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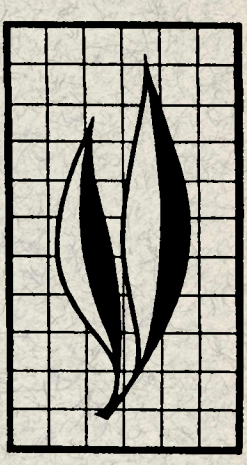
Biology and Immature Stages of *Antichaeta testacea* Melander (Diptera: Sciomyzidae)

T. W. Fisher and R. E. Orth

UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURAL SCIENCES



In the laboratory the terrestrial tetanocerine fly *Antichaeta testacea* Melander completes its life cycle in 35 to 44 days. The female fly oviposits only on the egg clusters of its snail host. Instar I feeds only on snail eggs. Instars II and III also feed extensively on snail eggs besides attacking certain aquatic snails of the families Physidae and Lymnaeidae, but all instars are reluctant to attack adult terrestrial snails in the Succineidae. However, in southern California, because of their distribution, seasonal occurrence, and placement, the eggs of the succineid snails—mainly those of *Oxyloma sillimani* Bland—are considered to be the preferred hosts of ovipositing adults and first-instar larvae of *Antichaeta testacea.*

The female fly can lay 10 eggs daily for more than 50 consecutive days. During its development in the laboratory, a single larva can consume an average of 306 eggs of *Physa virgata* Gould or 113 eggs of *Succinea californiensis* Fischer and Crosse. Pupation occurs in the substrate, and some pupae enter a probable summer diapause, which may persist in certain individuals for more than six months.

Biosystematic criteria which suggest phylogenetic affiliation with the subfamily Sciomyzinae are: reticulate egg chorion; larvae which possess ventral spinule bands; a dorsal bridge which connects the pharyngeal sclerites; a "window" which occurs in the ventral cornua of the cephalopharyngeal skeleton; and the first-instar larvae, which are markedly obligate predators. Characteristics possibly unique among sciomyzid larvae possessed by *Antichaeta* larvae are the pubescent-appearing third-instar larva and adnation of the pharyngeal and hypostomal sclerites in all larval instars.

THE AUTHORS:

T. W. Fisher is Associate Specialist in the Citrus Research Center and Experiment Station, Riverside. R. E. Orth is Senior Laboratory Technician in the Citrus Research Center and in the Experiment Station, Riverside.

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R. E. Orth

Biology and Immature Stages of *Antichaeta testacea* Melander (Diptera: Sciomyzidae)[1, 2]

INTRODUCTION

SINCE THE first accurately reported host relationship of six species of sciomyzid flies with their mollusk hosts (Berg, 1953), there have been six publications offering detailed biological information on eight different species. The authors are: Foote (1959, 1963); Foote, Neff, and Berg (1960); Neff and Berg (1961); Neff and Berg (1962); and Knutson and Berg (1963). The illustrations and descriptions of immature stages in this paper are presented in a manner similar to that of the aforementioned authors, in order to maintain a uniform standard for comparison of immature stages of species within the family. This study is the first detailed biology reported for the genus, and it reports host relationships not previously recorded for the family Sciomyzidae.

Because this study is concerned with phylogenetically distinct organisms, i.e., a species of fly and its mollusk host, the reader is advised to give particular attention to the various stages of both organisms as their predator-prey relationships are discussed. The life stages of the fly to be mentioned will be egg, larva, pupa (its covering is the puparium), and the adult or imago. Life stages of the mollusks to be mentioned will be egg (singly or as part of an egg mass or capsule), juvenile (from hatching to onset of ovigenesis), and snail.

IDENTIFICATION OF MATERIAL

Identification of flies was provided by G. C. Steyskal (United States National Museum, Washington, D.C.) and B. A. Foote (Kent State University, Kent, Ohio). However, we would like to point out that our adults fit better Foote's (1961*b*) color description of *Antichaeta borealis* Foote, particularly regarding the bivittate thoracic dorsum (figs. 1*a* and *b*). Correspondence from Foote indicates that color patterns in this genus are variable. The epandrium, however, is closely comparable to the illustration by Steyskal (1960, p. 23) for *A. testacea* Melander.

Identification of mollusks was provided by Wendell O. Gregg, M.D. (retired, specialist in fresh-water mollusks, and snail morphology), Los Angeles, California. Mr. Allyn G. Smith, Associate Curator of Invertebrate Zoology, California Academy of Science, San Francisco, earlier had examined the material, but because it lay outside his specialty interest, declined to make identifications to the species level.

[1] Submitted for publication November 26, 1963.
[2] This paper is a result of a current survey associated with Agricultural Experiment Station Project 2037, Biological Control of Noxious Land Snails and Slugs, and Aquatic Snail Hosts of Livestock Liverflukes.

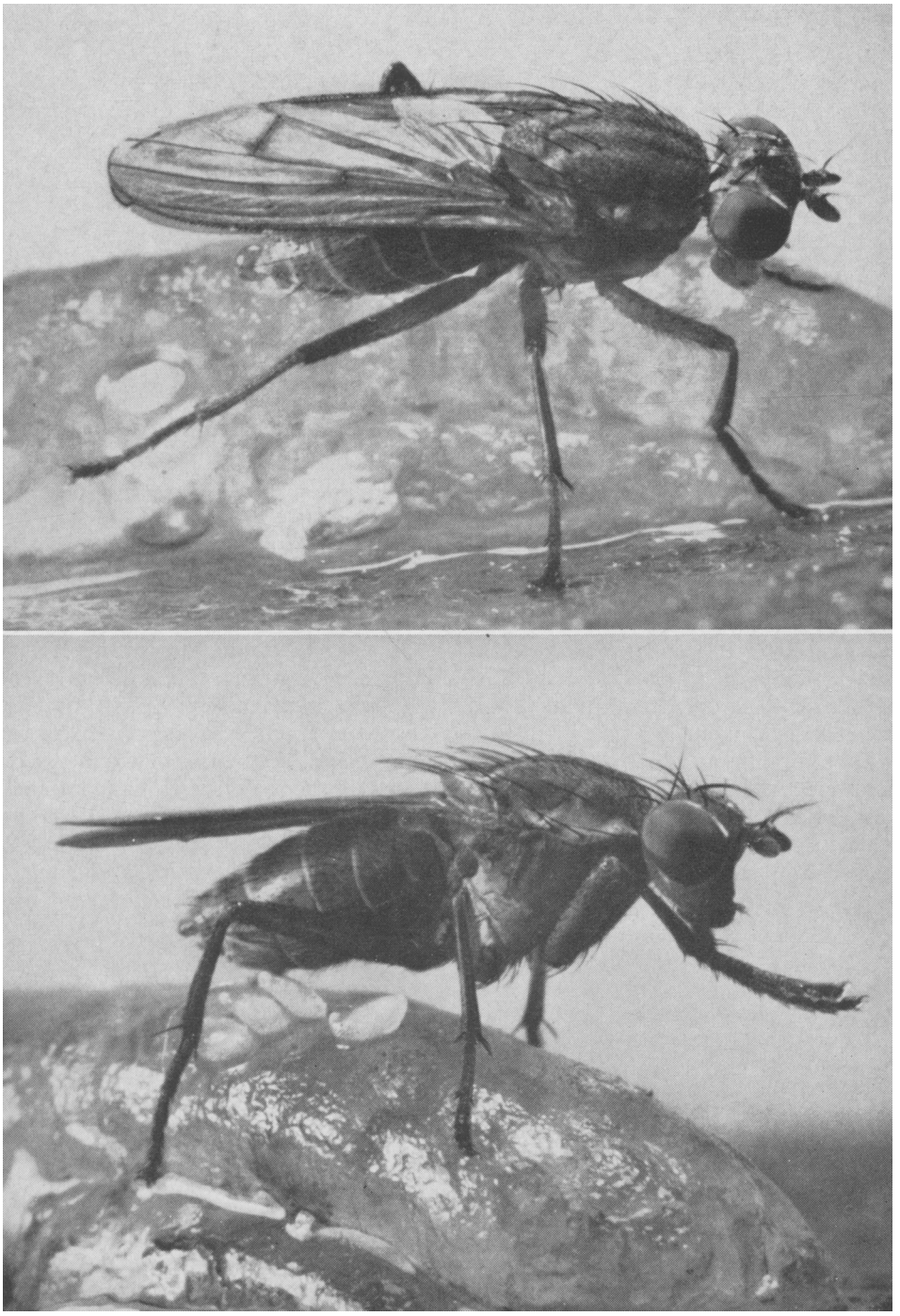


Fig. 1. Female *Antichaeta testacea* Melander. *a.* (top) View showing bivittate dorsum. *b.* (bottom) Lateral view showing certain typical characteristics of sciomyzid flies and newly laid eggs on egg capsule of *Radix auricularia.* Note upturned (respiratory?) cap on the eggs of the fly.

COLLECTION METHOD

A gasoline-powered "D-Vac" suction collector (distributed by D-Vac Company, Ventura, California) was used to collect the flies on vegetation emerging from the water or on banks close to the water (fig. 2). When taking a sample, the operator walks through the collecting area for 10 minutes, swinging the device in horizontal arcs, with the mouth of the collecting funnel just brushing the tops of the vegetation. Considering the scarcity of *Antichaeta testacea,* it is doubtful that conventional collecting nets would have captured sufficient material for this study. Further, it early became clear that flies collected with the machine were not damaged for subsequent biology or taxonomic studies, while net-collected specimens were frequently mutilated. Organdy bag inserts were removed from the machine and their contents released into cages. The desired species were then individually aspirated into individual vials.

STUDY AREA

Adults of *Antichaeta testacea* were collected mainly from commercial watercress beds, *Nasturtium officinale* R. Br., along a 400-yard section of the Santa Ana River, Riverside, Riverside County, California (fig. 2). At the periphery of the watercress and mixed with it were the following dominant emergent (aquatic) plants: *Hydrocotyle* spp., *Eleocharis* spp., *Bidens laevis* (L.), and *Scirpus* spp. Another inland locality from which this fly was taken during this study is Vail Lake, near Temecula, Riverside County. The third site, San Juan Creek, near San Juan Capistrano, is in coastal Orange County.

Fig. 2. Habitat of *Antichaeta testacea* at Riverside. Samples were taken by walking through the area and swinging the suction machine from side to side.

DISTRIBUTION AND ABUNDANCE

Between September 14, 1962, and December 31, 1963, attempts were made to collect sciomyzid flies at 61 sites in southern California. Single collections were made at 41 sites; 16 sites were visited from two to six times; and four sites were visited from eight to 19 times. The area surveyed extended from the Pacific Ocean eastward to the Colorado River, and from the California–Mexico border northward to the San Bernardino Mountains. Within this 24,000 square-mile area, *Antichaeta testacea* comprised 1.3 per cent of the total number of sciomyzids taken, but it was collected only at the three sites previously mentioned. Thirty-four flies were taken at Riverside, two at San Juan Creek,

and one at Vail Lake. Although never abundant, *A. testacea* was found most frequently during January, February, March, and April. During those four months, the 29 specimens of *A. testacea* taken at the three sites comprised 12.6 per cent of the total number of individuals among the nine species of Sciomyzidae collected at these locations.

