The Canadian Entomologist

Vol. 96

Ottawa, Canada, March 1964

No. 3

The Morphology and Functions of the Reproductive Systems of Dendroctonus monticola Hopk. (Coleoptera : Scolytidae)

By H. F. Canez

Forest Entomology and Pathology Laboratory, Calgary, Alberta

Abstract

The male and female reproductive organs of the mountain pine beetle, Dendroctonus monticola Hopk., are described, and interpretations given for functions of the parts on the basis of activity during mating, sperm transfer, egg formation and oviposition. Some morphological changes of the reproductive organs during the adult life cycle are also noted.

Three pairs of accessory glands associated with spermatozoa production are evident in the male beetle. One of these was previously termed the seminal vesicle. A complex muscular organ, the male genital organ during copulation. The female organs have four tetrapolar ovarioles with a posterior calyx region that has a possible accessory gland function. Evidence indicates that these organs previously termed "colletorial glands" have a digestive and reabsorbing function. The bursa copulatrix may be more closely allied with the function of the accessory glands than with the mating process. Parts of the spermathecae have been more precisely defined according to function.

Introduction

The mountain pine beetle, Dendroctonus monticola Hopk., has been the object of much investigation during the past 60 years, but few studies relating morphology to functional anatomy have been attempted (e.g. Hopkins 1909; Richmond 1935; and Reid 1958a, 1962c). Reproductive organs of North American bark beetles have generally been described to provide taxonomic information. European contributions provide more information in the field of comparative morphology (e.g. Stein 1847; Escherich 1894; Nüsslin 1911-12; Hebecker 1951; and Chancas 1956).

The reproductive organs of D. monticola were described briefly by Richmond (1935). Some of the important changes that take place in the organs of the adult male were shown by Reid (1958a, 1963). Reid (1958) also described the mating behaviour and other activities associated with fecundity. The present study was carried out during 1960-62 and describes the male and female reproductive systems from both a morphological and functional viewpoint. The terminology has been augmented and clarified in some instances. Much of this information may be applicable to other scolytids.

Materials and Methods

The mountain pine beetles were obtained from naturally infested lodgepole pine (Pinus contorta Dougall, var. latifolia Engelm.) near Invermere, British Columbia. Two rearing techniques were employed for obtaining reproductive structures in the desired stages of development and for observing adult behaviour within the egg gallery. In the first method broods of the mountain pine beetle were reared on freshly cut logs of lodgepole pine. Unmated males, unmated and mated females in the egg-laying condition and adults in the flight stage were thus available for study.

Acknowledgments

Contributions towards the costs of the publication of the Canadian Entomologist were received from the Ministère de l'Agriculture de la Province du Québec.
obtained. Secondly, observation plates (Reid 1962b) were made by scaling series of inner bark of pine between plates of transparent Lucite. A male and an egg-laying behaviour observed. The reproductive system of the male during specific periods of behaviour. Most rearing was carried out at room temperature.

Reproductive organs were fixed in either formal saline or alcohol Bouin 6-9%, stained with Delafield's haematoxylin and counterstained with cosin (Dawson 1957) and whole mounts were prepared of genital structures. Drawings were made to scale using a calibrated microtome eyepiece and a camera lucida. The terminology of the reproductive parts was obtained from Hopkins (1915), Richmond (1953), Snodgrass (1937), Franch-Grossmann (1948, 1950) and Lindroth and Pålman (1956).

Results and Discussion

General Features of the Metathorax and Abdomen

The combined abdomen (Abd) and metathorax (Metath) is roughly cylindrical and tapered sharply posteriorly. There are only slight morphological differences between the sexes in these two regions. Accordingly to English (1937) III to VIII (Fig. 1). Stermites I and II are apparently fused to sternites III and accessory structures are associated with the posterior segments. The segments that are associated with sexual differences and with attachment of the reproductive organs are described below.

Stermites VII is a prominent sclerite in both sexes (Richmond 1953) and carries an externally visible sex character. Two small submedian strip scrapper project from the posterior point of this sclerite in the male. The spicules produced by these scrapers provides a convenient method of separating the sexes of living beetles.

The tergite of the eighth segment is more conspicuous in the male; in the both sexes the eighth sternite is much reduced and is entirely concealed by the eighth tergite and seventh sternite except partly during mating and egg-laying (Figs. 4, 10). In the female the median portion is entirely membranous (Fig. 10). The lateral thickened portions of this sternite serve as points of attachment for the muscles that extend ventrally to the seventh sternite (Fig. 19). These muscles allow telescopic movement of the posterior abdominal segments.

The male reproductive system lies dorsally and entirely within the abdomen. Newly developed male has a separate system in a position similar to those of the male (SndAg) extends anteriorly from the posterior of the metathorax (Reid 1954; and 1981; and Fig. 1). The sinnusion of the main system is found on the posterior wall of the metathorax (Reid 1954; and Fig. 1). According to Reid the two systems are separate. Three pairs of dorsal longitudinal flight muscles and the tergosternal flight muscles undergo atrophy at the time of early vellelogenesis (Reid 1954; Atkins and Farris 1962).

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This study provides more data for the elaboration ovaries and may contribute nutritional material for growing oocytes (Ooc).

The posterior portion of the reproductive system is supported by muscle and membranous tissues (Figs. 4, 19). These are attached to tergites VIII and sternites VII and VIII which form the posterior enclosure of the genital opening (GenOp) and anus (An) (Figs. 4, 19, 18). In young females a tracheal network is more conspicuous over the posterior half of the ovarioles than the posterior half. During egg-laying this region expands most of the tracheal branches become more dispersed. Disappearance of the male organs was less noticeable. An important secondary role of the tracheae is to support the ovaries and testes (Tes) within the body cavity, especially during the contractions of the muscular ducts.

Male Reproductive System

The major components of the male reproductive system are two testes (Tes), each with a short vas deferens (Vd); three pairs of gland-like structures, two short seminal ducts (SndAg), a median ejaculatory duct (Jed) and a genital organ (Fig. 6).

Testis and vas deferens. The testis are dorso-ventrally flattened, bean-shaped, with structures measuring about 0.8 mm. at their maximum width. Each testis is divided into six equal follicles (Fol) (Fig. 6). At a median point on the testis a vas deferens projects posteriorly as a broad tube which apposes to almost the entire of the ejaculatory duct. Each vas deferens divides into two short vas efferents (Ve) within a testis and three testicular follicles appear to be continuous with each vas efferent (Fig. 6).

An epithelial sheath (Epsh) covers the outer testis and vas deferens. It is generally thicker at the base of the vas deferens and is continuous with the septum (Sep) which separate one follicle from another (Fig. 6). The epithelial sheath resembles a loose reticulate membrane. It has many oval-shaped nuclei and rests on basement membrane.

The four zones of sex-cell development that are generally recognized for the insect testes (Wigglesworth 1935) were not readily distinguishable but at least three of the more mature zones were seen (Fig. 14). The rate of development of the sex cells was similar in all follicles, with the earlier stage beginning at the outer extremity of each follicle and maturing toward the entrance of the vas efferentia. The spermatozoa (Spt) develop within the cysts and at maturity the spermatozoa rupture near the entrance of the vas efferentia. Dark (irregularly shaped structures believed to be remnants of ruptured cysts) were recognized near the base of the follicles (Fig. 6) but were not observed posterior to the vas efferentia. Disintegration of the cyst-cells probably takes place after rupturing as reported elsewhere for insects generally (Intono 1957).

The vas deferens and vas efferentia are thick-walled tubes with a inner lining of large epithelial cells (Figs. 6, 17). No musculature was found on the wall of either of these tubes except near the posterior region of the vas deferens wall. During early sex-cell development membranous sheaths form around the sex cells and these later produce the sperm cauda (SpCa) (Figs. 6, 14). The spermatocysts (Spt) develop within the cysts and at maturity the spermatozoa ruptured near the entrance of the vas efferentia. Dark (irregularly shaped structures believed to be remnants of ruptured cysts) were recognized near the base of the follicles (Fig. 6) but were not observed posterior to the vas efferentia. Disintegration of the cyst-cells probably takes place after rupturing as reported elsewhere for insects generally (Intono 1957).

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obtained. Secondly, observation plates (Reid 1926b) were made by sealing sheets of inner bark of pine between plates of transparent lucite. A male and egg-laying behaviour observed. This technique permitted the detection of female beetles during specific periods of behaviour. Most rearing was carried out at room temperature.

Reproductive organs were fixed in either formalin in alcohol or a mixture of Bouin 6:8:1, stained with Delafield's hematoxylin and counterstained with eosin (Daven and whole mounts were prepared of genital structures. Drawings were made to scale using a calibrated micrometer eyepiece and a few several sources including Hopkins (1911), Richmond (1915), Snodgrass (1935), Francke-Gromann (1946, 1950) and Lindroth and Palmin (1956).

