

LIFE HISTORY OF THE VARIEGATED CUTWORM TACHINA FLY,¹ ARCHYTTAS ANALIS²

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INTRODUCTION

This species was described originally by Fabricius (7, p. 311)⁴ in 1805 as *Tachina analis*. It was described as *Jurinia amethystina* by Macquart (10, pl. 3, p. 199) in 1842, as *Tachina apicifera* by Walker (21, p. 718) in 1849, and as *T. californiae* (22, p. 270) by Walker in 1856. During recent years several contributions to the distribution record have been made, most notable of which are those of Brimley (5, p. 21) and Johnson (9, p. 206), and it has several times been recorded as a valuable parasite of the variegated cutworm (*Lycophotia margaritosa* Haw.) and the army worm (*Cirphis unipuncta* Haw.). Sherman (14, p. 301) noted that this parasite emerges from the pupa of its host; and Reinhard (13) found that the adult is strongly attracted to flowers, and he listed the species to which it is attracted in Texas.

During the last two years the writer has been making a biological study of the tachinid parasites of Southern crop pests at the Mississippi Agricultural and Mechanical College. *Archytas analis* has been found to be one of the commonest and most beneficial tachinids in that section. It was discovered that very little concerning the details of its life history had been published, so a considerable part of 1924 was devoted to work with this insect. There are still many points in its biology which have not been definitely established, and others in which the data are rather limited. But considerable new information has been discovered, and since very few contributions to the biology of the group to which this species belongs have been made, the writer wishes to submit his results for publication at this time.

Biologically, this species belongs without question to Group IV of Pantel (11, p. 32) to which Baer (3, p. 203) has recently given the name *Echinomyia* group, and which Townsend has called the *Hystriicine* series (17, p. 132).

DESCRIPTION

The original description of the adult by Fabricius on specimens from South America, "America meridionale," is too superficial to be

¹ A common name suggested by its prevalence as a parasite of the variegated cutworm.

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⁴ Reference is made by number (*italic*) to "Literature cited," p. 434.

of much present-day value in differentiating the species. However, several detailed descriptions of the species are available, and it can be readily determined by the keys in Coquillett's "Revision of the Tachinidae" (6, p. 10, 142). In order to facilitate a preliminary determination, the following diagnostic characters are given.

The adult is a moderately large, robust fly with a tawny yellow pollinose thorax, and a coal-black abdomen. The eyes are naked, ocellar bristles lacking; the third antennal joint is scarcely longer than the second, and is prominently convex on the anterior margin; the proboscis is nearly or quite as long as the height of the head, and the palpi are normal. It is distinguished from the several other closely related species of the same genus by the color of the abdomen and by the sides of the face being clothed with numerous fine white hairs (but lacking bristles) and by the color of the calypteres, which are white.

FIRST-INSTAR LARVA

Elongate oval when viewed from above; strongly compressed; submarginate at the sides, with a distinct groove extending longitudinally between the two lateral ridges. Intersegmentary constrictions well defined. Color grayish-white above, becoming white as the maggot grows. Young maggots (fig. 1) are

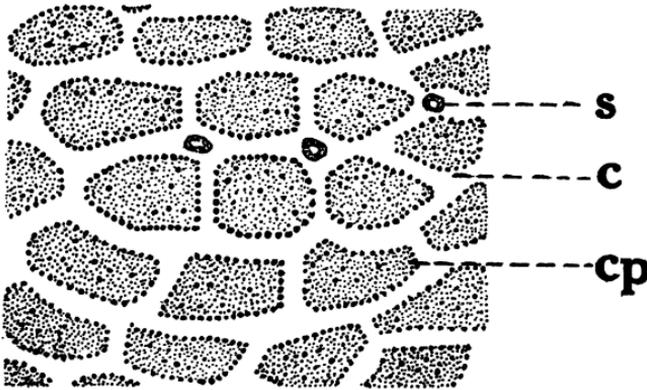


FIG. 1.—Section of the dorsal cuticula of a free living maggot, showing the thickened cuticular plates $\times 600$; c, thinly chitinized space between the cuticular plates; cp, cuticular plate; s, sensorium

covered dorsally by a mosaic of coarse blackish polygonal cuticular thickenings, separated by fine white reticulations, in older maggots becoming separated by wide areas of white cuticula. Cuticular plates are evenly distributed over the dorsum, except at the intersegmentary constrictions, where they are lacking, and extend slightly ventrad of the lateral margin; under high magnification they are seen to be coarsely stippled. Venter of each segment with transverse band of minute serrate spines, not in serried rows. Buccopharyngeal apparatus (fig. 2) without articulations, median hook moderately stout, bluntly tipped, without denticles or dorsal serrations, and with delicate recurved hooks on either side of the extreme front. Dorsal wings of the basal part narrower than the sinus and about as wide as the ventral wing when viewed from the side; lower wing slightly longer than the upper wing. Metapneustic, posterior spiracle with two papillae; atrium (felt chamber) two to three times as long as its width, tracheal system scarcely visible through the cuticula. Free living maggots 0.55 mm. long, 0.13 mm. wide.

This description applies particularly to free living maggots on foliage, and to the early parasitic life in the subcuticular position. In the very much larger first-instar maggot found in the body cavity of the host, the cuticula becomes stretched through growth, the spines and cuticular plates widely separated, and the white delicate maggot is scarcely to be recognized as of the same instar as its free living counterpart.

SECOND-INSTAR LARVA

Triangular in outline when viewed from above, flattened ventrally, dorsum strongly arched, perceptible lateral prolongations in the pleural regions. Color white, cuticula transparent. Small, but well defined black spines in long transverse rows on the anterior half of the ventral part of the thoracic segments; last four segments with extremely minute brown spines in long transverse rows on posterior third or more of the segment, extending ventrally except on the anterior two of the four; elsewhere without spinyarmature. Mouth parts with two articulations; hooks bifid, the two prongs parallel and separated by a deep, slitlike cleft, each provided with a strong rounded ventral denticle and an equal dorsal prolongation ending in a strong point. In profile view, the dorsal wings larger than the ventral, from which they are separated by a sinus scarcely one-third the width of the dorsal wing; basal piece evenly and heavily chitinized to posterior margin. Metapneustic; each posterior spiracle separated by three times width of one; spiracle with two slits, the sides of which are almost parallel to the horizontal plane.

