

THE MORPHOLOGY OF THE REPRODUCTIVE
SYSTEM OF THE BLACK VINE WEEVIL,
BRACHYRHINUS SULCATUS (F.)

by

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THE MORPHOLOGY OF THE REPRODUCTIVE SYSTEM OF THE
BLACK VINE WEEVIL, BRACHYRHINUS SULCATUS (F.)

INTRODUCTION

The black vine weevil, Brachyrhinus sulcatus (F.), is recognized as a serious pest of grape in Europe (4, p.767) and of certain nursery and greenhouse plants in North America (17, p.42; 11, pp.127-128; 12, pp.4-5; 20, p.72 and 1, p.4). Previous to 1950 this parthenogenetic species (4, p.767 and 19, p.119) was considered of minor importance as a pest of strawberry in the Pacific Northwest. The strawberry root weevil, Brachyrhinus ovatus (L.), was considered of greatest importance (17, pp.41-42; 3, p.3 and 20, p.72). Since 1950 the black vine weevil has become more abundant in strawberry plantings. On southern Vancouver Island and the lower Fraser Valley of British Columbia the pest has assumed a place of importance equal to, if not greater than, B. ovatus (1, p.4). In 1954 strawberry plantings in the Gresham area of Oregon were severely infested with B. sulcatus.

Since most of the damage is done by the larvae which feed on the strawberry roots, it is imperative to control the adults before they commence oviposition, especially in fields which have not previously been soil treated. The adults emerge during the first week of strawberry picking and, therefore, cannot be controlled immediately by the use of toxic dusts or sprays without contaminating the fresh fruit. If, however, the application of insecticide could be delayed until just prior to the commencement of general oviposition most, if not all, of

the crop could be safely harvested. Thus, information regarding the first date of general oviposition in the field is of great importance. Also it is important to know the stage of development of the ovaries of those few adults which successfully over-winter and are found in the strawberry fields in late March and April.

During studies on the biology and control of this weevil at the Canada Department of Agriculture, Fruit Insect Laboratory, Victoria, British Columbia the adults were observed to have an extended pre-oviposition period. The average pre-oviposition period of 35 weevils reared at 68°F. and 75 to 85 per cent relative humidity was 31.9 days with a minimum of 27 days and a maximum of 43 days. The pre-oviposition period in the field was somewhat longer, depending upon weather conditions.

The purpose of the gross morphological study undertaken and presented here is to determine if changes in the growth of the female reproductive system during the pre-oviposition period can be used as an indicator of the development of the ovaries of the adult and the commencement of oviposition in the field.

The gross morphology of the reproductive system of the ovipositing adult is discussed prior to a discussion of the growth of the female system during the pre-oviposition period.

TECHNIQUE

COLLECTING

In order to determine the exact age of adult weevils it was necessary to collect pre-pupae from soil under infested strawberry plants and rear these through the pupal stage to adults. Larvae were collected by the author and others during late April and May, 1954 at Corvallis and Gresham, Oregon. Dr. R.G. Rosenstiel collected larvae on April 15, 1954 and May 29, 1954 at Gresham. Dr. H.H. Crowell collected larvae on April 15, 1954 at Corvallis.

Adults were collected at periodic intervals throughout June, July and August. Collections were made by sweeping infested strawberry plantings at night between 9:00 p.m. and 11:00 p.m. Dr. Rosenstiel and the author used this method to collect large numbers of adults for the first time on June 7, 1954. Dr. Rosenstiel made the periodic collections of adults from the Gresham area and forwarded them to the author for study.

REARING

Larvae collected from soil under infested strawberry plants on April 15, 1954 were in the pre-pupal stage and had completed feeding. Both the larvae and the soil in which they were living were brought to the laboratory at Oregon State College where they were placed in plaster-of-paris rearing blocks. The rearing blocks measured 6 inches

long by 4 inches wide by 2 inches deep and had a centre well for soil which measured 5 inches long by 3 inches wide and 1 inch deep. The centre well was covered with a glass plate. The soil in the well was kept moist by the periodic addition of water to a separate watering well in the rearing block. Blocks were placed on the window sill and the window was usually kept open. No more than 20 larvae were placed in each block. Adults commenced emergence on May 12. The pupal period of 21 specimens averaged 16 days.

The newly emerged adults were placed singly in glass vials 3 inches long by 1/2 inch wide. The vials were closed with corks each having a 1/4 inch hole which was plugged with saran screening cloth for ventilation. Vials were placed on the window sill and contained a fresh strawberry leaf as food for the weevil. Weevils did not feed for the first four or five days but fed voraciously thereafter.

DISSECTING

When possible live dissections were made. Various dissecting fluids were tried such as; water, saline solution, 70 per cent alcohol and 5 per cent chloral hydrate. The 5 per cent chloral hydrate gave the best definition of organs but was not a satisfactory preservative.

Most of the dissections were made from preserved material. Weevils were killed in Kahle's fixative and after 24 hours removed to 70 per cent alcohol for storage. These specimens were dissected in 70 per cent alcohol.

Dissecting was begun by lifting off the hard elytra with fine forceps. The membranous tergum was removed by peeling it back from the anterior end of the abdomen. Jewellers' forceps with fine points were the only dissecting instruments used except for sharp razor blades used for making sections.

Drawings were usually made at the magnification of 50 diameters by the use of a square-ruled ocular micrometer disc in the binocular eyepiece and square-ruled drawing paper. Drawings were photographed and reduced in the usual manner.

Measurements of the size of the various structures were made by the use of a calibrated linear micrometer disc in the binocular eyepiece.

A Reichert stereo microscope (Mak K) was used for all dissections.

GROSS MORPHOLOGY OF THE FUNCTIONING REPRODUCTIVE SYSTEM

The general topography of the female system in B. sulcatus is similar to that of other parthenogenetic and gonorrhistic weevils that have been studied by various workers (14, pp.583-586; 2, pp.242-251; 15, pp.20-27; 5, pp.1-23 and 6, pp.447-484). The system consists of four parts, namely; the ovaries, the generative ducts, the accessory organs and the external organs.

OVARIES

The ovaries, or reproductive organs of mesodermal origin which contain the egg cells, represent that part of the internal reproductive system of insects anterior to the lateral oviducts (14, pp.39, 552 and 579). In weevils the internal system is generally represented by a single pair of ovaries with each ovary consisting of two ovarioles (6, pp.450-451). The thin membranous cover of each ovariole is called the tunica propria (14, p.553).

In B. sulcatus the ovaries lie in the latero-dorsal abdominal cavity where they are supplied with a dense network of trachea and are surrounded by layers of fat bodies. The two ovarioles of each ovary are not contained in a common membrane, nor are they connected except at their anterior ends by the union of their terminal filaments and at their posterior ends by the union of their ovariole pedicels at the lateral oviducts (Fig. 3). Each ovariole is comprised of three main parts, the terminal filament, the egg tube and the ovariole pedicel (14, p.553).

Terminal Filament:- The terminal filament arises generally as a direct anterior protraction of the outer ovariole cover, the tunica propria (14, p.554 and 6, p.453). The threadlike filament is a solid strand of cells which joins the filament of the adjacent ovariole to form the suspensory ligament. The suspensory ligament of each ovary may then be imbedded in the neighbouring fat tissue, the body wall, the dorsal diaphragm, or in some cases may be inserted in the ventral

wall of the dorsal blood vessel (14, p.552). In the genus Polydrosus the suspensory ligament is attached to the dorsal diaphragm (6, p.449). Nutting reports the atypical attachment of the suspensory ligament of acridoid grasshoppers in which the fused ligaments arise from the ventral heart wall (9, p.535).

In B. sulcatus the form and location of the terminal filaments remain without noticeable change throughout the life of the weevil. The filaments arise at the anterior end of the egg tube where the somewhat loose tunica propria of each ovariole constricts. The resultant filaments join to form a suspensory ligament. The ligament of each ovary joins on each side to a large median ligament which originates at the anterior loop of the proctodaeum. This proctodaeal ligament is inserted in the ventral wall of the dorsal blood vessel where the latter passes under the posterior tip of the scutellum of the thorax (Fig. 6). The presence of a dorsal diaphragm is not apparent in this area. Lenkova makes no mention of the presence of a large proctodaeal ligament in the genus Polydrosus.

Egg Tube:- The egg tube, according to Snodgrass, contains the germ cells and represents the principal part of the ovariole (14, p.553). The tube is in two parts, the germarium or end chamber and the zone of growth or vitellarium (14, p.555). Lenkova reports that Polydrosus mollis, also a parthenogenetic weevil, has a telotrophic or arotrophic ovariole in which some of the cells formed from the oogonia become nurse cells and remain in the anterior end of the germarium;

while the oocytes become removed but still connected to their associated nurse cells by long protoplasmic strands. The oocytes continue to receive nutrient material from the nurse cells through these protoplasmic strands. The oocytes leave the germarium and pass into the vitellarium where the protoplasmic connections with the trophocytes are lost as the follicular covering closes around the young ova. The nourishing function is then performed only by the follicular vesicles of the vitellarium. While in the vitellarium the oocyte receives an outer shell or chorion of chorionine which is produced by the follicle cells. The complete formation of the chorion marks the end of growth of the oocyte. The follicle cells surrounding the full-grown oocyte degenerate at the posterior end of the vitellarium and form a yellowish bulk called the yellow body or corpus luteum (6, pp.458-461).

In the mature system of B. sulcatus the tunica propria forms a loose, tough cover over each entire egg tube. Under this cover the anterior germarium is elliptical in shape and greatly enlarged, measuring from 1.04 mm. to 1.73 mm. in length and from 0.25 mm. to 0.47 mm. in width. The germarii lie in a position parallel to the ventriculus, usually sloping toward the median dorsal line at their anterior ends (Fig. 2). At the constriction of the posterior end of the germarium there is a division or change in tissue. This point of division marks the beginning of the follicular lining of the vitellarium (Fig. 6).

At the anterior end of the vitellarium oocytes are not visible under low magnification (X100). Only the white, dense follicular tissue can be seen through the tunica propria. More posteriorly the

oocytes soon become apparent in the vitellarium and their size increases as the tube progresses toward the ovariole pedicel. The vitellarium is tightly coiled in the abdominal cavity adjacent to the ventriculus and ventral to the enlarged germarium (Figs. 2 and 6).

