

# Key Aspects of the Biology of Snail-Killing Sciomyzidae Flies

William L. Murphy,<sup>1,\*</sup> Lloyd V. Knutson,<sup>2</sup>  
Eric G. Chapman,<sup>3</sup> Rory J. Mc Donnell,<sup>4</sup>  
Christopher D. Williams,<sup>5</sup> Benjamin A. Foote,<sup>6</sup>  
and Jean-Claude Vala<sup>7</sup>

<sup>1</sup>Research Collaborator, Smithsonian Institution, Fishers, Indiana 46038-2257; email: billmurphy8@sbcglobal.net

<sup>2</sup>Salita degli Albito 29, 04024 Gaeta LT, Italy; email: lvknutson@tiscali.it

<sup>3</sup>Department of Entomology, University of Kentucky, Lexington, Kentucky 40546-0091; email: ericgchapman@gmail.com

<sup>4</sup>Department of Entomology, University of California, Riverside, California 92521-0001; email: rjmcdonnell@gmail.com

<sup>5</sup>Behavioural Ecology and Biocontrol Laboratory, Department of Biology, National University of Ireland, Maynooth, County Kildare, Ireland; email: chris.david.williams@gmail.com

<sup>6</sup>Emeritus Professor of Biological Sciences, Department of Biological Sciences, Kent State University, Kent, Ohio 44242; email: bfoote@kent.edu

<sup>7</sup>Laboratoire des Ligneux et des Grandes Cultures, UPRES EA2107, Université d'Orléans, BP 6749, 45067 Orléans Cedex 2, France; email: jean-claude.vala@univ-orleans.fr

Annu. Rev. Entomol. 2012. 57:425–47

The *Annual Review of Entomology* is online at [ento.annualreviews.org](http://ento.annualreviews.org)

This article's doi:  
10.1146/annurev-ento-120710-100702

Copyright © 2012 by Annual Reviews.  
All rights reserved

0066-4170/12/0107-0425\$20.00


\*Corresponding author

## Keywords

Diptera, Mollusca, zoogeography, systematics, phylogenetics, ecology, biocontrol

## Abstract

The biology of snail-killing flies (Diptera: Sciomyzidae) has been studied intensively over the past half-century, especially over the past decade. Today, sciomyzids are biologically the best-known group of higher Diptera. The overarching research objectives are evaluation of sciomyzids as biocontrols of disease-carrying or agriculturally important snails and slugs and as a paradigm group for the study of the evolution of diverse feeding and associated behaviors in flies. We present reviews and analyses of some key features of particular scientific and societal interest, including behavioral and phenological groups; laboratory experimental studies on behavior and development; population biology, bioindicators, ecosystem service provision, and conservation; phylogenetics, molecular studies, and evolutionary biology; and biocontrol.

 Supplemental Material

## INTRODUCTION

With life cycles known for 240 of 540 species in 41 of 61 genera, and immature stages described for 176 species in 39 genera, the Sciomyzidae are, from those aspects, the most thoroughly studied family of Acalyptratae. We suggest that Sciomyzidae are emerging as a richer knowledge base for broad evolutionary studies, especially of larval feeding behavior and associated adaptations, than are larger but lesser-known families of higher Diptera; some outstanding research needs in this regard are noted herein. (Supplemental figures, a film, tables, and text provide further information relating to sections of this chapter. See **Supplemental Text 1** for a rationale for use of Sciomyzidae as a resource for the study of the evolution of life cycle strategies; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>.)

Sciomyzidae are of particular interest in regard to the feeding behavior and hosts/prey of the larvae and associated behavioral and morphological adaptations throughout the life cycle (**Supplemental Figures 1** and **2**). All known larvae are obligate natural enemies of Mollusca, except for three killers of freshwater Oligochaeta. Larvae range from overt rapacious predators of freshwater snails (**Supplemental Film 1**) to covert, intimately associated, insidious parasitoids of terrestrial snails or aestivating freshwater snails (one larva per snail, one snail per larva). Many species behave variably as predators, parasitoids, or saprophages during their development, depending, for example, on relative sizes of larvae and snails, intraspecific competition, age of larvae, and microhabitat condition.

In 1850 in France, Perris (98) first reared an adult sciomyzid from a larva found in a terrestrial snail; he did not know whether the snail was dead or alive when he collected it. For 100 years, most authors described sciomyzid larvae as general saprophages until, a continent away and a century later, in 1950 in Alaska, Berg (18) first proved the obligate snail-killing behavior of six species in five genera. Berg and 16 graduate students at Cornell University subsequently (1953–1978) pursued life cycle studies and descriptions of immature stages worldwide as well as studies on populations, physiology, natural enemies, and other aspects. Soon after the initial studies (e.g., 21) began, a closely knit international coterie of researchers developed. With the resurgence of interest in Sciomyzidae during the past decade, the current directory of sciomyzid enthusiasts (<http://www.sciomyzidae.info/news.php>) now lists 89 persons in 32 countries.

Basic resources for researchers are a nearly complete, alphabetical, serially numbered bibliography of 3,000+ publications on Sciomyzidae (ScioBiblio), upon which are based the citations in a Cornucopia, a new format for tabulating information—a table of nine key features for each of the known species of Sciomyzidae, with ScioBiblio numbers for publications documenting these features. Both resources are available on the Sciomyzidae Web site (Sciomyzidae.info, <http://www.sciomyzidae.info/news.php>) and are updated from time to time. **Supplemental Table 1** is a summary, by major zoogeographic region, of numbers of genera and species, extent of life cycle knowledge, and availability of descriptions of immature stages.

## DISTRIBUTION AND ZOOGEOGRAPHY

A wealth of data on the geographical distribution of sciomyzids, including tables and maps, has been published. Distribution of genera and species by major regions has been presented (101) and updated (67). Species distributions are best known for the Palearctic (by countries, 102) and Nearctic (by state/province, 62), whereas distribution of Oriental species is least known (see **Supplemental Table 2**). Species distributions closely follow classical delimitations of major zoogeographic regions. Except for 28 Holarctic species in six genera, few species are broadly shared with adjacent regions, and few are even slightly adventive from one region into adjacent regions.

Approximately 70% of the 540 species and 82% of the 61 genera occur in the Nearctic and Palearctic (Nearctic: 201 species/23 genera, Palearctic: 176 species/27 genera). The dominant genera, *Pherbellia* (tribe Sciomyzini, 95 species) and *Sepedon* (tribe Tetanocerini, 80 species), occur worldwide except in the Subantarctic (including New Zealand), where all 25 species in four genera are endemic. The third-largest genus, *Dictya*, comprises 42 Nearctic and Neotropical and 1 Palearctic species. No sciomyzid is cosmopolitan.

Zoogeographic research on Sciomyzidae suffers from a lack of cladistic analyses of species within most genera. Such analyses would facilitate vicariant zoogeographic studies. They are available only for the Neotropical genera *Protodictya* (75), *Thecomyia* (78), *Sepedonea* (77), and *Tetanoceroides* (138, phyletic analysis), and for the Nearctic *Tetanocera* (24). The only modern vicariant analysis is that of *Sepedonea* (99). No comparative sciomyzid/mollusc zoogeographic studies have been conducted. Zoogeography is discussed in some taxonomic and biological papers [Neotropical, *Perilimnia* and *Shannonia* (58) and *Tetanoceroides* (138); Nearctic, three *Sepedon* species (39); Palearctic, one *Elgiva* (64) and two *Pherbellia* species (128)] and in some faunistic studies (see Identification and Systematics, below). An overview of descriptive (dispersal) zoogeography focuses primarily on species and genera shared among regions, extent of endemism, and likely dispersal routes (67).

The distribution of many described genera/species is poorly known, as indicated by recent collections of species well beyond their documented range (e.g., *Dictya disjuncta*, known only from the holotype collected in Mississippi in 1927 and recently rediscovered in Indiana and Arkansas) and genera new to major regions (e.g., the Holarctic *Colobaea* and *Pteromicra* and the Holarctic-Neotropical *Ditaeniella* from sub-Saharan Africa). Several monotypic genera are known only from one or two specimens from the type and nearby localities: Palearctic (*Apteromicra*, *Ellipotaeonia*, *Neodictya*, and *Oligolimnia*), Afrotropical (*Tetanoptera* and *Verbekaria*), Neotropical (*Calliscia*), and Oriental (*Steyskalina*).

Many species and some genera remain undescribed. About 100 undescribed species in approximately 20 genera are listed at Sciomyzidae.info (<http://www.sciomyzidae.info/news.php>) by “species near sp.x,” locality, date, collector, number-sex, museum/current location, and specialist. This list serves as a request for more specimens, indicates areas for further exploration, and notes the locations of museum collections for further study.

## HOSTS/PREY

Sciomyzidae are the only dipteran family whose larvae are almost exclusively obligate killers of molluscs; a few other families include some obligate or opportunistic snail or slug killers. Of the eight families of Sciomyzoidea (sensu McAlpine, 80), all are saprophagous, coprophagous, fungivorous, or microflora grazers except for one dryomyzid that feeds on barnacles and some helosciomyzids that prey on ants.

Of the 240 reared species of the 540 valid species of Sciomyzidae, only 3 species, all Afrotropical, are not strictly malacophagous: *Sepedonella nana* and *Sepedon knutsoni*, which prey on freshwater oligochaetes, and *Sepedon ruficeps*, facultative on snails or oligochaetes. One species of the sister group Phaeomyiidae (subfamily Phaeomyiinae of Sciomyzidae in earlier classifications) is the only fly documented as a parasitoid of millipedes (4, 5).

Most sciomyzids are restricted to nonoperculate (pulmonate) freshwater, semiterrestrial (Succineidae), or terrestrial snails. A few species attack brackish or freshwater operculate (prosobranch) snails, one attacks marine coastal strandline *Littorina*, five attack only slugs, nine are restricted at least during early larval life to eggs of freshwater and semiterrestrial snails, and six species in three genera are the only Insecta proven to be natural enemies of bivalve Mollusca (Sphaeriidae). None is cannibalistic.

---

**Malacophagous:**  
killing and feeding on  
Mollusca, primarily  
snails or slugs

---

**Supplemental Table 3** lists 56 natural prey species (field records) in 43 genera of aquatic, terrestrial, and semiterrestrial gastropods representing 21 families. The natural prey of most of the many freshwater predators (all Tetanocerini) are unknown, as these larvae feed only until satiated and then leave the prey to rest before killing additional snails. The natural prey of only 11 such species have been documented (84). The most polyphagous is the Holarctic *Tetanocera ferruginea*, recorded to consume nine snail species in seven genera. Although freshwater predators kill most snails offered to them during laboratory rearings, their natural prey probably are more limited. Terrestrial parasitoids, restricted to one or a few genera of gastropods, are generally more host specific than are predators.

The natural hosts/prey of larvae of many terrestrial or semiterrestrial parasitoids and predators of the tribe Sciomyzini are better known than those of the Tetanocerini because (a) many Sciomyzini attack snails exposed in aquatic-terrestrial ecotone (shoreline) situations and thus are more easily collected, (b) such larvae remain feeding, often saprophagously, in the snail long after it has died, and (c) many Sciomyzini pupariate in the snail shell. Such infested shells are collected more easily than are freshwater snails with larvae feeding in them (**Supplemental Table 4**).

During laboratory rearings, one of the Palearctic Sciomyzini shoreline predator/parasitoid/saprophages, *Pherbellia dorsata*, killed and fed on 28 snail species in 20 genera, more than recorded for any other sciomyzid, although it was found only in the freshwater *Planorbis planorbis* in extensive collections in a well-studied habitat in nature (22). In the laboratory, larvae of some freshwater Tetanocerini, with morphological features such as elongate segment 12, elongate interspiracular processes, and elongate posterior spiracular disk lobes, obviously adapted to an aquatic existence (24, 122), readily kill and feed on terrestrial snails; e.g., the Palearctic *Pherbina coryleti* consumed terrestrial snails of five species in four genera (65).