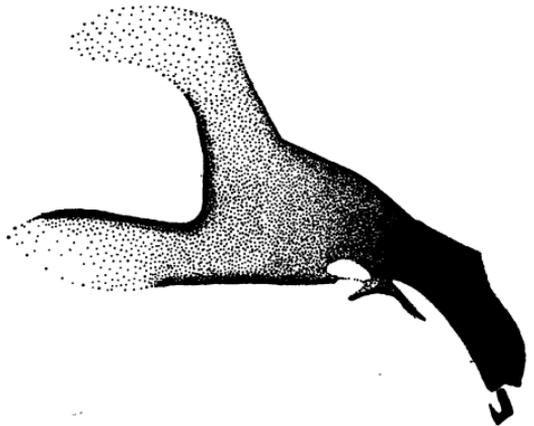


FIG. 2.—Buccopharyngeal apparatus of the first-instar maggot. $\times 400$.

The second-instar maggot occurs in a highly characteristic hump of the wing pad of the living pupa of its host, through the semitransparent walls of which it may often be clearly seen.

THIRD-INSTAR LARVA

Somewhat compressed; triangular in outline when viewed from above (pl. 1, F). Color white, cuticula thin, delicate, transparent. Cuticular armature scanty, consisting of several rows of minute black spines on the anterior part of the thoracic segments, similar spines in undulating rows on the whole surface of the last segment, dorsum and venter of the penultimate and antepenultimate, and venter of the intermediate abdominal segments. In the pleural region there is a very distinct series of three rows of fleshy callosities extending the length of the body. Buccopharyngeal apparatus (fig. 3, A) resembles that of the second instar, excepting that there are three articulations, and the mouth hooks are more bluntly pointed. Amphipneustic; anterior spiracle (fig. 3, D) consisting of two to three small black parallel slits or papillae not protruding conspicuously above the surface of the surrounding cuticula; posterior spiracles separated from each other by less than the width of one (fig. 3, C). Spiracle with three nearly straight slits on smooth, black, elevated ridges (fig. 3, B) converging on a black button located near the middle of the inside margin.

The large third-instar maggot occurs in the dead pupa of its host, the cavity of which is almost completely filled with its soft white body.

Greene's description of the puparium (8, p. 26) is as follows (fig. 4):

Large; dull, dark red, with a faint indication of a depression or stricture at the posterior end. Spiracles shining black, slightly raised above the surface, separated by a space nearly equal to the width of one plate. Each plate has three slits, each located at the top of a well-defined ridge. Button fairly large, round. Spiracles above longitudinal axis, about two-thirds the width of one plate. Anal opening very small, far below the spiracles. Length, 10.5 mm.; diameter, 4.75 mm.

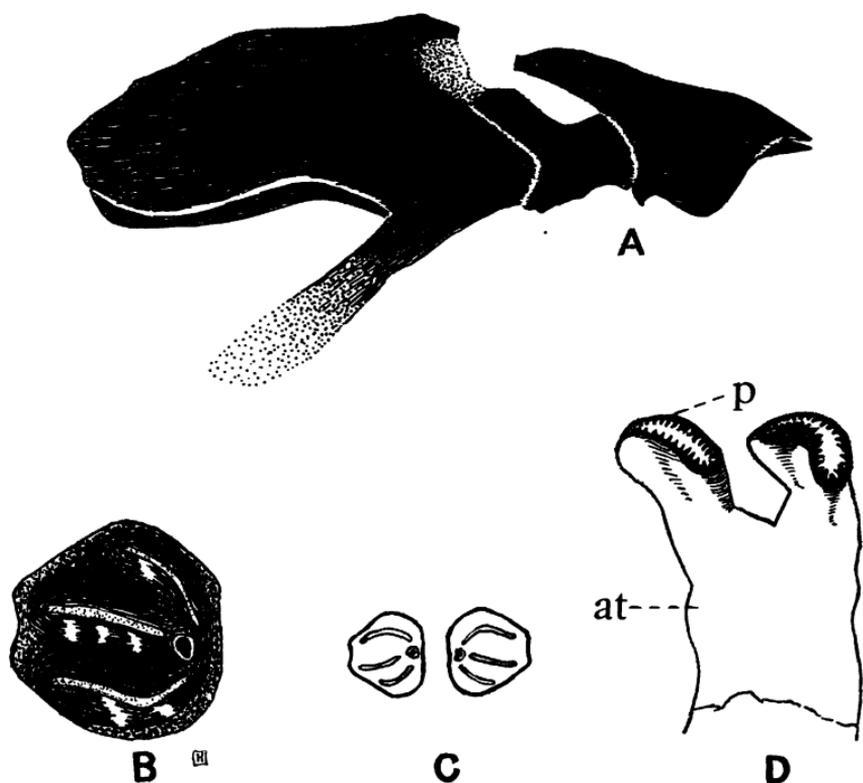


FIG. 3.—Details of structure of third-instar larva. A, buccopharyngeal apparatus, $\times 40$; B, posterior spiracle, $\times 20$; C, outline of both spiracles, showing their relative position, $\times 8$; D, anterior spiracle, lateral aspect, $\times 96$; at, atrium; p, papilla