At the union of the vitellarium with the ovariole pedicel the thick-walled follicular vesicles and the dense tracheation common throughout the vitellarium both cease. At this point, yellow tissue within a swelling of the tube indicates the presence of the corpus luteum. In weevils that have just commenced egg laying (Fig. 6) the yellow colour and swelling caused by the presence of the corpus luteum is not readily apparent; but as egg production progresses the yellow colour becomes more dense and the swelling increases in size (Fig. 13).

Ovariole Pedicel:- The ovariole pedicels are usually represented by short stalks connecting the egg tubes with the lateral oviducts (12, p.556). At the posterior end of the vitellarium the tunica propria ends and the simple elastic epithelium of the pedicel wall commences (6, p.462). In the genus Polydrosus, the pedicel or stipe of mature weevils is so distended that it is indistinguishable from the calyx. However, the pedicels are long and readily distinguishable in the young female (6, p.462).

Dissection of ovipositing B. sulcatus adults reveals that the pedicels are greatly distended but are distinguishable as separate tubes which join to form the lateral oviduct or calyx area (Fig. 13). Both the pedicels and the anterior ends of the lateral oviducts are

thin, elastic membranes which contain several mature eggs. Since there is no apparent difference between these two areas, the pedicels might be considered as part of the calyces.

GENERATIVE DUCTS

Oviducts:- Snodgrass states that the lateral oviducts are simple tubes without accessory structures (14, p.562). According to Metcalfe the lateral oviducts in the pupa of Sitodrepa panicea Linn. are derived partly from the union of the mesodermal ovariole pedicels and partly from the ectodermal paired lateral uteri which split off from the primary uterus invagination. These tissues join before the pupa matures (7, pp.95-97). Bissell in his description of the reproductive system of the pecan weevil, Curculio caryae (Horn.), (2, p.246) and Tissot in describing the white-fringed beetle, Naupactus leucoloma Boh., (16, p.26) have both, in the opinion of the present author, erroneously referred to the vitellarium and ovariole pedicels as the lateral oviducts.

Ssilantjew refers to the median oviduct of Otierrhynchus turca Bohem. as the vagina (15, p.585). Metcalfe has established that the median oviduct of Sitodrepa panicea is derived from the primary invagination of the eighth sternite. According to Sing Pruthi an invagination of the eighth sternite represents the uterus (7, p.90). Metcalfe, therefore, refers to the median oviduct as the uterus and the lateral oviducts as the paired lateral uteri. In the discussion of B. sulcatus the more commonly used terminology of Snodgrass is adhered to, namely, median oviduct and lateral oviducts.

In B. sulcatus there is apparently no difference between the tissues of the ovariole pedicels and the anterior portions of the lateral oviducts. However, a change in the tissue of the posterior portions of the lateral oviducts is evident (Fig. 10). The narrower posterior portion appears slightly sclerotized with longitudinal folds similar to the median oviduct. There is a definite line of union of the two portions of the lateral oviduct, especially evident in the newly emerged adult. This observation is in agreement with Metcalfe's findings.

The two lateral oviducts converge at the median line near the intersegmental membrane of the third and fourth sternites. The resultant median oviduct loops sharply dorsally and anteriorly. At the tip of the chitinous rod, the median oviduct loops sharply posteriorly and enters the thick musculature surrounding the vagina where it joins with the latter.

Vagina:- According to Snodgrass, where the median oviduct joins a genital chamber which serves both as an egg exit and as a copulatory entrance, the chamber may properly be distinguished as a vagina (13, p.23). The union of the median oviduct and vagina is marked by the opening of the spermathecal duct which enters dorsally into the anterior end of the vagina (14, p.563). A diverticulum of the vagina arises immediately posterior to the spermathecal opening to form the copulatory pouch. Accessory glands are usually absent in the Coleoptera (13, p.23).

Metcalf states that the single genital duct, the uterus or vagina, of Sitodrepa panicea is formed from the longitudinal fusion of the primary uterus invagination and the primary spermathecal invagination. The opening of the uterus invagination becomes closed. This closure leaves the opening of the spermathecal invagination in the ninth sternite to become the functional vulva. Thus, the vagina (and median oviduct) has three component parts; the anterior uterus portion (median oviduct), the median region of combined spermathecal and uterus origin, and the posterior spermathecal portion (7, pp.95-98). Lenkova's unsuccessful attempt to locate any divisions between the median oviduct, the uterus and the vagina (6, p.466) is probably because the median oviduct is, as Metcalfe suggests, the uterus.

The vagina of B. sulcatus is completely obscured anteriorly by heavy musculature and posteriorly by the ovipositor lobes. The vagina is a long, narrow tube with many longitudinal infoldings which permit its expansion during oviposition. The tube extends from about the anterior edge of the fourth sternite to the vulva at the apex of the ovipositor (Fig. 7). The wall of the vagina, although flexible and capable of considerable expansion, is extremely strong indicating a heavily chitinized tissue of ectodermal origin. When the vagina is pulled anteriorly the tissue does not break but readily causes the ovipositor to turn inside out exposing the continuation of the inner vaginal surface with the outer ovipositor surface.

The opening of the spermathecal duct is found at the anterior dorsal end of the vagina. Posterior to this opening the diverticulum

of the vagina, the copulatory pouch, arises dorsally. The vagina is slightly convoluted between the opening of the copulatory pouch and the basal plates of the ovipositor. These convolutions straighten when the ovipositor is extended.

The heavy musculature surrounding the vagina serves to extend and retract the ovipositor and to force eggs through the vagina (Fig. 9). The latter function is performed by the inner layer of circular muscles and the outer longitudinal muscles operate the ovipositor.

ACCESSORY ORGANS

Copulatory Pouch:- The copulatory pouch or bursa copulatrix is usually a dorsal pouchlike diverticulum of the vagina (13, p.23). The walls of the copulatory pouch are lined with a thick layer of soft chitin which is somewhat hardened on the ventral and anterior end in the genus Polydrosus (6, p.467).

In the black vine weevil the copulatory pouch is a relatively large dorsal sac off the vagina (Fig. 7). The pouch curves anteriorly and ventrally over the median oviduct. There is much infolding of the wall of the pouch especially at the blind anterior end. The muscles surrounding the pouch are largely circular. A circular muscle sheath encloses both the anterior end of the pouch and the median oviduct and holds them to the anterior tip of the chitinous rod (Fig. 9). The function of the pouch in this parthenogenetic weevil is no longer one of receiving the male organ during copulation, but probably serves to hold mature eggs prior to oviposition.

Spermatheca:- In insects generally the spermatheca or receptaculum seminis is a storage organ for sperms (14, p.566). Metcalfe states that the spermatheca arises as a primary ectodermal invagination of the body wall posterior to the ninth sternite of Sitodrepa panicea (7, pp.94-95). The spermatheca of weevils is generally represented by a sickle-shaped, heavily sclerotized structure lying on the right side of the vagina and possessing two tubular ducts, the spermathecal duct and the duct of the spermathecal gland (16, p.27; 5, p.132 and 6, p.473). The spermathecal duct is a long, elastic and very narrow tube, the outer wall of which is a layer of soft chitin (6, p.475). The spermathecal gland is a narrow chitinous tube surrounded by a thick layer of secreting cells (6, p.477). The spermathecal duct serves to convey sperms between the spermatheca and the vagina while the spermathecal gland secretes a fluid in which the sperms are transported (14, p.566). The spermathecal duct of Naupactus leucoloma enters the wall of the median oviduct at about its middle and runs posteriorly in the wall to the vagina where the duct opens into the vagina (16, p.27).

The spermatheca of B. sulcatus is a typically sickle-shaped, heavily sclerotized organ lying on the right side of the vagina (Fig. 3). The organ is imbedded in fatty tissue and is well supplied with trachea. The blunt 'handle' of the sickle-shaped spermatheca is postero-ventral with the back of the 'blade' dorsal and the point of the 'blade' antero-ventral. It is from the enlarged 'handle' or postero-ventral end that the two ducts emerge (Fig. 12). The spermathecal duct emerges from the ventral wall of the 'handle' and loops anteriorly around the

anterior end of the median oviduct into the muscle tissue surrounding the anterior tip of the chitinous rod and enters the vagina just anterior to the dorsal opening of the copulatory pouch (Fig. 7). The duct of the spermathecal gland emerges from the 'handle' posterior to the spermathecal duct. The tissue surrounding the short duct of the spermathecal gland is very white and contains the secreting cells of the gland (Fig. 12). A muscle sheath extends from the 'handle' to the back of the 'blade' (Fig. 12). This muscle sheath has the function of pumping the spermatheca to eject sperms through the spermathecal duct into the vagina (14, p.566).

Thus, although no males of B. sulcatus have ever been found, the spermatheca is present in full detail. Lenkova concludes that since there is no anatomical difference in the reproductive organs of the parthenogenetic species, Polydrosus mollis, and the two closely related gonohorristic species, Polydrosus sericeus and Polydrosus pilosus, the parthenogenesis in Polydrosus mollis originated recently, probably in the diluvial period (6, p.483).

EXTERNAL ORGANS

Ovipositor:- In Coleoptera the ventral ovipositor lobes represent the endopodites of the eighth sternite; the dorsal lobes, the endopodites of the ninth sternite, and the lateral lobes, the coxites of the ninth sternite (7, p.89). Then, according to Snodgrass, the ventral lobes are the first valvulae, the dorsal lobes are the second valvulae and the lateral lobes are the second valvifers. Michener claims that the third

valvulae are the styli of the ninth sternite and refers to them as the gonostyli (8, pp.336-337).

