THE GENITAL MUSCULATURE OF THE FEMALE MOTH EAR MITE DICROCHELES PHALAENODECTES

BY

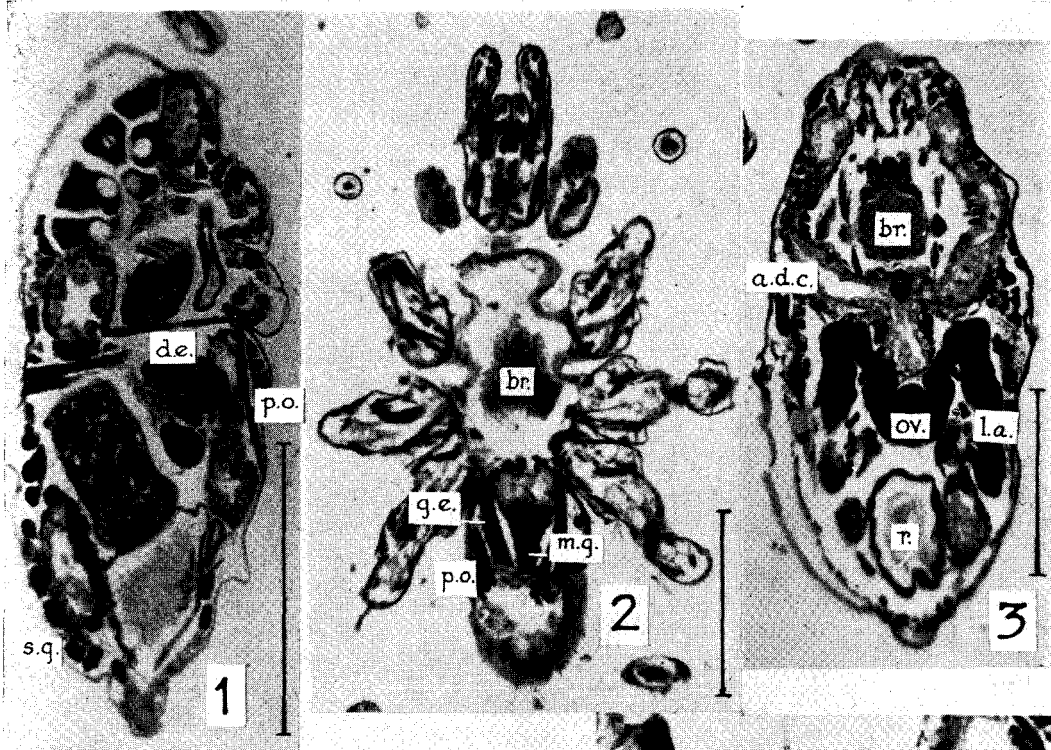Asher E. TREAT.

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ABSTRACT.

