl. u.*,upper (dorsal, posterior or lateral) vulvulae of ovipositor.

The inner or anterior margin of the above described reflection joined to the base of the lower valvulae of the ovipositor by means of a membrane which arches dorsally and posteriorly. The vaginal opening may be regarded as an aperture at the base of this membrane. On either side of the vaginal opening, this membrance is folded to form two shallow pits which are divided by a median ridge and open posteriorly.

Since they lie on either side of the female genital opening (andrium), they may be called the *paraandrial pits*. The pits do not appear to be of much morphological significance. Also in the vertical membrane, nearer the top than the base, there are a pair of nearly transverse, slit-like, apertures (Text-figs. 5 and 6) which are the openings of eversible pouches the *oviductary vesicles* (*od. vl.*). Their muscles are attached to the apodemes of the subgenital plate.



TEXT-FIG. 6.—*Schistocerca gregaria*, adult female. Dorsal view of posterior portion of abdomen, dissected to show the spermatheca and the oviductary vesicles *in situ*. Semidiagrammatic.

m. od. vl., muscles of oviductary vesicles ; *od. vl.*, oviductary vesicle ; *o. od. vl.*, opening of oviductary vesicle ; *sp. c.*, spermathecal canal ; *sp. h.*, head of spermatheca ; *sp. c.*, spermathecal opening ; *vl. l.*, lower (ventral or anterior) valvulae of ovipositor.

The oviductary vesicles were first described by Comstock & Kellog (1899) in *Melanoplus femur-rubrum*. Later, they were described in detail by Vardé in *Anacridium aegyptium* (1929) and *Schistocerca gregaria* (1934). Slifer (1936) found that out of 55 species of Acrididae examined by her, these vesicles occurred only in the subfamily Cyrtacanthacrinae, aud in none of the Acridinae, Oedepodinae and Pyrgomorphinae. According to Vardé (1929), they are new formations in the Acrididae

and are not homologous with the coxal glands of the eighth segment in the Thysanura.

2. *The female accessory glands* (boyau calicial)

There is a single pair of *female accessory glands* (*a.g.*), called "boyau calicial" by Fenard (1896). Each gland is a colourless, much-coiled "diverticulum" from the apical end of the egg-calyx and bends inwards to touch its fellow of the opposite side at the anterior tip of the ovary. In the young female the accessory glands are, like the ovaries, small and inconspicuous. They grow with maturity, and at the time of oviposition they are large and conspicuous, measuring, in the natural folded condition, about 8-12 mm. long and 0·8-0·9 mm. wide. They produce a whitish mucilaginous substance which is extruded along with the eggs at the time of oviposition and is the material which forms the basis of the "egg-pod" as well as of the "froth" over the eggs. Occasionally, the accessory gland may possess an additional pouch (Roonwal, 1935).

3. *The spermatheca*

The spermatheca is a blind, much-coiled tube which opens externally by means of a long, narrow canal into the genital cavity and serves to receive and store the sperms during coitus. The spermathecal opening (*sp.o.*) lies in a groove, between the bases of the lower ovipositor valvulae near the ventral side of the latter, in the membrane which connects the bases of the lower valvulae. This membrance is continuous with the vertical membrane mentioned previously and in which the oviductory vesicles also open. Over the groove is a chitinous arch formed by a localised thickening of the membrane. The opening leads into a small dome-shaped pouch, the *bursa copulatrix* (*br.c.*), which receives the male penis during coitus. From it a narrow, slightly sinuous canal, the *spermathecal canal* (*sp. c.*), leads inwards and ends in a coiled-up portion, the "head" (*sp.h.*) which has a tunic of connective tissue over which is a coating of fat. In the coiled condition the anterior end of the spermathecal head reaches up to the posterior end of the seventh abdominal sternum. When the head is uncoiled, the spermathecal canal is seen to end blindly (*sp.b.*), but near its blind end it gives off a blind pouch, the *seminal vesicle* (*s.v.*) where the sperms are presumably stored. The dimensions of the various portions of the spermatheca in a freshly enclosed female are approximately as follows :—

Portion of spermatheca	*Dimensions (approximate)*
1. Length of entire, coiled spermatheca (from mouth to anteriormost part of coiled mass)	7 mm.
2. Length of "head"	2·5 ,,
3. Width of "head"	1·5 ,,
4. Length of uncoiled spermatheca (from mouth to blind end, along curves, but excluding the seminal vesicle)	13·2 ,,
5. Length of uncoiled proximal portion (from mouth to opening of seminal vesicle)	11·5 ,,
6. Length of uncoiled portion distal to opening of seminal vesicle	1·7 ,,
7. Length of seminal vesicle	1·2 ,,

The width of the lumen of the spermatheca at various points varies from about 67-286μ as shown below, and it is of special interest to note that the opening by which the seminal vesicle opens into the spermathecal canal is very narrow, being only about 38μ wide :—

Portion of spermatheca	*Diameter of lumen (approximate)*
1. Bursa copulatrix (near opening) . .	276μ
2. Portion of seminal duct immediately following bursa copulatrix (for short distance only)	124μ
3. Portion of seminal duct following No. 2 (for a considerable length)	67μ
4. Portion of seminal duct following No. 3 (for a short length, posterior to opening of seminal vesicle)	124μ
5. Seminal vesicle (near its middle)	286 μ
6. Opening of seminal vesicle into spermathecal duct	38μ
7. Portion of spermathecal duct proximal to opening of seminal vesicle .	181—191μ

IV—POSTEMBRYONIC DEVELOPMENT OF INTERNAL FEMALE REPRODUCTIVE ORGANS

(Tables 1-4 ; Text-fig. 7 ; and Plates 11 and 12)

1. *General*

Developmentally considered, the female reproductive organs in *Schistocerca gregaria* may, as has been shown in another Acridid, *Locusta migratoria migratorioides* (Roonwal, 1937), and several other insects, be regarded as consisting of two portions : (i) a mesodermal portion which gives rise to all the parts of the ovary, its ducts and glands ; and (ii) an ectodermal portion which gives rise to the common oviduct or vagina and the spermatheca.

