Copulation in Two Species of Tetraopes: Behavior, Mechanics and Morphology (Coleoptera, Cerambycidae)

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COPULATION IN TWO SPECIES OF TETRAOPES: BEHAVIOR, MECHANICS AND MORPHOLOGY (Coleoptera, Cerambycidae)

by

Thomas John Pilat

A Thesis Submitted to the Faculty of the Graduate School of Loyola University in Partial Fulfillment of the Requirements for the Degree of Master of Science

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INTRODUCTION

*Tetraopes* Schönherr belongs to the subfamily Lamiinae, the most advanced of the seven subfamilies of the Cerambycidae. This family of long horned beetles is composed of individuals which feed on flowers as adults and which are wood-boring in the larval stages. The twenty-two species of the genus are found throughout the United States from Canada to Costa Rica. All are associated with one or more species of milkweed. As a member of the Phytophaga the milkweed beetle bears a number of similarities to the other members, especially in biology and morphology.

The published literature on the genus *Tetraopes* Schönherr is very scarce. The most recent and comprehensive work was done by Chemsak (1963). In that paper he revised the taxonomy of the genus and reviewed the previous work on the biology and natural history of the species. Most of these papers were brief accounts of oviposition (Gardiner 1961, Clench 1923) and life cycle (Williams 1941a, b). The information is neither detailed,
nor does it concern the mating process. Two species
are found in Cook County, Illinois. T. tetrophthalmus
(Forster) and T. femoratus LeConte can be collected on
Asclepias syriaca L. in open fields and along railroad
rights of way. T. tetrophthalmus is by far the most
common. The flight period lasts from May to October
in this region (Chemsak 1963). The morphological
variation between these two is not extreme and apparent
only under close examination.

The purpose of this study was to observe and analyze
the mating behavior of these two sympatric species to
determine if there is any specific taxonomic or isolating
value to their behavior. An investigation of the anatomy
of the reproductive structures is also a purpose of
this study. Knowledge of the anatomy is essential for
the understanding of the behavior. The genitalia of
beetles have been used extensively for taxonomic purposes
in most taxonomic papers on Coleoptera. There is no
published work which explains the real function of the
genital structures during copulation and sperm transfer.
This study's purpose has also been to provide factual
evidence to support or oppose the current theories. The
procedure involves integrating the behavior and anatomy
to formulate a composite description of the mechanics of
sperm transfer.
REVIEW OF LITERATURE

A number of texts provide a general discussion of the science of animal behavior (Klopfer and Hailman 1967, Thorpe 1961, Tinbergen 1951, Eibl-Eibesfeldt 1970). Baerends (1959) has reviewed the major works in insect behavior before 1959. Schneirla (1953) discussed various problems and areas for analysis in insect behavior. Studies of the mating behavior of a great many insects are available (Roth 1948, Michelson 1964, Selander and Mathieu 1969, LeCato and Pienkowski 1970, Tauber and Tauber 1967, Manning 1960, Spieth 1951, Batakatsch 1939, Heintze 1925 et al.). Michelson's paper is a comparative study of fourteen related species of Cerambycid beetles. Edwards (1961) has studied reproduction in another Cerambycid (Prionoplus reticularis White) and made remarks concerning the variations among the subfamilies, namely that the subfamily Lamiinae is the more specialized. Spieth (1952) studied comparative behavior in one hundred species of Drosophila. Ewing (1961, 1964, and Manning 1963) has investigated a number of morphological variations in Drosophila and the effects on mating success. Research has also been done to correlate behavior with isolation in various species of
Orthoptera (Perdeck 1957, Alexander 1957b) and Diptera (Tauber and Tauber 1967). Tauber and Tauber note that ethological isolation may be the sole mechanism preventing gene exchange between two species. Evans (1966) has correlated behavior and evolution in the sand wasps. LeCato and Pienkowski (1970) made observations of the mating behavior of the alfalfa weevil, *Hypera postica* (Gyllenhal). The genetics of behavior in insects has also received attention in articles by Manning (1965) and Bastock (1956).

A general description of the anatomy is found in Snodgrass (1935). Ehara (1954) studied 101 Japanese species of Cerambycid beetles and indicated that the morphology of the external male genitalia agreed closely with the taxonomy based on characters of external morphology. Bissell (1937) and Burke (1959) have described the genitalia and reproductive organs of two species of weevils and suggested their use in taxonomy. Sharp and Muir (1912) described the external male genitalia of a large number of beetles. Numerous papers deal with the homologies of the reproductive structures in insects, (Tuxen 1956, Wood 1952, Snodgrass 1957, Michener 1944). Many of these authors include remarks on the function of the structures during copulation. For the most part these remarks are based on conjecture. The functional relationship between the male and female structures has been determined in the milkweed bug, *Oncopeltus fasciatus* (Dallas), by Bonhag and Wick (1953). By temporarily immobilizing the bugs through refrigeration they were able to conduct in vivo dissections.
METHODS AND MATERIALS

The initial stages of the project consisted of gathering the available information on the life history of *Tetraopes* (Chemsak 1963). Knowledge of its emergence date in this region was facilitated by checking the collection data on specimens in the Field Museum of Natural History, Chicago. The earliest recorded date was found to be June 20. Collection sites in Cook County, Illinois were selected based on the presence of milkweed (*Asclepias* spp.) and the size and relative isolation of the fields. These sites were then sampled beginning in mid-June. The first specimen of *T. tetrophthalmus* was collected on June 21, 1971. Five different sites were used for collection and observation throughout the summer.

Observations of *T. tetrophthalmus* and *T. femoratus* were made primarily under laboratory conditions. All specimens were field collected and not necessarily virgin stock. Most lab observations were checked in the field and any variations or differences are included. The insects were maintained in the laboratory in clear plastic crispers measuring 13.0 in. x 10.0 in. x 3.5 in. and
The large crisper was used to hold a large number (30-50) of specimens from which copulating pairs were taken and isolated in the small crispers. The small crispers permitted close observations, photographing, and "fixing" of copulating pairs. Milkweed leaves were collected and placed in the crispers with a cotton water wick every two days due to the difficulty in keeping the host plant in the laboratory. Over one thousand individual copulations were observed for *T. tetrophthalmus* and sixty for *T. femoratus*.