Sciomyzid life cycle and biocontrol studies are deficient in prey-choice experiments. Most sciomyzid larvae recalcitrant to laboratory rearing generally have not been offered nonmolluscan food. However, the extensively studied (e.g., 92, 93) Nearctic *Sepedon fuscipennis*, a surface predator of nonoperculate freshwater snails in calm waters, was reared from hatching to maturity on a diet consisting solely of limpets (Ancyliidae) (93). These cone-shaped gastropods are common in streams (which are not *S. fuscipennis* microhabitats), where they adhere to riffle stones and feed by scraping biofilm. The aggressive larvae squeezed under the adhered shell and “flipped the limpet over for feeding.”

Many sciomyzids have been characterized as feeding on freshwater snails stranded on, foraging at, or migrating through shoreline situations. Taxonomic-ecological-behavioral analyses are needed of the snail and fly members of this major complex of hosts/prey of sciomyzid larvae in terms of diel, seasonal, climatic, and other factors. Such information might be useful, especially in selecting biocontrols of fluke-transmitting snails not in open water, i.e., aestivating, migrating, or stranded; such individuals are not susceptible to molluscicides.

The historical lack of joint research by entomologists and malacologists on sciomyzid larvae and their hosts/prey is a deficiency from theoretical and practical viewpoints. A theoretical perspective in regard to biocontrol possibilities from the viewpoint of malacologists has been provided (1, 7). Barker et al. (7) mapped a cladogram of sciomyzid genera onto a cladogram of potential molluscan prey (**Supplemental Figure 3**) and examined the pattern of prey diversification. They concluded that “the considerable number of molluscan clades not utilized as prey indicates the ecological conservatism of Sciomyzidae” and that operculate snails are strongly underrepresented as prey. Major categories of hosts/prey have been mapped above the cladogram of genera of Sciomyzidae (67). These considerations are further discussed below.

## LIFE CYCLES, LARVAL FEEDING BEHAVIOR, AND ASSOCIATED ADAPTATIONS

Life cycles, larval feeding behavior, and associated morphological, microhabitat, and phenological adaptations essential to evolutionary and biocontrol aspects continue as focal points of Sciomyzidae research. Over the past 50 years, information on the sciomyzid life cycle has been presented in over 100 publications on 240 species in 41 genera, for all major regions (see “A Cornucopia for Sciomyzidae and Phaeomyiidae” at [http://www.sciomyzidae.info/downloads.php?cat\\_id=1](http://www.sciomyzidae.info/downloads.php?cat_id=1)). Many ecological equivalents exist among regions, but some of these species show a multitude of special adaptations. Classification of Behavioral Groups, based on hosts/prey, feeding behavior, and microhabitats of larvae, has been used extensively to capture the essence and broad range of sciomyzid behaviors. Earlier reviews (21, 37, 48) recognized 7 or 8 groups on the basis of these descriptors, but Barker et al. (7), who included morphology of immatures as a descriptor, recognized 9 groups, whereas Knutson & Vala (67), who excluded morphology, recognized 15 groups (**Supplemental Text 2** depicts the classification as of 2011, with examples of species and genera). The diverse feeding behavior of Sciomyzidae and the coevolved behavioral and morphological adaptations throughout the life cycles suggest further refinement of behavioral or ecomorphological groups. Considering the many characters and character states, correspondence analyses or some numerical taxonomic or other analytic procedures probably would be useful. Here we take the opposite tack and simplify discussion to examples of the three extremes in feeding behavior: parasitoid, mixed parasitoid/predator/saprophage, and predation.

Sciomyzid life cycles have been elucidated either (*a*) by beginning with a collection of larvae and/or puparia (occasionally in snails) in nature, indicating microhabitats and potential hosts/prey for laboratory rearings, or (*b*) by beginning laboratory rearings with field-collected adults, obtaining eggs, and offering neonates various hosts/prey, the results indicating where to look in nature. The morphology of larvae and puparia often indicates whether the species is aquatic or terrestrial, also helping direct field collections. Rearing methods are described in many life cycle publications and are summarized in Reference 67.

### Parasitoid Behavior

The best studied of the highly parasitoid species (all in Sciomyzini) are the Nearctic *Sciomyza varia* and its almost exact ecological equivalent, the Palearctic *Colobaea bifasciella*; the Nearctic *Sciomyza aristalis*; the Nearctic and Palearctic subspecies of *Pherbellia schoenberri*; the Palearctic *Tetanura pallidiventris*; and the Nearctic *Oidematops ferrugineus*. Some Sciomyzini and Tetanocerini with partially similar parasitoid behaviors are placed in three parasitoid groups in the most recent Behavioral Group classification (see **Supplemental Text 2**). The best-studied example is the uncommon, univoltine *S. varia* (11, 19), which Barnes (11) characterized as having “one of the most fully developed suites of specialized habits found in the Sciomyzidae, including parasitoid feeding, host specificity, oviposition on the shell, solitary life in a single host, and completion of larval and pupal life in the host shell.” The strategy of this group seems to be one snail per larva and one larva per snail. Although several eggs are sometimes laid on one snail, only one larva survives. Unlike some true parasitoid sciomyzid larvae, in which the first instar penetrates far into the snail between the shell and mantle and is deprived of outside air, first-instar larvae of *S. varia* penetrate until only their posterior spiracles are exposed at the edge of the snail’s peristomal collar.

Barnes (11) provided the only thorough analysis of the sequence of snail organ destruction by a sciomyzid, dissecting snails after they had been fed upon by first, second, and third instars of *S. varia*. Host snails died 5–14 days after eggs were laid on them; larvae pupariated 6–14 days after entering snails. Host individuals of an amazingly broad size range were utilized. The shell-free

---

Uni-, bi-, or  
multivoltine:  
one, two, or several  
generations per year

---

dry weight of tissue available in field-collected snail shells 7.0–19.8 mm long, from which *S. varia* adults were reared, was calculated as 1.6–40.4 mg (11). Small snails produced small flies. Adults ranged in size (body length) from 3.6 to 6.5 mm.

### Mixed Parasitoid/Predator/Saprophage Behavior

The widely distributed Nearctic *Atrichomelina pubera* is an abundant, multivoltine, non-host-specific, opportunistic parasitoid/predator/saprophage of exposed semiaquatic and aquatic nonoperculate snails in diverse moist habitats (40). Eggs are laid on the shell or on other substrates. Larvae have been reared from five genera of field-collected snails. In the laboratory they feed on additional snail genera, including terrestrial species. Larvae can also develop on dead bivalves (59). They apparently kill and feed on an ecological assemblage of snail species, not on a particular taxonomic group. Feeding behavior is variable and depends on circumstances. The larvae display parasitoid, predatory, and saprophagous capabilities. Feeding behavior is variable and dependent upon availability of snails, relative sizes of larva and snail, and intraspecific competition. Such labile feeding behavior is typical of many other Sciomyzini and semiterrestrial Tetanocerini, especially during early larval life. Morphologically, the immature stages of *A. pubera* are typical of the Sciomyzini (e.g., reticulate egg chorion, unpigmented larval integument, ventral body spinules, microscopic interspiracular processes, and barrel-shaped puparia), but larvae share with a few *Pherbellia* only slightly elongate posterior spiracular disk lobes, indicating adaptation to wet microhabitats (22). Many saprophagous Diptera (including Ephydriidae, Phoridae, Piophilidae, and Sarcophagidae) have been reared from snails also containing *A. pubera*. No other sciomyzid has been reared from snails containing larvae of other families of flies. Such communal feeding might have been typical of ancestral sciomyzids.

### Predation

Predatory sciomyzid larvae exhibit a broad range of feeding behaviors, kinds of prey, and associated adaptations.

**Freshwater predators.** This largest group consists of 74 species in 14 genera, all in Tetanocerini, all in the terminal half of cladograms, occurring in all zoogeographical regions, and all with rather stereotyped larval feeding behavior (see “A Cornucopia for Sciomyzidae and Phaeomyiidae” at [http://www.sciomyzidae.info/downloads.php?cat\\_id=1](http://www.sciomyzidae.info/downloads.php?cat_id=1)). Although their behavior and associated adaptations differ somewhat, these larvae are the most overtly rapacious Sciomyzidae. Their prey range in the laboratory is broad (but probably narrower in nature). They attack and kill their prey within a few minutes, feed until gorged, and then rest away from the prey. They kill up to 50 snails of various sizes during the three stadia. They are wasteful predators, killing snails even when their gut is full. Whereas aquatic predaceous Tetanocerini probably evolved from shoreline predators early after divergence from a common stock with the Sciomyzini, they then probably acquired aquatic adaptations and became the basic line from which semiterrestrial and terrestrial Tetanocerini evolved (24). This group includes species that have been the main subjects of controlled laboratory experiments [*Illione albisetata* (46, 47), *Sepedon fuscipennis* (8, 31), *S. sphegea* (44, 50), *S. spinipes* (75, 83, 85, 86), and *Tetanocera ferruginea* (71–74, 124)] (see Laboratory Experimental Studies on Behavior and Development, below).

**Terrestrial predators.** A few Sciomyzini and 25 Tetanocerini in eight genera are considered terrestrial predators, although their behavioral, phenological, and morphological adaptations

and their polyphyletic ancestry likely represent several evolutionary lines (7, 24). Major differences and nuances in behavior are especially striking in this group, ranging from outright predation to aspects of parasitoid behavior (e.g., prey limited to a few species from one or two genera, slow death of the prey, and few prey individuals killed), especially during early larval life. Examples in Tetanocerini include four slug-killing *Tetanocera* species (24), a few *Sepedon* and *Tetanocera* parasitoids and predators of succineid snails, truly terrestrial predators such as *Tetanocera phyllophora* and *Trypetoptera punctulata* (119), and some Sciomyzini in *Pherbellia*, *Pteromicra*, and *Sciomyza* (see “A Cornucopia for Sciomyzidae and Phaeomyiidae” at [http://www.sciomyzidae.info/downloads.php?cat\\_id=1](http://www.sciomyzidae.info/downloads.php?cat_id=1)).

Evaluation of the life cycles of the highly specialized, apomorphic/apotypic fingernail-clam-killing species (in three unrelated genera), the snail-egg-feeding *Anticheta*, and the oligochaete-feeding *Sepedonella* and *Sepedon* species (all in Tetanocerini) in relation to their (unresolved) positions in cladistic analyses is critical to an evolutionary scenario of feeding behavior in Sciomyzidae.

The taxonomic value, phyletic significance, and functional morphology of sciomyzid eggs, larvae, and puparia have been presented (67). We summarize here important morphological adaptations of larvae relative to feeding behavior. Feeding behavior of Sciomyzini larvae, which generally feed in a somewhat insidious manner, differs strongly from that of Tetanocerini larvae, which are generally more overt feeders. All Sciomyzini lack accessory teeth below the mouthhook, indicating a less rapacious behavior than in Tetanocerini, in which accessory teeth are present, even in the derived terrestrial species. The ventral arch and pharyngeal sclerite of predatory Tetanocerini are much more expansive than those of Sciomyzini, providing increased area for muscle attachment. Although many larvae, especially Sciomyzini, feed for long periods in decaying, liquefying tissues of hosts/prey, only *Salticella fasciata* (one of three species of the plesiomorphic Salticellinae) has oral grooves around the mouth opening and ridges in the pharynx floor—adaptations common among saprophagous muscoid larvae for filtering microorganisms from decaying animal or plant tissues (66). Whereas *S. fasciata* is the only sciomyzid reared to pupariation and emergence solely on dead tissues of nonmolluscs (sowbugs and annelids), its first instars feed as parasitoids or saprophagously in terrestrial snails, and older larvae are strictly saprophagous.

