EARLY EMBRYOLOGY OF THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSKÅL). [ORTHOPTERA, ACRIDIDAE.]

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(Plates III-VI.)

CONTENTS.

INTRODUCTION.

The embryology of the Orthoptera, which are among the most primitive of the living Pterygota, is of considerable importance in throwing light upon the many disputed questions of insect development. The Desert Locust, *Schistocerca gregaria* (Forskål) (Fam. Acrididae), was chosen as the subject of study firstly, because of the ready availability of material; and secondly, because of the great economic importance of this insect.

The embryology of only two species of Acrididae, namely, *Stenobothrus* sp. (Graber 1888-1891*a*) and the African Migratory Locust, *Locusta migratoria migratorioides* (R. & F.) (Roonwal, 1935-1939*b*) has been studied more or less fully. In a third species, *viz.*, the Differential Grasshopper of N. America, *Melanoplus differentialis* Uhl., certain aspects of embryology have been studied by a number of workers thus : Sex differentiation and development of the gonads by Nelsen (1931-1934*a*); external morphology of the embryo, blastokinesis and the function of pleuropodia by Slifer (1931-1938*a*); egg-maturation and cleavage by Slifer and King (1934) ; the development of the male genitalia by Else (1934) ; the development of the mid-gut by Stuart (1935); and the development of the nervous system by Baden (1936). Packard (1883) had long ago studied a few aspects of the embryology of the Rocky Mountain Locust, *Melanoplus spretus* Walsh. The development of the external form of embryos has been recently described by Jannone (1940) in the Moroccan Locust, *Dociostaurus maroccanus* (Thunb.), and by Steele [Andrewartha] (1941) in the Australian grasshopper, *Austroicetes cruciata* Sauss. Husain and Roonwal (1933) have studied the structure of the egg-wall and the micropylar apparatus in *Schistocerca gregaria* and a number of other Acrididae.

In the present paper on *Schistocerca gregaria* I have described firstly, the external form of the embryos from the moment of the first formation of the germ band until hatching, recognizing, in all, 18 stages for convenience of reference. Secondly, the peculiar bi-triangular concentration of the cephalic appendages towards the medial line is described and the law recently given by Roonwal (1939) concerning that phenomenon is confirmed. Finally, the origin and early development of the coelom is described. The ultimate fate of the coelomic cavities and other aspects of organogeny will be presented in a subsequent paper. Cleavage and gastrulation were not studied, as suitable developmental stages were not available.

This work was carried out in the Department of Zoology, Lucknow University, Lucknow, during the author's tenure of a University Research Fellowship for the years 1943 and 1944. I am deeply grateful to Prof. K. N. Bahl for working facilities and every form of encouragement. To Major M. L. Roonwal of the Zoological Survey of India I am grateful for placing at my disposal his entire material of fixed eggs and embryos that he had collected earlier and for valuable help and suggestions in the course of my work. My thanks are also due to Dr. B. N. Chopra, Offg. Director, Zoological Survey of India, for library and other facilities on many occasions, and to Dr. G. B. Banerjea, Principal, Government College, Sambalpur, Orissa, for various facilities during the latter part of this work.

MATERIAL AND METHODS.

The material for this work consisted of a large collection of well fixed eggs and embryos of various stages made several years ago in Baluchistan by Major M. L. Roonwal who also kindly supplied the following information regarding them : " The eggs were laid in sand in laboratory cages and were allowed to develop under semi-natural conditions; individual eggs were removed from the pod at desired intervals, and the embryos dissected out and fixed. The fixatives employed were hot alcoholic Bouin's fluid for the younger eggs, aqueous Bouin's fluid for the younger embryos, and Carnoy's fluid (Formula No. 2) for the older eggs and embryos. The fixed material was preserved in 90-95 per cent. alcohol." When examined for study after nearly 7 years, it was found to have undergone no deterioration, and whole embryos and sections stained excellently. Up to blastokinesis, the age of the embryos in the original material was indicated in days. Since however, the eggs were incubated under varying conditions, a reference scale of embryos, with 18 stages in all, was drawn up from selected whole mounts, in order to obtain comparable stages. In the post-blastokinesis period, when differentiation is comparatively slow, the age is also referred to in terms of the number of days from the moment of blastokinesis, as indicated in the original material. Embryos were embedded in paraffin wax (M. P. 52° C.) for 2 to 10 minutes, depending on size, and sections 8 to 10μ thick were cut. The sections were stained with Delafield's haematoxylin and orange G,

REFERENCE SCALE OF EMBRYONIC STAGES.

(Plate III, Figs. 14-22 ; and Pl. IV, Figs. 23-31.)

Eighteen stages were recognized from the early formation of the germ band until hatching. The actual specimens in the reference scale consisted of stained whole mounts of embryos up to blastokinesis (Stages 1-12), and, thereafter, of spirit specimens, each stage being represented by a single embryo. All other embryos, whether for section-cutting or any other purpose, were referred to this standard scale. The distinguishing morphological characteristics, especially external, of the various stages are briefly described below ; some measurements are also given in Table I.

Stage 1 (Pl. III, Fig. 14). The germ band is differentiated into a protocephalon and a protocorm only, and is about 0·8 mm. long.

Stage 2 (Pl. III, Fig. 15). The embryo is similar to Stage 1, but is now about 1·3 mm. long.

Stage 3 (Pl. III, Fig. 16). The protocorm is now differentiated into 3 apparent segments—the anterior, posterior and middle—, thus making, along with the protocephalon, 4 segments in the embryo. This segmentation evidently corresponds to the primary segmentation in *Locusta* (Roonwal, 1936*a*), and later leads to the definitive body segmentation. The embryo is about 1·6 mm. long.

Stage 4 (Pl. III, Fig. 17). The mesodermal rudiments of the labrum and the antennae, and the rudiments of the eyes and the stomodaeum are developed on the protocephalon. The protocorm is now divisible into two parts—a broad anterior half comprising the 3 jaw and the 3 thoracic segments ; and a narrow posterior half comprising the abdomen. In the former the rudiments of the mandibles, the first and second maxillae and the three thoracic legs are seen, while in the latter the rudiments of the first two abdominal appendages are visible. The embryo is about 1·7 mm. long.