Monthly sampling, from May to December, 1963, resulted in the capture of *Antichaeta testacea* in the following numbers at Riverside: May (1), July (1), August (1), September (2), and October (1). San Juan Creek and Vail Lake each yielded one fly in June, but none were taken in the monthly samples thereafter. In January 1964, no *A. testacea* were collected at the three sites. By mid-February seven specimens had been taken at Riverside, none at San Juan Creek, and none at Vail Lake.

Specimens in the A. L. Melander collection (G. C. Steyskal, United States National Museum, personal correspondence) are from the following localities: Riverside (2 specimens), May 5, 1935; Ortega Highway, Mariana River (2), May 15, 1946; Oak Grove (4), May 8, 1945; and Morro Bay (3), July 27, 1940. With the exception of the flies from Morro Bay (San Luis Obispo County), all are from the same drainage systems as the specimens taken during our survey.

No *Antichaeta* spp. were seen in the collections of the University of California at Berkeley or Davis, nor at the California Academy of Science, San Francisco. The highly localized distribution and scarcity in numbers agree with the observations of Foote (1961*a*), who, during his survey in the northwestern United States, found that *A. testacea* was fairly common during late May and June in Idaho, which seasonally is similar to southern California two or three months earlier. He reported that out of approximately 70 collecting stations throughout Idaho, Utah, and Oregon, four species of *Antichaeta* were collected at eight sites. Curiously, only one species was taken per site. *A. testacea* was collected at five sites in Idaho and Utah; *A. melanosoma* Melander was found in Idaho; *A. robiginosa* Melander in Oregon; and *A. borealis* Foote (sp. A of Foote, 1961*a*) in Idaho. The only succineid snail listed, *Oxyloma* sp., was reported at four collecting sites; but only near Sandpoint, Idaho, was its presence correlated with a species of *Antichaeta.*

THE HOST SNAIL

The dominant aquatic snail species occurring at the collection sites where *Antichaeta testacea* was taken during this study are: *Stagnicola palustris nuttaliana* (Lea) (family Lymnaeidae); *Physa virgata* Gould (family Physidae); and *Helisoma tenue californiense* Baker (family Planorbidae). However, at Riverside the closest host association seems to be with the "amphibious" snail *Oxyloma sillimani* (Bland) (family Succineidae) (fig. 3). At the Riverside site in 1963 *Succinea californiensis* was present but rare.

Thus far *Antichaeta testacea* has been collected only where a succineid host occurs. Morphologically this family of snails is considered by malacologists to be *terrestrial* (Pilsbry, 1948, p. 771). However, in southern California *Oxyloma sillimani* is always closely associated with an aquatic habitat and may usually be seen within 12 inches of the water surface on the aerial portions of plants emerging from the water; it likewise is found virtually at water level among the plants, where it feeds and deposits its eggs in clusters on shaded low mud hummocks littered with fine wet debris—hence the appellation "amphibious." In mixed stands of aquatic plants, *Oxyloma* often occurs on *Eleo-*

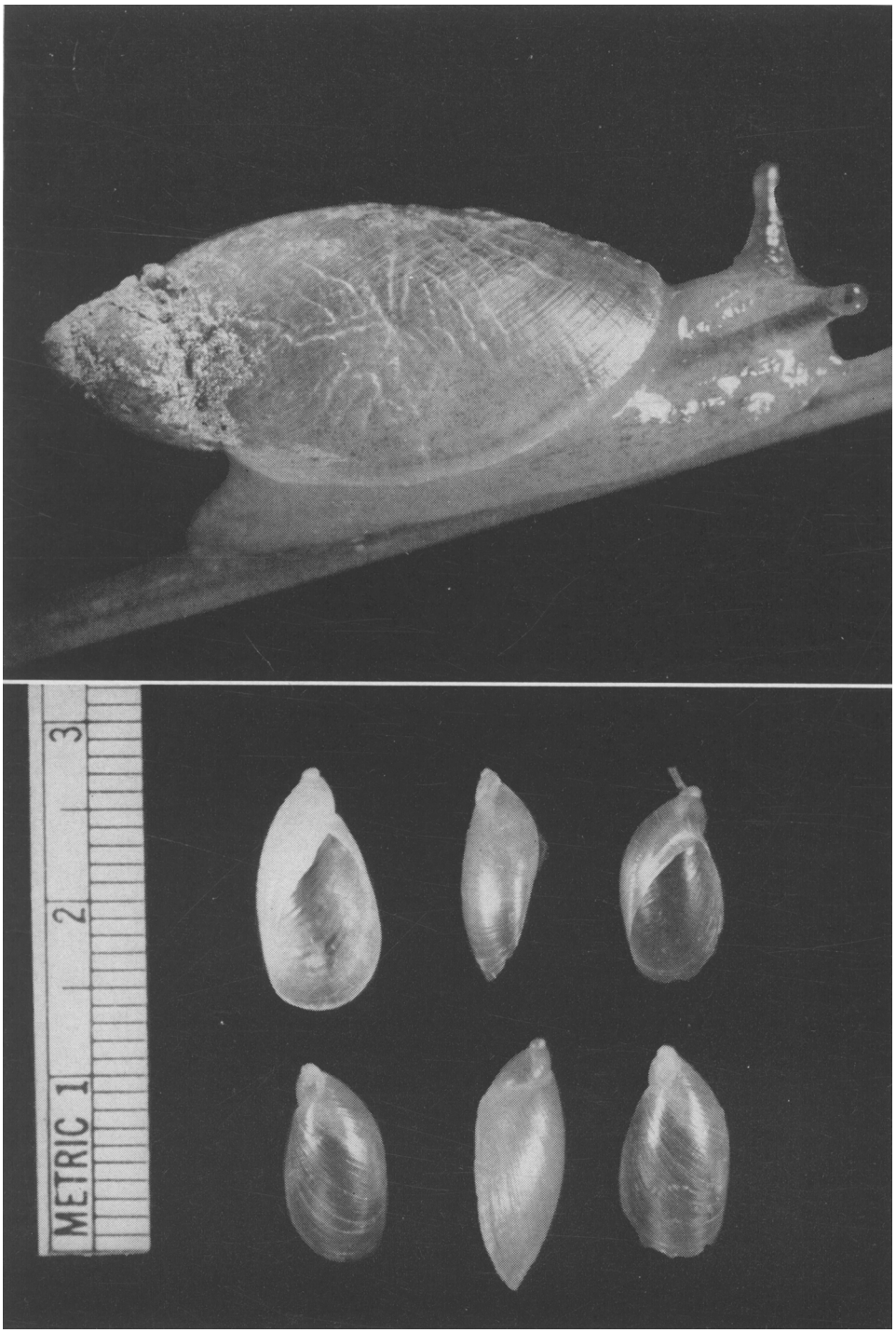


Fig. 3. *Oxyloma sillimani* (Bland). *a.* (top) Living mature snail. The greatest length and width of the shell of this snail were 14 mm and 7 mm, respectively. *b.* (bottom) Dorsal, lateral, and ventral views of shells.

charis; but it comprises a very low percentage of the total snail population. No damage to living plants by *Oxyloma* was observed, and this snail is presumed to feed primarily on the periphyton growing on the plants it frequents.

The only succineid snail found at Vail Lake and San Juan Creek was *Succinea californiensis* Fischer and Crosse. In the fall of 1963 at the lake several small shallow pools were formed by the receding water level and were distributed up to 80 feet from the lake margin. A rather dense stand of knot grass, *Paspalum distichum* L., interspersed with clumps of *Eleocharis,* occurred near these pools. Few *Succinea* sought the shade of the vegetation; rather, they were most commonly seen on the moist shore on exposed mats of algae up to 12 feet away from the pools or the lake. At San Juan Creek, *Succinea* occurs on the moist soil near the water exposed to view, or it may be found at the base of plants near the water. *Succinea* is not densely colonial, and its distribution is discontinuous even in areas where it occurs. Counts per linear 36 inch × 12 inch unit area at San Juan Creek ranged from 0 to 30 individuals. At Vail Lake the density was considerably lower.

Because *Succinea californiensis* was not commonly found at Riverside during the initial preparation period of this paper, it received little attention in laboratory testing. However, during early 1964 *S. californiensis* became more abundant than *Oxyloma sillimani* at Riverside and was therefore included in further testing procedures. Even though *S. californiensis* was rather common at Riverside in early 1964, *Antichaeta testacea* was collected there during that period in fewer numbers than in 1963—thus indicating that, of the two succineid snails, *O. sillimani* is the preferred species. The very few specimens of *A. testacea* collected at the two other localities, where we have never found *Oxyloma,* give further substantiation of this host preference.

In the dry climate of southern California the observed proximity of a succineid snail to water is probably accounted for by the prevailing temperature and humidity of the microhabitat. Even so, observation leads us to think that *Succinea* has greater tolerance to desiccation than has *Oxyloma.* The latter is more hydrophilic than *Succinea* in our study areas and therefore seeks a habitat which also meets the requirements of second- and third-instar *Antichaeta* larvae. In the laboratory at 70° to 74° F, the incubation period preceding hatching of the juvenile snails of *Oxyloma sillimani* was 14 days; of *Succinea californiensis,* 11 days; and of *Physa virgata,* 12 days.

LIFE HISTORY OF *ANTICHAETA TESTACEA*

On January 31, 1963, our first specimens of *A. testacea* were collected at Riverside. The first attempt to learn something of their biology was to offer the adults a free choice of a number of snails found at the collection site. Accordingly, a pair of feral flies was confined with a few mature *Physa virgata, Oxyloma sillimani,* and *Stagnicola palustris* in a one-pint plastic food container. *Physa* and *Stagnicola* were placed in a small glass reservoir of water on the bottom of the container, and damp peat moss was packed between the reservoir and the sides of the container. The latter procedure provided suitable conditions for the terrestrial *Oxyloma* and also assured the high humidity required by the flies. As a food supplement for the flies, a small patch of MRT-honey[3]

[3] Protein hydrolysate-MRT; manufactured by Marvin R. Thompson, Inc., Stamford, Connecticut: "A freely soluble enzymatic hydrolysate of primary grown brewers' type nutritional yeast, containing free amino acids, polypeptides with all factors of Vitamin B complex."

(equal parts by volume) was placed on the side of the container. The snap-on plastic lid contained a cloth-covered central opening. During the remainder of the day the flies were first caged, the female showed no interest in any of the snails and no eggs were deposited in the cage. Overnight *Oxyloma* deposited a cluster of eggs on the moist peat, and the next morning a number of fly eggs were seen on that egg cluster. Thus the key to an understanding of the biology of *A. testacea* resulted accidentally. If eggs had not been deposited by *Oxyloma,* and if *Antichaeta* had not oviposited on them, this study would not have been pursued, since at that time we were mainly interested in working out a sciomyzid biology for our own information.

During this preliminary test and subsequent studies, room temperature was 76° F ± 1°, and relative humidity was 50 to 60 per cent; the caged flies mated repeatedly and both sexes fed at the MRT-honey; no flies were observed feeding on mollusk eggs or egg capsules, and no interest in crushed snails was displayed by confined flies.