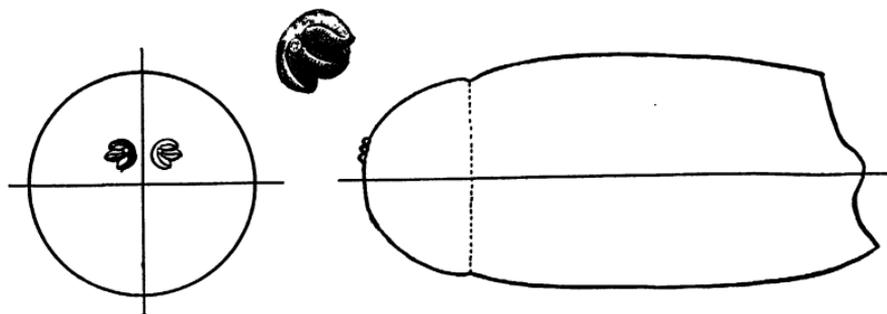
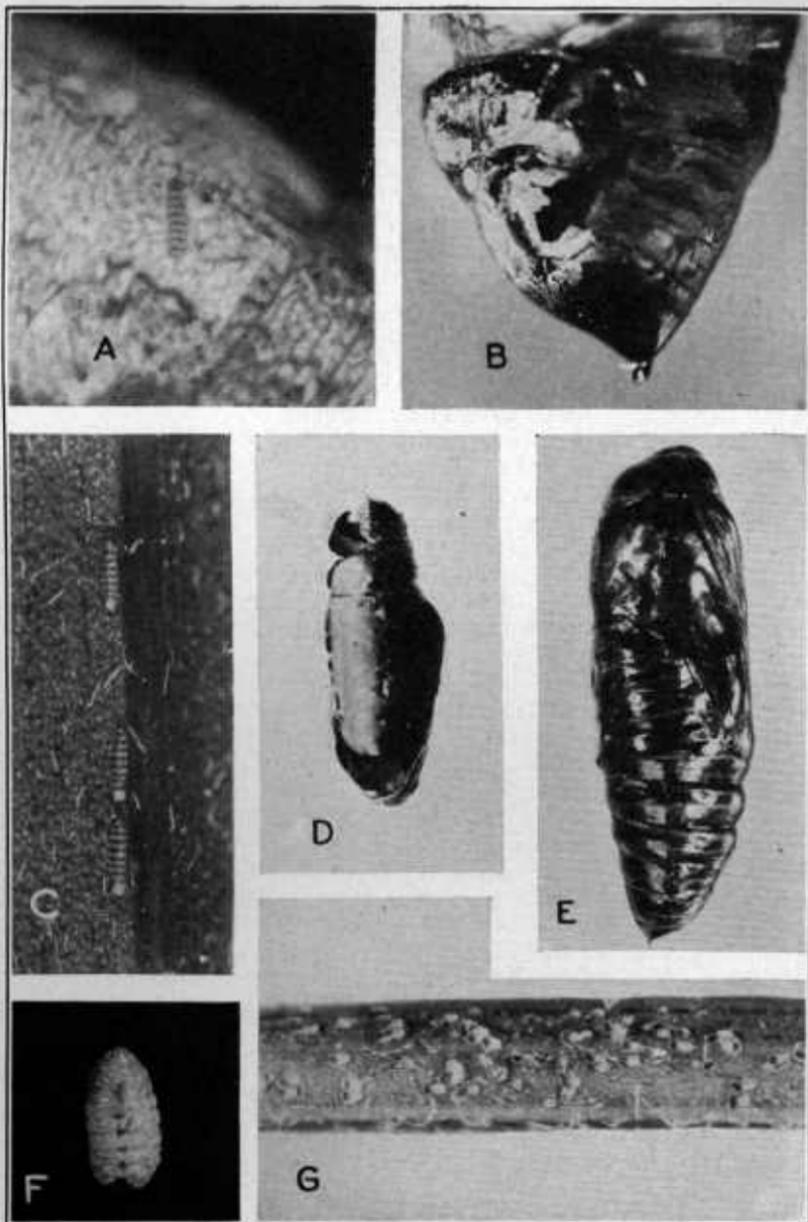


FIG. 4.—Details of the structure of the puparium, showing the outline when viewed from the side, the location of the posterior spiracle when viewed from behind, and the detailed structure of the posterior spiracle. (After Green)



A.—First-instar maggot in subcuticular position in variegated cutworm. $\times 25$
 B.—Posterior end of pupal case, showing characteristic breathing slit torn by the third-instar maggot of *Archytas analis*. $\times 25$
 C.—Free living first-instar maggots seated in cuplike attachment, and lying closely pressed to the substratum. $\times 25$
 D.—Puparium in position in pupal case of host, the upper half of which has been removed to show position of puparium. $\times 3$
 E.—Pupa of the variegated cutworm, showing the characteristic swelling of the wing-pad produced by the presence of the second-instar maggot of *Archytas analis*. $\times 5$
 F.—Third-instar maggot, dorsal view. $\times 2.5$
 G.—Membranous attachments of free living maggots remaining on the substratum after the maggots have disappeared. $\times 30$

LIFE CYCLE

The life cycle of this species was worked out under out-of-door insectary conditions. Adults were maintained very satisfactorily in wooden cages with a base 6 by 10 inches and a depth of 4 inches. The bottom of the cage was kept covered by moist earth, and over the top was placed a tightly fitting glass plate. In one end of the cage a 1-inch hole plugged with cotton served partly for ventilation, but particularly for added convenience in manipulation. Food and water were provided and changed daily. In order to facilitate the daily manipulations, a special cage was built inside the insectary, just large enough to give working space to one worker with a breeding cage. One wall facing the light was screened. All the other walls were covered with black cloth to shut off the light. It was found that flies leaving the cages, when food and water were being changed, would almost invariably remain on the outside screen, responding to their strongly positive phototropic instinct, and were readily picked up in small vials and returned to their proper cages when ready to receive them once more. Sugar water, diluted honey, and mashed banana spread on small pieces of cardboard were furnished for food, and whenever possible sprigs of melilotus bloom, or other favored host-plant flowers were placed in the cage with the stems in water, and maintained with the other food. Water was furnished from saturated sphagnum moss in 1-ounce salve boxes. Larviposition was readily obtained on herbaceous foliage in the insectary. From such stock, transfers of maggots from foliage to caterpillar were readily accomplished by laboratory manipulation. Infested caterpillars were thereafter maintained in 1-ounce tin salve boxes, jelly glasses partly filled with soil, or under inverted jelly glasses placed over flower pots filled with soil. Puparia were maintained most successfully in sphagnum moss just wet enough to feel moist to the touch.