Morphological adaptations to microhabitat limit the hosts/prey available to larvae and thus, to some extent, determine the type of feeding behavior (24, 122). Adaptations of many Tetanocerini to a surface or, rarely, subsurface existence (i.e., elongate last segment with upturned posterior spiracular disk having elongate lobes and interspiracular processes, pigmented integument with sensilla hairs) are lacking in Sciomyzini. The latter have a short last segment with a rear-facing posterior spiracular disk, short lobes on the disk, short interspiracular processes, unpigmented integument, and extensive ventral spinule patches that probably enhance mobility across substrates populated by “stranded” snails. Secondarily terrestrial Tetanocerini larvae (assuming a freshwater existence as the plesiotypic condition) have the same cephalopharyngeal skeleton features as do aquatic species but resemble Sciomyzini in having a short last segment with a rear-facing posterior spiracular disk, short lobes on the disk, short interspiracular processes, and colorless integument but no ventral spinule patches.

The 26 behaviorally, morphologically, and phenologically diverse reared species of *Tetanocera* (the fourth largest genus, with 39 species) are among the biologically best-known Sciomyzidae and have been the subjects of many experimental and life cycle studies (see “A Cornucopia for Sciomyzidae and Phaeomyiidae” at [http://www.sciomyzidae.info/downloads.php?cat\\_id=1](http://www.sciomyzidae.info/downloads.php?cat_id=1)). With a phylogeny (from a cladistic analysis of molecular characters) as a framework, analyses of the morphological features and microhabitats of 17 *Tetanocera* species suggested the freshwater habitat as the ancestral condition for the genus, with at least three parallel transitions to terrestrial habitat and one reversal (24). Hosts/prey, feeding behavior, and phenology were not included

---

**Plesiotypic:** describes a given behavior or habitat preference that is ancestral as opposed to derived

---

in the analyses, but the evolution of microhabitat selection delimited available hosts/prey and associated adaptations in feeding behavior and phenology.

## PHENOLOGY

Diverse phenological adaptations are associated with macrohabitats and microhabitats, hosts/prey, and feeding behavior. More species have been analyzed from cool temperate latitudes of North America than from elsewhere; five groups of voltinism and overwintering were proposed, as listed below (20). These groups are summarized and modified, with representative species included, in **Supplemental Text 3**; **Supplemental Figures 4** and **5** are graphic displays.

- Group 1: Multivoltine species overwintering in the puparium as diapausing or quiescent prepupae, pupae, or pharate adults
- Group 2: Multivoltine species overwintering as diapausing adults
- Group 3: Univoltine species overwintering within the egg membranes
- Group 4: Univoltine species overwintering partly or entirely in the larval stage
- Group 5: Univoltine species overwintering in the puparium

No sciomyzid has a life cycle lasting much more than one year, although in a few species, members of a cohort (i.e., larvae developing from eggs laid on the same day during autumn) may include individuals that overwinter either in the puparium or as adults, and some of these overwintering adults possibly live a few months more than a year. The capture, marking, and release of a female *Sepeidon fuscipennis* in Ithaca, New York, during August and her recapture in a reproductively active condition the following May (2) indicate a life cycle slightly longer than one year.

Berg et al. (20) summarized that most multivoltine species overwinter in puparia and that some overwinter as adults, whereas univoltine species overwinter as embryonated eggs, partly grown larvae, or in puparia. They concluded that multivoltinism with overwintering in the puparium is the most common and widespread phenology and that some species, especially some in Group 5, are labile and develop seasonally in alternative ways. Puparia of many aquatic and semiaquatic predatory species in cold-winter areas that eventually produce adults are often found at the surface during periods of ice melt during winter. Puparia of most species apparently survive freezing in the ice cover.

Many semiaquatic and terrestrial univoltine and multivoltine Sciomyzini form puparia in the host/prey shell. This behavior, especially in *Pherbellia* that produce a calcareous septum occluding the aperture, might be an adaptation for overwintering as well as for protection, the shell serving perhaps as a cocoon. In regions with cold winters, many species that overwinter as adults, e.g., most *Sepeidon* and *Elgiva* and some *Pherbellia* in southern parts of their ranges, are active on warm days during winter. Their apparent “basking” behavior likely raises their metabolic rate.

Stereotyped phenology characterizes aquatic and semiaquatic predators in tropical and warm areas. They appear to be multivoltine, with a variable number of generations (perhaps 4–12) per year that are not discrete but are successive and overlapping. In laboratory rearings they show no indication of diapause, develop promptly, have a short preoviposition period, a long oviposition period, and short egg, larval, and pupal periods. Similarly behaving species from warm areas of the Neotropical, Afrotropical, and Oriental regions have been consigned to a separate group, Group 6 (67). A few temperate-zone New Zealand and Neotropical species also seem to fit into Group 6.

## LABORATORY EXPERIMENTAL STUDIES ON BEHAVIOR AND DEVELOPMENT

Many aspects of Sciomyzidae have been studied experimentally, primarily in the laboratory and to a lesser extent in the field, but on relatively few species. We focus on laboratory experiments

▶ Supplemental Material




on key aspects of behavior and development conducted mostly under at least partially controlled conditions. Other aspects studied experimentally include the impacts of molluscicides on larvae (81), natural enemies of sciomyzids (57, 95), use of a salivary gland toxin by larvae to immobilize their prey (116), mass rearing potential (88), thermal constants (137), numerical responses (123), and coefficient of food for larval growth and energy gain (31).

Experimental conditions, especially water depth, varied significantly among studies. Although benchtop life cycle investigations conducted under ambient conditions might be considered experiments, we consider most of the results to be observations only. Such life cycle studies have often included simple short-term experiments resulting in conclusions that should be investigated further with current methods. Results of almost all experimental studies were reviewed recently (67), but the authors did not synthesize most research results to derive possibly new outcomes or to resolve conflicting conclusions. Among aquatic predators, the best studied are the multivoltine *T. ferruginea* (Holarctic), *Sepedon senex* (Oriental), *S. spegea* and *S. spinipes* (Palearctic), and *S. fuscipennis* (Nearctic); the univoltine *Ilione albiseta* (Palearctic); and among terrestrial parasitoids/predators the multivoltine *Pherbellia schoenberri schoenberri* and the univoltine *Salticella fasciata*, *Euthycera* spp. (all Palearctic), and *Sciomyza varia* (Nearctic), a parasitoid on aestivating *Lymnaea* snails.

Oviposition by several terrestrial and some semiterrestrial species appears to be triggered by various factors including number of available prey (123), size and maturity of suitable hosts (29), and presence of snail feces (28). Stimulatory cues for aquatic and semiaquatic species are unknown but could be worth researching, given the potential for the development of kairomones to attract potential biocontrols into target areas. During mass-rearing studies, addition of protein, e.g., crushed snails (25), reduced the preoviposition period while increasing the number of eggs laid and adult longevity. Sigmoidal oviposition curves have been described for many insects (55), including some Sciomyzidae (14, 47, 83, 119), and are useful indicators of egg production of wild-caught females, e.g., a curve truncated on the left indicates that oviposition had commenced in nature. Using oviposition data, Haab (50) identified 15°C as the oviposition threshold temperature for *S. spegea* overwintering as nonreproductive adults in France under natural autumn photoperiod (8:16); at 12°C, no females oviposited. Identifying such threshold temperatures will be useful in the future for matching sciomyzids to climates of areas where inoculative biocontrol programs are planned.

Hatching of submerged eggs of *Ilione albiseta* is facilitated by low oxygen levels (45). The thermal reaction norm is useful for determining whether an animal is cold or warm adapted (117). Eggs of the univoltine *I. albiseta* are significantly cold adapted (100). Cryopreservation of sciomyzid eggs for long-term storage or transportation has received little attention (83); there has been some success with other flies (e.g., *Musca domestica*, 129).

Much experimental research on Sciomyzidae has focused on larvae, the active malacophagous stage. The impact of prey species and prey and larval density on the duration of the larval stage has been elucidated for some aquatic species (**Supplemental Figure 6**). The length of time before attacking the first gastropod seems variable for neonate survival (13). Starvation of neonate larvae of *S. spegea* adversely affected survival of later instars, pupae, and adults (**Supplemental Figures 7 and 8**). Survival doubled at 20°C, 23°C, and 26°C when neonate larvae of *Sepedon spinipes* were fed one snail before starvation (82), an important finding in terms of release of larvae in biocontrol. However, determining which stage of sciomyzids to release remains a question. Prey searching by first instars tends to be random; efficacy depends on crawling speed, prey density and distribution, and water depth (17, 31, 43). Neonates of some freshwater predators actively pursued prey by following fresh snail mucus trails but not trails aged 45 min (86) (**Supplemental Figure 9**). Subsurface foraging is practiced by a few freshwater Tetanocerini (126); *I. albiseta* larvae use dissolved oxygen (47), but the means of uptake remains unknown.

 Supplemental Material

Many studies have examined photoperiod and temperature effects on survival and development time. In general, duration of all stadia decreased with increasing temperature (8, 85, 119, 137), percentage hatch was greater at lower temperatures, photoperiod manipulation caused *T. ferruginea* to bypass diapause (124), and the temperature at which the immature stages were reared influenced the longevity of adults of *S. spegea* (**Supplemental Table 5**). The above data are crucial for defining optimum conditions for mass-rearing purposes in biocontrol.

The amount of prey consumed by individual larvae depends on their feeding behavior, relative sizes of larvae and prey, and density of prey and larvae (**Supplemental Figure 10**). For strict parasitoids, the larval stage tends to be completed on one host, whatever its size; such larvae rarely forage for additional hosts. For predators attacking aquatic snails, the relationship tends to be size dependent, with neonate larvae killing smaller snails and later instars killing larger snails (42). In terms of prey density, a strong functional response has been reported, ranging from Type I (second- and third-instar *S. senex*; 17) to Type II (second- and third-instar *S. spegea*; 50) to Type III (third-instar *S. senex*; 17). Water depth appeared to be insignificant in governing functional response, but the addition of vegetation to experimental arenas increased snail biomass consumed (50) when prey density decreased (**Supplemental Figure 11**), apparently because it facilitated snail aggregation at the water surface. Eckblad (31), using equations to predict total number of snails killed per larva in shallow water, found that a simple power function might be more predictive than the predator models of Holling's classic work (53). At high snail densities, many freshwater predators showed high food conversion ratios when they killed many snails but only partially consumed them (120). Such wasteful feeding (56) can be related to optimal foraging theory because it might increase the energy-intake rate of predators by enabling them to consume only the most nutritious parts of their prey. Because more prey are killed in this scenario than otherwise, such behavior would be a useful trait in selection of potential biocontrols.

Many studies have investigated prey preference. The first, in regard to freshwater species (91), showed that larvae of 10 species killed only nonoperculate snails, all hosts of *Schistosoma* and all from outside the geographical range of the sciomyzids studied, thus highlighting their biocontrol potential. Larvae of the freshwater predator *T. ferruginea* displayed labile feeding behavior depending on the combinations of available snail species (73, 74). Those larvae chose prey providing the greatest return per unit of energy expended (72). As with other insects (e.g., Pteromalidae, 26), *T. ferruginea* displayed a "switching" phenomenon sensu Murdoch (89). As a measure of predation, biomass consumed (being independent of snail size and number of snails) has been the preferred index to number and sizes of snails killed. Larvae of *T. ferruginea* consumed more snails but less biomass when offered one prey species but consumed fewer individuals and more biomass when offered multiple prey species; overall they preferred large, sexually mature individuals (71). As a result, this species might have considerable impact on snail populations in the wild. Because *T. ferruginea* is one of the best-studied sciomyzids, it should be a priority for biocontrol in temperate areas. Number and biomass of snails consumed daily by *S. spegea* also increased with various combinations of temperatures (12°C–30°C) and photoperiods (8:16, 12:12, and 16:8) (44, 50).