Because there is no published comprehensive biology of the genus known to us, the present study was undertaken.

REARING PROCEDURE

After preliminary trials, the type of rearing cage developed and used in all subsequent group studies was a pint plastic container with a screened opening on top (fig. 4). A half-inch-thick pad of bleached, non-sterile cotton was placed in the bottom of the container and saturated with distilled water. (Subsequent tests showed that damp peat moss—pH = 3.7—had a deleterious effect on snail eggs. This problem will be elucidated in a subsequent paper.) Snail eggs were placed on the wet cotton and a drop of MRT-honey was placed near the top of the container. A piece of paper towel beneath the food prevented contamination of the cotton. A male and female fly were then added for an oviposition period of 24 to 48 hours, after which the flies and the remaining food supplement were removed—the latter to prevent development of mold. The flies were lightly anesthetized with CO_2 in order to minimize damage or loss during transfers.

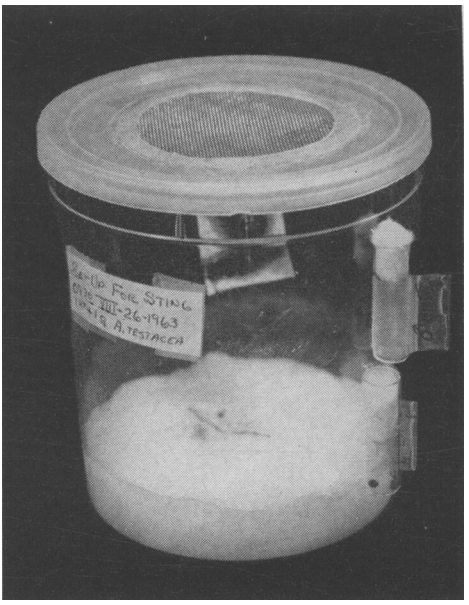


Fig. 4. Rearing cage. (Description in text.) Vials contain puparia from which adults used in this test emerged.

OVIPOSITION BEHAVIOR

Oviposition Stimulus

Preliminary tests utilizing several females indicated that snail eggs provide the stimulus for fly oviposition. When removed from host eggs, the female fly may, during the next few days, continue to oviposit up to a dozen eggs on a moist substrate. Thereafter,

TABLE 1

RELATIVE PREFERENCE FOR HOSTS OFFERED SINGLY TO ALL STAGES OF *ANTICHAETA TESTACEA*

Mollusk species	Mollusk host preferred by:						
	Female, for oviposition site, i.e., host eggs	Instar I		Instar II		Instar III	
		Eggs	Juvenile snails	Eggs	Juvenile snails	Eggs	Juvenile & adult snails
Oxyloma sillimani (Bland)	10*	10	0	10	0	10	0
Physa virgata Gould	10	10	0	10	2	10	9
Succinea californiensis Fischer and Crosse	10	10	0	10	0	10	2
Radix auricularia (L.)	8	10	0	—	0	10	5
Stagnicola palustris nuttalliana (Lea)	8	10	0	—	0	—	1†
Pseudosuccinea columella (Say)	8	10	0	—	—	—	3†
Helisoma tenue californiense F. C. Baker	2	0	0	0	0	1	4†
Helix aspersa Müller	1	0	0	—	—	—	0
Lehmannia poirieri (Mabille)	3	0	0	—	—	1	0

* Value of 10 = greatest preference; 5 = moderate; 1 = rarely attacked; 0 = refused; a dash indicates no data.
† Snails half grown or less in size.

oviposition resumes only if host eggs are present in the immediate environment of the female fly. In one instance, after a five-day interruption of oviposition, a female began ovipositing immediately after again being placed with host eggs. During the first half hour, this female laid 13 eggs, and within 24 hours had laid 93 eggs. Similarly treated, other females exhibited the same pattern.

Fecundity and Longevity

The average number of eggs deposited by female *Antichaeta testacea* and the longevity of the flies in nature are not known. In the laboratory, fecundity and longevity were probably affected by the MRT-honey diet supplement, but a comparison of effects with and without the supplement was not undertaken. Rather fragmentary data indicate that *A. testacea* is rather long-lived and highly fecund under laboratory conditions. For example, three females and two males captured early in the season (February 20) were placed together in a plastic oviposition cage. The females each laid from five to 10 eggs daily for 50 consecutive days, after which counts were discontinued; all five flies were vigorous at that time.

Host Preference

Laboratory studies on host suitability were conducted in the plastic rearing containers, using eight species of mollusks and their eggs exposed on wet cotton. Table 1 indicates the stages of the host preferred as oviposition sites and as sources of food for the developing larvae. A high degree of preference (10) indicates virtual exclusion of species with lower ratings. A rating of (0) indicates hosts refused when they alone were offered to adult flies as oviposition sites or to larvae as food.

In order to clarify the factor of host relationship it is necessary to present pertinent information on the reaction of first-instar larvae to the eggs and egg masses of the mollusks listed in table 1, and to mention that the combined duration of the egg- and first-instar stages of *Antichaeta* is five or six days.

By maintaining constant high moisture with the wet cotton it was possible to rear approximately 300 larvae of *Antichaeta* in egg masses of *Physa virgata* and the lymnaeid spp. when succineid eggs were not available. Although physid and lymnaeid eggs can serve admirably as substitute hosts for the laboratory propagation of first-

instar *A. testacea* (see further discussion of feeding tests with *Physa* eggs), it seems unlikely that the normally submerged egg masses of those snails would be available to the female *Antichaeta* in nature. Hence it appears incorrect to consider them as true alternate hosts. The manner in which the egg masses of the various species of snails respond to the laboratory method used in this study, as well as the response of newly hatched *Antichaeta* larvae to those egg masses, lends support to this idea. On wet cotton, *Oxyloma* eggs completed development in 14 days without exhibiting appreciable desiccation, whereas physid and lymnaeid egg masses usually began deteriorating in two or three days and had to be replaced in order to bring the younger fly larvae to the same stage of development (particularly if the gelatinous covering of the egg mass was ruptured). However, the egg mass of *Radix* (= *Lymnaea*) *auricularia* (L.) is more resistant to desiccation and will remain acceptable for six to eight days on wet cotton.

The flat egg mass of *Helisoma* may be satisfactorily maintained on wet cotton for approximately 24 hours. The external gelatinous coating of the *Helisoma* capsule appears to be tougher than that of lymnaeid snails, *Physa,* or *Oxyloma.* During this period a newly hatched larva of *Antichaeta* can enter the egg mass of *Helisoma,* but usually dies within a few hours; and it is presumed that the inability of the posterior spiracles to regain contact with air results in suffocation of the larva.

Eggs of the slug *Lehmannia* are deposited singly in groups of six to 15. Newly hatched *Antichaeta* larvae enter single eggs of this mollusk but soon die, presumably for the same reasons as stated for *Helisoma.*

In the absence of eggs of other mollusk species, *Antichaeta* will deposit its eggs on those of the brown garden snail (*Helix aspersa* Müller), but the first-instar larvae do not enter those eggs.

Further indications of the preferred host egg mass are seen in the way in which *Antichaeta* distributes its eggs on those of the host. The fly attaches its eggs at random to the air-exposed egg mass of *Oxyloma, Succinea, Physa,* and lymnaeid spp. (fig. 5). But only a few eggs are deposited directly on the eggs or egg masses of *Helisoma, Helix* and *Lehmannia,* most being scattered nearby on the substrate. Also, the total number of eggs deposited on the latter three hosts is less than 25 per cent of the number deposited on the more preferred hosts.

In our field-study areas, *Oxyloma* and *Succinea* are the snails which most often oviposit out of water. The aquatic snails in these areas oviposit only on submerged objects; hence, their eggs are not available to *Antichaeta* unless a lowered water level exposes them. But, unless adequate moisture is provided, the fragile aquatic snail egg masses will deteriorate before the first-instar fly larvae can complete their development.

Because of the normal oviposition site and the physical characteristics of the eggs of the mollusks mentioned; and in view of corroborative laboratory observations on host selection by *Antichaeta* and the direct correlation of numbers of *Oxyloma* and *Antichaeta* in the field, we conclude that at Riverside, California, the eggs of *Oxyloma sillimani* must be considered the host of first preference for ovipositing adults and first-instar larvae of *A. testacea.* (Eggs of *Succinea californiensis* are of secondary preference.) These observations suggest that other species of *Antichaeta* may likewise be closely associated with succineid snails, and it is possible that future collectors may be able to use these animals as indicators of each other's presence.

The host preference of *Antichaeta testacea* differs in degree from the specificity displayed by other sciomyzid flies for this family of snails. Foote (1959) reports that all known larvae of the genus *Sciomyza* Fallen are asso-

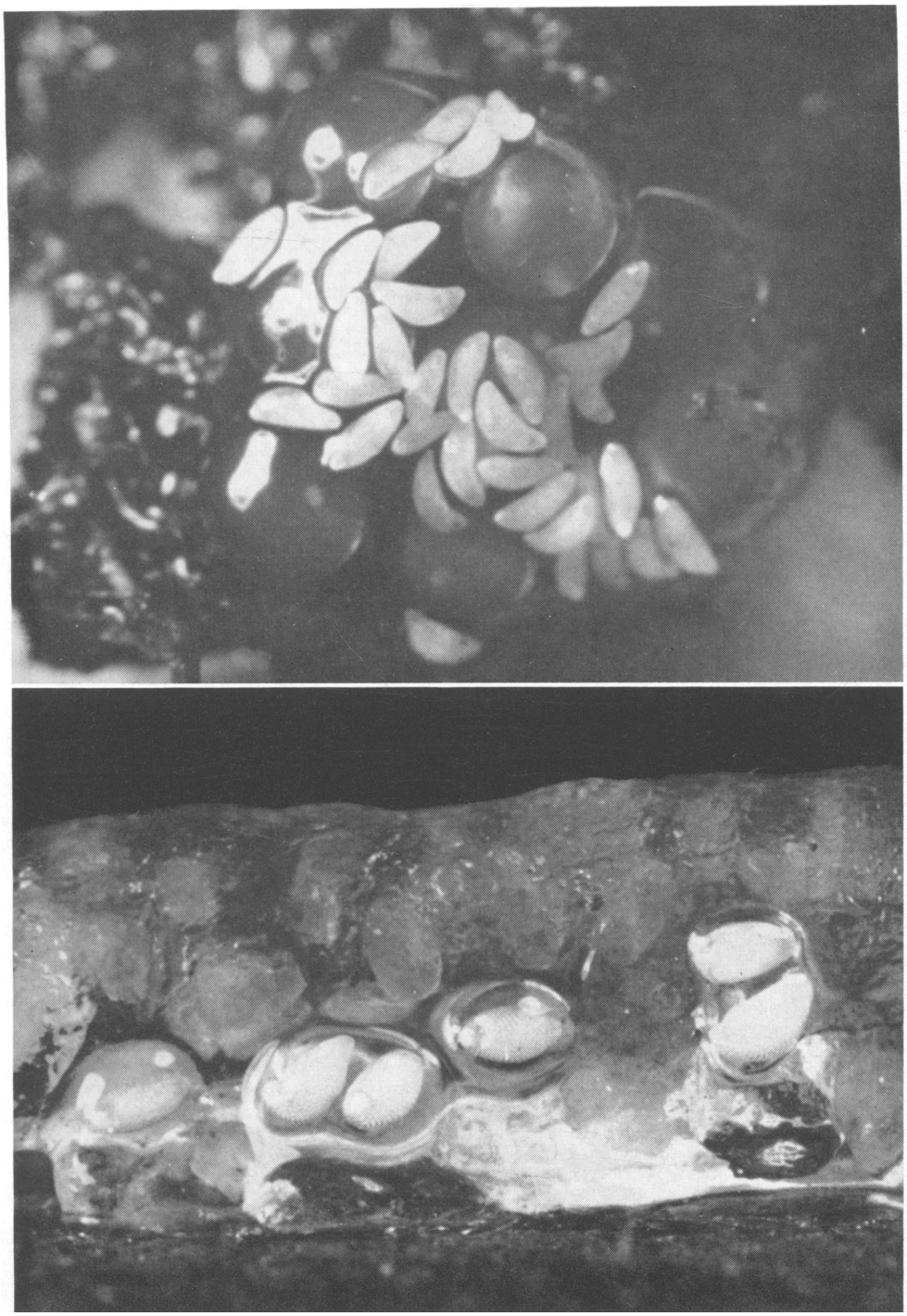


Fig. 5. *a.* (top) Eggs of *Antichaeta testacea* on "dry" eggs of *Oxyloma sillimani.* Capsules have dehydrated. The heavy concentration of fly eggs is abnormal. *b.* (bottom) Eggs of *Antichaeta testacea* showing "halo" effect of capsules on "wet" egg mass of *Radix auricularia.*