Adults mate almost immediately after the emergence of the female. Mating is followed by the preovispositional period during which time the ova in the body of the female are fertilized. During the same period the fertilized ova pass down the long, more or less quadrate uterovagina, where they develop into active maggots inclosed in a thin chorion sheath. Females, after reaching maturity, desposit minute maggots in enormous numbers on the stems, leaves, and flowers of the hosts' food plants. The maggot lies more or less quiescent on the substratum upon which it was deposited, until a suitable host caterpillar passes within reach, when the maggot attaches itself to the body of the caterpillar and crawls to some protected place where it again becomes quiescent. It then bores through the integument, a process requiring several hours, penetrating obliquely, and taking a position between the hypodermal layer and the cuticula. After spending several days in this position, the maggot penetrates the body cavity, in which it passes over into the pupal stage of the host. Here it occurs first in a sort of cradle in the bulging wing-pad, with a breathing pore to the outside. The death of the pupa soon takes place. In its rapidly putrifying contents the maggot completes its development and invariably pupates within the pupal case of its host, from which the fly emerges a few days later.

DURATION OF THE LIFE STAGES

The durations of the various life stages of *Analisis* have been summarized in Table I which may require a few words of explanation and qualification.

TABLE I.—Duration of the life stages of *Archytas analis*

Life stage	Time of experiments	Number in experiment	Duration in days		
			Minimum	Maximum	Average
Adult:					
Preovipositional	Middle of June to middle of August.....	9	8	19	10.6
Larvipositional	Middle of June to late August.....	7	3	30	13.3
Longevity—					
Males	Late June to early September.....	16	2	53	19.9
Females	do.....	20	1	47	23.9
Both sexes.....	do.....	36	1	53	22.0
Larva:					
Free living—					
Lot 1	Late April to early June.....	31	2	31	18.1
Lot 2	July.....	90	4	16	-----
Parasitic—					
Lot 1	May.....	1	24	24	24.0
Lot 2	Late June to late July.....	23	7	18	11.6
Lot 3	Late August to middle of September.....	3	13	18	16.0
Puparium:					
Lot 1—					
Males	Late May to middle of June.....	9	10	13	11.0
Females	do.....	6	11	12	11.8
Both sexes.....	do.....	15	10	13	11.4
Lot 2—					
Males	July.....	9	10	11	10.4
Females	do.....	12	11	13	11.6
Both sexes.....	do.....	21	10	13	11.1
Lot 3—					
Males	September.....	2	13	13	13.0
Females	do.....	2	14	14	14.0
Both sexes.....	do.....	4	13	14	13.5
Combined parasitic larva and puparium:					
Lot 1	Late June to early August.....	23	19	30	22.6
Lot 2	August.....	4	21	23	22.0
Lot 3	Late August and September.....	4	25	31	28.5

*Approximate.

The prelarvipositional and also the larvipositional period was determined for females copulating on the day of emergence, fed and watered daily, and allowed to run with males until the death of the latter. During the larvipositional period maggots were not deposited every day, 1 to 3 days frequently elapsing without larviposition. Death of the female was customarily preceded by 1 to 5 days of reproductive inactivity; in one case, after 5 days of normal larviposition, by 23 days of inactivity. Three-fourths of the maggots obtained in this experiment were deposited in from 10 to 20 days following the emergence of the female. Adult longevity was determined from specimens maintained in the insectary in the normal manner throughout the hotter summer months.

The free living first-instar maggots are remarkably hardy. Their longevity was found to vary considerably with the season, being longer in the cooler months. In lot 1, individuals attached to short

sections of melilotus stems were maintained in the insectary in covered jelly glasses, under somewhat unfavorable conditions. In lot 2, about 90 maggots were deposited on July 1, on a small potted melilotus plant, which was maintained in a vigorous growing condition throughout the experiment, and upon which the surviving maggots were counted each day. Maggots began to die on the fourth day, the death rate remaining very low until the eighth day, then increasing rapidly until the death of the last one on the sixteenth day. Maggots deposited on sprigs of Amaranthus and chrysanthemum, in the late fall, passed the short, mild winter successfully, the majority remaining vigorous for more than a month, some surviving until February 25, with a longevity of at least 52 days. At the end of this long period, the substratum had become incrustated with mold, more or less desiccated, and to all appearance highly unfavorable to the health of the attached maggots. In all probability, maggots deposited at the same time on the foliage of hardy plants in the field came through the winter in much better condition. The longevity of the free living maggots is not an exact measure of the period during which they are infective. Maggots on the substratum are often so weak for several days before they perish that they are unable to effectively establish themselves on a passing host. It was found, however, that the maggots, deposited and maintained on potted melilotus under conditions approximating the normal, were able to establish themselves readily and to penetrate the body of the host up to 14 days after deposition, even during the most unfavorable midsummer weather. The effective longevity of free living maggots during the cooler months was not determined, but is undoubtedly much longer.

The maggot duration on and in the host is highly variable, depending directly on the time required for the host to attain its pupal stage, and indirectly on the instar of the host infested, the degree of divergence from optimum temperature for the host, and other factors. Durations under the influence of variable temperatures are indicated in the three lots in Table I. The host for lot 1 was the variegated cutworm; for lot 2, the yellow-striped army worm (*Prodenia ornithogalli* Guen), in the last three instars; and for lot 3, *Cirphis juncicola* Guen, in the last two instars. The pupal period was determined at three different times, and it also was found to vary with the season, but not to such a marked degree as the parasitic larval stage. The combined maggot and pupal duration from the time of infestation of host to the emergence of the adult fly was determined for three different lots, and constitutes a more precise determination of the duration of this period than that obtained by combining the separate data of larval and pupal durations. Lots 1 and 2 were reared from the yellow-striped army worm, lot 3, from *Cirphis juncicola*.

The duration of the life cycle during the active developmental season was found to be as follows: Prelarvipositional adult life 8 to 19 days, larvipositional life up to 30 days, free maggot life 0 to 31 days, parasitic maggot life 7 to 24 days, puparium 10 to 14 days, with a minimum of 25 days and a maximum of 118 days for the completion of the cycle. The overwintering generation almost certainly has an even longer cycle, but its duration has not been determined.

