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Biology of a Limicolous Megadrile
(Annelida: Oligochaeta) from Louisiana

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Zoology and Physiology

by

Michael Lee McMahan

B.S., The University of Mississippi, 1968
M.S., The University of Mississippi, 1971
December, 1976

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TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES.	iv
LIST OF ILLUSTRATIONS	v
ABSTRACT.	vi
I. INTRODUCTION	1
II. TAXONOMY	3
III. ANATOMY.	11
IV. REPRODUCTION	24
V. LIFE HISTORY	26
VI. ECOLOGY.	33
VII. ETHOLOGY	38
VIII. FOLKLORE	42
IX. SYSTEMATICS.	43
LITERATURE CITED.	48
GLOSSARY.	72
VITA.	74

LIST OF TABLES

Table		Page
1.	Location of clitellum in <u>Lutodrilus multivesiculatus</u>	52
2.	Location of alae in <u>Lutodrilus multivesiculatus</u>	53
3.	Distribution of genital tumescences in <u>Lutodrilus multivesiculatus</u>	54
4.	Pattern of distribution of genital tumescences of three specimens of <u>Lutodrilus multivesiculatus</u>	55

LIST OF ILLUSTRATIONS

Figure	Page
1. Anterior end of <u>Lutodrilus multivesiculatus</u> , ventral view.	57
2. Diagrammatic longitudinal section of genital region of <u>Lutodrilus multivesiculatus</u>	59
3. Cross section of anterior body wall of <u>Lutodrilus multivesiculatus</u>	61
4. Cross section of body wall in clitellar segment of <u>Lutodrilus multivesiculatus</u>	61
5. Cross section of typhlosolar intestine of <u>Lutodrilus multivesiculatus</u>	63
6. Epidermal cross section from dorsal respiratory surface of <u>Lutodrilus multivesiculatus</u>	65
7. Epidermal cross section from dorsal respiratory surface of <u>Lutodrilus multivesiculatus</u>	65
8. Longitudinal section of ovarian egg string of <u>Lutodrilus multivesiculatus</u>	67
9. Cross section of spermathecae at 24/25 of <u>Lutodrilus multivesiculatus</u>	69
10. Oothecae of <u>Lutodrilus multivesiculatus</u>	71

ABSTRACT

The present study investigates the biology of Lutodrilus multivesiculatus McMahan, 1976, in the family Lutodrilidae. The existence of lumbricid ovaries places the family into superfamily Lumbricoidea. Features unique to the species include ten pairs of testes, in xii-xxi, 12 pairs of seminal vesicles, in xi-xxii, location of the ovaries in xxiii, and 11 pairs of hearts, in xi-xxi.

The species, which is hermaphroditic and likely amphimictic, deposits elongate, fusiform oothecae from which one or two young emerge. Postembryonic growth occurs by addition of segments and by enlargement of existing segments.

This megadrile is limicolous, inhabiting areas rich in organic detritus along shorelines of streams in southeastern Louisiana, and has undergone adaptations to an anaerobic, semi-aquatic habitat. It responds quickly to physical and chemical stimulation, often autotomizing sizeable body portions.

The relationship of the species to other oligochaete taxa is examined, and its status as a relatively primitive organism is demonstrated.

I. INTRODUCTION

The low temperatures characteristic of Pleistocene glaciation exterminated the megadrile fauna of North America in an area considerably greater than that actually glaciated (Gates, 1929, 1967, 1970, 1974b; Reynolds, 1973), and megadriles survived in only two refugia. Earthworms of one of these areas, the Pacific coast from northern California northward to the Canadian border, have not been studied adequately, and they presently are placed incorrectly in Australasian genera. The second refugium, the southern states from the Carolinas to Texas and Oklahoma, is characterized by five genera unknown elsewhere except as a result of transportation by man. These genera belong to four families (Sparganophilus - Sparganophilidae; Diplocardia - Acanthodrilidae; Eisenoides, Bimastos - Lumbricidae; Komarekiona - Komarekionidae) of which only one, the Lumbricidae, is not restricted to North and Central America (Gates, 1970, 1974a). The fact that five genera and three families are known only from the southern refugium (with the exception of Mexican species of Diplocardia) indicates the need for characterization of the megadrile fauna of the southeastern United States.

Eisen (1892) caught "Criodrilus or a related genus" in the Mississippi River but did not provide precise collecting data or description of specimens. Wurtz and Roback (1955) collected four megadrile specimens with copulatory appendages in northwestern Florida, but identification was not made. All of the specimens from the two

collections have disappeared without a trace (Gates, 1974a), resulting in two especially intriguing enigmas for North American researchers. Because neither species resembling Criodrilus nor megadriles with copulatory appendages are known from North America except as interceptions from plant shipments (e.g., McKey-Fender and MacNab, 1953), the discovery and loss of such specimens have taunted oligochaetologists.

M. A. Tidwell and the late R. E. Tandy, in 1965, collected specimens of an unusual and unidentifiable megadrile in Louisiana, and these specimens subsequently were stored for future investigation. Additional Louisiana specimens of the oligochaete were obtained in 1972 by Tidwell, who brought the megadrile to my attention. Tandy's collection was obtained, and recent collections of the earthworm have permitted a thorough examination and evaluation of the species, which was undescribed.

II. TAXONOMY

An ovary with a single terminal egg string is known only from the lumbricoid families: Hormogastridae, Komarekionidae, Lumbricidae, and Sparganophilidae (Gates, 1974a; 1974b). Likewise, the Glossoscolecidae (sensu Stephenson, 1930) are distinguished by a lengthy, multilayered clitellum which is located anteriorly on the body; male pores on or near the anterior clitellar segments; and intraparietal male ducts. In addition, aliform tubercula pubertates are known only from one microchaetid genus, Glyphidrilus (Stephenson, 1930; Gates, 1972). Mature specimens examined in this current study possess all of these traits that are diagnostic for the lumbricoid families, the Glossoscolecidae (sensu Stephenson), and the microchaetid genus Glyphidrilus. Since this Louisiana megadrile exhibits traits characteristic of two distinct familial assemblages, the erection of a new genus and family was necessitated (McMahan, 1976).

Lutodrilidae McMahan, 1976

Diagnosis

The family was diagnosed as for the type genus.

Type genus

Lutodrilus McMahan, 1976.

Distribution

Southeastern Louisiana.

Discussion

Study of any well-known megadrile family quickly demonstrates that it is difficult to anticipate, on the basis of a single species, those characteristics of diagnostic value for genus and family. Consequently, the family Lutodrilidae was diagnosed as for the genus until other representatives of the family are described.

The ovary is expected to be characteristic of all members of the family. The importance of ovarian structure in megadrile systematics was demonstrated by Gates (1974b), who stated that one ovarian configuration is characteristic of all members of any megadrile family. Thus, Gates (1974a, 1974b) allied the Lumbricidae, Sparganophilidae, Hormogastridae, and Komarekionidae into a major lumbricoid group on the basis of their possessing lumbricid ovaries (i.e., ovaries terminating distally in a single egg string). A similar configuration in the Lutodrilidae (Fig. 8) permitted the inclusion of this family as a fifth member of the lumbricoid group. As in all known members of the group, any species subsequently placed into family Lutodrilidae is expected to possess typical lumbricid ovaries.

With one exception, in no megadrile (excluding anterior regenerates) do testes exist posterior to xiv, nor do they number more than seven pairs (Gates, 1974b). The exception is Agastrodrilus multivesiculatus Omodeo and Vaillaud, with nine pairs of testes, in x-xviii (Omodeo and Vaillaud, 1967); however, the fact that this species likely is an anomaly produced by abnormal anterior regeneration is apparent from the description, and the species may be synonymous with its sole congener A. opisthogynous Omodeo and Vaillaud, which

itself may prove to be an abnormal anterior regenerate. Each of the two species of Agastrodrilus was described from perhaps only one or two specimens and therefore may be an abnormal regenerate of a species quite different from either described species (Gates, 1974b). Because of the uncertain status of A. multivesiculatus, its description does not preclude the statement that Lutodrilus may be characterized by the position of its ten pairs of testes, in xii-xxi, and that future members of the family are expected to possess numerous pairs of testes in a series extending posterior to xiv.

A somatic feature anticipated to be diagnostic for the Lutodrilidae is the 11 pairs of hearts and their position. No other megadrile possesses hearts behind xiii (Gates, in lit.) whereas they occur in xi-xxi in Lutodrilus multivesiculatus. Agastrodrilus multivesiculatus, also with 11 pairs of hearts, in ix-xix (Omodeo and Vaillaud, 1967), would negate Gates' statement except for the belief that the species was described from a specimen(s) suspected to be the product of abnormal anterior regeneration. No such suspicion is held for L. multivesiculatus since all examined specimens lack evidence of abnormal anterior regeneration.

Lutodrilus McMahan, 1976

Diagnosis

External characteristics. No dorsal pores. Nephropores inconspicuous, slightly lateral to B, presetal, absent anteriorly. Anus dorsal to dorsoterminal, triangular, with apex anteriad. Body rounded anteriorly, becoming quadrangular posterior to vii. Setae lumbricin, setal couples at the four angles of the body. Clitellum

annular, only slightly swollen with indistinct anterior and posterior delineation, and including many segments. Tubercula pubertates aliform, lateral to B, extending through most clitellar segments. Genital tumescences, each around a, b, beginning preclitellar and found in many clitellar segments. Male tumescence, enclosing both ventral setal couples of segments xxxii-xxxiii, with one pair of spermiducal pores on xxxii, slightly presetal in AA. One pair of oviducal pores, clitellar, in xxiv, slightly lateral to B, presetal. Genital apertures diminutive and superficial.

Internal anatomy. Digestive system lacking crop, gizzard, and calciferous glands. Pharyngeal bulb, ii-vi. Intestine dilating gradually in posterior gonadal segments. Posttesticular intestinal pouches, each extending several segments. Dorsal typhlosole with postgonadal origin. Nephridia holoic, avesiculate, absent in anterior segments. Seminal vesicles, 12 pairs, xi-xxii, trabeculate. Testes, 10 pairs, xii-xxi, terminating in numerous strings projecting into coelom. Vasa deferentia minute, intraparietal, lateral to B. Prostates lacking. Ovaries, in xxiii, separated from last pair of testes by one sterile segment. Each ovary triangular with a single egg string at posterior apex of triangle, six to eight maturing oocytes per string. Spermathecae ovoidal, intraparietal, dorsolateral ventral to C, intersegmental, beginning in gonadal segments and present in several successive intersegmentals. Lateral hearts, 11 pairs, in xi-xxi, some with connectives from the lateroparietal vessels. Ventral trunk complete, dorsal trunk aborted anteriorly. Subneural vessel within neural sheath, absent anteriorly. Single pair of lateroparietals and one pair of latero-esophageals anteriorly.