The moth ear mite, *Dicrocheles phalaenodectes* (Treat), possesses both a lyrate organ and a camera spermatis but lacks both a sacculus foemineus and intercoxal spermathecae. Insemination is vaginal. Ten pairs of muscles or muscle groups control the genital aperture and associated structures. Several of these are attached to skeletal elements comprising the genital apodemes and " arcs chitineux " of Fain. The posterior limbs of these arcs are continuous with the peritremal plates.
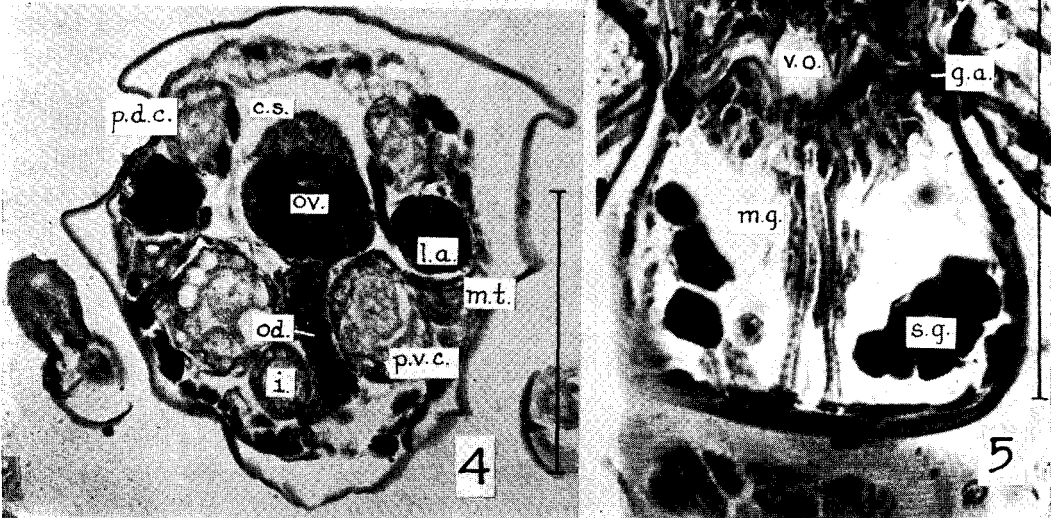
The immediate stimulus to this work was FAIN's (1963) description of the genital apodemes and associated " arcs chitineux " in various parasitic gamasines. According to FAIN, these parts are seen also in many free-living gamasines, and may perhaps extend throughout the Monogynaspida. While disclaiming definite knowledge of their function, FAIN plausibly suggests that the chitinous arcs may serve as points of attachment for ligaments or muscles, and that they may be derived from the deeper portions of the peritremal plates, perhaps with contributions from vestiges of the endopodal plates. My study of these structures in the moth ear mite, *Dicrocheles phalaenodectes* (Treat, 1954), supports FAIN's suggestions.

FIG. 1-5. — Five-micron sections of *D. phalaenodectes* females, 1 stained with Heidenhain's hematoxylin only, 2-5 with hematoxylin and eosin.

Fig. 1, sagittal plane through region of right genital apodeme. The large granular mass is a nearly mature egg. Fig. 2, frontal plane at level of genital eminence. Fig. 3, frontal plane at level of ovary and lateral arms. Fig. 4, transverse plane through ovary. Fig. 5, detail of a frontal section through genital eminence at level of vaginal orifice. Key to symbols : *a.d.c.*, anterior dorsal caecum ; *br.*, brain ; *c.s.*, camera spermatis ; *d.e.*, dorso-endopodal muscle ; *g.a.*, genital apodeme ; *g.e.*, genito-endopodal muscle ; *i.*, intestine ; *l.a.*, lateral arm of ovary (" lyrate organ ") ; *m.g.*, median genital muscles ; *m.t.*, malpighian tubule ; *od.*, " oviduct " ; *ov.*, ovary ; *p.d.c.*, posterior dorsal caecum ; *p.o.*, posterior oblique muscle ; *p.v.c.*, posterior ventral caecum ; *r.*, rectum ; *s.g.*, " skin gland " ; *v. o.*, vaginal orifice.

All scales = 100μ

Materials included living mites, whole mounts in Hoyer's medium, dissections, and serial sections. For dissection I used both fresh mites and specimens fixed in formalin or in alcoholic Bouin's solution. Dissection specimens were imbedded in a thin layer of fingernail polish as recommended by YOUNG (in press). YOUNG's suggestion for making dissecting instruments out of cactus spines was also very helpful. Various species of *Trichocereus* provide spines that are sufficiently strong and finely pointed. The dissecting microscope furnished magnification up to 178.5 ×. While this is not adequate for the genital muscles, it was helpful in freeing the genital field from most of the soft internal parts so that appropriate portions could then be mounted for study by both conventional and phase contrast microscopy. The main source of information was the serial sections of some 20 specimens prepared by Miss Helen GHIRADELLA, then of Cornell University. These mites were fixed in alcoholic Bouin's solution, dehydrated in ethanol, imbedded in 56-57° paraffin, and sectioned in various planes at 3 to 10 microns. Most of the sections were stained with Heidenhain's hematoxylin and eosin, a few with Mallory's phosphotungstic acid hematoxylin.

General anatomy of the female reproductive system.