SEASONAL CYCLE

The seasonal cycle has not been fully worked out. In north central Mississippi there seem to be two complete broods each year. The earliest-appearing individuals of each of these broods pass through to maturity in a comparatively short time, giving rise to several partial broods. But the life cycle of the late-appearing individuals of each brood is much extended, producing broadly overlapping generations from very early in the season. In the insectary during the season of 1924 the beginnings of five distinct broods were obtained, and in the field during the same period there may have been one or two more.

The manner in which *Archytas analis* hibernates has not been definitely determined. Free living maggots on substratum succeeding in passing the winter successfully in the insectary, some surviving as late as February 25, after withstanding more than one exposure to freezing temperature and a very long inactive period on the substratum. All died, however, in the early spring before suitable caterpillar hosts could be provided, and it appears to be by no means certain that in the field the winter is successfully passed in this stage.

HABITS OF THE ADULT

FEEDING

Reinhard (13) has collected adults of *analis* from broomweed (*Amphiacyris dracunculoides*), bitterweed (*Helenum tenuifolium*), wild aster (*Aster lateriflorus*), *Rudbeckia bicolor*, sweet clover (*Melilotus alba*), and prairie cacia (*Cecuan illinoensis*) in Texas. Townsend (16, p. 177) has taken them from flowers of *Lippia lanceolata* in the same State. Aldrich (2, p. 83) records taking them from sweet clover and golden rod.

In common with other tachinids possessing an elongate proboscis, this species is preeminently a flower-visiting, nectar-feeding species. Several flies collected on melilotus have been dissected and the crops examined. In all cases the crops were distended with a clear fluid, not mixed with pollen grains or other solid substances, and giving a strong positive reaction to Fehling's solution, indicating the presence of glucose. In Mississippi the adults are most commonly attracted to the flowers of herbaceous plants in open fields, they having been frequently observed in conspicuous swarms at the flowers of sweet clover, hairy vetch, smartweed (*Polygonum pennsylvanicum* L.), chrysanthemum, and at the flowers and nectaries of smooth vetch. They have also been noted less frequently at the flowers of crimson clover, *Chaerophyllum Teinturieri* Hook, *Geranium carolinianum* L., the wild sweet pea (*Lathyrus pusillus* Ell.), *Bidens aristosa* Brit., *Aster ericoides pilosus* Port., and soy bean. While they are usually attracted to herbaceous plants, shrubs or even tree tops are visited in search of food, a few adults having been observed feeding from the flowers of *Spirea vanhouttei*, and at the nectaries on the leaf petioles of peach. While nectar is unquestionably the principal food of the adult, honeydew is sometimes taken, adults having been observed feeding on honeydew-smearred foliage of tulip trees (*Liriodendron tulipifera* L.) beneath a heavy infestation of the tulip tree soft scale

(*Toumeyella liriodendri* Gmel), and on the foliage of turnips covered with the honeydew of the turnip aphid (*Rhopalosiphum pseudobrassicæ* Davis). In confinement, adults feed very freely on sugar, diluted honey, mashed banana, and similar sweets.

COPULATION

Copulation has never been observed in the field, but in insectary cages there was plenty of opportunity to observe it between females only a few hours from the puparium and males a day or more old. The sexes remain in coitu from four to five minutes. Fertilization of the female in the field undoubtedly takes place almost as soon as its wings have expanded.

LARVIPOSITION

Deposition of larvæ has been noted occasionally in the field, and many times in the insectary. As the female walks over the stems, she frequently touches the substratum with the tip of her abdomen, depositing thereon a maggot. Covering the posterior end of the maggots being deposited is a minute membranous cup. At the time of deposition the female fastens this cup securely to the substratum, furnishing the maggot with a fixed base but leaving the remainder of its body free. At the height of its larvipositional period the female may deposit as many as 10 to 12 maggots per minute. Periods of deposition alternate with periods of rest. With flies confined in cages it was found that on those plants having both stems and leaves a large majority of the maggots were deposited upon the stems, but some were also deposited on the leaf surface, stipules, blossoms, in fact, any succulent exposed part of the plant. When deposited upon leaf blades, the under side was preferred. Flies in confinement larviposited quite freely on the foliage of several species of herbaceous plants, none being avoided. Prell (12) has advanced the idea that adult tachinids are attracted to infestations by a more or less diffuse infestation odor, but that these flies, when once present in an infestation, utilize something other than the sense of smell to locate the individual parasite. Such a diffused infestation odor was undoubtedly present under insectary conditions, but larviposition was at all times readily obtained in cages without the stimulation of the actual presence in the cage of host caterpillars. Maggots are usually deposited with their axes parallel to that of the stem or leaf upon which they are placed.

SEGREGATION OF SEXES IN THE FIELD

Adults were collected at frequent intervals during the summer of 1924. The proportion of the two sexes bore no fixed relation to the normal, and indicated sexual segregation in the field, as may be noted in the following tabulation:

TABLE II.—Showing periodical fluctuation in proportion of sexes in the field

Date	Males	Females	Where collected	Date	Males	Females	Where collected
Apr. 15	0	2	Flowers of crimson clover.	Aug. 18	0	1	Flowers of soy bean.
Apr. 21	0	3	Smooth vetch.	Aug. 19	0	2	About colony of fall army worm.
May 15	0	1	On wild sweet pea.	Do.---	0	4	At nectaries of cowpea.
May 19	3	0	Nectaries of peach.	Aug. 23	0	1	About colony of fall army worm.
June 10	1	1	Flower of melilotus.	Aug. 24	0	1	At nectaries of cowpea.
June 17	4	0	Foliage under pecan trees.	Sept. 10	8	1	Over ground previously infested with fall army worm.
Do.---	15	0	Grass under apple orchard.	Do.---	1	1	Flowers of Bidens.
June 20	8	2	Flowers of melilotus.	Sept. 15	1	1	Over Johnson grass.
June 23	9	1	Do.				
July 6	2	3	Do.				
July 11	3	0	Do.				
July 26	1	0	Do.				