Etymology

The most frequently used common name for this megadrile is "mudworm." The generic name was derived from luo (Gr., loosen), via lutum (L., mud), and drilos (Gr., worm).

Type species

Lutodrilus multivesiculatus McMahan, 1976.

Distribution

Southeastern Louisiana.

Discussion

Generic characters are those that are constant in all species constituting a genus. Reservations similar to those at the familial level must be imposed upon traits included in a generic diagnosis based upon only one species.

Lutodrilus multivesiculatus McMahan, 1976

Diagnosis

With generic characters and the following:

External characteristics. In complete, contracted, mature specimens with no regeneration, length 20-40 cm. Width, up to 11 mm in gonadal segments, 3-5 mm posteriorly. Segments, 315-482. Prostomium zygalobous to prolobous. $\underline{AB} = \underline{CD}$, $\underline{AA} < \underline{BC} < \underline{DD}$, $\underline{DD} = 0.29-0.40$ C. Setal formula 7:1:10:1:13 in x, 8:1:12:1:15 in xxx, 6:1:8:1:11 in l. In vivo color green to blue-green anteriorly and far posteriorly, brown to brown-green in mid-body. Formalin-preserved material, gray to brown with little or no green. Nephropores, in xxiii and following, excluding xxiv. Clitellum extending 37-51 segments, xx-xxv to lxi-lxxi, red to red-brown in

color. Genital tumescences white to tan, rounded elevations around a,b, in some of xiii-lij, usually xvi-lii. Male tumescence, in xxxii-xxxiii, broad elevated area between alae, sometimes extending onto portions of xxxi and/or xxxiv. Alae prominent, 1.5-3 mm in height, in xxii-liii, usually xxviii-li.

Internal anatomy. Intestinal dilatation xxi-xxiv, pouches to region of 1. Dorsal typhlosole beginning gradually in xxxi-xxxiv. Nephridia absent anterior to xxv with exception of xxiii. Spermathecae, 15/16-25/26, 2-5 on each side of each intersegmental region, not bilaterally paired. Epidermal acinar glands, in xxii-xxvii, one gland associated with each ventral seta. Hearts of xi-xv, primary ventral junction with lateroparietals. Complete ventral trunk, very small anterior to v, bifurcating at subpharyngeal ganglion. Dorsal vessel absent anterior to septum 10/11. Subneural vessel complete posterior to xxi. Paired lateroparietal vessels extend anteriorly from junction with dorsal vessel at 22/23. Paired latero-esophageal vessels originate on dorsum of pharyngeal mass in ii and terminate by capillarization in seminal vesicle of xii.

Etymology

Among the features of the internal anatomy of Lutodrilus multivesiculatus, the most impressive is the series of twelve pairs of seminal vesicles. The specific name was derived from multus (L., many) and vesicula (L., small bladder).

Type material

The holotype is deposited in the collection of the U. S. National Museum, No. 53283 (clitellate specimen), as is a paratype, an

aclitellate, No. 53284. Additional paratypes are in the collection of the author, and paratypic material will be deposited in the Collection of Invertebrates, Louisiana State University, Baton Rouge, Louisiana.

Distribution

The distribution of Lutodrilus multivesiculatus is limited to the portion of southeastern Louisiana that lies between the Mississippi and Pearl rivers, and populations are located along the shorelines of streams and rivers in areas where accumulations of leaf litter occur.

Material Examined

All specimens used for measurements had been anesthetized in 10% ethanol as recommended by Ljungström (1970) and fixed and preserved in 10% formalin. Material for histological examination was fixed in 10% formalin as above, dehydrated in ethanol, embedded in paraffin, sectioned at 10 μ m, and stained with Harris' hematoxylin-eosin. Collections were as follows:

ST. HELENA PARISH. Amite River E Clinton, 28 July 1965, 0-1-0, M. A. Tidwell.

ST. TAMMANY PARISH. Tchefuncte River at Lake Ramsay Campground, N Covington, 9 June 1973, 0-2-0. M. L. McMahan.

TANGIPAHOA PARISH. Chappepeela Creek at La. 445, 8 June 1973, 0-3-0. M. L. McMahan. Tchefuncte River at La. 40, April 1972, 5-4-1. M. A. Tidwell. 24 May 1973, 5-1-2; 12 June 1973, 0-2-3; 6 August 1973, 4-2-0; 21 September 1973, 0-6-0; 26 October 1973, 2-0-0; 5 March 1974, 0-5-0; 3 May 1974, 0-5-0; 15 May 1974, 0-1-0; 10 June 1974, 0-4-0;

28 June 1974, 0-6-0; 13 August 1974, 5-5-0; 23 September 1974,
0-10-0. M. L. McMahan.

WASHINGTON PARISH. At the foot of the flood plain of Pearl River
just outside city limits of Bogalusa, 31 May 1965, 0-1-0. R. E. Tandy.
___ mi. South of State Line, La., in creek bottom on La. Hwy. 62.
? west fork of Pushepatapa (sic) Creek, 31 May 1965, 2-2-5. R. E.
Tandy. N State Line, La., west fork of Pushepatapa Creek at La. 62,
behind State Line Church (Sec. 12, R16E, T1S), 21 October 1974, 0-1-0;
25 October 1974, 9-9-0; 24 January 1975, 0-9-0; 22 March 1975,
4-5-0. M. L. McMahan. 0.85 mi E Mt. Hermon, La., on La. 438,
Silver Creek, 21 October 1974, 1-0-0. M. L. McMahan.

III. ANATOMY

External anatomy

Secondary furrows are present anterior to xxi-xxiv, and tertiary furrows begin in vii, occurring posteriorly to xiv-xxiv. Each type of intrasegmental furrow is most evident dorsally. Body shape is almost circular in anterior cross section and is quadrangular posteriorly, beginning approximately at vii. The quadrangular shape is most pronounced posterior to gonadal segments, with setal couples at the four angles of the body. Setal arrangement is lumbricin, with setae closely paired in a slightly postequatorial position. Setae are curved distally and have jagged, transverse ridges immediately proximal to the curved portion. A nodule is one-third of the setal length from the distal tip. In non-regenerates, the tip of the tail often is reflected over the posterior border of the anus. Nephropores are inconspicuous, identifiable only in histological sections.

The clitellum is annular and only slightly swollen, with indistinct anterior and posterior margins. The body in this region is compressed dorsoventrally, and the ventral surface is flattened or concave. The extent and location of the clitellum are variable, as indicated in Table 1. Intraclitellar intersegmental furrows are not obliterated by clitellar development. The clitellum is multi-layered dorsal to the alae only, not extending onto the ventrum; however, the coloration is annular with the exception of the genital

tumescences and ventral surfaces of the alae, both of which are white to tan in contrast to the reddened coloration of the clitellum.

The tubercula pubertates include 16-32 segments, xxii-liii (Table 2), are aliform, and extend 1.5 mm from the body in preserved material and 2-3 mm in living animals (Fig. 1). The alae originate lateral to B and in life are flared laterally. Genital tumescences are small, rounded elevations not sharply demarcated from the surrounding epidermis (Fig. 1). Each tumescence surrounds and includes one ventral setal pair, and the tumescences are superficial, being totally extramuscular. Each of segments xiii-xxx, usually xvi-xxviii, and xxxiv-lii may possess one, two, or no tumescences, each limited to the region around a, b (Tables 3 and 4). Frequently, genital tumescences are absent on most or all of segments xxxiv-xlvi. In clitellate individuals, genital tumescences are white to tan in contrast to clitellar coloration whereas, in aclitellates, the color of the genital tumescences is like that of the surrounding epidermis. The male tumescence is an elevated, flattened area on the ventrum of xxxii-xxxiii, sometimes extending onto portions of xxxi and/or xxxiv (Fig. 1). The male tumescence contacts the alae, thus including both ventral setal couples of each segment. The ventral setal pairs of xxxi-xxxiv are displaced medially. In xxxi and xxxiv, the amount of displacement is equal to half of AB whereas b of xxxi and xxxiii is in the A line of segments other than xxxi-xxxiv (Fig. 1). Spermathecal pores are minute, unrecognizable macroscopically, and are multiple in each intersegmental 15/16-25/26, ventral to C.

Internal anatomy

Septa are present posteriorly beginning with 3/4 and are thickened and heavily muscularized 7/8-23/24. Posterior to the pharynx, septa are markedly depressed posteriad. Muscles extend from the pharynx to parietal insertions, ending in vii.

Anteriorly, the body wall is distinctive, being ca. 1.5 mm thick in ix of a mature specimen and having five distinct muscle layers: subepithelial circular, diffuse longitudinal, median circular, trabeculate longitudinal, and retroperitoneal circular (Fig. 3). The median circular muscle layer diminishes posteriorly and ends in xviii. In midbody, the body wall is ca. 0.75 mm thick, and there are three muscle layers: two circular layers with a median trabeculate longitudinal layer (Fig. 4). The retroperitoneal circular layer is much thinner than anteriorly. Near the periproct, the body wall musculature is much reduced. The only distinct layer is the outer circular muscle, beneath which is a loosely-arranged layer of longitudinal fibers that are not organized into well-defined bundles. Immediately internal to the peritoneum, there is a muscle layer consisting of one to two thicknesses of circular muscle fibers.

In megadriles, the existence of distinct circular muscle layers other than immediately subepidermal in position is unknown. Such a condition would be expected to accompany reduction of the outermost layer of circular muscle; however, this is not the case. To the contrary, in L. multivesiculatus, the outermost circular muscle layer is thickest anterior to and including x - the portion of the body in which the two inner circular layers are best developed.

The proportional amount of circular muscle in this region is greater than in any other known megadrile and, comparatively, results in an extremely powerful probing capability with the anterior segments.

The retroperitoneal circular layer, always present throughout the body, is thickest anterior to x, posterior to which it diminishes to equal the thickness of the outermost circular layer. Near the periproct, the retroperitoneal circular musculature is one-sixth of the thickness of the subepidermal layer.

The trabeculate muscle layer is most highly developed in the region of xii, where it is ca. 1.2 mm thick. "Kästchen" are poorly defined, and they lack discernible internal organization. Fibers within a "kästchen" are arranged into small, randomly distributed bundles that are most dense ectally. Fascicles of connective tissue occasionally infiltrate between the bundles. This arrangement resembles that reported in Eisenia foetida (Savigny) and Allolobophora chlorotica (Savigny) by Harman (1960) although it is less organized than in either of these two species.

The outer longitudinal muscle layer consists of small, diffuse bundles of fibers that only occasionally are enclosed by connective tissue fascicles. The radial fascicles of connective tissue separating "kästchen" of the trabeculate layer sometimes penetrate the median circular layer and pass through the outer longitudinal layer, dividing its fibers into ill-defined bundles.

