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R. R. Miller

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 89

**Anatomy, Life History, and Evolution
of the Mites
Parasitizing Fresh-Water Mussels**

BY

RODGER D. MITCHELL

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
April 29, 1955

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ANATOMY, LIFE HISTORY, AND EVOLUTION
OF THE MITES
PARASITIZING FRESH-WATER MUSSELS*

INTRODUCTION

FOUR genera of Unionicolidae parasitize mollusks or sponges. These parasites are of particular interest because they are among the few water mites that attack animals other than insects and that are parasitic as nymphs and adults but not as larvae. Although these mussel parasites have been studied taxonomically, almost nothing has been published on their anatomy, life history, mode of life, and relationship to their hosts. This work was planned to deal with these subjects and to determine how the unique features of these parasites may have evolved.

All data from this and previous studies have been arranged under three main headings: systematics, anatomy, and life history. Systematic relationships, as presented by Viets and Lundblad, have been taken from the literature. The small amount of published information on anatomy and life history is integrated with the original studies here reported, and, in the light of available evidence, the possible trends in evolution and adaptation in the groups are discussed.

Since this paper was written Viets and Plate¹ have published a comprehensive review of the literature on the mites parasitizing mollusks. The nomenclature applied to the mollusks by Plate will be unfamiliar to many American malacologists. With reference to the exhaustive list of host associations for *Unionicola* cited in this work it is essential to keep in mind the limitations of the data. Frequency of parasitism by the mite and relative abundance of the mite in the host must be known in order to understand accurately host-parasite relationships.

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¹"Die ökologischen (parasitologischen) Beziehungen zwischen Wassermilben (Hydrachnellae, Acari) und Süßwasser-Mollusken," *Zeitschr. f. angew. Ent.*, 35:459-94.

SYSTEMATICS

Most of the systematic studies of water mites have been based on regional faunas. Familial, generic, and subgeneric names have been applied without clear definitions, and the groups came to be established on the basis of their specific contents rather than on any tangible structural features. A system which has developed in such a fashion may be sound, but cannot be accepted until it is supported by detailed knowledge of the comparative anatomy and life histories of the animals dealt with in the group. In spite of this limitation, the systematic literature serves as a suitable basis for comparative studies.

Viets's (1936) definition of the family Unionicolidae has been widely accepted. The family contains fifteen genera, all but four of which are free-living predators both as adults and as nymphs. All members of the family commonly inhabit permanent fresh waters, but no life histories are known except in the genus *Unionicola*. Ten genera are of limited distribution and have relatively few species assigned to them. All these are either African or South American except *Najadicola*, which is North American, and *Ecentridophorus*, which is European. The remaining five genera are at least holarctic in distribution and are represented by many species. This limited zoogeographic information adds little to the understanding of the evolution and development of phyletic lines within the family.

The mites parasitic on mussels belong to two subfamilies. In the subfamily Unionicolinae there are three genera, all of which are parasitic during certain advanced stages of their life history. Two of these, *Polyatacides* and *Atacella*, are neotropical, whereas the third, *Unionicola*, is a large cosmopolitan genus. The only member of the subfamily Najadicolinae is *Najadicola ingens* (Koenike), of North America. All these mites share a tendency to parasitize Unionidae during one or more of the postlarval stages. A few of the species of *Unionicola* are known to attack sponges (Wesenberg-Lund, 1918) and viviparid snails (Marshall, 1935; Lundblad, 1942).

Subgenera of *Unionicola* are based mainly on the number of genital acetabula, although the form of the coxae is also considered. The subgenera *Pentatax* and *Unionicola*, with five and six pairs of genital acetabula, respectively, are regarded as generalized forms. Those with numerous genital acetabula are usually more modified and are thought to be further removed from the ancestral stock. Although this conclusion lacks adequate documentation, the studies of behavior and life history presented and discussed below support this interpretation of relationships in the group.

Since the appearance of Wolcott's monograph (1899) little work has been done on the *Unionicola* in North America. The species known from North America were listed recently (Mitchell, 1954). The present studies were made upon species that were adequately defined by Wolcott (1899).

ANATOMY

Materials and Methods

Whole mounts, dissections, and sectioned material were used in anatomical studies. Exoskeletal structures were studied from glycerine jelly preparations and balsam mounts of specimens stained in basic fuchsin. The musculature was worked out from dissections, and certain points were checked against sectioned material. All studies of organ systems were made from paraffin sections 7μ to 15μ thick, generally stained by one of two procedures: Harris' hematoxylin with eosin counterstain, or methyl blue and eosin. A good nuclear stain was not obtained except in the oral glands.

Unionicola fossulata and *Najadicola ingens* were selected for detailed treatment. Comparative studies of the following species were also made from sectioned material and dissections:

Unionicolidae

- Unionicola crassipes* (Müller)
- Unionicola ypsilophora* (Bonz)
- Unionicola intermedia* (Koenike)
- Unionicola fossulata* (Koenike)
- Najadicola ingens* (Koenike)
- Neumania distincta* Marshall
- Koenikea* sp.

Anatomy of *Unionicola fossulata* (Koenike)

General appearance. — The mite is a comparatively slow-moving animal about 1 to 1.5 mm. in length and elongate oval in shape (Fig. 1A, B). The colors of the internal organs are clearly visible through the transparent integument and sclerites. Figure 2C and D shows the general arrangement of the organs seen in life. A deep greenish black or brown mid-gut occupies nearly the entire body. Lobes of the mid-gut are usually closely appressed or covered by other organs. A sharply defined white Y-shaped excretory organ rests on the dorsal surface of the mid-gut with the stem of the Y extending posteriorly. Oral glands, ganglia, muscles, and testes are rarely recognizable because of their small size and neutral white color. Yellowish ovaries cover nearly the entire ventral body surface and, in the older females carrying fully developed eggs, may extend up laterally.

Integument. — As in most unionicolids, the integument is thin and without any markings or structural modifications. Few structural details are apparent in the epidermis which appears as a thin layer of cytoplasm with a few scattered densely stained nuclei. No cell walls or other histological structure are demonstrable.

Exoskeleton and musculature. — The exoskeleton limits and defines the movements the animal can make, and action of the muscles induces movement. Together, these structures form an integrated system for feeding and locomotion which must be considered a functional unit. Accurate

knowledge of the origin and insertion of each muscle is essential for comparative work and is presented in tabular form (Tables I - III). Only general structure and function will be considered in the text.

The mouth parts are supported by a tubular sclerotized structure that is composed of four elements (Snodgrass, 1948): basis capituli, coxae of the palps; epistome and hypostome, dorsal and ventral sclerotizations of the projection bearing the mouth; tectum, a plate dorsal and caudad to the base of the chelicerae. In anatomical as well as taxonomic work, reference must be made to the discrete structure that may be formed by the fusion of the basis capituli and, in some cases, some or all of the above-mentioned structures. It has been common practice to call this structure the capitulum, and as so restricted the term is not synonymous with gnathosoma, which refers to a body region. Snodgrass (1948) and Gorirossi and Wharton (1954) hold these terms to be synonymous without considering this other common and useful definition of capitulum.

Previous accounts of musculature of mites enumerate the muscles present. So little is known that the body muscles cannot be homologized, and a natural classification is impossible. Some sort of organization is possible if the muscles are grouped according to function. The musculature of water mites may be separated into three groups on the basis of function: muscles originating on the coxae and inserting on the basal segment of the leg, coxal muscles; those originating on the body wall, coxae, or genital stirrup and inserting on the transverse coxal ligament, supportive muscles; those with both origin and insertion on the body wall, dorso-ventral muscles.

The coxae, the legs, and their segments are referred to by a numerical system. Roman numerals refer to the leg pairs and coxae beginning anteriorly. Arabic numerals 1 to 6 refer to the leg segments beginning with the first segment distad of the coxa.

Mouth parts (Fig. 2A, B). — The capitulum is reduced to a narrow collar supporting the palps and their muscles and those of the pharyngeal pump. It serves as a fulcrum for the chelicerae. The capitulum is longest ventrally (Fig. 1A, 2B), and a bulblike lateral expansion supports the palps. The walls of the capitulum bend mesally to form the dorsal surface, which is no more than a solid rod supporting the two sigmoid pieces (Fig. 2B). The capitulum is closed anteriorly and sclerotized to a level slightly above the mouth opening. Chelicerae hang over the front of the capitulum, which is produced into a cuplike expansion around their distal ends.

The mouth lies in the center of the anterior surface of the capitulum (Fig. 2B). There is a space between the capitulum and the chelicerae. That part of the space before the mouth, through which food must pass to reach the mouth, is called the preoral cavity, and the continuation of this space behind the mouth is called the postoral cavity.

The thick, rigid ventral wall of the pharynx is firmly attached to the floor of the capitulum by a series of ligaments. When relaxed, the flexible dorsal wall of the pharynx lies against the ventral surface. A series of muscles inserts on the dorsal surface of the pharynx and originates high on the lateral and dorsal surfaces of the capitulum (Fig. 2B). Contraction of these muscles, the pharyngeal dilators, pulls the dorsal wall of the pharynx

up and away from the ventral wall, thus drawing fluids into that cavity. The pharyngeal dilators do not originate in a discrete longitudinal row, and a distinct epistomal apodeme is not present.

The chelicerae consist of a main shaft with a movable cheliceral claw at its end. There is a small sclerite dorsal and posterior to the cheliceral shaft, tentatively referred to as the "tectum" (Fig. 2B). Elevation of the cheliceral claw is accomplished by three muscles that insert dorsally on the base of the claw and originate as follows: the posterior muscle from the ventral wall of the cheliceral shaft, the median muscle from the tectum, and the anterior muscle from the dorsal surface of the cheliceral shaft. The three depressors of the cheliceral claw insert ventrally on its base; one originates on the tectum, and two on the dorsal wall of the cheliceral shaft.

Protraction of the chelicerae is accomplished by the contractions of a muscle which inserts on the sigmoid piece and originates on the tectum (Fig. 2B). Contraction of the cheliceral protractor draws the posterior part of the sigmoid piece dorsally and the tectum ventrally, thus pushing the ventral wall of the cheliceral shaft outward and drawing the dorsal wall inward. The result is a raising of the tip of the chelicera. This movement of the cheliceral shaft along with the movement of the cheliceral claw would rip any tissue appressed to the capitulum.

Elevators and depressors insert on the basal segment of the palp and originate on the capitulum. There is one elevator which originates on the posterior margin of the ventral wall of the capitulum. Four depressors originate on the capitulum; one on the posterior margin of the ventral wall, two near the middle of the ventral wall, and a wide muscle on the lateral wall. The muscles of the palp segments are limited to three flexors (Fig. 2B, Table III). Apparently, extension of the palps is accomplished by pressure of the body fluids, as in the legs.

Two pairs of dorsoventral muscles originate on the anterior dorsal sclerite and insert on the posterior margin of the capitulum (Fig. 3); the dorsal pair on the margin just dorsal to the socket for the reception of the palp, the ventral pair at the ventrolateral angle of the capitulum. These muscles belong to the group of dorsoventral muscles which seem to function in giving rigidity and support to the sclerites of the body.

Supportive muscles (Fig. 3, Table I). — One pair of muscles originates at the lateral margin of coxa IV and inserts on the lateral extremity of the transverse coxal ligament. The ligament is very long, and the muscle at either end is short and obscure. Three pairs of muscles originate on coxa IV; two pairs of these originate on the lateral margin and insert halfway to the center of the transverse ligament, the third originates on the socket of coxa IV and inserts near the center of the ligament. Another pair of muscles inserts near the center of the ligament and extends posteriorly to its origin on the genital stirrup. All supportive muscles insert on the posterior surface of the transverse coxal ligament and must act to draw the ligament posteriorly. This opposes the muscles originating on the anterior surface of the ligament, the elevators of the first three legs.