ciated with succineid snails. The closest association is shown by *S. aristalis* (Coq.), which oviposits on the shell of the snail and in which larval development and pupation occur in the individual host. Foote, using Reuter (1913) for precedence, designates this host relationship "parasitoid."

Neff and Berg (1962) reported that the first-instar larvae of *Hoplodictya spinicornis* (Loew) prefer two succineid snails, *Oxyloma retusa* (Lea) and *Succinea avara* Say, over several other terrestrial or aquatic species. The second and third instars of *H. spinicornis* fed on snails refused by the first instar. The third instar of *A. testacea,* however, is reluctant to attack *snails* of *Succinea californiensis* or *Oxyloma sillimani,* even though their *eggs* (to repeat) are the obligate host of the first-instar and early second-instar larvae and are highly acceptable to late second- and third-instar larvae. Other sciomyzid larvae will feed on snail eggs; i.e., Knutson and Berg (1963) reported that *Hydromya dorsalis* (Fabr.) (Tetanocerinae) may be reared on a diet solely of *Lymnaea* eggs or snails. They surmise that the feeding in egg masses may be a means of larval survival in the moving, thin film of water which characterizes a madicole environment (Vaillant, 1956), even though the fly has not been reported to oviposit directly on the egg masses of the host snail.

Mating Behavior

In the laboratory, mating occurred readily in the plastic rearing cages at any time adults were placed together during the day, and was repeated many times throughout adult life.

In the mating stance the male assumes a position fully on the dorsum of the female, with his body tilted head uppermost (as in typical sciomyzid resting position) and with the wings folded together normally over the back. The fore tarsi are placed just laterad of the female's antennal bases and lie against her face, the tarsal claws being hooked either at the lower edge of the face or at the base of the antennae. The apical spines of the mesotibiae of the male rest on the base of the costal wing vein of the female, the tarsi hanging loosely over the edge of the wing. The metatarsi rest on the abdomen or wings of the female.

During mating the female is in a nearly horizontal standing position, with the postabdomen turned upward at an approximate angle of 90 degrees, in order to engage the genitalia of the male. This posture causes the female's wings to spread slightly, and the weight and position of the male cause the wings to assume a slightly downturned position. Pairs commonly remain *in copula* 30 minutes or longer.

Preoviposition Period

Groups of newly emerged females were placed with seven-day-old or older males in standard breeding containers. Snail eggs and protein hydrolysate supplement were constantly available. The first eggs were laid on the fourth to the seventh day.

DEVELOPMENT AND BEHAVIOR OF IMMATURE STAGES

In the laboratory the life cycle (egg to egg) was completed in 35 to 44 days at 76° F ± 1° and 50 to 60 per cent relative humidity ambient readings in the room. The observations which follow were made under those same conditions.

Egg

The eggs of *Antichaeta testacea* are deposited singly (although up to 40 may be deposited on one host egg mass in the laboratory) and are contained in individual hyaline capsules which appear to

be of a hygroscopic collagenous substance of very light density (figs. 1*b* and 5*b*). Each egg is surrounded by its individual capsule, in which it can actually float (behaving much like a ship's compass in liquid), with the upturned bald end opposite the micropyle prominently displayed and oriented upright in contact with the air. The posterior spiracles of the developing larva are pressed close against this domelike structure, which may have a respiratory function. The capsule is rather sticky and permits good adhesion even to very moist eggs of aquatic snails under laboratory conditions. On drier substrates, such as the eggs of *Oxyloma* (fig. 5*a*) or moist peat, the capsule undergoes a certain amount of drying, thus causing the eggs of the fly to adhere so tightly that some appear to be partially imbedded in the host egg mass. As the capsule dries, the bulbous upturned end remains upright. Capsules of closely contiguous eggs may appear to fuse; this gives the impression of more than one egg per capsule. When placed in water, such eggs readily separate and the capsules swell to three or more times the mass of the egg, imparting the appearance of a halo. Eclosion occurs early in the third 24-hour period. The larva emerges from the micropylar end of the egg and immediately bores into the matrix of the host egg mass.

Larva I

Within the matrix of the host egg mass, the first-instar larva moves from one snail egg to another, feeding on the developing embryos and cytoplasm. Newly hatched first-instar *Antichaeta* larvae were occasionally observed entirely within eggs of the host. Although larvae may be completely imbedded in the host's egg matrix as they actively move about in it, they scarcely move while ingesting the contents of an egg. During feeding, the posterior spiracles are in contact with the air at the surface of the gelatinous covering of the egg mass, and the cephalic segments are thrust into an egg. The body of the larva is nearly motionless, and the contents of the host's egg are slowly drained into the gut of the larva by means of peristaltic action. Evidence that a snail egg has been fed on is provided by a puckered appearance at the point where the larva "bit" into the chorion, by a clear hole in the shell, or by the collapsed vitelline membrane within the egg shell. Laboratory observations of 20 larvae individually isolated on clusters of young (less than 48 hours old) and old (seven- or eight-day-old) eggs of *Physa virgata* showed that seven to 16 (average = 12.1) young eggs and six to 10 (average = 8.1) old eggs were consumed during the first instar. The range in numbers consumed is in part associated with the ages of the developing snail embryos; but the preferred age, if any, of the embryonic snails was not determined. Five other individually isolated first-instar larvae completed development after each consumed an average of 2.6 *Oxyloma sillimani* eggs. An average of 3.8 eggs of *Succinea californiensis* was consumed by each of five additional first-instar larvae.

During individual feeding tests, larvae were isolated in small glass cells made by cutting off the bottom ¾ inch of standard 8-dram shell vials. Each cell was closed by a 25 mm microscope cover glass sealed on with silicone stopcock grease. As daily counts were made, mutilated eggs were removed, cells were flushed with distilled water and drained, and fresh eggs were added. Two or three drops of water were placed in each cell before the cover glasses were again sealed over the cells.

A group of first-instar larvae usually spend their entire development period within one egg mass of the host. But if all the snail embryos in the original egg mass are consumed, the larvae will leave and move about on the wet substrate in search of a fresh mass. During such movement there is no observed attempt

to feed on contacted juvenile or older snails. During their development, first-instar larvae double in length and increase in volume approximately four times. Ecdysis occurs after 1.5 to 2.5 days within the egg mass of the host, which by this time is usually devoid of viable embryos. In one instance, the actual process of ecdysis was observed within the matrix of a *Physa* egg mass. Transformation to the second instar occurred, of course, within the integument of the first instar. Because the integument of both instars is clear, it is difficult to follow exactly the sequence in which the various aspects of the transformation take place. The general movements of the larva were revealed because of the opaque cephalopharyngeal skeleton and tracheal system. After several minutes of rather violent twisting, contracting, and expanding motions, during which the structures of the second instar became divorced from those of the first instar, the second-instar larva ruptured, with its mouthhooks, the old first-instar larval skin near the anterior end. It then crawled out, leaving behind, still intact within the exuvium, the cephalopharyngeal skeleton.

After the first molt, cephalopharyngeal skeletons of first-instar larvae are readily seen in the egg matrix of the host against the white cotton substrate.

Larva II

Second-instar development begins in the egg mass where ecdysis occurred. Depending on the food supply, this instar completes development in two to eight days. We continued to feed the same 20 larvae mentioned in the previous section (p. 12) a diet solely of *Physa virgata* eggs. Ten larvae were offered only two-day-old embryos, and ten others were offered only seven- or eight-day-old embryos. Larvae fed younger embryos each consumed from 16 to 53 (average = 37) embryos. Larvae fed older embryos each consumed from nine to 21 embryos (average = 15) before molting.

Five individually isolated second-instar larvae each consumed an average of six *Oxyloma* eggs before molting. Feeding tests with eggs of *Oxyloma* and *Succinea* had to be suspended because of insufficient numbers for replication.

The second-instar larva shows a definite preference for mollusk eggs; and if undamaged snail eggs (embryos) remain in the egg mass, the larva will devour them before leaving in search of other food. During this search the larva will attack other egg masses immediately upon contact or, if hungry, juvenile *Physa,* which are strongly preferred to other snail species. A larva which has fed fully on *Physa* will commonly return for a resting (digesting?) period to any readily accessible snail egg mass. There seems to be no selectivity expressed regarding the characteristics of the refuge occupied, for it may be a *Physa virgata* or lymnaeid egg mass in various stages of decomposition, and it may or may not contain some viable embryos. If a fresh egg mass is contacted during the search instead of a snail, the larva will remain with it, alternately feeding on embryos and resting, rather than leave in search of other food. When offered a diet solely of several small juvenile *Physa virgata* and *Radix auricularia* in a one-pint rearing unit containing wet cotton, only one individual of a group of 16 newly transformed, second-instar *Antichaeta testacea* larvae survived. Mortality occurred as larvae became hungry and began searching for more desirable food. Those that crawled up the sides of the plastic container (away from the wet cotton) dried up and died.

In order to create closer confinement with the host and a more moist habitat, five larvae were individually isolated with *Physa* juveniles in the previously described cut-off 8-dram vials. Two refused to attack the snails and died six and seven days later respectively. Two made their first feeding on the second and third days of confinement, and one

larva attacked the host during the first 24 hours of confinement. Two of the larvae transformed to instar III after feeding on five snails each, and one larva fed on two snails before molting.

The larva reduces activity during the last day or two of the stadium. Ecdysis may occur within a snail egg mass or after the larva burrows slightly into the substrate.