Results and Discussion

General Features of the Metathorax and Abdomen

The combined abdomen (Abd) and metathorax (Metr) is roughly cylindrical, tapered sharply posteriorly. There are many internal morphological differences between the sexes in these two regions. According to Linnaeus (1758) III to VIII (Fig. 1). Stermites I and II are apparently fused to tergite III and accessory structures are associated with the posterior segments. The segments that are associated with sexual differences and with attachment of the reproductive organs are described below.

Tergite VII is a prominent sclerite in both sexes (Richmond 1935) and carries an externally visible sex character. Two small stridulatory scrapers project from tergite and provide a convenient method of separating the sexes of living beetles. The tergite of the eighth segment is more conspicuous in the male, in both sexes the eighth sternite is much reduced and is entirely concealed by the eighth tergite and seventh sternite except briefly during mating and egg-laying (Figs. 4, 10). In the female the median portion is entirely membranous (Fig. 10). The lateral thickened portions of this sternite serve as points of attachment for musculature that extends ventrally to the seventh sternite (Fig. 19). These muscles allow telescopic movement of the posterior abdominal segments.

The male reproductive system lies dorsally and entirely within the abdomen. Newly developed females have the organs in a position similar to those of the male. (Snd.Lig) extends anteriorly from each ovary (Ov) to the prepragmas (Prepo penes). Spermatozoa are stored in the prepragmas. In the present study the exact attachment was variable, and in some cases a fusion with the internal cavity of the spermatheca occurred. A small number of eggs develop the ovaries move towards the prepragmas. Three pairs of dorsal longitudinal flight muscles and the tergosternal flight muscles undergo atrophy at the time of early vitellogenesis (Reid 1924; Atkins and Faris 1962).

This study provides more room for the expanding ovaries and may contribute additional material for growing oocytes (Oo). The posterior portion of the reproductive systems is supported by muscles and musculature of various times (Figs. 4, 10). The three are attached to tegmina VIII and sternum VIII (GerOp) and anus (An) (Figs. 4, 10, 19).

In young females a tracheal network is more conspicuous over the posterior half of the ovaries than the anterior half. During egg-laying this region expands most and the tracheal branches become more dispersed. Tracheation to the male organs was not noticeable. An important secondary role of the trachea is to support the ovaries and testes (Tes) within the body cavity, especially during the contractions of the muscular ducts.

Male Reproductive System

The male genitalia are two testes (Tes), each with a short vas deferens (Vd), three pairs of gland-like structures, two short seminal ducts (SndD), a median ejaculatory duct (Edj) and a genital organ (Fig. 4).

Testes and Vas Deferentia. The testes are dorso-ventrally flattened, bean-shaped, structures measuring about 0.6 mm. at their maximum width. Each testis is divided into six equal follicles (Fol) (Fig. 8). At a median point on the testis a vas deferens projects posteriorly as a broad tube which tapers to almost the size of the ejaculatory duct. Each vas deferens divides into two short vasa efferentia (Ve) within a testis and these testicular follicles appear to be continuous with each vas efferentia (Fig. 8). An epithelial sheath (EphS) covers the outer testis and vas deferens. It is generally thicker at the base of the vas deferens and is continuous with the septum (Sep) which separate one follicle from another. The epithelial sheath resembles a loose reticular membrane. It has many oval-shaped nuclei and rests on a basement membrane.

The four organs of sperm development that are generally recognized for the insect testes (Wigglesworth 1973) were not readily distinguishable, but at least three of the more mature zones were seen (Fig. 14). The development of the sex cells was similar in all follicles, with the earliest stage beginning at the outer extremity of each follicle and maturing toward the entrance of the vas efferentia. While the testis contains two spermatogenic sheaths form around the sex cells and these latter produce the spermatozoa (SpGar) (Figs. 8, 14). The spermatids (Spex) develop within the cyst and at maturity the cyst membranes rupture near the entrance of the vas efferentia. Dark irregularly shaped structures believed to be remnants of ruptured cyst-cells were recognized near the base of the follicles (Fig. 8) but were not observed posterior to the vas efferentia. Disappearance of the cyst-cells probably takes place after rupturing as reported elsewhere for insects generally (Lampe 1957).

The vas deferens and vas efferentia are thick-walled tubes with an inner lining of large epithelial cells (Figs. 8, 17). No muscular tissue (Mc) was found on the wall of either of these tubes except near the posterior region of the vas deferens (Fig. 17). The anterior portion of the vas deferens becomes distended in all mature males and contains large masses of fully developed sperm (Fig. 17). This tube and the vas efferentia perform the function of sperm storage and therefore constitute the seminal vesicle (Svn). Previous workers have referred to the posterior accessory gland (Figs. 1, 4, 15) in male beetles as the seminal vesicle (Hopkins 1915; Richmond 1915; Atkins and Chapman 1977; Ryan 1959), but
there was no evidence for this in D. vonchicale, In terenale the quantity of mature spermatocytes increased within the vasa deferentia and vasa efferentia for the larval
separated sexually mature males of Tryphonotus lineatus (Olbr.) from young
males on the basis of sperm accumulation in the vasa deferentia and found no
sperm within the “seminal vesicles”. Francke-Groszmann (1950) reported that
the vasa deferentia in D. micans Kug. also perform the function of seminal vesicles
(“Semenblase”).

Testes male are apparently sexually mature when they emerge from the host
tree since their tissue always contains mature spermatocytes, but mating seldom
occurs before emergence (Reid 1958b). The time of sexual maturity in D.
micans and in D. pseudotangae Hopl. (Francke-Groszmann 1950; Vite and Rudin-
sky 1977) is similar to that in the mountain pine beetle.

LIST OF ABBREVIATIONS

Abd, abdomen
AcG, accessory gland
AcG1A, accessory gland A
AcG1D, accessory gland A duct
AcG2AFL, accessory gland A fluid
AcG2G, accessory gland B
AcG3G, accessory gland cell
Adu, aorum
Anl, anlebe
Apok, apode
Arr, arm of anchor
Bou, buccal apparatus
BoV, basal ovary
Cbo, chitin
Cch, corpus choroideum
CCh, eye
Ce, eye
CMe, circular muscle
CmpMe, compressor muscle
Cmhn, connective membrane
Cot, cuticle
Cym, epycranian
DFd, ejaculatory duct
EpEp, epithelial plug
EpEp, epithelial sheath
Fod, follicle
FolEp, follicular epithelium
Fux, fusion
Gc, genal opening
Gcr, gomphon
Gyr, gynipore
Ila, lateral lobe of internal sac
IlaMc, longitudinal muscle
IlaOd, lateral odont
IlaPm, lateral lobe of penis
Im, inner
M, M., muscles of male genitalia
Me1, muscle
Men, metaxenon
Mih, middle lobe of internal sac
MOd, median odonot
Myc, myocytes
Nc, muscle
N, nucleus
Nod, nucleolus
Oc, oocyte
Oc1, ootid
Or, ovary
Ov, ovule
Pit, penis
Prv, prothoracic epipharynx
Prp, prothoracic epipharynx
Rec, rectum
S, seminal
Sd, seminal
Sent, seminal fluid
Sentr, seminal vesicle
Spcl, spicle
SpG, sperm gland
Spn, spine
Sppl, sperm plug
St, spermatophore
Sph, spermatheca
Spm, spermatic sheath
SpmB, spermathecal duct
SpmP, spermathecal pump
SpmS, spermathecal sac
SpmW, spermatic valve
Spz, spermatic
Spor, spermatogonia
T, tegument
Tg, terebra
Tm, tegmen
t
Tf, terminal filament
Trp, terostrate
Trz, transitional zone
Vag, vagina
Vag, vas deferens
Ve, vasa efferentia
Vex, vasa efferentia
Vex, vaginalis
Vms, vasa efferentia
X, possible gland structure
X, fluid of X-structure
Y, possible atrium structure
Y, yolk

Figs. 1-4. 1, Lateral view of male and female reproductive organs during copulation.
2, Diagram of male accessory glands and ducts. 3, Transverse view of duct of accessory gland
A, vas deferens and X-structure. 4, Ventral view of male reproductive system with genital
organ in internal position.
there was no evidence for this in D. monicae. In general, the quantity of mature spermatozoa increased within the vas deferens and vasa efferentia for the first separated sexually mature males of Trypeta melanosoma (Oliv.) from yong sperm within the "aminal vesicles". Francke-Gromann (1950) reported that the vasa deferentia in D. micans Kug. also perform the function of seminal vesicles ("aminalvese").