Copulating pairs were killed in copula by immersing them in boiling water after intromission was initiated. The time period allowed for copulation was varied from five to thirty minutes before killing in order to demonstrate intromission stages. The copulating pairs were then kept for one to four hours in selected fixatives. FAA solution (Formaldehyde, Acetic Acid, Alcohol), Aerosol-OT (Dioctyl Sodium Sulfosuccinate), and Bouins solution (Ethyl alcohol, Formaldehyde, Glacial Acetic Acid, Picric Acid) were used to promote preservation of the internal anatomy. They were then transferred to and stored in 70% Ethyl alcohol (ETOH). Aerosol-OT was used similarly by Gilbert (1964) to provide information on the endophallic structures of the genus *Baris* Germar, a weevil. A large number of specimens were killed in this manner in order that subsequent dissections would provide new, factual data concerning the relation of the genitalia during copulation.
The dissections of both single individuals and "fixed" copulants was done in the following manner. From specimens which were relaxed (or stored) in 70% ETOH the entire abdomen was removed and secured in a block of paraffin. The sternites, or in some cases the tergites, were then removed individually to expose the internal anatomy. The fixed copulants were secured on their sides in the paraffin dish with pins in the normal copulating position before dissection. Extreme care was taken during handling to avoid even slightly separating the pairs. When fastened down securely, the female was dissected and as much of her reproductive system as possible was carefully removed. The female reproductive structures were then dissected to determine the condition and extent of the penetrant male structures. The primary dissection tools were jewelers' forceps and minuten pins. The individual specimens were eventually mounted on pins. The abdominal sclerites and genitalia were placed in a drop of glycerol in individual genitalia vials and the vials pinned below the proper specimens. The fixed specimens were returned to vials of 70% ETOH. A large number of single specimens were studied in this manner as were forty copulating pairs.

In some instances the sclerotized structures, especially of the male, were cleared in 10% Potassium Hydroxide (KOH) to provide a better view of the internal structures. The genitalia were placed in a small beaker with 25 ml. of KOH. In some instances the preparation was allowed to stand for
a period of hours and in others it was brought to a boil and allowed to cool. Varied treatment was necessary to provide differential clearing. The structures were removed and washed with 70% ETOH and examined. The procedure was repeated if necessary until adequately cleared. No attempt was made to investigate the genital muscles or the associated tracheae in detail although reference is made to the more obvious ones.

The photographs were made with an Alpa 10d 35mm. camera equipped with a 50mm. Kern-Macro-Switar f1.9 lens. The photographs were then mounted and reproduced as plates.

The drawings and measurements were made through the use of a reticule in the ocular of a binocular microscope. The reticule was calibrated with a millimeter rule at various magnification. The finished drawings were made in India ink and reproduced as plates. The abbreviations were selected from Snodgrass (1935) and Burke (1959) where applicable. Others were devised for the purposes of this study.
List of Abbreviations

AcG1.................. accessory gland
Aed.................... aedeagus
AedApo................ aedeagal apodeme
AedVal................ aedeagal valve
An....................... anus
Ant...................... anterior
CM1.................... first connecting membrane
CM2.................... second connecting membrane
Con..................... concavity
COvid................... common oviduct
CP...................... copulatory pouch
Cx...................... coxite
Cy...................... calyx
Den.................... denticle
DV...................... dorsal valve
EjD..................... ejaculatory duct
Enph................... endophallus
EnphPls................ endophallic plates (armature)
Ft...................... foretube
Fl...................... flagellum
GC...................... genital chamber
LOvid.................. lateral oviduct
LP1..................... lateral plate of SpiV
MO..................... median orifice
MS...................... muscular sheath
Ovl..................... ovarirole
Phb. . . . . . . . . . . . phallobase
Rec. . . . . . . . . . . . rectum
Rid. . . . . . . . . . . . ridge (on female VIII)
Set. . . . . . . . . . . . seta
SpiG. . . . . . . . . . . . spiculum gastrale
SpiV. . . . . . . . . . . . spiculum ventrale
Spt. . . . . . . . . . . . spermatheca
SptD. . . . . . . . . . . . spermathecal duct
SptGl. . . . . . . . . . . . spermathecal gland
STr. . . . . . . . . . . . shallow trough (on female VIII)
Sty. . . . . . . . . . . . stylus
Tes. . . . . . . . . . . . testis
VD. . . . . . . . . . . . vas deferens
Vu. . . . . . . . . . . . vulva
8S. . . . . . . . . . . . eighth sternum
8T. . . . . . . . . . . . eighth tergum
RESULTS AND DISCUSSION

Behavior

Stimulation and Recognition

There is no elaborate courtship behavior in *T. tetronphthalaxus* or *T. femoratus*. The adults congregate on *Asclepias syriaca* L. and are consequently in contact with each other. There is no evidence of pheromonal or stridulatory stimulation of either sex preceding the copulatory act. The animals were never observed to be attracted over long distances. Interspecific and sex recognition was only accurate from close range, (i.e. close enough for mechanical contact).

The initial identification of an individual as a possible mate is usually made visually and followed by a mating attempt. When the attempt is made, antennal investigation is the primary means of sensory reception. The information from the antennae may indicate that the individual is not suitable and the male will retreat. If the antenna stimulation indicates the opposite, a marked increase in the activity of the male is obvious as he begins to mount. However, some males have been repelled and attacked because they continued to approach
a resistant individual. The female has never assumed the dominant searching role but always remains passive. The female's responses to stimulation are more subtle than those of the male. It is probably a permissive behavior in which she simply allows the male to continue the process. The alternate behavior of the female is to escape.

When a male is without antennae his attempts to copulate are very few and only when first bumped into by the female. He loses all ability to recognize the female, except when actually in contact with her. A similar situation was observed by Heintze (1925) in the Lepturinae.

Males have also been observed to attempt copulation with both females and males while in a reversed position. No attempt has been made to determine the reasons for this behavior. This behavior is also reported for the alfalfa weevil (LeCato and Pienkowski 1970).

Approach

After locating the female, either visually or by contact, the male usually rushes toward or after her. The male attempts to mount from the rear or from either rear quarter and then aligns himself over the female (fig. 1).

The physical condition of the female does not affect the male, although attempts to copulate with dead females
have never been observed as in the alfalfa weevil (LeCato and Pienkowski 1970). The loss of all or part of the male's prothoracic or metathoracic legs makes copulation more difficult than the loss of part of a mesothoracic leg, since these are the appendages used in grasping the female.

