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# BIOLOGY AND IMMATURE STAGES OF *CHAETOPSIS MASSYLA* (DIPTERA: OTITIDAE), A SECONDARY INVADER OF HERBACEOUS STEMS OF WETLAND MONOCOTS

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*Abstract.*—The life cycles and larval feeding habits of *Chaetopsis massyla* (Walker), a saprophagous species that is a secondary invader of wetland monocots, are elucidated. The immature stages are described and illustrated. Suggestions are made concerning the possible evolution of larval feeding habits in the family Otitidae.

*Key Words:* Diptera, Otitidae, *Chaetopsis,* life cycles, feeding habits

The family Otitidae, containing some 650 species in the world, is divided into two subfamilies. The subfamily Otitinae is primarily north temperate in distribution, whereas the Ulidiinae is particularly well developed in the Neotropics. The family is widely distributed, with 178 species in the Palaearctic Region (Soos 1984, Zaitzev 1984); 130 in the Nearctic (Steyskal 1987); 285 in the Americas south of the United States (Steyskal 1968); 21 in the Afrotropical (Steyskal 1980); 11 in the Oriental Region (Steyskal 1977); and 25 in the Australasian and Oceanian Regions (Evenhuis 1989).

Information on life histories and larval feeding habits of Otitidae is available in Allen and Foote (1967), Foote (1976), and Ferrar (1987). The larval feeding habits are known for less than 32% of the Nearctic species, and immature stages have been described for only some 10%. Most of the larvae have saprophagous habits, although a few genera contain phytophagous larvae that are primary invaders of living plant tissue (Table 1).

In North America the genus *Chaetopis* is represented by five species: *C. aenea* (Wiedemann), *C. apicalis* Johnson, *C. major* (Wulp), *C. massyla* (Walker), and *C. quadrifasciata* Curran. The first two species are largely restricted to salt marshes along the Atlantic and Gulf Coasts, but the remaining three can occur in freshwater habitats.

Biological information is available for three Nearctic species. Larvae of most species apparently are saprophagous, having been found in damaged stems of corn (Gossard 1919), sugar cane (Braydon 1918), and cattail (Foote 1976). They have also been found in rotting pineapples (Illingworth 1926) and bananas (Oglivie 1925), as well as decaying bulbs of narcissus (Blanton 1938) and onion (Severin and Severin 1915, Merrill 1951, Merrill and Hutson 1953). The larvae of a few species may be phytophagous. Chittenden (1895) presented information on the life cycle of *C. aenea* and described the eggs and mature larvae, stating that the larvae damaged cereals such as wheat, oats, corn, and sugarcane. S. E. Neff (personal communication) collected larvae and puparia of *C. apicalis* from the pithy material of big cordgrass [*Spartina cynosuroides* (L.) Roth] growing on the shoreline of a brackish marsh. He felt that the larvae were primary invaders, as no larvae of other phytophagous insects were found. In con-

trast to these earlier workers who assumed a phytophagous way of life for *C. aenea* and *C. apicalis,* Strong et al. (1984) stated that these two species were saprovores in stands of smooth cordgrass (*Spartina alterniflora* Loisel) in northwestern Florida. No larval stages of any species of the genus have been described (Ferrar 1987).

The present paper elucidates the life cycle of *C. massyla* and describes its immature stages. A tabular summary of the larval foods of Otitidae is presented, and possible evolutionary trends in larval feeding habits within the family are discussed.

## Materials and Methods

*Collecting techniques:* Most of the field collections were made near Kent in Portage County, Ohio. A small burrow pit, located seven miles east of Kent bordered on the east and west by a vernal marsh and a small pond was the site of most of the field observations. A second productive site was a small marsh located along Horning Road in Kent.

Adults were collected by sweeping suitable habitats with a standard insect aerial net measuring 40 cm in diameter. Larvae were collected by examining damaged stems of wetland monocots. Puparia were collected in early spring by pushing emergent vegetation beneath the water surface.