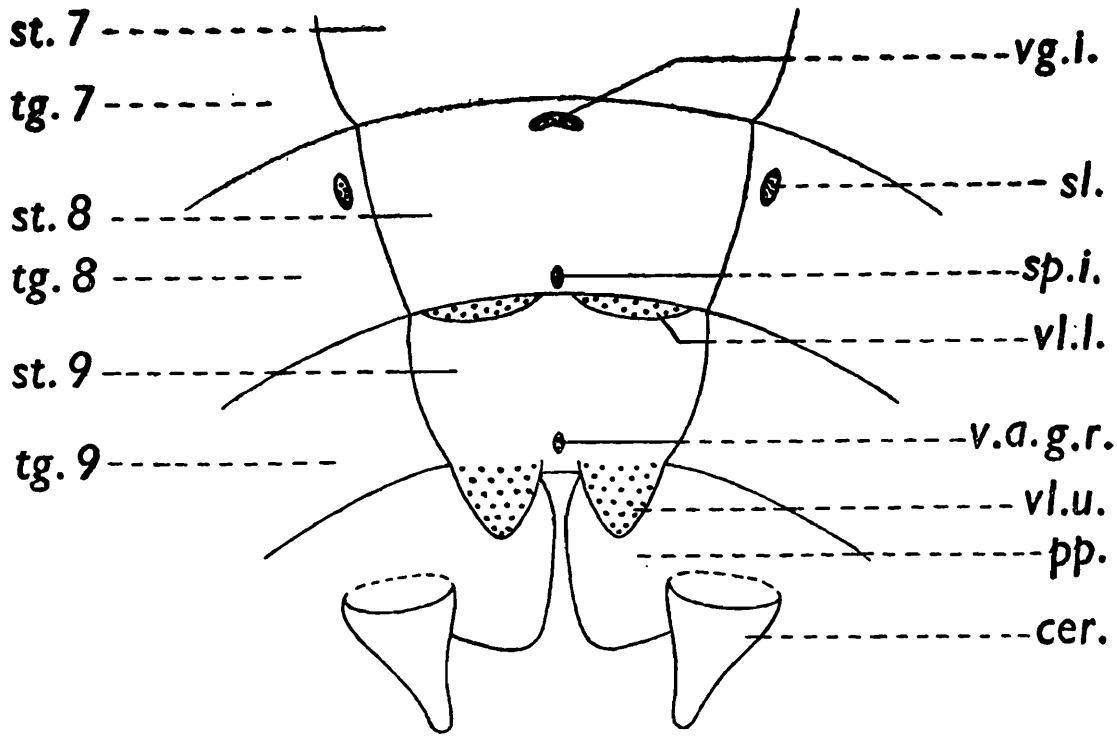
Excluding the "intermediate moult" immediately after hatching, there are normally five moults in *Schistocerca gregaria* and, consequently, five copper instars. Occasionally, one or two extra moults occur (*vide* Roonwal, 1946). The present postembryonic development was studied on the basis of the normal five moults.

2. *Condition at the time of hatching*

(Text-fig. 7 ; and Plate 11, Figs. 1-3)

At the time of hatching from the egg, the ovaries (*ov.*) consist of a flat, elongated and nearly rectangular plate of tissue, about 0·9 mm. long and 0·2 mm. wide, lying dorsal to the alimentary canal and extending from the

anterior border of the third abdominal segment to the middle of the fifth (Pl. 11, Fig. 2). On either side it is bordered by a strand of tissue, the oviduct. The two oviducts approach and meet each other beneath the alimentary canal in the region of the anterior portion of the eighth sternum. At this point there is also seen the rudiment of an ectodermal invagination, the common oviduct or vagina (*vg.i.*) whose inner end is fused with the junction of the two oviducts. Behind the vaginal invagination, near the posterior margin of the eighth sternum, there lies the rudiment of the spermathecal invagination (*sp.i.*), and behind the latter, at the posterior border of the ninth sternum between the two upper



TEXT-FIG. 7.—*Schistocerca gregaria.* Posterior end of abdomen of a freshly hatched first instar female hopper, treated with KOH and mounted on a Slide, to show the position of the female genital opening and associated structures. Semidiagrammatic.

cer., cercus ; *pp.*, paraproct ; *sl.*, last abdominal spiracle ; *sp. i*, spermathecal invagination ; *st. 7—st. 9.*, 7th to 9th sterna respectively of abdomen ; *tg.7—tg. 9.*, 7th to 9th trga respectively of abdomen ; *v. a. g. r.*, rudiment of future vestigeal accessory genital invagination ; *vg. i.*, invagination of vagina or common oviduct ; *vl. u.*, upper (dorsal. posterior or lateral) valvulae of ovipositor.

ovipositor valvulae, there lies the rudiment (*v.a.g.r.*) of the future vestigeal accessory genital invagination (*v.a.g.i.*).