Coxal muscles (Fig. 3, Table I). — All coxal muscles act upon a basal leg segment. Movement between leg segment 1 and the coxa is limited by

TABLE I

The Coxal and Supportive Muscles of *Unionicola fossulata* (Koenike)
According to Function, Origin, and Insertion (see Figure 3)

Functional Group	Origin	Insertion
Leg I Elevators	Transverse coxal ligament (three bands)	Dorsal margin, base of segment 1, leg I
	Posterolateral margin, coxa I Posterior extension, coxal group 1	Dorsal margin, base of segment 1, leg I Dorsal margin, base of segment 1, leg I
Depressors	Body wall between coxae IV (two muscles)	Ventral margin, base of segment 1, leg I
	Mesal margin, coxa I Posterolateral angle, coxa I	Ventral margin, base of segment 1, leg I Ventral margin, base of segment 1, leg I
Leg II Elevators	Transverse coxal ligament (three bands)	Dorsal margin, base of segment 1, leg II
	Posteromesal angle, coxa II Posterior margin, coxa II Posterior extension, coxal group 1	Dorsal margin, base of segment 1, leg II Dorsal margin, base of segment 1, leg II Dorsal margin, base of segment 1, leg II
Depressors	Mesal margin, coxa II Posteromesal angle, coxa II Posterior margin, coxa II	Ventral margin, base of segment 1, leg II Ventral margin, base of segment 1, leg II Ventral margin, base of segment 1, leg II
Leg III Elevators	Transverse coxal ligament (three bands)	Dorsal margin, base of segment 1, leg III
	Anteromesal margin, coxa III Mesal margin, coxa IV	Dorsal margin, base of segment 1, leg III Dorsal margin, base of segment 1, leg III
Depressors	Anteromesal angle, coxa III Posterior margin, coxa III	Ventral margin, base of segment 1, leg III Ventral margin, base of segment 1, leg III
Leg IV Elevators	Anterior margin, coxa IV Mesal margin, coxa IV	Dorsal margin, base of segment 1, leg IV Dorsal margin, base of segment 1, leg IV
	Depressors	Mesal margin, coxa IV (three muscles) Posterior extension, coxa IV
Supportive Muscles	Lateral margin, coxa IV (three muscles)	Lateral part, transverse coxal ligament
	Mesal extremity, coxal socket IV	Central part, transverse coxal ligament
	Anterior genital stirrup	Central part, transverse coxal ligament

TABLE II

Dorsoventral Muscles of *Unionicola fossulata* (Koenike) (see Figure 3)

Number	Origin	Insertion
I	Dorsal extension, anteromesal angle, coxa I	Anterior dorsal sclerite
II	Dorsal extension, posterior margin, coxa I	Anterior dorsal sclerite
III	Dorsal extension, posterior margin, coxa II	Anterior dorsal sclerite
IV	Posterior margin, coxa II	Body wall dorsal to coxal group 2
V	Posterior margin, coxa III	Body wall dorsal to coxal group 2
VI	Lateral margin, coxa IV	Posterior dorsal sclerite
VII	Posterior margin, coxa IV (two muscles)	Body wall posterior to coxa IV
Capitulum muscles	Base of the capitulum Dorsolateral margin, capitulum	Anterior dorsal sclerite Anterior dorsal sclerite

articulations and limiting membranes. Such an articulation is difficult to define accurately, and certain aspects of coxal muscle action cannot be analyzed. Since all muscles acting on the segment insert at one of two points, the movement of the segment must be relatively simple. Manipulation and examination of the musculature show that the motion of the first segment of all legs must be in or near a dorsoventral plane.

The coxal musculature is illustrated (Fig. 3) and tabulated as to origin, insertion, and function (Table I). Only certain general features of the musculature will be considered below.

The principal elevators of legs I-III are fairly thick elongate muscles that originate on the transverse coxal ligaments. Each muscle is made up of three separate bands. In addition to these elevators there are prominent elevators of legs I and II that originate on a posterior projection of the anterior coxal group. One or two small elevators of legs I-III originate on the respective coxae (Table I).

Each of legs I-III has two or three depressors that originate on the coxa mesal and posterior to the leg base. There is a striking contrast between the long thick elevators of the first three legs and the small short depressors opposing them. The functional significance of this arrangement is not clear.

A projection of the basal segment of leg IV (Fig. 1E) fits into a socket of the coxa, and the segment rotates in it. Two antagonistic muscle groups, almost balanced as to size and length, insert on the base of the first leg segment. Three depressors of leg IV originate together on the mesal margin of coxa IV; the fourth originates on an apodeme that forms a posterior extension of coxa IV. This apodeme, which serves as the origin of a depressor of the fourth leg, is a common feature of the family Unionicolidae.

Leg muscles (Fig. 1D, E; Table III). — Musculature of the leg segments is constant and rather simple in all legs. Leg segments 1 and 2 are the

TABLE III

The Segmental Muscles of the Legs and Palps of
Unionicola fossulata (Koenike) (see Figure 1D and 1E)

Function	Origin	Insertion
Legs		
Protractor 2	Anteroproximal wall, segment 1	Anterior margin, base of segment 2
Retractor 2	Posteroproximal wall, segment 1	Posterior margin, base of segment 2
Flexor 3	Proximoventral wall, segment 2	Ventral margin, base of segment 3
Flexor 4	Mesodorsal wall, segment 2	Ventral margin, base of segment 4
Flexor 5	Mesodorsal wall, segment 3	Ventral margin, base of segment 5
Flexor 7	Mesodorsal wall, segments 4 and 5	Ventrally, base of tarsal claw
Extensor 7	Mesodorsal wall, segment 6	Dorsally, base of tarsal claw
Palps		
Flexor 3	Proximally, ventral and lateral wall, segment 2 (two muscles)	Ventrally, base of segment 3
Flexors 4	Distally, dorsal wall, segment 2	Ventrally, base of segment 4
	Proximally, dorsal wall, segment 3 (two bands)	Ventrally, base of segment 4
Flexors 5	Distally, dorsal wall, segment 3	Ventrally, base of segment 5
	Dorsal wall, segment 4 (two muscles)	Ventrally, base of segment 5

only ones supplied with antagonistic muscles. Segment 1 is acted on by the elevators and depressors discussed above. The movement of segment 1 determines the dominant movement for the entire leg. In *U. fossulata* this plane is nearly vertical in all legs. Segment 2 is acted upon by a protractor and a retractor that originate on the wall of segment 1 (Fig. 1D, E) and insert on the proximal margin of segment 2.

Segments 3 through 6 are, with two exceptions, activated by flexors which originate on the dorsal surface of the second segment proximal to their insertion. The flexor of segment 3 originates on the venter of segment 2. No muscles insert on segment 6. The tarsal claw which is, in fact, a true segment (Snodgrass, 1952) is supplied with two flexors and an extensor; flexors originate on the dorsal wall of segments 4 and 5 and the extensor originates on the dorsal wall of segment 6. Since no muscles are provided for the extension of segments 3 to 6, extension must be caused by pressure of the body fluids.

Although the base of leg IV differs in insertion from legs I-III, there is no difference in leg musculature or function. A marked difference appears in the function of the two anterior legs as compared to that of the two posterior ones. Legs I and II act more to pull the animal forward. The power movement is started with the legs extended and depressed anterior to the body, and through elevation by the coxal muscles together with flexion of the segmental flexors the body is pulled forward. On the other hand, legs III and IV act to push the body forward. Beginning with the legs elevated and flexed parallel to the body, the depressors of segment 1 contract and press the leg down, which straightens out the leg as far as permitted by the segmental articulations.

Thus, only the segmental flexors and elevators of segment 1 develop power in the anterior legs. Interior body pressure appears to be the only means of extending the legs. In legs III and IV power is developed as flexed legs in contact with the substrate are depressed, and only the depressors of segment 1 develop power. Elevators and flexors of the posterior legs return them to position for a new power stroke.

The function of the leg in walking has been considered, and this explanation accounts for the facts of anatomy but remains only partly verified from observation. Walking is the major means of locomotion in *U. fossulata*. General body and leg structure of *U. fossulata* is similar to that of active swimming forms, but nothing is known of leg function in swimming.

Dorsoventral muscles (Fig. 3, Table II). — These muscles all seem to give a tonus and rigidity to the body. Possibly their periodic contraction produces pressures helpful in moving body fluids, and this, in the absence of other circulatory organs, may be of some importance. Probably these muscles also contribute to the maintenance of the body pressure essential for extension of the appendages.

Extrinsic muscles of the capitulum (discussed with the mouth parts) are assignable to this group. These muscles and dorsoventral muscles I-III originate on the anterior dorsal sclerite and pass between the median anterior lobe and the lateral anterior lobes of the mid-gut. Dorsoventral muscles I-III insert on the three laterodorsal extremities of the first coxal group (Fig. 3). Dorsoventral muscles IV and V extend obliquely from origins on coxae III and IV to points of origin on the lateral body wall. Only one muscle originates from the posterior dorsal sclerite, dorsoventral muscle VI, which inserts on the lateral margin of coxa IV. Dorsoventral muscle VII simply extends from the posterior margin of the coxa to the body wall lateral to the genital sclerite.

Genital field (Figs. 1A, C; 3). — The exoskeletal features associated with the gonopore are considered here. Six pairs of genital acetabula are present. Presumably, acetabula are sensory structures, but their function has not been established. In the female the region of the acetabula is hardly thicker than the rest of the integument (Figs. 1A, 3), but in the male the acetabula are on a sclerotized plate with an oval central opening (Fig. 1C).

Two accessory sclerites are present in the female and are designated the genital stirrups. The anterior genital stirrup is a knoblike protuberance at the anterior end of the gonopore and bears a pair of elongate rods that extend posteriorly along the wall of the gonoduct (Fig. 3). The posterior genital stirrup is similar, with lateral arms extending anteriorly and almost meeting those of the anterior genital stirrup. The posterior genital stirrup also bears a median rod on which originate two pairs of genital plate muscles: muscle I lateral to the acetabula, muscle II on the dorsum. Contraction of muscle I presses down on the gonoduct, opening the gonopore. Genital plate muscle II lifts the gonoduct and closes the gonopore.

Genital acetabula are situated immediately lateral to the gonopore, where the body wall is somewhat heavier. Two heavy setae are centrally located just lateral to the gonopore (Fig. 1A). As the egg is forced through the gonopore this fairly rigid part of the body wall spreads out, and it appears to spread a slit in the epithelium of the host through which the egg passes.

Oviposition involves the combined action of a series of structures. From anatomical evidence oviposition appears to be as follows: Prior to oviposition the female tears a slit in the host tissue with her mouth parts. The genital field is then pressed into the slit, and the four heavy setae engage the edges of the slit in the epithelium. Contraction of genital muscle I spreads the lips of the gonopore, and contractions of the circular muscles of the gonoduct push the egg through the open slit in the host's epithelium into the underlying loose connective tissue. Following extrusion of the egg, contraction of genital plate muscle II raises the posterior genital stirrup and closes the gonopore.

The so-called penis or copulatory organ of the male is a structure of the gonoduct wall. It is apparently a series of valves for the production and deposition of spermatophores. Musselius (1912) has worked out the anatomy of this structure in a related species. I have not studied this structure.