Larva III

Third-instar development is completed in nine to 16 days on a diet of snail eggs and snails. Although snails of *Physa virgata* are readily attacked, and third-instar development is in some cases completed on a diet solely of juveniles and adults of that species (see table 1), the young third-instar larva prefers mollusk eggs. Juvenile *Stagnicola palustris nuttalliana* and *Helisoma tenue californiense* were fed upon; but when mature snails of *S. palustris nuttalliana* and *Helisoma* and small *Helix aspersa* and *Lehmannia poireiri* were individually offered, none were attacked.

Three larvae which had been feeding on *Physa* snails and egg masses of *Radix auricularia* were placed in close confinement with four mature *Oxyloma sillimani.* After three days the snails were alive and no attempted attack had been observed. The fly larvae were returned to their previous diet, whereupon they immediately fed. Curiously, this test indicates a marked lack of preference for the snail species whose *eggs* are the host of first preference for the first instar and are highly acceptable to the second and third instars. This behavior might be interpreted as indicating an effect of a pre-conditioning diet, or learned preference, but other scattered tests with *Oxyloma sillimani* had the same negative result. The picture was somewhat different, however, when snails of *Succinea californiensis* were offered to five individually isolated third-instar larvae of *Antichaeta,* for within 24 hours three larvae had each killed and consumed a small *S. californiensis.*

The color of the gut of second- and third-instar larvae indicates the source of their food. Those that feed on the eggs and embryos of the host have a clear gut, whereas those that feed on the snail have a dark-colored gut.

A larval habit not yet mentioned is that of swallowing air. As previously pointed out by Berg (1961), this behavior assures greater buoyancy to aquatic tetanocerine larvae than is provided by their fleshy posterior lobes alone and permits them to support the weight of snails while floating and feeding in relatively deep water. Curiously, our observations in the laboratory with larvae of *Sepedon praemiosa* Giglio-Tos (an aquatic tetanocerine), kept on wet cotton substrate, and *Antichaeta testacea* (a terrestrial tetanocerine), repeatedly showed that the larvae sank when dropped into water, but upon removal immediately began swallowing air, even though they were placed on moist cotton and in no further danger. It appears that as a survival mechanism the air-swallowing reaction may on occasion be ineffective.

As the third-instar larva approaches its maximum development the integument becomes noticeably papillose and somewhat leathery in appearance. Three or four days before pupation the larva burrows into the substrate, where it remains quiet during the day, if fully fed. Further feeding usually occurs at night, and continues to within less than 24 hours of pupation.

Observations on the 20 individually isolated larvae mentioned in the two preceding sections (pp. 12, 13) were continued. By the *eighth* day of third-instar development the 10 larvae which had been offered only *young* embryos of *Physa virgata* had each consumed from 52 to 131 (average 96.6) eggs. On that day the gross appearance of the larvae indicated that they were reacting ad-

versely to the test conditions, and juvenile *Physa* were arbitrarily added to five of the cells in addition to the snail eggs. Although all five larvae attacked the snails, three larvae were dead by days 10, 11, and 12, respectively.The other five larvae of the group continued to be fed on a diet solely of young *Physa* embryos, and by days 10 and 11, respectively, two of those larvae were dead. The two surviving larvae from the snail-fed group and the three from the egg-fed group were removed from their individual cells and placed as a group in a ventilated wet-cotton rearing container. Both snails and eggs were placed in this container and all the larvae continued to develop. However, two subsequently died; one pupated in 23 days and two pupated later.

By the sixth day the 10 larvae which had been offered only *old* embryos of *Physa virgata* had each consumed from 72 to 218 (average = 156) eggs. During the sixth and seventh days five larvae died. The five survivors had consumed from 156 to 226 embryos (average = 200) by the *eighth* day, when they were transferred as a group to a ventilated rearing unit containing wet cotton. These five larvae continued to develop on a diet solely of old embryos, and each consumed an average of 83 additional embryos before forming puparia three to seven days later. All told, these five larvae each killed an average of 283 eggs of *P. virgata* while in the third instar.

Summary of Larval Feeding

The results of the continuous feeding tests (see table 2) may be summarized as follows:

(1) Instars I and II developed at virtually the same rate, but fed on more young eggs than old eggs.

(2) The two groups of instar III larvae showed a marked difference in the number of eggs consumed in eight days. Those kept on a diet solely of young *Physa virgata* eggs had consumed an average of 96.6 eggs each, whereas larvae reared on a diet solely of older eggs had destroyed an average of 200 eggs each. Further, the group reared on young eggs (plus snails after the eighth day) were approximately one week longer in reaching the pupal stage.

(3) Whereas instars I and II completed development in the small closed cells in a manner comparable to that which occurred in the standard ventilated rearing cage, instar III did not. Development of the latter appeared to proceed satisfactorily in the closed cells for six to eight days, after which the larvae became sluggish and the rate of feeding was either sharply reduced or stopped entirely. Third-instar larvae removed from the small cells and placed in moist but well-ventilated containers continued feeding, completed development, and formed puparia in three to seven days. If better ventilation were provided in the cells throughout the entire development of the third instar, the number of hosts consumed probably would have been larger than the presently described tests indicate.

Since death occurred in the assumed absence of microorganisms, we feel that the moisture-saturated environment of the closed cells was the main inhibiting factor. Indeed, the "leathery" integument of the third-instar larva indicates that it is not adapted to a virtually submerged type of aquatic habitat.

Although we could not obtain large enough numbers of succineid eggs to conduct definitive tests on species which we are reasonably certain are hosts of *Antichaeta testacea* in the field, we did feed small numbers of individual larvae on eggs of random ages of *Succinea californiensis, Oxyloma sillimani,* and *Physa virgata* and the results are shown in table 2. For comparison, the results derived from the previously described "continuous feeding tests" utilizing eggs of known ages are shown in the table also. Since the *Physa* egg is 0.8 mm in diameter and the succineid egg is 1.1 mm in diameter, or volumetrically 2.52

TABLE 2

RANDOM-AGE EGGS OF *SUCCINEA CALIFORNIENSIS, OXYLOMA SILLIMANI,* AND *PHYSA VIRGATA* DESTROYED BY LARVAE OF *ANTICHAETA TESTACEA* COMPARED WITH YOUNG AND OLD EGGS OF *PHYSA VIRGATA* DESTROYED BY LARVAE OF *A. TESTACEA*

Larval instar	Factor	Host			Young and old eggs of *Physa virgata* destroyed in continuous feeding tests	
		*S. californiensis**	*O. sillimani**	*P. virgata**	1- or 2-day-old eggs	7- or 8-day-old eggs
I	Number of larvae	11	5	5	10	10
	Av. no. of eggs destroyed	**3.2**	**2.6**	**8.3**	**12.1**	**8.1**
	Range of eggs destroyed (no.)	2–5	1–4	5–13	7–16	6–10
	Larval development time (days)	2–3	2–3	2–6	2–3	2–3
II	Number of larvae	5	5	6	10	10
	Av. no. of eggs destroyed	**5.6**	**6.0**	**34.7**	**37**	**15**
	Range of eggs destroyed (no.)	5–7	4–8	27–42	16–53	9–21
	Larval development time (days)	2–4	2–3	4–7	5–6	4
III	Number of larvae	3	...	...	5	5 (survivors)
	Av. no. of eggs destroyed	**104**	...	...	incomplete data	**283**
	Range of eggs destroyed (no.)	92–125	...	...	(90–154 plus snails)	239–309
	Larval development time (days)	14–16	...	...	23†	11–15
Total av. no. eggs destroyed per larva		**112.8**	...	...	...	**306.1**

* Eggs of random ages.
†One accurate record.

times larger than the *Physa* egg (and the third instar consumes approximately 2.5 more *Physa virgata* eggs than succineid eggs), it appears that the quantity of nutrient is the determining factor in larval developmental time rather than the nutritive value per se of eggs of the various host species.

In nature it is probable that late second-instar larvae and third-instar larvae include more snails (hence fewer eggs) in their diets than were permitted within the limits of our laboratory studies.

Pupa

Pupation occurs in the substrate, and the adult usually emerges 15 days later. In one group of approximately 60 larvae reared to pupation in the laboratory, on a diet of snail eggs and snails, no puparia were formed in the shells of the killed snails. Rather, all larvae had burrowed shallowly into the wet cotton or wet peat substrate.

During the summer, we first became aware that certain puparia of laboratory-propagated material failed to yield adult flies, and that dissection after three months revealed pale but seemingly healthy immature pupae. Eighteen isolated puparia, formed from July 22 to September 23, were divided into two groups on October 21. Eight puparia were placed in a lathhouse, where temperature extremes during the test period were 39° to 88° F. Ten puparia remained in the laboratory at 70° to 74° F. By December 12 six adults had emerged in the lathhouse (two pupae died). No emergence had occurred in the laboratory group as of December 30. The laboratory group was again divided, and of those placed in the lathhouse

some died and some emerged, and of those held continuously in the laboratory some also died and some emerged. It is probable that some of these 18 pupae were in diapause; this phenomenon is receiving further investigation. Because of the paucity of *Oxyloma* eggs as well as adult *Antichaeta* in the field during the summer, it seems reasonable to assume that diapause in at least a portion of the *A. testacea* population is necessary to carry the species over that unfavorable period.

Pupal parasites

Because no pupae of *Antichaeta testacea* were found in the field, it was not possible to assess parasite-caused mortality to that stage. However, a local uniparental parasite, *Phygadeuon* sp. (Ichneumonidae), was reared out of puparia of *Sepedon praemiosa* Giglio-Tos (Sciomyzidae), and in the laboratory this wasp readily oviposited on young pupae of *A. testacea* and completed its development as a solitary external pupal parasite.

DESCRIPTION OF IMMATURE STAGES

Because the present study is the first rather comprehensive biology in the genus, the following descriptive details are included. It is hoped that they may lead eventually to a better appreciation of the continuum of species in the family. A comparison of larval characteristics of the Sciomyzidae with larvae of closely related dipterous families may be found in Foote *et al.* (1960), and in the Ph.D. thesis of Neff (1960).

Egg

(See plate II, 7, 8, p. 25.) Elongate ovoid; micropylar end nearly truncate; end opposite micropyle rounded, prominent, and turned up. Length 0.70–0.75 mm; width 0.35 mm. Chorion white, with raised reticulations of irregular polygonal shape, which become more elongate at the micropylar end, and are absent on the bald upturned end opposite the micropyle.

Morphological and histological studies (Snodgrass, 1935; Fish, 1947; and West, 1951) agree that spermatozoa enter the anterior end of the egg through one or more micropyles, and that as the egg passes down the oviduct, posterior end first, fertilization occurs as the egg (*viz.*, its blunt anterior end as viewed *in vivo* in the oviduct) receives spermatozoa from the sperm duct. Dissections were made to establish accurate polar orientation of the *Antichaeta testacea* egg, and in the photograph (fig. 6) the bulbous upturned end on five eggs is clearly seen at their posterior end, and the truncate opposite end is clearly shown on a single egg at the center of the field.

It is generally accepted that the surface configurations of the chorion are reverse images of those in the follicular wall. However, around the edges of each enclosed "cell" are five to eight rather evenly spaced "granulae," whose origin and function are as yet obscure.