Studies have been conducted on intra- and interspecific competition (15, 16), but limitations include mixing of unlikely ecological equivalents (e.g., species partitioned spatially in different microhabitats) and exclusion of other malacophagous taxa (e.g., Lampyridae). As with some Tephritidae (3), intraspecific competition among the parasitoid *P. schoenherri schoenherri* (123) and the aquatic predator *Sepedon spegea* (44) often resulted in some larvae gaining and maintaining a competitive advantage at the expense of conspecifics (123). Emerging adults ranged widely in size (44) (**Supplemental Figure 12**).

Experimental studies on pupae have focused on sexual dimorphism and overwintering. It is possible to predict the adult sex of *Tetanocera ferruginea* and *Sepedon spinipes* adults prior to eclosion

by measuring puparium length (69) and weight (85), respectively; this method could be used to determine differences in hymenopteran parasitoid load between sexes. Its use also would facilitate establishment of cultures for mass rearing because puparia are more easily manipulated than motile adults are and sex ratios of cultures could be set prior to the emergence of adults. Puparia can be dissected to determine the overwintering stage within (i.e., young or old prepupae, pupae, or pharate adults), and temperature can be manipulated to elucidate their physiological state (i.e., quiescence or true diapause) (20). This area, critical for fine-tuning phenologies for selecting biocontrols and for studying the overall evolution of the family, is in need of further research.

## POPULATION BIOLOGY, BIOINDICATORS, ECOSYSTEM SERVICE PROVISION, AND CONSERVATION

Populations of adult Sciomyzidae are found in metacommunities over large areas of similar habitat. Within these macrohabitats are egg, larval, and puparial microhabitats, of which the last two may be sampled by a variety of methods (**Supplemental Text 4**). Adults move infrequently within a macrohabitat and between nearby macrohabitats (**Supplemental Text 5**), but the wide geographical ranges of many sciomyzids suggest broader saltatory movements. Peacock (97) studied the movements of the Nearctic aquatic predator *Sepedon fuscipennis* using mark-recapture techniques and suggested in his unpublished thesis that movements of adults were more extensive in lotic macrohabitats than in lentic macrohabitats. Restricted movement of Sciomyzidae also has been noted in a number of Palearctic studies (109, 121, 133). Four mark-recapture studies on Sciomyzidae, two of which concern *S. fuscipennis*, have been published. Adult populations of approximately 1 (32) and 0.53 (2) flies per m<sup>2</sup> were reported from a backwater habitat and an experimentally flooded area, respectively, in New York, and population estimates of an assemblage of 10 species were as high as 6.08 flies per m<sup>2</sup> in an Irish turlough (temporary karstic lake) (133). Although the latter estimates are 6–12 times higher than the former estimates, they are consistent with a wider study in Irish turloughs (133, 135). In a study of an assemblage of sciomyzids (three *Sepedon* and one *Sepedonella* species), with emphasis on *Sepedon ruficeps* (42), in temporary and permanent freshwater habitats in Bénin, West Africa, the population of *S. ruficeps* in both habitats peaked three months after maximal rainfall, but adults were present continually in the permanently wet habitat. This was one of the few studies, in addition to those by Eckblad & Berg (32) and Arnold (2), in which snail and sciomyzid populations were studied simultaneously.

Substantial information has been published on seasonal variation in population sizes of sciomyzids, especially adults, but more precision and variety are needed in sampling methods throughout the year. Mark-recapture was used to illustrate diel fluctuations in a forest population of *Trypetoptera punctulata* and eight associated species in southern France (118). High temperatures reduced activity during midday. In a turlough in Ireland, sweep-net collecting showed that five species tended to peak between the end of July and mid-August, although some *Tetanocera* peaked earlier (133). In a study on a different turlough, the proportion of individuals of *Illione albiseta* captured in two vegetation zones on either side of a hillock shifted seasonally (134) (**Supplemental Text 5**). The shift was interpreted as an effect of water depth on the temperature at which each subpopulation developed. A succession of population peaks (May/June, July/August, October) was found for 14 species by sweep-net collecting in a temporarily inundated habitat in southern France (125). The same study showed a peak in species richness in June/July that coincided with a dip in equitability (species evenness), suggesting dominance of one or a few species.

Although scant explicit work has been conducted on Sciomyzidae as biodiversity indicators (94, 103), sciomyzids often appear in a supporting role in studies of wetlands and forests (**Supplemental Text 6**). Sciomyzidae as bioindicators may be considered in a normative framework, i.e., in terms of

---

**Metacommunity:** a set of local communities linked by dispersal

**Biodiversity indicator:** group of taxa or functional group whose diversity reflects diversity of other higher taxa in a habitat or set of habitats

---

#### Environmental

**indicator:** a species or group of species responding predictably to environmental disturbance or to a change in environmental state

#### Ecological

**bioindicators:** species representing the response of at least a subset of other organisms to stresses in the environment

#### Fuzzy-coded

**databases:** means of representing expert knowledge of species habitat/trait associations, coding species 0-3 by strength of association with habitats/traits

#### Economic

**externality:** a cost or benefit not transmitted through prices

### Supplemental Material

a set of ideal rules as to their selection, verification, and application (87), and in terms of pragmatic constraints, i.e., ease of collection, ubiquity, taxonomic stability, and availability of literature. The latter factors were considered in a European context, and Sciomyzidae were suggested as an auxiliary group especially suited to wetland habitats (108). Sciomyzidae were listed along with Chloropidae, Ephydriidae, Scathophagidae, and Sphaeroceridae as among the most important families of Diptera in freshwater wetlands in North America in terms of population size and species richness (60). Microhabitat selectivity and the significant role played in food webs add to the flies' utility as bioindicators. Populations of the relatively sedentary adults display qualitative and quantitative changes in species composition and relative abundance with habitat type, habitat management (e.g., grazing), and hydrology. Species richness and biomass productivity typically are their highest at medium hydroperiods (130, 135), consistent with the intermediate disturbance hypothesis (132).

Species lists and faunistic studies can be extremely useful in conservation work, especially in interpreting site history and management factors (110). Fuzzy-coded habitat-association and species-trait databases are ideal means of integrating expert knowledge and powerful multivariate statistical techniques. Such databases have proven useful for different taxa in a number of ecological contexts (**Supplemental Text 7**). A similar database being prepared for the European Sciomyzidae will widen their application as ecological bioindicators. Similar projects on the well-known Nearctic fauna would be useful, but wider sampling and more detailed ecological and basic biological research are needed before such projects can be attempted in Afrotropical, Neotropical, and Oriental regions.

Much interest in ecosystem service provision has resulted from the realization that services provided by nature can no longer be regarded as economic externalities of zero value (30). The value of insects as dung buriers, pollinators, pest controllers, and food for wildlife has been estimated to be US\$57 billion per year in the United States alone (68). The snail-killing impact of Sciomyzidae has not been included in published assessments of ecosystem services, yet it is well known that dam construction and concomitant environmental change result in expanded distributions of freshwater snails serving as intermediate hosts of flatworms that cause diseases of humans and livestock.

One of the best-known Sciomyzidae faunas is that of Britain and Ireland. Early collation of these records is continually supplemented, with new records regularly reported for both areas (**Supplemental Text 8**). Even in such relatively small, well-known faunas, baseline data are lacking on which to judge the importance of conservation of Sciomyzidae. Nevertheless, attempts have been made to list species of greatest concern and to attribute causes of decline of populations (36, 107) (**Supplemental Table 6**). With few invertebrates protected through legislation [no Diptera are listed in Annex II of the European Habitats Directive (34)], the most effective means of conserving Sciomyzidae is probably through the coarse filter of habitat protection. A third approach to conservation, between the fine filter provided by species lists—faunistic studies—and the coarse filter, is the so-called mesofilter of critical ecosystem elements (54). Many of these elements are not recorded in standard vegetation surveys but are critical to documenting insect communities. Sensitive management for invertebrates can be attained even in the absence of surveys by gross habitat protection (61, 105). Data on macrohabitat/microhabitat associations and species traits will contribute to adoption of a mesofilter approach to Sciomyzidae conservation and improved use of Sciomyzidae as bioindicators and ecosystem service providers (111).

## IDENTIFICATION AND SYSTEMATICS

Adult sciomyzids are readily recognized by porrect, projecting to slightly decumbent or drooping antennae; parallel to slightly divergent postocellar setae; lack of oral vibrissae; unexposed clypeus;

unbroken costal vein without strong setae; vein  $A_1 + CuA_2$  (anal vein) usually reaching the wing margin; and one or more tibiae with a dorsal preapical seta but no medial setae. The ease of identifying live adults of many species in the field or in a vial under the microscope—as well as the sedentary behavior, longevity, and tolerance of both adults and larvae—renders the family ideal for field and laboratory studies.

The most complete source of generic keys to sciomyzid adults and larvae (and to Nearctic and Palearctic puparia) by zoogeographic region, for all regions, is by Knutson & Vala (67). Also listed therein and in **Supplemental Texts 9 and 10** are other publications with keys, primarily to adults, for regions or subregions.

Species-level taxonomy for Sciomyzidae is well developed. Molecular studies of several species complexes are needed, e.g., several so-called subspecies, Holarctic species, the Nearctic *Sepedon fuscipennis* complex (70), and many Afrotropical *Sepedon* species. Taxonomic catalogs are available for all regions (**Supplemental Text 11**). The Smithsonian Institution, with 411 species and type specimens of 110 species, holds the most complete, authoritatively identified collection. A world checklist of valid species, with location of type material (in 64 collections in 27 countries), is available (67).

Sciomyzidae seem well placed in the superfamily Sciomyzoidea (which also includes Coelopidae, Dryomyzidae, Helosciomyzidae, Natalimyziidae, Phaeomyiidae, Ropalomeridae, and Sepsidae) (9, 10, 12, 51, 52, 80, 131), although some authors (e.g., 79) disagree as to which families should be included in Sciomyzoidea and whether the superfamily is monophyletic. We follow McAlpine (80) in considering Lauxanioidea as the sister group to Sciomyzoidea. Using maximum likelihood (ML) and Bayesian (BI) methods, Wiegmann et al. (131) analyzed a comprehensive Diptera data set [ $>200$  taxa; 149 of 157 families; 5 nuclear genes: 7 kilobases with 42 taxa having sequences from 14 nuclear genes, complete mitochondrial genomes (approximately 30 kilobases), and 371 morphological characters]. The analyses recovered a clade for Sciomyzoidea containing six families traditionally classified as Sciomyzoidea + Huttoninidae and Conopidae and the recently described family Natalimyziidae (12). Previously, family status was proposed for the generally recognized sciomyzid subfamily Phaeomyiinae (which then included only three Palearctic *Pelidnoptera* species, one of which is an obligate parasitoid of millipedes) (49). That placement generally has been followed, with Phaeomyiidae considered the sister group to Sciomyzidae, but a revision of *Pelidnoptera* that described the new genus *Akebono* (Japan) placed both genera in the Phaeomyiinae without discussion (113). Other segregates, especially the Helosciomyzinae and Huttonininae, have been included in or excluded from the Sciomyzidae by various authors (see **Supplemental Table 7**).

Before recent cladistic analyses of genera within Sciomyzidae and Phaeomyiidae (7, 23, 76) (see next section), major works were published on the suprageneric classification of Sciomyzidae (9, 10, 49, 51, 52, 112, 127). Although Steyskal's (112) and Verbeke's (127) papers were not couched in Hennigian (51) cladistic terminology, those authors were well acquainted with and sometimes used Hennigian principles.

Several genera, especially the species-rich worldwide genus *Pherbellia*, are obviously polyphyletic, and several subgenera in various genera probably should be raised to generic level. Taxonomy of Sciomyzidae lacks rigorous, comparative diagnoses, as pointed out in a major study of Sciomyzidae of the U.S. mid-Atlantic states (L.V. Knutson, W.L. Murphy & W.N. Mathis, unpublished manuscript). Many genera are based on descriptions/figures of only a few key characters. Studies of underutilized character systems are needed, especially of female abdomens.