Nervous system.—As in all Acarina, the ganglia are fused, and the neuropile masses representing them can be demonstrated only by histological studies of the ganglionic mass. Four subesophageal neuropile masses, each innervating one pair of legs, are present (Fig. 2). Other mites (*Tetranychys*, Blauvelt, 1945; *Dormacentor*, Douglas, 1943) show a slight distinction of a fifth neuropile mass, but there is no such indication in *U. fossulata*. The supraesophageal ganglion shows two neuropile masses (Fig. 2A). The lower innervates the mouth parts, but the nerves of the dorsal mass could not be traced.

Excretory system.—The excretory organ is a large thin-walled trilobate chamber without any openings. A pair of small tubular lobes extends anteriorly between the median and lateral anterior lobes of the mid-gut (Fig. 2A, C), and a large posterior lobe lies between the paired posterior lobes of the mid-gut. The walls of the excretory organ are made up of a single layer of simple cells that are uniform throughout the organ.

Reproductive system.—Gonads appear as a mass of tissue on the ventral surface of the body, extending anteriorly from the gonopore nearly to the nerve mass (Fig. 2A, D). The testes or ovaries have no clear structural organization, and reproductive products in various stages are noted throughout the gonads. Accessory glands are absent in both sexes. The function of accessory glands in males is not known, but in females one of their functions is to produce a protective covering for the egg or egg mass. None of the species of *Unionicola* examined has been noted to produce an egg covering. Evidently these eggs require neither external protective covering nor means of adherence.

Ova are carried from the median ovary by a single simple tube. The process of oviposition has been discussed in connection with the external genital structures. Sperm are carried from the testes by a pair of inconspicuous, thin-walled vasa deferentia to the chamber of the complex male copulatory organ. The function of this organ has not been studied here.

Digestive system.—In discussing the system the whole complex of organs involved in the ingestion and digestion of food must be considered together. The structure and operation of the mouth parts have been discussed above.

Oral glands (Fig. 2A).—Because of reduction and modification certain oral glands in *U. fossulata* cannot be homologized by comparison with Bader's

(1938) detailed account for other water mites. One pair of glands, designated "F" by Bader, is absent. Two other pairs are also absent, but these belong to a group of four pairs of glands which Bader called L(A), L(D), M(B), and M(E). These glands occur together and are so similar in structure and cytology that any attempt to homologize them is difficult. The tracheal gland is a small ovoid mass of cells just posterior to the chelicerae and is drained by a short median duct leading into the end of the post oral cavity.

Tubular glands are also present although very much modified. Only zones 2 and 3 of the three Bader (1938) recognized in *Hygrobatas* are present here. Terminally, the gland is a simple, straight tube about 15μ in diameter which is appressed to the ventral surface of the lateral anterior lobe of the mid-gut. The central lumen is a very obscure passage. A single layer of radially arranged, lightly staining cells forms the gland, and the centrally placed cell nucleus contains a rather large nucleolus but is without other structures.

The main mass of glandular tissue is formed by two pairs of large, anteriorly placed reniform glands. Usually the smaller is anterior and median to the main mass of the large one. This smaller, more or less ovoid gland is made up of a group of conical cells with attenuated ends that meet in the center, and this area is drained by a simple duct. Two zones are apparent in each cell: the darkly staining granular region at the base where there are very few vacuoles, and the lightly staining vesicular area at the tip. A nucleus over 5μ in diameter is situated in the basal region and contains a nucleolus half the diameter of the nucleus together with a few very fine chromatin granules.

The larger, irregularly shaped gland is situated dorsolaterally and is made up of cells of various shapes. These coarsely granulate cells usually stain lighter than those of the smaller gland and show a central region where vacuoles accumulate. The basally situated nucleus may reach 10μ in diameter and contains a nucleolus about 2μ in diameter together with many fine chromatin granules. The gland lacks a distinct cavity for the accumulation of secretions and is drained by a branched duct which passes ventrally to join the duct from the other reniform gland and thus to form paired common ducts. These extend down to the roof of the capitulum, where the two common ducts empty into either side of the dorsal extremity of the post-oral cavity (Fig. 2B).

Mid-Gut. — Liquid food material, presumably partly liquefied by action of the oral gland secretions, is drawn into the pharynx and pumped into the mid-gut by action of the pharyngeal pump. The mid-gut is a large, blind, thick-walled cavity without prominent histological differentiation. Several layers of irregular, ill-defined cells in various stages of activity make up the wall of the gut. Bader (1938), in reference to *Limnesia koenikei*, stated that the cells of the gut function in various ways: secretion, ingestion and digestion of particles, and accumulation of wastes. Vacuoles, inclusions, and waste products obscure much of the cell structure in *U. fossulata*, but none of my observations conflicts with Bader's account of digestion.

There are five main lobes of the mid-gut (Fig. 2A), three anterior and two posterior; the median anterior lobe is dorsal to the lateral anterior

ones. Oral glands lie on the lateral anterior lobes of the mid-gut and are appressed to the sides of the median anterior ones. Very large posterior lobes of the mid-gut nearly fill the posterior region of the body.

Comparative Anatomy of the Genus *Unionicola*

There is little variation in structure in the genus. The internal organs are basically similar, but there are slight differences in shape and proportions. Descriptions of internal organs of *U. fossulata* apply to all species of *Unionicola* studied. Species of this genus differ mainly in exoskeletal features, which are used in taxonomic work. These features indicate modifications in the form of sensory organs, musculature, and body shields.

In *Unionicola* proportions, chaetotaxy, and leg shape vary considerably and are closely correlated with swimming habits. Free-living planktonic forms have long, slim, setigerous legs (Fig. 5), whereas in parasitic forms legs are short and thick and bear fewer setae (Fig. 1). Even with such marked differences in structure and, presumably, in function no prominent variation was found in the musculature of the segments or coxae. In all species studied the coxal muscles are similar in number and placement. One marked variation was observed in the depressor muscle of leg IV (Fig. 3), which originates on a projection of the posterior margin of coxa IV. This projection, characteristic of the Unionicolidae, is often reduced in the subgenera *Pentatax* (Fig. 5) and *Hexatax*, and is absent in *U. ypsilophora*. With the loss of this apodeme the origin of the muscle is found on the body wall just posterior to coxa IV.

Dorsoventral muscles are the most difficult to follow, and comparisons are not reliable. The pattern described for *U. fossulata* seems to fit all the species examined.

The number of acetabula and structural modifications of the genital plates are among the most useful diagnostic features for species and subgenera. Of course, the significance of the differences in genital acetabula will be obscure as long as their function is unknown. Females of *Unionicola* bear certain processes on the median margin of the genital plates, either heavy setae or outwardly directed, bladeliike margins. These are adaptations for spreading an opening in the host tissue for the deposition of eggs. In some species (e.g., *U. fossulata*, Fig. 1A) the region lateral to the gonopore, which bears the genital acetabula, is very little thickened, and the lips are divided into two parts by transverse folds. Others (e.g., *U. intermedia*) show four sclerites with expanded margins. All polyacetabulate forms have a pair of lateral plates with expanded margins. This unique development of movable genital plates in females of the genus *Unionicola* represents the only clear structural adaptation to parasitism.

Anatomy of *Najadicola ingens* (Koenike)

Najadicola ingens, the only member of the genus, was originally described as a species of *Unionicola*. It is a common parasite of a number

TABLE IV

The Coxal and Supportive Muscles of *Najadicola ingens* (Koenike)
According to Function, Origin, and Insertion (see Figure 4B)

Functional Group	Origin	Insertion
Leg I Elevators	Transverse coxal ligament Anterolateral margin, coxa I Posterior margin, coxa I (two muscles) Posterior extension, coxal group 1	Dorsal margin, base of segment 1, leg I Dorsal margin, base of segment 1, leg I Dorsal margin, base of segment 1, leg I Dorsal margin, base of segment 1, leg I
Depressors	Body wall between coxa IV Mesal margin, coxa I Posterolateral margin, coxa I (two muscles)	Ventral margin, base of segment 1, leg I Ventral margin, base of segment 1, leg I Ventral margin, base of segment 1, leg I
Leg II Elevators	Transverse coxal ligament Posterolateral margin, coxa II Posterior extension, coxa II	Dorsal margin, base of segment 1, leg II Dorsal margin, base of segment 1, leg II Dorsal margin, base of segment 1, leg II
Depressors	Anteromesal margin, coxa II Posteromesal margin, coxa II Mesoposterior margin, coxa II Lateroposterior margin, coxa II	Ventral margin, base of segment 1, leg II Ventral margin, base of segment 1, leg II Ventral margin, base of segment 1, leg II Ventral margin, base of segment 1, leg II
Leg III Elevators	Transverse coxal ligament Mesal margin, coxa III Posterior margin, coxa IV	Dorsal margin, base of segment 1, leg III Dorsal margin, base of segment 1, leg III Dorsal margin, base of segment 1, leg III
Depressors	Anteromesal margin, coxa IV Mesal margin, coxa III Posterior margin, coxa III Lateroposterior angle, coxa III	Ventral margin, base of segment 1, leg III Ventral margin, base of segment 1, leg III Ventral margin, base of segment 1, leg III Ventral margin, base of segment 1, leg III
Leg IV Elevators	Anterior margin, coxa IV Lateral margin, coxa IV	Dorsal margin, base of segment 1, leg IV Dorsal margin, base of segment 1, leg IV
Depressors	Lateral margin, coxa IV Posterior margin, coxa IV	Ventral margin, base of segment 1, leg IV Ventral margin, base of segment 1, leg IV
Supportive Muscles	Lateral margin, coxa IV Body wall dorsal to coxa IV Projection, posterior margin, coxa IV	Lateral tip, transverse coxal ligament Lateral tip, transverse coxal ligament Lateral tip, transverse coxal ligament

of North American unionids (Humes and Jamnback, 1950). Nymphs and adults live in the suprabranchial chambers. Movement of these large short-legged mites in the mussel is slow and labored; outside the mussel, movement is impossible. The larva, as yet undescribed, is probably motile and is the only stage at which the mite is able to move to new hosts. A comparison of *Unionicola* with *Najadicola* is especially necessary in order to clarify the relationships of the two parasitic groups. Living animals of *Najadicola* are very large; some females reach 6 mm. in length, but most are about 3 mm. Males are usually just under 2 mm. At first, the mites appear to be of a uniform cream color, but with careful observation the oral glands, excretory organ, and ovaries may be distinguished by their slightly lighter color. The oral glands are paired translucent white masses situated anteriorly and slightly separated from the mid-gut.

The opaque white excretory organ is irregularly divided and extends over the dorsal surface of the mid-gut. As in *Unionicola*, the mid-gut fills nearly the entire body; in *Najadicola* it is cream colored and none of its lobes can be distinguished. The ovaries in mature females are indicated by the outlines of the eggs.

The anatomy of *Najadicola* is so similar to that of *Unionicola* that the previous account of *U. fossulata* serves as an adequate basic description. Attention is called to identical features in the two forms, and a detailed description is given only if the structures differ.

In relative size the mouth parts are small in *Najadicola* (Fig. 4A), and the chelicerae are more nearly on a horizontal plane; the musculature of the mouth parts is the same as in *Unionicola fossulata*.

The coxae are relatively narrow and elongate, and the muscles are very narrow (cf. Figs. 3 and 4B). Each of the elevators of legs I-III that originate on the transverse coxal ligament is reduced to a single narrow muscle band, and all originate together near the center of the ligament. With few exceptions the coxal muscles are the same as in *Unionicola* (Tables I and IV). Differences, in most instances, are due to the fact that one broad muscle in *Unionicola* is represented by two or three very narrow muscles in *Najadicola*.

Proportions of the various muscle groups of coxae I-III differ greatly from those in *Unionicola*. All elevators are much reduced in width, whereas the depressors are not so altered. As a result, the opposing muscle groups of the coxae are nearly balanced in the amount of muscle tissue. Balanced elevators and depressors are commonly noted in nonswimming forms.