The ovipositor of B. sulcatus is represented by the characteristically telescoped female genitalia of Coleoptera (Fig. 7). Externally the abdomen has five sternites and seven tergites visible. The sixth and seventh sternites are unsclerotized segments folded anteriorly above the fifth sternite. The spiculum gastrale (defined p.17) lies between the seventh and eighth sternites. The eighth and ninth sternites are not readily visible as segments since each is incorporated in the ovipositor. The sternum dorsal to the spiculum gastrale folds anteriorly to the base of the ovipositor, forming the ventral wall of the ovipositor's outer sheath. The sternum then folds posteriorly and forms the plates or lobes of the tubular ovipositor (Fig. 7). At the base of the ovipositor the coxite of the eighth sternite, the first valvifer, is visible in cross-section as a sclerotized, latero-ventral plate (Fig. 11). The first valvifer fuses with the sclerotized, main lateral plate, the second valvifer, which is the coxite of the ninth sternite (Fig. 8). The ventral lobes are membranous and represent the gonopophyses of the coxites of the eighth sternite or the first valvulae. The dorsal lobes are likewise membranous and represent the gonopophyses of the coxites of the ninth sternite or the second valvulae. Figure 8 is a drawing of an ovipositor much swollen by preservative. Normally the sclerotized second valvifers obscure the dorsal and ventral lobes of the ovipositor. Apically the second valvifer gives rise to a stylus which, according to Michener, is the gonostylus. The

sclerotized plates of the ovipositor have a limited number of setae. The apical portion of the second valvifers and the gonostyli have pronounced setae (Fig. 8).

The dorsal wall of the ovipositor continues anteriorly for a short distance beyond the sclerotized plates before it rolls back posteriorly to form the dorsal wall of the ovipositor's outer sheath. Near the apex of the ovipositor this sheath again folds anteriorly and gives rise to an anal flap which covers the anal opening (Fig. 7).

The seventh and last visible tergite, although membranous at its anterior end, is heavily sclerotized around its posterior edge. The eighth tergite, which lies concealed beneath the seventh tergite, is separated from the latter by a deep intersegmental fold. The eighth tergite, often called the mantle (5, p.130; 16, p.25 and 2, p.247), may be visible during oviposition when the ovipositor is everted. There are no spiracles on the eighth tergite. Additional tergites are not readily discernible (Fig. 7).

Spiculum Gastrale:- The presence of a spiculum gastrale or chitinous rod is common in weevils. Metcalfe describes the development of this organ and claims that it is definitely not of appendicular origin, but, instead, is formed from an invagination of the intersegmental membrane between the seventh and eighth sternites (7, p.97).

The spiculum gastrale of B. sulcatus is a spoon-shaped organ lying beneath the ovipositor and the vagina. Anteriorly the spiculum gastrale narrows to a slender, chitinous rod which extends into the

abdominal cavity beneath the vagina as far as the intersegmental membrane of the second and third sternites (Fig. 7). The anterior tip of the rod is slightly broadened and to this area, are attached many of the muscles which operate the ovipositor (Fig. 9). The broad, spoon-shaped, posterior end of the spiculum gastrale is heavily sclerotized at the lateral tips. These sclerotized areas converge anteriorly at the chitinous rod. Non-sclerotized tissue forms an open pocket in each of the antero-lateral wings of the spiculum. Into these pockets are inserted the muscles from the vagina and tergum (Fig. 10). The main function of the spiculum gastrale is to form a rigid base for the attachment of the muscles which cause the eversion and retraction of the ovipositor.

GROWTH OF THE REPRODUCTIVE SYSTEM

The main object of this study was to determine if changes in the growth of the reproductive system of B. sulcatus during the pre-oviposition period can be used as an indicator of adult development and subsequent oviposition in the field.

OBSERVATIONS OF LABORATORY-REARED WEEVILS

Adults reared from larvae at Oregon State College were killed on June 12. These adults represented roughly four age groups of zero, 15, 25 and 28 days. Unfortunately older adults were not obtained. However, one adult in the last group had laid four eggs and afforded an example of a mature adult of known age (Fig. 6).

Examination of ten weevils from each age group was made.

Measurements were recorded of the ratio of the anterior growth of the more advanced germarium of the right ovary to the abdomen length (Tables 1, 2, 3 and 4). The advance of the germarium was measured from the posterior tip of the fifth sternite to the anterior tip of the germarium. The length of the abdomen was measured from the posterior tip of the fifth sternite to the posterior tip of the scutellum.

Newly Emerged Adult:- In the newly emerged adult (Fig. 3) the ovaries are small and largely transparent. The most conspicuous portion is the short, slender, white germarium of each ovariole (Fig. 2). The germarium is from 0.43 to 0.79 mm. long and from 0.1 to 0.14 mm. wide (Table 1). In the right ovary the germarii lie with their anterior ends directly dorsal to the posterior margin of the coxal cavity of the metathoracic leg, or from 3.2 mm. to 4.5 mm. from the posterior tip of the fifth sternite (Table 1). A dense network of trachea enters the tunica propria surrounding the germarium of each ovariole and holds them close together, giving the appearance of connective tissue. Immediately posterior to this heavily tracheated area the ovariole pedicel of each ovariole of the right ovary extends posteriorly for a distance of approximately 0.5 mm. where it joins the adjacent pedicel at the anterior end of the lateral oviduct. The ovariole pedicels are noticeably lacking in tracheation. It is important to notice that there is no indication of a vitellarium between the germarii and the ovariole pedicels. The dense tracheation of the germarii continues to

TABLE 1

MEASUREMENTS IN MILLIMETERS OF THE SIZE AND ANTERIOR ADVANCE OF THE GERMARIUM¹ OF NEWLY EMERGED B. sulcatus ADULTS REARED IN THE LABORATORY FROM PRE-PUPAE COLLECTED IN THE FIELD

NO.	GERMARIUM ¹		ANTERIOR ADVANCE OF GERMARIUM ²	ABDOMEN LENGTH ³	RATIO OF ANT. ADV. OF GERMARIUM TO ABDOMEN LENGTH
	LENGTH	WIDTH			
1	.72	.14	4.5	7.4	.61
2	.79	.14	3.9	6.3	.62
3	.72	.14	4.0	6.6	.61
4	.76	.14	4.5	6.9	.65
5	.58	.14	4.0	5.7	.70
6	.54	.14	4.0	6.2	.65
7	.68	.14	4.4	6.2	.71
8	.43	.10	3.8	6.0	.63
9	.58	.14	3.4	5.2	.65
10	.54	.14	3.2	4.8	.66
AV.	.63	.14	4.0	6.1	.65

¹Larger germarium of the right ovary.

²Measured from anterior tip of the larger germarium of the right ovary to the posterior tip of the fifth sternite.

³Measured from the posterior tip of the scutellum to the posterior tip of the fifth sternite.

beyond the anterior tip of the germarii, and close examination reveals that the tracheation enters the thin, transparent tunica propria of each ovariole. Each tunica propria with its dense tracheation extends to the anterior end of the abdomen where it constricts and a terminal filament arises. Trachea supplying the germarii at this early age originate at the third abdominal spiracle; whereas, the trachea supplying the anterior transparent tubes originate at the first and second abdominal spiracles (Fig. 3).

The tissue of the anterior portion of the lateral oviducts is similar in appearance to that of the ovariole pedicels. However, the

posterior one-third of the oviducts is different, being slightly darker in colour and exhibiting longitudinal grooves with very slight sclerotization. There is a definite point of demarkation between these two tissues of the lateral oviducts.

The musculature of the vagina is not fully developed (Figs. 2 and 3). The remainder of the reproductive system is not significantly different from that of the mature adult.

Fifteen Day Old Adult:- The difference between the fifteen day old weevil (Fig. 4) and the newly emerged weevil, although very slight, is discernible. Measurements of the anterior growth of the germarium through the tunica propria show a very slight advance in the 15 days. (Table 2 and Fig. 1); however, these measurements are not sufficiently different to be of value. The main point of difference that can be detected readily is the slight formation of the vitellarium. Close examination reveals that each germarium has moved slightly anterior. There is now visible a short length of tunica propria, posterior to each germarium, that is heavily tracheated and is in close association with its adjacent tunica propria. This part of the tunica propria was previously occupied by the germarium which has grown forward, leaving the short tube of follicular tissue behind. The beginning of the ovariole pedicels is readily marked by their relative absence of tracheation.

The 15 day old weevil has also acquired a considerable amount of fatty tissue which obscures the ovaries.

TABLE 2

MEASUREMENTS IN MILLIMETERS OF THE SIZE AND
ANTERIOR ADVANCE OF THE GERMARIUM¹ OF FIFTEEN
DAY OLD *B. sulcatus* ADULTS REARED IN THE
LABORATORY FROM PRE-PUPAE COLLECTED IN THE FIELD

NO.	GERMARIUM ¹		ANTERIOR ADVANCE OF GERMARIUM ²	ABDOMEN LENGTH ³	RATIO OF ANT. ADV. OF GERMARIUM TO ABDOMEN LENGTH
	LENGTH	WIDTH			
1	.76	.14	4.0	6.3	.63
2	.94	.22	5.0	6.6	.76
3	.90	.22	4.0	6.3	.63
4	.90	.18	4.6	6.8	.68
5	.90	.18	4.2	6.6	.64
6	.65	.14	4.0	5.6	.71
7	.86	.18	4.6	6.8	.68
8	.86	.18	3.9	6.2	.63
9	.79	.18	4.0	6.0	.67
10	.76	.18	4.2	6.4	.66
AV.	.83	.18	4.2	6.4	.67

¹See table 1.

²See table 1.

³See table 1.

Twenty-five Day Old Adult:- The 25 day old adult (Fig. 5) shows a marked difference from either the newly emerged or the 15 day old adult. Not only have the germarii advanced a considerable distance but also they have increased noticeably in size. The vitellarii are now readily discernible, and in the right ovary have developed a single convolution just posterior to the germarii and immediately dorsal to the coxal cavity of the metathoracic leg. The tunica propria surrounding the vitellarium appears wrinkled and slightly distended. Under the tunica propria is the dense follicular tissue of the vitellarium. The union of the vitellarii with their respective ovarian pedicels remains marked by the dense tracheation of the tunica propria surrounding the vitellarii

TABLE 3

MEASUREMENTS IN MILLIMETERS OF THE SIZE AND
ANTERIOR ADVANCE OF THE GERMARIUM¹ OF TWENTY-
FIVE DAY OLD *B. sulcatus* ADULTS REARED IN THE
LABORATORY FROM PRE-PUPAE COLLECTED IN THE FIELD

NO.	GERMARIUM ¹		ANTERIOR ADVANCE OF GERMARIUM ²	ABDOMEN LENGTH ³	RATIO OF ANT. ADV. OF GERMARIUM TO ABDOMEN LENGTH
	LENGTH	WIDTH			
1	.90	.22	4.6	6.9	.67
2	1.15	.22	4.5	6.6	.68
3	1.22	.25	5.2	6.4	.81
4	1.08	.22	4.0	6.4	.62
5	1.08	.22	5.4	6.4	.84
6	1.26	.22	5.1	6.4	.80
7	1.11	.22	3.9	6.3	.62
8	1.26	.29	5.4	6.3	.86
9	1.01	.22	3.9	5.6	.70
10	1.19	.22	4.8	6.0	.80
AV.	1.13	.23	4.7	6.3	.74

¹See table 1.