Morphological studies of immature stages generally support the suprageneric classification based on adults, but systematics research and cladistic analyses of immatures are needed at the generic level. Detailed analyses of character states of features of immature stages are available, with diagnoses at the family, subfamily, and tribe levels (67).

## PHYLOGENETICS, MOLECULAR STUDIES, AND EVOLUTIONARY BIOLOGY

Only two family-wide phylogenetic studies of adult Sciomyzidae, and four studies of species within a genus (*Protodictya*, *Sepedonea*, *Tetanocera*, and *Thecomyia*; see below), have been conducted. The first family-level phylogeny used maximum parsimony (MP), analyzing 38 characters (36 adult, 1 larval morphological, and 1 larval behavioral) scored for the type species of 50 of the 61 genera (76). Seven adult morphological characters were added to those data, the larval characters were removed, and they were reanalyzed with MP (7). Both analyses recovered a monophyletic Salticellinae, Sciomyzini, and Tetanocerini. An MP bootstrap analysis of the former data set revealed that whereas relationships among most genera received relatively low support, relationships were well supported among *Sepedon* and five related genera that share derived states of eight characters. Most notably, the *Sepedon* lineage completely lacks a ptilinum (present in all other 42,000 ± *Schizophora* species) (67). Studies of individual genera using MP included 21 adult morphological characters scored for all 8 *Protodictya* species (75), 21 adult morphological characters analyzed to produce a phylogeny for all 12 *Thecomyia* species (78), and 27 adult morphological characters analyzed for all 13 *Sepedonea* species (77). The only published molecular-based phylogenetic study analyzed a concatenated four-gene data set (*COI*, *COII*, *16S*, *28S*; 3,787 characters) of 31 species among nine genera (54 specimens) focusing on *Tetanocera*, using BI, ML, and MP methods (24).

Five approaches (7, 21, 37, 48, 63) were used to categorize sciomyzids into Behavioral Groups on the basis of commonalities in larval microhabitat (aquatic, damp shoreline, terrestrial), mode of feeding (parasitoid, predator, saprophage), and prey type (freshwater and terrestrial nonoperculate snails, littoral and brackish-water operculate snails, succineid snails, snail eggs, slugs, fingernail clams, oligochaetes) (see Life Cycles, Larval Feeding Behavior, and Associated Adaptations, above). Of these, the ordination analysis by Barker et al. (7) used semistrong, hybrid, multidimensional scaling of 36 egg and larval morphological characters, larval behavior (omitting prey type), and habitat, recognizing nine “Eco-Groups.” However, without placement in a phylogenetic context, it cannot be determined whether closely related species in these groupings represent monophyletic lineages or whether feeding behaviors evolved in parallel.

Knutson & Vala (63) mapped their own Behavioral Groups onto the Marinoni & Mathis cladogram (76), numbering their groups in an evolutionary sequence. Utility of this approach was limited because the cladogram was relatively unresolved and did not estimate species-level evolutionary relationships within genera, but we provide some generalizations on the basis of that effort: (a) Ancestral sciomyzid habitat undoubtedly was terrestrial because Salticellinae and Sciomyzini (the basal lineages in the cladogram) are terrestrial (although some Sciomyzini occur on moist surfaces along terrestrial-aquatic interfaces)—as are all but the most derived members of other families of Sciomyzoidea. (b) Ancestral feeding behavior was likely similar to that of the extant *Atrichomelina pubera* because both are facultative (parasitoids/predators/saprophages depending upon food availability, level of intraspecific competition, etc.) and both attack assemblages of aquatic and semiaquatic snails in diverse moist habitats. (c) Aquatic habitats were invaded early during the phylogenesis of Tetanocerini (based upon phylogenetic relationships of aquatic and terrestrial Tetanocerini) and occurred multiple times in parallel, once followed by parallel reinvasions of terrestrial habitats, or both.

ML was used to optimize larval habitat onto a molecular phylogeny of *Tetanocera* (24). Results of this optimization were consistent with the hypothesis that larvae invaded aquatic habitats early during Tetanocerine evolution and that *Tetanocera* invaded terrestrial habitats multiple times from their aquatic ancestry. The latter study is one of the first to use phylogenetic comparative methods to explore morphological adaptations to both aquatic and terrestrial habitats of insects.

Ferrar (37) concluded that sciomyzid “larval morphology is predominantly functional and that larvae show a number of interesting examples of parallel evolution.” This hypothesis was examined using the program Discrete<sup>®</sup> (96) to test for correlated evolution among larval habitat and four larval morphological characters apparently associated with larval habitat (24). (Discrete<sup>®</sup> uses an ML framework and examines distributions of character states across a phylogeny, testing for potential correlations among two binary characters.) Correlations were significant between transitions in larval habitat (aquatic versus terrestrial) and changes in the states of the four morphological characters. These analyses demonstrated at least three parallel aquatic-to-terrestrial larval habitat transitions in *Tetanocera*. In each transition, larvae of terrestrials lost pigmentation, and float hairs and ventrolateral lobes of posterior spiracular disks and the last segment became shortened, resulting in a rear-facing spiracular disk (upturned in aquatics). These analyses supported Ferrar’s (37) hypothesis regarding the functionality and parallel evolution of larval morphology.

Sciomyzid phylogenetic studies have focused primarily on adult and secondarily on larval morphological characters. One study (24) included molecular characters and, in an ecological context, attempted to reconstruct habitat transitions of ancestral species. As of September 2011, DNA sequence data for only 32 of the 540 sciomyzid species were available from GenBank. Researchers currently are developing molecular phylogenies of Sciomyzidae using a combination of mitochondrial and nuclear genes. A molecular phylogeny that included 61 sciomyzid species in 22 genera was presented (115). In his PhD dissertation, Chapman (23) presented a molecular phylogeny with 65 sciomyzid species in 22 genera (123 terminal taxa). He optimized feeding group transitions on the phylogeny and found multiple examples of parallel evolution of feeding behaviors within the family. More extensive phylogenetic work on adult and larval morphological and molecular characters, combined with explicit tests of hypotheses related to evolutionary transitions in ancestral species, will provide a more complete understanding of the family as a paradigm for the evolution of parasitoid/predator/saprophage feeding habits along a terrestrial-aquatic ecological gradient.

## BIOCONTROL

Researchers have evaluated sciomyzids for use as biocontrols of freshwater snails (Hydrobiidae, Lymnaeidae, and Planorbidae) that serve as obligate intermediate hosts of the flatworm parasites *Schistosoma*, which cause schistosomiasis of humans and cattle in tropical and subtropical areas (see **Supplemental Figure 13**), and *Fasciola*, which cause fascioliasis of humans and livestock worldwide. Biocontrol potential has also been studied for two sciomyzids against snail pests of pasture and grain crops in Australia (27). Among reviews of biocontrol of snails and slugs by sciomyzids, that by the malacologist Barker (7) is a particularly valuable analysis of the use of sciomyzids in relation to modern ecological and biocontrol theory.


Advantages of using predatory sciomyzids as biocontrols, by augmentation and/or introduction of exotics, include the following: (a) They are obligate natural enemies of gastropods. (b) Many species have several generations per year. (c) They feed voraciously. (d) They live long and have high survival rates. (e) Natural enemy pressure on them is apparently low (research is under way). (f) Their diverse feeding behaviors and microhabitat preferences enable researchers to select “tailor-made” agents. (g) They are broadly distributed both geographically and across macrohabitats, i.e., traits advantageous to selecting agents targeted to diverse recipient environments. (b) They are easy to mass rear. Other specific biological advantages are noted throughout this review. The wealth of background information and active research by many cooperators are significant, synergistic advantages.

---

**Schistosomiasis:** an important parasitic disease of humans caused by three *Schistosoma* species; also called bilharzia

**Fascioliasis:** a disease of humans and certain animals caused by *Fasciola* trematode flatworms in temperate and warm parts of the world

---

 [Supplemental Material](#)

Aquatic, predaceous sciomyzids were field tested in a preliminary manner as biocontrols, e.g., through inoculative releases on Hawaii and several other Pacific Islands and augmentative trials in Iran. The first, best-documented inoculative release was of *Sepedomerus macropus* from Nicaragua into Hawaii (where there are no native sciomyzids) against a liver-fluke host (25). Only a few pupae were shipped to persons inexperienced with sciomyzids but who reared many adults for release. Larvae subsequently have been found feeding on target snails in nature (67); the species is established (33). This trial showed that sciomyzids could be shipped effectively, reared with local expertise and materials, and released effectively and could establish and disperse. In Iran, a native predator, *Sepedon sphaegee*, was mass reared and released as larvae in rice fields against a snail host of *Schistosoma* (114).

A three-year study was conducted at six sites in South Africa to determine, in an augmentative approach managed at the rural community level, the value of the endemic *Sepedon neavei* and *S. scapularis* against host snails of *Schistosoma* (1). The authors considered mainly their laboratory results on aspects of predation, prey specificity, prey range, and competition. They projected the cost of operating a mass-rearing facility to treat several foci of transmission to be about US\$700 per year (1992 US\$), not including salaries. Their study reached Stage 3 b (controlled field trials—effectiveness under local conditions) of the WHO 1984 Plan for Development of Biological Vector Control Agents (136), the stage of final laboratory tests for indigenous control agents. On the basis of extensive laboratory studies and a brief, preliminary, small-scale field trial (with no evidence that the sciomyzid became established), the authors concluded that *S. neavei* satisfied most criteria proposed by Samways (104) and WHO (136) for an effective, predaceous biocontrol agent. They also concluded that *Sepedon* spp. used in large numbers likely would be effective only in shallow transmission foci and as part of an integrated control program.

Efforts to control snail intermediate hosts of flatworms with molluscicides and habitat management waned recently as emphasis shifted toward use of antihelminthic drugs for the vertebrate-definitive hosts. However, interest in Sciomyzidae and other biocontrols of snail intermediate hosts and conservation of sciomyzids as ecosystem service providers likely will grow because of increasing costs of and resistance to antihelminthics (35). Snail populations are increasing as a result of extensive construction of dams and irrigation systems in many countries. As early as 1972, Bardach (6), reviewing the ecological implications of water resource development projects in the Lower Mekong Valley, noted “there can easily be a sharp rise in schistosomiasis” and at least five other diseases, with snails and mosquitoes being of greatest concern as vectors. In their 2008 analysis of the global burden of schistosomiasis, Finkelstein et al. (38) found the impact of symptoms associated with *Schistosoma japonicum* to be 7–46 times greater than 1996 estimates (90). Schelle et al. (106) focused on environmental impacts of dam construction, especially biodiversity of natural ecosystems; for example, despite the known risks, the World Bank provided US\$270 million in 2005 to construct a 38-m-high dam on a Mekong River tributary in Laos (41).

In conclusion, field research is needed on sciomyzids as biocontrols, particularly predation levels in natural populations, natural host/prey preferences, hymenopterous parasitoid pressure, numerical and functional response to predation, integrated control methods, and laboratory studies on cryopreservation, acclimatization, and mass rearing.

### SUMMARY POINTS

1. Larvae of Sciomyzidae are obligate natural enemies of freshwater, brackish-water, littoral, semiterrestrial, and terrestrial snails, snail eggs, slugs, and fingernail (sphaeriid) clams; three species feed on freshwater oligochaetes.