Testicular mites are apparently sexually mature when they emerge from the host tree since their taste always contain mature spermatogenesis, but mating seldom occurs before emergence (Reid 1958b). The time of sexual maturity in D. micans and in D. pseudomelas Hopk. (Francke-Gromann 1950; Vités and Rudinsky 1957) is similar to that in the mountain pine beetle.

LIST OF ABBREVIATIONS

Abd, abdomen
AgG, accessory gland
AgGI, accessory gland A
AgGIc, accessory gland A duct
AgGIb, accessory gland B
AgGc, accessory gland C
AgGd, accessory gland D
c
AgGIe, accessory gland cell (Ile)
An, anus
Aope, anopale
Arv, arista of antenna
Bou, buccula copulatrix
BoT, basal oostegite
Cho, chitin
Cil, corpus linear
Cilc, cilia
Cm, cercus
Cmcl, circular muscle
ComPM, compound muscle
ConM, connective membrane
Cor, corne
Cyt, cytoplasm
EID, excretory duct
EpE, epidermal plug
Eplb, epidermal sheath
Fix, follicle
FoEpf, follicular epithelium
Fm, femur
GenOp, genital opening
Germ, germarium
Gyr, gonopore
Int, internal sac
IntL, lateral lobe of internal sac
lMCL, longitudinal muscle
LOCL, lateral oviduct
LOPo, lateral ovoid
Lb, lumen
M., m. muscles of male genitalia
Md, muscle
Ment, mentomebman
MLb, medial lobe of internal sac
MOOl, median oviduct
Myct, mycetocyte
Nac, median
Nuc, nucellus
Oec, oocyte
Oec, oecum
Oen, oenocyte
Ovi, ovule
Pr, penis
PrEt, epiploric epithelium
Prep, prepragnum
PrSc, proscroum
S, spermatophore
Scl, sclerite
SensPr, sensilla of penis
Sep, sperm
SdD, seminal duct
SdF, seminal fluid
SdL, seminal lobe
Sdv, seminal vesicle
Spd, spicule
SpEc, spermatocyte
Sph, spermaphore
SpM, spermatotheca
SpMSc, spermatic duct
SpMScP, spermatophalangeal pump
SpMScS, spermatic sac
SpMScV, spermatophalangeal valve
SpS, spermatozoa
SpSg, suspensory ligament
Tgm, tegmum
Ten, testis
To, torma
Trl, terminal filament
Tro, tracheal propria
Trt, trachae
Tn, tenebrivae
Tz, tritromatine range
Vag, vagina
VAc, vas deferens
VAc, vas efferens
VAc, vaefer
c
Volv, volvulus
VoL, vitelline membrane
X, possible gland structure
XpF, fluid of X-systeme
Y, possible sensory structure
Ylk, yokk

Figs. 1-4. 1, Lateral view of male and female reproductive organs during copulation. 2, Diagram of male accessory glands and ducts. 3, Transverse view of duct of accessory gland. 4, Ventral view of male reproductive system with genital organ in internal position.
Mature spermatozoa are long and thread-like (4x, length 0.116 mm.) with head and flagellar mechanisms. The head contains a single nucleus, and the flagella are long and sinuous. The flagella extend from the anterior end of the spermatozoon and are used for movement through the female reproductive tract.

The accessory glands of the male reproductive system are complex and varied. They produce substances that aid in the transport and nourishment of spermatozoa. The accessory glands include the seminal vesicles, the prostate gland, and the Cowper's glands. The seminal vesicles produce a thick, frothy fluid rich in fructose, which provides energy for sperm motility. The prostate gland secretes a fluid that contains enzymes that break down the gelatinous semen, and the Cowper's glands secrete a clear fluid that lubricates the urethra.

In females, the accessory glands play a crucial role in ovulation and fertilization. The ovaries produce eggs and are surrounded by the corpus luteum, which produces the hormone progesterone during pregnancy. The Fallopian tubes transport the egg to the uterus, and the uterus prepares for implantation if fertilization occurs. The cervix is the lower part of the uterus and is responsible for expelling the fetus if necessary.

The transport system of the male reproductive system includes the epididymis, the vas deferens, and the urethra. The epididymis is a convoluted tubule where sperm matures and becomes motile. The vas deferens transport sperm from the epididymis to the seminal vesicles. The urethra is a tube that carries semen from the base of the prostate gland to the outside of the body. The女孩子生殖系统包括卵巢、输卵管、子宫、宫颈和阴道。卵巢产生卵子，卵巢周围有黄体，孕时分泌黄体酮。输卵管输送卵子到子宫，子宫为胚胎提供生长环境。宫颈是子宫的下部，分娩时胎儿由这里排出。

The female reproductive system is designed to facilitate reproduction. The female ovulates, or releases an egg, in response to the hormone luteinizing hormone (LH) from the pituitary gland. The egg travels through the Fallopian tubes to the uterus, where it can be fertilized by a sperm. If fertilization occurs, the fertilized egg, or zygote, implants in the uterine wall and begins to divide and form a developing embryo. If fertilization does not occur, the egg is released and the female enters a new cycle.

The male reproductive system is designed to ensure the delivery of sperm to the female reproductive tract. The testes produce sperm cells, which are transported through the epididymis and vas deferens. The sperm is released into the urethra, which leads to the penis, allowing it to exit the body during sexual intercourse. The transport system also includes the urethra, which carries urine from the bladder and semen during ejaculation.
Mature Spermatozoon is long and thread-like (av. length 0.116 mm.) with in- and also by muscular contractions of the posterior vas deferens and ejaculatory \nconspicuous heads. They move through the vas deferens by their own muscular duct. The vas deferens leads directly to the funnel (Fig. 2) to some visibility in the general morphology of the testes and the pine beetle. The vas deferens in D. valens Lec. are visible externally as each testis subdivided into two equal lobes (Hopijs 1911). In D. imicatu the vas (Francke-Grossmann 1930). The arrangement in D. pseudotangenti (Ryan 1919) monticola has each testis subdivided with short vas efferentia visible external to the testes. This variation was illustrated by Richnaden 1915.

Accessory glands. Three pairs of gland-like structures (AcGila, AcGIB, were also located in six other Dendroctonus species and are similar to those found in D. monticola. Two pairs of the therefore regarded as accessory glands A and B, but the function of the glands has been termed the seminal vesicle and the more anterior as a mucous or accessory gland (Hopijs 1917). These two vessels run forward from the base of the testes. (Fig. 3). The seminal fluid is secreted from these glands and enters the seminal vesicle before entering the ducts of the spermatozoa. (Fig. 4). The Ejaculatory duct. The ejaculatory duct (EJD) divides anteriorly into two short branches (SnMd) and all portions appear to be identical in structure and function. The two branches terminate at a median position on the posterior end of accessory gland B and are usually termed seminal ducts (Fig. 4). The ejaculatory duct is lined with a thick-walled muscular tube which conducts the seminal fluid released from the testes and accessory glands (Fig. 10). Its wall consists of several layers of circular muscles (CMc) with an inner longitudinal epithelium (Fig. 10). No distinct intra fluid was observed. The posterior end of the ejaculatory duct is fixed to the genital organ.

Genital organ. The genital organ consists of four sclerotized structures with associated muscle and membrane tissues (Figs. 4, 5), and forms the seminal duct fluid to the female during copulation. Its secretory parts include the penis (Pen), and its accessory apparatus consisting of seminal vesicle (SnMod) and anchor (Anch), its capacity and structure of the seminal vesicle. The seminal vesicle (SnMod) and sperm (Sp) attached to the penis (Pen) in the two principal sections of this organ, one accompanying the penis and the tegmina and spermatic region adjacent to the penis but are attached to it by muscle and membrane.

The penis is tubular with a basal orifice (BOE) at the anterior rim and an orifice (Or) at the posterior end (Fig. 5). Two heavily sclerotized regions and three additional segments of the lateral walls of the main body of the penis. These serve as points of attachment for muscles connecting to all of the accessory sclerites associated with the penis except the spinous lobes (Apod) extend anteriorly from the lateral walls of the main body of the penis. These serve to separate the muscle body from the external sheath to eject the glans. The accessory glands are of two main types, the anterior wall is thin, rigid and rectangular and yellow in fresh preparations. An X-sclerotized substance (XSF) is usually present within the bulbous. Both glands are not uncommon in the Polyphaga (Insect 1977).

Accessory gland B. This is circular, flattened anteriorly and posteriorly, and has six to seven defined lobes (Figs. 2, 4). The lobes are postero-
The penis has three sensory areas (SensPen), one at the ventral posterior end and one on each of the dorsal lobes (Fig. 5). These areas have many short conical sensilla (Fig. 7) which probably function as tactile receptors.

