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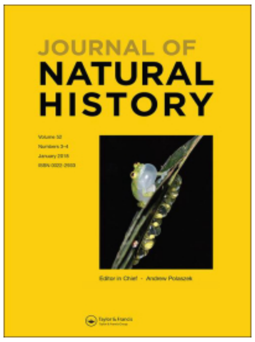

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First tabulation and analysis of natural enemies of snail-killing flies (Diptera: Sciomyzidae), their position in the fly/mollusc ecosystem, and implications for use of sciomyzids in biological control

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ABSTRACT

In this first tabulation and analysis of natural enemies of Sciomyzidae (snailkilling flies), 218 records are presented for 97 species and morphospecies in 44 genera of parasitoids, predators and pathogens. These represent 27 families in 7 orders attacking 64 of the 548 valid sciomyzid species in 23 of the 60 genera, in all major biogeographical regions, mainly North America and Western Europe. Our objectives are (1) to cast the data on natural enemies of a group of flies, with analysis, into a broad biological perspective; and (2) to provide specific data for selection of biocontrol agents. Parasitoid Hymenoptera are the primary natural enemies, 67 species and morphospecies in 25 genera of egg, larva/pupal and pupal parasitoids having been reared in nature from 24 sciomyzid species in 8 genera. Notably, all of our records of larval/pupal and pupal parasitoids are of rearings from isolated puparia, unlike many of the records of parasitoids of Tephritidae, reared from mass cultures of fruit, in which several species of Tephritidae (and other Diptera) were feeding. Herein we take a broad view of the complex of natural enemies, relating them to the extensive knowledge on the biology of the family, and analyse them in relation to the classification, phylogeny, distribution, habitats, and phenological and behavioural groups of Sciomyzidae. Parasitoid genera in the hymenopterous families Braconidae, Chalcididae, Diapriidae, Ichneumonidae, Pteromalidae and Trichogrammatidae are characterised briefly in regard to geographical distribution, host range, habitats, phenology and other aspects. Background information on Sciomyzidae and keys to the families and genera of parasitoid Hymenoptera attacking Sciomyzidae are included to encourage collection of and research on parasitoid natural enemies. Natural enemies are evaluated as to their impact on the use of Sciomyzidae as biological control agents of disease-carrying freshwater snails and pestiferous terrestrial snails and slugs in fieldcrop and greenhouses.

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Introduction

This is the first compilation of all published and numerous unpublished records of natural enemies of Sciomyzidae, analyses of their relationships with and impact on Sciomyzidae, and with special reference to the fly/mollusc/natural enemy ecosystem. The few publications specifically on the hymenopterous natural enemies of Sciomyzidae and the several publications on biology of Sciomyzidae that include some detail on natural enemies are reviewed below.

Globally, the natural enemies of few groups of Diptera have been thoroughly documented and analysed, notable exceptions being a few pest groups (eg some Tephritidae) and biological control agents (eg some Tachinidae). In addition to being of interest to Diptera and parasitoid Hymenoptera biology, data on and analyses of natural enemies of Sciomyzidae are important to further application of the flies as biological control agents. Important biocontrol targets are freshwater snails that are intermediate hosts of flatworm (Trematoda) parasites of humans (eg schistosomiasis) and livestock (eg fascioliasis), and terrestrial snails and slugs that are agricultural pests.