Mites of such a size range (2 mm. to 6 mm. long) living in the supra-branchial chamber of a mussel are very limited in activity. Within the restricted area available locomotion is most difficult because the mite, in order to accommodate its body, must spread apart the walls of the supra-branchial chamber. To do this, the legs must be very short and powerful. The musculature of the legs and palps, although identical in pattern with that of *Unionicola* (Table III), is heavier and appears much stronger. The very short legs are essential adaptations for activity in the mussel, but they are useless in any other situation.

Dorsoventral muscles are narrow (Fig. 4, Table V). Muscles I and III

TABLE V

The Dorsoventral Muscles of *Najadicola ingens* (Koenike)
According to Function, Origin, and Insertion (see Figure 4B)

Number	Origin	Insertion
I	Dorsal extension, anteromesal angle, coxa I	Center of dorsal body wall
III	Dorsal extension, posterior margin, coxa II	Center of dorsal body wall
IV	Posterior margin, coxa II	Body wall, dorsal to coxa III
V	Posterior margin, coxa III	Body wall, dorsal to coxa IV
VI	Body wall dorsal to coxa IV	Center of dorsum
"A"	Venter, posterior to genital field	Center of dorsum
"B"	Lateral body wall, posterior to coxae IV	Lateral body wall, posterior to coxa IV
Capitulum Muscles	Base of the capitulum Dorsolateral margin, capitulum	Center of dorsal body wall Center of dorsal body wall

and the two extrinsic muscles of the capitulum insert together at an undifferentiated region of the dorsum. The dorsal sclerites are absent. Dorsoventral muscles II and VII are absent. The other muscles are as in *Unionicola*.

Two additional sets of dorsoventral muscles are present. These may function to support the expansive posterior part of the body. The dorsoventral muscles which are homologous with those of *Unionicola* are crowded anteriorly. A series of six to eight poorly defined muscles are situated in a median row posterior to the gonopore and extend dorsally between the paired posterior lobes of the mid-gut to insert on the dorsum. These are called dorsoventral muscles "A." The second pair, designated "B," are muscles attached in the posterior third of the lateral body wall and have a transverse orientation.

The transverse coxal ligament is very short, with extremely long supportive muscles at either end. Although much longer, the supportive muscles do not differ from those of *Unionicola* in origin and insertion.

The genital field in the female of *Najadicola* (Fig. 4B) is not modified from the typical unionicolid form. On either side of the gonopore is an elongate, lightly sclerotized plate bearing many genital acetabula. This structure, an immovable thickening of the body wall, is homologous with the genital plates of *Unionicola* which, in the females, are movable and are modified for oviposition in mussel tissue. *Najadicola* merely deposits masses of eggs loosely between the gill lamellae. Of the water mites parasitic on mollusks *Najadicola* is the only one in which the genital plates of the female are unmodified. A further contrast is noted in the firm gelatinous matrix in which *Najadicola* eggs are imbedded. No covering is present in those of *Unionicola*.

The membranous lips of the gonopore are between the genital plates. Genital plate muscle I inserts on the margin of the lips of the gonopore

(Fig. 4B) and is divided into two bands, one inserting just anterior to the genital plate and one just posterior. Genital plate muscle II is absent, and this seems to confirm its function as a retractor of the genital plates in *Unionicola*.

Internal organs of *Najadicola* and *Unionicola* are very similar (Figs. 2A, 4A), but in cytology *Najadicola* is a most exceptional mite. Cells of the oral glands are of several types and very large, with those of the reniform glands nearly .5 mm. in length. The large, clear, well-defined mid-gut cells are quite unlike the irregular, indistinct, granule-filled cells in *Unionicola*.

Oral glands of *Najadicola* are similar in location and general form to those of *Unionicola*, but in size and cytology there are many differences (Fig. 4A). The two pairs of reniform glands are so close together that they appear to be a single structure. Regions can be distinguished cytologically and components of a fused gland may be identified. Anteroventrad there is a mass of attenuated granular cells that stain densely at the base and have an area of secretory accumulations at their tips. These cells reach a length of 500μ , with a base 200μ in diameter. Nuclei of the cells are over 25μ in diameter and are filled with coarse chromatin granules, but lack a distinguishable nucleolus.

The remainder of the gland is made up of lightly staining, irregularly shaped, vacuole-filled cells up to 200μ in diameter. Nuclei of the cells exceed 30μ in diameter and are filled with fine chromatin granules. In some preparations a nucleolus 8μ in diameter is present. The absence of this structure in some cases is probably an artifact. Each group of cells centers around a lumen into which the secretions of the cells are released. The ducts from these two glandular regions join to form a common duct that leads through a tortuous course to the preoral cavity.

The convoluted tubular glands are much longer than those of *Unionicola* but show only two parts, the glandular tube and the duct. A simple tube about 50μ in diameter is formed by a single layer of undifferentiated cells with distinct nuclei about 5μ in diameter. There is a distinct nucleus containing several coarse granules of chromatin. A fine thin-walled duct leads anteriorly from the gland and joins the duct of the reniform glands just behind the opening of the duct into the postoral cavity.

In *Najadicola* the tracheal gland is a large, saclike median structure with walls of simple, lightly staining, cuboidal cells about 20μ in height. The nucleus, 1μ in diameter, contains only a distinct nucleolus. The gland is situated just behind and dorsal to the base of the chelicera and opens into the postoral cavity. The opening of the gland appears only in sagittal sections.

Tracheae are present as thin-walled tubes of uniform diameter and are distributed throughout the body. Spiral thickenings are not apparent in the walls of the tracheae and branching is uncommon. The ends of the tracheae appear to be attached to the sigmoid piece as in other mites, but there is no chamber in the sigmoid piece with which the tracheae communicate.

The many-branched excretory organ extends throughout the body and empties through an excretory pore, which is opened by means of a pair of muscles that extend laterally from its lips to the body wall. The dendritic form of the excretory organ in *Najadicola* is in marked contrast to the trilobate structure in *Unionicola*. This form merely represents the modification

necessary to provide the body of *Najadicola* with adequate excretory tissue. The body volume of *Najadicola* is about fifteen times that of *Unionicola*.

Najadicola and *Unionicola* differ slightly in the shape of the excretory organ, the oral glands, minor features of the musculature, and the genital field. Although none of the differences is particularly striking, the distinction of the subfamily Najadicolinae is supported, but not enough is known of the anatomy of the family to suggest phyletic relationships.

Discussion of the Anatomy of the Unionicolidae

The anatomy of the Unionicolidae is simpler than that reported for any other water mite (Thor, 1904; Vitzthum, 1940-43). Several features appear common to the family and might well be of importance in its evaluation and redefinition. Two constant exoskeletal features are found: an elongate projection of coxal group 1 on which the elevators of legs I and II originate, and the posterior projection of coxa IV on which a depressor of leg IV originates. Internally the simple five-lobed mid-gut, the absence of accessory genital glands, and the presence of only five paired oral glands are distinctive features of all unionicolids considered in this study.

None of the parasitic forms shows any modification in internal organs that might be related to its habits. Food and feeding mechanisms need not be different in parasitic and predatory unionicolids because neither group is distinguished by special feeding habits. Like many ectoparasites, the prominent adaptations of the Unionicolinae and the Najadicolinae lie in the locomotor mechanism. Modifications in the locomotor apparatus are most obvious; but in considering them it is essential to eliminate consideration of secondary sexual modifications in the legs of the male, the function of which is unknown.

Anatomical modifications that accompany the shift from a swimming to a highly modified crawling form are very clear in the family Hydryphantidae. It is instructive to contrast the adaptive structural modifications of the hydryphantids with those of the unionicolids. The locomotor apparatus is similar in swimming and walking forms of the family Hydryphantidae except for the shortened legs of the latter. Crawling forms living in water-margin habitats are pressed to the substrate by the surface film, and certain modifications make the leg action more effective. These are: rotation of the plane of movement of legs I and II, disproportionate development of certain coxal muscles, and changes in the size, shape, and chaetotaxy of the leg segments.

Most Unionicolidae are swimming forms with long legs, a feature of all free-living members of *Unionicola*. Parasitic species of *Unionicola* tend to have shorter legs and are weak erratic swimmers. Nonswimming forms of *Unionicola* do not show any of the changes in articulation and musculature noted in crawling members of other families. In various species of *Unionicola* the musculature of the shorter nonsetigerous legs is similar to that of swimming forms, just as was observed in the Hydryphantidae. The remarkably disproportionate development of the elevators of legs I-III, a characteristic of the Unionicolidae, seems to be related to some swimming function

(Fig. 5). None of the nonswimming forms of *Unionicola* shows any modification from this pattern, but in *Najadicola*, the most modified nonswimmer of the family, the size of the elevators is greatly reduced. Opposing groups of muscles of legs I-III are nearly balanced in size and shape.

Structure of the genital field is constant in all members of the family except the three genera of Unionicolinae parasitic on mollusks: *Unionicola*, *Polyatacides*, and *Atacella*. Females of these genera have modified genital plates which function in depositing eggs in the tissue of the host. *Najadicola*, which does not deposit eggs in the host tissue, has no modification of the genital field.

LIFE HISTORY

Published information on the life history of water mites is very limited, and there is only one accurate account for a species of *Unionicola* (Uchida and Imamura, 1940). Even host associations are rarely mentioned. An examination of the Wolcott collection at the Chicago Natural History Museum shows that the material recorded in the most important monograph of the genus (Wolcott, 1899) was not carefully separated as to host and locality. Because of this failing the host associations reported by Wolcott are considered unreliable.

The intramolluscan stages of four species of *Unionicola* that parasitize *Lampsilis siliquoidea* (Barnes) are considered together with their behavior and their effect on the host. These species plus *Najadicola ingens* make up the normal mite fauna of this mussel in the vicinity of Ann Arbor, Michigan. The rarity of *Najadicola* made it impossible to obtain accurate life history information. Periodic collections were made from Bass Lake, four miles east of Pinckney, Livingston County, and Four Mile Lake, two miles east of Chelsea, Washtenaw County, during 1952 and 1953. The results obtained at those localities were checked with numerous irregular collections from the following stations: Washtenaw County — Base Line Lake, five miles north of Dexter; Portage Lake, five miles north of Dexter; South Lake, five miles north of Chelsea; Bruin Lake, six and one-half miles north of Chelsea; Livingston County — Zukey Lake, Lakeland.

Fresh-water mussels have never been reared successfully in the laboratory, although they may be maintained for a few months under conditions approximating those in the field. Furthermore, the host is killed in any examination for parasites. With such limitations experimental rearing of *Unionicola* is not feasible, and life history information must be obtained through periodic field collections.

Several factors make field data of limited value. At a given locality there was always a constant representation of species, but the numbers of parasites per mussel were always extremely variable. Seasonal occurrence was difficult to define because the adults of one generation may live until the adults of the succeeding generation first appear. The following life histories may seem to lack precision and detail, but local, seasonal, and individual variation in level of parasitism makes further refinement of little value for this general treatment.

Additional knowledge of life histories may be gained by experiments involving retardation of development at low temperatures and by transplantation. Such an experimental approach, however, could not be planned without the basic life history outline. These studies provide the data needed for the planning of future experimental work.

Identifications of immature and transforming stages were obtained in several ways. Oviposition sites were determined for the various species by one of two approaches: by comparisons of populations in which certain mites are absent in one and present in the other, or by correlating the appearance and decline of gravid females in the population with the appearance of eggs in the mussel. Quiescent stages can be removed from the host tissue and will hatch out in water. The uniform success of this method with all mites parasitic in *Lampsilis* showed that no nutrient was needed during these stages. Nymphs may be identified to species, but larval identifications are, as yet, impossible except through association.