The brain, located in ii-iii, is bilobed and gives rise to two circumpharyngeal commissures at 2/3. Each commissure is one-third the diameter of the single ventral nerve cord, which the commissures

join in iii. Five pairs of nerves branch anteriorly from the brain: two to the roof of the buccal cavity and three to the prostomium, peristomium, and parietes. Segmentally, three pairs of lateral nerve trunks arise from the nerve cord.

The digestive tube lacks crop, gizzard, and calciferous glands. The pharynx is in ii-vi, with muscle fibers to the parietes extending to vii. An esophageal valve originates from the dorsal wall of the esophagus in vii. The esophageal mucosa becomes folded longitudinally in xvi, with vascular sinuses in xvi-xx. The gut widens at 20/21, and intestinal pouches begin in xxi-xxiv, extending to the region of l. Each pouch, a dilatation of the intestine, is variable in length, extending up to 10 segments. The dorsal typhlosole begins as a low proliferation of tissue in xxxi-xxxiv and may obliterate the intestinal lumen posteriorly. The peduncle of the typhlosole is nearly as broad as the distal portion (Fig. 5). Chloragogen is present from the anterior segments, with greatest accumulations in xx and succeeding segments.

Nephridial tubules extend into the upper portion of the coelom and adhere closely to the parietes. Nephrostomes are single.

Seminal vesicles are largest in xiv-xxi, where they often fill the coelom to the mid-dorsal line (Fig. 2). Vesicles are attached to the posterior faces of their respective septa with the exception of the vesicles of xi and xii, which attach to the anterior faces of septa 11/12 and 12/13, respectively. Testes are digitate, ending distally in numerous strings. The large, polypliate spermiducal funnels surround ventrolateral portions of the seminal vesicles.

The vasa efferentia are microscopic, having diameters of 50-75 μm . They enter the parieties one segment posterior to their respective funnels and orient posteriorly in a retroperitoneal position. One, or sometimes two, segments posterior to their origins, the vasa efferentia join the intramuscular vasa deferentia, which also are microscopic (ca. 75 μm in diameter). The vasa deferentia are embedded in the trabeculate longitudinal muscle layer approximately half the distance through the body wall; however, they move toward the coelom at the junction with each vas efferens. Each vas deferens is lateral to B until 31/32, where it begins medial orientation through the ventral parieties toward the spermiducal pore in xxxii. Prostates are lacking.

Each ovary resembles a rounded triangle with a posterior apex tapering to a single egg string containing 6-8 maturing oocytes that are visible through the ovarian wall (Fig. 8). The crenellate oviducal funnels are smaller than and more closely attached to the septum than are the spermiducal funnels. Oviducts pass posteriorly through septum 23/24, which is depressed posteriad by seminal vesicles of xxii, and the ducts then orient anteriad toward their entrance into the parieties lateral to B and presetal.

Spermathecae are ovoidal, averaging ca. 150 x 200 x 275 μm , and are intraparietal in the outer layer of longitudinal muscle in intersegmentals 15/16-25/26 (Fig. 9). Spermathecal number varies, 2-5, on each side of a segment, and these structures often are not paired bilaterally. Spermathecae are ventral to C. Thecal ducts are simple, adiverticulate tubes ca. 90 μm in diameter and 150-300 μm in length leading to superficial pores in the intersegmental furrows.

Epidermal glands are associated with the ventral setae of xxii-xxvii. One acinar gland is associated with each of setae a and b, posterior to the seta. Glands are limited solely to the epidermis, and straight ducts open on a slight surface elevation.

Vascular system

According to Gates (1970), the artificiality of the classical system of oligochaete systematics, as rendered in Das Tierreich, Vol. 10 (Michaelson, 1900) and later supported by Stephenson (1930), was due largely to unwarranted emphasis of reproductive structures and lack of attention to somatic structure. Gates (1962) determined that vascular features provide diagnostic characteristics for natural taxa, perhaps to the familial level. Brinkhurst (1971) stated that the potential value of the vascular system in oligochaete systematics is not fully utilized due to inadequate knowledge concerning many taxa. Recent papers devoted exclusively to vascular system studies (e.g. Johansen and Martin, 1965; Righi, 1972; Righi and Bittencourt, 1972) reaffirm the significance of this system. Because of the uniqueness of the vascular system in Lutodrilus multivesiculatus, a comprehensive discussion of this system follows.

The vascular system is described from three regions: (1) anterior to xxiii, where much differentiation occurs due to cephalization; (2) intestinal segments, where vascular elements are metameric; and (3) the pre-periproct region, where there is extensive parietal vascularization. Nomenclature of the vessels follows that of Righi (1972), with modifications.

Anterior to xxiii. There are four primary longitudinal vascular trunks anteriorly: the ventral and dorsal vessels and a pair of lateroparietal vessels. Less prominent longitudinal vascular features are subneural sinuses and a pair of latero-esophageal vessels.

Ventral vessel. This vessel, continuous throughout the body, undergoes a great decrease in diameter anterior to v. In iv, the ventral vessel bifurcates, and each branch circles the pharyngeal bulb near the circumpharyngeal nerve commissure. Many branches of the circumpharyngeal vessels vascularize the pharynx, brain, commissures, and body wall of the first three segments.

Dorsal vessel. This trunk begins at septum 10/11 and follows a sinuous path along the dorsum of the alimentary tract. Anterior to its juncture with heart xi, the diameter of the dorsal vessel is very small, and it is disjunct from the digestive tract and surrounded by chloragogue. The size of the vessel increases to heart xiv, behind which it is uniform except for septal constrictions. Two pairs of dorso-intestinal vessels extend from the dorsal vessel to the esophagus segmentally posterior to x.

Lateroparietals. These bilaterally-paired vessels, present anterior to 22/23, are located slightly lateral to B and are retroperitoneal or immediately external to the innermost layer of circular muscle (Fig. 3). In iii, they terminate by forming circumferential vessels which branch to capillarize adjacent portions of the parieties and digestive tract. Segmentally, the lateroparietals give rise to large retroperitoneal circumferential vessels with

radial branches passing through the longitudinal muscle to vascularize the outer body wall. In xxii, the lateroparietals cross the coelom and join the dorsal vessel at 22/23. In the coelom of xxii, each lateroparietal gives rise to a large branch to the subneural vessel, which greatly increases in diameter posterior to this point.

Subneural vessel. Although the subneural vessel is not continuous anterior to xxii, a succession of sinuses, 2-3 per segment, is present in that region. Each of these sinuses, present in iv-xxii, originates by the union of capillaries within the neural sheath, vessels from the parieties, and a branch from each latero-esophageal, and the sinuses lose their identity in a similar fashion. Their position within the neural sheath is identical to that of the subneural vessel, which is not continuous until xxii, where it receives a large connective from each lateroparietal vessel.

Latero-esophageal vessels. The pair of latero-esophageals originate from capillaries on the pharyngeal dorsum in ii. They enlarge while on the dorsum of the pharyngeal mass and begin to orient ventrally around the pharynx in vi. In vii, they join smaller trunks that form ventrolaterally on the pharynx. Posterior to vii, the latero-esophageals, surrounded by chloragogen, are positioned ventrolaterally on the alimentary tract; therefore, they differ from extra-esophageals, which are free from the esophagus for much of their length and are more ventral with respect to the digestive tract than are latero-esophageals (Righi, 1972). Anterior to each septum 7/8-12/13, there is a large connective from each lateroparietal to the latero-esophageals, which also receive branches

from the alimentary tract and subneural vessels. In ix, there is a pair of connectives from the dorsum of the gut to the latero-esophageals, which terminate posteriorly by capillarization in the seminal vesicles of xii, immediately after branching to the lateroparietals.

Hearts. The most conspicuous vascular features anteriorly are the hearts, eleven pairs, one pair segmentally in xi-xxi. Only eight pairs, in xiv-xxi, are highly contractile whereas those of xi-xiii are smaller and are easily mistaken for commissural vessels. Every heart is muscularized, contains up to eight valves, and enters the ventral vessel. Hearts are lateral, i.e. connecting the dorsal and ventral vessels; however, the junction of the heart and ventral vessel is not the primary route for blood in xi-xv. In each of these five segments, there is a large ventrolateral branch from the heart to the parieties that eventually enters the lateroparietals. Such branches are termed ventrotegumentary vessels and are known from several megadrile genera (Perrier, 1881; Bourne, 1891; Righi, 1972). Hearts of xi-xv have very small diameters (ca. 25 μ m in xi) as they enter the ventral vessel; therefore, anteriorly, the major afferent vessels are the lateroparietal vessels because they receive blood from the first five hearts.

Intestinal region. In intestinal segments posterior to xxiii, there are three longitudinal trunks: dorsal, ventral, and subneural. Constrictions at the septa occlude the lumens of all three vessels. Vascularization is metameric.

Dorsal vessel. The dorsal vessel, the efferent trunk, is embedded within the chloragogue on the intestinal dorsum and receives three pairs of vessels per segment: a pair of commissural vessels and two pairs of dorso-intestinal vessels. The commissural vessels penetrate the posterior septum to carry blood from the posteriorly adjacent segment to the dorsal vessel. There are five tributaries of each commissural:

a) Ventroseptal vessel. Each commissural vessel originates in the ventral septum from numerous capillaries that coalesce to form the ventroseptal vessel, which therefore drains the ventral portion of the septum.

b) Ventroparietal vessel. This vessel drains the ventro-lateral body wall, where it originates as numerous smaller vessels draining the parieties. The union of the ventroparietal and ventroseptal vessels creates the ventral extremity of the commissural vessel, which courses dorsally a considerable distance before receiving the next efferent trunk, the lateral septoparietal vessel.

c) Lateral septoparietal vessel. Two small blood vessels arise in the lateral parieties and unite to give rise to the lateral septoparietal vessel. While coursing across the septum, this vessel receives many capillaries from the septum.

d) Nephridioparietal vessel. Two efferent vessels, one each from the lateral body wall and from the nephridium, join near the commissural vessel to form the nephridioparietal vessel.

e) Dorsal septoparietal vessel. The dorsalmost efferent trunk emptying into the commissural vessel is the dorsal

septoparietal vessel, which crosses the dorsal septum. This vessel originates in the dorsolateral body wall and receives septal vessels as it traverses the dorsal septum.

Two pairs of dorso-intestinal vessels, equally spaced between septa, arise from the dorsolateral portion of the intestinal blood sinus and extend dorsomedially to the dorsal vessel, which they join on its ventrolateral aspect. These vessels also receive smaller vessels that drain the gut surface. There is an extensive submucosal vascular sinus in the typhlosole, from which numerous vessels convey blood to the ventrum of the dorsal vessel.