2. With life cycles known for 240 of 540 species in 41 of 61 genera, Sciomyzidae are a resource for studying the evolution of feeding behavior, as biocontrol agents of gastropods that are intermediate hosts of flatworms that cause diseases of humans and livestock or are agricultural pests, as ecosystem service providers of snail and slug control, and as bioindicators.
3. Characterizations of 15 Behavioral Groups and 6 Phenological Groups provide templates for evolutionary studies and guidelines for further research on life cycles.
4. Focal points of research are coevolved features of larval microhabitat, parasitoid/predatory/saprophagous feeding behavior, phenology, and morphology of immature stages.
5. Phylogenetic work has focused on adult and larval morphological characters, but some work, notably on *Tetanocera*, has included molecular characters, and studies have included an ecological context in an attempt to reconstruct habitat transitions of ancestral species.
6. Research is needed to determine hosts/prey in nature, many aspects of natural populations, natural enemies, impact of sciomyzids on gastropod populations in the wild, databases on microhabitats and macrohabitats and species characteristics, priority bioindicators for a range of protected habitats, efficacy of potential biocontrol agents under controlled field trials, cladistic analyses of species and genera including molecular and morphological characters, and internal anatomy of larvae and adults.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

For reviewing the manuscript we thank J. Abercrombie, R. Anderson, J. Badmin, J.K. Barnes, J.B. Coupland, T. Gittings, K.C. Kim, W.N. Mathis, I. McLean, R.E. Orth, T.D. Paine, R. Rozkošný, M.C.D. Speight, and K.R. Valley. For permission to use data in the supplemental materials we thank S.A. Marshall for the photo of mating sciomyzids; M. Schlabach and the Division of Rare and Manuscript Collections, A.R. Mann Library, Cornell University, for including the film by K. Sandved and the late C.O. Berg; M. Ghamizi, C. Haab, and D. Peacock for use of unpublished material from their theses; and authors and copyright holders for reproduction of figures and tables.

## LITERATURE CITED

1. Appleton CC, Miller RM, Maharaj R. 1993. Control of schistosomiasis host snails in South Africa—the case for biocontrol by predator augmentation using sciomyzid flies. *J. Med. Appl. Malacol.* 5:107–16
2. Arnold SL. 1978. Sciomyzidae (Diptera) population parameters estimated by the capture-recapture method. *Proc. Entomol. Soc. Ont.* 107(1976):3–9
3. Averill AL, Prokopy RJ. 1987. Intraspecific competition in the tephritid fruit fly, *Rhagoletis pomonella*. *Ecology* 68:878–86
4. Bailey PT. 1989. The millipede parasitoid *Pelidnoptera nigripennis* (F.) (Diptera: Sciomyzidae) for the biological control of the millipede *Ommatoiulus moreleti* (Lucas) (Diplopoda: Julida: Julidae) in Australia. *Bull. Entomol. Res.* 79:381–91

7. Reviews the biology of Sciomyzidae, especially predators/ parasitoids of terrestrial gastropods and behavior/biocontrol potential in a theoretical framework.

11. Life cycle study of an intimately associated parasitoid of snails, incorporating analysis of larval feeding sites.

24. Shows the parallel evolution of larval morphology and habitat in the snail-killing fly genus *Tetanocera*.

5. Baker GH. 1985. Parasites of the millipede *Ommatoiulus moreletii* (Lucas) (Diplopoda: Julidae) in Portugal, and their potential as biological control agents in Australia. *Aust. J. Zool.* 33:23–32
6. Bardach JE. 1972. Some ecological implications of Mekong River development plans. In *The Careless Technology: Ecology and International Development: The Record of the Conference on the Ecological Aspects of International Development*, ed. MT Farvar, JP Milton, pp. 236–44. Garden City, NY: Nat. Hist. Press. 1030 pp.
7. **Barker GM, Knutson L, Vala J-C, Coupland JB, Barnes JK. 2004. Overview of the biology of marsh flies (Diptera: Sciomyzidae), with special reference to predators and parasitoids of terrestrial gastropods. In *Natural Enemies of Terrestrial Molluscs*, ed. GM Barker, pp. 159–219. Wallingford, UK: CABI. 644 pp.**
8. Barnes JK. 1976. Effect of temperature on development, survival, oviposition, and diapause in laboratory populations of *Sepedon fuscipennis* (Diptera: Sciomyzidae). *Environ. Entomol.* 5(6):1089–98
9. Barnes JK. 1979. The taxonomic position of the New Zealand genus *Prosochaeta* Malloch (Diptera: Sciomyzidae). *Proc. Entomol. Soc. Wash.* 81(2):285–97
10. Barnes JK. 1981. Revision of the Helosciomyzidae (Diptera). *J. R. Soc. N. Z.* 11(1):45–72
11. **Barnes JK. 1990. Biology and immature stages of *Sciomyza varia* (Diptera: Sciomyzidae), a specialized parasitoid of snails. *Ann. Entomol. Soc. Am.* 83(5):925–38**
12. Barraclough DA, McAlpine DK. 2006. Natalimyzidae, a new African family of acalyptrate flies (Diptera: Schizophora: Sciomyzoidea). *Afr. Invertebr.* 47:117–34
13. Beaver O. 1972. Notes on the biology of some British sciomyzid flies (Diptera: Sciomyzidae). II. Tribe Tetanocerini. *Entomologist* 105:284–99
14. Beaver O. 1973. Egg laying studies on some British sciomyzid flies (Diptera: Sciomyzidae). *Hydrobiologia* 43(1–2):1–12
15. Beaver O. 1974. Laboratory studies on competition for food of the larvae of some British sciomyzid flies (Diptera: Sciomyzidae). I. Intra-specific competition. *Hydrobiologia* 44(4):443–62
16. Beaver O. 1974. Laboratory studies on competition for food of the larvae of some British sciomyzid flies (Diptera: Sciomyzidae). II. Interspecific competition. *Hydrobiologia* 45(1):135–53
17. Beaver O. 1989. Study of effect of *Sepedon senex* W. (Sciomyzidae) larvae on snail vectors of medically important trematodes. *J. Sci. Soc. Thail.* 15:171–89
18. Berg CO. 1953. Sciomyzid larvae that feed in snails. *J. Parasitol.* 39(6):630–36
19. Berg CO. 1964. Snail control in trematode diseases: the possible value of sciomyzid larvae, snail-killing Diptera. *Adv. Parasitol.* 2:259–309
20. Berg CO, Foote BA, Knutson L, Barnes JK, Arnold SL, Valley K. 1982. Adaptive differences in phenology in sciomyzid flies. In *Recent Advances in Dipteran Systematics: Commemorative Volume in Honor of Curtis W. Sabrosky*, ed. WN Mathis, FC Thompson, pp. 15–36. *Mem. Entomol. Soc. Wash.* 10. 227 pp.
21. Berg CO, Knutson L. 1978. Biology and systematics of the Sciomyzidae. *Annu. Rev. Entomol.* 23:239–58
22. Bratt AD, Knutson LV, Foote BA, Berg CO. 1969. Biology of *Pherbellia* (Diptera: Sciomyzidae). *N. Y. Agric. Exp. Stn. Itabaca Mem.* 404:1–247
23. Chapman EG. 2008. *Bayesian phylogenetics of snail-killing flies (Diptera: Sciomyzidae) and freshwater mussels (Bivalvia: Unionidae): implications of parallel evolution, feeding group structure and molecular evolution*. PhD diss. Kent State Univ., Kent, Ohio
24. **Chapman EG, Foote BA, Malukiewicz J, Hoeh WR. 2006. Parallel evolution of larval morphology and habitat in the snail-killing fly genus *Tetanocera*. *J. Evol. Biol.* 19(5):1459–74**
25. Chock QC, Davis CJ, Chong M. 1961. *Sepedon macropus* (Diptera: Sciomyzidae) introduced into Hawaii as a control for the liver fluke snail, *Lymnaea ollula*. *J. Econ. Entomol.* 54(1):1–4
26. Cornell H, Pimentel D. 1978. Switching in the parasitoid *Nasonia vitripennis* and its effects on host competition. *Ecology* 59(2):297–308
27. Coupland JB. 1996. The biological control of helcid snail pests in Australia: surveys, screening and potential agents. In *Slug and Snail Pests in Agriculture: Proceedings of a Symposium Held at the University of Kent, 24–26 September 1996*, ed. IF Henderson, pp. 255–61. Br. Crop Prot. Counc. Symp. Proc. 66. 450 pp.
28. Coupland JB. 1996. Influence of snail faeces and mucus on oviposition and larval behavior of *Pherbellia cinerella* (Diptera: Sciomyzidae). *J. Chem. Ecol.* 22(2):183–89

29. Coupland JB, Espiau A, Baker G. 1994. Seasonality, longevity, host choice, and infection efficiency of *Salicella fasciata* (Diptera: Sciomyzidae), a candidate for the biological control of pest helixid snails. *Biol. Control* 4:32–37
30. Daily GC, Söderqvist T, Aniyar S, Arrow K, Dasgupta P, et al. 2000. The value of nature and the nature of value. *Science* 289(5478):395–96
31. Eckblad JW. 1973. Experimental predation studies of malacophagous larvae of *Sepedon fuscipennis* (Diptera: Sciomyzidae) and aquatic snails. *Exp. Parasitol.* 33(2):331–42
32. Eckblad JW, Berg CO. 1972. Population dynamics of *Sepedon fuscipennis* (Diptera: Sciomyzidae). *Can. Entomol.* 104(11):1735–42
33. Englund RA, Arakaki K, Preston DJ, Evenhuis NL, McShane KK. 2003. Systematic inventory of rare and alien aquatic species in selected O'ahu, Maui, and Hawai'i Island streams. *Contrib. No. 2003–17, Hawaii Biol. Surv.*
34. ECE (Eur. Commission Environ.). 1992. Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. *Off. J. L 206*, July 27, 1992. Brussels
35. Fairweather I, Boray JC. 1999. Mechanisms of fasciolicide action and drug resistance in *Fasciola hepatica*. In *Fasciolosis*, ed. JP Dalton, pp. 225–76. Wallingford, UK: CABI. 552 pp.
36. Falk SJ. 1991. A review of the scarce and threatened flies of Great Britain (Part 1). *Res. Surv. Nat. Conserv.* 39. Peterborough, UK: Nat. Conserv. Council. 194 pp.
37. Ferrar P. 1987. A guide to the breeding habits and immature stages of Diptera. Cyclorrhapha. In *Entomograph*, ed. L Lyneborg, 8:329–40, 815–27. Leiden/Copenhagen: Brill/Scand. Sci. Press. 907 pp.
38. Finkelstein JL, Schleinitz MD, Carabin H, McGarvey ST. 2008. Decision-model estimation of the age-specific disability weight for *Schistosomiasis japonica*: a systematic review of the literature. *PLoS Negl. Trop. Dis.* 2(3):e158
39. Fisher TW, Orth RE. 1972. Resurrection of *Sepedon pacifica* Cresson and redescription of *Sepedon praemiosa* Giglio-Tos with biological notes (Diptera: Sciomyzidae). *Pan-Pac. Entomol.* 48(1):8–20
40. Foote BA, Neff SE, Berg CO. 1960. Biology and immature stages of *Atrichomelina pubera* (Diptera: Sciomyzidae). *Ann. Entomol. Soc. Am.* 53(2):192–99
41. Fountain H. 2005. Despite worries, push to build big dams is strong. *N. Y. Times*, Le Monde ed., June 11, p. 3
42. Gbedjissi LG, Vala J-C, Knutson L, Dossou C. 2003. Predation by larvae of *Sepedon ruficeps* (Diptera: Sciomyzidae) and population dynamics of the adult flies and their freshwater prey. *Rev. Suisse Zool.* 110(4):817–32
43. Geckler RP. 1971. Laboratory studies of predation of snails by larvae of the marsh fly *Sepedon tenuicornis* (Diptera: Sciomyzidae). *Can. Entomol.* 103(5):638–49
44. **Ghamizi M. 1985. *Predation des mollusques par les larves de Sepedon sphegea* Fab. (Diptera: Sciomyzidae) aspects de la dynamique proie-predateur. PhD thesis. Acad. Montpellier, Fr. 180 pp.**
45. Gormally MJ. 1985. The effect of temperature on the duration of the egg stage of certain sciomyzid flies which predate *Lymnaea truncatula*. *J. Therm. Biol.* 10(4):199–203
46. Gormally MJ. 1988. Studies on the oviposition and longevity of *Ilione albiseta* (Diptera: Sciomyzidae)—potential biological control agent of liver fluke. *Entomophaga* 33(4):387–95
47. Gormally MJ. 1988. Temperature and the biology and predation of *Ilione albiseta* (Diptera: Sciomyzidae)—potential biological control agent of liver fluke. *Hydrobiologia* 166:239–46
48. Greathead DJ. 1981. Arthropod natural enemies of bilharzia snails and the possibilities for biological control. *Biocontrol News Inf., CIBC* 2:197–202
49. Griffiths GCD. 1972. *The Phylogenetic Classification of Diptera Cyclorrhapha with Special Reference to the Structure of the Male Postabdomen*. Ser. Entomol. No. 8. The Hague: Junk. 340 pp.
50. Haab C. 1984. *Etude expérimentale de la biologie de Sepedon sphegea (Fabricius, 1775) et aspects de sa prédation larvaire (Diptera: Sciomyzidae)*. PhD thesis. Acad. Montpellier, Univ. Sci. Tech. Languedoc, Montpellier, Fr. 136 pp.
51. Hennig W. 1958. Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. *Beitr. Entomol.* 8:505–688
52. Hennig W. 1965. Die Acalypratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteran-Gruppe. *Stuttg. Beitr. Naturkd.* 145:1–212