²See table 1.

³See table 1.

and the noticeable absence of tracheation in the pedicels.

The size of the germarii has now increased noticeably, measuring from 0.90 mm. to 1.26 mm. long and from .22 mm. to .29 mm. wide (Table 3).

Twenty-eight Day Old Adult:- Under laboratory rearing conditions the twenty-eight day old adult (Fig. 6) has a system that is essentially mature. From the twenty-fifth day the ovary undergoes rapid growth. Measurements of the size and anterior advance of the germarium of 10 weevils appear in table 4. The germarium of each ovariole attains the anterior extremity of the tunica propria. The convolution of the

TABLE 4

MEASUREMENTS IN MILLIMETERS OF THE SIZE AND ANTERIOR ADVANCE OF THE GERMARIUM¹ OF TWENTY-EIGHT DAY OLD B. sulcatus ADULTS REARED IN THE LABORATORY FROM PRE-PUPAE COLLECTED IN THE FIELD

NO.	GERMARIUM ¹		ANTERIOR ADVANCE OF GERMARIUM ²	ABDOMEN LENGTH ³	RATIO OF ANT. ADV. OF GERMARIUM TO ABDOMEN LENGTH
	LENGTH	WIDTH			
1	1.33	.29	5.8	7.0	.83
2	1.26	.29	5.2	7.0	.74
3	1.48	.29	5.7	6.6	.86
4	1.37	.29	5.8	6.4	.91
5	1.37	.29	5.0	6.6	.76
6	1.29	.29	5.2	6.6	.79
7	1.26	.29	5.2	6.3	.82
8	1.19	.29	4.8	6.3	.76
9	1.62	.29	6.0	6.8	.88
10	1.80	.40	6.0	6.9	.87
AV.	1.40	.29	5.5	6.6	.82

¹See table 1.

²See table 1.

³See table 1.

vitellarium becomes more pronounced, forming a complete loop which extends to the antero-lateral abdominal cavities. The vitellarium of each ovariole is swollen with developing ova which attain mature size just anterior to the union of the vitellarium with the ovariole pedicel.

OBSERVATIONS OF FIELD-COLLECTED ADULTS

Dr. R.G. Rosenstiel sent to the author periodic samples of preserved B. sulcatus adults collected in the field from the Gresham area. This series was collected from June 7, 1954 until August 31, 1954 and was comprised of ten samples for the 12 week period.

Ten specimens from each field sample were examined and measured in the same manner as the weevils reared in the laboratory (Fig. 1). Also the presence or absence of mature eggs in the calyces of the right ovary was determined.

Weevils collected on June 7 had no development of their reproductive organs. Those collected on June 17 had very slight development. This lack of development was expected as the emergence of B. sulcatus in the Gresham area commenced during the first week of June. Collections on June 30 indicated some development of the system but none of the 10 weevils examined had eggs in its calyces. Although one specimen from the July 7 series was producing eggs, the series generally was not so far developed as the previous collection. The reason for this variation was probably related to the adverse, cold weather experienced during June which probably delayed the emergence of many weevils. Similarly, the series collected on July 15 was not quite so advanced as the one collected on June 30, but one specimen in the July 15 series was producing eggs. Weevils collected on July 24 were generally well advanced with five of the ten specimens producing eggs. Thus, according to these data, July 24 was the time of first general egg production by weevils that emerged in June, 1954. The July 30 series had 7 of 10 weevils producing eggs; August 9, all 10; August 18, 9 of 10 and August 31, 7 of 8 (Fig. 1).

RELATIONSHIP BETWEEN LABORATORY AND FIELD ADULTS

Figure 1 represents a graph of the average of 10 ratios of

germarium advance to the abdomen length plotted against the age or date of collection of the weevils. The figure contains data from both the weevils reared in the laboratory and those collected in the field. The assumption is made that the first field collection of adults on June 7 represents the date of emergence of the weevils, since all of these specimens were soft when collected. The average age of weevils from subsequent collections is the number of days between June 7 and the date of collection. These ages appear on the ordinate together with the known ages of adults reared in the laboratory. The graphs of the above average ratios show a more rapid development of the weevils reared in the laboratory (Fig. 1). However, there is a similarity in the rate of development of the two groups for the first 23 days; after that age, the weevils from the field appear to develop more slowly than the weevils in the laboratory. The laboratory weevils reach full development after 28 days. The weevils in the field do not appear to reach full development until approximately 47 days after emergence. The sudden drop in the average development of the July 7 field sample was probably due to the emergence of a large number of weevils between June 30, the date of the previous sample, and July 7. The appearance of this new and later population of weevils was probably the result of weather conditions. First, the low daily maximum and minimum temperatures experienced during the month of June probably extended the developmental period of many pupae in the soil and inhibited their metamorphosis to adults (Fig. 1). Second, on June 29 and 30 there was a sudden increase in maximum temperature to 84°F. and 80°F., respectively,

along with a corresponding increase in minimum temperatures on June 30 and July 1 to 56°F. (Fig. 1). These increased temperatures probably caused a large number of pupae to undergo metamorphosis to the adult. After a period of several days during which they darkened and hardened in their soil pupation cells, the newly developed adults appeared on the soil surface (1, p.1). These newly emerged adults were, therefore, present in the field at the time of the July 7 collection. Examination of the development of the ovaries of the specimens in the July 7 sample revealed a low average ratio (.65) of germarium advance to abdomen length (Fig. 1). This low average ratio indicated the presence of a newly emerged adult population. The single, mature weevil collected on July 7 probably emerged with the first weevils on, or about, June 7. Similarly, in the July 15 sample, the single, mature weevil belonged to the early group, while the majority of the remaining nine weevils emerged just prior to July 7. Therefore, if these assumptions are correct, there were in reality two populations of different ages present in the field after June 30. Although general oviposition by the later and more abundant population did not occur until July 24, members of the earlier and less abundant population commenced oviposition on approximately July 7.

CONCLUSIONS

The gross morphological study of the reproductive system of B. sulcatus has led to the following conclusions:

1. The suspensory ligaments of each ovary join with a large, median, proctodaeal ligament which is subsequently inserted into the ventral wall of the dorsal blood vessel.
2. The egg tubes receive extensive tracheation from the first, second and third abdominal spiracles. The presence of this tracheation readily marks the location of the egg tubes in relation to the relatively non-tracheated ovariole pedicels of each ovariole.
3. During times of extensive oviposition the egg tubes are greatly swollen with developing ova and fill the antero-lateral abdominal cavities.
4. The ovariole pedicels are greatly distended in ovipositing adults and serve for the storage of many mature eggs.
5. A change in the tissue of the lateral oviducts appears to mark the union of mesodermal and ectodermal tissues.
6. The median oviduct and vagina are a continuous tube leading to the vulva.
7. Although this species is entirely parthenogenetic, both the copulatory pouch and spermatheca are present in full detail.
8. The ovipositor has as its base the first valvifers which fuse with the large sclerotized lateral plates, the second valvifers. The membranous first and second valvulae or ventral and dorsal lobes, respectively, are largely obscured by the second valvifers which overlap them. Each second valvifer gives rise to a gonostylus at its apex.

A study of the development of the internal reproductive organs during the pre-oviposition period has led to the following additional

conclusions:

9. The egg tubes of the newly emerged adult have no vitellarii. The small, undeveloped germarii are situated immediately anterior to the ovariole pedicels. Anterior to the germarium the transparent tunica propria, which extends to the anterior end of the abdomen, is an empty tube.
10. In the 15 day old adult the germarium is located slightly anterior to its previous location. A short vitellarium is apparent in each egg tube between the germarium and the ovariole pedicel.
11. In the 25 day old adult the germarium is noticeably increased in size and is located much more anteriorly. The vitellarii of each egg tube are readily apparent, with those of the right ovary having a single convolution just posterior to the germarii.
12. Under laboratory rearing conditions, the 28 day old adult has essentially a mature system. Mature eggs may be found in the calyces. The vitellarii are swollen with developing eggs and the germarii are almost at the anterior extremity of the tunica propria.
13. The developing weevils may be divided into four stages: no development or newly emerged, slight development or approximately 15 days old, some development or approximately 25 days old and full development or over 28 days old. These four stages are similar to those mentioned by Ritcher for the development of the reproductive system in Tyloderma fragariae (Riley) (10, p.13).
14. Observations of small, periodic field collections of weevils indicate that, although very few adults commenced oviposition as early as

July 7, general oviposition did not commence at Gresham, Oregon in 1954 until July 24.

15. The examination of the reproductive systems of developing weevils appears to be a successful means of determining the stage of development of the ovaries of weevils. It also aids in the prediction of the commencement of general oviposition.

SUMMARY

The gross morphology of the reproductive system of the black vine weevil, Brachyrhinus sulcatus (F.), a parthenogenetic species, is discussed in detail. There is a pair of ovaries, one on each side of the abdominal cavity. Each ovary has two ovarioles. Each ovariole is covered with a thin, transparent tissue, the tunica propria. The terminal filaments of each ovariole unite to form a suspensory ligament which joins with a large median proctodaeal ligament. The proctodaeal ligament is then inserted into the ventral wall of the dorsal blood vessel. The egg tube of each ovariole consists anteriorly of a large germarium and posteriorly of a convoluted vitellarium which contains the developing ova in follicular vesicles. The corpus luteum or yellow body is at the posterior end of the vitellarium. Posterior to the corpus luteum the ducts have very little tracheation in comparison to the heavily tracheated egg tube. The long and greatly distended ovariole pedicels contain many mature eggs. The large calyces at the union of the two ovariole pedicels of each ovary comprise the anterior ends

of the lateral oviducts. The posterior portions of the lateral oviducts are narrower than the anterior calyces and have longitudinal infoldings with faint sclerotization, the presence of which indicates the probable ectodermal origin of this part of these ducts. At the union of the lateral oviducts the median oviduct loops antero-dorsally and then postero-dorsally to enter the musculature of the vagina. The vagina is a slightly convoluted tube which leads posteriorly to the vulva at the tip of the ovipositor. The spermathecal duct enters the vagina at its antero-dorsal end and leads to the sickle-shaped spermatheca situated to the right of the vagina. A single spermathecal gland lies posterior to the spermatheca. Postero-dorsal to the entrance of the spermathecal duct into the vagina arises the diverticulum of the vagina called the copulatory pouch. The extensive musculature of the vagina serves to force mature eggs posteriorly and to aid in the eversion and retraction of the ovipositor during oviposition.