The ovarioles (*ovr.*) have become differentiated and are seen attached to the median suspensorium (*m.s.*), each by means of single row of cells, the terminal filament (*t.f.*) of the ovariole. The terminal suspensorium is also present. The egg-calyx (*e.clx.*) of each side has not yet been fully differentiated from the oviduct, nor has the latter yet become extended auteriorly to form of the female accessory glands.

3. *Position of ovary in the abdomen*

TABLE 1.—Schistocerca gregaria. *Position of the ovary in the abdomen in various instars*

Stage	Extent and position of ovary in abdomen
1. First instar hopper (just hatched)	Anterior border of 3rd to middle of 5th abdominal segments.
2. Second instar hopper (just moulted)	As in first instar hopper.
3. Third instar hopper (just moulted)	Also as in first instar hopper. (In some cases, however, the anterior end lies about middle of 2nd abdominal segment.)
4. Fourth instar hopper (just moulted).	Hind portion of 3rd to middle of 5th abdominal segments.
5. Fifth instar hopper (just moulted)	Middle of 4th to anterior border of 6th abdominal segments.
6. Imago (just enclosed)	Middle of 4th to middle of 6th abdominal segments.

In the first instar hopper just hatched from the egg, the ovary extends from the anterior border of the third to the middle of the fifth abdominal segments. Thence onwards there is a gradual posterior shifting of the ovary until, in the recently enclosed imago, it extends from the middle of the fourth to the middle of the sixth abdominal segments.

4. *Differentiation of ovarioles, ova, etc.*

(a) *Number of ovarioles*

At the time of hatching, the ovary is already differentiated into ovarioles which are disposed in their characteristic position, forming a compact mass. Due to this compactly packed condition of the ovarioles and to their small size, it is difficult to count accurately their number in the first instar hopper. In a recently moulted second instar hopper, however, this number could be easily counted and was found to be 59-63 in each ovary. It was further noted that the disposition of the ovarioles along the oviducts is two or three deep.

As shown by me earlier (Roonwal, 1946), in eight hoppers of 2nd and 5th stages, the number of ovarioles in each of the paired ovaries in an individual varied from 54-68. It is noteworthy (and in striking contrast to the condition occurring in the adult) that in all cases the number in the right and left ovaries was the same in each individual. It was further shown by me that the proportion of symmetrical ovaries (with an equal number of ovarioles in the right and left ovaries) is higher in freshly eclosed young females (42 per cent) than in females nearing maturity (29 per cent). This progressive decrease in symmetry with

maturity (100 per cent in hoppers and 29 per cent in nearly mat ure females probably arises by an irregular (unequal) resorption of ovarioles in the two ovaries. This view, as shown in the above mentioned paper, finds support from the fact that while in the freshly hatched hopper all the ovarioles in an ovary are of approximately the same size, already in the fourth stage some ovarioles are markedly smaller than the others and in the ripe female about to oviposit for the first time, though the majority of ovarioles are large and contain a ripe egg, there are some which are extremely underdeveloped and do not contain a ripe egg. (For further discussion, see Roonwal, 1947, p. 382.)

(b) *Structure of the ovarioles*

The structure of the ovarioles at the time of hatching is essentially the same as in a fully developed adult female, except that definite ova have not yet been differentiated as such. Even in this early stage, three distinct regions are distinguishable as follows :—

(i) *The vitellarium* (*vt.*).—This is the basal part of the ovariole which abuts on the oviduct and contains actively dividing cells with large, lightly staining nuclei, about 13-17μ in diameter. These nuclei (*nu.o.* ; *nu. fol.*), which are the future germinal-vesicles, are arranged irregularly and not in a single row. The egg-cells are not yet differentiated. The nuclei of the follicular cells (*nu.fol.*) in this region are fewer in number and much smaller in size.

(ii) *The germarium* (*gr.*).—This is the most deeply staining portion of the ovariole and lies towards the apex. The deep-stainting property is due to the presence of a large number of small (diameter *ca.* 6·5μ) nuclei in the cells.

(iii) *The terminal filament* (*t.f.*).—The terminal filament consists of a single row of cells connecting the apex of the germarium with the median suspensorium (*m.s.*) of the ovary. The cells of the terminal filament are disc-like and are arranged close to each other in a row, with the nuclei flattened in a direction at right angles to the longitudinal axis of the ovariole. Each nucleus measures about 10μ in its maximum diameter and 4μ in the minimum.

At the time of hatching, the nuclei of the future ova are arranged irregularly and the follicular cells have not yet "dipped in" to enclose each egg separately. By the end of the first instar, however, these nuclei have marshalled themselves into a single file, starting from the base of the vitellarium, and the follicular cells have "dipped in" so as to enclose each nucleus with its surrounding cytoplasm to form a definite, closed sac. Such a body may now be called a "differentiated egg-cell" With the growth of the insect the size of the ovarioles as well as the number of differentiated egg-cells in them increase. This differentiation proceeds from the base of the ovariole upwards. At the beginning of the second instar hopper, 3-5 egg-cells are differentiated in each ovariole, and this number gradually increase with growth until it has reached about 8-12 in the freshly eclosed adult and 14-20 in an actively ovipositing female. The number of differentiated egg-cells, the average length of the ovarioles, the average dimensions of the basal and the subbasal egg-cells and of their nuclei at various stages of development are given in Table 2.