Ventral vessel. This vessel is suspended in the medial mesentery between the intestine and the nerve cord. A pair of ventrotegumentary vessels and two or three unpaired ventro-intestinal vessels leave the ventral vessel segmentally. Ventrotegumentary vessels, arising in midsegment, penetrate the posterior septum, bifurcate, and then branch to supply the nephridium, posterior septum, and body wall. There are three ventro-intestinal vessels per segment, decreasing to two posteriorly, where the segments are narrow. The ventro-intestinals arise from the dorsum of the ventral vessel and move dorsally through the mesentery to the vascular sinus of the intestine.

Subneural vessel. This tiny vessel, located within the neural sheath, capillarizes the nerve cord and has one pair of parietal branches per segment.

Pre-periproct segments. Near the posterior extremity of the animal, the dorsal vessel receives a pair of commissures comparable

to those found further anteriorly, draining the parieties and nephridium of each segment. In addition to two ventro-intestinal vessels, the ventral vessel gives rise segmentally to only one pair of vessels, which vascularize the septum, parieties, and intestine. The subneural vessel gives rise to a pair of nephridial vessels in each segment in addition to vascularizing the nerve cord.

The three longitudinal trunks extend nearly to the anal area, where they capillarize to supply the parieties. Extensive parietal vascularization is pronounced dorsally, and capillaries infiltrate the epidermis, frequently forming subcuticular capillary beds (Figs. 6, 7). Such extra-epidermal capillarization is unknown in other megadrile taxa. There also is extensive vascularization of the intestine, forming sinuses which often constitute one-third of the intestinal wall.

IV. REPRODUCTION

Spermatozoal iridescence was present on spermiducal funnels and in spermathecae of clitellates. Observation of mature sperm in these two structures in histological sections confirms the completion of spermatogenesis and the transfer of sperm during copulation. Additionally, a single, scalelike spermatophore containing sperm was present on the ventrum of each of three clitellates at xxv-xxvi (Fig. 1). Therefore, the species is hermaphroditic and likely amphimictic. A definitive statement that Lutodrilus multivesiculatus is amphimictic cannot be made because pseudogamy is known to occur in megadriles (Reynolds, 1974), and this possibility has not been excluded.

Sperm morulae are released from the testes into the coelom, where they have been observed frequently in histological studies, and they pass to the seminal vesicles, in which completion of spermatogenesis and sperm maturation occur. Mature sperm move from the seminal vesicles to the spermiducal funnels, where the gametes aggregate with their heads aligned on the internal face of the funnel. No sperm have been observed in the male ducts, indicating that the gametes are retained upon the funnels until their release.

The single ovarian egg string, which extends posteriorly toward the oviducal funnel, is a region of growth for the developing oocytes. Within each egg string are 6-8 maturing oocytes that

increase greatly in size as they approach the distal (posterior) tip of the egg string, the point of their release from the ovary (Fig. 8).

No worms in copula have been observed.

Oothecae are fusiform with a quadrangular cross section, and they are 5-6 mm wide, 3-5 mm high, and 5-8.5 cm long (Fig. 10). Although one end is closed tightly, the other end is broad and plugged with mucus, and the broad end is the point of exit for the young worms. The number of ova deposited within each cocoon is unknown although 1-2 worms have been observed to emerge. Of four cocoons hatched in the laboratory, two produced one worm, and two produced two worms each.

V. LIFE HISTORY

Lutodrilus multivesiculatus has been collected in every month of the year except December and February. Lack of collections during these months resulted from the frequency of rains and consequently widely fluctuating water levels that affected habitats and prevented the collection of specimens during these two months each year of this study. The distribution of the species in southeastern Louisiana coincides with a geographical area in which the topography is rolling hills, and even light rainfalls cause great fluctuations in water levels in waterways of the region. Throughout the year, no specimens have been sighted during or immediately after sudden variations in water levels.

Clitellate specimens, comprising 5.7% of all specimens studied (245), were collected April to July. Within these months, clitellates constituted only 12% of the lutodrilids that were collected.

Oothecae. Cocoons were found August-September, and unhatched cocoons were collected only in early August. Of 26 cocoons that were collected, only six were unhatched. Because a large proportion of the cocoons had hatched prior to collection and were in various stages of decomposition and because young of the year were collected as early as June, deposition must have begun prior to June. Cocoons had been deposited at depths to 20 cm within a meter of the lowest waterline. Only one cocoon was recovered from the surface.

Incubation times in the laboratory were 12, 16, 23, and 36 days from the dates of collection for the four cocoons which hatched. Because it was unknown when the cocoons had been deposited, the total time required for development was uncertain. The maximal incubation time of 36 days for Lutodrilus multivesiculatus compared favorably with 24-33 days in Sparganophilus eiseni Smith (Hague, 1923; Harman, 1965) and with 26 days in Eisenia foetida (Herlant-Meewis, 1954).

Oothecae were incubated in aged tap water in the laboratory. Of the six unhatched cocoons, two did not hatch and were examined when it was determined that no movement was detectable inside the cocoons. A round hole was present in the side of one cocoon, indicating possible predation. Although no worms or worm fragments were found inside the cocoon, it did contain several albuminous masses containing nematodes and protozoa. The other unhatched cocoon was opened after eight days of incubation, and it contained three partially decomposed worms or fragments with lengths of 5, 4, and 2 cm.

Oothecae were dark brown to green-brown and translucent at the time of collection; therefore, it was difficult to detect movement of developing worms. As incubation progressed, the thecal walls became semitransparent, and the young were visible within the cocoons. Worms moved actively about the interiors of the cocoons, and they appeared to feed on the thecal albumin. Worms in the cocoons frequently exhibited phenomena similar to those associated with the respiratory phase in adults: widened body posteriorly, reddening

of the posterior segments, and undulations of the hindbody (cf. section on ecology).

The broad end of the cocoon began to enlarge at 8-32 days before hatching, occurring within one week in all oothecae despite the time remaining to hatching. Simultaneously, the mucus that had plugged the opening began to extend from the opening, lengthening to 1 cm during the first day. At the time of emergence of the young, the mucus of two cocoons had reached a length of 8-10 cm, which was equal to or greater than the length of the cocoons.

Worms often extended one or both ends of the body through the oothecal opening prior to emergence. Most frequently, the posterior was extended to the surface in typical lutodrilid respiratory fashion (cf. section on ecology). This behavior was exhibited for up to 12 days before hatching, proportional to the total time of incubation in the laboratory.

Worms emerged from the cocoons at night. In one instance, a worm emerged one night, reentered the cocoon 24 hours later, and did not reemerge for eight days, at which time two worms emerged from the cocoon. In the case of the other cocoon that produced two young, both worms emerged within one 24-hour period.

Growth. At emergence, worms were 5-10 cm in length and contained 140-209 segments, the number of segments being proportional to the length. The two shortest lengths were recorded in individuals that were the second individuals to emerge from their respective cocoons. Width was 4-5 mm anteriorly, decreasing to ca. 1 mm posteriorly. Young worms were red in color except for the anterior 4-5 mm of the body, which was green.

In newly-hatched worms, greater body length is accompanied by a greater number of segments. The number of segments in a newly-hatched worm is approximately one-half the maximum recorded number in mature adults (400-500), indicating that postembryonic growth occurs through addition of segments as well as by enlargement of existing segments. This method of growth occurs commonly in megadriles (Gates, 1948). The posterior extremity of the body is a zone of rapid growth that measures 0.5-2.0 cm in length and consists of very small, inconspicuous segments. In the vicinity of the anus, external indications of segmental limits become indistinguishable.

The position of the anus is dorsal throughout postembryonic life with the exception of regenerates, in which the anus is terminal to dorsoterminal. In regenerative growth, the anus initially is terminal and later moves to a dorsal position, a characteristic of certain "aquatic" glossoscoleids (Gates, 1948). The anus is associated with several rudimentary segments that are developing simultaneously.

New segment formation in L. multivesiculatus apparently continues throughout life. All specimens that are free of regenerative growth possess short, terminal growth zones resembling those of newly-hatched worms. This concurs with Gates' conclusion (1948) that growth by segment formation in some megadriles is possible throughout life.

Anomalies of metamerism. Two types of metameric anomalies occur in Lutodrilus multivesiculatus: (1) anomalies of segmentation and (2) asymmetric sexual characters. Segmental abnormalities occur

with great frequency and are of two basic varieties: (a) the compound (split) metamere and (b) spiral segmentation (Morgan, 1895).

According to Morgan (*idem*), the compound metamere, which is doubled on one side of the body and single on the other, is the most common segmental anomaly in oligochaetes, and this is true in L. multivesiculatus. In one instance, there occurred a compound metamere that bore normal setal complements on the left and triple setal couples dextrally. On the right side, there was one intra-segmental furrow that extended half-way across the segments, between two of the three setal couples. Morgan (*idem*) termed this anomaly a double compound metamere and stated that it was one of the least common metameric abnormalities of the Oligochaeta.

In L. multivesiculatus, the segmental anomaly that was second in frequency of occurrence was spiral segmentation, in which a single metamere united dorsally with two metameres. For instance, the left half of the metamere dorsum united with the next anterior segment, and the right half with the next posterior segment.

Another segmental anomaly observed frequently in these worms was an inserted half-metamere. This aberration results from the development of a partial segment which is wedge-shaped when viewed dorsally (Morgan, 1895).

Asymmetric sexual characters in this megadrile were of two types: (1) asymmetry of genital tumescences and (2) asymmetry of the male tumescence. Occurring commonly was asymmetry of genital tumescences, which often were paired bilaterally but frequently were not. Both conditions were present in every mature lutodrilid as

was the absence of genital tumescences on numerous segments within the longitudinal extent of these structures (Table 4).

Asymmetry of the male tumescences was rare, being observed only once. On the left side, the tumescence covered the ventrum of xxxi-xxxii, and the spermiducal pore was on xxxi whereas, on the right, the tumescence was on xxxii-xxxiv, and the male pore was on xxxii, the normal position. Morgan (1895) reported the asymmetric position of the spermiducal pores as being a relatively common phenomenon in the oligochaetes.