The biology of Sciomyzidae has been studied extensively over the past 50+ years from basic research viewpoints, especially life cycles, descriptions of immature stages, and evolution of predatory/parasitoid behaviour (see summaries of biology in Knutson and Vala 2002, 2011; Barker *et al*. 2004; Murphy *et al*. 2012). There have been some studies and practical attempts to use Sciomyzidae as inoculative or augmentative biocontrol agents to help control pestiferous snails, for example in California (Mc Donnell *et al*. 2007), Hawaii (Chock *et al*. 1961; Berg 1964), Iran (Tirgari 1986), South Africa (Appleton *et al*. 1993), Australia (Coupland 1996) and Ireland (HopeCawdery and Lindsay 1977; Gormally 1985, 1987a, 1988b; Mc Donnell *et al*. 2005; Mc Donnell and Gormally 2007; Hynes, Giordani *et al*. 2014, Hynes, Mc Donnell *et al*. 2014; D'Ahmed *et al*. 2019; Bistline-East, Williams *et al*. 2020, Bistline-East, Burke *et al*. 2020). Globally, there have been increased incidences of anthelmintic resistance in livestock (Fairweather and Boray 1999; O'Brien and Scully 2002). Also, the recent resurgence of dam-building projects throughout the world, eg Bujagali Dam, Jinja, Uganda (Mulkeen, pers. comm.) and the Nam Theun 2 Dam project underway in Laos with World Bank support (Bakker 1999), is resulting in increased trematode host-snail habitats and thus increased disease transmission (Zeigler *et al*. 2013). With these developments and the wealth of information gained on Sciomyzidae over the past several decades, there are compelling reasons to look at these insects again as biocontrol agents. For further analysis of Sciomyzidae in the context of current ecological and biological control theory, see Barker *et al*. (2004) and our Discussion below.

Background information on Sciomyzidae

Systematics, distribution and biology

The family Sciomyzidae includes three subfamilies, the Phaeomyiinae, Salticellinae and Sciomyzinae. The Phaeomyiinae consist of two extant genera and five species in the Palearctic and Oriental regions. The Salticellinae consists of one Palaearctic species and one Afrotropical species in the genus *Salticella* Robineau-Desvoidy[1] and one extinct Baltic amber genus with one species. The subfamily Sciomyzinae is the most abundant and comprises two tribes (Sciomyzini and Tetanocerini) with 57 genera and 541 described species (W.L. Murphy, unpublished), with at least 100 species remaining to be described.

Globally, 547 valid species of Sciomyzidae have been recorded in all biogeographical zones, with the greatest representation being in the Northern Hemisphere, but with many Neotropical, Afrotropical, and Oriental genera and species (Table 1). There is an online bibliography of about 2000 publications (https://sciomyzidae.info/downloads.php?cat_id=1&download_id=19) that will expedite further research, including research on natural enemies. There is a world checklist (as of 2013) of all valid species annotated with references to publications in which the biology and morphology of immature stages have been described as well as geographical distribution, phenological and behavioural groups, and major features of DNA analysis (Vala *et al*. 2012). Keys to genera of adults, larvae and puparia by major biogeographical regions are presented in Knutson and Vala (2011). Keys to species of larvae and puparia of some large North American genera are available, such as *Sepedon* (Neff and Berg, 1966), *Pherbellia* (Bratt *et al*., 1969), *Dictya* (Valley and Berg, 1977) and *Tetanocera* (Foote 2013). Publications by Rozkošný (1987, 1997, 1998, 2002) provide keys to genera of adults, larvae and puparia of Palaearctic Sciomyzidae, the 2002 publication including keys to species. There are no published keys to immature stages of Sciomyzidae species in the other major biogeographical regions, except for the Neotropical *Sepedonea* (Freidberg *et al*., 1991). There are keys to the immature stages of species of the Neotropical genus *Protodictya* Malloch in the unpublished parts of the PhD thesis by Abercrombie (1970). Very detailed biological information is available, including in most cases the complete life cycle, for 260 species in 41 of the 60 genera (see Table 2 which clearly indicates the need for more research in tropical areas). Thus, the group is one of the biologically best-known families of flies (Knutson and Vala 2011; Murphy *et al*. 2012). Adults of many species are found in a wide variety of moist to freshwater habitats where hygrophilous snails, slugs and fingernail clams (Sphaeriidae) occur. Some species are found in and near mesophytic woods, for example *Tetanocera elata* (Fabricius) (Knutson *et al*. 1970), and others in very dry habitats, such as *Trypetoptera punctulata* (Vala, 1986). Larvae are primarily obligate predators and parasitoids of non-operculate (pulmonate) freshwater and terrestrial snails. The larvae of a few species are restricted to snail eggs, slugs, fingernail clams or freshwater oligochaete worms (Knutson and Vala 2002, 2011). The puparia of freshwater species are well adapted for floating, whereas semi-terrestrial and terrestrial species pupariate[2] in leaf litter, in soil or even inside the shell of the host snail; some of these can be translocated by flood waters.