**Position**

The copulatory position of *T. tetrophthalmus* is typical of beetles. The male is above the female, actually standing on the elytra of the female (fig. 2).

In *T. tetrophthalmus* the position of the male tarsi is characteristic. The protarsi are on or very near the humeral angle. The protarsi are used for maintaining grasp. The claws are hooked over the side of the elytra but not over the costal edge. The mesothoracic tarsi are on the side of the elytra between the mesothoracic and metathoracic legs of the female. The metathoracic legs are not used in grasping the female but are used for support when the male adjusts the position of the other legs. This is usually the only time they contact the substrate. He has difficulty maintaining the position if a large number of tarsal segments are broken off, but can copulate effectively if the female does not attempt to remove him too vigorously.

The position of the protarsal segments in *T. femoratus* is extremely characteristic (fig. 3). It was never seen to copulate in the position typical of *T. tetrophthalmus*. 
The first and second segments of the tarsi are in contact with the elytral surface, but rarely are the remaining segments in contact. They are held suberect or perpendicular to the elytral surface (fig. 3). When in this position they are rubbed forward and backward, bringing about the calming effect on the female. Rarely (one observation) in _T. tetrophthalmus_ are the protarsi positioned medially on either side of the female's elytral suture. The efficacy of this protarsal behavior (calming) was greater in _T. tetrophthalmus_ during this one observation than in _T. femoratus_ at any time.

The position of the two abdomens (fig. 4) is as follows. The female's abdomen is not bent or contorted but rather in a normal position as if not copulating. The male must curve the abdomen almost 180° in order that the terminal sclerites of each come into contact. When in contact the male slightly separates the female's seventh sternite and tergite with the partly protracted eighth abdominal segment. The female is thereby stimulated to further separate them herself. At the onset of intromission the eighth abdominal segment of the male is also protracted and contacts the female sclerites, but is secondarily retracted, leaving only the aedeagal valves in contact.

The curvature of the male's abdomen when in copulating position is generally characteristic of the species. The angle through which the abdomen is bent is greater, on the average, in _T. femoratus_ than in _T. tetrophthalmus_. This
characteristic could be due to the relative sizes of the specimens observed.

**Antennal Behavior**

The position of the antennae during copulation is very constant. The female holds the antennae at approximately a 90° angle to the side of the head when resting. If she is investigating and/or moving about, the antennae move in a typical, investigating, non-copulatory manner.

The male holds the antennae in a variety of positions. If resting securely in copulation position, they are held at approximately 80° to 90° to the side of the head. If the female becomes restless and moves about, the male seems to calm her by movements of the antennae. The antennae are used to "tap" or "pat" the female on the sides of the pronotum, head, antennal base and humeral angle. Sometimes the antennae also tap the eyes of the female. The movement is primarily horizontal, bringing the antennae toward each other rapidly (fig. 5). Rarely is the motion vertical. The male also uses this behavior extensively while mounting and attempting intromission. The method is successful even after long periods of repeated copulations (one hour or more). The female does not have to move about to stimulate the male to this behavior.

If the male is missing parts or all of an antenna, it takes a longer time to calm the female and the probability is greater that she will escape his grasp rather than be
calmed. *T. femoratus* exhibits a characteristic difference with regard to antennal behavior. The female behavior is similar but the male on many occasions uses only one antenna at a time, leaving the other in a resting position. The male often alternates the tapping from one antenna to the other or he may tap simultaneously (fig. 6).

At this time it is difficult to postulate why or how this behavior operates. Perhaps the resonance of the female's exoskeleton or the location of the special nerve endings in the female is the important factor. Other authors have described various aspects of antennal behavior during mating in beetles (Michelson 1964, LeCato and Pienkowski 1970, Funke 1957). Michelson states that in the Lepturinae the antennae never hit the female and do not have a stimulating effect. He attributes the stimulatory effect described in the Lamiinae (Funke 1957) to the fact that the antennae are often used as weapons in this subfamily. The females of *T. tetrophthalmus* and *T. femoratus* were not stimulated by the antennal tapping, rather calmed. LeCato and Pienkowski (1970) state the antennae tapping in the alfalfa weevil is an external manifestation of the male's excitement and probably does not calm the female. This evaluation agrees with Michelson's comment on the role of the behavior in the Lepturinae.

**Copulation**

After the copulatory position is assumed and intromission is begun there is little visible behavior
associated with sperm transfer. Contractions of the male's abdomen and intromittent organ are visible. This does not occur as a rigidly rhythmic process, but is rather sporadic in occurrence.

The female usually occupies herself by feeding on leaves or blossoms, or with cleaning operations. When the female cleans the appendages (sometimes all of them) she rarely disturbs the male (fig. 7). The male will occasionally investigate the female's elytra and base of the pronotum with his mouthparts. The behavior is only by means of tapping with the palps, never a licking type movement. The tapping of the palps is similar to that defined by Michelson (1964). The palpal behavior in these species of Tetraopes does not act as a strong stimulus for the female as described for other Cerambycids by Michelson (1964).

If the copulating pair is disconnected and in a "riding" position they are relatively stable. If disturbed, the female begins to move as if rejecting and the male reacts with the antennal calming behavior and extends the aedeagus to attempt reunion. The male is usually successful.

Pairs of both species have been observed to copulate repeatedly for a great length of time. Each copulation (time aedeagus is inserted to time of retraction) lasted twenty minutes on the average. Some pairs have remained in position for an hour or more and traveled long
distances (18-24 in.). The average copulation time decreased later in the season. This is probably due to the fact that the females are already well supplied with sperm and are more prone to reject mating behavior in favor of oviposition behavior as indicated by LeCato and Pienkowski (1970), Richards (1927) and Gilbert (1964). It is possible this does not occur in the field where encounters are less frequent.

In the field, the copulating pair is usually found on the upper 1/4 of the host plant. Most pairs were found on the apical blossoms or buds, but some were also observed on the upper leaves. The occurrence of all the individuals, not only the pairs, is greater on the upper part of the plant. Many times the copulating pairs are found hanging upside down from the blossoms. This position does not seem to impair the behavior.

Postcopulation

As mentioned above the male occasionally withdraws the aedeagus from the female genital chamber and remains in the riding position if the female is calm. They will remain in this position unless disturbed or until the male attempts intromission again. In the field, the female wanders over the plant for long distances when in the copulatory position. When the male withdraws the aedeagus the curvature of his abdomen decreases and the terminus is directed ventrally and posteriorly. In this position
it occasionally contacts and rests on the substratum behind the female.