The life history of water mites includes three active stages: (1) the six-legged larva, (2) an eight-legged, sexually immature nymph, and (3) the adult. Each active stage is preceded by a sedentary developmental stage: (1) the egg, (2) the nymphochrysalis (stage of transformation from larva to nymph), and (3) the teleiochrysalis (stage of transformation from nymph to adult). These stages (Fig. 5) appear in the life history of *Unionicola aculeata*.

Normally, the water mite larvae are parasitic, but the function of this stage in ancestral forms is difficult to establish. Variability in the extent of parasitism by various water mites shows this habit to be influenced by many factors other than transportation and nutrition. A parasitic larval stage is typical of water mites in general; in many unrelated groups, however, the larvae are facultative parasites, or the larval stage may even be by-passed in the egg.

Nymphs and adults are usually active predators; there are only two groups that contain exceptions to this habit. The remarkable *Parasitalbia sumatrensis* (Viets), of the family Axonopsidae, is an ectoparasite of an ephemerid as an adult (Viets, 1935). The other exceptions are the four genera of Unionicolidae, many species of which as nymphs and adults are ectoparasites of fresh-water mussels. Parasitism by nymphs and adults is a very obvious exception to the general life history plan of water mites.

Of the four species of *Unionicola* found in *L. siliquoidea*, three — *U. fossulata*, *U. abnormipes*, and *U. serrata* — are resident parasites; the remaining species, *U. aculeata*, is a transient. A resident parasite is one which lives in the mantle cavity of its host throughout one or more of the active stages. In the three species mentioned above both the nymph and adult live in the host. The transient parasite, *U. aculeata*, only enters the host to pass the transforming stages; the active stages are always free-living. Details of life history for each of these parasites are as follows:

Unionicola aculeata (Koenike)

This ubiquitous holarctic form is closely related to a well-developed

assemblage of neotropical species. The various life history studies on this species in Europe (Viets, 1936) agree with the main points established below. *U. aculeata* is a common parasite of *Lampsilis siliquoides*, but is an occupant of the host only during transformation stages, and the extent of its parasitic action is open to question.

Eggs of *U. aculeata* are usually deposited in the incurrent siphon (Figs. 5, 6E) or rarely in the adjacent mantle. Clusters of 25 to 30 eggs are laid in the loose connective tissue just below the surface epithelium. Oviposition begins in the middle of August and continues through the fall. By the end of November the entire inner wall of the incurrent siphon is filled with eggs. Embryonic development is completed before winter. A few weeks after the mussel resumes activity in the spring the larvae hatch and immediately leave the host.

Early in the summer the larvae re-enter the mussel and work into the tissue lining the water tubes of the gills to form the nymphochrysalis. In sectioned material the larvae are seen to lie just below the epithelium, forming projections on the surface of the tissue (Fig. 6C). These transforming larvae are not perceptibly larger than the newly hatched ones, a condition which indicates that there is no extensive feeding prior to transformation. Nymphochrysalises are most abundant in the posterior part of the outer gill. This region is closest to the walls of the excurrent siphon; consequently, it appears that the larvae probably invade a host via the excurrent siphon. Five to 20 transforming larvae may be found in a mussel at nearly any time of the year. At peak abundance, during the early summer months, 25 to 100 are found in each host.

On emergence the nymph leaves the mussel and lives as a free-swimming form in open waters. It is presumed that the nymphs are predatory. Following a period of active life, the nymph enters a host via the excurrent siphon and may imbed itself there or in the gills to form the teleiochrysalis (Figs. 5, 6B). Maximum abundance of teleiochrysalises, 15 to 30 per mussel, occurs from late July through September. The teleiochrysalis lies rather deep in the tissue of the excurrent siphon (Fig. 6B).

Adults of *U. aculeata* leave the host immediately on emergence. The only records for collections of adults were from still, open waters. This species represents one of the few planktonic mites and presumably is predatory.

Unionicola aculeata is of particular interest because it shows a pattern of development that may have existed at an early stage in the development of parasitism in *Unionicola*. This animal may use its host only as a protected place to spend quiescent periods, although the possibility that the mite feeds on the mussel has not been excluded. The uniform success with nearly complete emergence of such stages when removed from the host and placed in water is evidence that the feeding, if it occurs, is not essential. This holarctic mite parasitizes a great variety of mollusks, and its flexible host-parasite relationships indicate the absence of any specific bond between the mite and its hosts.

It appears that *U. aculeata* has no serious effect on the host nor is its own life history greatly modified. As illustrated in Figure 6, none of the stages of the mite imbedded in the mussel causes any noticeable cytological response or pigmentation in the host tissue.

Unionicola abnormipes (Wolcott)

This mite is a common parasite of *Lampsilis siliquoidea*. Nymphs, teleiochrysalises, and often adults can be found imbedded in the tissue of the foot at nearly any time of the year. From 20 to nearly 100 adult mites were found in every specimen of *Lampsilis siliquoidea* collected from Bass Lake during late July and August. The species was absent from Four Mile Lake but was found in all other collections of the host. Faust's observations (1918) refer to *U. abnormipes*, not to *U. aculeatus* as Faust claims. The few observations in that paper agree with the following, but the conclusions are confused because of the erroneous identification.

Eggs are laid irregularly throughout the mantle tissue (Fig. 6D), as well as in the tissue at the base of the foot. They lie in the loose connective tissue just below the epithelium. In some instances a mild hyperplasia develops in the adjacent host tissue. Gravid females are found in the fall and spring. Oviposition begins in late August and continues through the fall and into the spring. Eggs deposited during the fall undergo complete embryonic development but do not hatch until spring. Throughout May and during the first two weeks of June larvae emerge from mussels that are brought into the laboratory and placed in aquaria. By the first week of July only a few old or undeveloped eggs are left in the mantle or foot.

Nymphs appear in the host in late June and are found crawling about in the mussel until late summer. Nymphs usually burrow into the tissue at the base of the foot (Fig. 6A), rarely into the tissue of the mantle, to form the teleiochrysalis. The adults, after leaving the teleiochrysalis stage, remain inactive in the mussel tissue for an undetermined length of time. A period of activity follows, during which they are found moving about freely on the base of the foot. Specimens may be found on the gills and mantle, but generally a higher proportion of individuals frequents the foot.

Only adults of *U. abnormipes* are present in early spring, and at this time they are never buried in the tissue of the foot. From early June until late fall transforming nymphs and inactive adults are present.

Some differences were found between specimens of *L. siliquoidea* from Bass Lake and those from Four Mile Lake (where *U. abnormipes* was absent). Mature mussels from Bass Lake were twice the size of those from Four Mile Lake. The mantle of Bass Lake specimens had a deep, mottled, yellowish deposition of pigment, and the tissue at the base of the foot was soft and rather loose. On the other hand, specimens from Four Mile Lake had no marked mantle pigmentation, and the tissue at the base of the foot was firm. Whether the difference in size, mantle pigmentation, and tissue firmness has any bearing on the presence of the mite is uncertain.

Unionicola fossulata (Wolcott)

All individuals of *L. siliquoidea* examined contained this species, but there were usually fewer than ten specimens to a mussel. *U. fossulata* was the only resident parasite of *L. siliquoidea* in Four Mile Lake.

Eggs are laid only along the outer margin of the outer gill. The long

axis of the egg is usually at right angles to the gill edge, and the head of the larva is most often pointed toward the gill edge. Usually, the eggs are so abundant that they rest side by side for the full length of both outer gills. In female mussels, in which the posterior part of the outer gill is used as a marsupium, no eggs are deposited in that region. Eggs first appear in early spring, and oviposition continues through the early part of June. By late June most of the mussels are free of eggs.

The larvae leave the mussel, and the next stage found in the mussel is the nymph, which is commonest in August. Nymphs crawl about on the surface of the gills or in the water tubes. A teleiochrysalis is formed in the gill. When the adults emerge, they are found crawling about on the surface of the gills. Adults become abundant in late July or August. The females are gravid in the fall, but do not lay eggs until the following spring.

Unionicola serrata (Wolcott)

This is the rarest *Unionicola* in *L. siliquoides*. The incidence of parasitism by this mite is as great as in the other species. It was recorded from all but one of the localities, but there were never more than ten adults to a mussel and usually fewer than five.

The first life history stage identified in the mussel is the nymph, which is found in the host from August to early November. Sometime during the fall the nymph attaches itself with its mouth parts to the epithelium of the mantle or the base of the foot. There it forms the teleiochrysalis, which is usually in a cuplike depression of the epithelium.

Most of the nymphs and adults of *U. serrata* are on the labial palps, though a few are on the epithelium of the base of the foot. No other species of *Unionicola* was ever found on the labial palps.

TABLE VI

Location and the Period of Abundance of the Active Stages of the *Unionicola* Parasitizing *Lampsilis siliquoides* (Barnes)

Species	Larva	Nymph	Adult
<i>Unionicola abnormipes</i>	Free living May through June	Base of the foot, rarely on the mantle June to September	Base of the foot, rarely on the mantle September through May
<i>Unionicola aculeata</i>	Free living May through June	Free living June to September	Free living June to October
<i>Unionicola fossulata</i>	Free living June through July	Gills August	Gills August through June
<i>Unionicola serrata</i>	Free living Unknown	Labial palps August through June	Labial palps September through June

Parasites of *Lampsilis siliquoidea* (Barnes)

The normal fauna of parasitic mites in *Lampsilis siliquoidea* in this region consists of *Najadicola ingens* and four species of *Unionicola*. At six of the collecting stations in the vicinity of Ann Arbor all four species of *Unionicola* were recovered from nearly every host examined. At only one locality, Four Mile Lake, was there an unexplained absence of *U. abnormipes* and *U. serrata*. *Najadicola* was too rare to permit any reliable estimate of its occurrence.

Comparisons of the life histories of these parasites in *Lampsilis siliquoidea* show no great amount of competition among any of the four mite species either as to the area occupied by the parasite or with regard to the time of the life history stages (Table VI). Adults and nymphs of the resident parasites generally remain concentrated in particular regions of the mantle cavity of the host mussel: *U. abnormipes* on the mantle or base of the foot, *U. fossulata* on the gills, and *U. serrata* on the labial palps. As the level of parasitism increases, so does the restriction of mites with respect to regional distribution. This breakdown of territory at low levels of parasitism was observed in *U. serrata* more than in any of the other species.

A similar specialization was shown in the host tissues occupied by the mites during the transformation stages (Table VII). There is very little overlapping and competition for a place for transformation among the four species. It should be noted that in addition to these marked seasonal and behavioral differences, the four species of *Unionicola* that parasitize *L. siliquoidea* are sufficiently dissimilar in structure to be assigned to different subgenera.

TABLE VII

Location and Seasonal Abundance of the Quiescent Stages of
Unionicola Spent Within *Lampsilis siliquoidea* (Barnes)

Species	Egg	Nymphochrysalis	Teleiochrysalis
<i>Unionicola abnormipes</i>	Imbedded in the tissue at the base of the foot, rarely in the mantle August through May	Same location as the egg June to November	Same location as the egg June to November
<i>Unionicola aculeata</i>	In the connective tissue of the incurrent siphon August through May	In the walls of the water tubes of the gills June to September	In the walls of the water tubes of the gills or the excurrent siphon July to October
<i>Unionicola fossulata</i>	In the tissue at the margin of the outer gill June	Unknown	In the walls of the water tubes of the gills July through September
<i>Unionicola serrata</i>	Unknown	Unknown	Attached to the mantle or the base of the foot July through September

EVOLUTION OF PARASITISM IN THE UNIONICOLINAE

Certain facts from the previous discussion of anatomy and life history indicate the nature of the ancestral stock of the Unionicolinae. With assumptions based on these facts it is possible to propose a plausible explanation of the evolution of parasitism in the family. The assumptions concerning the ancestral stock of the Unionicolinae and the supporting evidence are as follows:

1. Parasitism as exhibited in the Unionicolinae is unrelated to, and fundamentally different from, that of other water mites.