Freshwater species of Tetanocerini kill snails quickly and feed on their fresh tissue for a relatively brief period (several hours to a day). They then rest or forage away from the prey. They do not form their puparia in snail shells. Larvae of the Sciomyzini tend to remain feeding in their host's/prey's shell for relatively long periods (several days). Many of them form their puparia in the host's/prey's shell. From laboratory rearings, most aquatic and semi-aquatic predaceous Tetanocerini have a broad prey range, whereas most of the terrestrial and semi-terrestrial larvae (both Sciomyzini and Tetanocerini) are more specialised. However, some Sciomyzini, for example *Atrichomelina pubera* (Sciomyzini), have a very broad food range, feeding on an ecologically wide-ranging assemblage of snails (Foote *et al*. 1960). The most host-specific sciomyzids are the few species of terrestrial to semi-terrestrial parasitoid Sciomyzini that have highly intimate relationships with their host (eg *Sciomyza varia*; see Barnes 1990). That is, the female

Table 1. Enumeration of genera and species of world Sciomyzidae by geographical region.

	Region									Described-
Genus	H	N	P	NT	AF	O	A	OC	SA	species
1. *Akebono*			1							1
2. *Anticheta*		8	7	1						16
3. *Apteromicra*						1				1
4. *Atrichomelina*		1		(1)						1
5. *Calliscia*				1						1
6. *Chasmacryptum*			1							1
7. *Colobaea*		3	11		2	(1)				16
8. *Coremacera*			9							9
9. *Dichetophora*			5			1	6			12
10. *Dictya*		43 (2)	1	13 (4)						57
11. *Dictyacium*		2								2
12. *Ditaeniella*		2	1	1 (1)	2	(1)				6
13. *Ectinocera*			1							1
14. *Elgiva*	1	2								3
15. *Ethiolimnia*					7					7
16. *Eulimnia*									2	2
17. *Euthycera*		2	19	1						22
18. *Euthycerina*				2						2
19. *Eutrichomelina*				2						2
20. *Guatemalia*				2						2
21. *Hedria*		1								1
22. *Hoplodictya*		5		(2)						5
23. *Hydromya*			1		(1)	(1)				1
24. *Ilione*			8			(1)				8
25. *Limnia*		17	5							22
26. *Neolimnia*									13	13
27. *Neuzina*				1						1
28. *Oidematops*		1								1
29. *Oligolimnia*			1							1
30. *Parectinocera*				3						3
31. *Pelidnoptera*			4			(1)				4
32. *Perilimnia*				2						2
33. *Pherbecta*		1								1
34. *Pherbellia*	9	32	34 (1)	7 (1)	3	3 (2)	2	1		91
35. *Pherbina*			3							3
36. *Poecilographa*		1								1
37. *Protodictya*				8						8
38. *Psacadina*			4							4
39. *Pseudomelina*				1						1
40. *Pteromicra*	3	11	3		2	1				20
41. *Renocera*	1	5	2							8
42. *Retellia*				2						2
43. *Salticella*			1		1					2
44. *Sciomyza*	2	2	2							6
45. *Sepedomerus*		(1)		2						2
46. *Sepedon*		20	4 (4)		42	10 (1)	3 (1)	3		82
47. *Sepedonea*				13						13
48. *Sepedonella*					5					5
49. *Sepedoninus*					2	1				3
50. *Shannonia*				2						2
51. *Steyskalina*						1				1
52. *Tetanocera*	12	17	8	(1)		2				39
53. *Tetanoceroides*				7						7
54. *Tetanoptera*					1					1
55. *Tetanura*			1							1
56. *Teutoniomyia*		(1)		2						2
57. *Thecomyia*				13						13
58. *Trypetolimnia*			1							1
59. *Trypetoptera*		1	1							2
60. *Verbekaria*					1					1

(*Continued*)

Table 1. (Continued).