A brief description of the female reproductive organs will aid in understanding the genital musculature. The ovary is a globular mass lying between the stomach and the rectum. From it a pair of lateral arms extends forward to about the level of the third leg pair. Here each arm turns abruptly rearward to end blindly, one on either side of the rectum (fig. 3, 4). These lateral arms represent the " lyrate body " of MICHAEL (1892) and of WARREN (1940), and the " ovulogenous glands " of YOUNG (in press). Transparent or whitish, and slightly granular in living specimens, they contain large, strongly basophilic cells, much more clearly defined in sections of young adults than in those of older ones. In mature females, no lumen is seen in the lateral arms, and the cells contain scattered, densely staining basophilic masses of irregular shapes and of various sizes. Warren regards these organs, in the species he studied, as accessory glands which form precursors of yolk for the developing eggs. Young believes that in *Haemogamasus ambulans* they are the source of the germ cells.

In both young and mature adults, the dorsal part of the central ovarian mass contains a superficial layer of cuboidal or columnar cells with vesicular nuclei (fig. 4). Since it is in this layer that the smallest recognizable ova appear, it is likely that this is the true germinal tissue in *Dicrocheles*, and that the lateral arms are accessory structures.

Surmounting the central ovarian mass is a lenticular cap consisting of a homogeneous, non-cellular ground substance enclosing several to many globular, hyaline bodies of 2 to 2.5 microns' diameter, each with a compact central mass which in some specimens appears to be basophilic and in others acidophilic (fig. 4). These bodies resemble cells seen in the lower parts of the testes and ejaculatory ducts of sectioned

males. It may be supposed that they are spermatozoa and that the lenticular cap represents the *camera spermatis* of MICHAEL. In one series of 5-micron cross-sections of a gravid female, two fine cellular, but apparently non-tubular strands converge from the intercoxal regions of legs IV to the antero-ventral portion of the central ovarian mass. While these might conceivably be vestiges of the *rami sacculi* and *tubuli annulati* of MICHAEL, there is no trace of a *sacculus foemineus*, which in MICHAEL's experience was always found in species possessing a lyrate organ. The cellular strands are not evident in most specimens. In several pairs of mites fixed in copula the spermadactyls of the males are deeply inserted into the vagina. This, together with the fact that there are no intercoxal spermathecae, convinces me that insemination in *Dicrocheles* is vaginal.

From the ventral part of the ovarian mass in non-gravid females, there emerges a flattened, tubular column of large, more or less columnar, nucleated, basophilic cells (fig. 4). In some specimens this column passes to the left of the intestine, in others to the right. Since this structure leads toward the genital orifice it may represent the oviduct, although WARREN regards its counterpart in *Dermanyssus gallinae* as merely a dorsal outgrowth of the vagina, which invades the ovary but does not convey eggs. In gravid specimens, much of the region between the stomach and the rectum is occupied by eggs of various sizes, the larger ones heavily laden with yolk granules. As seen in the sections, an occasional egg is enclosed in a thin cellular covering, but in most instances the eggs appear to be free in the body cavity. WARREN believes that each ovum develops its own " brood chamber ", which is later somehow " invaded " by a posterior outgrowth of the vagina to provide egress for the egg. Whether this occurs in *Dicrocheles* I cannot say. I have not seen eggs in the " oviducts " of young females, and in my material, where well developed eggs are present the oviduct is not recognizable.

As it approaches the genital orifice, the genital tract broadens and acquires a cuticular intima. This vaginal portion is like a wrinkled and flattened funnel with its lips extending laterally to the genital apodemes (fig. 5). The cells investing the vagina are smaller than those of the oviduct. Their shape varies from globular to fusiform, but both shape and arrangement are probably much modified during oviposition. Although the eggs when laid are about 180 microns in cross-sectional diameter (compared with a distance of only about 140 microns between the fourth coxae), they are passed through the vaginal orifice quickly and without appreciable deformation. The entire passage takes only one or two seconds and is accomplished without visible strain.