The internal accessory apparatus is fixed to the inner dorsal wall of the penis and moves in a hinge-like manner. At this point the postpenis body, termed end plates by Hopkins (1915) and Francke-Gromann (1948).

The internal accessory apparatus appears to serve three functions. It provides posterior support for the ejaculatory duct, provides the gonopore (Gort) for the seminal fluid (S) during copulation. Hopkins (1915) suggested a valve-like function for the internal apparatus in D. solen but this was doubted by Sharp and Muir (1912). No evidence was found to suggest a valve-like function for either the seminal rod or the anchor in the mountain pine beetle. The ejaculatory duct does not join the anterior end at the median point on its dorsal side, and is attached to the anchor as well as to the seminal rod (Figs. 6, 13). This arrangement corresponds closely to the condition reported for D. micans (Francke-Gromann 1948). The gonopore of the internal structure lies between the areas of the anchor and the seminal rod (Fig. 6).

The internal sac (IntS) is a membranous component of the penis. It connects to the arm of the anchor and encloses the internal accessory apparatus, which is fixed to the accessory apparatus. The internal sac is also continuous with the end of the penis (Figs. 11, 12). When fully coiled for mating (ML), that is partly coiled from the dorsal side and with two prominent lateral lobes (LL), the lateral lobes have an uneven distribution of conical spines. The lateral lobes become smaller towards the posterior tip of the lobes and no conical spines were observed on their ventral side. A small, circular, yellow structure (Y) lies at the posterior tip of the median lobe and appears to serve a sensory function (Figs. 12, 16). The outer wall is mucus and cytoplasmic differentiation is suggested (Fig. 16). A similar structure was observed in D. micans by Bollag (1928) who suggested that it serves a role in sensing and regulating blood pressure within the sheathed sac.

The tegmen is a narrow, U-shaped sclerite located on the ventral side of the penis with the ends curved dorsally. It is situated near the posterior end of the abdomen, and may be partially sclerotized. The tegmen provides muscle attachments and during copulation it is circular in cross-section and has a central canal extending through most of its length. From the posterior end it curves laterally and posteriorly and divides into two posterior prongs. The larger of these is the smaller bends dorsally on the opposite side. The two prongs form a semi-loop around the penis. Muscles are attached to all three terminal points of the spicile as well as to the transverse portion of the larger prong. The spicile provides the major support for the genital organ (Figs. 4, 9, 10).

**Musculature of the genital organs.** Muscles M, M, and M are paired and one of each pair originates from near the tip of the two posterior spicile prongs (Figs. 9, 10). These hold the spicile relatively stationary. M is attached to the...
The penis has three sensory areas (SensPm), one at the ventral posterior end sensilla (Fig. 5) which probably function as tactile receptors. The internal accessory apparatus is fixed to the inner dorsal wall of the penis, near its posterior end and moves in a hinge-like manner. At this point the posterior seminal groove and dorsal plates by Hopkins (1911) and Francke-Graumann (1948).

The internal accessory apparatus appears to serve three functions. It provides posterior support for the ejaculatory duct, orients the gonopore (Gp) cistern. Hopkins (1911) suggested a valvular function for the internal apparatus found to suggest a valvular function for the anterior seminal rod or the anchor in of the internal apparatus as suggested by Richmond (1915), but rather at a more internal rod and is attached to the anchor as well as to the seminal rod (Figs. 6, 13). This arrangement corresponds closely to the concretion rod of D. micans (Francke-Graumann 1948). The gaskets of the ejaculatory duct lies between the arms of the anchor and the seminal rod (Fig. 6).

The internal sac (IntS) is an important membranous component of the penis. It connects to the arms of the anchor and encloses the internal accessory apparatus. The ejaculatory duct is external to the sac except for the terminal end which is fixed to the accessory apparatus. The internal sac is also composed of the internal sac is seen as a thin, semi-transparent membrane with a large median lobe (ML) and a lobe-like lateral lobe (LLh). Two patterns of spiny sclerites are present on the outer surface of the lobe (Figs. 11, 12). The lateral lobes have an even distribution of spines and the median lobe has smaller spines in evenly spaced groups. The latter spines become smaller towards the posterior tip of the lobe and no sclerites were observed on the ventral side of the lobe and appear to serve a sensory function (Figs. 12, 16). The outer wall is firm and may be partly sclerotized. It is nucleated and cytoplasmic differentiation is suggested (Fig. 16). A similar structure was observed in D. micans by Hopkis and in the "epithehial body". She suggested a role in sensing and regulating blood pressure within the ejaculatory duct.

The tegmen is a narrow, U-shaped sclerite located on the ventral side of the penis with the ends curved dorsally. It is situated near the posterior end of the esopodes. The tegmen provides muscle attachment and during copulation it is circular in cross-section and has a central excav extending through most of its length. It is slightly enlarged at the anterior end where it rests in a median dorsal and posteriorly and divides into two posterior prothoraces. The space of these is the smaller bend dorsally on the opposite side. The two prothoraces thus form a semi-loop around the penis. Muscles are attached to all three terminal points of the spicule as well as to the transverse portion of the lateral prothorace. The spicule provides the major support for the genital organ (Figs. 4, 9, 16).

Musculature of the genital organ. Muscles M1, M2 and M3 are paired and one of each pair originates from near the tips of the two posterior spicule prothoraces (Figs. 9, 10). These hold the spicule relatively stationary. M3 is attached to the
inside lateral margins of tergum VIII. M. connects to the inside lateral margins of sternum VIII and M. extends ventrally and posteriorly to sternum VIII.

A single muscle, M., is attached to both spicule prods and completes a loop around the posterior end of the penis (Fig. 9). The connecting membrane passes between this loop and the penis. Relaxation and contraction of M. probably controls the rigidity of the genital organ while it is extended during mating activity. It also serves as a guide through which the penis can slide.

Muscles M. and M. also attach onto the spicule but oppose one another in function. M. originates on the anterior end of the spicule and divides with one branch passing around each side of the epodemes extending to the lateral arms of the tegumen (Figs. 9, 10). Muscle M. forms a single band extending from the tegumen to the transverse portion of the spicule. When the genital organ is internal, M. is relaxed while M. is contracted (Fig. 9).

Muscle M. is paired, one muscle extending on the ventral side of the penis from each of the anterior epodemes tips to the anterior projection of the tegumen (Fig. 9). The ejaculatory duct passes between the two muscles to enter the penis tube. Part of the function of these muscles is to retract the penis after copulation. They may also lessen lateral movement of the anterior end of the genital organ during copulation.

Muscles M. and M. withdraw the internal sac after copulation. M. consists of two large muscles that originate from the anterior tips of the epodemes (Fig. 9). They extend posteriorly within the penis tube where each divides into at least three branches. One branch from each muscle attaches to the anterior end of the internal accessory apparatus while the other two branches spread out over the lining of the internal sac (Figs. 11, 12). Muscle M. is also paired and extends from the inside lateral wall of the lateral lobes to the wall of the median lobe (Figs. 11, 12).

Exversion of the genital organ. Observations were made on the musculature of the genital organ when fixed in the internal (Fig. 9) and external (Figs. 10, 11, 12) positions. Exversion begins with the contraction of M. and M. with a simultaneous relaxation of M. Contraction of M. probably causes a slight counter clockwise rotation of the penis to orient the gonopore dorsally. The activities of these muscles project the penis posteriorly through the genital opening. The anterior tips of the epodemes and the tegumen are pulled posteriorly to the transverse portion of the spicule (Fig. 10). A relaxation of M. and the lateral muscles of the eighth sternum probably facilitates the projection of the penis. Muscles M. and M. may also shift the spicule nearer to the posterior abdominal wall. At this stage the penis is at maximum extension for copulation (Figs. 10, 11).

The internal sac is unfolded after the penis is extended. Exversion of the sac is probably caused by blood pressure with a simultaneous relaxation of muscles M. and M. At the sac is forced backward the unfolded posterior sclerotizations of the penis fold out laterally, curving the sac and the internal accessory apparatus posteriorly. This movement swings the seminal rod and anchor backward at a slight angle to the penis. Fronckel-Grotrmann (1948) suggested that the stiffening and pumping action of the muscular ejaculatory duct also helps to force the accessory apparatus posteriorly. The internal sac finally unfolds in balloon-like fashion, bringing the gonopore adjacent to a mid-dorsal point at the base of the median lobe (Fig. 11). The internal sac is completely everted only when in the vagina. Retraction of the male genital organ progresses in a reverse manner to eversion.

Female Reproductive System

The female reproductive system consists mainly of two ovaries (Ov.), each with a pair of oviducts (Ovd.), a suspensory ligament (Sus.Lig.) for each ovary, two short lateral oviducts (L.Ovd.), a median oviduct (M.Ovd.), a burst copulatory (Bcoph.), a spermatheca (Spin.) and a pair of accessory glands (Ac.Gi.) (Figs. 18, 22).
inside lateral margins of tergum VIII. Ml connects to the inside lateral margins of sternum VIII and M2 extends ventrally and posteriorly to sternum VIII.