Genus	H	N	P	NT	AF	O	A	OC	SA	Described-species
	Region									
Total species/region	28	177	139	86	68	20	11	4	15	**548**
Total genera/region	**6**	**23**	**29**	**23**	**12**	**13**	**3**	**2**	**4**	–
Endemic genera/region	**3**	**5**	**9**	**14**	**4**	**2**	**0**	**0**	**4**	–

Table 2. Biological information published on Sciomyzidae by zoogeographical region.

Zoogeographic region	Total number of genera	Total number of species	Life cycles known, by number of genera	Life cycles known, by number of species
Palaearctic	35	167	23	79
Nearctic	29	205	17	107
Neotropical	23	86	13	36
Oriental	13	20	6	17
Afrotropical	12	68	2	9
Subantarctic	4	15	2	9
Australian	3	11	4	2
Oceanic	2	4	1	1

oviposits onto the shell, larvae feed for a relatively long period (several days) on the less vital tissues before the snail dies and generally there is only one larva per snail. These larvae also tend to feed on only one snail, and the puparium is formed within the shell upon which the egg had been laid. Among the many species of Sciomyzini and Tetanocerini that have mixed parasitoid–predatory behaviours there is a tendency for the somewhat parasitoid first-instar larvae to be more host/prey specific than the more predatory older larvae.

Behavioural groups and microhabitats

Behavioural groups. Eight behavioural groups within the Sciomyzidae were highlighted by Berg and Knutson (1978): aquatic predators, terrestrial parasitoids, scavengers, slug killers, egg or embryo eaters, subsurface foragers, operculate snail killers and clam killers. A more finely dissected classification of behavioural groups (17) was proposed by Knutson and Vala (2002), Knutson and Vala (2011) and summarised by Murphy *et al*. (2012). This arrangement of behavioural groups is an *a posteriori* classification of all the biologically known species of Sciomyzidae of the world, each group or subgroup based on knowledge of the actual attributes of one to many species in each group. The attributes of the groups of Knutson and Vala (2002, 2011) are type of food, the manner of killing and feeding, and the microhabitat. Their groups are more similar to 'functional groups' rather than to the 'guilds' of the ecological literature and are not limited to sympatric species or members of a community. Barker *et al*. (2004) recognised 10 ecomorphological groups in the Sciomyzidae based on feeding behaviour of larvae, habitat, 13 morphological features of eggs and larvae, and – for a few groups – very general host/prey ranges, but the latter were not specified as precisely as in Knutson and Vala (2002, 2011).

Ovruski *et al*. (2000, p. 85) centred their analysis of parasitoids of some Tephritidae in part on parasitoid guilds. For their purposes, they defined guilds as 'two or more *sympatric* [emphasis ours] species exploiting a given developmental stage of the host or a group of species that exploit the same class of environmental resources in a similar way'. They

Table 3. Natural enemies of Sciomyzidae. Taxon authorities for genera and species of natural enemies are given in Table 5; those for Sciomyzidae in Table 6.