Stage 5 (Pl. III, Fig. 18). The rudiments of the various appendages of Stage 4 have now grown into lateral evaginations, and the early rudiments of the third and fourth abdominal appendages are seen. The stomodaeum first appears in this stage. The embryo is about 2 mm. long.

Stage 6 (Pl. III, Fig. 19). The stomodaeal invagination is deepened and is about 0·08 mm. long. The early rudiments of the fifth and sixth abdominal appendages are now visible. The embryo is about 2·4 mm. long.

Stage 7 (Pl. III, Fig. 20). The stomodaeum is about 0·12 mm. long. The first six abdominal appendages are now in the form of lateral outgrowths, and the early rudiments of the seventh and eighth abdominal appendages are visible. The proctodaeal invagination makes its appearance. The embryo is about 2·5 mm. long.

Stage 8 (Pl. III, Fig. 21). The stomodaeum is about 0·14 mm. long. The body appendages are considerably elongated but not yet segmented. The first pair of abdominal appendages or pleuropodia are now much larger than the remaining abdominal appendages. The rudiments of the seventh, eighth, and ninth pair of abdominal appendages now appear. The proctodaeum elongates and is about 0·16 mm. long. The embryo is about 2·6 mm. long.

Stage 9 (Pl. III, Fig. 22). The labrum has now shifted to the ventral side and covers the oral aperture. The stomodaeum measures about 0·32 mm. and the proctodaeum about 0·26 mm. in length. The jaw and thoracic appendages exhibit segmentation. In the first maxillae the rudiments of the lacina, galea and maxillary palps are differentiated; in the second maxillae the palps are distinguishable; the thoracic legs show differentiation into 5 joints, thus: joint representing the combined segments of the subcoxa, coxa and trochanter; femur; tibia; tarsus; and the terminal joint. All the eleven abdominal appendages are now developed. The embryo is about 2·9 mm. long.

Stage 10 (Pl. IV, Fig. 23). The stomodaeum measures about 0·38 mm. and the proctodaeum about 0·36 mm. in length. The thoracic appendages, especially the metathoracic ones, have grown considerably. The embryo is stouter and broader and measures about 3 mm. in length.

Stage 11 (Pl. IV, Fig. 24). The stomodaeum is about 0·44 mm. and the proctodaeum 0·5 mm. long. The two labial appendages have shifted close to each other in the median line prior to complete fusion. The pleuropodia are considerably enlarged. The embryo measures about 3·1 mm. in length.

Stage 12 (Pl. IV, Fig. 25). Blastokinesis occurs in this stage, and the embryo is bent double into a U-shape before turning round completely. The mouth-parts tend to concentrate around the oral aperture. The embryo is about 3·5 mm. long.

The remaining stages are timed in days after blastokinesis.

Stage 13 (Pl. IV, Fig. 26), one day after blastokinesis. The head thorax and abdomen are clearly demarcated from one another. The two compound eyes are very large and prominent and show the beginning of pigmentation (*vide* Roonwal, 1947*a*, p. 170). The tarsal joint of the thoracic legs becomes differentiated into its components. All the abdominal appendages disappear with the exception of the pleuropodia (1st), the 7th and those forming the genitalia (8th and 9th in females; and 9th and 10th in males) and the cerci (11th in both sexes). All along the anterior part of the abdomen a pair of closely apposed nerve cords with ganglia can be seen through the transluscent wall of the embryo. The embryo is about 4 mm. long.

Stage 14 (Pl. IV, Fig. 27), two days after blastokinesis. The ganglionic rudiments of the ventral nerve cord can be clearly seen up to the posterior end of the abdomen. It is possible at this stage to easily differentiate the sexes by means of differences in the genitalia. The embryo measures about 5·2 mm. in length.

Stage 15 (Pl. IV, Fig. 28), three days after blastokinesis. The terminal tarsal joint of the thoracic legs develops a pair of claws. The genitalia become better defined. The embryo measures about 5·6 mm. in length.

Stage 16 (Pl. IV, Fig. 29), six days after blastokinesis. The embryo has grown considerably and now measures about 7·2 mm. in length. The hind-femur is greatly elongated and the genitalia are prominent.

TABLE 1.

Measurements of embryos, in mm.

Stage No.	1	2	3	4	5	6	7	8	9	10	11	12*	13	14	15	16	17	18
Total length of embryo	0·8	1·3	1·6	1·7	2·0	2·4	2·5	2·6	2·9	3·0	3·1	3·5	4·0	5·2	5·6	7·2	8·7	9·0
Width of protocephalon (later, head in level of eyes).	0·5	0·6	0·7	0·6	0·5	0·6	0·7	0·7	0·9	1·1	0·8	1·4	1·5	1·6	1·4	1·3	1·4	1·4
Length of protocorm (later, thorax plus abdomen)	0·6	0·9	1·2	1·5	1·7	2·2	2·3	2·3	2·4	2·6	2·8	2·7	3·2	4·2	4·4	5·5	6·9	7·0
Length of thorax	..	..	..	0·6	0·8	0·8	0·8	1·1	1·0	1·1	1·1	0·8	0·8	1·0	1·0	1·0	1·1	1·5
Length of abdomen	..	..	..	0·8	0·9	1·4	1·4	1·2	1·4	1·5	1·7	1·9	2·4	3·2	3·4	4·5	5·7	5·5
Width of anterior region of protocorm (just posterior to 2nd thoracic legs).	0·3†	0·3†	0·36†	0·4	0·2	0·3	0·3	0·5	0·7	0·8	0·8	1·0	1·2	1·4	1·4	1·5	1·9	2·0
Width of posterior region of protocorm (in level of 4th abdominal segment).	0·3†	0·3†	0·36†	0·2	0·2	0·2	0·2	0·4	0·7	0·7	0·6	0·8	1·0	1·6	1·4	1·6	1·7	1·7
Vertical length of eye	..	..	..	..	..	..	..	..	..	..	..	0·57	0·63	0·65	0·65	0·7	0·95	1·3
Length of hind-femur	..	..	..	..	..	..	..	..	..	..	..	0·5	0·96	1·1	1·1	2·5	2·9	3·3

*Blastokinesis.