A single muscle, M, is attached to both spicule prongs and completes a loop around the posterior end of the penis (Fig. 9). The connecting membrane passes between this loop and the penis. Relaxation and contraction of M probably control the rigidity of the genital organ while it is extended during mating activity. It also serves as a guide through which the penis can slide.

Muscles M1 and M2 also attach onto the spicule but oppose one another in function. M1 originates on the anterior end of the spicule and divides with one branch passing around each side of the apodemes extending to the lateral arms of the tegumen (Figs. 9, 10). Muscle M2 forms a single band extending from the tegumen to the transverse portion of the spicule. When the genital organ is internal, M1 is relaxed while M2 is contracted (Fig. 9).

Muscle M3 is paired, one muscle extending on the ventral side of the penis from each of the anterior apodeme tips to the anterior projections of the tegumen (Fig. 9). The ejaculatory duct passes between the two muscles to enter the penis tube. Part of the function of these muscles is to retract the penis after copulation. They may also lessen lateral movement of the anterior end of the genital organ during copulation.

Muscles M4 and M5 withdraw the internal sac after copulation. M4 consists of two large muscles that originate from the anterior tips of an apodeme (Fig. 9). They extend posteriorly within the penis tube where each divides into at least three branches. One branch from each muscle attaches to the posterior end of the internal accessory apparatus while the other two branches spread out over the lining of the internal sac (Figs. 11, 12). Muscle M5 is also paired and extends from the inside lateral wall of the lateral lobes to the wall of the median lobe (Figs. 11, 12).

**Eversion of the genital organ.** Observations were made on the mucous membrane of the genital organ when fixed in the internal (Fig. 9) and evaginated (Figs. 10, 11, 12) positions. Eversion begins with the contraction of M4 and M5 with a simultaneous relaxation of M3. Contraction of M4 probably causes a slight counter clockwise rotation of the penis to orientate the gonopore dorsally. The activities of these muscles project the penis posteriorly through the genital opening. The anterior tips of the apodemes and the tegumen are pulled posteriorly to the transverse portion of the spicule (Fig. 10). A relaxation of M4 and the lateral muscles of the eighth sternum probably facilitates the projection of the penis. Muscles M4, M5, and M6 may also shift the spicule nearer to the posterior abdominal wall. At this stage the penis is at maximum extension for copulation (Figs. 10, 11).

The internal sac is unfolded after the penis is extended. Eversion of the sac is probably caused by blood pressure with a simultaneous relaxation of muscles M4 and M5. As the sac is forced backward the infolded posterior sclerotizations of the penis fold out laterally, carrying the sac and the internal accessory apparatus posteriorly. This movement swings the seminal rod and anchor backward at a right angle to the penis. Francke-Gromann (1948) suggested that the stiffening and pumping action of the muscular ejaculatory duct also helps to force the accessory apparatus posteriorly. The internal sac finally unfolds in balloon-like fashion, bringing the gonopore adjacent to a mid-dorsal point at the base of the median lobe (Figs. 11). The internal sac is completely exerted only when in the vagina. Retraction of the male genital organ progresses to a reverse manner to eversion.

**Female Reproductive System.** The female reproductive system consists mainly of two ovaries (Orv), each with a pair of oviducts (Ovd), a suspensorial ligament (SMLig) for each ovary, two short lateral oviducts (LOvd), a median oviduct (MOvd), a bursa copulatrix (Bcpx), a spermatheca (Spth) and a pair of accessory glands (AcGl) (Figs. 10, 22).
Oviducts. The median oviduct extends from the posterior genital opening (GenOp) to the base of the ovaries where it divides into two lateral ducts (Fig. 18, 22). They consist of an inner layer of longitudinal muscle fibers (LinM3) surrounded by several layers of circular muscles (CirM3) (Fig. 25). The inner minute spines line the epithelium with a posterior orientation and are more numerous near the caudal end of the median oviduct. The musculature surrounding the posterior opening of the oviduct is greatly thickened (Fig. 19) and forms a sphincter type of mechanism which closes the oviduct off from the genital opening and from the vagina.

Copulatory pouch. This is dorsal to the posterior end of the median oviduct and includes the vagina (Vag) and bursa copulatrix (Bcpux) (Fig. 19). There is a single external opening common to both the vagina and the median oviduct. The portion of the walls of these tubes is lined with muscle tissue (Fig. 19). The muscular wall of the vaginal region is thinnest than the wall of the oviduct and may consist only of circular muscles on its dorsal side. Thickened musculature surrounds the posterior end of the vaginal tube (Fig. 19). The bursa copulatrix forms a dorsal diverticulum that is continuous with the dorsal view curves to the left (Figs. 18, 22). It resembles the ovotestis in cross section but only one layer of outer circular muscles could be found (Fig. 26). The inner convolutions appear to consist mostly of thick membranous tissue with muscle fibers also likely to be present. The musculature surrounds the inner wall of the vagina as well as the bursa copulatrix and carries numerous spines that are larger than those of the median oviduct. These spines occur only on the dorsal wall of the vagina and they project anteriorly. The muscular wall is slightly constricted near the basal end of the bursa copulatrix and immediately posterior to this are two spiny sclerites (ScI) which the sclerites occupy a lateral position (Fig. 27) with their spines almost vertical. When it is filled they may move to a dorsal position (Fig. 22). The sclerites are convex and carry about ten well defined spines on the outer curvature (Fig. 21). These curve posteriorly within the lumen of the bursa copulatrix.

Examination of five other North American species, including D. brevistomus chrysophalus, showed that only the first three postulated sclerites in the bursa copulatrix are also widely known throughout the Elateridae (Stein 1847; Williams 1945; Becker 1956; Karg 1962).

Accessory Glands. Only one pair of accessory glands (AcG) was found in the posterior dorsal part of the reproductive cavity (Fig. 24A). When dissection and elongated to the posterior ramus (Fig. 22). The glands of wing-forming females are at least partly filled. There is no distinct duct connection peripheral walls are lined with long spines (Spn) that project toward the gland opening (Fig. 24A). The accessory glands are lined with densely packed, dome-shaped cells to the gland opening become smaller and their spines correspondingly larger.

Large nuclei were evident at the base of the cells and a cytoplasmic substance was present in the dome portion. Surrounding the outer gland wall is a basement membrane which imparts a smooth appearance. It was not determined whether there was any secretion from the gland cells, but substances including cholinergic cells (Cho), yolk-like material (YLM), remnants of spermatogonial (Spd) and spermatogonial (Sp) were recognized within the glands. These material accounts for most of the increased volume (Fig. 29). As many as seven cholinergic membranes were found in the glands. In another instance six spermatogonial were found in a female, one in the vagina, four in one accessory gland and one in the other. This occurred when females were stored with a greater proportion of males. The elongated spines surrounding the accessory gland opening probably prevent outward movement of the contents and may help in their maturation.

When egg production was halted in females by rapidly drying the bark tissue the accessory glands invariably contained cholinergic membranes and yolk-like material. These materials accumulated at variable rates and were often in one gland more than in the other. If the females were left for several days much of the accessory-gland content consisted of a yellow oil liquid which usually separated from the rest of the gland content. This condition often appeared in egg-laying females collected from infested logs during the summer as well as in
Oviducts. The median oviduct extends from the posterior genital opening (GenOp) to the base of the ovaries where it divides into two lateral ducts surrounded by several layers of circular muscles (CMel) (Fig. 25). The inner Musculare spines line the epithelium with a posterior orientation and are more numerous near the caudal end of the median oviduct. The muscular walls surrounding the posterior opening of the oviduct are greatly thickened (Fig. 18) and carry numerous circular muscles on its dorsal side. Thickened muscular walls the posterior end of the oviduct and vagina. It is blind at the anterior end, slightly larger than one millimeter and in section but only one layer of outer circular muscles could be found (Fig. 26). The inner convolutions appear to consist mostly of thick membranous tissue with large nuclei. Some longitudinal muscles fibers are also likely to be present. The muscular wall surrounds the inner wall of the vagina as well as the bursa copulatrix and carries numerous spines that are longer than those of the median oviduct. These spines occur only on the dorsal wall of the vagina and they project from the bursa copulatrix and immediately posterior to this are two spiny sclerites (ScL) when the sclerites occupy a lateral position (Fig. 22) with their spines almost touching. When it is filled they may form a dorsal position (Fig. 22). The sclerites are convex and carry about ten well defined spines on the outer curvature (Fig. 21). These curves posteriorly within the lumen of the bursa copulatrix.