Natural Enemy	Identifier	Sciomyzidae	Dates collected/emerged	Collected	Reference	Museum
(A) Parasitoids						
1. EGG PARASITOIDS						
Hymenoptera						
Trichogrammatidae						
Trichogramma japonicum	KY	*Sepedon aenescens*[1]	3.vi/?	Japan	Nagatomi and Kushigemachi (1965) and Yasumatsu (1967)	
"	?	*Sepedon aenescens*[1]	?	?	Hayat and Subba Rao (1986)	
"	A	*Sepedon aenescens*[1]	?	India, Japan	Nagarkatti and Nagaraja (1971) CIBC-B	
"	?	*Sepedon aenescens*[1]	?	Hawaii, India	Nagarkatti and Nagaraja (1977)	
"	?	*'Sciomyzidae'* in lab trials	?	China	Wong *et al*. (1984)	
"	A	*Sepedon aenescens*[2]	?	Philippines	Barrion and Litsinger (1982)	
"		*Sepedon sphegea*			Universal Chalcidoidea Database	
Trichogramma sp. 'probably *japonicum*'	A	*Sepedon aenescens*	?	Hawaii	Davis (1971)	
Trichogramma julianoi	GP	*Elgiva solicita*	?	New York	Juliano (1981)	
?????		*Elgiva sundewalli (=solicita)*			Universal Chalcidoidea Database	
"	GP	*Sepedon fuscipennis*	?	New York	Juliano (1981)	
Trichogramma julianoi		*Sepedon fuscipennis*	?		Universal Chalcidoidea Database	
Trichogramma kalkae	A	*Sepedon 'angularis'*[3]	?	Malawi	Schulten and Feijen (1978)	
Trichogramma kalkae	?	*Sepedon 'angularis'* [3]	?		Universal Chalcidoidea Database	
Trichogramma pinneyi	A	*Sepedon 'angularis'*[3]	?	Malawi	Schulten and Feijen (1978)	
Trichogramma sp.[4]	?	*Sepedon aenescens*	?	Hawaii	Knutson and Orth (1984)	
" spp.	A	*Sepedon ferruginosa*	?	Thailand	Yasumatsu *et al*. (1982)	
" sp.	HEE	*Sepedon fuscipennis*	?	New York	Neff and Berg (1966)	
"	?	*Sepedon fuscipennis*[5]	?	New York	Barnes (1976)	CU
"	RM	*Sepedon fuscipennis*[6]	vii/?	New York	Arnold (1978)	CU
?????????		*Sepedon fuscipennis*	(L3-2)		Universal Chalcidoidea Database	
?	?	?	?	?	Cowan (1979)	
Trichogramma spp.	A	*Sepedon* spp. (4)	?	Thailand	Yasumatsu *et al*. (1981)	
Trichogramma sp.	GP	*Elgiva solicita*	?	New York	Juliano (1981)	
nr. *californicum*	GP	*Sepedon fuscipennis*	?	New York	Juliano (1981) and 1982)	
"	GP	*Tetanocera* sp.	?	New York	Juliano (1981)	
Trichogramma sp. nr. *semblidis*	GP	*Sepedon fuscipennis*[7]	?	New York	Juliano (1981)	
Trichogramma semblidis		*Sepedon fuscipennis*			Universal Chalcidoidea Database	

(*Continued*)

Table 3. (Continued).

"		*Sepedon sphegea*			Universal Chalcidoidea Database	
		Tetanocera sp.			Universal Chalcidoidea Database	
Trichogrammatoidea bactrae	?	*Sepedon aenescens*[1]	?	?	Hayat and Subba Rao (1986)	
"	?	*Sepedon aenescens*[1]	?	India	Nagarkatti and Nagaraja (1977)	
Trichogrammatoidea nana		*Sepedon aenescens*[1]			Universal Chalcidoidea Database	
Trichogrammatoidea simmondsi	?	*Sepedon 'angularis'*			Universal Chalcidoidea Database	
Unidentified	A	*Sciomyza aristalis*[8]	?	New York	Foote (1959)	
"	A	*Sepedon spinipes*[9]	?	Denmark	Neff and Berg (1966)	
2. PUPAL PARASITOIDS						
Hymenoptera						
Diapriidae						
Spilomicrus barnesi	JWE and DSH	*Neolimnia tranquilla*	(P-35) 18.iii, 4.iv, 26.vii, 7xii/ [333]	New Zealand	Barnes (1979) and Early and Horning (1978)	
Spilomicrus sp.	CFWM	*Sepedonea trichotypa* [10]	(L3-1) 16.iv(19.iv)/19.v [4]	Argentina	Abercrombie (1970)	
"	CFWM	*Sepedonea trichotypa* [10]	(P-1) 16.iv/16.v [7]	Argentina	Abercrombie (1970)	
Trichopria atrichomelinae	CFWM	*Atrichomelina pubera* [11]	20-27.vii/25-26.viii [9,11,11]	New York	Muesebeck, (1972) and O'Neill (1973)	
"	CFWM?	*Sepedon fuscipennis* [12]	Oviposition, no emergence	New York	O'Neill (1973)	
"	CFWM?	*Elgiva solicita* [12]	"	New York	O'Neill (1973)	
"	CFWM?	*Dictya* sp. [12]	"	New York	O'Neill (1973)	
Trichopria popei	?	*Dictya floridensis*	(P-4) 29.iii/? [19]	Florida	Valley and Berg (1977)	
"	CFWM	*Dictya* sp.	(P-1) 13.viii/31.viii [5]	Minnesota	Knutson and Berg (1963)	
"	CFWM	*Dictya* sp.	(P-1) 29.x/1.xi [10]	New York	Knutson and Berg (1963)	
"	CFWM	*Elgiva solicita*	(P-1) 2.viii/12.viii [16]	New York	Knutson and Berg (1963)	
"	CFWM	*Sepedon fuscipennis*	(P-1) 28.vi/1.vii [30]	Michigan	Muesebeck (1949) and Berg (1953) and Knutson and Berg 1963)	CU
"	CFWM	*Sepedon fuscipennis*	(P-1) 16.vii/21.vii [17]	Michigan	Berg (1953) and Knutson and Berg 1963)	CU
"	CFWM	*Sepedon fuscipennis*	?/vi, vii	New York	O'Neill (1973)	
"	CFWM	*Atrichomelina pubera*[12]	-	New York	O'Neill (1973)	
"	CFWM	*Sepedon fuscipennis*[12]	-	New York	O'Neill (1973)	
"	CFWM	*Elgiva solicita*[12]	-	New York	O'Neill (1973)	