---

44. Analyzes the influence of intraspecific competition on a wide variety of biotic factors involving *S. sphegea*.

---

53. Holling CS. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91(7):385–98
54. Hunter ML Jr. 2005. A mesofilter conservation strategy to complement fine and coarse filters. *Conserv. Biol.* 19(4):1025–29
55. Jarvis JL, Brindley TA. 1965. Predicting moth flight and oviposition of European corn borer by the use of temperature accumulations. *J. Econ. Entomol.* 58(2):300–3
56. Johnson DM, Akre BG, Crowley PH. 1975. Modelling arthropod predation: wasteful killing by damselfly naiads. *Ecology* 56(5):1081–93
57. Juliano SA. 1982. Influence of host age on host acceptability and suitability for a species of *Trichogramma* (Hymenoptera: Trichogrammatidae) attacking aquatic Diptera. *Can. Entomol.* 114:713–20
58. Kaczynski VW, Zuska J, Berg CO. 1969. Taxonomy, immature stages, and bionomics of the South American genera *Perilimnia* and *Shannonia* (Diptera: Sciomyzidae). *Ann. Entomol. Soc. Am.* 62(3):572–92
59. Keiper JB. 2006. Snail-killing flies (Sciomyzidae). In *Cleveland Museum of Natural History: Research & Collections: Invertebrate Zoology*. <http://www.cmnh.org/site/ResearchandCollections/InvertebrateZoology/Research/Diptera.aspx>
60. Keiper JB, Walton WE, Foote BA. 2002. Biology and ecology of higher Diptera from freshwater wetlands. *Annu. Rev. Entomol.* 47:207–32
61. Kirby P. 1992. *Habitat Management for Invertebrates: A Practical Handbook*. Sandy, Bedfordshire: R. Soc. Prot. Birds. 150 pp.
62. Knutson L, Orth RE, Fisher TW, Murphy WL. 1986. Catalog of Sciomyzidae (Diptera) of America North of Mexico. *Entomography* 4:1–53
63. Knutson L, Vala J-C. 2002. An evolutionary scenario of Sciomyzidae and Phaeomyiidae (Diptera). *Ann. Soc. Entomol. Fr.* 38(1–2):145–62
64. Knutson LV, Berg CO. 1967. Biology and immature stages of malacophagous Diptera of the genus *Knutsonia* Verbeke (Sciomyzidae). *Bull. Inst. R. Sci. Nat. Belg.* 43:1–60
65. Knutson LV, Rozkošný R, Berg CO. 1975. Biology and immature stages of *Pberbina* and *Psacadina* (Diptera: Sciomyzidae). *Acta Sci. Nat. Acad. Sci. Bohem.-Brno* 9(1):1–38
66. Knutson LV, Stephenson JW, Berg CO. 1970. Biosystematic studies of *Salpicella fasciata* (Meigen), a snail-killing fly (Diptera: Sciomyzidae). *Trans. R. Entomol. Soc. Lond.* 122(3):81–100
67. Knutson LV, Vala J-C. 2011. *Biology of Snail-Killing Sciomyzidae Flies*. Cambridge, UK: Cambridge Univ. Press. 584 pp.
68. Losey JE, Vaughan M. 2006. The economic value of ecological services provided by insects. *BioScience* 56(4):311–23
69. Manguin S. 1989. Sexual dimorphism in size of adults and puparia of *Tetanocera ferruginea* Fallén (Diptera: Sciomyzidae). *Proc. Entomol. Soc. Wash.* 91(4):523–28
70. Manguin S. 1990. Population genetics and biochemical systematics of marsh flies in the *Sepedon fuscipennis* group (Diptera: Sciomyzidae). *Biochem. Syst. Ecol.* 18(6):447–52
71. Manguin S, Vala J-C. 1989. Prey consumption by larvae of *Tetanocera ferruginea* (Diptera: Sciomyzidae) in relation to number of snail prey species available. *Ann. Entomol. Soc. Am.* 82(5):588–92
72. Manguin S, Vala J-C, Reidenbach JM. 1986. Prédation de mollusques dulçaquicoles par les larves malacophages de *Tetanocera ferruginea* Fallén, 1820 (Diptera, Sciomyzidae). *Can. J. Zool.* 64(12):2832–36
73. Manguin S, Vala J-C, Reidenbach JM. 1988. Action prédatrice des larves de *Tetanocera ferruginea* (Diptera: Sciomyzidae) dans des systèmes à plusieurs espèces de mollusques-proies. *Acta Ecol./Ecol. Appl.* 9(3):249–59
74. Manguin S, Vala J-C, Reidenbach JM. 1988. Détermination des préférences alimentaires des larves de *Tetanocera ferruginea* (Diptera: Sciomyzidae), prédateur de mollusques dulçaquicoles. *Acta Ecol./Ecol. Appl.* 9(4):353–70
75. Marinoni L, Barros de Carvalho CJ. 1993. A cladistic analysis of *Protodictya* Malloch (Diptera, Sciomyzidae). *Proc. Entomol. Soc. Wash.* 95(3):412–17
76. Marinoni L, Mathis WN. 2000. A cladistic analysis of Sciomyzidae Fallén (Diptera). *Proc. Biol. Soc. Wash.* 113(1):162–209
77. Marinoni L, Mathis WN. 2006. A cladistic analysis of the Neotropical genus *Sepedonea* Steyskal (Diptera: Sciomyzidae). *Zootaxa* 1236:37–52

---

67. The single most comprehensive review of all aspects of the Sciomyzidae worldwide, with keys.

---

78. Marinoni L, Steyskal GC, Knutson L. 2003. Revision and cladistic analysis of the Neotropical genus *Thecomyia* (Diptera: Sciomyzidae). *Zootaxa* 191:1–36
79. McAlpine DK. 1991. Relationships of the genus *Heterocheila* (Diptera: Sciomyzoidea) with description of a new family. *Tijdschr. Entomol.* 134:193–99
80. McAlpine JF. 1989. Phylogeny and classification of the Muscomorpha. In *Manual of Nearctic Diptera*, ed. JF McAlpine, 3:1397–505. Ottawa: Res. Branch, Agric. Can. Monogr. No. 32. vi + 1333–1518
81. McCoy LE, Joy JE. 1977. Tolerance of *Sepedon fuscipennis* and *Dictya* sp. larvae (Diptera: Sciomyzidae) to the molluscicides Bayer 73 and sodium pentachlorophenate. *Environ. Entomol.* 6(2):198–202
82. Mc Donnell RJ. 2004. *The biology and behaviour of selected marsh fly (Diptera: Sciomyzidae) species, potential biological control agents of liver fluke disease in Ireland*. PhD thesis. Natl. Univ. Irel., Galway. 236 pp.
83. Mc Donnell RJ, Gormally MJ. 2007. Thermal effects on the egg stage of four sciomyzids with reference to phenology and biocontrol potential. *J. Appl. Entomol.* 131(2):65–70
84. Mc Donnell RJ, Knutson L, Vala J-C, Abercrombie J, Henry P-Y, Gormally MJ. 2005. Direct evidence of predation by aquatic, predatory Sciomyzidae (Diptera, Acalyprata) on freshwater snails from natural populations. *Entomol. Mon. Mag.* 141:49–56
85. Mc Donnell RJ, Mulkeen CJ, Gormally MJ. 2005. Sexual dimorphism and the impact of temperature on the pupal and adult stages of *Sepedon spinipes spinipes*, a potential biological control agent of fascioliasis. *Entomol. Exp. Appl.* 115:291–301
86. Mc Donnell RJ, Paine TD, Gormally MJ. 2007. Trail-following behaviour in the malacophagous larvae of the sciomyzid flies *Sepedon spinipes spinipes* and *Dictya montana*. *J. Insect Behav.* 20(3):367–76
87. McGeoch MA. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev. Camb. Philos. Soc.* 73:181–201
88. McLaughlin HE, Dame DA. 1989. Rearing *Dictya floridensis* (Diptera: Sciomyzidae) in a continuously producing colony and evaluation of larval food sources. *J. Med. Entomol.* 26(6):522–27
89. Murdoch WW. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335–54
90. Murray CJL, Lopez AD, eds. 1996. *The Global Burden of Disease: A Comprehensive Assessment of Mortality and Disability from Diseases, Injuries and Risk Factors in 1990 and Projected to 2020*. Cambridge, MA: Harvard Univ. Press. 1022 pp.
91. Neff SE. 1964. Snail-killing sciomyzid flies: application in biological control. *Verh. Int. Ver. Limnol.* 15(2):933–39
92. Neff SE, Berg CO. 1966. Biology and immature stages of malacophagous Diptera of the genus *Sepedon* (Sciomyzidae). *Va. Agric. Exp. Stn. Bull.* 566:1–113
93. Nelson M, Keiper JB. 2009. Observations of the snail-killing fly *Sepedon fuscipennis* (Sciomyzidae) consuming limpets in the laboratory. *Fly Times* 43(Oct.):8–10
94. O'Halloran J, Harrison S, Gittings T, O'Callaghan E, O'Mahony L. 2011. Effects of habitat loss and fragmentation on the biodiversity maintenance function of remnant wetland and pond habitats within typical Irish agricultural landscapes. In *Biodiversity and Environmental Change: An Integrated Study Encompassing a Range of Scales, Taxa and Habitats*, ed. L Scally, S Waldre, pp. 9–25. (2005-CD-B2-M1). Techn. Proj. Rep. Wexford: Environ. Prot. Agency
95. O'Neill WL. 1973. Biology of *Trichopria popei* and *T. atrichomelinae* (Hymenoptera: Diapriidae), parasitoids of the Sciomyzidae (Diptera). *Ann. Entomol. Soc. Am.* 66(5):1043–50
96. Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. Ser. B* 255:37–45
97. Peacock DB. 1973. *Ecology of the snail-killing fly, Sepedon fuscipennis Loew (Diptera: Sciomyzidae) in lentic and lotic habitats*. MS thesis. Univ. Conn., Storrs. 61 pp.
98. Perris E. 1850. Histoire des métamorphoses de quelques diptères. *Mem. Soc. Sci. Lille* 1850:122–24
99. Pires AC, Marinoni L, Barros de Carvalho CJ. 2008. Track analysis of the Neotropical genus *Sepedonea* Steyskal (Diptera: Sciomyzidae): a proposal based on the phylogenetic analysis of its species. *Zootaxa* 1716:21–34
100. Pritchard G, Harder LD, Mutch RA. 1996. Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. *Biol. J. Linn. Soc.* 58:221–44