*Rearing techniques:* The temperature of the rearing room ranged from 22 to 25°C. Adults collected in nature were placed in 5 × 7 cm breeding jars for mating and oviposition. The bottom of each jar contained a moist layer of commercial peat moss. A moistened pellet of brewer's yeast mixed with honey supplied the nutritional requirements of the adult flies. A small piece of decaying cattail stem served as an oviposition stimulant. As eggs appeared, they were removed from the jars with a fine jeweler's forceps or camel hair brush, counted, and transferred to the surface of moist peat moss in small (6.5 × 1.5 cm) petri dishes.

Larvae were reared individually or col-

Table 1. Larval foods of North American Otitidae.

| Genus | Larval Food |
|---|---|
| | Otitinae |
| *Callopistromyia* | Decaying cambium of deciduous trees |
| *Cephalia* | Unknown |
| *Ceroxys* | Decaying vegetation, manure |
| *Curranops* | Unknown |
| *Delphinia* | Decaying vegetation |
| *Diacrita* | Rot pockets in cactus |
| *Dyscrasis* | Unknown |
| *Haigia* | Unknown |
| *Herina* | Unknown |
| *Hiatus* | Unknown |
| *Idana* | Decaying vegetation |
| *Melieria* | Unknown (phytophagous?) |
| *Myrmecothea* | Decaying vegetation |
| *Myiomyrmica* | Unknown |
| *Notogramma* | Rot pockets in cactus, decaying fruits |
| *Psaeropterella* | Unknown |
| *Pseudotephritina* | Decaying cambium of deciduous trees |
| *Pseudotephritis* | Decaying cambium of deciduous trees |
| *Pseudoseioptera* | Decaying vegetation |
| *Seioptera* | Decaying vegetation, manure |
| *Tetanops* | Sugarbeet roots, decaying bulbs |
| *Tetropismenus* | Unknown |
| *Tritoxa* | Onion and garlic bulbs |
| *Tujunga* | Unknown |
| *Ulidiotites* | Unknown |
| *Xanthracrona* | Unknown |
| | Ulidiinae |
| *Acrosticta* | Unknown |
| *Axiologina* | Decaying tissues of palm trees |
| *Chaetopsis* | Decaying vegetation, stems of salt marsh grasses |
| *Eumecosomyia* | Inflorescences of corn (damaged?) |
| *Eumetopiella* | Inflorescences of grasses |
| *Euxesta* | Decaying vegetation, fruits, cambium, cactus, manure |
| *Homalocephala* | Decaying subbark tissues of coniferous trees |
| *Oedopa* | Unknown |
| *Paroedopa* | Rot pockets in cactus |
| *Physiphora* | Decaying vegetation |
| *Steneretma* | Unknown |
| *Stenomyia* | Unknown |
| *Stictomyia* | Rot pockets in cactus |
| *Texasa* | Unknown |
| *Zacompsia* | Unknown |

lectively in small petri dishes containing either lengths of decaying cattail stem or rotting bits of lettuce. The rearings were inspected daily to determine larval feeding behavior, time spent in each of the three larval stadia, and site of pupation. Food and water were added as needed. As puparia appeared, they were transferred to eight-dram shell vials (one puparium per vial) containing a moistened peat moss substrate. Recently emerged adults were placed into breeding jars for information on premating and preovipositional periods, number of eggs laid, and longevity.

*Preparation techniques:* Eggs were preserved and stored in Peterson's egg preservative. For gross examination eggs were removed from the preservative and placed in a small depression slide containing KAAD solution. A representative sample of the eggs for each species was measured.

Larvae were killed in hot water and stored in 80% ethanol. To study gross morphological structures, larvae were transferred to a petri dish containing KAAD. The spiracular discs were removed with a pair of iridectomy scissors and placed on a microscope slide in a small amount of glycerin jelly.