The actual sequence of events in breaking union is as follows. The male pulls the abdomen backward, breaking the contact inside the female genital chamber. Then the aedeagus is withdrawn slightly from the female chamber. The force of drawing the organ back into the abdomen results in the organ being completely removed from the female (fig. 8) and she seems to walk out from under him. The entire organ is not retracted quickly inside the male. A small section of the aedeagus and endophallic sac remains outside the body and the male raises the abdomen to facilitate retraction of these structures, (fig. 8, showing incomplete retraction). This process does not require much time and semen was never seen on the exposed organs as described in Lecato and Pienkowski (1970). He then flexes abdominal muscles rhythmically and opens and closes the genital plates a few times before the genitalia is aligned properly inside. The male usually completes this operation before he moves very far.

*T. femoratus* spends a longer time retracting the organ than *T. tetrophthalmus*. The reason for this difference is not known. The males of both species keep the abdomen bent at 90° while retracting the aedeagus.

Sometimes after a long period of copulation (30-45 min.), and after the pair has separated and moved away, one or both expels a fecal pellet. The abdominal
Muscular activity necessary in copulation probably exerts pressure on the terminal portion of the intestine, which is in close proximity to the reproductive organs. This has been observed in both sexes of both species primarily in the laboratory.

**Repulsion**

The female exercises control over the copulatory act by rejecting the male's advances. The two methods the female uses are: 1) running, escaping the male before he mounts, or 2) by trying to dislodge the male after he has mounted, yet before penetration. In the field, she runs on the plant, usually toward the top, where she takes flight to escape. In the cage, she runs about bumping into stems of plants and other debris, attempting to knock the male off, and flight was attempted infrequently. At this time the male is using the calming behavior extensively. Sometimes the female will use her metathoracic legs to kick and dislodge the male and thereby remove the aedeagus from her genital chamber. Some individuals ran about pressing their venters against the substrate, effectively blocking the male's advances, as described by LeCato and Pienkowski (1970).

If the female is lacking parts of or entire legs, she has more difficulty rejecting and escaping. In attempting to dislodge the male, an injured female walks about and will even climb the side of the container to
the lid. If she hangs from the lid, the combined weight with the male on her back causes her to lose grasp and fall. Sometimes the pair will land on the male's back and they are unable to right themselves unless the male breaks his grasp and they both regain their footing.

The female will exhibit a rejection behavior even during an act of copulation. This behavior takes approximately the same form as that mentioned above and in Michelson (1964). It is not known what factor stimulates the female to reject and terminate a specific act. However, she can be successful even when the male is very close to forcing union.

Other Types of Behavior

When the beetles are confined to the cages in the laboratory and there is a surplus of males, the females are almost constantly mated. The males show more aggressive behavior under these circumstances than in the field, (LeCato and Pienkowski 1970). Occasionally an unpaired male will harass a copulating pair by trying to bump and dislodge the male. This attack is made toward the head and is rarely successful. The mating female is never harassed directly but may become anxious as an attack is directed in her vicinity. The intruding male has also been observed to walk over the copulating pair from the anterior to the posterior. The reason is unclear, but the direction may be due to the fact that the female's head is lower and easier to climb onto than the male's abdomen.
An overt response to this behavior of an intruding male by a copulating pair has never been observed.

Males have been observed to assume the copulatory position in reverse on the backs of the females. The females did not react but continued to eat as before the intrusion. The male curved his abdomen over the vertex and between the antennae of the female and made searching movements with the tip of the abdomen while opening and closing the genital plates. The aedeagus was never protruded in this position. After a few minutes the male moved off the female and they both moved away. Similar behavior has been observed in the alfalfa weevil and other insects (LeCato and Pienkowski 1970).

The two species of Tetraopes also exhibit two other actions which are typical of beetles. When encountered in the field they either move about quickly, attempting to flee, or will fall, as if dead. In the death feigning process the beetle draws the legs beneath the body and tumbles from the plant. If he falls from the top of a milkweed plant he sometimes circles the stalk in stages from leaf to leaf. When he falls to the ground the gray ventral surface is invariably uppermost and he is easily overlooked.

Linsley (1961) describes another type of behavior common in Cerambycids as "bumping" behavior. These two species are a good example. When two males meet head on, especially on a stalk or branch of the host plant, they
may commence bumping heads (fig. 9). First they bump, then one or the other steps back and stridulates. Then they both advance and bump again. This may continue for some time and just as quickly as it started it stops. Occasionally one beetle tried to pass the other and the bumping was begun again. This behavior was observed both in the field and in the laboratory. The increase in population density in the laboratory did not markedly increase the occurrence. I am unable at this time to contribute any theories concerning the advantage or purpose of this behavior. It was never seen to occur as a competition device, nor was a female ever observed to be a participant. The species of Tetraopes stridulate by rubbing the rear of the pronotum against the front edge of the mesonotum (see fig. in Linsley 1961). Both species studied stridulate almost constantly while feeding and walking on the host plant. My observations agree with Alexander (1957a), who describes two separate sounds as "squeaking" and "purring". The stridulatory activity was never observed as a component of pre-copulatory or copulatory behavior. Specimens of T. femoratus exhibited a slight alteration of stridulatory behavior. After being picked up or disturbed both males and females firmly brace themselves on the substrate and stridulate very rapidly. This was not observed in T. tetrophthalmus, and was the loudest noise produced in either species. The specimens continued this strong stridulation for at least a minute.
At this time it is not possible to determine further purpose for stridulation in *Tetraopes* beyond the obvious purpose as a protective device which startles a potential predator.
Morphology

The organs concerned with the reproductive process can be separated into two groups. The internal genitalia consists of those structures which function in gamete production and protection, in insuring fertilization and in discharging the germ cells from the body. The external genitalia are the structures concerned with sexual mating and egg deposition. The internal genitalia are primarily mesodermal derivatives and the external genitalia are primarily ectodermal derivatives. The external genitalia are used to bring the sexes into intimate contact and are the structures of the greatest interest both functionally and taxonomically.