TABLE 2.—Schistocerca gregaria. *Number of differentiated egg-cells in ovarioles, length of ovarioles, demensions of egg-cells, etc., in various stages of postembryonic development.*

Stage	Number of differentiated egg-cells	Average length of ovariole	Average dimensions of basal egg-cell		Average dimensions of subbasal egg-cell		Maximum diameter of nuclei of	
			Length	Width	Length	Width	Basal egg-cell	Subbasal egg-cell
First stage (just hatched) .	None. (Differentiation occurs during this instar.)	0·088 mm.	—	—	—	—	Nuclei in vitellarium 13—17μ	
Second stage (just moulted)	3—5	0·19 mm.	44·4μ	45·2μ	35·2μ	45·9μ	28·3—32·6μ	23·9—30·5μ
Third stage (just moulted)	3—6	0·35 mm.	130·5μ	73·5μ	72·2μ	73·1μ	43·5—56·6μ	26·1—41·9μ
Fourth stage (just moulted)	5—11	0·8 mm.	150 μ	101 μ	107·7μ	93·3μ	60·9—67·4μ	47·9—60·9μ
Fifth stage (just moulted)	7—11	1·5 mm.	215·2μ	132·7μ	180·8μ	107·7μ	69·6—80·5μ	58·7—71·8μ
Imago (just eclosed)	8—12	2·4 mm.	441·3μ	151·9μ	338·5μ	164·4μ	69·6—100·1μ	65·3—100·1μ
Imago (about to lay its first batch of eggs)	12—17 (mostly 13—15)	*ca.* 8 mm.	6900 μ	1250μ	?	?	?	?
Imago which has laid thrice (would probably die in a few days)	14—20 (mostly 16—18)	*ca.* 8 mm.	6900 μ	1250 μ	?	?	?	?

By the beginning of the second instar hopper the terminal filament of the ovariole no longer consists of a single row of cells, and the nuclei are arranged irregularly. Further growth of the filament consists of an increase in the number of cells.

5. *The ovarian suspensorium*

At the time of hatching, both the median and the terminal portions of the ovarian suspensorium are present. The median suspensorium (*m.s.*) consists of a long, flat strand of tissue lying between the two ovaries. Its nuclei are generally scattered but are specially arranged at the sides where they form a row of deeply-staining bodies along either border of the suspensorium where they are met with by the terminal filaments (*t.f.*) of the ovarioles. The other nuclei stain somewhat less deeply and are slightly oblong in shape. By the beginning of the second instar the nuclei forming the edge of the median suspensorium are not distinguishable as such. Except for simple growth, no further change occurs in the structure of the median suspensorium.

The terminal suspensorium is a mere continuation of the median suspensorium and has much the same structure as the latter. The nuclei are slightly elongate, stain rather lightly and are not specially arranged along the edges. The anterior attachment of the terminal suspensorium appears in all the hopper instars, as in the imago, to be attached to the mesonotum.

6. *The oviducts, the vagina and the accessory glands*

(Table 3 ; Text-fig. 7 ; and Plates 11 and 12)

(a) *The lateral oviducts*

At the time of hatching (Pl. 11, Fig. 1), each oviduct (*ovd.*) is represented by a strand of tissue running along the outer side of the ovary of its side and continuing posteriorly to meet its fellow of the other side in the anterior region of the eight sternum where they are met by the vaginal invagination (*vg. i.*). The nuclei of these ducts stain deeply and have nearly the same appearance and size as those of the follicular cells of the ovary. There is at first no distinction between the various portions of the ovarian duct. By the beginning of the fourth instar hopper, however, the anterior region of the oviducts (lying alongside the ovaries) is seen to be more densely packed with nuclei than the posterior one and is also somewhat wider than the latter. By the end of that stage this region has become markedly thick and muscular and it ultimately becomes the egg-calyx (*e. clx.*). The posterior portion of the oviducts becomes the right and left oviducts. The entire oviduct, including the egg-calyx, of each side is about 2 mm. long in the first instar hopper and 8·3 mm. long in the freshly eclosed imago (Table 3).

TABLE 3.—Schistocerca gregaria. *Approximate length of oviduct, vagina and female accessory glands in various stages of postembryonic development.*

Stage	Length of oviduct (including egg-calyx portion)	Length of vagina (common oviduct)	Length of female accessory gland
1. First stage (just hatched)	2 mm.	Only a tiny rudiment yet	Not yet differentiated
2. Second stage (just moulted)	2·4 mm.	0·5 mm.	0·05 mm.
3. Third stage (just moulted)	2·9 mm.	0·7 mm.	0·26 mm.
4. Fourth stage (just moulted)	3·9 mm.	1·4 mm.	0·9 mm.
5 Fifth stage (just moulted)	6·1 mm.	2·1 mm.	1·9 mm. (Folds not yet acquired)
6. Fifth stage (about to moult)	——	——	2·2 mm. (Folds acquired)
7. Imago (just eclosed)	8·3 mm.	3·1 mm.	3·1 mm.
8. Imago (about to lay eggs)	2.6 mm	——	8·1 mm.