To study minute morphological structures, larvae were cut along the mid-dorsal line and the soft parts teased away from the integument with #3 insect pins. Anterior and posterior spiracles were dissected from the integument with insect pins that were sharpened to a fine point. To prepare permanent slides, the parts were carefully positioned on a slide, dehydrated in 80% ethanol, cleared in xylol, and finally mounted in Permount. Temporary wet mounts were prepared by mounting these structures in a small drop of glycerine.

The cephalopharyngeal skeletons were either dissected from preserved larvae or recovered from cast exuviae. The skeletons were first treated in a warm KOH solution for two or three minutes and then cleared in glacial acetic acid. Permanent slides of the sclerites comprising the cephalopharyngeal skeleton were prepared. A representative sample of the cephalopharyngeal skeleton for each instar was measured.

Larvae were prepared for SEM by immersing them in Super Skipper for 30–60 seconds, and then placing them in Carl's Solution for 24 h (Grodowitz et al. 1982). They were subsequently dehydrated in a standard ethanol series, subjected to critical point desiccation, and finally sputter-coated with gold/palladium. Prepared larvae were examined with a Cambridge Stereoscan Electron Microscope. Photographs were obtained with a high resolution camera and Polaroid film No. 52.

Puparia which failed to produce adults were fixed in KAAD and stored in 80% ethanol. Puparia which had produced adults were placed in #4 gelatin capsules and pinned beneath the adult. A representative sample of the puparia was measured.

Voucher specimens have been deposited in the insect collections of Kent State University and Ohio State University.

## Figure Abbreviations

AS, anterior sclerite; AT, accessory tooth; DC, dorsal cornu; DS, dentate sclerite; HS, hypostomal sclerite; IP, interspiracular process; M, mandible (bp, basal part; hp, hook part); PB, parastomal bar; Pa, papilla; PhR, pharyngeal ridge; PP, perianal pad; PS, posterior sclerite; SO, spiracular opening; SP, spiracular plate; SS, spiracular scar; TS, tentoropharyngeal sclerite; VC, ventral cornu.

## Life History

A strictly Nearctic species, *C. massyla* ranges from Alberta to Maine, and south to New Mexico (Steyskal 1965). We collected adults most commonly in open marshes and barrow pits containing stands of cattail (*Typha latifolia* L.), sedges (*Carex* spp.), and rushes (*Juncus* spp.). Most were taken between early June and late September and were particularly common during mid and late June. The earliest collection was made

on May 6 (1 male); the latest, November 6 (1 male).

Adults were not very active until approached, when they suddenly ran sideways and retreated to the opposite side of the cattail leaf. The lateral movements were as fast or faster than the forward movements. Both sexes constantly flicked their wings. Adults were not attracted to sweet smelling fragrances, and Frost (1929) collected only 2 adults (as *C. fulvifrons* (Macquart)) during a two year period using sugarwater bait pails. Adults were frequently seen running up and down the leaves of common cattail. However, they were not confined to that species and were nearly equally abundant in stands of cattail, reed canary grass (*Phalaris arundinacea* L.) and two species of sedges (*C. lacustris* Willd., *C. stricta* Lam.) during our summer-long study of a freshwater marsh near Kent (Fig. 12).

Laboratory-reared adults lived 15–62 days ($\bar{x}$ = 25, n = 8). Wild caught females lived 40–45 days (n = 4); males, 30–36 days (n = 6). The premating period was not determined, although it was probably less than 2 or 3 days, as viable eggs were obtained from reared females within 3 days after emergence. No mating was observed either in the laboratory or field.

Gravid field-collected females placed in breeding jars with pieces of mechanically damaged cattail leaves began ovipositing 1–2 days after capture. They inserted their ovipositors into decaying portions of the cattail leaves, and clusters of 3–10 eggs subsequently were found between the epidermal layers. Very few eggs were laid on the sides of the jars, on decaying lettuce, or on the peat moss substrate. Fecundity for reared females (n = 4) ranged from 150 to 398. Larvae hatched by rupturing the chorion near the micropylar end of the egg. The incubation period lasted 2–3 days (n = 12).