Profusely scattered throughout the subepidermal fatty and connective tissues, both in the genital area and elsewhere, are large, deeply staining cells of unknown function, probably corresponding to the " skin glands " of WINKLER (1888) and of WARREN. These cells are more prominent in engorged than in unengorged females. They often contain large vacuoles, but no ducts or other outlets have been seen. A number of such cells are found in the posterior sternal region and beneath the genital plate, where they obscure the muscles in a troublesome way.

Integumentary structures.

The genital (genito-ventral or epigynial) shield is of conventional monogynaspid form (fig. 6). It has a spatulate anterior prolongation bearing tree-like cuticular thickenings along its axis, while the thin lateral margins extend toward the lateral angles of the genital orifice (" la fente vulvaire " of FAIN). The posterior part of the genital shield is broadly rounded rearward. It bears a wedge-shaped pattern centrally and crescentic areas laterally. At the narrow, anterior end of the wedge there is a pattern of clear oval areas obscurely bordered by intertwining longitudinal
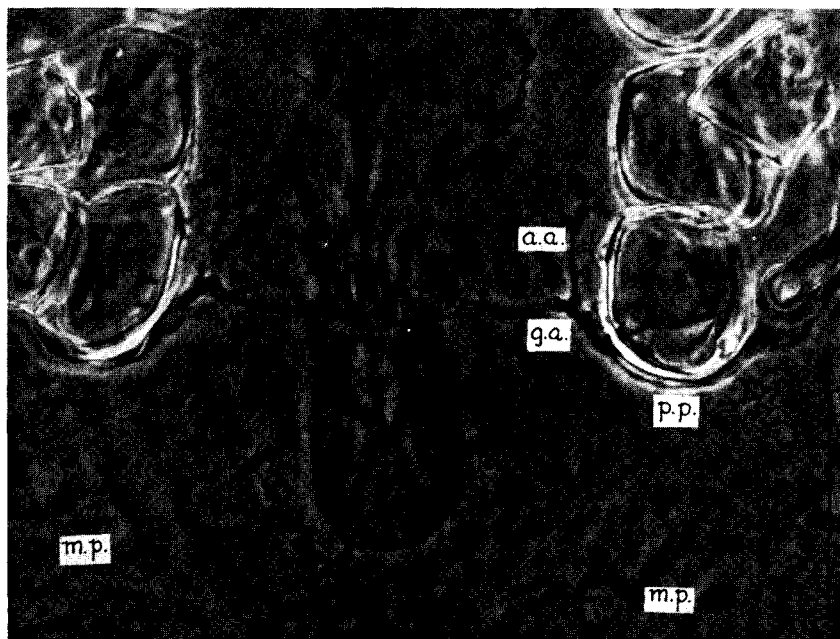

FIG. 6. — Genital area of an engorged female mounted in prone position, flattened, and cleared in Hoyer's medium ; *a.a.*, anterior arm of endopodal arc ; *g.a.*, genital apodeme ; *m.p.*, metapodal plate ; *p.p.*, peritremal plate. Dark phase contrast illumination. Compare fig. 7.

thickenings. In addition to the usual faint punctations commonly seen in sclerotized regions, there are scattered clear spots with dark borders, especially along the ridges in the middle of the shield. In appearance these suggest pores.

In living specimens seen by reflected light at 150 magnification, the genital shield occupies the summit of a low eminence whose general outline is bell-shaped. The posterior border of this eminence, forming the " mouth " of the bell, is a transverse fold or groove in the striated integument, crossing the venter at or just behind the rear border of the genital shield. This groove makes a line which is slightly concave anteriorly. It extends laterally beyond the borders of the genital shield

to the region between the fourth coxae and the metapodal plates. The sides of the genital eminence extend obliquely forward and medially from the extremities of the transverse fold, along the median borders of the fourth coxae toward the metasternal region. The genital eminence is usually not seen in mounted mites, although the transverse fold is sometimes visible if the specimen is not flattened.