(b) *The vagina (common oviduct)*

At the time of hatching (Pl. 11) the common oviduct or vagina forms a small median invagination of the body-wall in the anterior region of the eight sternum and meets the two oviducts in that region. It grows rapidly and measures about 0·5 mm. in length at the beginning of the second instar hopper, about 2·1 mm. at the beginning of the fifth and 3·1 mm. in the just enclosed imago (Table 3). With growth, the position of the vaginal opening (*vg.o.*) undergoes a shifting posteriorward. While its primary position (at the time of hatching) is in the anterior region of the eight sternum and about 0·44 mm. distant from the spermathecal opening (which lies near the posterior margin of the eight sternum), by the beginning of the second instar hopper the distance is reduced to about 0·25 mm. and by the beginning of the third it has shifted to the posterior border of the same sclerite in close proximity to the spermathecal opening.

The first step towards this displacement of the vaginal opening is the backward extension, in the later part of the first instar hopper, of the vaginal tissue as a narrow slip from either side of the original vaginal rudiment. During the later stages this process is simply carried a step farther. However, the exact mode of the posterior shifting of the vaginal opening itself is not clear. By the end of the fourth instar hopper, the opening of the vagina lies on the inner, reflexed border of the eighth sternum—the floor of the future genital cavity. This condition is maintained in the imago. At the beginning of the fifth instar hopper, the portion of the intersegmental membrane between sterna 8 and 9, anterior to the origin of the lower ovipositor valvulae, begins to extend itself, and by the end of that instar the membrane becomes considerably extended. As a result, the proximity of the vaginal and the spermathecal openings is no longer maintained and the two openings again become widely spaced apart.

(c) *The female accessory glands* (boyau calicial)

The female accessory glands or *boyau calicial* (*a.g.*) are formed as forward outgrowth of each egg-calyx anterior to the base of the first (anteriormost) ovariole. At the time of hatching, the outgrowth is absent ; it is formed during the first instar. At the beginning of the second instar hopper the outgrowth is about 0·05 mm. long, and thence onwards it grows rapidly (Table 3). In the recently moulted fifth instar hopper

the accessory glands have not yet acquired their characteristic folds, but by the end of that instar folds have been developed. The glands attain their maximum development just prior to egg-laying when they measure about 8-12 mm. in length in the "unfolded" condition.

7. *The spermatheca*

(Table 4 ; Text-fig. 7 ; and Plates 11 and 12)

At the time of hatching (Pl. 11, Figs. 1 and 2) the rudiment of the spermathecal invagination (*sp.r.*) is seen as a small, rounded median mass of actively dividing cells on the eighth sternum close to its posterior border and about 0·44 mm. behind the vaginal invagination. By the beginning of the second instar hopper (Pl. 11, Fig. 4), this distance has become reduced to about 0·25 mm. by the backward extension of the vaginal tissue, and the spermatheca has approached the posterior margin of the eight sternum. At the beginning of the third instar hopper (Pl. 12, Fig. 4) the spermathecal rudiment consists of an anterior ball-shaped portion (*sp.a.*) representing the coiled spermathecal "head" round which a connective tissue coating is evident, and a narrow posterior portion (*sp.p.*) representing the posterior portion of the spermathecal canal. In the natural, coiled position the spermatheca now measures about 0·22 mm. in length. It is to be noted that its position has by now shifted from the posterior margin of the eighth sternum to the intersegmental membrane between sterna 8 and 9. Also, as already stated, due to the backward extension of the vaginal tissue, the vaginal and spermathecal openings have become approximated but remain separate.

By the end of the third instar hopper (Pl. 12, Fig. 5) the spermatheca has become greatly elongated and has also developed a small pouch-like outgrowth, the seminal vesicle (*s.v.*) near its blind inner end (*sp.b.*). The posterior end of the spermathecal canal near its opening to the exterior (*sp.o.*) has also become slightly enlarged to form the bursa copulatrix (*br.c.*). Changes in the fourth (Pl. 12, Figs. 6 and 7) and fifth instar hoppers consist of a lengthening of the spermatheca, a thickening of its internal chitinous lining and a clear differentiation of its connective tissue tunic into an inner muscular and an outer fatty portion. Subsequent development consists in little else but increase in size. Measurements of the spermatheca in various stages are given in Table 4.

TABLE 4.—Schistocerca gregaria. *Length, etc., of spermatheca and vestigeal accessory genital invagination in various stage of postembryonic development.*

Stage	Spermatheca		Vestigeal accessory genital invagination	
	Length in natural (coiled) condition. (Straight distance from spermathecal opening to the most anterior end of coiled mass.)	Length in uncoiled condition. (Total length along curves, from spermathecal opening to blind end, but excluding the seminal vesicle.)	Length	Width (maximum)
1. First instar (just hatched)	Only a small rudiment	——	A tiny rudiment	——
2. Second instar (just moulted)	0·12 mm. rudiment	——	Very small	——
3. Third instar (just moulted)	0·22 mm. rudiment	——	80μ	16μ
4. Fourth instar (just moulted)	8·0 mm. rudiment	2·3 mm.	173μ	20μ
5. Fifth instar (just moulted)	2 mm. rudiment	4·8 mm.	400 μ	40μ
6. Adult (just enclosed)	7 mm. rudiment	13·2 mm.	1360μ	88μ

8. *The vestigeal accessory genital invagination*

(Table 5 ; and Plate 11, Fig. 1)

Between the upper ovipositor valvulae on the ninth sternum there is seen, in the recently hatched hopper, a mass of cells (*v.a.g.r.*) looking very much like the spermathecal rudiment but much less developed than the latter. It grows very slowly as compared to the spermathecal rudiment and develops an invagination in the beginning of the third instar hopper. It persists in the adult as a small vestigeal accessory genital invagination between the inner or middle ovipositor valvulae. Its length is about 80μ at the beginning of the third instar hopper when the invagination is first clear, 400μ at the beginning of the fifth instar and 1960μ in the freshy enclosed imago (Table 4). The structure does not develop further and remains vestigeal.