In contrast to the general pattern found in all major groups of water mites, the Unionicolinae are parasites as nymphs and adults. In related mites only the larva is parasitic. Feeding and parasitism are suppressed in the larvae of Unionicolinae, but such modifications are common among other mites. These facts suggest that the parasitism by nymphs and adults of Unionicolinae was not persistence of the larval habit through later ontogeny. Feeding habits of the adults and nymphs are quite different from those of other water mite larvae. Individuals of *Unionicola* are active ectoparasites, and feeding is not limited to a prolonged engorgement at one site as in all other known parasitic larvae.

Not only does the parasitic stage and the behavior of the Unionicolinae contrast with those of other water mites but also the hosts attacked are quite different. Unionicolinae attack mollusks and sponges, animals that are, in general form and habits, vastly different from the insects parasitized by all other water mites.

2. Members of the ancestral stock oviposited in animal tissue.

In the previous section on anatomy the function of the genital structures of female *Unionicola* was discussed. Highly modified genital plates bear a musculature which is radically different from that of any other species of Unionicolidae. This structure was shown to be an adaptation for oviposition in animal tissues, particularly the soft epithelium found in sponges and mollusks. Since this structure is common to all members of the subfamily, it seems safe to assume that the family was derived from a stock which oviposited in animal tissue.

3. The ancestral Unionicolinae fed on plankton during the nymph and adult stages.

The evidence supporting this assumption is based on the habits of the primitive members of the genus *Unionicola*. These forms, with *U. crassipes* and *U. aculeata* as well-known examples, are planktonic animals that live free of the host as nymphs and adults. In all known cases water mites are predatory, hence these forms are thought to feed on zooplankton.

4. The host originally served as a protected site for the mite during the transformation stages.

As has been pointed out, certain species of *Unionicola* live free of the host as nymphs and adults. In these forms only the transformation stages are spent buried in the tissue of the host. Protection is obtained in this way, and if any feeding occurs it is limited to the time when the mite is burrowing into the host.

The following account of the steps in the evolution of parasitism in

Unionicolinae is proposed as logical and consistent with the current knowledge of the group and is based on the assumptions and data discussed above. The listing is not necessarily sequential. It is the most satisfactory sequence I can suggest, although others are possible.

Unionicola crassipes and *U. aculeata* are thought to be very similar to the ancestral form in behavior and structure and illustrate the initial step in parasitism, which is the use of a host as a protected place for oviposition. The nymphochrysalis and the teleiochrysalis of the ancestral form may have been passed in the host, or this association may have developed later. At any rate, these species do spend all transforming stages in the host and seem to illustrate one of the earliest stages in the development of parasitism. The only demonstrable function of the host is to provide protection during the quiescent stages.

Any plankton feeder resident in the filter chamber of a filter-feeding animal would be provided with an abundance of food. It is consistent with the data at hand to conclude that parasitism in the Unionicolinae developed through just such a step. After transformation the active stages did not leave the mussel in which they transformed. Instead, they remained within the mussel and fed either on plankton collected by the host or on host tissue. As previously discussed, adults and nymphs of the genus *Unionicola* show a progressive modification to the sedentary life of a parasite, whereas the larvae remain free living and are the means of distribution. Parasitism, then, may have developed as an extension of an adaptation originally established to obtain protection.

The differentiation of a line of parasites may be interpreted through comparative morphology, host specificity, and behavioral modifications. A refined analysis of group differentiation in the Unionicolinae is, as yet, impossible, but certain general indications are worthy of note.

Studies of the systematics of hosts and parasites may sometimes give evidence concerning the relative ages of the groups. It is well established that the parasites of many vertebrates have been associated with their host over a long period of time. As a consequence, parasites of a group limited to hosts of one phyletic line are usually closely related to each other. In these instances one may conclude that the host and the parasites evolved together.

Such is probably not true in *Unionicola*. Although host distribution is not well known in *Unionicola*, the allied *Najadicola ingens* parasitizes mussels belonging to different subfamilies: *Elliptio complanatus* (Dillwyn) (Unioninae), *Anodonta cataracta* Say (Anodontinae), and *Lampsilis radiata* (Gmelin) (Lampsilinae) (Humes and Jamnback, 1950). Although *Elliptio complanatus* was found to be heavily parasitized, the closely related *Elliptio dilatatus* was not parasitized even in waters where *Najadicola* occurs. Similar unexplainable host specificities are common in *Unionicola* also, indicating that there has been no long-term, host-parasite relationship. Adaptation and host selection are both based on biological features that are not necessarily phyletic, and in the Unionicolinae host specificity seems to have developed only after the host species differentiated.

Parasites of mussels do not indicate degrees of relationship in the hosts, although species of mussels may be distinguished on the basis of their parasite fauna. It is clear that when different species or groups of mussels show

consistent differences in their parasites, some biological difference exists between the hosts, which is the basis for host selection. Actually, there are a few situations where such information has proved of value in understanding host relationships. As an example, there has been a dispute for over forty years as to the species of *Anodonta* in Europe, based on a difference of opinion regarding the importance of certain characters. Recent statements of the problem are those of Bloomer (1938), who gives a division into two species, and of Haas (1940), who recognizes but one species. Studies of the parasites of *Anodonta* (Mitchell and Pitchford, 1953) appear to have established that the British representatives of *Anodonta* are members of two species. Records of the parasites from 238 specimens of *Anodonta* collected from nine localities in central England were as follows:

Parasites	Hosts	
	<i>Anodonta cygnea</i>	<i>Anodonta anatina</i>
<i>Unionicola ypsilophora</i>	356	0
<i>Unionicola intermedia</i>	4	712

These data are of limited value, but they do illustrate what can be contributed to a knowledge of the hosts by studying their parasites and, moreover, reveal the necessity of recording frequency of parasitism and abundance of parasites.

Specialization in behavior among the species of *Unionicola* is well established in the preceding life history section on the four species parasitic on *Lampsilis siliquoides*. Together the four species reside in the mussel during fourteen life history stages, none of which overlaps in spatiotemporal occurrence. Among the observations now available there is no example in which closely related species occur in the same host. Members of the parasitic fauna of a given mussel appear to be distantly related systematically and to differ markedly in behavior.

SUMMARY

1. The structure of those unionicolids that are parasitic on mussels is relatively unmodified as compared to that of related free-living forms.
2. There are two structural adaptations to parasitism: reduction in leg length and chaetotaxy; and, in the Unionicolinae, development of specialized genital structures for oviposition in animal tissue.
3. Two types of parasitism are found in the Unionicolinae: transient parasitism during transformation stages, and resident parasitism during transformation stages and as adults and nymphs.
4. *Lampsilis siliquoides* supports a parasitic fauna of four species of *Unionicola*. Altogether these spend fourteen different life history stages in the host, all of which are spatiotemporally separated.

5. Proceeding from assumptions based on the facts of anatomy and life history of Unionicolinae, it is suggested that the steps in the evolution of parasitism were as follows: (a) loss, at some time, of all parasitic traits normally exhibited by water-mite larvae; (b) association with the host during transformation stages for protection; (c) development of a tendency of the adults and nymphs to remain in the host and feed on plankton collected by it; (d) adaptation to a sedentary parasitic life within the filter chamber of the host.

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FIGURES 1-6

- Fig. 1. General external anatomy of *Unionicola fossulata* (Koenike).
- A. Ventral aspect, female, palps removed. x 45.
 - B. Dorsal aspect. x 45.
 - C. Genital field, male. x 85.
 - D. Musculature, leg I, anterior aspect, left leg. x 80.
 - E. Musculature, leg IV, anterior aspect, left leg. x 80.

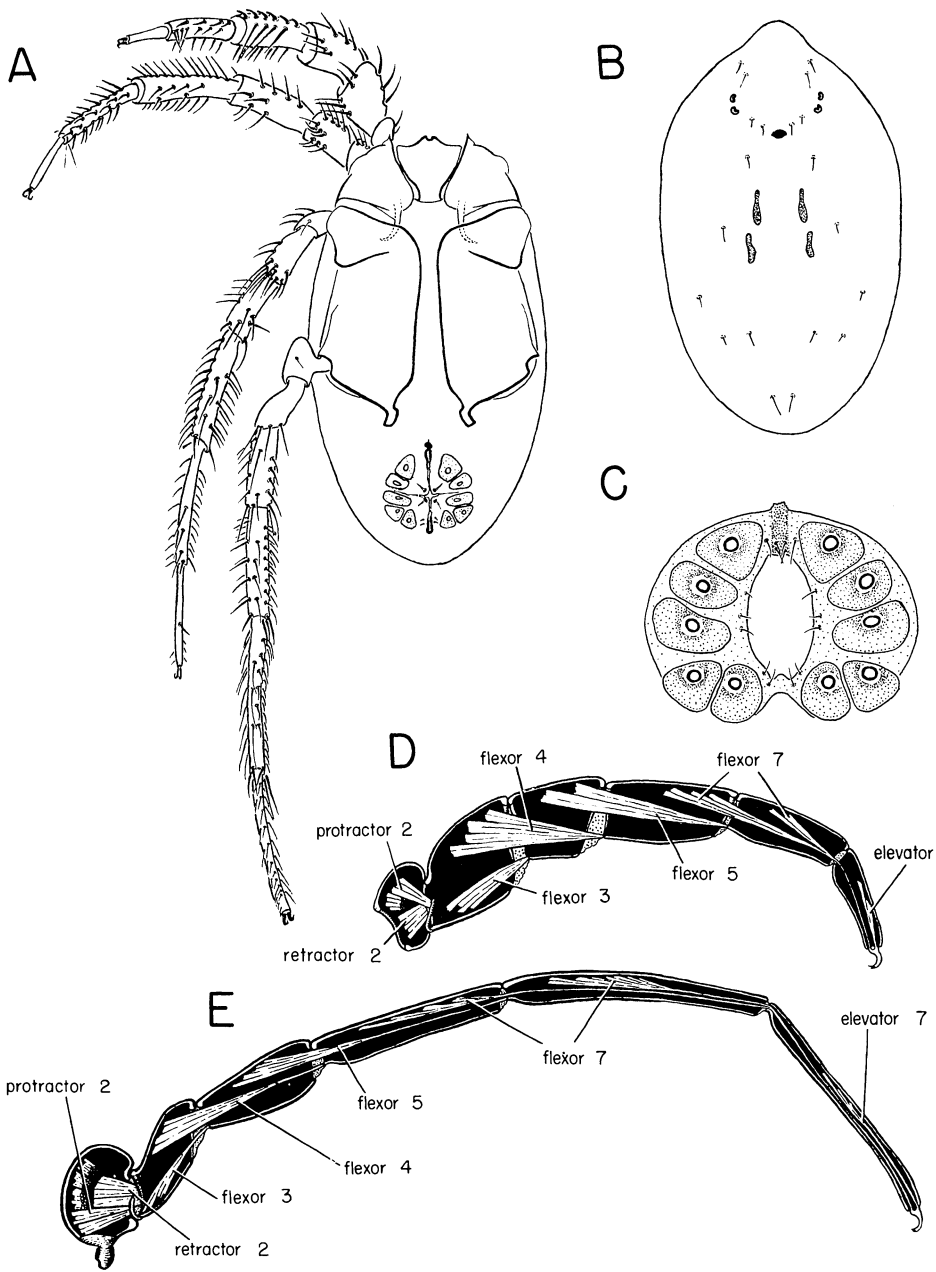


Fig. 1

- Fig. 2. Internal anatomy of *Unionicola fossulata* (Koenike).
- A. Diagrammatic representation of the internal organs (exclusive of the musculature) in a lateral view. x 40.
 - B. Feeding organs and their musculature. x 180.
 - C. Dorsal aspect showing position of the organs in the intact animal. x 45.
 - D. Ventral aspect showing location of the organs in the intact animal. x 45.