Maturation. Juvenile worms, i.e. those individuals with no indication of maturity, and aclitellates, i.e. worms with sexual characters but without clitellum, were collected throughout the year. Greatest abundance of newly hatched juveniles occurred June-August, a reflection of cocoon production and hatching during these months. The fact that young of the year appeared in June-August while juveniles occurred year-round indicated that L. multivesiculatus has a minimal two-year life cycle and does not mature until the second year. Throughout the reproductive season, even at the earliest dates at which clitellate worms were found, juveniles were present; therefore, some worms, possibly all, do not reach sexual maturity until the second year. Attempts to maintain colonies in the laboratory to observe growth and maturation have failed because lutodrilids were affected significantly by unfamiliar stimuli, and clitellate individuals placed into artificial habitats quickly lost their clitellate characteristics. Worms maintained in simulated shoreline habitats to approximate natural conditions were

removed from the mud for examination, and digging them from their burrows frequently induced autotomy and death. Additionally, small, artificial habitats were susceptible to extreme temperature fluctuations to which the worms were not subjected in nature. Consequently, field observations and study of preserved material are the sole sources of information concerning maturation.

Earliest manifestation of maturation is early development of the male tumescence. Initially, ventral setal couples of ~~xxxi~~-~~xxxiv~~ are displaced medially as described for mature specimens (cf. section on anatomy). Thickening of the ventral epidermis of ~~xxxii~~-~~xxxiii~~ produces the mature male tumescence. Simultaneously, genital tumescences appear, and they reach greatest prominence during early development of the clitellum. Reddening of the clitellum is preceded by enlargement of the body diameter in the anterior clitellar region. Last sexual characters to develop are the alae, which do not develop until all other external characteristics of sexual maturity are complete.

VI. ECOLOGY

Habitat

Lutodrilus multivesiculatus is limicolous, living along shorelines of slowly-moving streams and rivers, and is restricted to a zone extending ca. one meter on either side of the shoreline. Populations are disjunct and restricted to sites sheltered from the force of the current by logs, sandbars, or other obstacles. Habitats, most frequently situated along small tributaries, are characterized by heavy accumulations of organic detritus that often exceed a meter in depth. The decomposing matter, primarily leaves of deciduous trees and shrubs, is compacted tightly and is water-saturated, thus creating an anaerobic, or very nearly anaerobic, habitat. The anaerobic habitat has been confirmed by the use of a Yellow Springs Model 51 Oxygen Meter, with which no reading greater than 0.75 ppm dissolved oxygen has been recorded beneath the surface of habitats.

Respiratory adaptations

Habitats with limited oxygen necessitate special respiratory adaptations in inhabitants. L. multivesiculatus extends the posteriormost 1-3.5 cm of its body from the burrow and flattens this body region on the soil at the mouth of the burrow or at the water surface. This region then expands to ca. twice its normal width, and a longitudinal concavity develops on the dorsum. Reddened coloration of the region is indicative of increased blood content. Histological studies of this region show extensive epidermal

vascularization, including subcuticular capillaries (Figs. 6, 7), that transforms this body region into a blood-laden sac, greatly enhancing its respiratory function. The subcuticular vascularization is most pronounced dorsally although it occurs ventrally to a lesser degree. The dorsal body wall of the respiratory region undergoes an anteriorly-directed peristalsis which may serve two functions. The muscular contractions may aid in circulating blood through the area. In addition, peristalsis may distribute external secretory products that moisten the exposed surface. When the mouth of the burrow is under water, the posterior end of the worm extends to the water surface and functions in a similar manner. Under natural conditions, respiratory activity continues indefinitely until the organism is disturbed by vibration or by tactile stimuli, at which time the tail is withdrawn rapidly into the burrow; however, it is repositioned within a short time.

Similar phenomena occur in some microchaetids, most notably in species of Alma, the African swampworm (Beadle, 1957), and Drilocrius (Carter and Beadle, 1931). The respiratory activity of Lutodrilus multivesiculatus is similar to that of these species with one exception. The microchaetids extend and flatten the tail, the edges of which then are rolled dorsally to form a tube as the tail is withdrawn into the burrow. The opening of this tube is held at the mouth of the burrow until the organism is disturbed (Carter and Beadle, 1931; Beadle, 1957). Respiratory tube formation has not been observed in L. multivesiculatus, which holds the tail flat on the surface with maximum exposure to the air.

Effects of low oxygen concentrations on the respiratory activity of these Louisiana megadriles have been investigated experimentally. Specimens were maintained in lucite flow-chambers through which water flowed in which the oxygen concentration was regulated, being monitored with an oxygen meter. Air was flushed over the water surface to simulate natural conditions. At oxygen concentrations greater than 4.5 ppm, respiratory activity was not evident. At concentrations between 4.5 and 1 ppm, a slight flaring and reddening of the posterior extremity occurred intermittently, with the tail only occasionally raised to the surface. At concentrations less than 1 ppm, portions of the posterior, usually 1.5-2.5 cm but up to 3.5 cm in length were extended to the water surface with red coloration intensifying and the expansion and flattening becoming maximal (i.e. ca. twice the normal width). The dorsal concavity and peristalsis always were preceded by extension of the tail to the water surface. At 0.5-0.75 ppm oxygen, animals remained in the respiratory position with the tail extended to the surface for varying intervals, 5-15 min. Each respiratory phase was followed by submersion of the tail for an interval approximately equal to the preceding period of activity. At all times, worms continually probed the flow-chambers with their anterior extremities.

Since the burrows of this earthworm frequently extend to depths greater than one meter, the ability to utilize the posterior 5-10% of the body as a respiratory organ and to keep this organ at the mouth of the burrow is a distinct advantage. Individuals have been observed to extend to a length of more than one meter; therefore,

the worm can feed at considerable depths while being assured of constant gas exchange despite the anaerobic nature of the burrows.

Temperature

Habitats of Lutodrilus multivesiculatus are well shaded by a thick canopy of plants and, therefore, receive little direct sunlight. Consequently, these habitats are not subject to the great temperature fluctuations that might occur if there were direct exposure to the sun, and earthworm activity is not inhibited by high summer temperatures. Likewise, the relatively mild winters in southern Louisiana permit the worm to be active year-round.

Temperatures of ambient mud, usually measured in late a.m. or early p.m., consistently ranged 15-20°C, with little seasonal variation. A single temperature of 25°C was recorded in mid-August at an unshaded site. At this location, worms seemingly were not inhibited by the temperature although none was near the surface as is typical for the species.

Activity of the worms was affected markedly below 15°C. Days on which habitats registered below 15°C were preceded by night-time atmospheric lows of 0-15°C. At such temperatures, worms were located 2-8 cm below the surface and were inactive, positioned in a ventrad flexure. With handling and exposure to warmer air temperatures, such individuals rapidly became active. The optimal range for activity is 15-20°C and compares favorably with optimal soil temperatures for development of other earthworm species (Voisin, 1961).

Moisture

Water possibly is the limiting requirement of earthworms because of the lack of water conservation mechanisms and because of its value to respiration through the body wall (Reynolds, 1973). The limicoline habitat of Lutodrilus multivesiculatus provides a constant source of water which, in addition to its direct physiological importance, also protects the worms from rapid temperature fluctuations.

Parasites

L. multivesiculatus is parasitized by trematodes and protozoans. During warmer months of the year (April-September), nearly 100% of the adult worms contain numerous encysted trematodes that are largely restricted to posteriormost portions of the body. Trematodes usually are in the coelom although they occasionally are encysted in the seminal vesicle.

Monocystid gregarines are common in the seminal vesicles of Louisiana megadriles (McMahan, 1975); however, that study reported none from coelomic fluid. Monocystids are absent in seminal vesicles of Lutodrilus multivesiculatus whereas unidentified monocystid trophozoites do occur in the coelom.

According to Stephenson (1930), nematodes are the most common parasites of earthworms; however, they have not been observed in individuals of L. multivesiculatus.

VII. ETHOLOGY

Lutodrilus multivesiculatus deposits castings around the mouth of its burrow, as might be expected of an earthworm with deep burrows. Castings at the mouth of a burrow above the water line accumulate to form a mound that measures up to 5 cm in height and breadth. The mounds resemble small crayfish chimneys, and the mouth of the burrow emerges from the peak of the mound. When a mound of castings is present, and the worm is in the respiratory position, the tail is laid in a concavity in the top of the castings, resulting in the posterior portion being camouflaged and difficult to detect.

Burrows often are below the water line, and castings do not accumulate because of water action. Worms in these burrows respire as previously described, and the tail is held motionless except for peristalsis. The only other evident motion is due to movement of the water, and the tail resembles a dead leaf floating on the surface.

Reactions to stimuli

Withdrawal into the burrow occurs in response to any disturbance of the soil or water or to a tactile stimulus. The tail resumes its respiratory position unless the stimulus is very strong or is continuous. Vail (1972) reported that Diplocardia mississippiensis surfaces rapidly in response to disturbances in the soil, and similar phenomena have been observed in other earthworm species. In contrast, L. multivesiculatus withdraws rapidly into its burrow in response

to disturbances. If the anterior end of a worm were anchored deeply in the burrow, retraction would be a matter of rapid body contraction.

Photoreceptors have not been detected in the posterior extremity, contrary to the case in numerous megadriles (Stephenson, 1930). Responses to sudden changes in light intensity have not been noted in Lutodrilus multivesiculatus. Worms may be shaded totally from sunlight very rapidly, and equally rapid removal of obstruction to light has no effect upon the worms. An extended tail is susceptible to predation, and photoreceptors would be of value in escaping predation by potential predators (e.g., hogs). The absence of photoreceptors posteriorly in these worms may result in high rates of predation and may explain the large number of animals which are regenerating at collection.

Although photoreceptors are absent posteriorly, chemoreceptors are not. The posterior one-third to one-half of the worm reacts violently to ethanol anesthetization. An anterior response also occurs, but it is not as pronounced as is that occurring posteriorly. Stimulation with ethanol elicits an almost instantaneous twisting and coiling of the tail region whereas no response is detected anteriorly for as long as 2-3 min, varying inversely with the concentration of ethanol. Autotomy often occurs posteriorly in response to any concentration of ethanol greater than 7%.

Autotomy

Autotomy was observed with great frequency in L. multivesiculatus in response to handling, electrical and chemical stimulation, and injury. Sixty-four percent of all specimens studied were regenerating at the time of collection, and it is believed that the majority of

regenerating specimens were doing so as a consequence of spontaneous autotomy or predation rather than human activity since the habitats were undisturbed. Loss of the posterior extremity would be advantageous in that it would distract a predator by the continued movement of that fragment, thus protecting the anterior fragment. The viability of small anterior fragments was illustrated by an anterior fragment ca. 5 mm long (contracted) and consisting of segments i-vi. The fragment, maintained in artificial pond water, 0.5 mM NaCl, 0.05 mM KCl, 0.40 mM CaCl₂, 0.20 mM NaHCO₃ (Dietz and Alvarado, 1970), remained responsive to stimuli and retained the ability to burrow for two months after amputation.