Examination of five other North American species, including D. brevicorpus Hopk., D. complessis Ted. and D. engelmanni Hopk., showed that only the first three possessed sclerites in the bursa copulatrix. Hopkins (1951) had earlier found them in D. vulgum. Sclerites of the bursa copulatrix are also widely known throughout the Eulateridae (Stein 1847; Williams 1945; Becker 1956; Karg 1962).

Accessory Glands. Only one pair of accessory glands (AcG) was found in the females. These glands are located near the posterior end of the reproductive ducts and curled open laterally from the lower region of the vagina (Fig. 24A). When these glands were dissected and elongated on the posterior-ventral side (Fig. 22). The glands of the females are empty, but glands during and after egg-laying and in between the glands and the vagina, the gland openings are loose and their interior (Fig. 24A).

The accessory glands are lined with densely packed, dome-shaped cells (AcGDC), each with a short spine at the tip (Figs. 24D, 24C). The cells adjacent to the gland opening become smaller and their spines correspondingly larger.
females in the overwintering period. Nine females collected in November 1960 all showed either partly or fully expanded glands (Fig. 22) with yellow contents. This fluid was immiscible and floated in Ringer's solution and had characteristics similar to the corpus luteum. The presence of the yellow fluid may suggest that the glands is to conserve nutrients by operating in a digestive and reabsorbing capacity.

Previous workers termed the female accessory gland in the mountain pine beetle "coelenterial" (Richmond 1935; Reid 1938) but such terminology was not supported by the present study. There was no adhesions substance found on the surface of eggs. No reports of a nutrient conserving function for the female glands of other bark beetles could be found in the literature. Chapman (personal communication) observed spermatophores in the "coelenterial" glands of D. ponderosa and a substance resembling a mycocytes (Myct) is (Polycha) and the outer sheath (EpS) in a mature adult is similar to the spermatheca. The spermatheca is usually seen curved to the right of the median oviduct when viewed dorsally (Figs. 18, 22). It consists of a pump organ (Sph/Pn) with compressing muscles (Comp/Me) and a sac (Sph/S) (Fig. 20), a U-shaped, sclerotized capsule with a small projection at its distal end and a muscle extends from the sclerotized capsule to the basal portion of the capsule. The muscle extends from the outer curvature of the spermathecal sac (Fig. 20), a condition, which appears necessary to ensure bending of the spermatheca in the proper plane during pumping action. The pump organ is contained in a thick-walled, nucleated and vacuolated (Fig. 20), which suggests a glandular function. Hopkins (1965) termed the spermatheca and the sac portion of the "spermathecal gland". Richmond (1937) showed that the structure of the spermatheca of D. ponderosa was identical with that of D. valens, but differed in the number of nuclei of the spermatheca. In the present study the pump organ and the sac were designated as the spermatheca proper on the grounds that living spermatheca stored in both structures simultaneously (Fig. 20). The pump organ appears to perform the function of sperm ejection. Francke-Grommann (1950) suggested that the spermathecal pump in D. ponderosa may act both ways, i.e. pump males in the overwintering period. Nine females collected in November 1960 all showed either partly or fully expanded glands (Fig. 22) with yellow contents. This fluid was immiscible and floated in Ringer's solution and had characteristics similar to the corpus luteum. The presence of the yellow fluid may suggest that the glands is to conserve nutrients by operating in a digestive and reabsorbing capacity.

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females in the overwintering period. Nine females collected in November 1960 all showed either partly or fully expanded glands (Fig. 22) with yellow contents. This fluid was immiscible and floated in Ringer's solution and had characteristics similar to the corpus luteum. The presence of the yellow fluid may suggest that autolysis had taken place. The foregoing evidence suggests that the function of these glands is to conserve nutrient material by operating in a digestive and re-absorbing capacity.

Previous workers termed the female accessory gland in the mountain pine beetle "collateral" (Richmond 1935; Reid 1936a) but such terminology was not supported by the present study. There was no adhesive substance found on the surface of eggs. No reports of a nutrient conserving function for the female accessory glands of other bark beetles could be found in the literature. Chapman (personal communication) observed spermatozoa in the "collateral" glands of T. sinuata and Francke-Grovesmann (1950) reported that a yellowish fatty substance occurred in the collereral glands of D. melitaen. She suggested that the substance acted as a lubricant during oviposition and copulation.

Symbiotic organisms occur in association with the reproductive organs of many insects (Buchner 1917; Scholtzmann and Bonhag 1956; Richards and Brooks 1918; Bonhag 1959; Aslan 1960) and according to Aslan symbiotic containing structures are present adjacent to the vagina in two scolytid subfamilies. No pronounced-like structures were observed in the female accessory glands of the mountain pine beetle, but a structure resembling a myocyte (Myce) is illustrated in Fig. 37. This structure lies between the follicular epithelium (FedEp) and the ovarian sheath (EpSh) in a mature adult and is similar to the myocytes illustrated in the cockroach ovary (Bonhag 1959).

Spematheca. The spematheca is usually seen curved to the right of the median oviduct when viewed dorsally (Figs. 2, 18). It consists of a pump organ (SphPrn) with compressor muscles (ComMo) and a sac (SphSr) (Fig. 18). The spematheca stores sperm and releases it for fertilization. The pump organ is a U-shaped, sclerotized capsule with a small projection at its distal end and a duct (SpPrD) extending from its proximal end (Fig. 20). The compressor muscle extends from the sclerotized projection to the basal portion of the capsule. On the inner surface of the posterior half of the capsule, sclerotization is irregularly thick (Fig. 20), a condition which appears necessary to ensure bending in the proper plane during pumping action. The pump organ is contained in a thin nucleated epithelial sheath (EpSh) (Fig. 20). The spemathical sac extends from the outer curvature of the pump organ where it surrounds a small valve-like opening (SphV1) (Fig. 20). It is thick-walled, nucleated and vacuolated (Fig. 20), which suggests a glandular function. Hopkins (1935) termed the pump organ in D. calglans the "spematheca" and the sac portion the "spemathical gland" (Fig. 19). Richmond (1935) showed that the structure of the spemathica of D. monticola was identical with that of D. varius, but referred to the pump organ as the "spemathical sac." In the present study the pump organ and the sac were designated as the spemathica proper on the grounds that living spermatozoa are stored in both structures simultaneously (Fig. 20). The sac may provide nutritive material for sustaining the spermatozoa while the pump organ appears to perform the function of sperm ejection. Francke-Grovesmann (1950) suggested that the sclerotized pump in D. melitaen may act both ways, i.e., the spemathica is filled and emptied by pumping.

The spemathical duct passes posteriorly from the pump organ and medially between the vaginal chamber and the median oviduct. It opens into the median oviduct below the posterior end of the vagina (Fig. 19). The duct is cylindrical.
of the vagina and oviduct (Fig. 10). It consists of cells arranged radially above the central canal and has an inner lining of epithelium. No muscle fibers were observed in the duct wall.

Ovarioles: The complement of two ovarioles per ovary in the mountain pine beetle conforms with the number found in rhynchophorine beetles (Ermen 1967; Adam 1961; Robertson 1961). Each ovariole is enclosed in an epithelial sheath (Fig. 20), and has a short terminal filament (TIF), a germarium (Ger), a vitellarium (Vit) and a basal calyx (Cal) (Fig. 31). No distinct pedicle was observed.

The terminal filament is short and nucleated and extends anteriorly from the tip of each ovariole. It is separated from the germarium by a septum (Sep) and forms a suspensory ligament. The epithelial sheath surrounding an ovariole is continuous over the terminal filament and the calyx. It appears to consist of numerous nuclei scattered among the fibers. The outer layer is covered by tissue under the sheath. The epithelial sheath of terminal female ovarioles is often loosely arranged (Fig. 33). In addition to the outer epithelium, a thin inner sheath or tunica propria (Tun) encloses the germarium and vitellarium portions (Fig. 32).

The germarium is cylindrical and separated from the vitellarium by a transition zone (TZn) (Figs. 32, 33). These are densely packed nurse cells within the germarium from which the nutritive and oocyte cells differentiate. In these females two sites of nuclei were observed, the larger of the two were more numerous and were distributed uniformly throughout the germarium (Fig. 34). In egg-laying females the germarium expands as the germ cells enlarge and become more densely packed. During this stage the smaller nuclei could not be found. The larger nuclei are the trophocytes (Troc) (Figs. 28, 34, 35) while the smaller may represent the precursors of the follicular epithelial cells (PreEpith) found at the anterior end of the vitellarium (Figs. 32, 33). The trophocytes are circular and apparently undifferentiated. Scholtzmann and Boulog L. (1952) reported small scattered nuclei within the germarium of Tenebrio molitor and applied the term "interstitial nuclei" to them. They suggested that these nuclei gave rise to or contributed to the follicular tissue.