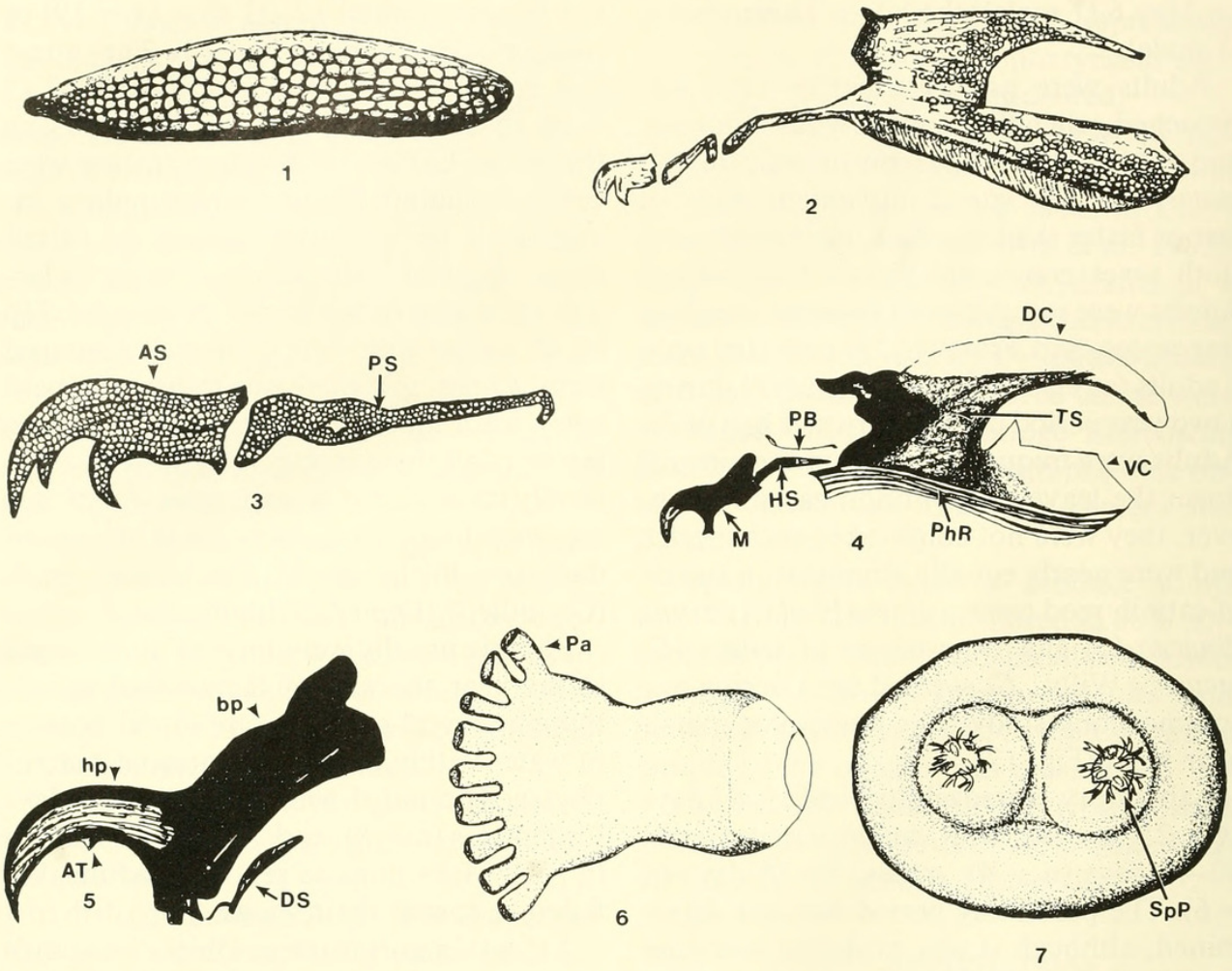
Newly hatched larvae were reared on decaying cattail leaves, lettuce, watermelon and pumpkin rind, and guinea pig and woodchuck dung. Larvae feeding on decaying cattail leaves required 12–23 days ($\bar{x}$ = 19) to complete development (n = 10). They spent 2–4 days ($\bar{x}$ = 3) in the first instar; 3–7 ($\bar{x}$ = 5), in the second; and 7–15 ($\bar{x}$ = 11), in the third. Larvae of all three instars were found in nature feeding as secondary invaders in decomposing tissues of cattail stems that had been damaged by moth larvae belonging to the family Noctuidae. Up to 40 larvae were found in each damaged stem. Apparently there was little movement away from moth-damaged tissues, as eggs, larvae of all three instars, and puparia commonly co-occurred in such sites. A few larvae were found in *C. lacustris* Willd. stems damaged by larvae of *Epichlorops exilis* (Coquillett) (Diptera: Chloropidae).