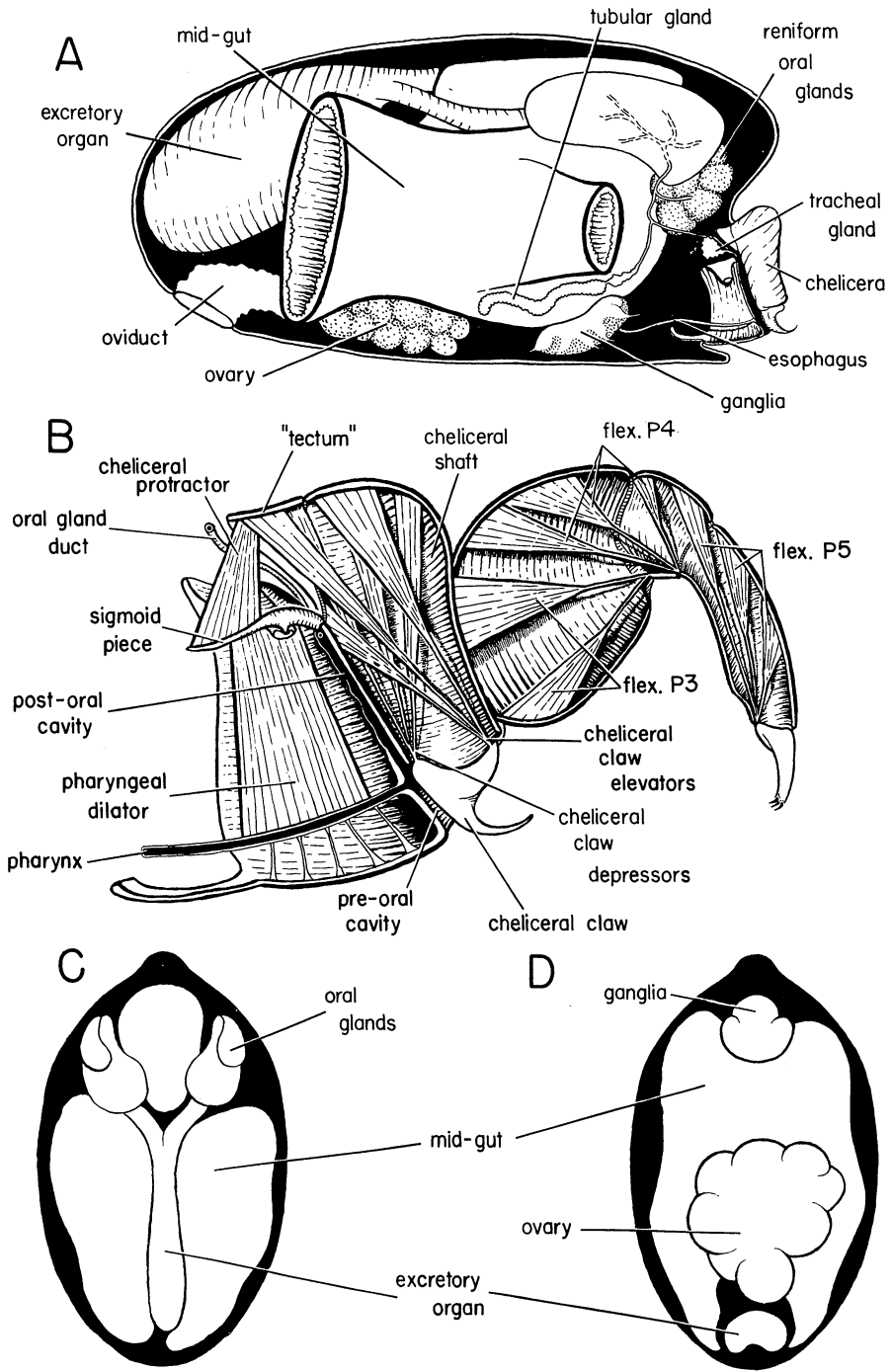


Fig. 2

Fig. 3. Dorsal aspect of the coxae, genital sclerites, and associated musculature of a female of *Unionicola fossulata* (Koenike). The full complement of muscles is shown on the left side of the drawing, and the deep muscles, after the removal of the superficial layer of muscles, on the right side. Tables I and II list all the muscles as to insertion, origin, and function. Legs and their musculature are designated by Roman numerals, starting anteriorly. Numbering of the dorsoventral muscles is given in Table II and is discussed in the text.

Abbreviations

elev.	Elevator muscle of leg segment 1.
depr.	Depressor muscle of leg segment 1.
dors.-vent.	Dorsoventral muscle.

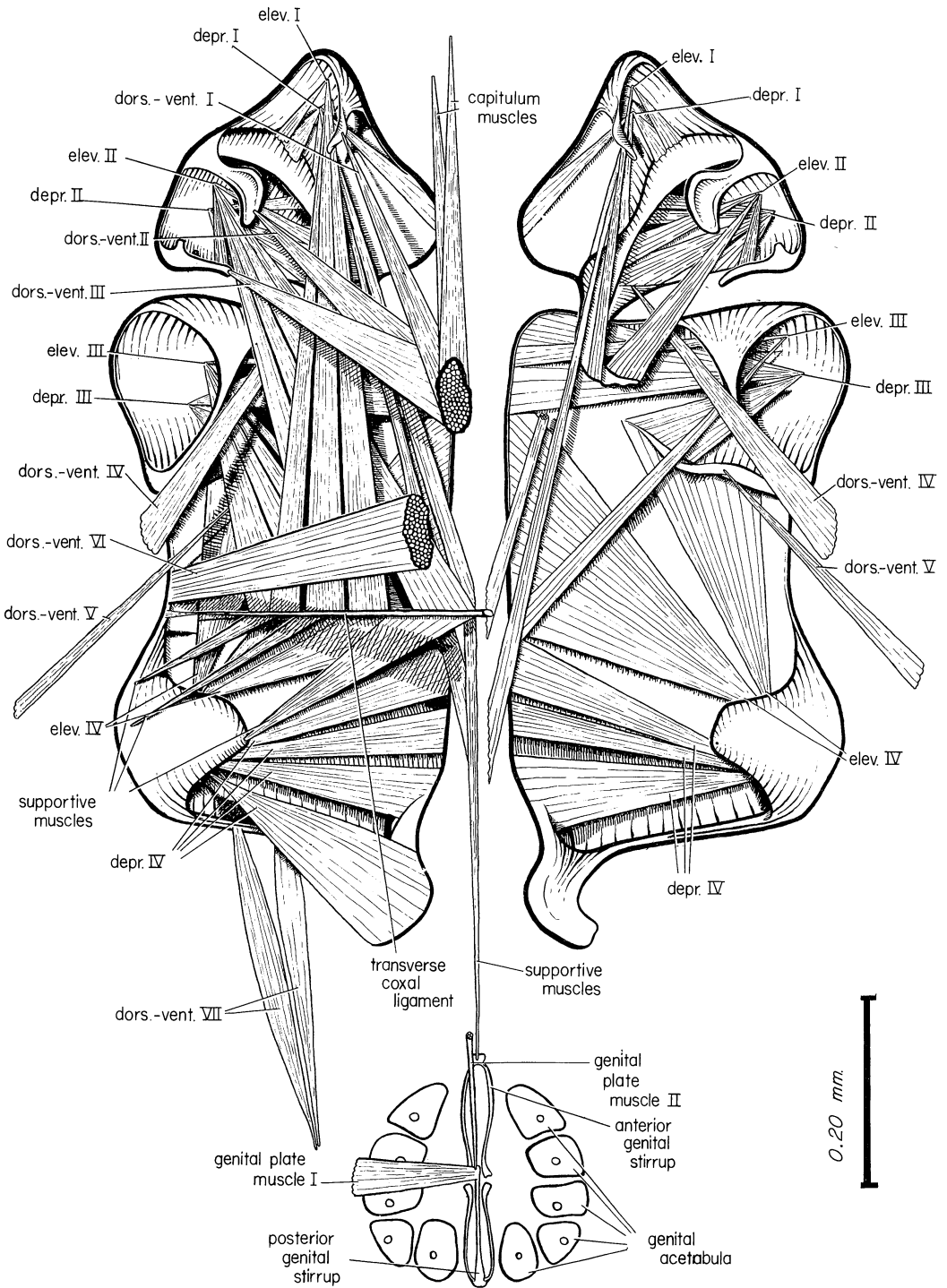


Fig. 3

- Fig. 4. Anatomy of *Najadicola ingens* (Koenike).
- A. Diagrammatic representation of the internal organs exclusive of the musculature. x 144.
 - B. Dorsal aspect of the coxae, genital sclerites, and associated musculature. The full complement of muscles is shown on the left side of the drawing and the deep muscles, after removal of the superficial layer of muscles, on the right side. Tables IV and V list all the muscles as to insertion, origin, and function. Legs and their musculature are designated by Roman numerals, starting anteriorly. Numbering of the dorsoventral muscles is given in Table V and is discussed in the text. x 360.

Abbreviations

- | | |
|-------------|-------------------------------------|
| elev. | Elevator muscle of leg segment 1. |
| depr. | Depressor muscles of leg segment 1. |
| dors.-vent. | Dorsoventral muscle. |