The ovipositor is a telescoped tube comprised of the coxites of the eighth and ninth sternites. The fused first and second valvifers are sclerotized lateral plates which almost meet on both the dorsal and ventral surfaces. The membranous ventral and lateral lobes, the first and second valvulae, respectively, are largely obscured by the second valvifers. Setaceous gonostyli arise apically from the second valvifers. The spiculum gastrale is a heavily sclerotized organ which serves as a point of attachment for many of the muscles which operate the mechanism for oviposition.

The development of the ovaries during the pre-oviposition period

is represented by the anterior advance and increase in size of the germarium within the tunica propria, accompanied by the formation of the vitellarium posterior to the advancing germarium. In newly emerged weevils the germarium lies posterior to the coxal cavities of the meta-thoracic leg. No vitellarium is present between the germarium and the ovariole pedicel. After approximately 15 days the germarium has advanced slightly through the tunica propria and leaves behind a short, dense follicular epithelium which is the start of the vitellarium. After 25 days the germarium is noticeably larger and more anterior. Also the vitellarium is longer and has developed a single convolution in the right ovary. Any time after 28 days the system may be fully developed with the germarium at the anterior extremity of the tunica propria and the vitellarium extensively coiled in the antero-lateral cavities of the abdomen. The calyces will usually contain mature eggs.

The examination of small periodic field collections of weevils from Gresham, Oregon during the summer of 1954 indicates that, although a very few adults commenced oviposition as early as July 7, general oviposition did not commence until July 24.

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APPENDIX

All drawings and photographs are of Brachyrhinus sulcatus (F.).

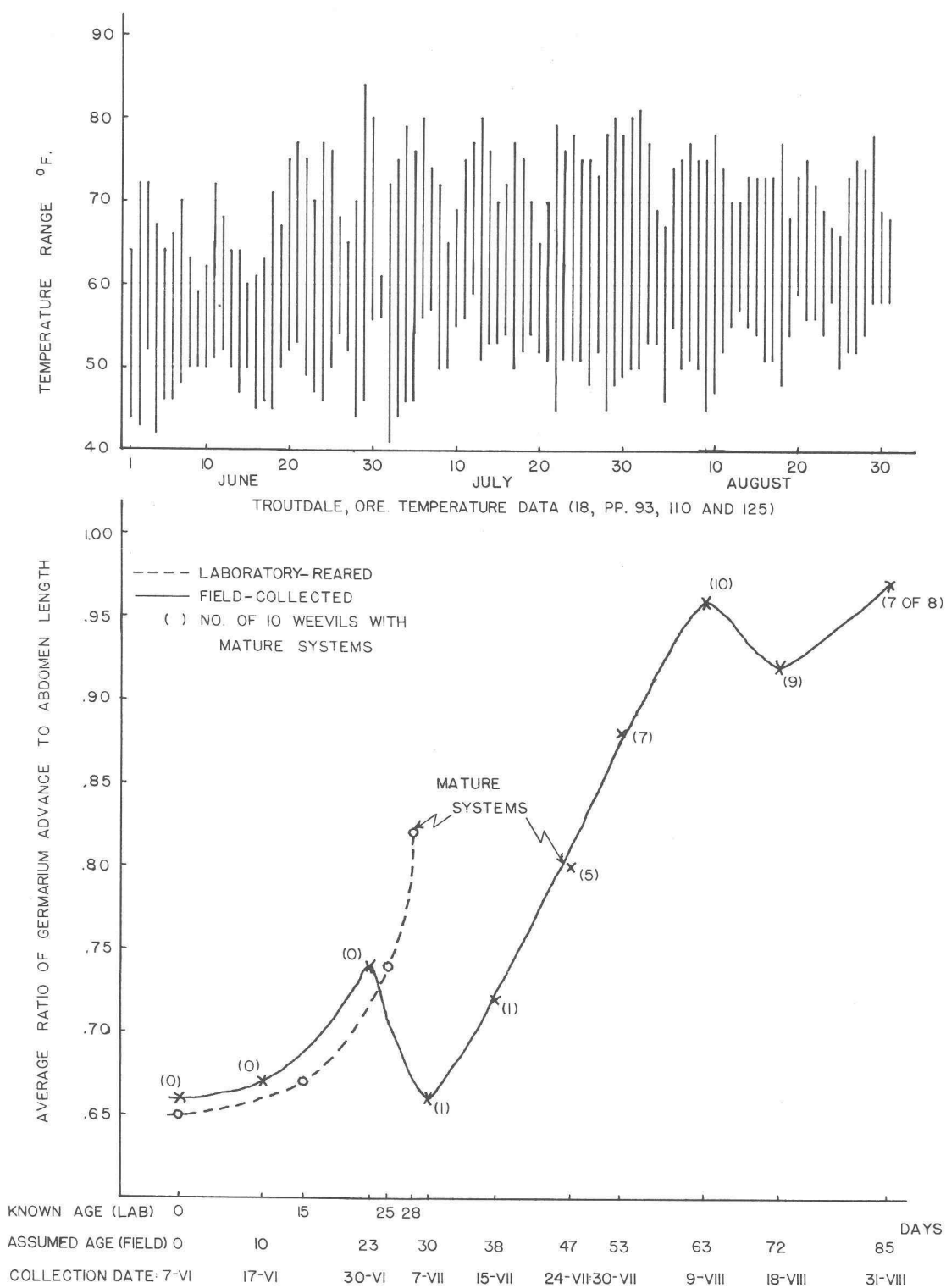
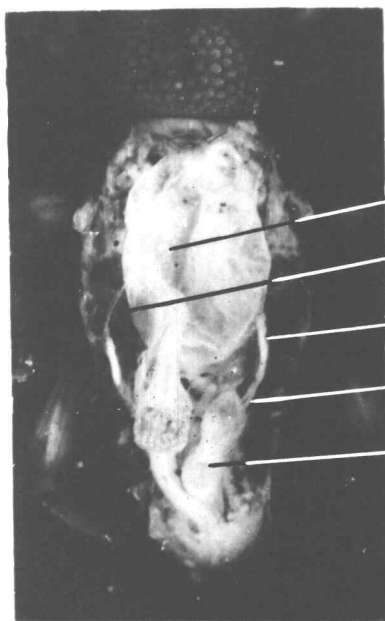
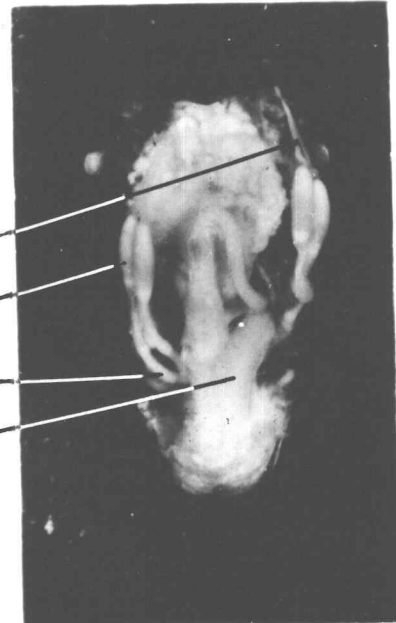


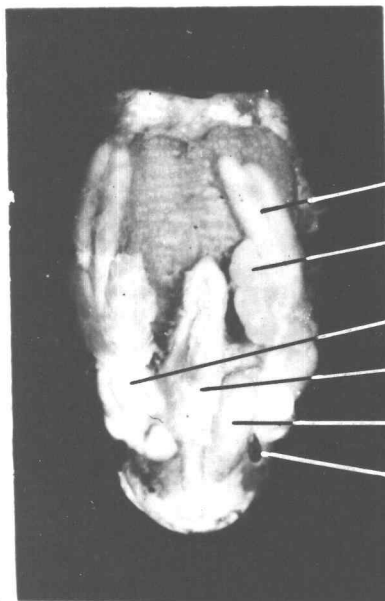
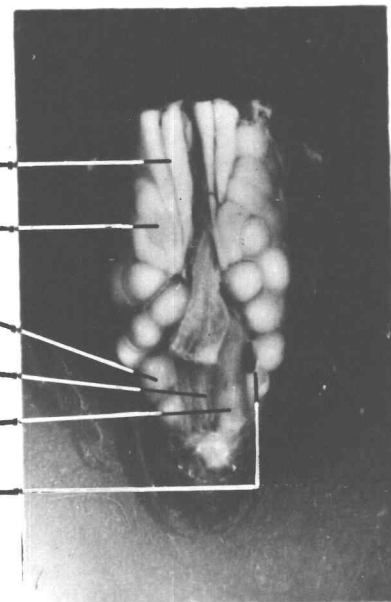
FIG. 1. RELATIONSHIP BETWEEN THE DEVELOPMENT OF THE REPRODUCTIVE SYSTEMS OF LABORATORY-REARED AND FIELD-COLLECTED WEEVILS (AVERAGES OF 10 RATIOS) WITH DAILY TEMPERATURE RANGES IN THE GRESHAM AREA DURING THE TIME OF FIELD COLLECTING.



NEWLY EMERGED ADULT



25 DAY OLD ADULT

28 DAY OLD ADULT
(JUST COMMENCED OVIPOSITION)

ACTIVELY OVIPOSITING ADULT

FIG. 2. DORSAL DISSECTIONS OF ADULTS SHOWING VARIOUS STAGES OF DEVELOPMENT OF THEIR REPRODUCTIVE ORGANS.