A study of the above grouping will show that in regard to the proportion of sexes, four rough seasonal divisions can be made. The first, from April 15 to May 15, in which only females were encountered, coincides roughly with the period of local infestation of the variegated cutworm when the caterpillars were abundant. The second, from May 19 to July 26, represents the main swarming period for analysis for the season, when adults were present in enormous numbers at the flowers of melilotus. During this period both sexes were present, but males were several times more numerous than the females. This period was contemporaneous with the emergence of analysis and the surviving host adults from the heavy local infestation of variegated cutworm. Reestablishment of the infestation failed to occur, and no suitable hosts were at that time locally abundant. The third period, from August 18 to August 24, was again marked by the presence of numerous females, and practically no males. This period coincided with heavy outbreaks of the fall army worm (*Laphygma frugiperda* Guen) mixed with *Cirphis juncicola*, about which the adult flies were abundant. The fourth period, from September 10 to September 15, was marked by the presence of many males and only a very few females, similar to the second period. It coincided with the emergence period of parasites and host adults from the colonies of the fall army worm and *Cirphis juncicola*. Here again the hosts failed to reestablish the infestation, practically vanishing from the locality, and no caterpillars suitable for parasite attack could be found in the vicinity.

The underlying reasons for this segregation, from the limited nature of the data, are highly conjectural. The preponderance of males at one time and females at another can not be explained by differences in proportion of sexes, which were always nearly equally divided in insectary rearings; nor by differing times of emergence, for in all insectary work, the males come out only a day or two at the most before the females; nor by the early death of the males, for their longevity, as determined in the insectary, is only slightly less than that of the female. Adults of analysis are powerful in flight, and it seems quite likely that females, after being fertilized, if suitable hosts are not locally abundant, migrate out of the region in which they have passed their parasitic existence, leaving the males behind to mate with the other females as they emerge from day to day.

It is certain that the seasonal fluctuations in abundance of adults in the field, which are so conspicuous, should in no way be interpreted as the flight periods of well differentiated broods, but rather as variations in the status of the parasite due to the constantly changing conditions in the abundance of foods and favored hosts.

ACTIVITY IN RELATION TO METEOROLOGICAL CONDITIONS

Adults of *analis* are active in the field under wide extremes of atmospheric conditions. In midsummer they frequently have been observed displaying normal activity in dry open fields, at midday with the temperature as high as 94° F. and the relative humidity from 52 to 59 per cent. The normal hosts are not usually found in abundance under such extreme conditions of heat and dryness. These observations indicate that the adult parasite can withstand any degree of heat and dryness not inhibitive to the host. At the other extreme, it has been observed that adults may be found in the cold, early winter days, when nearly all other adult tachinids have disappeared. Thus adults of *analis* have been taken flying about flowers on a chilly, cloudy day with the temperature at 67° F. In insectary experiments, adults were inactive at temperatures below 63° F.; from 63° to 73° their activity was limited to walking, running, and sluggish flying; at temperatures above 73° they were very active.

HABITS OF THE LARVAE

FIRST INSTAR

So long as they are not disturbed, the free living maggots remain seated in the basal cuplike membrane, as deposited by the female, with the body lying quiescent and closely pressed to the substratum (pl. 1, C), in a position in which they are manifestly protected from the rigors of adverse atmospheric conditions by the dorsal covering of thickened cuticular plates. As Prell has indicated in the nearly related *Panzeria rudis* (12), further protection is afforded by the basal membrane, which partially seals the only functional spiracle possessed in this stage. Whenever the substratum is disturbed, the maggot rears upwards (fig. 5) on its posterior end, swinging the head about in wide circles in an attempt to touch its host. Frequently, in its excess of excitement, a maggot will deliberately crawl away from its basal attachment to the substratum in order to bring itself within striking distance of its host, whose presence it has perceived. A maggot failing to make a suitable contact subsides to the original position closely pressed to the substratum. If, however, it strikes the body of a passing host it immediately releases itself from the basal membrane, which remains attached to the substratum (pl. 1, G), and crawls onto the body of the host. Maggots attach themselves readily to at least the last three larval instars. Maggots on substratum exhibit some powers of differentiation of possible hosts, but this power is manifestly not very highly developed. For instance, maggots attach themselves quite readily to caterpillars of the variegated cutworm, the army worm, the fall army worm, all of which serve as normal hosts, as well as the yellow-striped army worm and *Cirphis juncicola*, from which they have been reared after artificial infestation. But they will also attach themselves readily to the beet army worm (*Laphygma exigua* Hueb.), the grape leaf-folder (*Desmia*

funeralis Hueb.), the garden webworm (*Loxostege similalis* Guen.), and the dingy cutworm (*Feltia subgothica* Haw.). Into two of the latter, namely the beet army worm and the dingy cutworm, the maggots were able to penetrate in a normal manner, but they failed to complete their development, and there is no record that any of these ever serve as normal hosts. On the other hand, some caterpillars are deliberately refused. Maggots brought into contact with the caterpillars of the corn-ear worm (*Heliothis obsoleta* Hueb.), the granulate cutworm (*Feltia annexa* Treit.), the cabbage looper (*Autographa brassicae* Riley), and the bagworm *Thyridopteryx ephemeraeformis* Haw.) persistently refuse to attach themselves. None of these caterpillars are normal hosts.

After attaching itself to the body of its host the maggot crawls about for a few minutes, usually coming to rest in some more or less protected fold of the cuticula. Among 257 maggots allowed to establish themselves on host caterpillars confined with them in breeding cages, it was found that the venter and pleuron of the host body was preferred to the dorsum, and that many more sought out the first five segments than the other segments of the body, though maggots were generally scattered over all parts of the body, except the heavily chitinized head. The maggot exudes a liquid substance which on drying fastens its body securely to the cuticula of the host, where it may remain quiescent for 24 hours or more. It finally cuts a hole in the cuticula, and slowly works its way into the body, entering at an extremely oblique angle, so that it lies just beneath the cuticular and between it and the hypodermal layer, where it can be distinctly seen from the outside in caterpillars having a thin cuticula (pl. 1, A). Penetration is effected without leaving a scar, and no surface breathing pore with the attached breathing funnel is maintained. Subcuticular maggots, while still in the first instar, and while the host is still an active caterpillar, bore through into the body cavity, where they appear to wander freely about until the end of the feeding period of their host. At this time the maggot takes up a fixed position in the thoracic region, molting there to the second instar as the host is transforming to the pupal stage. Many maggots may penetrate the body of the host, but rapid reduction in numbers takes place among those which penetrate the body cavity, so that when the second instar is reached only two or three remain alive.