Young oocytes (Ooc) are first distinguishable at the transition zone where they descend into the follicular epithelial tissue (Fig. 13). The transition zone separates the germ-cell tissue from follicular tissue. Females show a sharp transition zone (Fig. 22) but in egg-laying females it may be more diffuse posteriorly and the end of the germarium of an egg-laying female the young oocytes of the nutritive cells. From here the oocytes enter the follicular tissue and proceed to maturity as they migrate posteriorly in the vitellarium.

The follicular epithelial cells are elongate and arranged more or less in the same direction as the ovariole (Fig. 32). These cells surround the oocyte in maturity. No distinctive cytoplasmic cords were observed extending from the vitellarium to the developing oocytes. It appeared that the early stage of the completion of the follicular layer. During later stages of vitellogenesis nutritive substances are probably mediated through the follicular epithelial cells.

Many investigators have described ovarioles in Polyphagous beetles and most resemble the telephoric type (Wieman 1910; Kame 1967; Leyn 1954; McArter 1954; Scholtzmann and Boulog L. 1952; Zacharias 1918). Nutritive cords were present in most of these beetles, but Boulog L. (1958) pointed out that the cords of Polyphagous beetles appear to be generally inapparent and may even be missing in some species. According to him the presence of trophocytes in the germarium, rather than oogonia, forms the criterion used to distinguish the telephoric ovariole from the parasitic type. It is fairly clear therefore, that the ovarioles in D. monticola are telephoric or a modification of that type.

The bulbous calyx (Cal) joins the posterior end of the vitellarium with the lateral oviduct (Figs. 18, 22, 23). The inner epithelial wall is thick, strongly con-
of the vagina and oviduct (Fig. 10). It consists of cells arranged radially about the central canal and has an inner lining of epithelium. No muscle fibers were observed in the duct wall.

Ovarioles. The complement of two ovarioles per ovary in the mountain pine beetle conforms with the number found in thripsophoruses beetles (Immon 1957; Atlan 1960; Robertson 1961). Each ovariole is enclosed in an epithelial sheath (Tf8h) and has a short terminal filament (Tf18i), a germarium (Germ), a vitellarium (Vit) and a basal calyx (Cyl) (Fig. 23). No division pedicle was observed.

The terminal filament is short and nucleated and extends anteriorly from the tip of each ovariole. It is separated from the germarium by a septum (Sep) and forms a suspensory ligament. The epithelial sheath surrounding an ovariole is two layers of flat fibers arranged at right angles giving a net-like appearance. Numerous nuclei are scattered among the fibers. The outer layer is covered by a basement membrane and no trabecular endings were observed penetrated the fibers around the ovariole (Fig. 34) and stretched greatly during egg development (Fig. 35). In addition to the outer epithelium, a thin inner sheath of tunica propria (Tup) covers the germarium and vitellarium portions (Fig. 32).

The germarium is cylindrical and separated from the vitellarium by a transition zone (Tr/Zn) (Figs. 32, 33). There are densely packed germ cells within the germarium from which the nutritive and oocyte cells differentiate. In female beetles two sizes of nuclei were observed; the larger of the two were more numerous and were distributed uniformly throughout the germarium (Fig. 34). In egg-laying females the germarium expands as the germ cells enlarge and are packed. During this stage the smaller nuclei could not be found. The larger nuclei are in the trophocytes (Troc) (Figs. 26, 34, 35) while the smaller may represent the precursors of the trophocytes. The oocyte cells (Ooct) found at the anterior end of the vitellarium (Figs. 32, 33). The trophocytes are circular and appear as individual cells in the germarium. Scholtmann (1956) reported small scattered nuclei within the germarium of Tenebrio molitor and applied the term "anterior nuclei" to them. They suggested that these nuclei gave rise to or contributed to the trophocyte tissue.

Young oocytes (Ooct) are first distinguishable at the transition zone where they descend into the trophocytes (Troc) (Fig. 33). The trophocytes are a diffuse transition zone (Fig. 32) but in egg-laying females it may be more diffuse posterior to the germarium of an egg-laying female the young oocytes are of the nutritive cells. From here the oocytes enter the pedicellate pedicle and proceed to maturity as they migrate posteriorly in the vitellarium.

The trophocytes (Troc) are elongated and arranged more or less transversely to the main axis of the ovariole (Fig. 32). These cells surround the oocyte to maturity. No distinctive cytoplasmic cords were observed directly from the germarium to the oocytes. It appeared that the early division of the completion of the follicular layer. During later stages of viti-
voluted, non-muscular and has large nuclei (Fig. 42). These features suggest a secretory function.

Egg Formation and Ovulation

Each ovariole in a general female contains seven to nine egg follicles (FoI) which are arranged uniserially (Fig. 18). At this time the ovaries are generally translucent. The oocytes and germ cells enlarge after feeding commences within the gallery. Differentiation of more oocytes takes place from the germarium and the ovarioles become notably distended. At maximum egg production 13 or more egg follicles may be distinguished within the vitellarium (Fig. 23) when the ovarioles assume a compact S-configuration within the abdomen.

The first oocytes differentiated are small and have prominent nuclei. With enlargement and the formation of the prefollicular epithelium, the oocyte moves to a median position in the vitellarium tube. Young oocytes have a thick layer of columnar follicular cells (Fig. 36) and uniformly granulated cytoplasm (CyI). The egg nucleus (Nuc) is less acidophilic than the nucleolus (NucI) (Fig. 40). As the egg enlarges the follicular cells also enlarge and become cuboidal with prominent nuclei (Fig. 38). The follicular cells of mature eggs are squamous and cell boundaries are distinct (Fig. 39). The follicular cells are always uninucleate and evidently accommodate the growing oocyte by growth in size and by change in shape.

An increase in both nuclear and cytoplasmic material occurs during egg growth. The nucleus is a prominent structure until yolk material appears (Fig. 40). During later stages the nucleus does not seem to increase in size and is often found situated inconspicuously near the lateral margin of the egg. The nucleolus, in insects generally, is known to undergo a slow transformation during vitellogenesis, serving a special function in yolk formation (Bongard 1958). It has been termed the "permanent vitelline". With the accumulation of yolk (Yk) there is a progressive decrease in cytoplasmic basophilia (Fig. 42).

Development of the oocyte is completed in the last follicle and is followed by the secretion of the chorion (Ch) which is a product of the follicular cells (Fig. 42). The chorion is a thin, filially sculptured, transparent membrane which encloses the mature egg. Immediately beneath the chorion is a thicker layer (VII) which is either nucleolated or is regularly thickened (Figs. 41, 43). It is probably homologous with a vitelline membrane produced by a condensation of the outermost layer of egg yolk (Wigglesworth 1937).

The follicular cells break down after the secretion of the chorion and the nuclei are often indiscernible. The mature egg, oval in shape and about one millimeter long, is now ready for ovulation.

An epithelial plug (EpIg) extends from the base of the vitellarium and partly fills the calyx, and is apparently composed of the degenerative follicular cells. An accumulation of this cellular mass occurs after each ovulation and numerous follicular cell nuclei can be recognized within it (Fig. 42). Soon after each ovulation the follicular cells undergo autolysis (Wigglesworth 1935; Schleiman and Bongard 1956) and cell boundaries become indiscernible. At this stage the cellular mass is bright yellow and is called the corpus lutum (Cl).

Some of this material may be reabsorbed through the ovariole epithelium, but some is evidently discharged through the egg tube during ovulation.

Ovulation begins when the egg ruptures the epithelial plug and enters the ovicellus, stretching it to about three times its normal diameter. The egg moves posteriorly by the peristaltic activity of the ovicellus musculature and is probably...
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*Egg Formation and Ovulation*

Each ovariole in a teratoid female contains seven to nine egg follicles (Fo) which are arranged uniseriately (Fig. 18). At this time the ovarioles are generally translucent. The oocytes and germ cells enlarge after feeding commences within the gallery. Differentiation of more oocytes takes place from the germarium and the ovarioles become notably distended. At maximum egg production 13 or more egg follicles may be distinguished within the vitellarium (Fig. 23) when the ovarioles assume a compact S-configuration within the abdomen.

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An increase in both nuclear and cytoplasmic material occurs during egg growth. The nucleus is a prominent structure until yolk material appears (Fig. 36). During later stages the nucleus does not seem to increase in size and is often found situated incooperatively near the lateral margin of the egg. The nucleus, in insects generally, is known to undergo a slow transformation during vitellogenesis, serving a special function in yolk formation (Bouhag 1958). It has been termed the "germinal vesicle". With the accumulation of yolk (Yolk) there is a progressive decrease in cytoplasmic basophilia (Fig. 42).