The genital apodemes and " chitinous arcs " are hard to see in living specimens but show plainly in well cleared and severely flattened whole mounts. The portion of each arc posterior to the apodeme is in direct continuity with the posterior limb of the corresponding peritremal plate (fig. 6). Favorable specimens show this plate to be a flat, ribbon-like structure capable of being twisted so that a portion
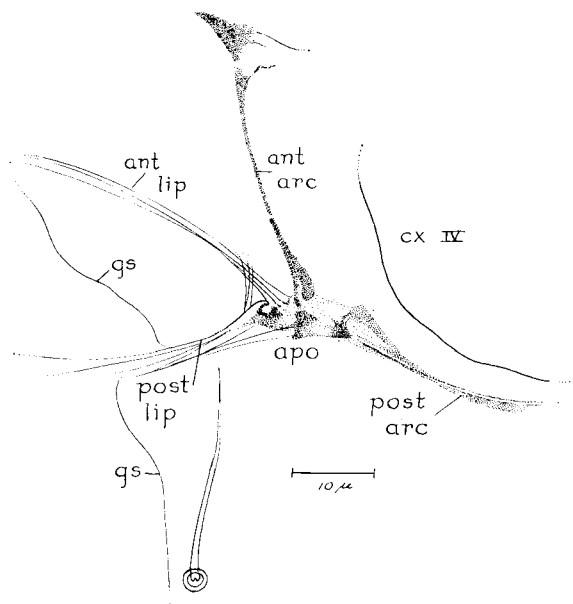

FIG. 7. — Details of right apodemal region in the specimen shown in fig. 6 ; *ant arc*, anterior limb of endopodal arc ; *ant lip*, anterior lip of vaginal orifice ; *apo*, genital apodeme ; *cx IV*, base of fourth coxa ; *gs*, lateral margin of genital shield ; *post arc*, posterior limb of endopodal arc ; *post lip*, posterior lip of vaginal orifice.

of it may be presented in edge-on view. Whether or not these arcs actually contain chitin I do not know ; under the dark contrast phase objective they appear darker than the surrounding elements. Because of their position, and with a reasonable surmise regarding their origin, I prefer to call them endopodal arcs. The portion of each arc anterior to the apodeme is very slender and is often broken into two or more pieces in flattened specimens. At its free end it is characteristically knobbed and toothed [1]. From the knobbed end, faint strands suggesting ligaments

1. Moth ear mites from various parts of the Orient differ from *D. phalaenodectes* in the shape of the endopodal arcs and in several other features probably indicating divergence of at least specific rank. These await description.

pass between the third and fourth coxae and become lost to view. I have not been able to follow these strands in sections ; if they are truly ligamentous, they might help to anchor the arcs against tensions in some of the muscles to be described, or against those incident to oviposition.

At the junction of the anterior and posterior limb of each endopodal arc is a minute element bearing a blunt hook which projects slightly forward and inward and thus a little deeper beneath the surface than the arcs themselves (fig. 7). This element is evidently the genital apodeme of FAIN. From it arise the integumentary folds that form the lips of the genital orifice. In *Dicrocheles* the genital apodemes are by no means as distinct from the endopodal arcs as they are in most of the species figured by Fain. The anterior and posterior limbs of the arcs appear to meet them in a complex articulation in which no clear separation of the elements is detected. I cannot tell whether relative movement among these parts is possible.

The anterior or deep lip of the genital orifice is a rippled integumentary fold forming a broad arch, convex anteriorly, between the genital apodemes (fig. 6, 7). Across the base of the arch, connecting the two apodemes, is another integumentary fold or ridge which I consider the posterior or superficial lip of the orifice. The free, spatulate portion of the genital plate extends forward from this fold, underlapping the anterior lip and the posterior part of the sternal shield. It is the margin of this free portion rather than the fold at its base that Fain designates in his figures as the superficial lip of the genital orifice. The difference is only one of interpretation.

The genital muscles.

Ten muscle pairs are associated directly or indirectly with the genital apparatus (fig. 8). Two of these are divided into several parallel slips which could be regarded as separate muscles but which are here treated collectively. Five anatomical groups may be recognized : (1) dorsoventral, (2) lateral, (3) ventral, (4) epigynial, and (5) endostylar. The individual muscles are assigned provisional names based upon their positions and apparent attachments.