Puparia usually were formed in damaged stems near the site of larvae feeding, although several puparia were found floating in water within stands of emergent macrophytes. The pupal period lasted 8–10 days for females (n = 8), and 7–9 days for males (n = 5). Many puparia produced adults that failed to spread their wings.

At least in northeastern Ohio, *C. massyla* was a multivoltine species. In the laboratory, the whole life cycle was completed in 33 days. Reproduction occurred continuously during the warm season, stopping only in response to low temperatures in early fall. Overwintering occurred as larvae, prepupae, and pupae. Larvae collected in nature during late December and March quickly resumed feeding on decaying cattail in the laboratory, suggesting that overwintering does not involve a larval diapause. The first seasonal record for puparia was obtained in early March in a stand of cattail. The early and late capture records for adults, May 6 and November 6, indicate a flight period of ca. 180 days.

## Descriptions of Immature Stages

*Egg* (Fig. 1): Length 0.86–0.94 mm; maximum width 0.15–0.18 mm. White, semipolished. Spindle shaped. Chorion striated.



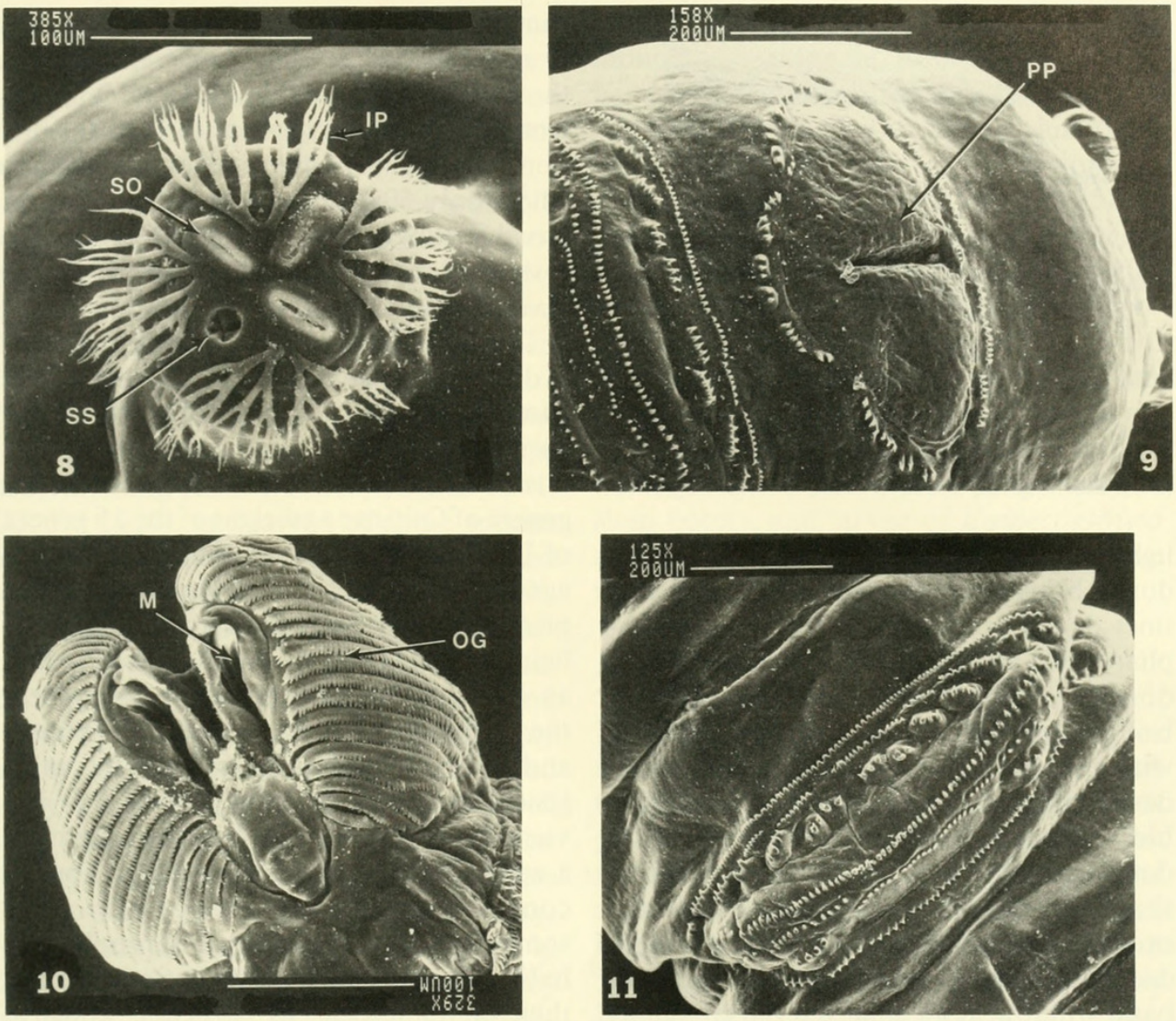

Figs. 1–7. *Chaetopsis massyla.* 1, Egg. 2, Cephalopharyngeal skeleton of first instar. 3, Mandible of first instar. 4–7, Third-instar larva. 4, Cephalopharyngeal skeleton. 5, Mandible. 6, Anterior spiracle. 7, Posterior spiracular disc.

Terminal micropyle shielded by small tubercle (n = 20).

*First-instar larva:* Similar to third instar except in following characters. Length 1.12–2.14 mm; maximum width 0.15–0.32 mm. White, integument transparent. Intersegmental constrictions well defined. No anterior spiracles. Posterior spiracular plates raised on two dome-like