The genital apparatus of the male is a simple tube which has been telescoped upon itself. Sharp and Muir (1912) described this structure comparatively in a large number of beetles. The female's genitalia serves two functions; it forms the pathway for the male intromittent organ and for the exit of the eggs. Tanner (1927) reviewed and described the female structures in a large number of beetles. The genital structures in insects are highly variable in form and both of these studies indicate their valid use as taxonomic characters. Bruhn (1947) and Ehara (1954) have underscored the use of the male genitalia in taxonomy. Besides having taxonomic value there is reason to believe the structure of the genitalia may have isolating value. Considering the specific character of the genital
anatomy, the discussion of the reproductive behavior will be more full understood as a result of this description.

The Genital System of the Male

In *T. tetrophthalmus* the testes (fig. 10, Tes) are located in the ventral lateral portion of the abdominal cavity at the level of the second, third and fourth visible sterna. They are oval, lobe shaped bodies. The vas deferens (VD) is obvious along the medial surface of each organ. Beyond the posterior edge the vas deferens join in the midline (fig. 21). Before this union to form the ejaculatory duct (Ejd) a long accessory gland (AcGl) is evident. A seminal vesicle was not noted as an obvious structure, but the vas deferens is expanded slightly before the point of union. From this point of union the thin ejaculatory duct leads posteriorly and dorsally to the end of the aedeagal apodemes (AedApo) where it enters the muscular sheath (MS).

Within the wider muscular sheath the ejaculatory duct continues as a tightly coiled structure. The anterior edge of the muscular sheath is attached to the tips of the aedeagal apodemes by means of a muscle which issues from the massive muscle connecting the phallobase (Phb) to the aedeagal apodemes. The muscular sheath continues ventrally and is folded upon itself slightly. Eventually it narrows sharply and ends in fusion with the endophallic sac. This point is indicated by the base of the flagellum (Fl, fig. 10), a long thin sclerotized tube, at which point the ejaculatory duct also ends.
The remaining genital structures are derived from the ectoderm and are thus labeled external genitalia. These structures include the endophallus, the aedeagus (fig. 12, Aed) and its apodemes, and the phallobase (fig. 16-19, 24, Phb). The spiculum gastrale (SpiG) is associated with these intromittent structures as are a number of membranes and muscles to facilitate protraction and retraction during copulation. The flagellum (fig. 20) is a posterior extension of the true gonopore within the endophallic sac. The true gonopore is that point at which the ejaculatory duct terminates distally. The endophallic sac continues as a lobular, membranous structure into the barrel of the aedeagus and attaches near the posterior opening of the aedeagal valves. The opening of the endophallus at this posterior point is labeled the phallobase or median orifice (MO).

The endophallus is a complicated structure with various sclerotized denticles and plates on its inner surface. The patches of small denticles seem to be characteristic for the species, especially at the anterior end covering the flagellum (fig. 20). The sclerotized plates are located within the body of the aedeagus when the endophallic sac is in repose (fig. 12, Enph Pls). The shape of all three in each species is unique (fig. 22, 23). The various lobes and protuberances of the membranes indicate the probable relationship of these structures when protruded. The endophallus is not a simple sac, rather it is complex and the way in which it is
bent is a result of the differences in surface area on each side. In *T. tetraphthalmus* the endophallus is formed into a characteristic wedge (fig. 31-33) between the most anterior pair of plates. This wedge is slightly sclerotized and probably operates closely associated with the endophallic armature.

The aedeagus (fig. 12) is the main intromittent organ. It is located in the posterior half of the abdomen and is composed of the posterior valves, the tubular body or median lobe and the anterior apodemes. The aedeagal apodemes are two laterally concave, dorso-ventrally oriented plates extending anteriorly from the base of the tube. They are sites of muscle insertion and origin. The apodemes curve and join dorsally and continue posteriorly with the dorsum of the median lobe. The lateral edges also join more posteriorly and continue as the ventral portion of the tubular body. The endophallus extends from the gonopore anteriorly and passes out of the median lobe between the aedeagal apodemes. The median lobe is not perfectly cylindrical, but rather slightly depressed. This flattening becomes extreme distally where the lobe continues as plate-like horizontal valves. The valves comprise approximately the distal one-third of the median lobe. These valves are shaped into a point, the apical "bill", and fit closely upon each other. The point of insertion of the endophallus (MO, fig. 12) can be located inside the edge of the valves.

The phallobase (Phb) (fig. 24 & fig. 16-19) is a thin sclerotized oval ring around the median lobe. It
bears a pair of lobes at the posterio-dorsal apex which are moderately setose. The ventro-lateral segments of the ring meet in the midline and continue a short distance anteriorly side by side to a point between the aedeagal apodemes. Major muscles of protraction and retraction of the aedeagus are attached to the phallobase and its proximal end. It is free to slide over the aedeagus and has been observed in a variety of positions relative to the median lobe.

When in repose in the abdomen the aedeagal valves (AedVal) are concealed within the eighth abdominal segment which is retracted within the seventh. The eighth tergum (8T) is large in relation to the sternum (8S). The sternum is small and protracted into a small anteriorly projecting, peg-like apodeme. Dorsal to this structure the union of the eighth tergum and sternum is continuous with the spiculum gastrale (SpiG). This Y-shaped apodeme is a sclerotized rod which bends to the right side of the abdomen (fig. 25). The spiculum gastrale is found in various positions along side the aedeagal apodemes and a number of muscles insert along its length. The anterior edges of the eighth abdominal segment are attached by membranes to the posterior edge of the seventh abdominal segment. The posterior hindgut of the alimentary tract is in close proximity to the reproductive structures in the abdomen. The anus is located in a supporting membrane connecting the eighth tergum and the phallobase (CM, fig. 10).
The variation of the morphology of these structures between the two species is not great. A number of structures do indicate species differences. *T. femoratus* genitalia are generally larger than *T. tetrophthalmus*. The endophallic sac and its protuberances are larger, as is the flagellum which may be three times as long. The aedeagal apodemes are longer and more deeply concave in *T. femoratus* than in *T. tetrophthalmus*. The phallobase and spiculum gastrale are consequently larger also.

Besides the length of the flagellum, the major differences are the shape of the aedeagal valves and the phallobase lobes. The valves in *T. tetrophthalmus* are more rounded marginally and narrow to the point abruptly (fig. 14). The dorsal and ventral valves are similarly shaped, the dorsal one being slightly smaller overall and lying slightly within the edge of the ventral valve. Both valves are heavily sclerotized along the edge and the pigment reduces slightly in the middle.