†In stages 1-3, these two regions are not distinguishable.

Stage 17 (Pl. IV, Fig. 30), eight days after blastokinesis. The embryo measures about 8·7 mm. in length. Spines appear on the metathoracic tarsi.

Stage 18 (Pl. IV, Fig. 31), hatching. The embryo is about 9·0 mm. long.

LAW OF MEDIAL SHIFTING OF CEPHALIC APPENDAGES.

Some years ago Roonwal (1939) gave a new law of the bi-triangular medial concentration of the cephalic appendages in the Chilopoda and the Insecta, which runs as follows (p. 7) :—

" The cephalic appendages lying in front of and behind the intercalary pair of appendages undergo a concentration,[1] both in phylogeny and in ontogeny, towards the median line. In this way, two hypothetical triangles, termed the ' anterior or procephalic triangle ' and the ' posterior or gnathocephalic triangle ' are formed, having a common base in the level of the intercalary appendages. The cephalic appendages occupy roughly either the sides or the apices of the triangles and *the degree of their final medial concentration is in direct proportion to their distance from the triangular base.* Before the final bi-triangular condition is achieved by the appendages, varying types of transitory shiftings are passed through."

Observations on positions at the time of the first appearance and subsequent shifting of the cephalic appendages in the embryonic development of *Schistocerca gregaria* has shown (Pl. III, Figs. 1-13 ; Text-figs. 1 and 2 ; and Table 2) that Roonwal's Law is fully applicable to this insect.

Thirteen embryonic stages[2] (Pl. III, Figs. 1-13) from the time of the first appearance of the cephalic appendages until hatching were compared with regard to the position of these appendages. The bases or exact points of attachment of the appendages were determined by dissecting them out at the base. In the last three stages (Pl. III, Figs. 11-13) the clypeus, labrum and antennae were removed so as to fully expose the remaining cephalic appendages.

If the centres of the bases of the cephalic appendages, as they make their first appearance in the early embryo (Pl. III, Fig. 1), are joined, an outline diagrammatically represented in Text-fig. 1 is obtained ; this is a modified H-position of Roonwal. The intercalary appendages are not quite clear in *Schistocerca*[3], but their position is indicated by

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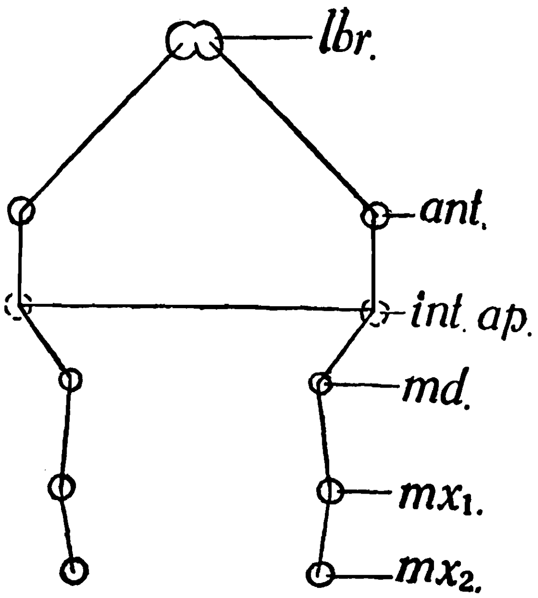
[1] This concentration in *Schistocera gregaria,* as will be noticed in Table 2, is at first only *relative* to the increasing size of the embryo ; the absolute distance between the appendicular bases of a segmental pair at first actually increases. Finally, of course, a decrease even in the absolute distance occurs towards the triangular apices, but not in those appendages which lie towards the triangular base. These points are implied in Roonwal's law, but need reemphasis.

[2] These " stages " are not synonymous with Stages 1-18 of the Reference Scale of embryos (Pl. III, Figs. 14-22 ; and Pl. IV) described above, but refer to the figures 1-13 on Pl. III.

[3] In Stage 8 a pair of small appendage-like evaginations is seen (Text-fig. 3*a*) between the antennae and the mandibles in longitudinal sections ; they could not, however, be demonstrated in surface views of embryos. In *Locusta* (Roonwal, 1937) intercalary appendages are marked by mere thickenings of the body-wall and develop rather late.

that of the intercalary mesoderm masses representing modified coelom sacs. Starting from that position, the antennae are the first pair of



Text-fig. 1.—Diagrammatic representation of the cephalic appendages of *Schistocerca gregaria* as they first appear in the embryo.
ant., antennae; *int. ap.*, probable intercalary appendages; *lbr.*, labrum; *md.*, mandibles; *mx_1.*, first maxillae; *mx_2.*, second maxillae.

TABLE 2.

Distance (in mm.) between the centres of the bases of the two rudiments of each segmental pair of cephalic appendages.

(Figs. 1—8 before blastokinesis; Figs. 9—13, after blastokinesis.)