spiracular tubes; each plate with B-shaped opening and four branched interspiracular processes. Cephalopharyngeal skeleton (Fig. 2) length 0.26–0.31 mm; maximum width 0.04–0.07 mm (n = 5). Tentoropharyngeal sclerite lightly to deeply pigmented, lacking parastomal bars. Each mandible (Fig. 3) with two sclerites; anterior sclerite bearing three teeth, with accessory tooth lying in same plane as hook; posterior sclerite with small window (n = 20).

*Second-instar larva:* Similar to third instar except in following characters. Length 2.24–4.85 mm; maximum width 0.26–0.58 mm. Anterior spiracles rosette shaped, with 9–12 fingerlike marginal papillae. Posterior spiracular plates with three oval openings; trabeculae reduced in number; interspiracular processes two- or three-branched at base. Cephalopharyngeal skeleton length 0.46–0.60 mm; maximum width 0.14–0.21 mm (n = 20).

*Third-instar larva:* Length 4.50–9.90 mm; maximum width 0.57–1.28 mm. Subshining white, integument transparent; fat bodies becoming yellowish just prior to pupation. Conical cylindrical, tapering anteriorly




Figs. 8–11. Third-instar larva of *Chaetopsis massyla*. 8, Posterior spiracular plate. 9, Perianal pad. 10, Facial mask. 11, Creeping welt of segment 5.

from second abdominal segment, bluntly rounded posteriorly. Cephalic segment bilobed apically, each lobe bearing short fleshy two-segmented antenna anteriorly and maxillary palp ventrally, palps without basal sclerotized rings; facial mask (Fig. 10) with 20–25 unbranched grooves leading into oral opening, each groove bordered anteriorly by single row of 5–20 unpigmented spinules. Spinule bands restricted to eight ventral creeping welts (Fig. 11). Perianal pad (Fig. 9) ellipsoidal, slightly protruding; bordered by single row of unpigmented spinules.