SECOND INSTAR

The presence of the young second-instar maggot in the newly formed pupa induces the production of a delicate membranous sheath, which is somewhat more heavily constructed toward the wall of the host. The maggot within this sheath is found in the newly formed pupa cradled in a highly characteristic bulge of the wing pad (pl. 1, E). No breathing funnel is developed, but the posterior



FIG. 5.—Free living, first-instar maggot, in characteristic erect position, seated in its cuplike attachment to the substratum. $\times 50$

spiracles of the maggot are applied to a rupture at the lower end of the wing pad, through which air is obtained. After pupation of the host, maggot development is much accelerated, the maggot growing rapidly, killing its host at the end of the second or the beginning of the third instar.

THIRD INSTAR

At the death of the pupa the third-instar maggot grows very rapidly, living largely on decaying tissues, all of the softer parts being consumed, the maggot becoming so large as nearly to fill the interior of the host pupa with its bulk. In this instar the maggot obtains its necessary supply of air by cutting a minute hole in the extreme front of the pupal case, to which the anal spiracles are applied as it works toward the posterior end of the pupa. When feeding is nearly completed, several much larger slits are torn about the periphery of one of the segments near the anal end (pl. 1, B), so that the latter is frequently nearly severed. The maggot then faces about so that its anterior end lies in the anterior end of the pupal case, and pupates, the puparium completely filling the middle part of the host pupal case (pl. 1, D).

RELATION OF THE PARASITE TO ITS HOST

The host caterpillar displays no marked irritation when the maggots attach themselves to its body, crawl over the surface, or even when they penetrate the cuticula. Unless heavily overstocked with maggots, it completes its development to the pupal stage in a normal manner, the presence of several maggots in their first instar producing neither abnormal symptoms nor appreciable lesions in their host. In the variegated cutworm, pupation normally occurs in an earthen cell an inch or more beneath the soil surface. During its early pupal life in this cell the host succumbs to the parasite, which completes its development on the disintegrated contents of its host, transforming to a puparium in its empty pupal case.

Rather early in the season a number of variegated cutworms were dissected to study the development of the parasite within its host. In this lot it was found that first-instar maggots occur in the subcuticular position up to about 15 days from time of penetration, second-instar maggots were encountered from the sixteenth to the twenty-second day, and the third instar from the twenty-second to the twenty-sixth day.

The speed of development of the parasite, which must necessarily await the pupal stage of the host before being enabled to complete its parasitic existence, is largely dependent on the rate of development of its host. This is shown very clearly in Table III. Those caterpillars infested in their last instar allowed the parasite to complete its development to the adult in 20 days and those infested in the penultimate instar in 22.2 days.

TABLE III.—Difference in speed of development of maggot attacking different instars of the host

Instar of host when infested	Number in experiment	Number of days from—						
		Infesting to host, a prepupa	Host, a prepupa, to host a pupa	Host, a pupa, to pupal death	Pupal death to formation of puparium	Total maggot duration	Formation of puparium to fly emergence	Total maggot and pupal duration
Last.....	10	4.0	1.5	1.6	1.5	8.6	11.6	20.0
Penultimate.....	6	4.5	2.2	2.0	2.6	11.3	10.9	22.2
Antepenultimate.....	6	9.1	1.8	2.1	1.8	14.8	10.6	25.4
Averages.....		5.9	1.8	1.9	2.0	11.6	11.0	22.6

The antepenultimate-instar caterpillars, which required considerably longer time to attain the pupal stage allowed their parasites to emerge only after 25.4 days. It was also determined that the rate of development of the parasitic life was not appreciably influenced by the duration of the preceding free living maggot stage, whether the latter was of only a few hours duration or a matter of days.

FECUNDITY

The reproductive power of *Archytas analis*, as with other parasites depositing their progeny on the food plant of the host, is very high. The largest number of maggots deposited by an insectary-reared female was 579, and by any captured female, 531. The average number produced by insectary-reared females was 270, and the numbers deposited daily ranged from 0 to 290. These numbers are very probably less than in the field under more favorable conditions. One laboratory-reared female, dissected before larviposition began contained 890 maggots and undeveloped ova. This great reproductive power is largely counterbalanced by the high percentage of ineffectives among the free living maggots, comparatively few of which are ever confronted with an opportunity to establish themselves on a host.

DISTRIBUTION

Archytas analis is generally distributed throughout the United States (fig. 6), where it has been reported from all sections, excepting the extreme Southwest. It also occurs in southeastern Canada (1, p. 485), Santo Domingo, Jamaica, St. Vincent, Colombia, and Venezuela. It has not been reported outside of the Americas. While it appears that this parasite is present only in the Western Hemisphere, it has, within the limits of its range, become adjusted to a very wide variation of climatic conditions, being present from the north temperate to well into the tropical zone, and in the United States from the semi-arid Southwest to the humid forest region of the East and far West.

HOSTS

This species is moderately polyphagous, so far as known, attacking only caterpillars. It has been reared from seven different hosts represented by two families, the Noctuidae and Lasiocampidae. The variegated cutworm is undoubtedly its principal host throughout most of its range. It is also of considerable importance as a parasite of the army worm. Vickery (18, p. 391), records it as a parasite of the two nearly related species, *Cirphis latiuscula* H. and S. and *C. multilinea* Walk. In Colorado it has been reared from 2 species of tent caterpillars, *Malacosoma californica* Pack (15, p. 70) and *M. fragilis*