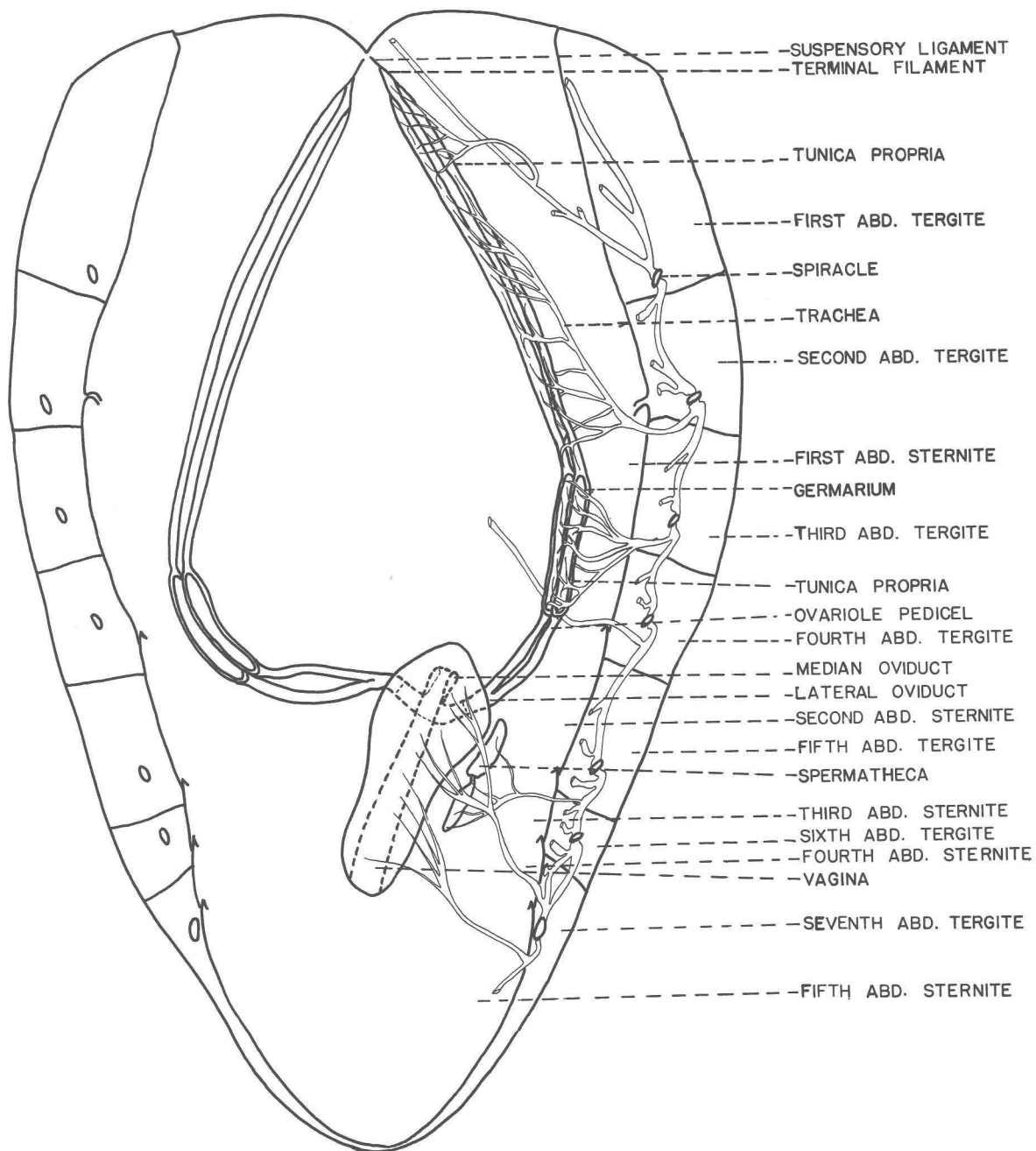


FIG. 3. DORSAL VIEW OF THE INTERNAL REPRODUCTIVE ORGANS OF A NEWLY EMERGED ADULT.

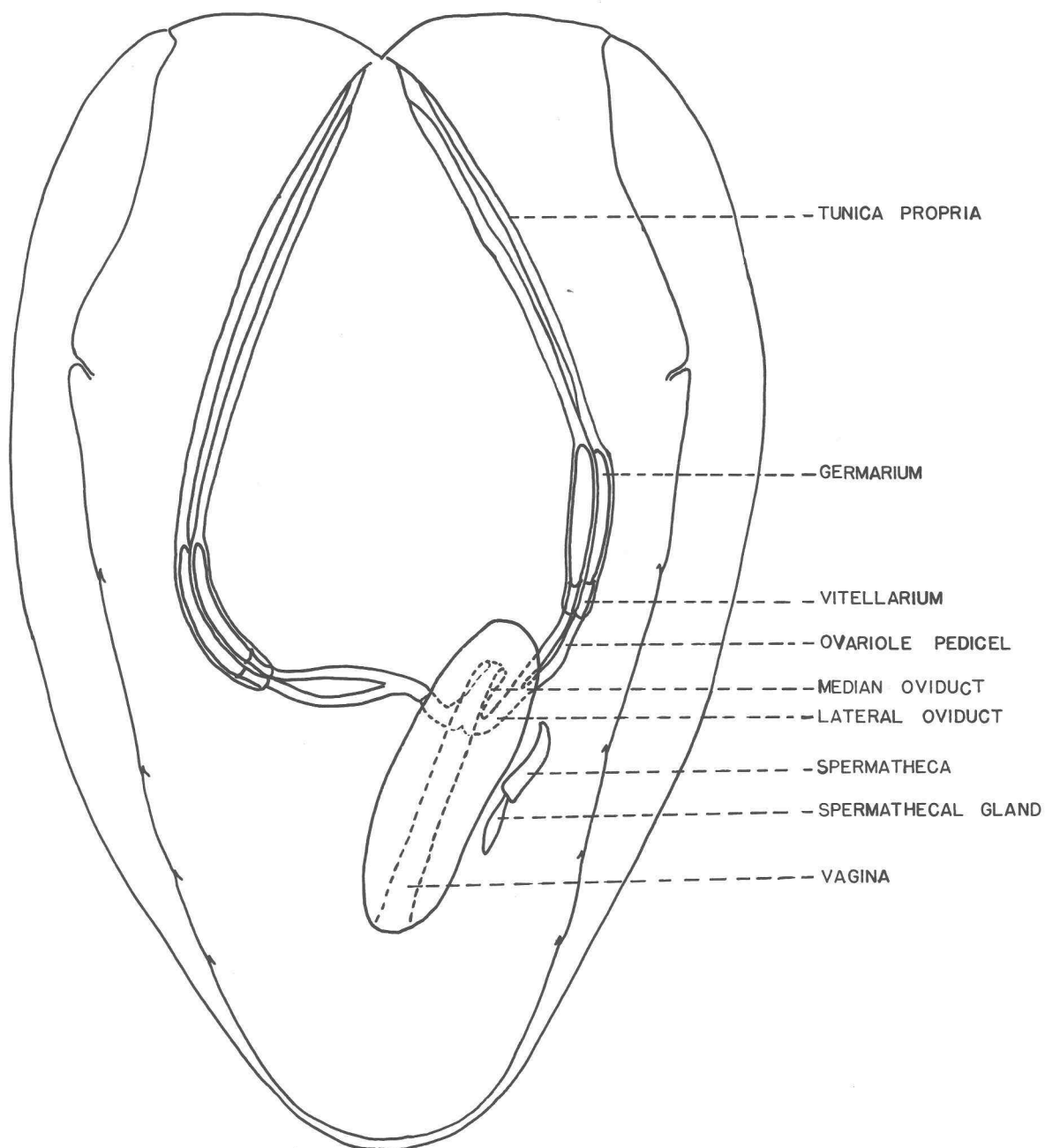


FIG. 4. DORSAL VIEW OF THE INTERNAL REPRODUCTIVE ORGANS OF A 15 DAY OLD ADULT.

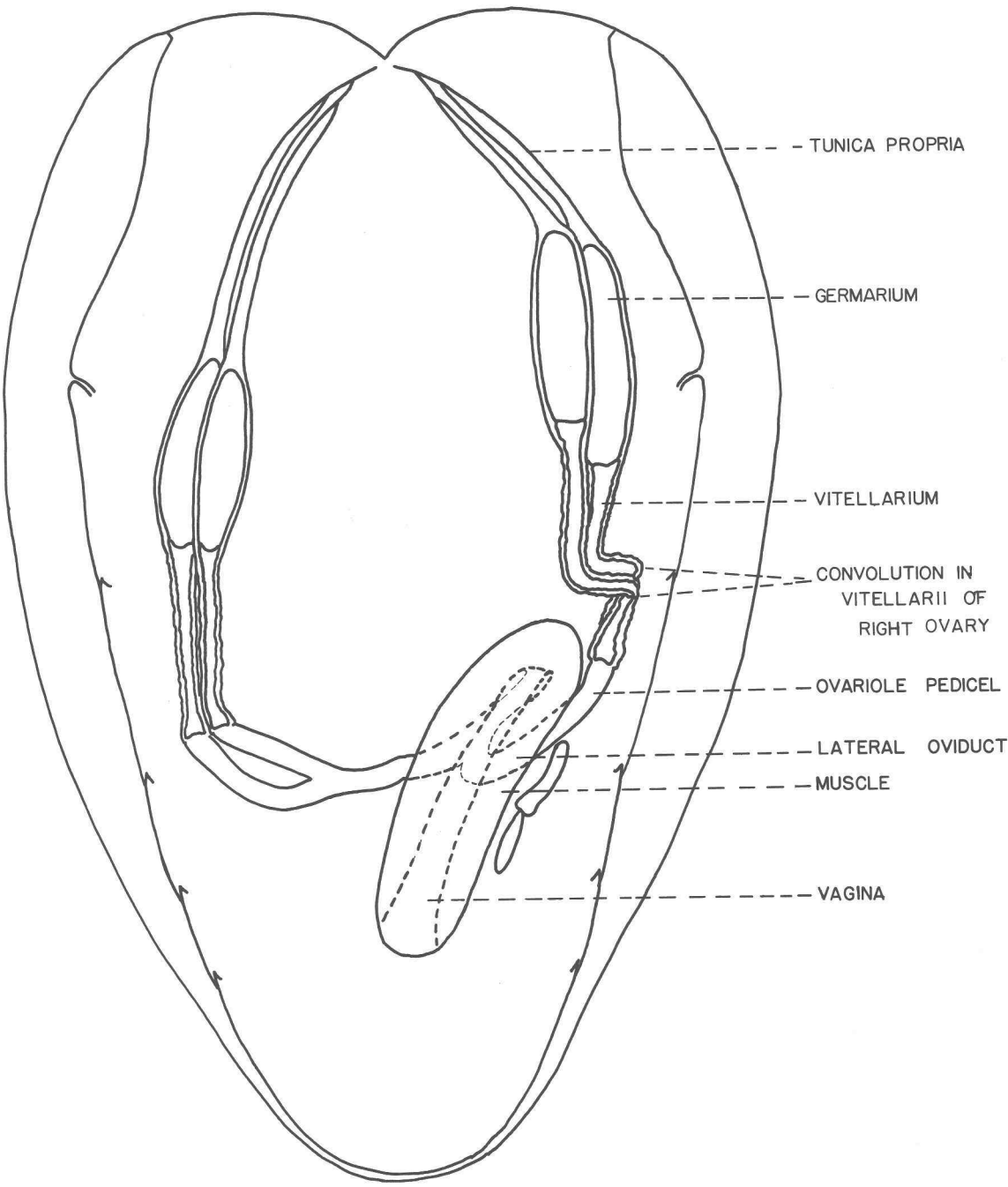


FIG. 5. DORSAL VIEW OF THE INTERNAL REPRODUCTIVE ORGANS OF A 25 DAY OLD ADULT.