9. *Discussion*

(a) *Number of ovarioles*

There is some indication to suggest that the number of ovarioles found in the first instar hopper at the time of hatching represents the full quota for that individual, and subsequent development consists not in an increase in number but rather in a decrease due to resorption of the ovarioles caused presumably by overcrowding. This is suggested by their initially large number and also by their symmetry in the young hoppers. Furthermore, all the ovarioles in the younger hopper stages (first to third) are, in each stage, almost identical in development in each individual. Already in the fourth stage hopper it is seen that some of the ovarioles are distinctly smaller than the others. This phenomenon is accentuated with growth and is very marked in the maturing imago.

(b) *The genital ducts and their openings*

Both Qadri (1940, for *Locusta migratoria*) and Gupta (1950, for *Schistocerca gregaria*) have stated that the median external opening of the common oviduct or vagina is first developed in the intersegmental membrane between the abdominal sterna 8 and 9, but embryos were not studied. On the other hand, I have found in these very insects (Roonwal, 1937 for *Locusta* ; and the present account for *Schistocerca*) that in the freshly hatched first instar hopper the vaginal opening lies at the anterior end of the eighth sternum. It is obvious that this difference can only be resolved by a careful study of embryos. It is, however, clear that subsequently during postembryonic development, the position of the vaginal opening undergoes a shifting posteriorward until it comes to lie at the posterior margin of the eighth sternum. This displacement of the vaginal opening from an initially anterior position was also observed by Nel (1929) in Acridids of the genera *Locustana* and *Colemania*.

(c) *The spermatheca and the vestigeal accessory genital invagination*

The spermathecal opening both in *Locusta migratoria* (Roonwal, 1937) and in *Schistocerca gregaria* (Roonwal, 1946 ; and present account ; and Gupta, 1950) is quite separate from the opening of the vagina or common oviduct. The curious statement of Qadri (1940, p. 156) that in *Locusta migratoria* the spermatheca "opens on the common oviduct" is certainly an error.

The vestigeal accessory genital invagination on the ninth sternum evidently corresponds to a similar structure described by Nel (1929) in the Acridids *Locustana* and *Colemania* as arising on the ninth sternum and developing slowly, exactly as in *Schistocerca gregaria* where it was correctly described by Gupta (1950).

V—SUMMARY

1. The internal female reproductive organs (the ovaries and their ducts, the female accessory glands and the spermatheca) in the adult of the Desert Locust, *Schistocerca gregaria* Forskal (Orthoptera : Acrididae) are described in detail.

2. The postembryonic development of these structures is also studied from the moment of hatching from the egg to the ripening of the adult female.

3. The ovary, which in the freshly hatched hopper lies from the anterior border of the 3rd to the middle of the 5th abdominal segments, occupies a position from the middle of the 4th to that of the 6th abdominal segment in the freshly enclosed imago.

4. The number of ovaries is already large, about 59-63, in the freshly moulted second instar hopper and probably represents the full quota for that individual. This number in the right and left ovaries in an individual is symmetrical up to the 5th instar hopper, but thereafter a symmetry develops in the imago (due presumably to resorption of some ovarioles) and increases progressively as the female matures.

5. The structure and development of the ovarioles are described. Even in the freshly hatched first instar hopper, three parts are distinguishable in an ovariole, *viz.*, a basal vitellarium, a distal germarium and a terminal filament.

6. The ovary is attached to the dorsal body-wall by a long ovarian suspensorium.

7. The two oviducts are already well developed in the freshly hatched first instar hopper. The portion of the duct abutting on the ovaries becomes differentiated into a thick-walled egg-calyx by the end of the fourth instar hopper.

8. At the time of hatching, the median external opening of the common oviduct or vagina is situated at the anterior end of the 8th abdominal sternum. In subsequent hopper stages it shifts posteriorly and ultimately comes to lie on the posterior margin of that same sclerite.

9. The female accessory glands (*boyau calicial*) are first differentiated in the first instar hopper from the anterior end of the oviducts. The glands attain their maximum development in the adult just prior to egg-laying.

10. The rudiment of the spermathecal invagination is first seen in the freshly hatched first instar hopper on the posterior border of the 8th abdominal sternum. Thereafter it grows rapidly.

11. A vestigeal accessory genital invagination is first clearly developed on the 9th abdominal sternum in the 3rd instar hopper though its rudiment, as a cell-mass, is seen in the same position in the beginning of the first instar.

VI—REFERENCES

AGARWALA, S.B.D. 1952*a*. A comparative study of the ovipositor in Acrididae. I.—*Indian J. Ent.*, New Delhi, **13**(2) [Dec 1951], pp. 147-181.