(*Continued*)

Table 3. (Continued).

"	CFWM	*Elgiva solicita*	?/vi, vii	New York	O'Neill (1973)	
"	CFWM	*Dictya* sp.[12]	-	New York	O'Neill (1973)	
"	CFWM	*Dictya* sp.	29.iii/?	Florida	O'Neill (1973)	
"	CFWM	*Dictya* sp.	?/vi, vii	New York	O'Neill (1973)	
"	CFWM	*Tetanocera plebeja*[13]	-	New York	O'Neill (1973)	
"	CFWM	Sciomyzidae (sp.)	iii, iv, xii/?	Florida, Louisiana	O'Neill (1973)	
"	CFWM	Sciomyzidae (sp.)	summer to 29.x/?	Michigan, Minnesota Illinois, New York	O'Neill (1973)	
*Trichopria*sp.	CFWM	*Atrichomelina pubera*	(P-1) 19.viii/?	New York	Foote *et al*. (1960)	
Undetermined species	CFWM	*Anticheta brevipennis*	(P-1) 3.v - 4.v	Denmark	Knutson (1966)	
3. LARVAL-PUPAL PARASITOIDS [14] **Hymenoptera** **Ichneumonidae**						
Mesoleptus declivus	CFWM	*Atrichomelina pubera*	(P-24) 9.iv-21.viii/?	New York	Foote *et al*. (1960)	
"	HKT	*Dictya* sp.	(P-4) 30.iv/?	New York	Knutson, unpub.	
"	HKT	*Ditaeniella humilis*	(P-2) 20,25.vi/?	Idaho	Bratt *et al*. (1969) and Bratt, unpub.	
"	HKT	*Pherbellia albovaria*	(P-several)/?	New York	Bratt *et al*. (1969) and Bratt, unpub.	
"	HKT	*Pherbellia griseola*	(P-1) 7.iv/?	New York	Bratt *et al*. (1969) and Bratt, unpub.	
"	HKT	*Pherbellia n. nana*	(P-1) 5.vii/?	New York	Bratt *et al*. (1969) and Bratt, unpub.	
"	HKT	*Pherbellia quadrata*	(P-1) 21.iv/?	New York	Bratt *et al*. (1969) and Bratt, unpub.	
"	HKT	*Pherbellia s. maculata*	(P-6) 7-9.iv/?	New York	Bratt *et al*. (1969) and Bratt, unpub.	
"	HKT	*Pteromicra pectorosa*	3.iv/?	New York	Foote, unpub.	
"	HKT	*Sciomyza varia*	(P-5) 27.vii / 21,22,23,27. viii, 9.ix	Michigan	Berg, unpub.	
"	HKT	*Sciomyza varia*	x/ 20-28 days later 23.xi/?	New York	Gower-Teece, unpub.	
"	HKT	*Sepedon armipes*	3.iii/? "early spring"	New York	Neff and Berg (1966)	Same
"	HKT	*Sepedon fuscipennis*	(L,P) various dates	New York, Michigan	Neff and Berg (1966)	
"		*Sepedon fuscipennis*	?/24.viii	New York	Ashmead (1901)	USNM
Mesoleptus sp. nr. *declivus*	WRMM	*Anticheta melanosoma*	28.iv/6.v	New York	Knutson and Abercrombie (1977)	