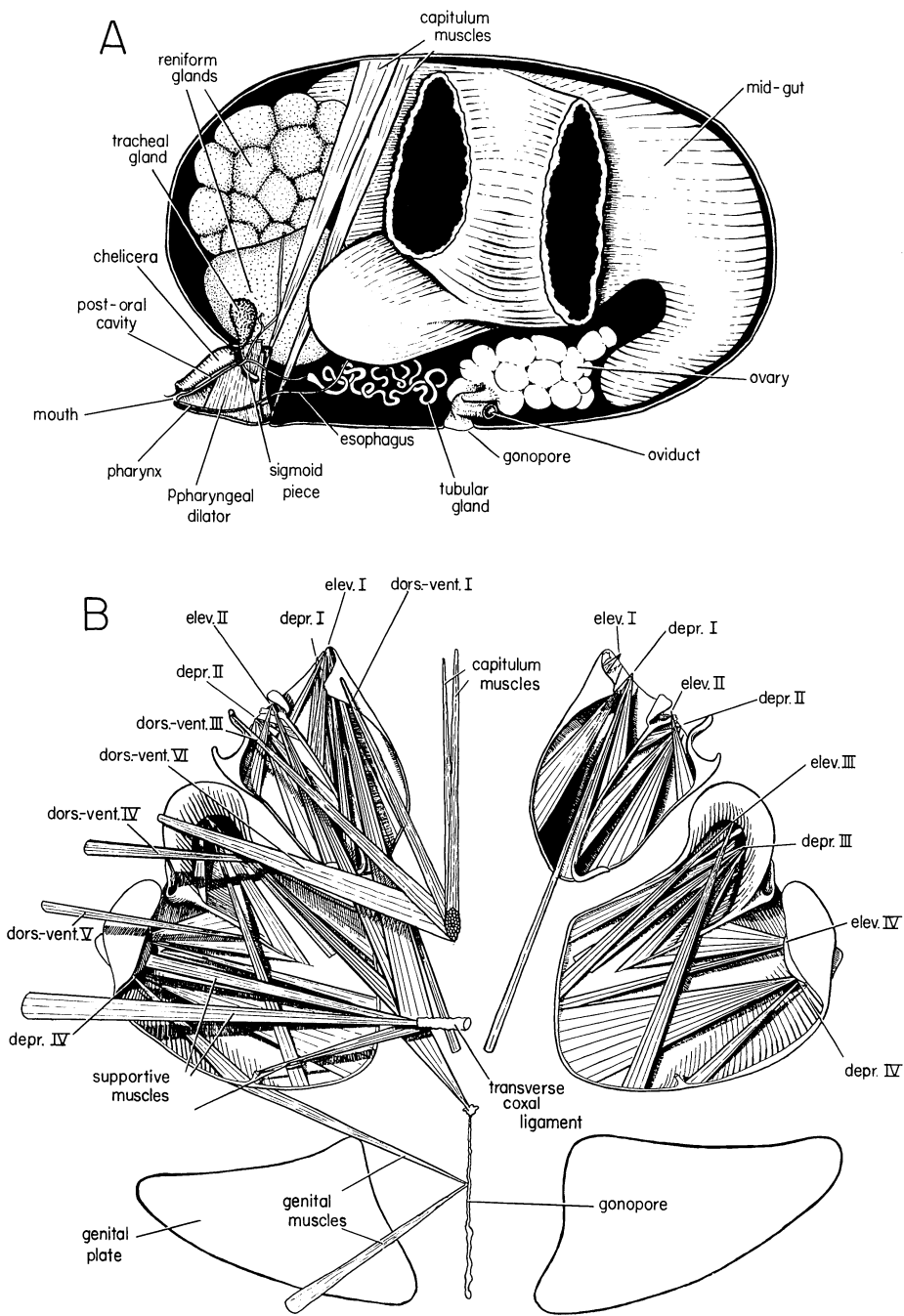


Fig. 4

- Fig. 5. Life history of *Unionicola aculeata* (Koenike) in *Lampsilis siliquidea* (Barnes). Sequence of the six life history stages is indicated by arrows. The three active stages, all of which live outside of the host, all illustrated by drawings of the ventral aspect. Locations of the quiescent stages, indicated in the sketch of *L. siliquidea*, are as follows: eggs in the incurrent siphon, nymphochrysalis in the gills, teleiochrysalis in the excurrent siphon or the incurrent siphon gill. Adult and nymph x 50.
Larva x 100.

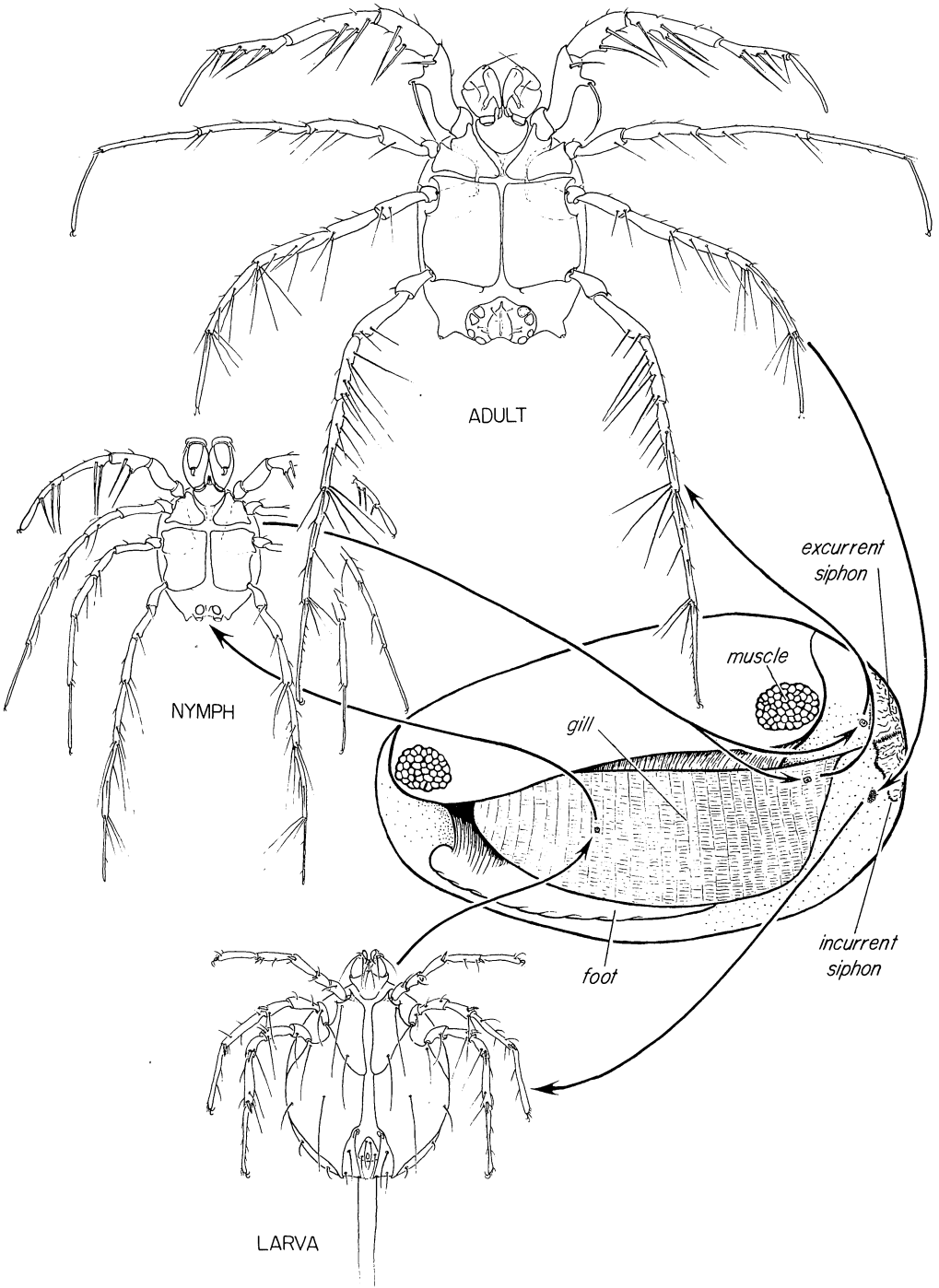


Fig. 5

- Fig. 6. Sections of mussel tissue of *Lampsilis siliquidea* showing location in the host of certain transforming stages of the mites parasitizing this unionid.
- A. Base of foot. Teleiochrysalis of *Unionicola abnormipes*.
 - B. Mantle tissue, excurrent siphon. Teleiochrysalis of *Unionicola aculeata*.
 - C. Cross section of the gill. Nymphochrysalis of *Unionicola aculeata*.
 - D. Mantle tissue. Eggs of *Unionicola abnormipes*.
 - E. Mantle tissue, incurrent siphon. Eggs of *Unionicola aculeata*.

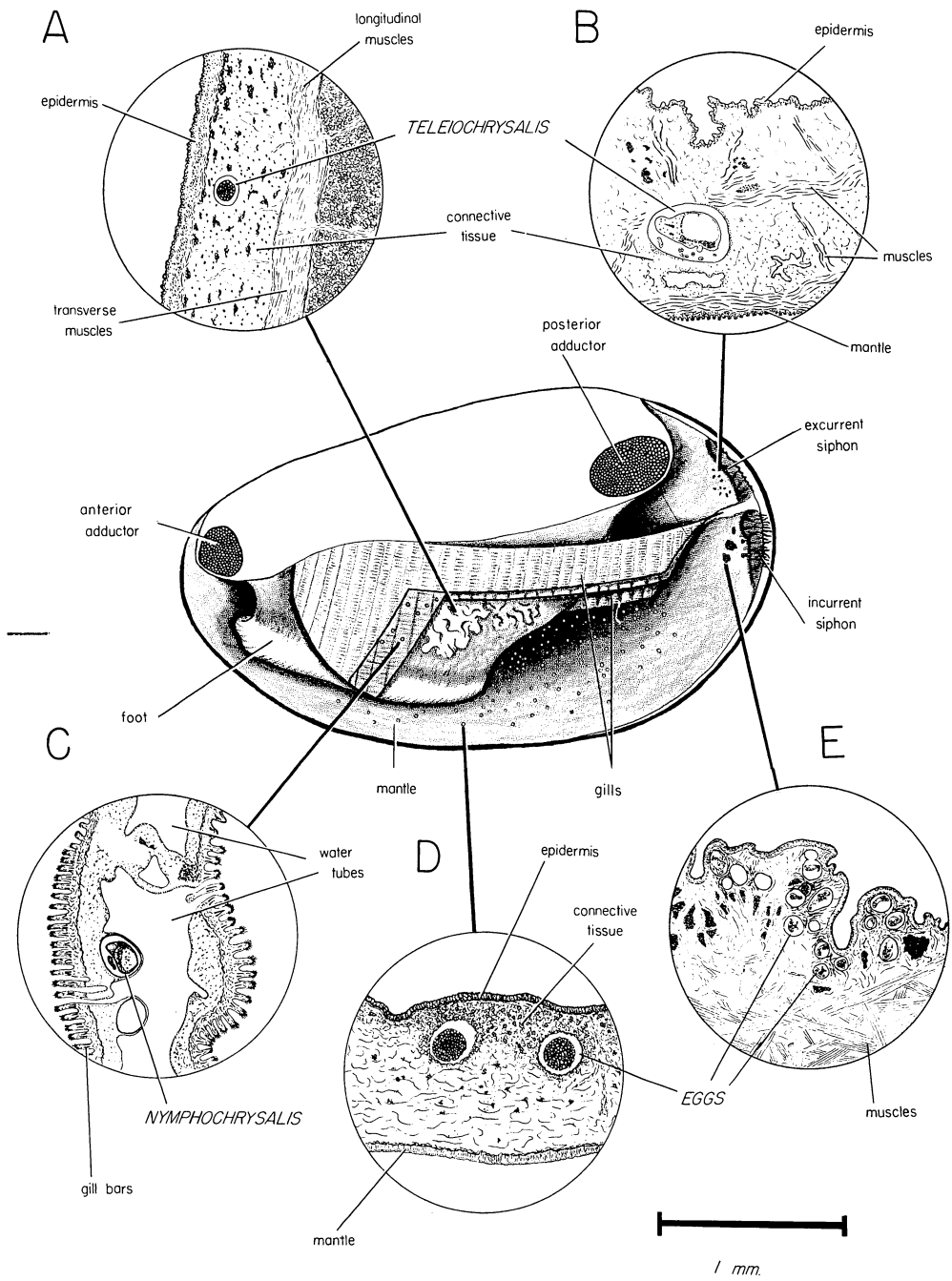


Fig. 6

- No. 30. The Darters of the Genera *Hololepis* and *Villora*. By Carl L. Hubbs and Mott Dwight Cannon. (1935) Pp. 93, 3 plates, 1 figure
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- No. 33. The Discovery of the Nest of the Colima Warbler (*Vermivora crissalis*). By Josselyn Van Tyne. (1936) Pp. 11, colored frontis., 3 plates, 1 map
- No. 34. Mollusca of Petén and North Alta Vera Paz, Guatemala. By Calvin Goodrich and Henry van der Schalie. (1937) Pp. 50, 1 plate, 1 figure, 1 map
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