AGARWALA, S.B.D. 1952*b*. A comparative study of the ovipositor in the Acrididae. II [in part].—*Indian J. Ent.*, New Delhi, **14** (1), pp. 61-75.

AGARWALA, S.B.D. 1953. A comparative study of the ovipositor in the Acrididae. II (*contd.*).—*Indian J. Ent.*, New Delhi, **15** (1), pp. 53-69.

ANDER, K. 1956. Orthoptera Saltatoria. *In* S.L. TUXEN (ed. by) : *Taxonomist's Glossary of Genitalia in Insects*, pp. 53-62.—Copenhagen (E. Munksgaard).

COMSTOCK, J. H. and KELLOG, V L. 1899. *The Elements of Insect Anatomy*. (Revised ed.). 134 pp.—New York (Comstock Publ. Co.).

FÉNARD, A. 1896. Recherches sur les annexes internes de l'appareil génital femelle des Orthoptères.—*C.R. Acad. Sci. Fr.*, Paris, **122**, pp. 1137-1139.

FÉNARD, A. 1897. Recherches sur les organes complémentaires internes de lappareil génital des Orthoptères.—*Bull. Sci. Fr. Belg.*, Paris, **29**, pp. 390-532, 4 pls.

GUPTA, P.D. 1950. On the structure, development and homology of the female reproductive organs in Orthopteroid insects.—*Indian J. Ent.*, New Delhi, **10** (1) [1948], pp. 75-123.

HEBERDEY, R.F. 1931. Zur Entwicklungsgeschichte, vergleichenden Anatomie und Physiologie der weiblichen Geschlechtsausführwege der Insekten.—*Z. Morph. Ökol. Tiere*, Berlin, (A) **22** (2-3), pp. 416-586.

KARANDIKAR, K.R. 1942. External structures of the Desert Locust (*Schistocerca gregaria* Forsk.) [II].—*J. Univ. Bombay*, Bombay, (N. S.) **9** (3), pp. 1-29.

NEL, R.I. 1929. Studies on the development of the genitalia and the genital ducts in insects. I. Female of Orthoptera and Dermaptera.—*Quart. J. micr. Sci.*, London, **73**(1), pp. 26-85, 4 pls.

NELSON, O.E. 1931. The development of the ovary in the grasshopper *Melanoplus differentialis* (Abstract).—*Anat. Rec.*, Philadelphia, **51,** Suppl., p. 76.

NELSON, O.E. 1934*a*. The development of the ovary in the grasshopper *Melanoplus differentialis* (Acrididae, Orthoptera).—*J. Morph.*, Philadelphia, **55**, pp. 515-543 (6 pls.).

NELSON, O.E. 1934*b*. The segregation of the germ cells in the grasshopper *Melanoplus differentialis* (Acrididae, Othroptera).—*J. Morph.*, Philadelphia, **55,** pp. 545-575 (4 pls.).

QADRI, M.A.H. 1940. On the development of the genitalia and their ducts in Orthopteroid insects.—*Trans. R. ent. Soc. Lond.*, London, **90** (6), pp. 121-175, 7 pls.

ROONWAL, M.L. 1935. An abnormality in the *boyau calicial* (female accessory glands) of the Desert Locust, *Schistocerca gregaria* Forsk.—*Nature*, London, **135,** pp. 394-395.

ROONWAL, M. L. 1936. Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* R. and F.—I. The early development with a new theory of multiphased gastrulation among insects.—*Philos. Trans. roy. Soc. Lond.*, London, (B) **226** (538), pp. 391-421, 3 pls.

ROONWAL, M.L. 1937. Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* Reich. and Frm. II. Organogeny. (Orthoptera, Acrididae).—*Philos. Trans. roy. Soc. Lond.*, London, (B) **227** (543), pp. 174-244, 7 pls.

ROONWAL, M.L. 1945. Presence of reddish pigments in eggs and ovarioles of the Desert Locust, and its probable phase significance.—*Nature*, London, **156,** p. 19.

ROONWAL, M. L. 1946. Studies in intraspecific variation. II. New rules governing the correlation between normal- and extra-moulting and directional reversal of the elytron-wing complex in the Desert Locust and other Acrididae (Orthoptera).—*Indian J. Ent.*, New Delhi, **7** (1 & 2) [Dec. 1945], pp. 77-84.

ROONWAL, M. L. 1947. On variation in the number of ovarioles and its probable origin in the Desert Locust, *Schistocerca gregaria* (Forskal) (Orthoptera, Acrididae).—*Rec. Indian Mus.*, Delhi, **44** (4) [1946], pp. 375-384.

ROONWAL, M.L. 1949. On reddish pigments in eggs, ovarioles, embryonic eyes, etc. in the Desert Locust, *Schistocerca gregaria* (Forskal) (Orthoptera, Acrididae).—*Indian J. Ent.*, New Delhi, **8** (2) [1946], pp. 186-194.

ROONWAL, M.L. 1954*a*. The egg-wall of the African Migratory Locust, *Locusta migratoria migratorioides* Reich. and Frm. (Orthoptera, Acrididae).—*Proc. nation. Inst. Sci. India*, New Delhi, **20** (4), pp. 361-370, 2 pls.