Stage (Fig. number in Pl. III).	Distance.			
	Antennae.	Mandibles.	First maxillae.	Second maxillae.
Fig. 1	0·26	0·18	0·20	0·18
Fig. 2	0·20	0·18	0·20	0·20
Fig. 3	0·33	0·23	0·20	0·20
Fig. 4	0·38	0·33	0·33	0·38
Fig. 5	0·28	0·46	0·48	0·43
Fig. 6	0·45	0·52	0·39	0·28
Fig. 7	0·52	0·66	0·50	0·38
Fig. 8. (Just before blastokinesis.)	0·42	0·51	0·38	0·31
Fig. 9. (One day after blastokinesis.)	0·50	0·80	0·80	0·50
Fig. 10. (Two days after blastokinesis.)	0·48	0·72	0·90	0·40
Fig. 11. (Four days after blastokinesis.)	0·48	0·62	0·86	Fused
Fig. 12. (Eight days after blastokinesis.)	0·75	0·90	0·96	Fused
Fig. 13. (Hatching.)	0·75	1·0	0·75	Fused

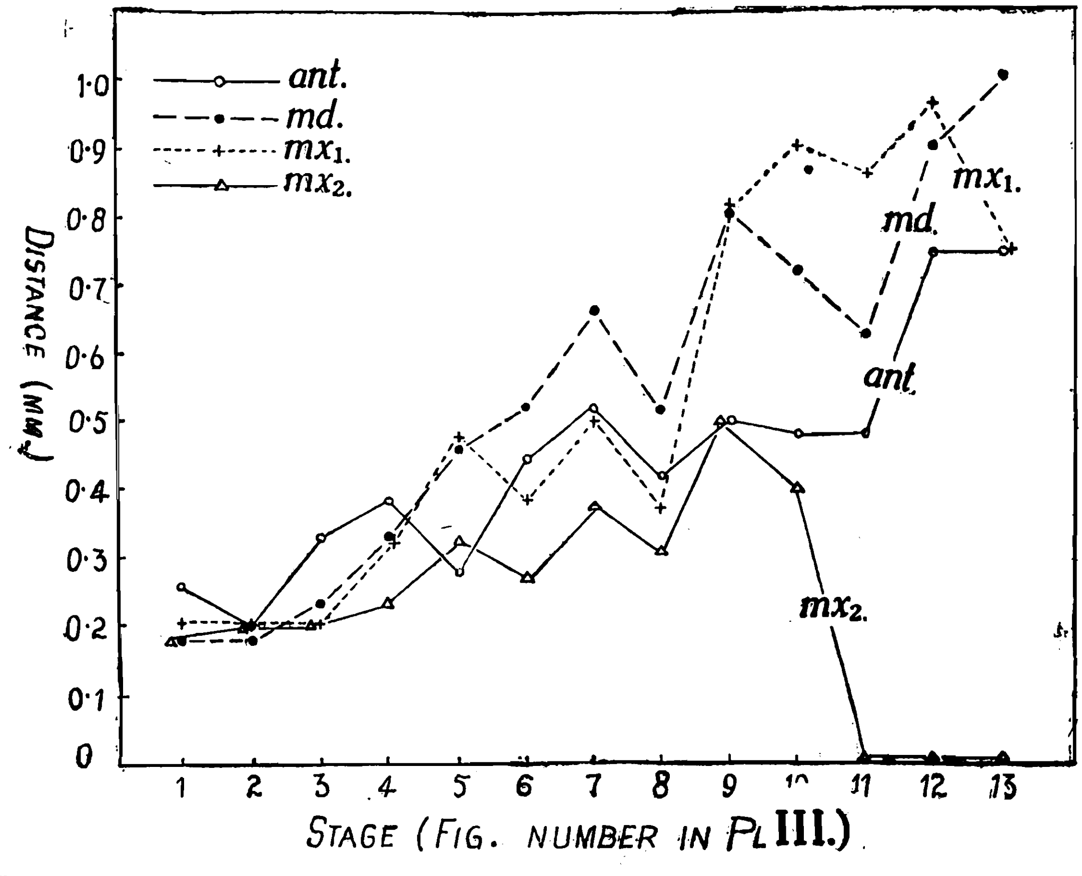
appendages on the procephalic side (Pl. III, Fig. 1); the preantennar appendages are absent in *Schistocerca*. The apex of the "procephalic triangle" is occupied by the labrum. On the gnathocephalic side (Pl. III, Fig. 2), the mandibles and the first and second maxillae follow in the order stated. The distances between the two members of each pair of appendages, as they vary from stage to stage (Pl. III, Figs. 1-13), are given in Table 2. It will be noticed that the three gnathocephalic appendages are almost equidistant from the median line at the moment of their first appearance (Pl. III, Fig. 1). During further development Pl. III, Figs. 2-11 and Text-fig. 2), the second maxillae, which are he farthest from the triangular base, undergo the greatest degree of *final* medial concentration and the two rudiments ultimately fuse together to form the labium (Pl. III, Fig. 11). The degree of final medial concentration of the first maxillae is less than that of the second maxillae, and that of the mandibles the least (Pl. III, Figs. 11-13), this being in accord with their respective distances from the triangular base.

In the procephalon the labral rudiments have evidently undergone a considerable degree of medial concentration in phylogeny as is indicated by their earliest rudiments appearing close to the median line (Pl. III, Figs. 1 and 17). The antennae, which are closer to the triangular base, undergo a lesser degree of medial concentration than the labrum.

FORMATION AND EARLY DEVELOPMENT OF COELOM.

Origin and Mode of First Formation of Coelomic Cavities.

The formation of coelom in *Schistocerca* first takes place in Stage 4. The germ band in Stage 3 (Pl. III, Fig. 16) is more or less semilunar in transverse section and measures about 0·7 mm. broad in the protocephalonic region and about 0·36 mm. in the protocormic. Soon afterwards (Stage 4), the germ band develops an outpushing in the mid-ventral area (Pl. V, Fig. 32) extending from a point slightly posterior



TEXT-FIG. 2.—Graph showing the developmental changes in the distance (in (mm.) between the bases of a segmental pair of cephalic appendages in *Schistocerca gregaria* from the moment of their first appearance until hatching. The numerals on the abscissa correspond to stage of embryo as indicated by corresponding figure number in Plate III.

ant., antennae; *md.*, mandibles; *mx*$_1$., first maxillae; *mx*$_2$., second maxillae.

to the protocephalon to almost the tip of the protocorm. This outpushing quickly assumes the shape of a dorso-ventrally flattened puoch (Pl. V, Fig. 33). It enlarges with further development and, at the same time, its mouth widens. Both the ectoderm and the inner layer[1] are involved in the pouching. After the completion of pouching, one sees, along the lateral edges of the germ band, an incomplete tube open medially and composed of inner layer cells (Pl. V, Fig. 33). Soon afterwards, the two tubes close medially, and thus arise the coelom sacs (Pl. V, Figs. 34 and 35) of the jaw segments and of those that follow them.