Larval Morphology: General

All three larval instars possess 12 segments, and in addition share certain other characteristics as follows:

Head. The head segment consists of an anterior pseudocephalic portion and a posterior cephalic portion. The pseudocephalon is weakly bilobed, and each "lobe" bears a slightly sclerotized ring-like sensillum anterodorsally. The anteroventral portion of the cephalon bears the post-oral spine band and forms the atrium.

The post-oral spine band covers most of the venter of the flexible cephalic segment, being comprised of 11 or 12 diverging rows of spines directed posteriorad in the extended larva and continuing to the dorsum, gradually taper-

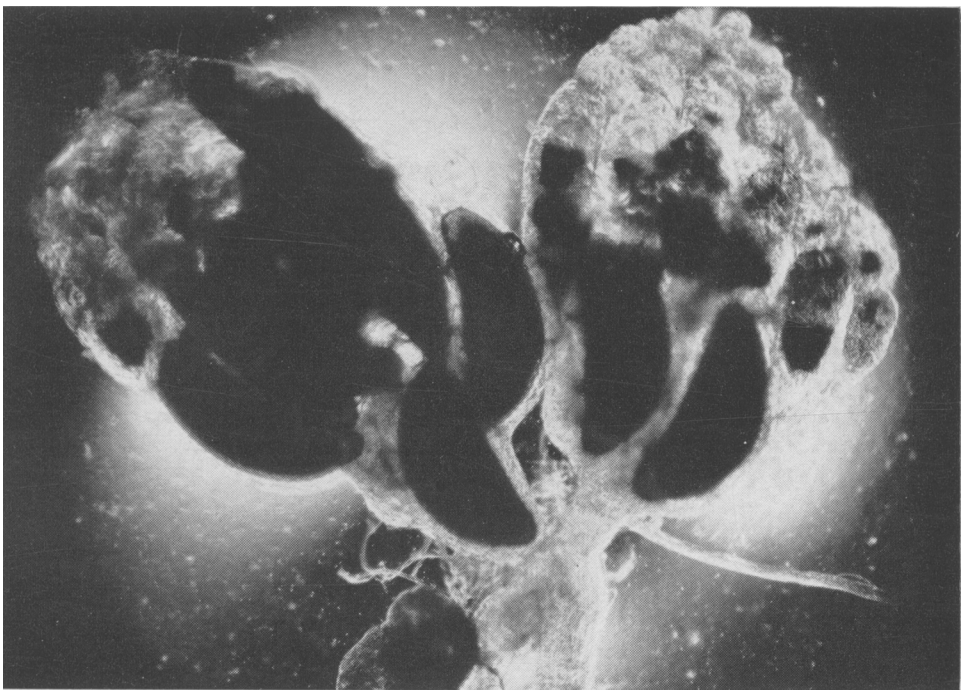


Fig. 6. Photomicrograph of reproductive organs freshly dissected out of an ovipositing female *Antichaeta testacea*. Antero-posterior orientation is from top to bottom of the photo.

ing to three or four rows of spines. When the larva contracts, the head segment is pulled in and the spine band invaginates. The spines then become directed anteriorly.

Thorax. The second segment (prothoracic segment) bears the anterior spiracles dorsolaterally toward the posterior margin in the second- and third-instar larva. Segments 3 and 4 are the meso- and metathoracic segments.

Abdomen. Segments 5 to 12 comprise the abdominal segments. The twelfth segment is the caudal segment, or eighth abdominal segment, and dorsally bears the single pair of stalked posterior spiracles. All three instars possess four groups of short, palmately branched and bifurcate float hairs on each posterior spiracular plate. In the first instar the exact points of origin of the groups are obscure, but in the second and third instars the float hairs are located alternately with the spiracular slits. When the hairs are floating, none are directed toward the lengthwise dorso-ventral midline of the larva. The float hairs are clear and can best be viewed in the CO_2-anesthetized larva in water. The bilobed anal plate is located ventrally on the eighth abdominal segment.

Cephalopharyngeal Skeleton (Plate I). In all three instars a ventral arch is present, and the hypostomal sclerite is fused with the pharyngeal sclerite.

The cephalopharyngeal skeleton is a bilaterally symmetrical structure consisting anteriorly of one dextral and one sinestral mandibular sclerite, each articulating posteroventrally with the anterior apophysis of the fused hypostomepharyngeal sclerites, which are surmounted by paired peristomal bars that anteriorly fuse with the epistomal sclerite. After each molt and accompanying size increase, sclerotization increases, the hypostomal area becomes relatively shorter, and the cephalo-

pharyngeal skeleton becomes more massive in appearance. Each half of the pharyngeal sclerite possesses a dorsal and a ventral cornua. The space between the dorsal cornua and the ventral cornua (those on the same half of the pharyngeal sclerite) measured lengthwise we prefer to call the "pharyngeal indentation"—terminology which we feel is more descriptive than "sinus," as this space has been termed by Berg and his associates.

The *mandibular sclerites* (after West, 1951, fig. 48*c*) are joined transversely by a weak fusion in only the first instar. Two small foramina are located on the mandibular sclerite: one is located anterodorsally near the base of the mouthhook; the second is located posteroventrally near the point of articulation of the ventral arch in the second and third instars.

The *hypostome* is fused with that portion of the pharyngeal skeleton which bears the ventral cornua. The hypostomal sclerites are joined transversely by a sclerotized bar whose point of attachment is indicated by a slight convexity on the venter of the hypostomal area when viewed laterally. In the second and third instars a second, more lightly sclerotized bar appears posterior to the heavy bar (plate II, 11). The hypostomal sclerites become relatively shorter and wider with each molt in proportion to the change in size of the pharyngeal cornuae. The two halves of the pharyngeal sclerite are joined anterodorsally by a curved thin dorsal bridge. Anteriorly, each half of the pharyngeal sclerite consists of a dorso-ventral sclerotization which widens with each molt.

Epistome. The anterior portion of the horizontally oriented epistomal sclerite lies between the posterior limits of the mandibular sclerites. Lateral extensions (peristomal bars) continue posteriorly parallel to and above the hypostomal sclerite, ultimately fusing with the pharyngeal sclerite. Preceding that point of attachment, a thinly sclerotized area may connect the peristomal bars and the hypostomal sclerite.

Lingual sclerite. The ligulate sclerite of Neff and Berg (1961); the lingual sclerite of Neff and Berg (1962). Lying ventrad to the epistome, the lingual sclerite begins as a simple, very lightly sclerotized loop in the first instar. In the second and third instars it becomes increasingly sclerotized; and other structures which may be associated with it develop within the area enclosed by the hypostome (plate II, 11). Its function and true relationship to the other cephalopharyngeal sclerites remain to be learned.

Integument. Clear in all instars. When viewed by transmitted light at 100X and 430X magnification, the integuments of instars 1 and 2 appear to be weakly papillose, and that of instar 3 is markedly papillose and pubescent.

In addition to the spinule arrangement as discussed in the following sections on larval morphology, mention is here made regarding clear, stiff spinules quite different from "typical" spinules. Although their exact function is not clear, it is presumed that they may be either secretory or sensory (tactile). They are perpendicular to the segment and seated on a broad, elevated base midlaterally on the segments concerned. They may be seen in profile (one to each side of the segment) only when the larva is viewed from a dorsal or ventral aspect (plate III, 16*e*). In the first-instar larva these spines are visible on segment 2, but their occurrence on other segments is uncertain. In the second instar these occur singly and midlaterally on segments 2 to 12. In addition, one such spine occurs apically on each ventral lobe, and two on each ventral-lateral lobe of the twelfth segment. In the third instar two such spinules occur on segment 2, but they are not clearly discernible in the heavy spinulation on the segments that follow.

Tracheal System. The longitudinal tracheal trunks extend from the poste-

rior spiracles to the second segment, but at the sixth or seventh segment they abruptly change character, the anterior section appearing less dense and smaller in diameter than the posterior section. In the posterior portion of the third segment the dorsal tracheal trunks are connected by a major transverse tracheal commisure. Another major commisure connects the dorsal tracheal trunks in the anterior portion of the twelfth segment. Other minor transverse commisures occur in most, if not all, of segments 3 to 11.

Larva I

In gross aspect the first-instar larva appears whitish, its integument is transparent; length is 1.0 to 1.8 mm, width is 0.25 to 0.55 mm.

Respiratory System. Metapneustic (anterior spiracles are absent). The yellowish posterior spiracular stalks are longer in relation to the general size of the larva than in instars 2 and 3, and the same is true of the float hairs (.038 to .043 mm), which are as long as the spiracular plate is wide.

Cephalopharyngeal Skeleton (Plate I, 4). Length is approximately 0.23 mm; sclerotized, and blackish-brown in color.

The triangular *mandibular sclerite* dorsally possesses a densely sclerotized bifid mouthhook. *Accessory teeth* are lacking. The ventral arch is located ventrad of the mouthhooks and articulates with the antero-ventral apophysis of the mandibular sclerite.

The *ventral arch* (plate I, 1) possesses 14 to 16 anteriorly directed teeth. The point of articulation is a forward-directed U-shaped structure in the center of the arch, which appears to fit over the ventral projecting apophyses of the mandibular sclerites. These latter, to repeat, are lightly fused together dorsally in this instar. On both sides of the "U" are six or seven slender, sharp-pointed teeth and one thicker blunt tooth which terminates the arch.

The *epistomal sclerite* is lightly sclerotized, appearing as a simple loop, and possesses no visible foramina anteriorly. The peristomal bars extend to the pharyngeal sclerite as described in the introductory section. The cornuae of the *pharyngeal sclerite* lack distinct windows. The dorsal cornua tapers evenly to a point. The ventral cornua appears truncate and is shorter than the dorsal cornua.

Integument. Clear. Tubercles absent. Ventral creeping welts are not pronounced but appear as two transverse bands of spinules, located intersegmentally and converging ventrolaterally between segments 5 to 12. In addition, these segments and segments 4 and 12 ventrally possess a short patch of spinules arranged transversely on the segment.