The apical "bill" or distal end of the aedeagal valves in *T. femoratus* (fig. 15) is not rounded but rather straight and obtuse. The sides of the ventral valves converge gradually to the terminal point. The much smaller dorsal valve lies on the ventral valve and between the outer margins, but its shape does not correspond to the ventral valve as it does in *T. tetrophthalmus* (fig. 14). The posterior edge of the dorsal valve does not lie on top of the same edge of the ventral valve. The body of the aedeagus is characteristically
marked by a split in the dorsal midline which is covered by a slightly sclerotized area. The edges of the valves are also darkly pigmented as in *T. tetrophthalmus*.

The shape of the apical lobe of the phallobase is valuable in delimiting these species. In *T. tetrophthalmus* the area of the underside is much smaller than the same area in *T. femoratus*. The part of the phallobase which makes contact with the aedeagus dorsally is more narrow. The lobes are longer and larger in *T. femoratus* (fig. 17, 19) and the medial cleft is deeper than that of *T. tetrophthalmus* (fig. 16, 18). The ventral edge of the dorsal portion of the ring in *T. femoratus* is equipped with a small peg-like knob. It seems this knob would be aligned with the less sclerotized slit in the dorsal surface of the aedeagus when the structures are in repose.

The sclerotized plates found within the endophallus show species variation (fig. 22, 23, 31-34). These structures are best viewed from the dorsal through the top of the aedeagus. The first plate from the posterior (plate I) is free along the medial edge in both species and along the posterior edge in *T. femoratus*. It curves under the medial portion of the endophallus from the lateral surface when in the protracted position (fig. 33). A concavity is then formed between the pair. This medial free edge is square in *T. tetrophthalmus* and rounded in *T. femoratus* and is heavily sclerotized. Plate II is a large structure in *T. tetrophthalmus* and shaped like a half circle, the
round edge being medial (fig. 22). The posterior edge is sculptured and more deeply sclerotized and a corner of it projects slightly as a hooked edge. In *T. femoratus* the same plate is shaped like a right triangle, the hypotenuse being located medially (fig. 23). Plate III, the most anterior, is very similar in both species, being somewhat shaped like a cane. The anterior tip of this structure coincides with the edge of the anteriorly projecting endophallic wedge described previously (fig. 32, 33). This pair of plates is actually the lateral basal edge of the wedge which has been secondarily sclerotized to a greater degree than the rest of the wedge.

The Genital System of the Female

The reproductive system of the female (fig. 11, 13, 26-28) consists of a pair of ovaries and the associated glands and ducts. The ovaries are composed of eight ovarioles (fig. 11, Ov1) which are joined by a suspensory ligament which attaches in the anterior portion of the abdomen. The ovaries vary in size depending on the reproductive condition and in most of the specimens dissected the abdomen was full of large eggs. The ovaries usually occupy the space from the third to the sixth visible abdominal sterna. Posteriorly, the ovarioles open into a common chamber, the short calyx, which is on either side and slightly below the copulatory pouch (CP) and the genital chamber (GC). The lateral oviducts (LOvid) extend posterior
from the calyx (Cy) and are then acutely bent anterior to a point near the terminus of the copulatory pouch. From this point they bend posteriorly and medially and join beneath the copulatory pouch to form the common oviduct (COvid). The common oviduct then enters the wall of the copulatory pouch and opens into it a short distance posteriorly. The entire oviduct is slightly sclerotized and darker in color than the other ducts. The membranes of the oviducts are thrown into numerous longitudinal folds that allow for extensive lateral expansion.

The ovipositor is not an extremely long structure. It is the posterior extension of the gonital chamber (GC). The sclerotized plates and rods described in various other species (Bissell 1937) were not observed in the membranes of the ovipositor. When in repose in the abdomen, it is enclosed entirely within the foretube (Ft), a slightly sclerotized tube derived from the first connecting membrane. The posterior edges of the foretube are attached to the posterior edge of segment VIII which is retracted inside segment VII. The cavity within segment VIII is known as the vestibule. The anterior end of the foretube supports the rectum (Rec) and anus (An) and the ovipositor and its aperture, the vulva (Vu). The vulva is the true gonopore of the female and is the point of attachment of the gonocoxites and styli (Sty).

The eighth abdominal tergum (8T) is a large plate attached laterally to the sternum (8S) which is smaller.
The large spiculum ventrale (SpiV) is attached to the anterior edge of the sternum. It continues anteriorly as a thin apodeme and bends slightly to the right side of the abdomen. A large number of muscles connect this rod and the other reproductive organs, especially the copulatory pouch (CP).

The genital chamber (GC) passes posteriorly beneath the foretube from its point of attachment to the foretube. It bends anteriorly at a point near the eighth sternum to which it is attached by a band of muscle (fig. 28). These two bends I have labeled I and II respectively (fig. 11, 31) for purposes of clarity. From bend II the chamber narrows acutely and then expands anteriorly into the copulatory pouch (CP). The common oviduct enters the chamber at the posterior edge of bend II. The long, coiled spermathecal duct (SptD) is attached on the right side and near the antero-ventral end of the copulatory pouch. The duct leads to an oval shaped spermatheca (Spt, fig. 26, 27) which is situated on the right side of the abdominal cavity. The spermatheca and 1/3 of the duct connected to it are densely sclerotized and pigmented, but there is no muscle as described by Burke (1959). At the point where the sclerotized and membranous parts of the duct join, two rather long fingerlike spermathecal glands (SptGl) open. The spermatheca is considered the primary storage space for the sperm.

The lateral oviduct is connected to the anterior
edge of the foretube by means of a ligament. This ligament probably plays a major role in aiding the posterior movement of the lateral oviduct during oviposition. Beyond bend I the membranous chamber has characteristic folds and protruding bumps on its surface. One of these protuberances is especially obvious on the anterior of bend II (fig. 11). Anterior beyond this point there is a constriction of the chamber prior to its enlargement into the copulatory pouch. The copulatory pouch is sparsely lined internally with thin setae (fig. 31).