ROONWAL, M.L. 1954*b*. Size, sculpturing, weight and moisture content of the developing eggs of the Desert Locust, *Schistocerca gregaria* Forskal (Orthoptera, Acrididae).—*Proc. nation. Inst. Sci. India*, New Delhi, **20** (4), pp. 388-398, 2 pls.

SNODGRASS, R.E. 1931. Morphology of the insect abdomen. Pt. I. General structure of the abdomen and its appendages.—*Smithson. misc. Coll.*, Washington, **85** (6), pp. 1-128.

SNODGRASS, R. E. 1933. Morphology of the insect abdomen. Pt. II. The genital ducts and the ovipositor.—*Smithson. misc. Coll.* Washington, **89** (8), pp. 1-148.

SNODGRASS, R.E. 1935*a*. *Principles of Insect Morphology*. ix+666 pp. —New York & London.

SNODGRASS, R.E. 1935*b*. The abdominal mechanisms of a grasshopper —*Smithson. misc. Coll.*, Washington, **94** (6), pp. 1-89.

SLIFER, E.H. 1936. An internal structure in the Cyrtacanthacrinae (Orthoptera, Acrididae) of possible taxonomic value.—*J. New York, ent. Soc.*, New York, **44**, pp. 345-348.

SLIFER, E.H. 1940. The internal genitalia of Omexechinae and Cyrtacanthacridinae (Orthoptera, Acrididae).—*J. Morph.*, Philadelphia, **67**, pp. 199-239 (2 pls.).

TUXEN, S.L. (Ed. by.) 1956. *Taxonomist's Glossary of Genitalia in Insects*. 284 pp., 215 figs.—Copenhagen (E. Munksgaard).

VARDÉ, V.P. 1929. Contribution a létude morphologique et éthologique des Orthoptères Acridide. I. Les vésicules oviductaires de *Anacridium aegyptium*.—*Bull. Soc. zool. Fr.*, Paris, **54** (3), pp. 477-483.

VARDÉ, V.P. 1934. The protrusible vesicles in Cyrtacanthacrinae-Acridiinae (Orthoptera).—*J. Univ. Bombay*, Bombay, (N.S.) **2** (5), pp. 53-57.

WALKER, E.M. 1919. The terminal abdominal structures of Orthopteroid insects. A phylogenitic study. [Pt. 1.]—*Ann. ent. Soc. Amer.*, Columbus, **12**, pp. 267-316, 9 pls.

WALKER, E.M. 1922. The terminal abdominal structures of Orthopteroid insects. A phylogenitic study. Pt. 2.—*Ann. ent. Soc. Amer.*, Columbus, **15**, pp. 1-75, 11 pls.

LETTERING USED IN PLATES

a.g., female accessory glands (*boyau calcial*).

al. cn., alimentary canal.

an., anal opening.

br. c., bursa copulatrix.

cer., cercus.

cr., crescentic chitinized areas on reflected portion of subgenital plate.

c. vg., cells in continuation of vaginal cells.

e., egg or ovum.

e. clx., egg-calyx.

ed. phr., endo-phargma.

e.g., egg-guide.

gan., ganglion of ventral nerve cord.

g.c., genital cavity.

gr., germarium.

ints. 8/9, intersegmental region between abdominal sterna 8 and 9.

mem., membrane.

m.g., mid-gut wall.

m. od. vl., muscles of oviductary vesicle.

m.s., median suspensorium of ovary.

m.t., Malpighian tubules.

nt., notch.

nu. f.o., nuclei of future ova.

nu. fol., nuclei of follicular cells.

nu. o., nuclei of ova.

od. vl., oviductary vesicles.

o. od. vl., opening of oviductary vesicle.

or., mass of orange-red pigment.

ov., ovary.

ova. paired oviduct.

ovr., ovarioles.

pd., pedicel or basal chamber of ovariole.

pp., paraproct.

rt., rectum.

sa. p., supraanal plate.

sg. p., subgenital plate.

sl., last abdominal spiracle.

sp., spermatheca.

sp. a., anterior end of spermatheca.

sp. b., blind end of spermatheca.

sp. c., canal of spermatheca.

sp. h., head of spermatheca.

sp. i., spermathecal invagination.

sp. o., spermathecal opening.

sp. p., posterior end of spermatheca.

sp. r., rudiment of spermatheca.

st. 2.—*st.* 9, second to ninth sterna respectively of abdomen.

s.v., seminal vesicle.

t.f., terminal filament of ovariole.

tg., tergum.

tg. 4—*tg.* 9, fourth to nin th terga respectively of abdomen.

t.s., terminal suspensorium of ovary.

t.v.t., transverse-ventral tracheal trunk of its segment, in cross-section.

v.a.g.i., vestigeal accessory genital invagination.

v.a.g.r., rudiment of vestigeal accessory genital invagination.

vg., vagina or common oviduct.

vg.d., deep-staining portion of vaginal rudiment.

vg.i., invagination of vagina or common oviduct.

vg.l., light-staining portion of vaginal rudiment.

vg.o., opening of vagina or common oviduct.

vg.r., rudiment of vagina or common oviduct.

vl.i., inner (middle) valvulae of ovipositor.

vl.l., lower (ventral or anterior) valvulae of ovipositor.

vl.u., upper (dorsal or posterior) valvulae of ovipositor.

vt., vitellarium.

y., yolk spheres in mid-gut.

y.c., yolk cells in mid-gut.