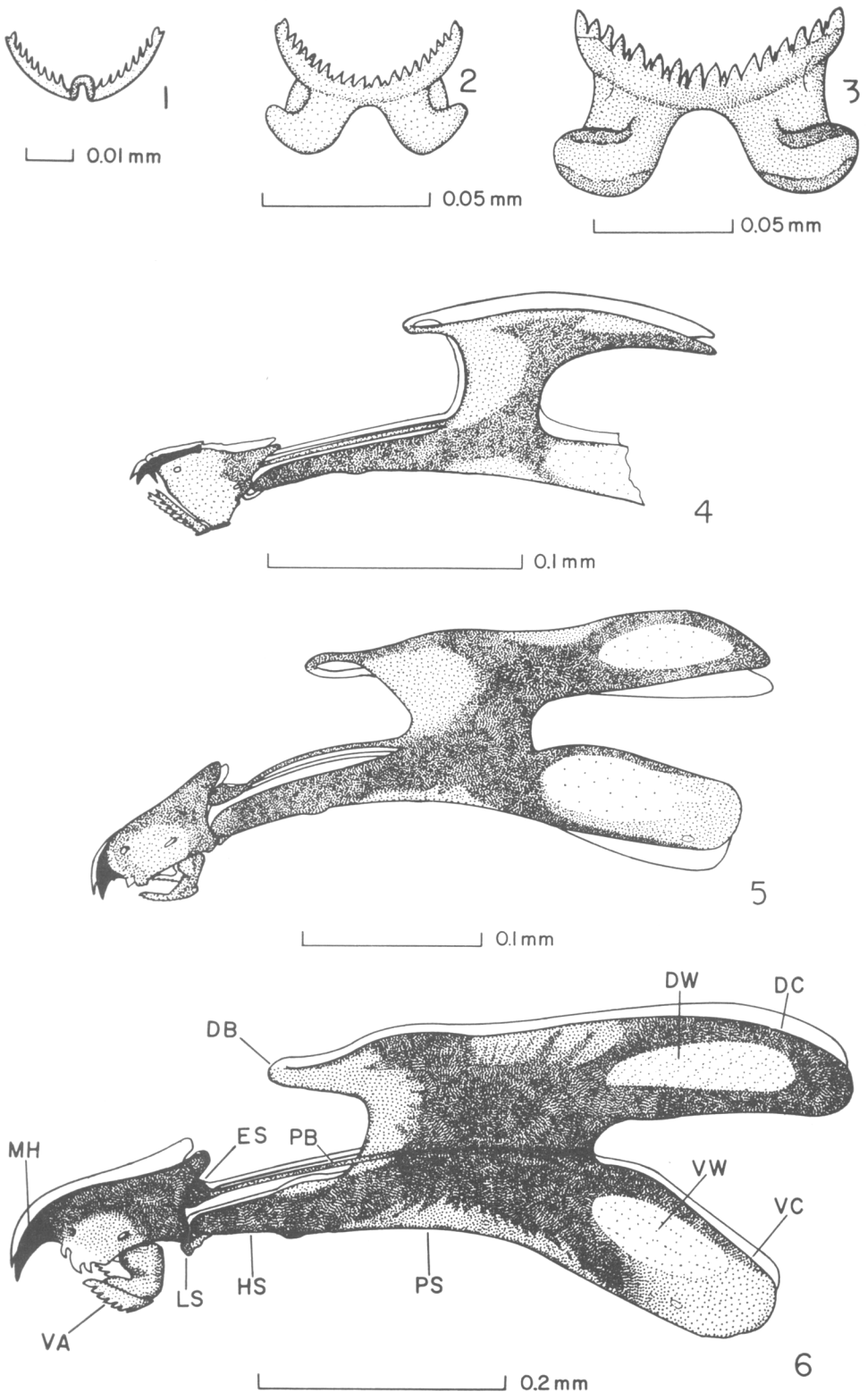
In the first and second instars the apices of the spinules in each spinule band of the creeping welts are directed either forward or to the rear in a regular sequence. When magnified, apices of

PLATE I* (*opposite page*)

Antichaeta testacea

1. Ventral arch of first-instar larva. Flattened ventral aspect.
2. Ventral arch of second-instar larva. Flattened ventral aspect.
3. Ventral arch of third-instar larva. Flattened ventral aspect.
4. Cephalopharyngeal skeleton of first-instar larva. Lateral aspect.
5. Cephalopharyngeal skeleton of second-instar larva. Lateral aspect.
6. Cephalopharyngeal skeleton of third-instar larva. Lateral aspect. DB—dorsal bridge, DC—dorsal cornua, DW—dorsal "window," ES—epistomal sclerite, HS—hypostomal sclerite, LS—lingual sclerite, MH—mouthhook, PB—parastomal bar, PS—pharyngeal sclerite, VA—ventral arch, VC—ventral cornua, VW—ventral "window."

* Drawings were made with the aid of a microprojector after boiling the material in 10 per cent KOH and mounting it in glycerine. Cover slips were ringed with "Zut" (Bennett's Zut Slide Ringing Compound, manufactured by Bennett's, Salt Lake City, Utah).


1
0.01 mm
2
0.05 mm
3
0.05 mm
4
0.1 mm
5
0.1 mm
DW
DC
DB
ES
PB
MH
VW
VC
LS
HS
PS
VA
0.2 mm
6

spinules appear black. All spinules on segments 2 to 11 are directed caudad except those on the anterior band of the creeping welt (which is actually a double band composed of forward-directed spines anteriorly, and caudad-directed spines posteriorly).

Ventrad to the spiracles on segment 12 and posterior to the anal plate is a patch of spinules. A larger patch of longer spinules lies anterodorsally to the spiracles. A sparsely spinulate area lies between the larger dorsal and ventral patches joining them.

Segments 3, 4, and 5 possess continuous bands of spinules directed caudad around the anterior margins. Segment 2 bears an inconspicuous band of spinules dorsally.

Bands of spinules occur dorsally on segments 6 and 7, the latter being less distinct. Dorsal bands on segments 8 to 10 are reduced to a few scattered spinules. A spinule band appears to be located along the posterodorsal margin of segment 11.

Laterally, small, somewhat elongated patches of minute spinules appear as denser patches in the spine bands on segments 4, 5, and 6; but at segment 7 the lateral patch becomes separated from the anterodorsal band; and from that segment through segment 11 the lateral patches occur as pairs, one member located on the posterior margin of its segment immediately opposite the other member of the pair on the anterior margin of the following segment.

Larva II

Whitish in gross aspect, integument clear, length 1.6 to 2.8 mm, width 0.6 to 1.0 mm.

Respiratory System. Amphipneustic; two anterior spiracles are located dorsolaterally on the first thoracic segment. They are thin, flattened, fan-shaped, with 14 to 16 lobes at the convexly rounded periphery. When the larva is extended, the anterior spiracles project at an angle of approximately 45°, with their greatest width oriented dorsoventrally. When the larva contracts, the anterior spiracles are forced by the overlapping second thoracic segment to pivot forward from their bases and lie flat against the first thoracic segment. Dorsal tracheal trunks terminate anteriorly in the second segment, where they merge with the stalks of the two anterior spiracles.

There are three spiracular slits on each posterior spiracular plate alternating with four groups of float hairs, which are .041 to .045 mm in length.

Cephalopharyngeal Skeleton (Plate I, 5). Length is approximately 0.37 mm. The *mandibular sclerite* becomes subrectangular. The mouthhook is simple and decurved, and its length is approximately equal to the width of its base. A single *accessory tooth* occurs immediately ventrad of the mouthhook, and in some specimens one or two small toothlike buds are seen close to the base of the accessory tooth.

Ventral arch (plate I, 2). Possesses 20 to 22 anteriorly directed teeth. Three or four of the teeth are about one-fourth the size of the majority. The major teeth are not regularly symmetrical nor equal in number on the two sides of the arch.

The ventral arch articulates ventrally with the mandibular sclerites by two processes (prolongations) which are approximately perpendicular to the arch.

The *epistomal sclerite* is thin and convex, and along its rounded anterior margin are six foramen-like openings.

The *pharyngeal sclerite* has a dorsal and a ventral cornua, each of which possesses a clearly defined, broadly ellipsoidal "window" of thin chitin.

Integument. Clear; a group of five to seven short, broad-based, anteriorly directed black spines of various lengths appear in a single transverse row midventrally, nearly touching the posterior margin of the anal plate. Otherwise the spinule arrangement appears to be the same as in instar I, but the spinules are larger.

Larva III

Whitish-gray in gross aspect, becoming somewhat darkened as pupation approaches. During its development the size increases approximately from 3.0 to 8.0 mm in length and from 1.0 to 2.2 mm in width. (See plate II, 9.)

Respiratory System. Amphipneustic; anterior spiracles (plate II, 10), usually with 16 lobes. On the boot-shaped base is the inner scar (Snodgrass, 1935, p. 447), marking the point of attachment of the second-instar anterior spiracle. Float hairs on the posterior spiracular plate (plate III, 13) are .049 to .054 mm long.

Cephalopharyngeal Skeleton (Plate I, 6). Length is approximately 0.69 mm; color is nearly black and sclerotization is considerably heavier than in the second instar.

Mandibular sclerite. Subrectangular. The *mouthhook* is simple, decurved, and twice as long as the width of its base. Three well-defined *accessory teeth* are arranged in a row below the mouthhook along the anterior margin of the mandibular sclerite. The center tooth is the largest of the three, those on either side being smaller and about equal in size.

Ventral arch (plate I, 3). Possesses 22 to 24 anteriorly directed teeth; approximately one-third are small and are interset irregularly between those in the majority. When compared to the second-instar ventral arch, the third-instar arch is a mechanically stronger structure; the processes which articulate midventrally with the mandibular sclerites are quite massive.

The *epistomal sclerite* is more massive laterally, and the foramen-like openings along the anterior margin are more distinct than in the second instar.

The most heavily sclerotized portion of the *hypostomal sclerite* (plate II, 11) is H-shaped. Between the anterior projections are seen the lingual sclerite and the hypostomal plates (after Hennig, 1952, p. 120). A lightly sclerotized transverse bar extends between the posterior projections of the hypostome.

Pharyngeal sclerite. The dorsal and ventral cornua each possess a clearly defined "window" of chitin which is denser and smaller in proportion to the size of the cornua than that same size relation is in the second instar. The pharyngeal indentation is approximately one-half the length of the pharyngeal sclerite to its anterior margin (dorsal bridge not included).

Integument. Almost clear, slightly translucent (probably because it is thicker than in the second instar), markedly papillose, and covered with large, clear spinules from segments 3 through 12 (plate III, 12). These are the largest of the various types of spinules on the third-instar larva (plate III, 16*a*). In moist terrestrial habitats these large spinules lie flat against the integument and are virtually indiscernible with reflected light. Such spinules are totally lacking in first- and second-instar larvae, which spend most of their time in the egg mass of the host. It is possible that in the third instar their function may be to reduce loss of moisture through the integument. In water these spinules stand out from the integument, imparting a pubescent appearance to it at 35X with transmitted light. Such spinules are lacking from third-instar larvae of local *Atrichomelina pubera* Loew, *Dictya texensis* Curran, and *Sepedon praemiosa* Giglio-Tos, and have not been mentioned previously in the published works on sciomyzid biology.

Black-tipped spinules (plate III, 16*c*) occur as indistinct bands in contrast to the well-defined bands of the first- and second-instar larvae, and become virtually obscure on segments 7 through 10.

The short spines just posterior of the anal plate have become 18 to 22 in number and are roughly arranged in two transverse rows. Three or four of these spines are bidentate and are situated singly on an enlarged, slightly pigmented basal area ("pad"). The remain-

der of these spines are simple and one to three occur for each "pad." (See plate III, 16*b*.)

Dorsally, on the ventral lobes of the twelfth segment, occur five or six rows of short small black spines which are arranged in groups of four to seven (plate III, 16*d*).

Puparium (Plate III, 14, 15). The puparium is 4.3 to 5.4 mm in length and 1.8 to 2.2 mm in width. Newly formed puparia are reddish-brown and semi-translucent, becoming nearly brown by the fifth day at 76° F and barely translucent. The puparium in median cross section is nearly circular. The anterior end is flattened dorsoventrally. Segment 1 appears to be invaginated, leaving the second segment with the anterior spiracles prominently displayed as the first apparent segment.