Hitherto two modes of formation of coelom sacs have been known among insects. These are : (i) By the appearance of clefts in the solid inner layer, as in *Gryllus* (Heymons, 1895), *Gryllotalpa* (Graber, 1888, 1890, 1891*b*), *Calandra oryzae* (Mansour, 1927 ; Tiegs and Murray, 1938), *Formica* (Graber, 1888, Strindberg, 1913), and in all the abdominal segments, except the first, in *Locusta* (Roonwal, 1937). (ii) By the lateral margins of the germ band bending inward and dorsalward, the inner layer cells thus enclosing a cavity which forms the coelom, as in *Blatella* [=*Phyllodromia, Blatta*] *germanica* (Heymons, 1892, 1895), *Eutermes* (Strindberg, 1913), *Sialis* (Strindberg, 1915), *Diacrisia* (Johannsen, 1929), *Calandra callosa* (Wray, 1937), and in the cephalic, thoracic and the first abdominal segments in *Locusta* (Roonwal, 1937). *Schistocerca* shows an entirely new mode of coelom formation. In the jaw segments and those that follow them the coelom sacs arise before the body segmentation and as a result of the mid-ventral pouching of the germ band. In the remaining segments the coelom sacs arise by the first method described above.

Early Development of Coelom.

Nineteen pairs of coelom sacs are developed in *Schistocerca gregaria*—5 in the cephalic region, 3 in the thorax, and 11 in the abdomen. Their early development proceeds as follows.

Cephalic coelom sacs.

The five pairs of cephalic coelom sacs belong to the labral, antennary, mandibular, first maxillary and labial segments.

Labral coelom sacs (Pl. V, Figs. 36 and 37). A distinct pair of small and short-lived labral coelomic sacs arises in *Schistocerca* and are best developed in Stage 8. The labral mesoderm mass first makes its appearance in Stage 4 by the migration of cells from the stomodaeal mesoderm. In Stages 5-7 it becomes paired, but no cavities are as yet visible. These latter appear in Stage 8 (Pl. V, Figs. 36 and 37), and by Stage 9 they have disappeared. In Stage 8 a few mesoderm cells are seen lying in between the two labral coelom sacs and probably connecting them. In the same stage it is seen that the labral mesoderm is also connected with the stomodaeal mesoderm by means of loose cells lying between the two structures. In these features *Schistocerca* differs

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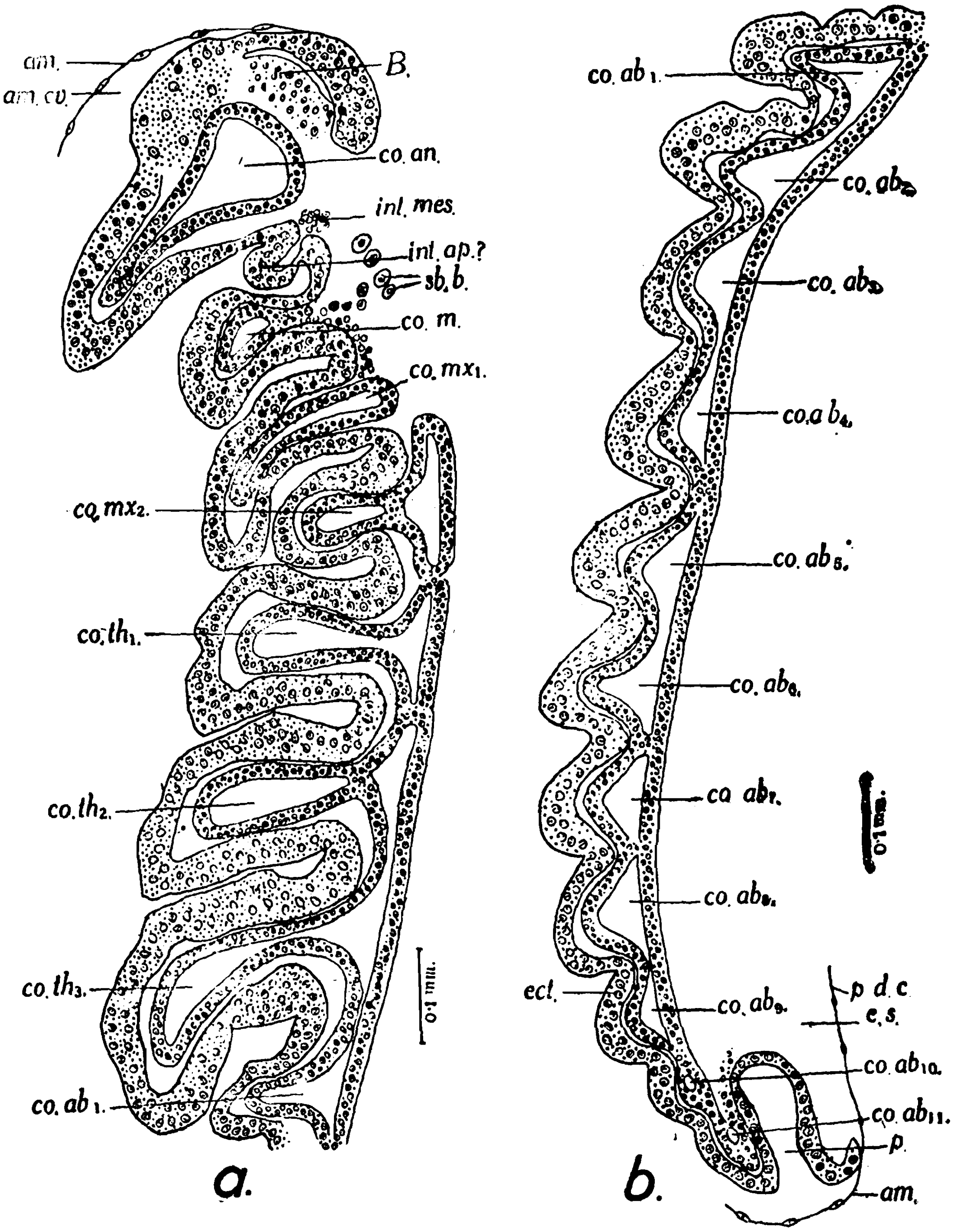
[1] See Roonwal (1936*a*, 1937, 1939*a*) for a discussion of the terminology of the various germ layers in insects and other Arthropods.

from *Locusta* in which, according to Roonwal (1937), the labral coelom sacs are neither connected with each other medially nor with the stomodaeal mesoderm. In *Schistocerca*, even after the obliteration of the labral coelom sacs, the labral mesoderm remains connected with the stomodaeal mesoderm.