The dorsoventral group includes two pairs of muscles, both originating on the posterior portion of the dorsal shield and passing medial to the posterior dorsal caeca of the gut, to the lateral arms of the ovary, and to the malpighian tubules. The more posterior of the dorsoventral muscles insert upon the metapodal plates and are therefore designated *dorso-metapodal* muscles. The metapodal plates, which I overlooked in the original description of the moth ear mite, are minute, oval sclerotizations, about 9 by 7 microns, lying behind the fourth coxae at about the level of the posterior margin of the genital shield (fig. 6) near the terminations of the transverse fold that forms the rear border of the genital eminence. The more anterior of the dorsoventral muscles appear to be inserted upon the posterior limbs of the endopodal arcs just posterior to the genital apodemes, and are here referred to as the *dorso-endopodal* muscles. The convergence of several muscles

toward this region tends to obscure the apodemal articulation and makes the exact positions of some of the muscle insertions difficult to determine.

The lateral group is represented by a single pair of muscles, the *lateral metapodals*, which connect the metapodal plates with the endopodal arcs. Their attachments are the rearmost ones upon these arcs, and accordingly are farthest from the apodemal articulations.

The ventral muscles are here termed the *anterior* and *posterior obliques*. The length of these muscles is somewhat exaggerated in the figure. The fibers of the *anterior obliques* arise from the ventral integument between the sternal shield and the anterior lip of the genital orifice, whence they converge on each side to the anterior limb of the endopodal arc near the genital apodeme. The fourth pair of sternal setae is lacking and metasternal plates are not recognizable in the moth ear mite, but the origins of the anterior oblique muscles are approximately where these plates might once have been. The *posterior obliques* are represented by two or more slips on each side. Their posterior attachments are upon the integumentary areas posterolateral to the genital plate, from which they pass to the posterior limbs of the endopodal arcs. I have not been able to determine unequivocally the relation of the posterior oblique muscles to the transverse fold. It is possible that this fold is actually created by the muscle attachments. I can see no trace of any sclerotized element in this region.

The epigynial muscles are those most closely associated with the genital shield. They include the *median genitals*, and a pair each of *transverse genitals, posterior genitals*, and three-part *genito-endopodals*. The median genital muscles comprise several slender but clearly striated fibers passing from the posterior margin of the genital plate, or from just behind it, to the vaginal floor (fig. 5, 8). These fibers are interspersed with fusiform, nucleated cells optically similar to those that invest the vaginal canal. The *transverse genital* muscles arise broadly from the medial portions of the genital shield just posterior to the superficial lip of the orifice. They insert, as nearly as I can tell, upon the genital apodemes or the region of their junction with the endopodal arcs. The *posterior genital* muscles arise just ventrolateral to the origin of the median muscles at the posterior margin of the genital plate. They pass forward and slightly laterally. Although their insertions are obscure in the few sections that show them, they appear to be very close to those of the transverse genitals, probably on the genital apodemes. The three slips of the *genito-endopodal* muscles arise side by side from the posterior margins of the genital plate or from just behind it. Their stout bundles (fig. 2) pass obliquely forward and outward to their distinct insertions on the posterior limbs of the endopodal arcs.

The endostylar group is represented by a single pair, the *vulvar* muscles. These slender fibers, interspersed with fusiform cells like those of the median genital, converge from the posterior parts of the endostyle, passing downward and rearward to the median portion of the anterior lip of the genital orifice (fig. 8).