Anterior spiracles (Fig. 6) posterolateral on segment 2 (prothoracic), yellowish tan, fan shaped with 9–12 ($\bar{x}$ = 10) fingerlike marginal papillae.

Posterior spiracular plates at tips of short spiracular tubes (Fig. 7); each plate (Fig. 8) with circular spiracular scar, three spiracular slits arranged in "T" configuration, and four branched interspiracular processes; each process two- or three-branched at base; spiracular tubes, slit margins and trabeculae dark brown, interspiracular areas and slits yellowish white.

Cephalopharyngeal skeleton (Fig. 4) length 0.99–1.10 mm; maximum width 0.29–0.34 mm. Tentoropharyngeal sclerite mostly

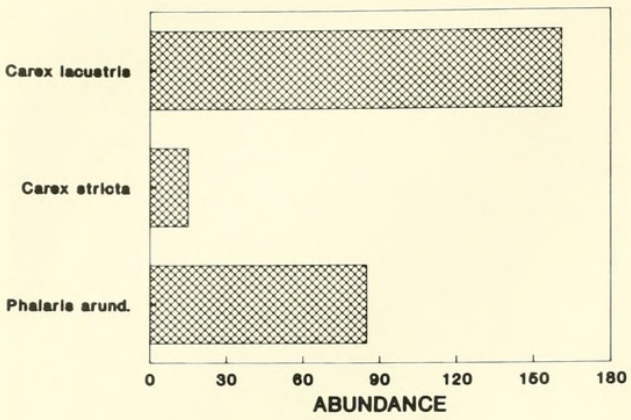



Fig. 12. Occurrence of adults of *C. massyla* in stands of *Carex lacustris, C. stricta,* and *Phalaris arundinacea* at the Horning Rd. marsh in Kent, Ohio during 1990.

lightly pigmented, deeply pigmented on dorsal bridge, each ventral cornu with distinct dorsal projection near base; tentoropharyngeal and hypostomal sclerites fused; dorsal cornua joined anterodorsally by bridge; floor of tentoropharyngeal sclerite with numerous ridges; parastomal bars well developed and reaching nearly to mandibles; hypostomal sclerite bent abruptly downward anteriorly in lateral view and H shaped in ventral view, lightly pigmented except near anterior end. Mandibles (Fig. 5) deeply pigmented except at tips, each with basal window, not connected dorsally; narrow, elongate paired dentate sclerite lying ventrad of each mandible (n = 20).

*Puparium:* Length 3.06–5.50 mm; maximum width 0.96–1.63 mm. Reddish brown, smooth and translucent, darker near cephalic caps and posterior spiracles. Cylindrical, rounded posteriorly; narrowed anteriorly, flattened dorsoventrally to form lateral ridges on cephalic caps. Anterior spiracles on anterolateral margins of dorsal cephalic cap, fan shaped, reddish brown, yellowish at tips, with 9–12 ($\bar{x}$ = 10) marginal papillae. Posterior spiracles on two knoblike spiracular tubes; tubes black, spiracular slits reddish yellow. Perianal pad ellipsoidal, slightly depressed (n = 20).

## Discussion

The known larval foods of 23 of the 41 North American genera of Otitidae are summarized in Table 1. The numerous gaps in our knowledge of many genera reduces the usefulness and value of the table in detecting evolutionary trends in food utilization, especially in the subfamily Otitinae where only 50% of the genera have known larval feeding habits. However, it is possible to derive a few generalizations about trophic diversification in the family.