Clearly defined labral coelom sacs have hitherto been found only in four other insects, *viz.*, *Carausius* (Wiesmann, 1926), *Rhodinus*, (Mellanby, 1935, 1936), *Locusta* (Roonwal, 1937, 1939*b*) and *Pteronarcys* (Miller, 1940). In agreement with these authors, I am of the opinion that these sacs in *Schistocerca* represent true coelom sacs belonging to



TEXT-FIG. 3.—Reconstruction, from camera lucida drawings, of several longitudinal-vertical sections of an embryo near Stage 9, showing the various coelomic cavities, etc.

(*a*), anterior half; and (*b*) posterior half of embryo. (Explanation of lettering as in Plates, p. 200.)

the labrum. They are not mere extensions of the supposedly preantennary coelom, as opined by Manton (1928) for *Carausius*. Nor can they be regarded, as Snodgrass (1938) suggests, as unsegmental in nature merely by virtue of their acquiring a radial instead of a bilateral symmetry.

Antennary coelom sacs (Pl. V, Figs. 38, 39, 41 and 43). The antennary mesoderm first appears in Stage 4 as a pair of mesodermal cell-masses immediately posterior to the stomodaeal invagination and near the junction of the protocephalon with the protocorm. Soon afterwards, each of these masses develops a cavity, thus giving rise to the antennary coelom sacs. They first lie (Pl. V, Fig. 38) in the appendicular outgrowths which forms the antennae. From the time of its first appearance, the antennary mesoderm is connected with the stomodaeal mesoderm by loose mesodermal cell-strands. As in *Locusta* (Roonwal, 1937), the antennary coelom sacs are at first subcircular in shape, but with the growth of the antennae they elongate. Though composed throughout of a single layer of cells, the sac-walls do not remain uniformly thick. The ventro-median portions are considerably thickened, while the dorso-lateral portions are thinned down. By Stage 8 (Pl. V, Figs. 39 and 42) each antennary coelom sac has developed a large dorso-rostral pouch and a comparatively small dorso-anal pouch—for terminology of these pouches *vide* Wiesmann (1926) and Roonwal (1937). The antennary coelom thus has three pouches, *viz.*, a ventral, a dorso-rostral and a dorso-anal. The ventral pouch lies in the hollow of the antenna. The dorsal pouches occupy an extensive area in the head—the dorso-rostral reaching almost up to the labrum, and the dorso-anal up to the mandibles. Gradually, the two dorso-rostral pouches move towards each other and ultimately, by Stages 9-10 (Pl. V, Figs. 42 and 43), unite over the stomodaeum.

Intercalary mesoderm. Well defined intercalary coelom sacs do not occur in *Schistocerca,* but are represented, near Stage 9, by a pair of solid mesodermal cell-masses (Text-fig. 3*a*). In *Locusta* (Roonwal 1937), on the other hand, there occurs a distinct pair of intercalary coelom sacs.

Mandibular coelom sacs (Pl. VI, Fig. 44; and Text-fig. 3*a*). The mandibular coelom sacs first appear in Stage 4 as a pair of very small cavities in the mandibular segment. They gradually increase in size until they become quite large. They do not develop dorsal pouches which are characteristic of the coelom sacs of the antennary and some other segments—the mandibular coelom sacs correspond to the ventral pouches of these segments. From the dorsal wall of the mandibular coelom sacs certain cells move off medially, congregate in the middle below the oesophagus and thus constitute the suboesophageal body. The mandibular coelom sacs are connected with the maxillary sacs by means of mesodermal cell-strands, as in *Carausius* (Wiesmann, 1926) and *Locusta* (Roonwal, 1937).

First maxillary coelom sacs (Pl. VI, Fig. 48; and Text-fig. 3*a*). Like the mandibular coelom, the coelom of the first maxillary segment arises as a pair of very small cavities in the first maxillary mesoderm.

These cavities subsequently become considerably enlarged. The coelom sac of each side develops a small dorsal outgrowth which probably represents, in a rudimentary form, the well-developed dorsal pouches of the antennary coelom; this outgrowth does not develop any further. In *Locusta* (Roonwal, 1937) the dorsal pouch is not developed at all. The walls of the first maxillary coelom sacs are connected with those of the mandibular segment by means of a pair of mesodermal cell-strands.

Second maxillary or labial coelom sacs (Pl. V, Figs. 48-50; and Text-fig. 3*a*). The labial coelom first makes its appearance in Stage 4 as a pair of mesodermal sacs in the hollow of the second maxillary appendages. These sacs grow rapidly, and by Stage 7 they develop extensive dorso-rostral and rather smaller dorso-anal pouches. The former extend almost up to the first maxillary segment, while the latter extend towards the prothoracic legs but without reaching them. In the intersegmental area between the first and second maxillary segments, as well as in the latter segment itself, the dorso-rostral pouches of the labial coelom send down mesodermal cells towards the mid-ventral line where, in Stages 8-9, they meet. In this way a layer of median mesoderm connecting the two sacs is formed just above the ectoderm (Pl. VI, Fig. 49).

At the junction of the ventral pouch with the dorsal there develops, in Stage 8, a furrow which deepens and ultimately separates the two pouches (Pl. VI, Fig. 50).