The action of some of these muscles may be deduced from their anatomical

relationships ; that of others is not so obvious.   Muscles inserting upon the metapodal plates and upon the unsclerotized ventral integument may provide some of the compression required to move the eggs toward the genital orifice, and may furnish support for the opisthosoma when it is distended by engorgement and egg production.   In engorged, living females one often sees periodic, deep, dimple-like depressions of the metapodal areas.   These movements do not visibly affect the position of the eggs, and they evidently are not required for the movement of food in the gut or of waste in the excretory tubules, since these organs, though they appear to lack striated muscles, show independent contractility.   The metapodal depressions may help to circulate the haemolymph, or they may serve to ventilate the tracheae.
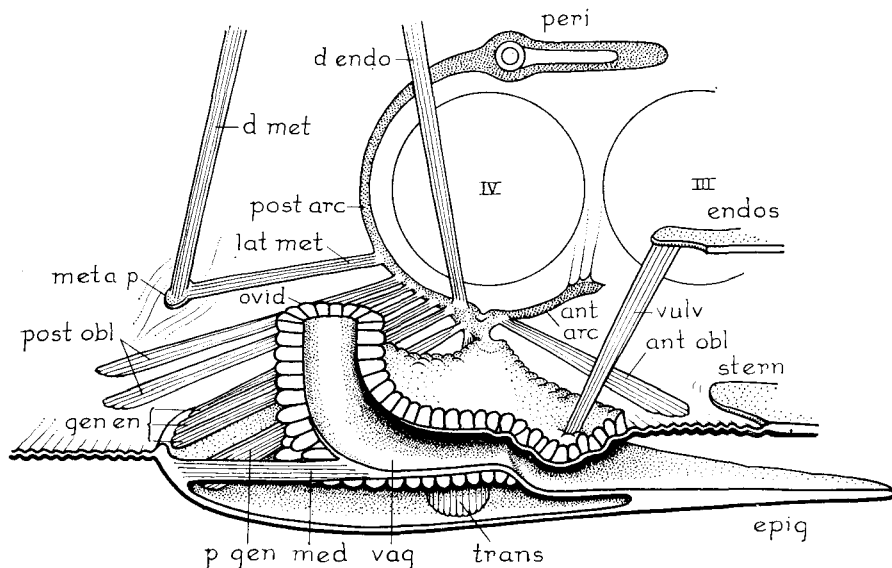

Fig. 8. — Schematic visualization of the left half of the genital apparatus as viewed from the mid-sagittal plane.   The transverse fold is not shown.   *III*, *IV*, third and fourth leg bases ; *ant arc*, anterior limb of endopodal arc ; *ant obl*, anterior oblique muscle ; *d endo*, dorso-endopodal muscle ; *d met*, dorso-metapodal muscle ; *endos*, endostyle ; *epig*, epigynium ; *gen en*, genito-endopodal muscles ; *lat met*, lateral metapodal muscle ; *med*, median genital muscle ; *meta p*, metapodal plate ; *ovid*, " oviduct " ; *p gen*, posterior genital muscle ; *peri*, peritreme ; *post arc*, posterior limb of endopodal arc ; *post obl*, posterior oblique muscle ; *stern*, sternal shield ; *trans*, transverse genital muscle ; *vag*, vagina ; *vulv*, vulvar muscle.

The vulvar muscles and the median genitals might help to dilate the genital orifice during oviposition and possibly during insemination.   In both of these processes, however, dilatation is probably passive, at least in part.

The transverse and posterior genital muscles are probably appressors of the genital shield.   Their relaxation is probably required in order to permit the passage of the egg.   The dorso-endopodal and anterior oblique muscles may help to anchor the endopodal arcs against the forces produced during the actual expulsion.   The

dorso-endopodals might also aid the transverse genitals in maintaining the normally appressed position of the genital shield.

If these views are correct, the skeletal complex comprising the peritremal plates, the endopodal arcs and their ligaments, and the genital apodemes, may be conceived as a sort of harness, anchored around the fourth leg bases, suspending the distensible chute through which the eggs are expelled. The differential fluid pressures required in order to move the eggs to and through this chute may be achieved by adjustment of the relative tensions of idiosomal compressor and epigynial appressor muscles. Having the suspending harness separate from the coxal sclerotizations would permit freedom of leg movement at all times.

The phyletic relations of the moth ear mites, like those of many parasitic gamasines, are still obscure. These mites differ in significant respects from those of the other genera which KRANTZ and KHOT (1963) included with them in their revision of the family Otopheidomenidae. Lacking the intercoxal spermathecae of *Treatia*, *Hemipteroseius* (EVANS, 1963), and the phytoseioid mites, they differ in chaetotaxy and in other features from the type genus *Otopheidomenis*. Comparative study of internal structures would perhaps shed light on the evolution of these and of other mites.

Acknowledgements.

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