The most striking external characteristic of the dry puparium is the *pubescent appearance* imparted by the clear spinules (described for the third-instar larva) projecting from the integument. In a study of pubescence in the dry state the segmentation of the puparium becomes clearly apparent.

Viewed externally, the *anal plate* (plate III, 17) lies transversely near the anterior margin of the twelfth sternite and appears black in color. Its generally oval outline takes on a bilobed appearance because of the prominent, broadly elliptical and longitudinally oriented anal opening located medially. When excised and viewed anteriorly, the anal plate is seen to be much thicker than the surrounding integument, and the anal atrium extends below it as a blind invagination approximately as long as half the width of the anal plate.

In lateral profile the posterior spiracular stalks are prominent. Lobes of the posterior spiracular disc are inconspicuous.

DISCUSSION

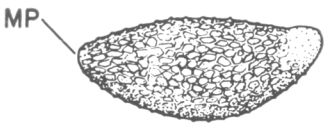
The biologies of the approximately 440 known species (worldwide) within the family Sciomyzidae are not sufficiently known to permit detailed treatment of their phylogenetic relationships nor to determine if they are monophyletic. Berg (1961) delineates a probable continuum based primarily on biology studies of varying depth with 84 species.

Steyskal (1960) considers the genus *Antichaeta* to be "... one of the more highly specialized (apomorphic) of the Sciomyzidae, as shown by the strongly asymmetrical epandrium, the reduced hypandrium and aedeagus, and the extension of the fifth sternite under the postabdomen." Basing his phylogenetic interpretation on adult postabdominal characters of five of the seven known American species (there are also five known Palaearctic species), he considers that the three yellow forms (*A. testacea* Melander, *A. robiginosa* Melander, and *A. fulva* Steyskal) are the least specialized (most plesiomorphic) as evidenced by least-developed asymmetry, least extension of the fifth sternite, and least reduction of the

PLATE II (*opposite page*)

Antichaeta testacea

7. Dorsolateral aspect of the egg. MP—micropyle.
8. Semi-diagrammatic detail of reticulate egg chorion.
9. Mature third-instar larva. Lateral aspect, spinulation not shown. (Refer to text for discussion of characteristic pubescence.)
10. Anterior spiracle of third-instar larva.
11. Ventral aspect of hypostomal sclerite of third-instar larva. HP—hypostomal plates: corresponds in location to Hennig's (1952, p. 120) illustration; HS—hypostomal sclerite; LS—lingual sclerite.



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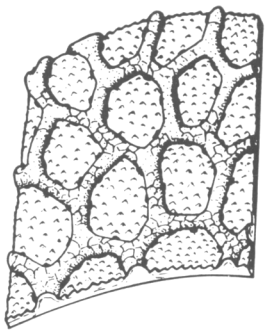

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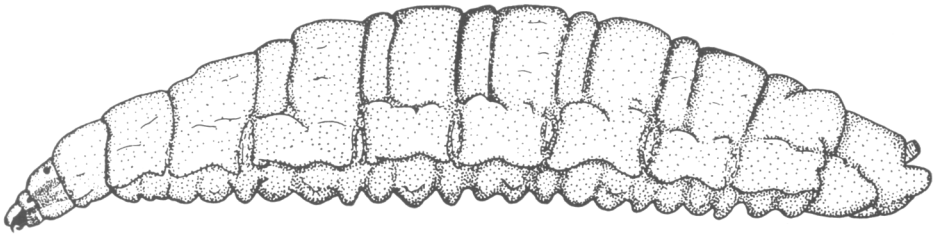

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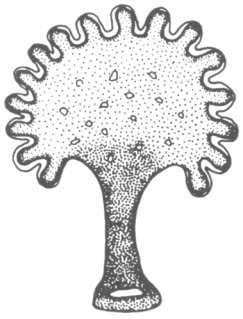

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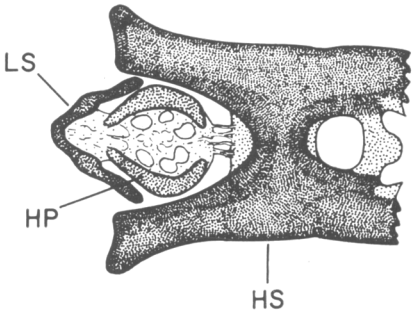

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hypandrium and aedeagus. Foote's (1961*b*) description of *A. borealis* Foote indicates that it should also be included in this group.

Because only two fragmentary biologies of *Antichaeta* (*A. analis* Meigen, *A. melanosoma* Melander) preceded this study (alluded to in Steyskal, 1960; Knutson, 1963), it is not possible at this time to make comparisons based on larval characters or biologies. However, we would like to call attention to certain cross-generic comparisons which seem to lend a unique aspect to the phylogenetic position of *Antichaeta* (Tetanocerinae) among the genera of the family.

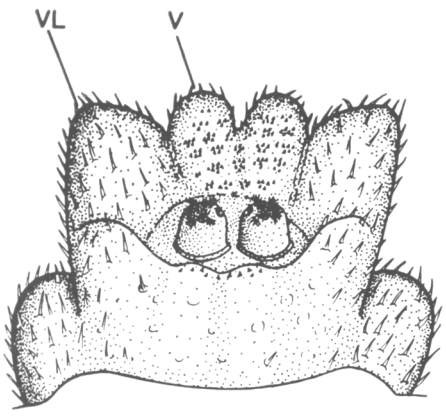
In their publications Berg (of Cornell University, Ithaca, New York) and his former students Foote, Knutson and Neff (see Literature Cited) have stated certain of the characteristics which are considered to be typical of the two American subfamilies of Sciomyzidae. Columns 1 and 2 of table 3 list those characteristics as seen in the Sciomyzinae and *terrestrial* Tetanocerinae respectively. Column 3 gives the status of the same characters for *A. testacea*.

Although dipterists assign the imago to the subfamily Tetanocerinae, and this study places *Antichaeta testacea* among the terrestrial species, it is apparent from table 3 that *A. testacea* possesses characteristics which seem to place it well toward the Sciomyzinae in a credible phylogenetic continuum of species within the family; i.e., the adult exhibits high host selectivity in choosing an oviposition site; first-instar larvae are markedly obligate predators; larvae possess ventral spinule bands (although weakly developed); a dorsal bridge connects the pharyngeal sclerites; a "window" occurs in the ventral cornua; the chorion of the egg is reticulate. It may be significant that toward the beginning of the developmental cycle sciomyzine-like characteristics are rather definite. If these ontogenetic implications are valid, it would appear that *A. testacea* may indeed be more closely related to known sciomyzine flies than to tetanocerines. In addition, two third-instar larval characters not reported for any other known sciomyzid species are: (1) fusion of the hypostomal sclerite with the pharyngeal sclerite; and (2) the "pubescent" integument. S. E. Neff (personal correspondence) has noted these characters in larvae of *Antichaeta borealis* Foote and *A. melanosoma* Foote. We call attention to the fact that the pharyngeal indentation (sinus) is almost exactly half the length of the pharyngeal sclerite. The same length ratio was figured for *Hydromya dorsalis* by Knutson and Berg (1963) without comment. It is possible that this characteristic should

PLATE III (*opposite page*)

Antichaeta testacea

12. Dorsal aspect of eighth abdominal segment of third-instar larva. V—ventral lobe, VL—ventro-lateral lobe. (The large, clear spinules—shown here semi-diagrammatically—are more numerous.)
13. Dorsal aspect of right posterior spiracular plate of third-instar larva. FH—float hairs, SP—spiracular plate, SS—spiracular slit, SSC—stigmatic scar.
14. Dorsal aspect of puparium.
15. Lateral aspect of puparium.
16. Larval spinules.
    a. Clear spinules of third-instar larva.
    b. Bifid spinules just posterior to anal plate of third-instar larva.
    c. Creeping welt spinules of third-instar larva.
    d. Spinule patch caudad to posterior spiracles of third-instar larva.
    e. Lateral stiff spinule on segment two of second-instar larva.
17. Anal plate of puparium.



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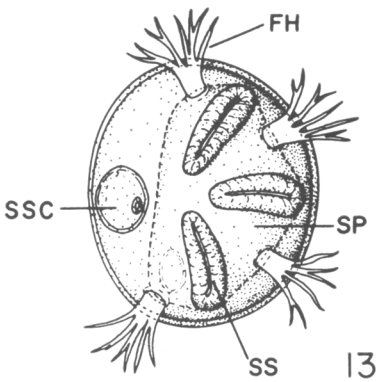

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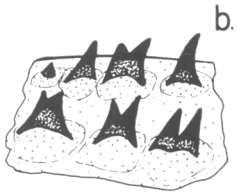

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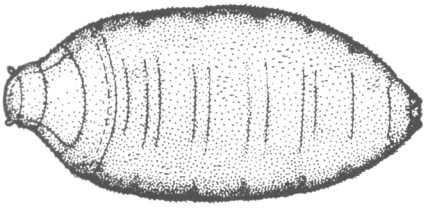

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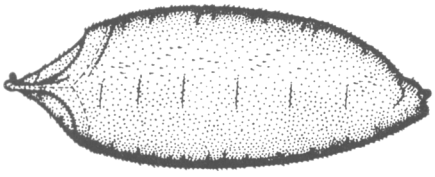

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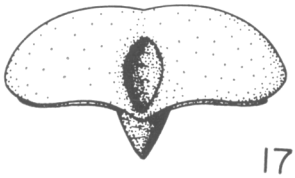

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TABLE 3

BIOSYSTEMATIC COMPARISON OF *ANTICHAETA TESTACEA* WITH SUBFAMILIAL CHARACTERISTICS

Characters	Sciomyzinae	Terrestrial Tetanocerinae	*Antichaeta testacea*
Adult characters:			
Propleural bristle	present	absent	absent
Oviposition site	on or near host snail	on or near host snail	on eggs of host snail*
Pupa:			
Habitat	in shell of host	away from host	in substrate away from host
General appearance	smooth	smooth	pubescent
Larval characters:			
Head retraction	slight	marked	marked
Integument	distinct "creeping welts" of ventral spinule bands; no wartlike tubercles	ventral spinule bands lacking; wartlike tubercles reduced	indistinct "creeping welts" and spinule bands; no wartlike tubercles;* "pubescent" third instar†
Float hairs	absent	reduced to lacking	reduced
Third-instar cephalopharyngeal skeleton:			
Accessory teeth	absent	present	present
Dorsal bridge	present	absent	present*
Hypostomal sclerite	independent	independent	fused with pharyngeal sclerite†
"Windows" in dorsal cornua	present	absent	present*
Pharyngeal indentation (sinus)	>one-half length of pharyngeal sclerite	<one-half length of pharyngeal sclerite‡	closely approximating one-half length of pharyngeal sclerite
Egg:			
Chorion	reticulate	striate	reticulate*

* Sciomyzine attributes.
† Unlike any known Sciomyzinae or Tetanocerinae.
‡ Except in *Hydromya dorsalis* (Knutson and Berg, 1963), wherein this measurement is similar to *A. testacea*.

be considered when contemplating a continuum of sciomyzid species. To speculate, when enough complete biologies are known, sciomyzid genera may be regrouped into more than the four subfamilies now recognized worldwide, and *Antichaeta* may serve as the type genus of a new subfamily.

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