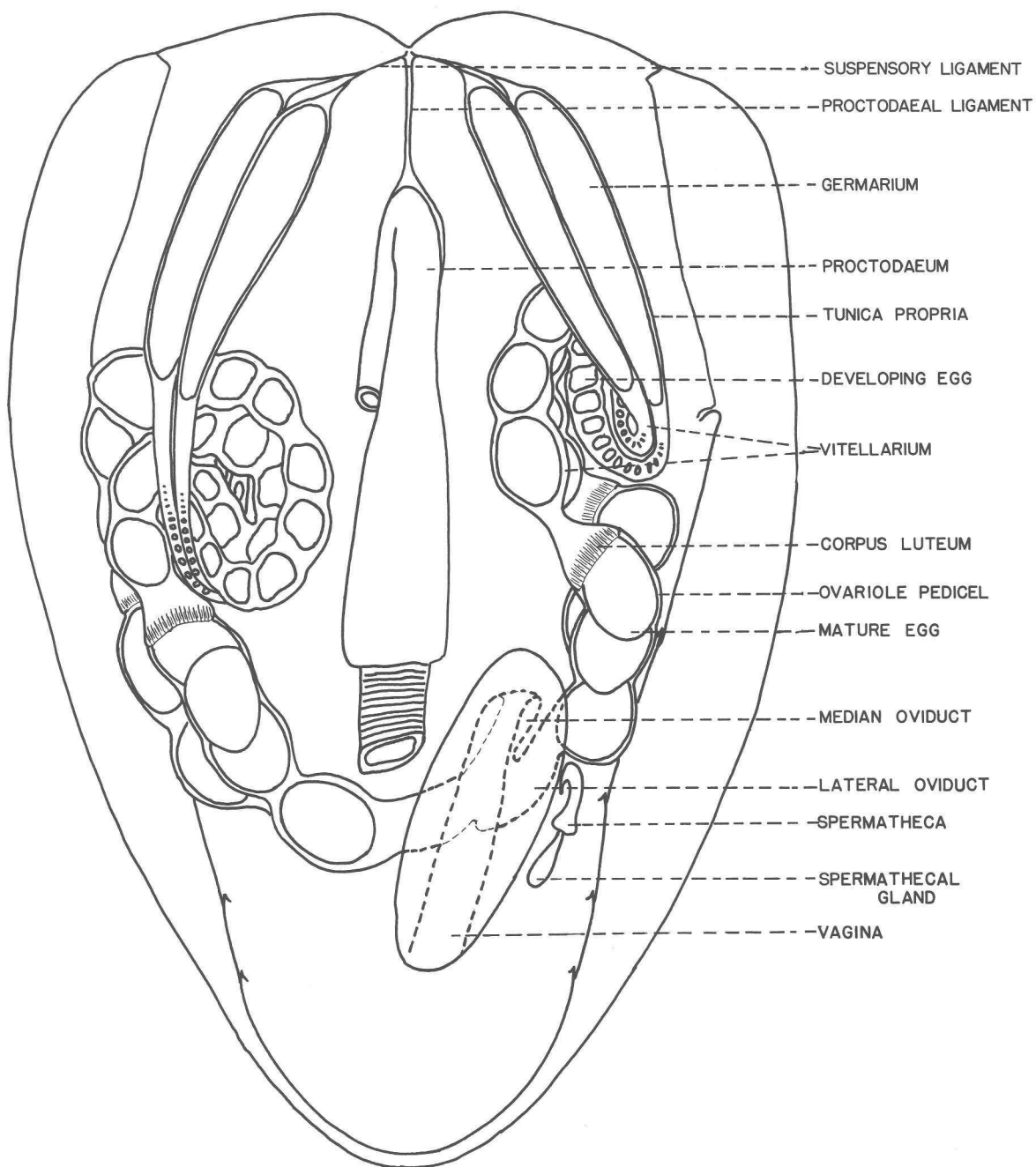


FIG. 6. DORSAL VIEW OF THE INTERNAL REPRODUCTIVE ORGANS OF A 28 DAY OLD ADULT WHICH HAS JUST COMMENCED OVIPOSITION.

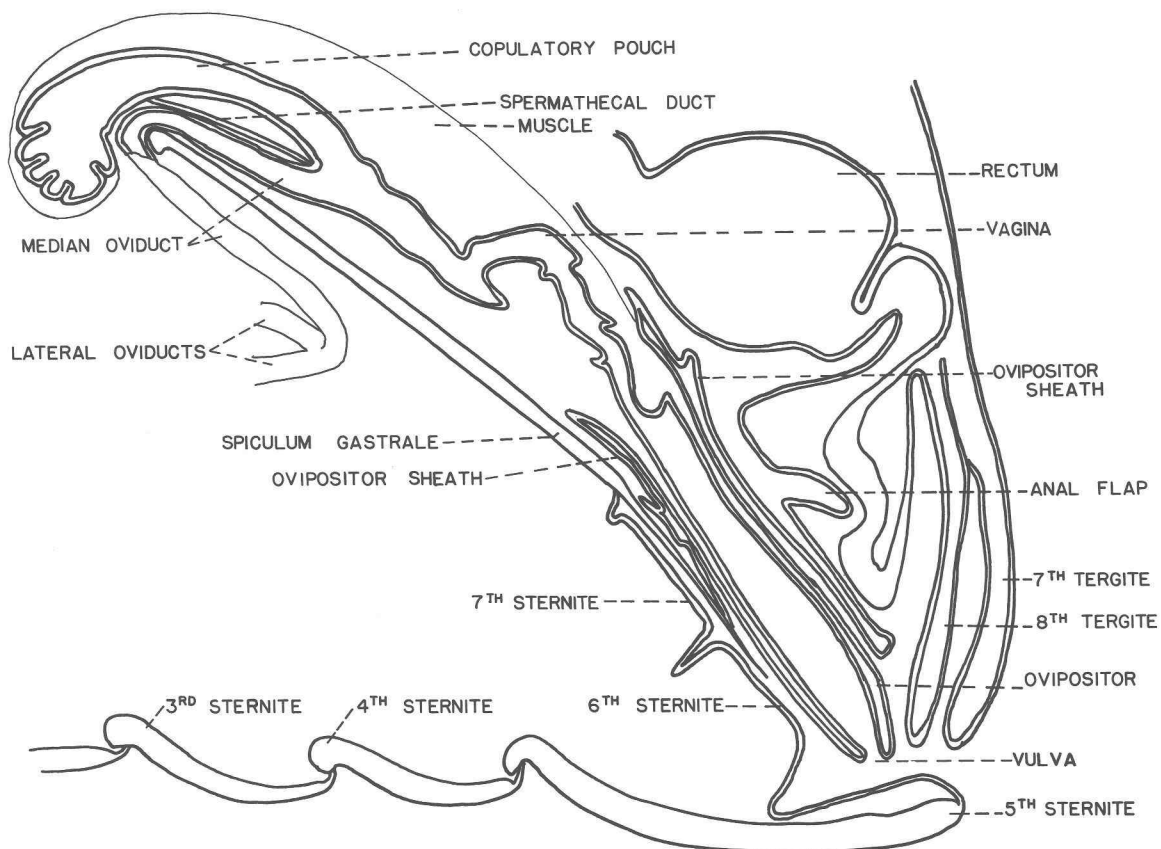


FIG. 7. MEDIAN LONGITUDINAL SECTION OF OVIPOSITOR.

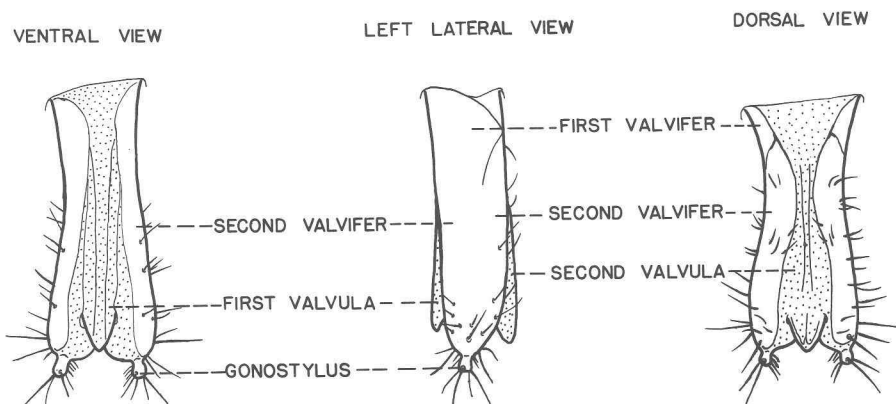


FIG. 8. OVIPOSITOR SOMEWHAT DISTENDED TO SHOW THE VARIOUS PARTS.