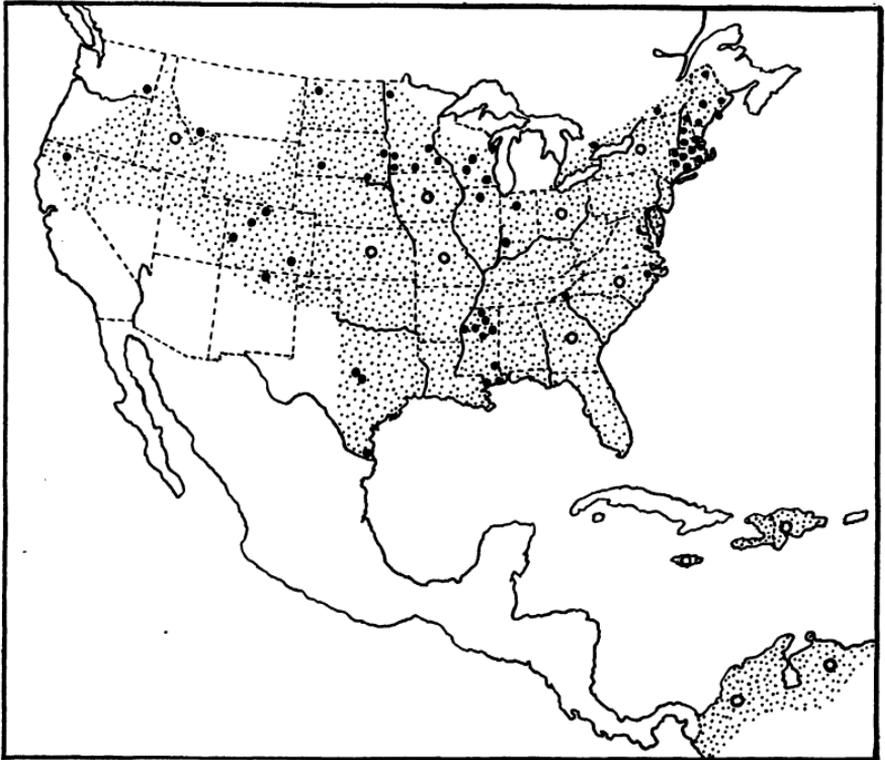


FIG. 6.—Map showing distribution of *Archytas analis*. Large dots represent locality records. Circles represent state or national records

St. (4, p. 174). In Mississippi it has been reared from the variegated cutworm and the fall army worm. It has been inoculated upon and reared quite successfully upon the army worm, *Cirphis juncicola*, and the yellow-striped army worm. Though the latter proved to be an excellent host for insectary work, *analis*, strange to say, has never been reared from material of this species collected in the field.

ECONOMIC IMPORTANCE

During the spring of 1924, in Mississippi, this species was reared from 14.9 per cent of the variegated cutworms captured during the last three instars. Last-instar caterpillars were most heavily parasitized, in one lot 36 per cent being destroyed by this parasite. During 1925, 22 per cent were parasitized. These percentages are

undoubtedly somewhat less than the total proportion of the infestation destroyed by *analisis*, for while the earlier instars are readily attacked, the last-instar caterpillars are naturally much more liable to be parasitized, since they have lived a longer time exposed to infestation. *Archytas analisis* has also been cited as a natural control of the variegated cutworm in Colorado (20, p. 18), and Wadley (19, p. 276) states that this pest was heavily parasited by it in Kansas in 1915 and in Iowa in 1919. Though it has been mentioned from several localities as a parasite of the army worm, no precise information is available as to its effectiveness on this host. During the last two seasons, at the Mississippi Agricultural and Mechanical College, with moderate numbers of army worm present, *analisis* parasitism has been negligible. The writer was surprised at obtaining the parasite from the fall army worm; however, the record is unquestionable, since determination of the host was checked by examination of the pupal case after the fly had emerged. Its occurrence in the fall army worm is not common, and as a natural control of this pest is not important. It has been reported as a parasite of tent caterpillars, but its true value as a natural control for these pests has not been determined.

The possibilities for manipulation of this parasite, for the purpose of increasing its effectiveness, are much greater than for most tachinids. It displays great fondness for the nectar of certain food plants. Some of these, fortunately, are valuable legumes, the cultivation of which would not only serve to induce beneficial concentrations of these parasites, but they have an important place in improved farming methods. Melilotus and the vetches are particularly favored by *analisis* adults. Certain other plants, such as *Polygonum pennsylvanicum*, which grow in great profusion on waste land and attract great numbers of the adult flies of this species, and which are regarded as weeds, might often be left standing with profit until after the blooming period is past.

It was found that free living maggots on stems of melilotus, the bases of which were wrapped in a ball of moist sphagnum moss, were able to withstand a five-day trip by mail, even in hot mid-summer weather, coming through with a fairly high percentage of active living maggots. Such material could be readily obtained, shipped several hundred miles, and colonized. Free living maggots packed in sphagnum moss did not, however, respond favorably to retention in cold storage, none surviving a 30-day exposure to temperature varying from 37° to 40°.

The ease with which this species can be reared in confinement, and infestation of its hosts obtained, together with its enormous powers of reproduction, combined with the fact that it is an effective parasite of at least two highly important crop pests which are not always controlled by artificial methods, makes it a highly promising subject for experimentation in the field of biological control.

SUMMARY

Investigations were made upon the life history of *Archytas analisis*, at the Mississippi Agricultural and Mechanical College in 1924. The parasite was found to be one of the group which deposits maggots on the foliage frequented by the host. These free living maggots,

which may live on the substratum for many days, attach themselves to passing caterpillars, if they are acceptable hosts, and bore through the cuticula to a position between it and the hypodermal layer, later passing into the body cavity, where they persist in the host until its pupal stage. The puparium is formed in the pupa of the host, only one parasite completing its development in each pupa. The time durations of the different stages differ widely with the season, the instar of the host when infested, and the time spent as a free living larva. There appear to be at least two complete and several partial broods each season. Adults are preeminently nectar suckers, and congregate in swarms at the flowers of sweet clover and a number of other common wild and cultivated plants. They are powerful flyers and there is some reason to believe that they migrate rather freely. They are present from early spring to late fall and are adapted to activity in wide extremes of weather. The parasite is broadly distributed over North America and parts of South America. It is moderately polyphagous, attacking several species of Lepidoptera. It is undoubtedly a valuable natural control for the variegated cutworm, and is also of some value as a parasite of several other caterpillar pests. It offers more promise than some species as a possibility in the field of biological control.

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