The basic food of otitid larvae probably is decaying organic matter, particularly accumulations of rotting plant material occurring in moist to mesic terrestrial habitats. Twelve of the 26 North American genera of Otitinae and eight of the 15 genera of Ulidiinae have larvae that are saprophagous. The otitid flies thus largely retain the primitive acalyptrate dipterous habit of utilizing compost (Oldroyd 1964). Such genera as *Ceroxys, Delphinia, Idana, Myrmecothea, Pseudoseioptera, Seioptera, Euxesta* and *Physiphora* appear to have the most generalized feeding habits in that their larvae apparently are capable of developing in a wide spectrum of decaying vegetation. In contrast, other genera seemingly have somewhat more specialized saprophagous habits, as they concentrate or even restrict their larval feeding to particular kinds of rotting vegetable matter. For example, larvae of species of *Callopistromyia, Pseudotephritina, Pseudotephritis,* and *Homalocephala* feed on decomposing cambial and other tissues under the bark of dead and dying trees (Allen and Foote 1967, Steyskal 1979). Further specialization has occurred even within this group, as larvae of the first three genera are associated with deciduous trees, whereas *Homalocephala* larvae have been found only under bark of conifers. A second set of saprophagous genera are specialized for feeding on rotting cactus tissues in the arid lands of the Southwest (Foote 1976). This feeding habit undoubtedly represents convergent evolution, as the genera involved, *Diacrita, Notogramma, Paroedopa,* and *Stictomyia,* belong to both subfamilies and certainly did not evolve from a single common ancestor. A third group of

saprophytic genera, including *Chaetopsis* and possibly *Eumecosomyia,* are secondary invaders of herbaceous plants that have been damaged by other, truly phytophagous insect species.

Saprophagous larvae of Diptera probably ingest and assimilate populations of decomposer microorganisms that flourish in rotting vegetation. Some studies have shown that decomposed vegetable matter when sterilized is unsuitable as larval food. Larvae of numerous species of *Drosophila* consume the abundant yeast flora that develops in fermenting plant tissues (Wagner 1944, Cooper 1960), and larvae of some species of saprophagous Ephydridae are postulated to ingest bacteria (Eastin and Foote 1970). Other saprophagous dipterous larvae, including some species of Lauxaniidae that develop in rotting leaf litter (Miller and Foote 1975, McDonald et al. 1974), may utilize bacteria and/or fungi. A detailed study of saprophagous otitid larvae may well show that each species utilizes a particular spectrum of microorganisms. Thus, species that co-occur in rotting plant tissues (e.g. rot pockets in cactus) may actually be in different trophic niches, even though they occupy the same spatial and temporal niches. Rearings of different saprophagous species of otitid larvae in monocultures of a variety of bacterial, fungal and yeast substrates would give meaningful insights into trophic niche segregation occurring within the family.

A second generalization concerning larval food preferences in Otitidae is that several genera have abandoned the saprophagous way of life and are now phytophagous. Adoption of herbivory apparently has occurred repeatedly during the evolutionary history of the family as shown by the fact that the phytophagous genera do not constitute a single phyletic line. Phytophagous habits occur in at least two Nearctic genera of Otitinae (*Tetanops* and *Tritoxa*) and one genus of Ulidiinae (*Eumetopiella*).

Larvae of the phytophagous genera attack a fair diversity of plant hosts, although there is a strong tendency to utilize herbaceous monocots. Larvae of *Eumecosomyia* and *Eumetopiella* attack grasses (Gramineae) (Steyskal 1966, Valley et al. 1969), and those of *Tritoxa* feed on bulbs of wild onion and garlic (Liliaceae) (Allen and Foote 1975). At present, only larvae of *Tetanops myopaeformis* (Roder) are known to attack a species of Dicotyledoneae (sugar beet, Chenopodiaceae) (Mahrt and Blickenstaff 1979). Specialization for particular plant parts has also occurred. Thus, larvae of *Tetanops* attack roots, those of *Tritoxa* feed within bulbs, larvae of *Chaetopsis apicalis* may be stem borers, and larvae of *Eumecosomyia* and *Eumetopiella* consume reproductive tissues in developing inflorescences.

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