There are not many variations between females of the two species. The structures are generally larger in T. femoratus, especially the region including the constriction and the copulatory pouch. The form of the base of the spiculum ventrale and segment VIII is slightly variable. The triangular lateral plate is more acutely shaped (fig. 13) whereas it has rounded edges in T. tetrophthalmus (fig. 11). The sternum of segment VIII immediately inside the vestibule is a flat or only slightly concave plate in T. tetrophthalmus (fig. 35). T. femoratus is more concave (fig. 36) in the lateral aspect of the sternum such that the interior of the vestibule is actually a depression between the concavities. This characteristic may indicate the relationship between this structure and aedeagal valves of the male (fig. 37). The pointed dorsal valve could be positioned so that the point fits into this depression. The dorsal valve of T. tetrophthalmus is not pointed and
could not fit this depression, effectively blocking introduction of the endophasallic sac by not allowing separation of the valves. It is likely the valves must be pushed firmly against the wall of the depression to allow separation through increased pressure. The shape of the spermatheca is also a variable structure. *T. tetrophthalmus* has a broadly rounded or flattened spermatheca (fig. 26) and in *T. femoratus* it is more narrow and slightly larger and longer (fig. 27). In *T. femoratus* the union of the duct which is more densely sclerotized and the spermatheca forms a right angle.
Discussions of the function of the genitalia of beetles during copulation have been limited to interpretation. Burke (1959) and Bissell (1937) have considered this aspect for the species they described. Burke gave an especially good account of the probable functions of the various structures. No report has ever been made in which actual dissections have indicated the relationship of male and female genitalia. Bonhag and Wick (1953) were able to immobilize milkweed bugs in copulo by refrigeration. In vivo dissections were then undertaken to determine such a relationship. Gilbert (1964) has indicated the relationship of the male and female structures for selected species of the genus Baris Germar. His observations on the amount of penetration of the aedeagus indicates interspecific variation. He did not however investigate the actual relation of the membranous structure even though he used similar fixing techniques to determine the shape of these non-sclerotized parts.

The remainder of this discussion is based primarily on evidence gathered in the manner outlined previously. All work was done on T. tetrophthalmus.

As described before, the male initiates the copulatory act by mounting and attempting union with the female. He does this by bending the abdomen so the orifice is directed anteriorly. At this time he protracts the aedeagus, the phallobase, the spiculum gastrale and
abdominal segment VIII. By flexing the muscles associated with the spiculum gastrale, segment VIII is exerted first and the terminal edges probe and tap the female venters. The apical lobes of the phallobase protrude from the opening and are utilized in this probing action, especially the sensory setae on the lobes. When these structures make contact with the female vestibule and the opening in segment VIII, the aedeagus is protruded by means of muscular action (Burke 1959). The farthest extension of this structure is such that the base of the valves is still inside the male's eighth segment. The flattened scoop-like aedeagal valves function in locating and securing entrance to segment VIII within segment VII of the female. The aedeagus most likely never enters the foretube.

It is difficult to determine what response the female makes to the intromission. She very likely pushes segment VIII and the foretube posterior slightly in order to withstand the force of the entrance of the aedeagus.

After the male is in position and has effected intromission of the aedeagus he begins eversion of the endophallic sac. A combination of blood pressure and muscular contraction bring about this eversion. The endophallic sac is everted from the median orifice in an anterior direction in relation to the female, which is similar to the expansion of an inverted glove finger. It is feasible that the female may facilitate entrance of the endophallic sac by contracting longitudinal muscles along
the genital chamber, effectively shortening the path to the copulatory pouch. The female's role, then, is one of permission externally and internally. As the eversion becomes greater the median orifice is moved more anteriorly. When everted the endophallic sac is actually a tube within a tube, the inner tube being the ejaculatory duct. As the sac is everted the endophallic armature, which was described inside the body of the aedeagus, becomes a set of effective claspers inside the foretube. The arrangement is reversed when the claspers are everted and the most anteriorly directed is the cane shaped plate. This is the same position as described in repose because it is reversed when the sac is everted. The dorsal valve of the aedeagus contacts the female's eighth sternum and the ventral valve is in contact with the tergum. When the endophallic sac is everted the cane shaped claspers are located on the dorsal surface with respect to the female, but they are on the ventral side of the endophallic sac and aedeagus (fig. 31). The other two (posterior in relation to the female when everted) are on the ventral surface (with respect to the female) when everted. When eversion has proceeded such that the anterior cane shaped claspers are evident the membranous wedge becomes the most anterior structure between these two claspers. At this point the eversion effects the placement of the tip of the wedge deeply into the foretube. It seems that this slightly sclerotized structure is used to locate and secure the vulva (fig. 31). The remainder of the
endophallus then issues from below the wedge and moves into the genital chamber. Neither the claspers nor the wedge were ever observed inside the chamber, but always associated with the vulva. The final position of the claspers is in the interior of the foretube from segment VIII to the vulva and they are effective in maintaining a grasp on the lining of the foretube.

After entering the chamber the endophallic sac continues to be everted beyond bend I. If the endophallus is removed from the region of bend I it is obvious that the sac itself is bent in a peculiar manner (fig. 31). This condition could be a result of fixation in a position dictated by the female's anatomy or it could be due to the position of local protuberances or expansions of the sac membrane itself. Based on the dissections of the structures in repose, I feel the correct reason is the latter.

The endophallus continues into bend II where another characteristic protuberance of the female chamber aligns with an expansion of the endophallic sac. The remainder of the endophallus is very narrow and conforms to the constriction of the chamber. This part of the endophallus corresponds to the narrow region found around the flagellum in the relaxed specimen (fig. 20). The endophallus which is heavily covered with denticles in this region (fig. 31) everts to fill the copulatory pouch. This situation is like that described for the boll weevil by Burke (1959).
The boll weevil lacks a flagellum and consequently the gonopore is in the copulatory pouch when the endophallic sac is fully exserted.