Autotomy, as evidenced by observations of the process and by locations of regeneration zones, may occur at any intersegmental furrow in the intestinal region of the body. No area of the body is characterized by increased frequency of autotomy, and there is no correlation between number of body segments and location of the first plane of autotomy. Autotomy can occur far anteriorly, as illustrated by a specimen of only 96 segments that was regenerating from 68/69 and a specimen of 213 segments that attempted autotomy at 76/77. Posteriorly, autotomy has been observed as far back as 414/415, in a worm 424 segments in length. The number of segments lost through each autotomy was variable, ranging 10-300⁺, with 50-100 segments being the most frequent.

The process of autotomy in Lutodrilus multivesiculatus is similar to that described for other megadriles (Stephenson, 1930; Vail, 1972). A muscular constriction occurs at one or more

intersegmental furrows and is accompanied by a twisting motion. The portion of the body posterior to the first plane of autotomy usually twists and turns in a direction opposite to that portion of the body anterior to the constriction. The first break in the body wall occurs ventrally, and the opening quickly extends circumferentially in the intersegmental groove. A sphincterlike contraction of circular musculature on either side of the plane of autotomy prevents excessive loss of body fluids. For a variable period of time, the two body fragments are connected only by the intestine, which eventually breaks. Time necessary for the completion of autotomy varies, usually ranging from less than a minute to more than 10 min. Frequently, autotomy is multiple, occurring at numerous intersegmental furrows simultaneously.

Newly-hatched worms are capable of autotomy, as has been observed in one instance. A worm which measured 10 cm at emergence from the ootheca autotomized an 8 mm body fragment within one hour after emergence.

VIII. FOLKLORE

Lutodrilus multivesiculatus is well-known locally by three common names, the most frequently encountered being "mudworm," from the limicoline habitat of the worm. Next in frequency is the name "bloodworm," after the reddened coloration of the clitellum and the tendency to bleed excessively when broken. Use of the name "bloodworm" is to be avoided due to the inevitable confusion with other annelids and some insects that are known by that name. One informant supplied the name "hogworm," used in reference to the "fondness" of hogs for the worms. Reputedly, porcines enter streams and root up the banks to find lutodrilids.

The mudworm is valued as fishbait, especially for catfish, due to its great volume of blood. Fishermen within the known distribution of the species are familiar with the use of the worm for bait and eagerly seek it for that purpose, primarily in the spring. Most anglers who dig for mudworms are able to describe habitats very well. They know of the accumulations of organic detritus, protection of habitats from swift water currents, and the location of habitats at or near shorelines. Additionally, collectors describe the length of mudworms as being up to 40 cm and the development of the reddened clitellum during "certain times of the year." Also, mudworms are said to "come all to pieces" when they are handled, of course referring to autotomy.

IX. SYSTEMATICS

The relationship of the Lumbricidae and Glossoscolecidae long has been recognized. Michaelsen (1918) included all of the genera of these two families within one family Lumbricidae s. lat., which he divided into six subfamilies: Lumbricinae, Glossoscolecinae, Sparganophilinae, Microchaetinae, Criodrilinae, and Hormogastrinae. Through the ensuing years, numerous revisions of Michaelsen's scheme have been proposed. Most workers have retained the Lumbricinae as family Lumbricidae with relatively little change in content of the taxon (Gates, 1972); however, opinions concerning the status and relationships of the other five subfamilies of Michaelsen have varied widely (Jamieson, 1971c).

Jamieson (1971b), in his examination of aquatic megadriles, retained the family Glossoscolecidae of Stephenson (1930) although he reorganized the subdivisions of the family. Jamieson described six glossoscolecoid subfamilies: Glossoscolecinae, Kynotinae, Alminae, Biwadrilinae, Hormogastrinae, and Sparganophilinae. Gates (1974b) considered the Glossoscolecidae of Jamieson (1971b) to be "bloated beyond capability of definition." The Hormogastrinae and Sparganophilinae are considered as families by other authors (Gates, 1959; Reynolds, 1974), who more closely relate them to the Lumbricidae, all three families being included with the Komarekionidae in superfamily Lumbricoidea (Gates, 1974a, 1974b). Criodrilus, of Jamieson's Alminae, is considered by Gates (1959) to constitute the monogeneric

family Criodrilidae, and Ljungström (1974) raised the remaining Alminae to the status of a family that included four genera: Alma, Drilocrius, Callidrillus, and Glyphidrillus. While recognizing Gates' superfamily Lumbricoidea and family Criodrilidae and Ljungström's Alminidae, it is deemed prudent at the present time to elevate the remaining glossoscolecid subfamilies of Jamieson to familial status and to unite them into the superfamily Glossoscolecoidea, consisting of the Glossoscolecidae, Alminidae, Criodrilidae, Kynotidae, and Biwadrilidae.

Phylogenetic unity of the Alminidae is indicated by a number of characteristics that differentiate members of this taxon from glossoscolecid genera with which they were grouped formerly. Such features of the Alminidae are: a posterior quadrangular cross section with setal couples at the angles; usual presence of a dorsal respiratory groove; a dorsal or dorsoterminal anus; DD less than 0.3 C; absence of genital setae, of their glands, and of testis sacs; absence of calciferous glands; nephropores near B; absence of anterior nephridia; absence of nephridial sphincters and caeca; and presence of a medial subneural vessel in all except two highly evolved genera (Jamieson, 1971b). These features, considered to be primitive by Jamieson (*idem*), have been demonstrated in the Lutodrilidae and therefore ally this family to the Alminidae. The phylogenetic conservatism of somatic anatomy in megadriles has been demonstrated by Gates (1970). Since most of the features common to the Alminidae and Lutodrilidae are somatic, these characteristics by their accepted degree of conservatism are indicative of the kinship of the two taxa. A further similarity

between these two families is the formation of elongate, fusiform oothecae. The cocoons of some aluids (Janda, 1926; Nair, 1938; Khalaf el-Duweini, 1951) and Criodrilus lacuum Hoffmeister (Örley, 1887), which was considered an aluid by Jamieson (1971b), resemble those of lutodrilids, and the shape differs vastly from the ovoid cocoons of other megadrile families (Jamieson, 1971a).

The relation of the Lutodrilidae to the lumbricoid families has been demonstrated, and this new family has been placed as a fifth member of superfamily Lumbricoidea on the basis of its possession of lumbricid ovaries. In addition, lutodrilid genital tumescences are not sharply demarcated from the surrounding epidermis, a typical lumbricoid condition (Stephenson, 1930; Gates, 1972). These features differ from similar structures in other megadriles, in which they are set distinctly apart from the surrounding epidermis by a peripheral rim and are termed genital markings rather than genital tumescences (Jamieson, 1971a).

Numerous authors, noting similarities between the Criodrilidae and the Lumbricidae, have proposed that Criodrilus, or a criodrilidlike megadrile, was the ancestral form for the Lumbricidae (Michaelson, 1918; Stephenson, 1930; Omodeo, 1956; Jamieson, 1971c). Criodrilus, included in the Aluidae by Jamieson (1971b), is viewed as having developed directly from the aluid ancestor, which also gave rise to lumbricids. Lutodrilus further serves to demonstrate affinities between the Lumbricoidea and the Glossoscolecoidea. Features common only to the Lutodrilidae and Aluidae demonstrate a close degree of kinship between these two taxa. Since the Lumbricidae and Aluidae

are described as having arisen from a criodrilidlike ancestor and since the superfamilies Lumbricoidea and Glossoscolecoidea are accepted to be closely related and of common ancestry, Lutodrilus, a form possessing numerous features diagnostic for the two taxa, is viewed as having arisen from a common ancestor for the two as is Criodrilus.

The lutodrilid battery of 10 pairs of testes is more extensive than in any other known megadrile. Likewise, the position of the posteriormost gonad, the ovary, in xxiii, extends the hindmost location for oligochaete gonads one segment, previously being xxi in some Opistocystidae (Gates, 1974b). Gates (1971) proposed that early oligochaetes possessed a series of gonads extending through xxiv. The constant presence of ovaries in xxiii in Lutodrilus multivesiculatus lends more credibility to Gates' statement and leads to a conclusion concerning the phylogeny of lutodrilids. Gonads that are present in such numbers as they are in Lutodrilus, a primitive characteristic, may be viewed in one of two manners: (1) the existence of the primitive feature is a reversion to an ancestral condition, or (2) the existence of the primitive feature is a retention of an ancestral trait.

The frequency of reversions to ancestral conditions in megadriles has been demonstrated by Gates (1971), who stated that such reversions may involve organs in a single segment or a set of organs extending through several segments. His studies of several species, especially Pheretima anomala, in which extensive gonadal series were observed frequently, led to the conclusion that the gonads can and do revert to an ancient stage in oligochaete evolution. Evidence that such variations from the normal condition are reversions rather than

retentions of ancestral traits is found in the fact that these alterations occur in species that otherwise certainly are not to be considered primitive (Gates, 1971).

Lutodrilus multivesiculatus possesses numerous somatic features known to be primitive: quadrangular body shape, dorsal respiratory groove, dorsal to dorsoterminal anus, DD ca. 0.3 C, nephropores near B, absence of anterior nephridia, absence of nephridial sphincters and caeca, and presence of medial subneural vessel. In addition, the number and position of the testes, 10 pairs in xii-xxi, and the position of the pair of ovaries in xxiii have been demonstrated to be primitive. Consequently, the species is viewed as a relatively primitive species possessing a combination of characteristics that are retentions of, rather than reversions to, the ancestral state. Lutodrilus multivesiculatus is considered to have arisen from, and as possessing numerous features of, oligochaetes ancestral to the Lumbricoidea and Glossoscolecoidea.

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TABLE 1. Location of clitellum in Lutodrilus multivesiculatus.

Segments Included	Number of Segments	Number of Specimens
xx-lxvi	47	1
xxi-lxiv	45	1
xxi-lxvi	46	1
xxi-lxviii	48	1
xxi-lxxi	51	1
xxii-lxv	44	1
xxii-lxvi	45	1
xxv-lxi	37	1

TABLE 2. Location of alae in Lutodrilus multivesiculatus.

Segments Included	Number of Segments	Number of Specimens
xxii-li	30	1
xxii-liii	32	1
xxvii-xlii	16	1
xxviii-xlix	22	1
xxviii-l	23	1
xxviii-li	24	2
xxix-xxvi	18	1
xxix-xxviii	20	1
xxix-xlix	21	2
xxix-l	22	3
xxix-li	23	3
xxx-xxvi	17	2
xxx-li	22	1

TABLE 3. Distribution of genital tumescences in Lutodrilus multivesiculatus.

First and Last Segments of Series	Number of Segments	Number of Specimens
xiii-lii	40	1
xv-li	37	1
xvi-xlvi	33	1
xvi-xlix	34	2
xvi-li	36	2
xvi-lii	37	2
xvii-li	35	2
xvii-lii	36	1
xviii-li	34	1
xix-li	33	1

TABLE 4. Pattern of distribution of genital tumescences of three specimens of Lutodrilus multivesiculatus.