Discussion : *Segmentation of the head.* In recent years Hanström (1927-1930), on the basis of the morphology of the brain, has revived Holmgren's (1916) view of a 4-segmental insect head. The value of this view is greatly reduced by the fact that Hanström completely ignores the embryological evidence not only as regards coelom sacs and appendages but also as regards neuromeres. Apart from this highly improbable view, the insect head is most commonly regarded as either 6- or 7-segmental. The evidence in support of these two views has been discussed by a number of authors, *e.g.*, Wiesmann (1926), Eastham (1930), Imms (1937), Roonwal (1937, 1939*b*), Snodgrass (1935, 1938) and Weber (1938). Eastham, Imms and Weber support the 6-segmental view, and Wiesmann and Roonwal the 7-segmental view. The existence of the last five segments, *viz.*, the antennary, intercalary or premandibular, mandibular, first maxillary and second maxillary, is accepted by both groups of authors. In front of the antennary segment, however, some authors accept the existence of only one oral segment (given a variety of names), while others accept two, *viz.*, preantennary and labral. Until recent years the evidence for the oral segment was based only on the presence of its neuromere, *viz.*, the protocerebrum; no coelom sacs were known. Since the discovery of the labral and preantennary pairs of coelomic cavities by Wiesmann (1926) in *Carausius*, and the demonstration of the former alone in a number of other insects (*vide supra*), the evidence for the existence of 1 to 2 segments became stronger. Evidence for 2 segments based on the presence of 2 pairs of coelom sacs and 2 pairs of appendages (labral and preantennary in *Carausius*) was available, but the evidence from the neuromeres was lacking as only one neuromere, the protocerebrum, had until recently been demonstrated. Recently, however, Roonwal (1939*b*, pp. 27-44), has provided a new interpretation of the composition of the protocerebrum. He has conclusively demonstrated, from developmental evidence in *Locusta* and other insects, that the protocerebrum is composite in nature and is composed of two pairs of neuromeres, and not of one. As will be shown in a subsequent paper, the protocerebrum in *Schistocerca* develops in the same way as in *Locusta*. Judging from these three pieces of evidence, the head of *Schistocerca* must be regarded as 7-segmental (Table 3).

TABLE 3.

Evidence for the composition of Schistocerca gregaria *head.*

+ present ; — absent.

Segment.	Coelom.	Neuromere.	Appendages.
1. Labral	+	+	+
2. Preantennary	—	+	—
3. Antennary	+	+	+
4. Intercalary	—*	+	+
5. Mandibular	+	+	+
6. First maxillary	+	+	+
7. Labial	+	+	+

*Doubtful.

Thoracic coelom sacs.

(Pl. VI, Figs. 45 and 52 ; and Text-fig. 3*a*.)

Each of the three thoracic segments, the pro-, meso-, and metothorax, develops a pair of coelomic cavities. These cavities first appear in Stage 4 as small sacs in the hollow of the appendages of each segment. Soon they develop dorso-rostral and dorso-anal pouches. These attain considerable development by Stage 8 when they extend lengthwise such that the posterior end of the dorso-anal pouch of one coelom sac abuts, in the intersegmental area, on the anterior end of the dorso-rostral pouch of the following segment (Pl. VI, Fig. 45). In *Locusta* (Roonwal, 1937), in the intersegmental areas, the distal tip of the rostral pouch of one segment lies beneath the proximal tip of the anal pouch of the preceding segment. In *Schistocerca* such an overlapping does not occur, When the coelomic cavities first develop in Stage 4, the ventral wall of the mesoderm of each side extends towards the median line in the intersegmental area. These extensions later, in Stages 7 and 8, unite in the mid-ventral position and form the median mesoderm or blood cell-lamellae lying immediately above the ectoderm. In the segmental areas this change occurs in a later stage.

In Stage 8 a furrow develops at the junction of the dorso-rostral pouch with the ventral one. It gradually deepens and ultimately separates the two pouches in the same way as in the labial coelom. There thus come to exist in the labial and the three thoraric segments four pairs of dorsal pouches arranged serially, one set on either side of the mid-ventral line (Pl. VI, Fig. 45).

In Stage 12 there develops a horizontal partition in the dorsal pouch (in both the rostral and anal divisions) of the coelom, thus dividing this portion into upper and lower chambers. Graber (1888) had already recorded it in *Stenobothrus*, and Roonwal (1937) described it in *Locusta*. The later author has suggested that this partition is characteristic of the family Acrididae.

Abdominal coelom sacs.

(Pl. V, Fig. 40 ; Pl. VI, Figs. 51, 53 and 54 ; and Text-fig. 3.)

Eleven pairs of abdominal coelomic cavities are developed in *Schistocerca*, one pair in each segment. Their development proceeds from the anterior to the posterior end simultaneously with the differentiation of the respective abdominal segments. By Stage 9 all the abdominal coelom sacs are formed. As in the thorax, the abdominal coelomic cavities are differentiated into dorsal and ventral pouches. The latter are the first to appear and lie in the hollow of the appendages of their respective segments. Soon afterwards, dorsal pouches appear which quickly differentiate into dorso-rostral and dorso-anal portions. The dorsal pouches extend lengthwise from one end of the abdomen to the other (Text-fig. 3). Unlike the thoracic coelom sacs, the ventral pouches here do not get cut off from the dorsal pouches. The abdominal coelomic cavities become smaller as we proceed towards the posterior end of the abdomen, the cavities of the eleventh segment being the smallest (Pl. VI, Fig. 54). In *Locusta* (Roonwal, 1937) the eleventh abdominal coelom sacs differs from the others ; they consist of a pair of long, narrow cavities running dorsally along the proctodaeum. In *Schistocerca* this is not the case and the cavities are essentially similar to the other abdominal sacs, except in being smaller.