101. Rozkošný R. 1995. World distribution of Sciomyzidae based on the list of species (Diptera). *Stud. Dipterol.* 2:221–38
102. Rozkošný R, Knutson L. 2005. Sciomyzidae. In *Fauna Europaea: Diptera Brachycera*, ver.1.2. ed. T. Pape. <http://www.faunaeur.org/>
103. Ryder C, Moran J, Mc Donnell RJ, Gormally MJ. 2005. Conservation implications of grazing practices on the plant and dipteran communities of a turlough in Co. Mayo, Ireland. *Biodivers. Conserv.* 14:187–204
104. Samways MJ. 1981. *Biological Control of Pests and Weeds*. London: Edward Arnold. 57 pp.
105. Samways MJ. 2007. Insect conservation: a synthetic management approach. *Annu. Rev. Entomol.* 52:465–87
106. Schelle P, Collier U, Pittock J. 2004. Rivers at risk—dams and the future of freshwater ecosystems. Presented at *7th Int. River Symp., Brisbane, Aust.*
107. Shirt DB, ed. 1987. *British Red Data Books: 2. Insects*. Peterborough, UK: Nat. Conserv. Counc. 402 pp.
108. Speight MCD. 1986. Criteria for the selection of insects to be used as bio-indicators in nature conservation research. In *Proc. 3rd Eur. Congr. Entomol., Amsterdam*, ed. HMW Velthuis, pp. 485–88
109. Speight MCD. 2004. Predicting impacts of changes in farm management on sciomyzids (Diptera, Sciomyzidae): a biodiversity case study from southern Ireland. *Dipter. Dig.* 11:147–66
110. Speight MCD, Castella E. 2001. An approach to interpretation of lists of insects using digitized biological information about the species. *J. Insect Conserv.* 5:131–39
111. Speight MCD, Knutson LV. 2011. Species accounts for Sciomyzidae and Phaeomyiidae (Diptera) known from the Atlantic Zone of Europe. *Dipter. Dig.* 19(1):1–38
112. Steyskal GC. 1965. The subfamilies of Sciomyzidae of the world (Diptera: Acalyrtratae). *Ann. Entomol. Soc. Am.* 58(4):593–94
113. Sueyoshi M, Knutson L, Ghorpade KD. 2009. A taxonomic review of *Pelidnoptera* Rondani (Diptera) with discovery of a related new genus and species from Asia. *Insect Syst. Evol.* 40:389–409
114. Tirgari S, Massoud J. 1981. Study on the biology of snail-killing flies and prospect of biological control of aquatic snails *Sepedon spbegea* (Fabricius) (Insecta, Diptera, Sciomyzidae). Sci. Publ. 2051, Sch. Public Health, Inst. Public Health Res. Teheran Univ.
115. Tóthová A, Rozkošný R, Kutty SN, Wiegmann BM, Meier R. 2010. A molecular analysis of Sciomyzidae (Diptera). *Proc. 7th Int. Congr. Dipterol., San Jose, Costa Rica* (Abstr.)
116. Trellka DG, Berg CO. 1977. Behavioral studies of the slug-killing larvae of two species of *Tetanocera* (Diptera: Sciomyzidae). *Proc. Entomol. Soc. Wash.* 79(3):475–86
117. Trudgill DL, Honek A, Li D. 2005. Thermal time—concepts and utility. *Ann. Appl. Biol.* 146(1):1–14
118. Vala J-C. 1984. Phenology of Diptera Sciomyzidae in a Mediterranean forestry biotop. *Entomol. Basiliensis* 9:432–40
119. Vala J-C. 1986. Description des stades larvaires et données sur la biologie et la phénologie de *Trypetoptera punctulata* (Diptera, Sciomyzidae). *Ann. Soc. Entomol. Fr.* 22(1):67–77
120. Vala J-C. 1989. *Diptères Sciomyzidae Euro-méditerranéens. Faune de France. France et Régions Limitrophes*. No. 72. Paris: Féd. Franc. Soc. Sci. Nat., 300 pp.
121. Vala J-C, Brunel C. 1987. Diptères Sciomyzides capturés dans le Département de la Somme. *Bull. Soc. Linn. Lyon* 56(6):187–91
122. Vala J-C, Gasc C. 1990. Ecological adaptations and morphological variation in the posterior disc of larvae of Sciomyzidae (Diptera). *Can. J. Zool.* 68(3):517–21
123. Vala J-C, Ghamizi M. 1992. Aspects de la biologie de *Pherbellia schoenherri* parasitoïde de *Succinea elegans* (Mollusca) (Diptera, Sciomyzidae). *Bull. Soc. Entomol. Fr.* 97(2):145–54
124. Vala J-C, Haab C. 1984. Etude expérimentale du développement larvaire de *Tetanocera ferruginea* Fallén 1820. Influences de la température et de la photopériode, diapause pupale, biomasse alimentaire. *Bull. Ann. Soc. R. Belg. Entomol.* 120(7–8):165–78
125. Vala J-C, Manguin S. 1987. Dynamique et relations Sciomyzidae—Mollusques d'un biotope aquatique asséchant dans le sud de la France (Diptera). *Bull. Ann. Soc. R. Belg. Entomol.* 123(2):153–64
126. Valley KR, Berg CO. 1977. Biology and immature stages of snail-killing Diptera of the genus *Dictya* (Sciomyzidae). *Search Agric. Entomol.* 187(2):1–44
127. Verbeke J. 1950. Sciomyzidae (Diptera Cyclorrhapha). Fasc. 66. In *Exploration Parc Natl. Albert, Miss. G. F. de Witte (1933–35)*. Brussels: Inst. Parcs Nat. Congo Belge. 97 pp.

128. Verbeke J. 1967. Contribution à l'étude des diptères malacophages. IV. L'identité de *Pherbellia obtusa* (Fallén) (1820) et la description d'une espèce paléarctique nouvelle *Pherbellia argyra* sp. n. (Diptera: Sciomyzidae). *Bull. Inst. R. Sci. Nat. Belg.* 43(2):1–9
129. Wang WB, Leopold RA, Nelson DR, Freeman TP. 2000. Cryopreservation of *Musca domestica* (Diptera: Muscidae) embryos. *Cryobiology* 41(2):153–66
130. Whiles MR, Goldowitz BS. 2001. Hydrologic influences on insect emergence production from Central Platte River wetlands. *Ecol. Appl.* 11(6):1829–42
131. Wiegmann BM, Trautwein MD, Winkler IS, Barr NB, Kim J-W, et al. 2011. Episodic radiations in the fly tree of life. *Proc. Natl. Acad. Sci. USA* 108(14):5690–95
132. Wilkinson DM. 1999. The disturbing history of the intermediate disturbance hypothesis. *Oikos* 84(1):145–47
133. Williams CD, Gormally MJ, Knutson LV. 2010. Very high population estimates and limited movement of snail-killing flies (Diptera: Sciomyzidae) on an Irish turlough (temporary lake). *Biol. Environ. Proc. R. Ir. Acad.* 110B:81–94
134. Williams CD, Moran J, Doherty O, McDonnell RJ, Gormally MJ, et al. 2009. Factors affecting Sciomyzidae (Diptera) across a transect at Skealaghan Turlough (Co. Mayo, Ireland). *Aquat. Ecol.* 43(1):117–33
135. Williams CD, Sheahan J, Gormally MJ. 2009. Hydrology and management of turloughs (temporary lakes) affect marsh fly (Sciomyzidae: Diptera) communities. *Insect Conserv. Divers.* 2:270–83
136. World Health Organ. (WHO). 1984. Report of an Informal Consultation on Research on the Biological Control of Snail-Intermediate Hosts. Unpubl. *TDR/BCV-SCH/SIH/84*:13–16. Geneva
137. Yoneda Y. 1981. The effect of temperature on development and predation of marsh fly, *Sepedon aenescens* Wiedemann (Diptera: Sciomyzidae). *Jpn. J. Sanit. Zool.* 32(2):117–23
138. Zuska J, Berg CO. 1974. A revision of the South American genus *Tetanoceroides* (Diptera: Sciomyzidae), with notes on colour variations correlated with mean temperatures. *Trans. R. Entomol. Soc. Lond.* 125(3):329–62



# Contents

Insect Responses to Major Landscape-Level Disturbance <i>T.D. Schowalter</i> .....	1
Sound Strategies: The 65-Million-Year-Old Battle Between Bats and Insects <i>William E. Conner and Aaron J. Corcoran</i> .....	21
Approaches and Incentives to Implement Integrated Pest Management that Addresses Regional and Environmental Issues <i>Michael J. Brewer and Peter B. Goodell</i> .....	41
Transmission of Flea-Borne Zoonotic Agents <i>Rebecca J. Eisen and Kenneth L. Gage</i> .....	61
Insect Nuclear Receptors <i>Susan E. Fabrbach, Guy Smagghe, and Rodrigo A. Velarde</i> .....	83
<i>Plasmodium knowlesi</i> : A Malaria Parasite of Monkeys and Humans <i>William E. Collins</i> .....	107
Group Size and Its Effects on Collective Organization <i>Anna Dornhaus, Scott Powell, and Sarah Bengston</i> .....	123
Mosquito Genomics: Progress and Challenges <i>David W. Severson and Susanta K. Behura</i> .....	143
Reevaluating the Arthropod Tree of Life <i>Gonzalo Giribet and Gregory D. Edgecombe</i> .....	167
Morphology and Diversity of Exocrine Glands in Lepidopteran Larvae <i>Francesca Vegliante and Ivar Hasenfuss</i> .....	187
Insects as Weapons of War, Terror, and Torture <i>Jeffrey A. Lockwood</i> .....	205
Mites (Acari) as a Factor in Greenhouse Management <i>Uri Gerson and Phyllis G. Weintraub</i> .....	229
Evolutionary Ecology of Odonata: A Complex Life Cycle Perspective <i>Robby Stoks and Alex Córdoba-Aguilar</i> .....	249



Insect Transgenesis: Current Applications and Future Prospects <i>Malcolm J. Fraser Jr.</i> .....	267
The Ecology of Nest Movement in Social Insects <i>Terrence P. McGlynn</i> .....	291
Molecular Bases of Plant Resistance to Arthropods <i>C. Michael Smith and Stephen L. Clement</i> .....	309
Prospects for Managing Turfgrass Pests with Reduced Chemical Inputs <i>David W. Held and Daniel A. Potter</i> .....	329
Managing Social Insects of Urban Importance <i>Michael K. Rust and Nan-Yao Su</i> .....	355
Systematics, Biodiversity, Biogeography, and Host Associations of the Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha) <i>G. Cassis and R.T. Schub</i> .....	377
Essential Oils in Insect Control: Low-Risk Products in a High-Stakes World <i>Catherine Regnault-Roger, Charles Vincent, and John Thor Arnason</i> .....	405
Key Aspects of the Biology of Snail-Killing Sciomyzidae Flies <i>William L. Murphy, Lloyd V. Knutson, Eric G. Chapman, Rory J. Mc Donnell, Christopher D. Williams, Benjamin A. Foote, and Jean-Claude Vala</i> .....	425
Advances in Insect Phylogeny at the Dawn of the Postgenomic Era <i>Michelle D. Trautwein, Brian M. Wiegmann, Rolf Beutel, Karl M. Kjer, and David K. Yeates</i> .....	449
<b>Indexes</b>	
Cumulative Index of Contributing Authors, Volumes 48–57 .....	469
Cumulative Index of Chapter Titles, Volumes 48–57 .....	474

## Errata

An online log of corrections to *Annual Review of Entomology* articles may be found at <http://ento.annualreviews.org/errata.shtml>