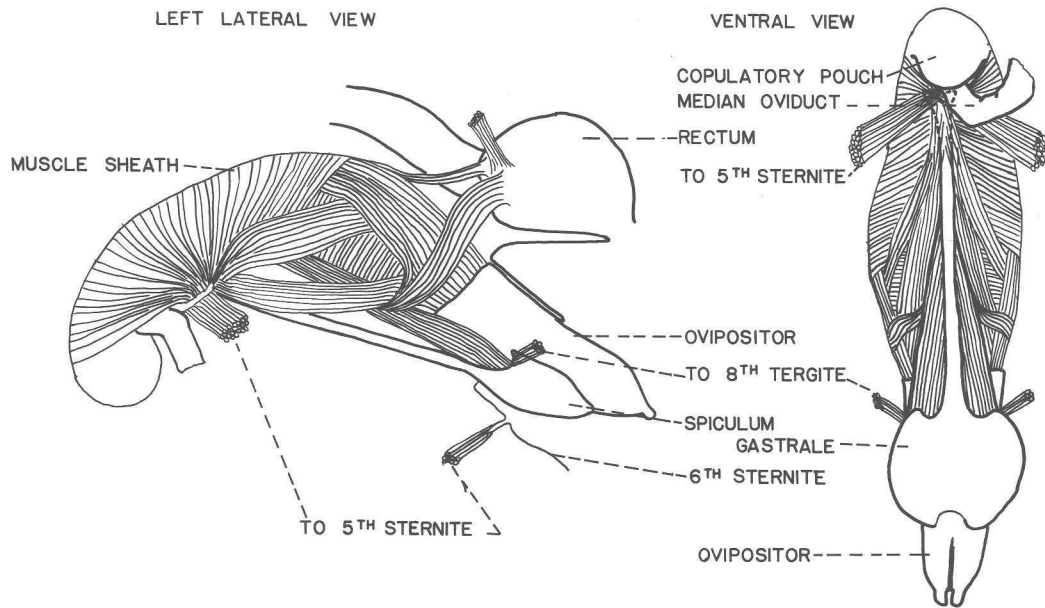


FIG. 9. PRINCIPAL MUSCLES OF THE VAGINA AND OVIPOSITOR.

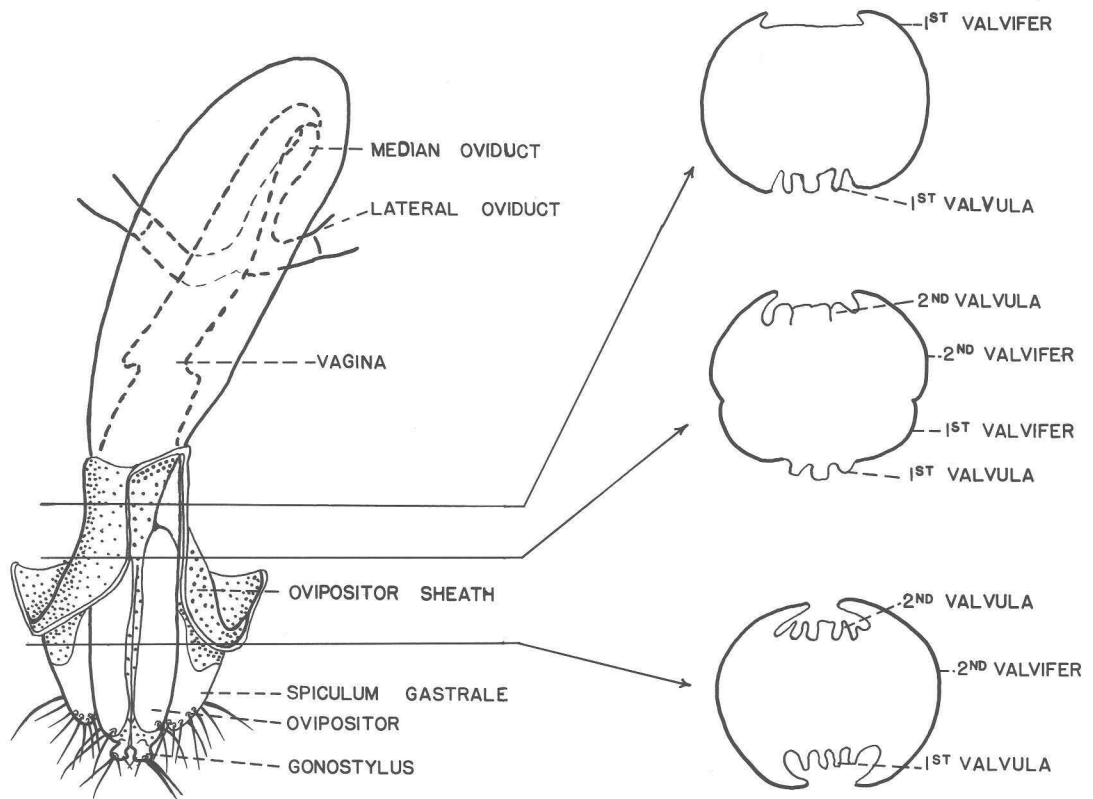


FIG. 10. DORSAL VIEW OF OVIPOSITOR.

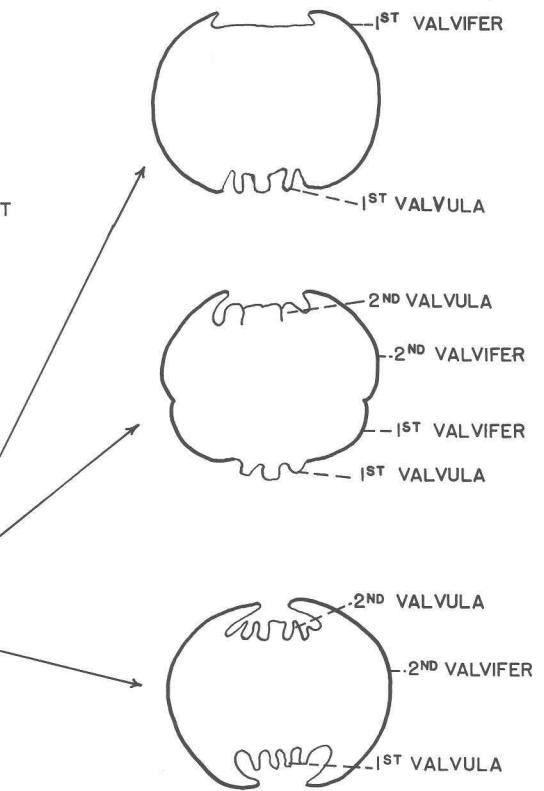


FIG. 11. CROSS SECTIONS OF OVIPOSITOR.

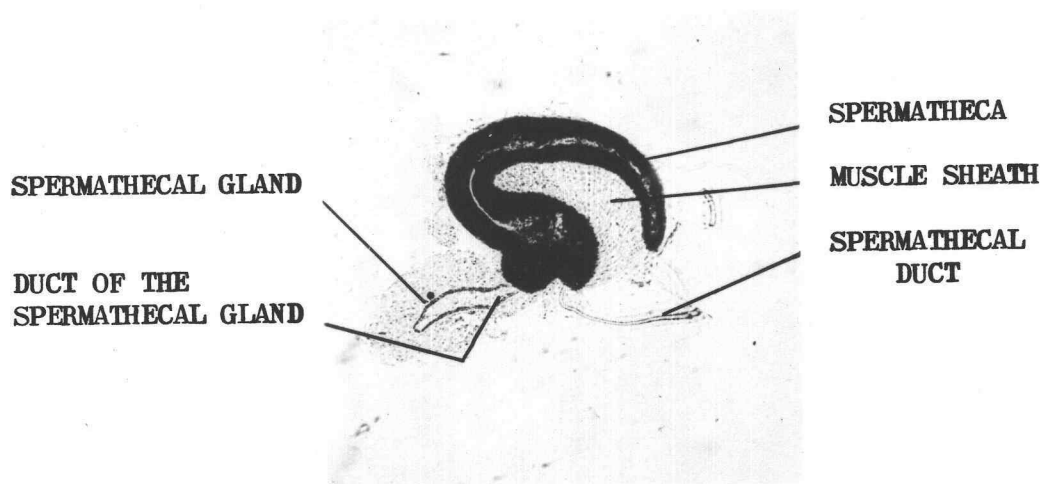


FIG. 12. RIGHT LATERAL VIEW OF SPERMATHECA AND ASSOCIATED DUCTS (GREATLY ENLARGED).

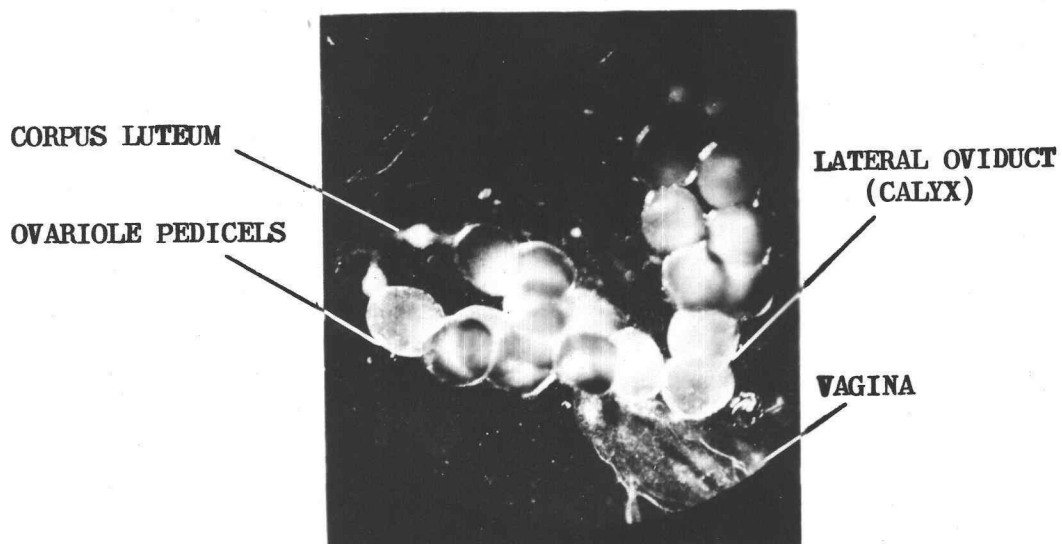


FIG. 13. VENTRAL VIEW OF MATURE EGGS IN THE OVARIOLE PEDICELS AND CALYX (GREATLY ENLARGED).