Segment	Position on Segment		
	1	2	3
pre-xv	none	none	none
xv	right	none	none
xvi	left	bilateral	none
xvii	bilateral	left	none
xviii	bilateral	right	left
xix	bilateral	right	none
xx	bilateral	left	right
xxi	bilateral	bilateral	bilateral
xxii	bilateral	bilateral	right
xxiii	bilateral	bilateral	right
xxiv	bilateral	bilateral	bilateral
xxv	bilateral	bilateral	bilateral
xxvi	bilateral	bilateral	bilateral
xxvii	bilateral	none	bilateral
xxviii	bilateral	none	left
xxix	right	none	none
xxx	bilateral	none	none
xxxi	bilateral	none	right
xxxii	male tumescence	male tumescence	male tumescence
xxxiii	male tumescence	male tumescence	male tumescence
xxxiv	bilateral	none	none
xxxv	none	none	none
xxxvi	none	none	none
xxxvii	right	none	none
xxxviii	left	none	none
xxxix	none	right	none
xl	none	none	none
xli	left	none	none
xlii	none	none	none
xliii	none	none	none
xliv	none	none	none
xlv	none	none	none
xlvi	none	none	none
xlvii	bilateral	bilateral	none
xlviii	bilateral	bilateral	right
xlix	right	right	none
l	right	none	none
li	right	none	bilateral
lii and following	none	none	none

Figure 1. Anterior end of Lutodrilus multivesiculatus, ventral view.

a, ala; gt, genital tumescence; mt, male tumescence;
op, location of oviducal pore; s, spermatophore; sp,
location of spermiducal pore

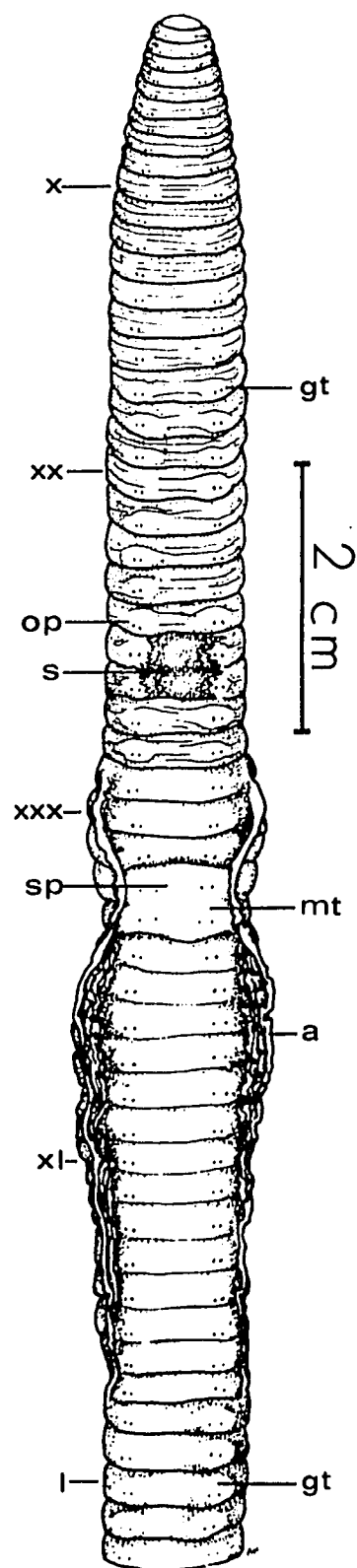


Figure 1

Figure 2. Diagrammatic longitudinal section of genital region of Lutodrilus multivesiculatus.

o, ovary; of, oviducal funnel; op, oviducal pore;
s, spermatheca (spermathecae illustrated in only three intersegmentals); sfp, posteriormost spermiducal funnel; sp, spermiducal pore; sva, anteriormost seminal vesicle; svp, posteriormost seminal vesicle;
ta, anteriormost testis; tp, posteriormost testis;
vd, vas deferens; ve, vas efferens

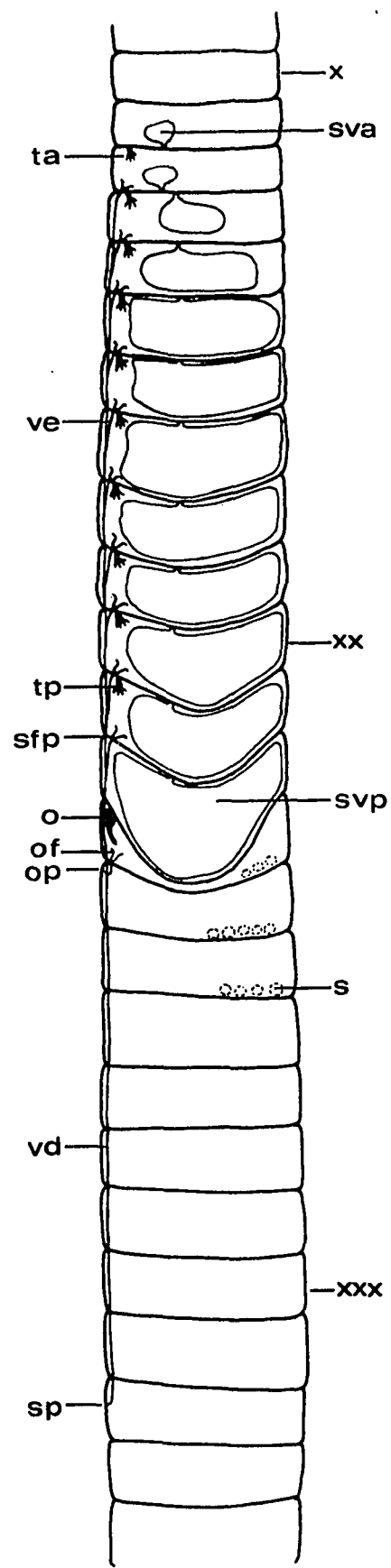


Figure 2

Figure 3. Cross section of anterior body wall of Lutodrilus multivesiculatus, scale 100 μm .

Figure 4. Cross section of body wall in clitellar segment of Lutodrilus multivesiculatus, scale 100 μm .

a, subepithelial circular muscle; b, diffuse longitudinal muscle; c, median circular muscle; d, trabeculate longitudinal muscle; e, retroperitoneal circular muscle; f, lateroparietal vessel

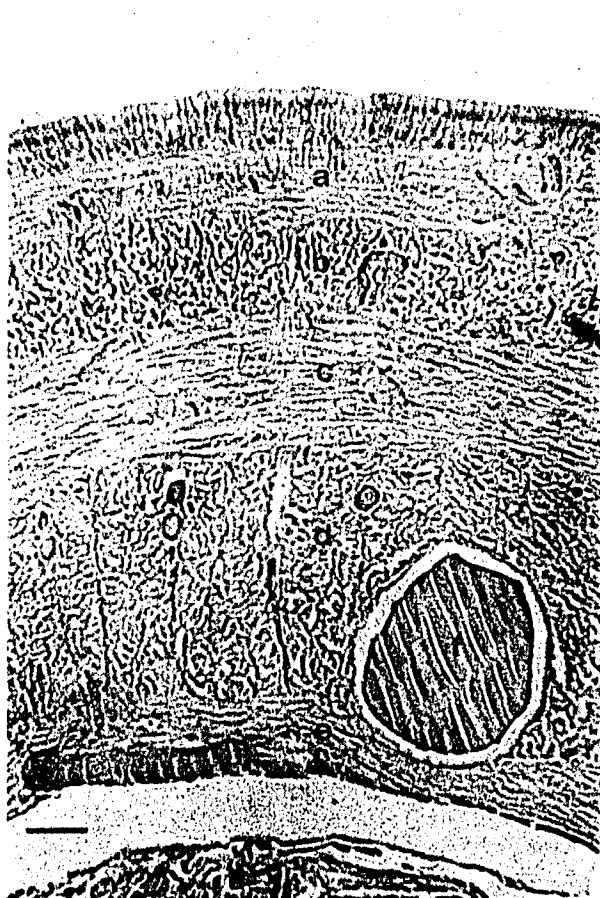


Figure 3



Figure 4

Figure 5. Cross section of typhlosolar intestine of Lutodrilus multivesiculatus, scale 100 μm .



Figure 5

Figure 6. Epidermal cross section from dorsal respiratory surface of Lutodrilus multivesiculatus, scale 10 μm .

Figure 7. Epidermal cross section from dorsal respiratory surface of Lutodrilus multivesiculatus, scale 10 μm .
c, extra-epidermal capillary; v, blood vessel entering basal layer of epidermis

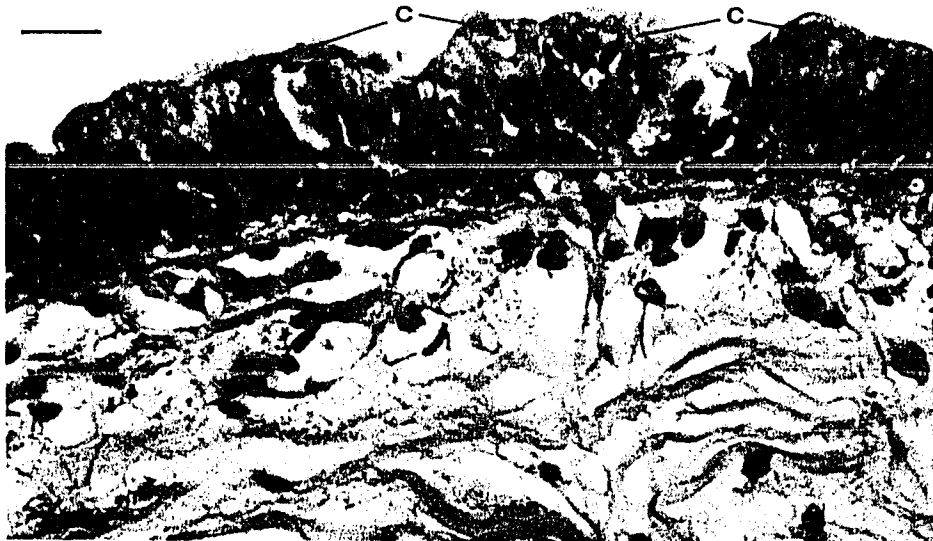


Figure 6

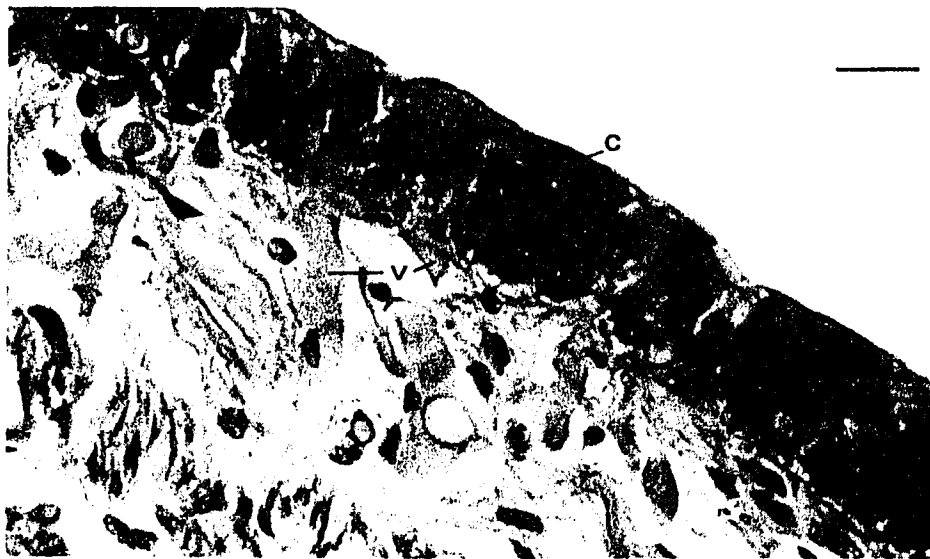


Figure 7

Figure 8. Longitudinal section of ovarian egg string of
Lutodrilus multivesiculatus, scale 100 μ m.
o, mature oocyte at distal end of egg string