Development of the oocyte is completed in the last follicle and is followed by the secretion of the chorion (Chor) which is a product of the follicular cells (Fig. 42). The chorion is a thin, faintly sculptured, transparent membrane which encloses the mature egg. Immediately beneath the chorion is a thicker layer (Yolk) which is either nucleated or is regularly thickened (Figs. 41, 42). It is probably homologous with a vitelline membrane produced by a concretion of the outermost layer of egg yolk (Wigglesworth 1931).

The follicular cells break down after the secretion of the chorion and the nuclei are often indistinguishable. The mature egg, oval in shape and about one millimeter long, is now ready for ovulation.

An epithelial plug (Epip) extends from the base of the vitellarium and partly into the calyx, and is apparently composed of the degenerative follicular cells. An accumulation of this cellular mass occurs after each ovulation and numerous follicular cell nuclei can be recognized within it (Fig. 42). Soon after each ovulation the follicular cells undergo autolysis (Wigglesworth 1951; Schleisinger and Bouhag 1956) and cell boundaries become indistinct. At this stage the cellular mass is bright yellow and is called the corpus lutenum (Cl).

Some of this material may be reabsorbed through the ovovitellar epithelium, but some is evidently discharged through the egg tube during ovulation.

Ovulation begins when the egg ruptures the epithelial plug and enters the ovovitellar tube. Stretching it to about two-thirds its normal diameter. The egg moves posteriorly by the peristaltic activity of the ovovitellar musculature and is probably

assisted by the spiny chitinous intima. Fertilization is believed to occur when the egg passes the opening of the spermathecal duct (Fig. 19). The approach of the egg to this point may be synchronized with the contraction of the spermathecal pump to provide spermatozoa. The egg then moves through the genital opening and is deposited in a specially constructed egg niche within the egg gallery.

According to Reid (1918b) one egg niche is excavated at the anterior end of the gallery for each egg deposited, and a variable time occurs between excavations. After the niche is constructed the female must reverse herself before exuviation. These events signify a warning period for ovulation but the exact mechanism of ovulation in insects is not understood (Wigglesworth 1953; Imms 1972). Four of five females which had just completed egg niches contained one mature oocyte in each of the median oviducts and all five had well developed ovaries. This suggests that the stimulus to construct an egg niche is received in advance of egg deposition and that a few minutes are necessary for the mature oocyte to pass from the last follicle into the calyx region. Some eggs, instead of
assisted by the spongy chitinous intima. Fertilization is believed to occur when the egg passes the opening of the spermathecal duct (Fig. 19). The approach of the egg to this point may be synchronized with the contraction of the spermathecal pump to provide spermatozoa. The egg then moves through the genital opening and is deposited in a specially constructed egg niche within the egg gallery.

According to Reid (1958b) one egg niche is excavated at the anterior end of the gallery for each egg deposited, and a variable time occurs between excavations. After the niche is constructed the female must reverse herself before oviposition. These events signify a warning period for ovulation but the exact mechanism of ovulation in insects is not understood (Wigglesworth 1955; Innes 1977). Four of five females which had just completed egg niches contained one mature oocyte in each of the median oviducts and all five had well developed ovaries. This suggests that the stimulus to construct an egg niche is received in advance of egg deposition and that a few minutes are necessary for the mature oocyte to pass from the last follicle into the calyx region. Some eggs, instead of
being laid, pass dorsally into the vaginal chamber and then to the bursa copulatrix where they are apparently destroyed. The morphological features already described for the vagina and bursa copulatrix are believed to be responsible for this, especially the spiny setae of the bursa copulatrix. These may represent the chiton or since they are capable of some rasping action. Partly crushed eggs, chiton setae, and cuticular fragments were often found in the bursa copulatrix (Fig. 27). From the bursa copulatrix and vagina the egg contents and spermatophores are transferred to the accessory glands. The reason for the dorsal passage of some eggs is not understood, but an interruption of delay during the events between egg niche construction and oviposition is likely to be an important factor.

Mating

The mating behaviour of the mountain pine beetle as described and illustrated by Reid (1978h) is similar to that of D. micans and Pityogenes chalcographus (Francke-Großmann 1910). The observations made during and after mating support their data and are in accordance with the anatomical structures already mentioned. Measurements of the male genitalia of the mountain pine beetle at full erection and of the female copulatory pouch suggest that the male genital organ does not extend into the bursa copulatrix during copulation; the distal tip of the internal sac extends only to the bursa copulatrix setae. Full erection of the sac takes place in the female vagina. Within the vaginal pouch there is a median depression (Fig. 26b), which the median lobe of the internal sac fits, while the lateral lobes project laterally to secure a fixed position until the male seminal fluid has been deposited. Since the male is upside down during mating (Fig. 25a) the dorsally located male gonopores inject the seminal fluid ventrally in the female, depositing it in the median groove of the pouch. This position is close to the spermathecal duct opening. An examination of females immediately after mating revealed the spermatheca in the median position. In D. micans the male genital organ extends into the bursa copulatrix during copulation where the spermatheca is deposed at the opening of the spermathecal duct (Francke-Großmann 1910).

The length of time required for copulation was variable, but lasted about 30 seconds (Reid 1978h). When mating was observed under magnification a series of wave-like motions could be seen through the connecting membrane of the genital organ. These were probably a result of contractions of the ejaculatory duct which ejects the male seminal fluid posteriorly. The fluid deposited forms a single ball-like mass for which the term spermatophore has been used. No attempt was made to determine the period required for transfer of sperm from the spermatheca to the spermatheca.

Acknowledgments

Dr. B. Hocking, Head of the Department of Entomology, University of Alberta, Edmonton, supervised this study and other members of the Department of Entomology gave valuable suggestions and encouragement. Staff members of the Forest Entomology and Pathology Laboratory, Calgary, Alberta, gave a critical review of the manuscript.

References


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March 1964

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References

species has only 21 pairs of setae on the dorsal shield, not counting the humeral pair (cf of the setal system of Hirschmann (1957)), 11 pairs on the anterior region and 10 pairs on the posterior region. Neither the total number of setae nor the presence of particular pairs of setae on the dorsal shield can be used as a consistent criterion for separating physoideus from blattisocidae.

From the discussion above, it is evident that Acoecurodes warrants no more characteristic distinction other groups in the Blattisocidae when many characters are considered. Accordingly, the subfamily Acoecurodes is here synonymized under the subfamily Blattisocidae.

Genus Acoecurodes Muma


Type species by original designation and monotypy: Acoecurodes crassus Muma, 1961.

Description. The dorsal shield of adults has a reduced number of setae that is reminiscent of the Physoideus, but a well developed series of marginal setae remains on the lateral margin. The chaetotaxy of the legs is normal for the Blattisocidae and differs from that of the Physoideus (Evans 1961a). Species of Acoecurodes and Latioceratidae have a number of similar features as mentioned above. However, the uniliated sternum of the spermatheca, the shape of the genital and ventral shield, and the number of setae on the gena of legs II and III separate the two groups.

Dorsum. Dorsumulateral incisions of dorsal shield absent on adults. Body dorsum with 35 to 38 pairs of setae: 11 pairs on anterior region of dorsal shield, seven to 11 pairs on posterior region, and seven pairs of marginals on lateral membranous of females. True vertical and paraventral setae absent.

On females, anterolateral, genal, ventral shield well sclerotized (Fig. 2) or partly desclerotized so that some setae seemingly free on membrane (Fig. 7). Sternal shields with three, four, or five pairs of setae on the anterior setae of female, unpaired oral, and unpaired lateral.

Tegument with anterior margin convex, smooth or desclerotized. Cervical field simple, weakly sclerotized. Seven transverse rows of denticles on ventral side of each seta, each row multidentate, all bidentate on the third and fourth pairs of setae. Palps with six terminal segments normal for subfamily, without ventral shield on third seta.

Spermatheca of females not sclerotized. Ovaries normal for subfamily, with ovipositor normal for subfamily, without ventral shield on third seta.

Remarks. The genus of legs II and III each have one less seta than found on most blattocerids. The arrangement of the setae on gena II of the X-type of Evans (1963b) scheme of leg chaetography, and that on genu III of the VIII-type scheme of dorsal setal number of Acoecurodes and the most anterior pair of setae on the dorsal shield may have up to 23 pairs of setae, including as many on the posterior region of Chilistus cameroni, 10 pairs of species of Acoecurodes and Chilistus cameroni, and 10 pairs of species of Acoecurodes in the Blattisocidae, as L. confusus, L. confusus (Hornemans) (Evans 1958), L. physoideus Chant (1958), and L. youngi Attias-Henle (1959). The last named species is Acoecurodes crassus (Muma, 1961).