It will be seen that the dorsal pouches of the coelom form a continuous chain of cavities from the labium to the posterior tip of the abdomen. Later, with the disappearance of the intervening cellular walls between the dorso-rostral pouch of one coelom sac and the dorso-anal pouch of the preceding sac, these cavities are converted into a pair of mesodermal tubes running from the labium to almost the tip of the last abdominal segment.

Segmentation of the Body.

From developmental evidence, the body of *Schistocerca gregaria* is to be regarded as composed of 21 segments, thus : Cephalic 7, thoracic 3 and abdominal 11. The same has been shown for *Locusta* by Roonwal (1937, 1939*b*).

The 7-segmental nature of the head has been discussed above. No acron is developed in *Schistocerca*. Snodgrass (1938, p. 94) has suggested a new definition of the acron as meaning " a primarily unsegmented archicephalon corresponding with the annelid prostomium " Such an acron, according to Snodgrass, is represented in the Arthropod embryos by the cephalic lobes bearing the eyes, labrum, preantennae and first antennae. Snodgrass has not brought forward any considerable evidence in favour of this view. To me there appears to be no justification for altering the usually accepted definition of the acron as meaning the unpaired apical part of the Arthropod head lying in front of the first true segment. Such an acron is seen in the embryos of certain insects and Myriapods.

The three thoracic segments are clear and call for no comment.

The existence of eleven abdominal segments is supported by the presence of a corresponding number of paired coelom sacs, appendages and neuromeres, one set in each segment. The telson, found in some insect embryos, is absent in *Schistocerca*.

SUMMARY.

1. The external form of the embryos of the Desert Locust, *Schistocerca gregaria* (Forskål), from the time of the first formation of the germ band until hatching, is described. For convenience, a reference scale of 18 embryonic stages, whose characteristics are described, was made.

2. The first origin and the subsequent medial shifting of the cephalic appendages has been studied. It is shown that this shifting occurs in accordance with Roonwal's Law (1939) of " bi-triangular medial concentration ".

3. Three pairs of thoracic and eleven pairs of abdominal appendages are developed. The first three form the legs, while the majority of the latter are transitory.

4. The formation and early development of the coelom is described. A new mode of coelom formation, not hitherto described in insects, occurs in *Schistocerca*.

5. In the head the following five pairs of coelom sacs are developed : the labral, antennary, mandibular and first and second maxillary. Intercalary and preantennary coelom sacs are absent. The question of head segmentation is discussed and the *Schistocerca* head shown to be 7-segmented.

6. Three pairs of thoracic and eleven pairs of abdominal coelom sacs are developed, one pair to each segment.

7. The suboesophagaeal body arises from the dorsal wall of the mandibular coelom sacs.

8. The body of *Schistocerca* is regarded as composed of 21 segments —7 cephalic, 3 thoracic and 11 abdominal. Neither the acron not the telson are developed.

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EXPLANATION OF LETTERING IN PLATES III TO VI.

a_1-a_{11}., 1st to 11th abdominal appendages; ab_1.-ab_{11}., 1st to 11th abdominal segments; *am.*, amnion; *am. cv.*, amniotic cavity; *ant.*, antenna; *B.*, Brain; *b.c.*, blood cells; *cbl.*, cardioblasts; *cer.*, cercus; *cl.*, clypeus; *co.*, coelom; *co.* ab_1.-*co.* ab_{11}., 1st to 11th abdominal coelomic cavities; *co. an.*, antennary coelom; *co. lb.*, labral coelom; *co. m.*, mandibular coelom; *co.*mx_1., first maxillary coelom; *co.* mx_2., second maxillary or labial coelom; *co.* th_1.-*co.* th_3., 1st to 3rd thoracic coelomic cavities; *da.co.*, dorso-anal pouch of coelom; *d.* co_1., *d.* co_2., upper and lower portions of the dorsal coelomic pouches; *d. co.* mx_2., dorsal pouch of second maxillary coelom; *dr.co.*, dorso-rostral pouch of coelom; *dr.co.an.*, dorso-rostral pouch of antennary coelom; *dr. co.*mx_2., dorso-rostral pouch of 2nd maxillary coelom; *d.y.c.*, degenerating yolk cells; *e.*, eye; *ect.*, ectoderm; *ect.lbr.*, labral ectoderm; *e.s.*, epineural sinus; *f.*, furrow between dorsal and ventral pouches; *gl.*, galea; *h.l.*, head lobes; *h.s.*, horizontal septum; *in. l.*, inner layer; *int. ap.?*, probable rudiments of intercalary appendages; *int. mes.*, intercalary mesoderm; l_1.-l_3., 1st to 3rd thoracic legs; *lbr.*, labrum; lbs_1., lbs_2., 1st and 2nd lateral blood sinuses. *lc.*, lacinia; *l.mb.*, lateral myoblast plate; *md.*, mandible; *mes. lbr.*, labral mesoderm; *mm.*, median mesoderm; mx_1., mx_2., 1st and 2nd maxillae; mx_1.*p.*, mx_2.*p.*, 1st and 2nd maxillary palps; *nb.*, neuroblasts; *n.gr.*, neural groove; *n.c.*, nerve cells; *o.*, oral aperture; ovp_8., ovp_9., lower and upper ovipositor valves; *P.*, mid-ventral pouch of germ band, leading to coelom formation; *p.*, proctodaeum; *pcl.*, protocephalon; *pcr.*, protocorm; *pcr.a.*, anterior portion of protocorm; *pcr. m.*, middle portion of protocrom; *pcr. p.*, posterior portion of protocorm; *p.d.c.*, provisional dorsal closure; *p. ect.*, proctodaeal ectoderm; *pgs.*, paraglossa; *p.mes.*, proctodaeal mesoderm; *sb.b.*, suboesophageal body; *spl.m.*, splanchnic mesoderm; *st.*, stomodaeum; *st.m.*, stomodaeal mesoderm; *t*., anterior tentorial invagination; *v.co.*, ventral pouch of coelom; *v.co.an.*, ventral pouch of antennary coelom; *v.co.*mx_2., ventral pouch of second maxillary coelom; *v.w.*; ventral wall of coelom; *y.*, yolk.