In the specimens dissected, the flagellum was never found totally everted. It has been located in the area of bend II even though the endophallus is protracted to the level of the constriction. Based upon the fact that the endophallus was observed as not yet fully everted into the copulatory pouch, it is not unreasonable to expect that at full eversion of the endophallus the flagellum and part of the endophallus would enter and proceed into the spermathecal duct. The copulating pairs were startled and disturbed when they were moved to the boiling water and in the short time before killing it is possible that the male withdrew the flagellum a slight distance. The fullest extension of the endophallus was observed in a specimen which had copulated for at least twenty minutes. This was the longest period of copulation permitted before fixation. It is possible the male requires more time for complete penetration, yet this does not seem likely based upon the observed duration of copulation. If the flagellum is totally everted and enters the spermathecal duct the muscular sheath would be stretched to a great length due to its attachment to the aedeagal apodemes. This sheath around the uncoiled ejaculatory duct is involved in propelling the semen out the flagellum.
The process of retraction is essentially the reverse of protraction. The decrease in blood pressure and some small muscles attached to the walls of the endophallus (also described in A. grandis Boh. by Burke 1959) are responsible for restoring the endophallus within the aedeagus. The aedeagus is effectively restored within the abdomen by large masses of muscle attached to the phallo-base and spiculum gastrale. The complex structures of the male require one or two minutes for proper realignment. This is the probable reason why the male hesitates before walking away after breaking contact with the female.
CONCLUSIONS

A number of statements can be made regarding the results of this study. The mating behavior described was constant throughout the study period. The antennal calming behavior was more effective than the protarsal rubbing. These calming devices show specific variation between the species. The act of calming the female is essentially an act of communicating and may be considered a species identification technique. A more thorough analysis of this behavior is necessary to indicate whether or not it is partially responsible for the isolation of *T. tetrophthalmus* and *T. femoratus*. The specimens observed during this study occur in the same region, where the ranges overlap. I feel that the results of similar observations on specimens from areas extreme in the range may indicate the reinforcement of these isolation mechanisms.

The genitalia have proven to be diagnostic taxonomic characters. The variation is greater in the males than the females. A study of a larger number of specimens is necessary to determine the extent of intraspecific variation. At that time it might be possible to analyze more closely the morphological isolating mechanisms alluded to previously.
The reproductive structures are indeed complicated structures and their description was aided greatly by analysis of the fixed pairs. The function of these structures becomes much clearer after observing their position and condition in the fixed specimens. The structure of the aedeagal valves becomes more important when one considers that they must come into close contact with a specifically structured genital aperture. It is obvious that the aedeagal valves never enter the foretube and the major organ of intromission is the endophallus. The endophallic wedge functions as a vulvar opening mechanism insuring entrance of the endophallus into the genital chamber. The variation in size and placement of various protuberances of the endophallus becomes very important when one considers that the female chamber is accordingly shaped and the two have a "lock and key" arrangement. Based upon the dissections it is probable that the flagellum enters the spermathecal duct at full protraction. It is unknown if this situation is necessary for ejaculation. The fixing procedure works very well and more can be learned from it. The extraneous conditions, such as vibration and air current, which may disturb the copulants should be stringently controlled. These precautions will definitely improve the results.

A closer investigation is suggested in a number of areas. The site and mechanism of the antennal tapping
behavior could be studied through the use of slow motion photography and the use of a colored indicator. More detailed, in depth study of the copulating behavior might indicate other, subtle devices by which the copulants communicate. A histological study of the ejaculatory duct and muscular sheath tissue may indicate the structure of the muscle tissues and therefore provide evidence of its function during ejaculation. The variation evident in the endophallic armature could be endorsed by a study of a larger number of specimens. The precise clasping mechanism utilized between the armature and foretube should be studied in freshly fixed pairs which would still be attached and more pliable.

I intend to continue this research in a number of the areas mentioned above. I feel much can be learned by becoming familiar with the insect over its entire range. By doing this one can address himself to the dynamics of isolation and the role of behavior and morphology in that process.
1. *T. tetrophthalmus* (Forst.), male mounting female, note male abdominal flexure.

2. Same, male in "riding" position.


4. *T. tetrophthalmus* (Forst.), abdominal relationship prior to intromission.

5. Same, horizontal tapping of male antennae.


7. *T. tetrophthalmus* (Forst.), female cleaning antenna during copulation.

8. Same, abdominal position after breaking contact. Note abdominal segment VIII of male still extended.

9. Same, male bumping behavior.
EXPLANATION OF FIGURES 10-11

10. *T. tetraphthalmus* (Forst.), male, sagittal section of abdomen showing position of reproductive organs, 20x, (right testis omitted).

11. Same, female, 20x. (left lateral oviduct and ovary omitted)
EXPLANATION OF FIGURES 12-13

12. *T. femoratus* LeC., male, median lobe of aedeagus, lateral view, 30x.

13. Same, female reproductive system, lateral view, 20x.
EXPLANATION OF FIGURES 14-21


16. *T. tetrophthalmus* (Forst.), detail of apical phallobase, dorsal view, 30x.

17. *T. femoratus* LeC., detail of apical phallobase, dorsal view, 30x.

18. *T. tetrophthalmus* (Forst.), phallobase apex, lateral view, 30x.


20. *T. tetrophthalmus* (Forst.), flagellum within endophallic sac, 24x.

22. *T. tetrophthalmus* (Forst.), detail of endophallic armature, dorsal view, 64x. Right half of pair shown.

23. *T. femoratus* LeC., detail of endophallic armature, dorsal view, 64x. Right half of pair shown.

24. Same, phallobase, dorsal view, 20x.

25. Same, spiculum gastrale, dorsal view, 20x.

26. *T. tetrophthalmus* (Forst.), spermatheca, 30x.

27. *T. femoratus* LeC., spermatheca, 30x.

28. *T. tetrophthalmus* (Forst.), female genitalia, diagrammatic, ventral view, 20x.
EXPLANATION OF FIGURES 29-31

29. Same, detail of apex of ovipositor, dorsal view, 30x.

30. *T. femoratus* LeC., detail of apex of ovipositor, dorsal view, 30x.

31. *T. tetrophthalmus* (Forst.), diagrammatic representation of protracted endophallus within genital chamber of female. Note the wedge shaped protuberance and denticile patches, lateral view, 24x. (muscular sheath is omitted)
EXPLANATION OF FIGURES 32-37

32. Same, partially protracted endophallus, note armature and wedge, lateral view, 30x.

33. Same, ventral view, 30x.

34. T. femoratus LeC., endophallic armature, lateral view, 30x.

35. T. tetrophthalmus (Forst.), sternum of eighth abdominal segment, ventral view, 24x.

36. T. femoratus LeC., sternum of eighth abdominal segment. Note areas of deep concavity (Con), ventral view, 30x.

37. Same, diagram indicating relationship between the sternum of abdominal segment VIII of the female and the dorsal valve of the male during intromission, ventral view; 30x.
LITERATURE CITED


APPROVAL SHEET

The thesis submitted by Thomas John Pilat has been read and approved by members of the Department of Biology.

Furthermore, the final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated, and that the thesis is now given final approval with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

5-22-72
Date

Dr. R. W. Hamilton
Signature of Advisor