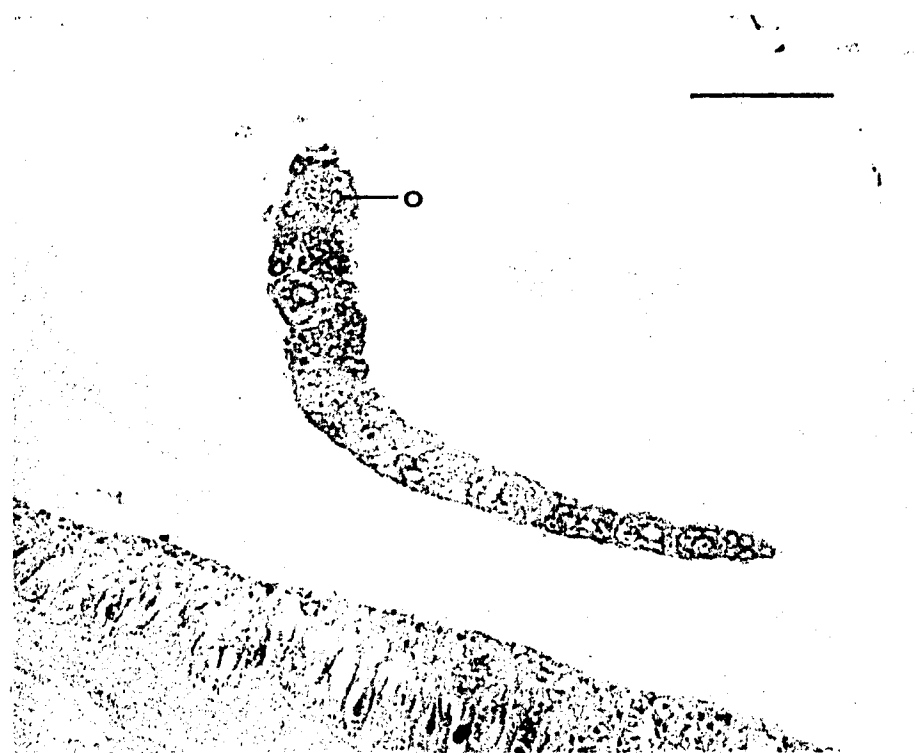


Figure 8

Figure 9. Cross section of spermathecae at 24/25 of Lutodrilus multivesiculatus, scale 100 μm .

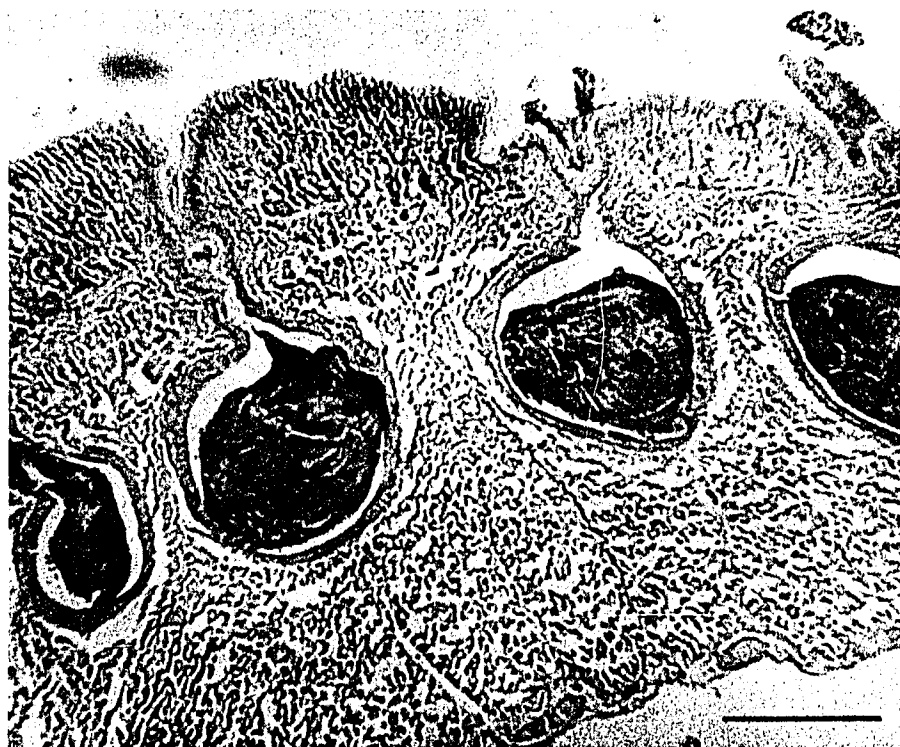


Figure 9

Figure 10. Oothecae of Lutodrilus multivesiculatus.

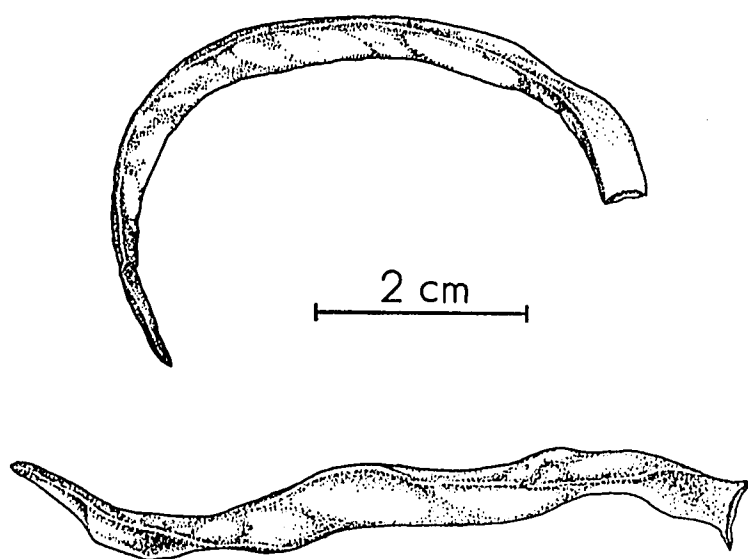


Figure 10

GLOSSARY

Oligochaetologists use a considerable number of abbreviations and conventions which are enigmatic to workers unfamiliar with oligochaete literature. The following explanations are derived from Gates (1972).

Abbreviations

- a - the ventralmost seta on each side of a segment
- A - a meridian of longitude passing anterioposteriorly along apertures of the a setal follicles
- AA - median, ventral space between the two A meridians
- AB - space between A and B meridians
- b - the seta next lateral to a
- B - a meridian of longitude passing anterioposteriorly along apertures of b follicles
- BC - space between meridians of longitude B and C
- c - the seta next lateral to b
- C - circumference
- C - a meridian of longitude passing along apertures of the c follicles
- CD - space between meridians of longitude C and D
- d - the seta next lateral to c. Dorsalmost of the four setae of each side of a segment
- D - a meridian of longitude passing along apertures of the d follicles
- DD - the space dorsally between the two D meridians

Conventions

i, ii, iii, iv, v - Roman numerals indicate the segments of the body in an anterioposterior direction beginning with the peristomium.

1/2, 2/3, 3/4, 4/5 - Numbers so printed (never as fractions) designate the intersegmental furrows or septa. Thus, 1/2 indicates the junction of segments i and ii.

1-1-1 - Any such set of three figures indicates from left to right the number of juvenile, aclitellate, and clitellate specimens. A juvenile has no readily discernible genital structures whereas an aclitellate has at least rudimentary external genital features although lacking a clitellum.

VITA

Michael Lee McMahan was born 17 May 1946 in Memphis, Tennessee. He attended public school in Batesville, Mississippi, where he graduated from South Panola High School in 1964. He immediately entered The University of Mississippi, from which he graduated with the Bachelor of Science Degree in 1968 and the Master of Science Degree in 1971. In January, 1971, he entered the Ph.D. program in the Department of Zoology and Physiology of Louisiana State University, where he was awarded a Graduate Teaching Assistantship. In August, 1975, he assumed the position of Assistant Professor of Biology at Campbellsville College, Campbellsville, Kentucky.

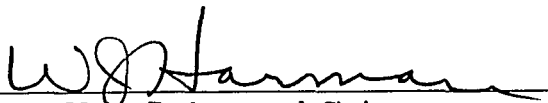
EXAMINATION AND THESIS REPORT

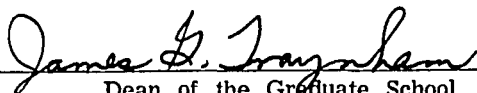
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Major Field: Invertebrate Zoology


Title of Thesis: Biology of a Limicolous Megadrile (Annelida: Oligochaeta)
from Louisiana

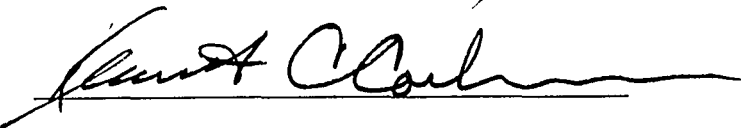
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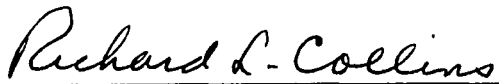

Major Professor and Chairman



Dean of the Graduate School

EXAMINING COMMITTEE:









Date of Examination:

July 29, 1976