(*Continued*)

Table 3. (Continued).

Mesoleptus variator	MGF	*Tetanocera ferruginea*	-	Ireland	Mc Donnell and Gormally, unpub.
Mesoleptus vigilatorius	HKT	*Sepedon sphegea*	(L) 7.viii/?	Sweden	Neff and Berg (1966)
Mesoleptus laticinctus	MGF	*Tetanocera ferruginea*		Ireland	Mc Donnell and Gormally, unpub.
Mesoleptus sp.	JFA	*Sepedon sphegea*	(P-38) 10.vi/?	S. France	Vala and Manguin (1987)
*Mesoleptus*sp. A	HKT	*Dictya* sp.	1.vii/?	New York	Knutson, unpub.
"	HKT	*Dictya* sp.	27.viii/?	Minnesota	Knutson, unpub.
"	HKT	*Sepedon armipes*	'early spring'	New York	Neff and Berg (1966)
"	HKT	*Sepedon fuscipennis*	(L,P) various dates	New York, Michigan	Neff and Berg (1966)
"	HKT	*Tetanocera* sp.	4.xi/?	New York	Knutson, unpub.
*Mesoleptus*sp. B	HKT	*Pherbellia griseola*	"primarily spring"	New York	Bratt *et al*. (1969) and Bratt, unpub.
"	HKT	*Pherbellia seticoxa*	(P-79) 12.iv - 18.v/?	New York	Bratt *et al*. (1969) and Bratt, unpub.
Mesoleptus sp. C	HKT	*Pherbellia albovaria*	(P-1) 27.v/?	New York	Bratt *et al*. (1969) and Bratt, unpub.
"	HKT	*Pherbellia dorsata*	(P-17) 17.vii-8.viii/?	Denmark	Bratt *et al*. (1969) and Bratt, unpub.
"	HKT	*Pherbellia s. schoenherri*	(P-1) 11.viii/?	Germany	Bratt *et al*. (1969) and Bratt, unpub.
Mesoleptus sp. D	HKT	*Tetanocera arrogans*	(L-1) 25.vi(3.vii)/31.vii	England	Vala and Knutson, in prep.
"	HKT	*Tetanocera arrogans*	(L-1) 25.vii(7.viii)/12.ix	Denmark	Vala and Knutson, in prep.
Mesoleptus sp. E	HKT	*Pherbina coryleti*	(P-21) 7, 9.iv/20.iv-18.iv	Italy	Knutson *et al*. (1975)
Mesoleptus sp. F	HKT	*Tetanocera rotundicornis*	(P-1) 5.v/?	New York	Foote, unpub.
Mesoleptus sp. G	HKT	*Sepedon* sp.	23.viii/?	Minnesota	Knutson, unpub.
*Mesoleptus*sp. 1		*Ilione albiseta*	24.vi/7.vii	Wales	Beaver O. (1972)
"		*Tetanocera arrogans*	4.xi/18.vi	Wales	Beaver (1972)
Mesoleptus sp. 3	WRMM	*Anticheta melanosoma*	21.iii - ?; 27.iv - ?	New York	Knutson and Abercrombie (1977)
*Mesoleptus*sp.	RWC	*Sciomyza varia*	late iv-mid vi/?	New York	Barnes (1990)
"	WRMM	*Anticheta borealis*	late v-mid vi/?	Ohio	Robinson and Foote (1978)
"	HKT	*Tetanocera ferruginea*	spring/?	New York	Foote (1999)
"	CFWM	*Atrichomelina pubera*	–	New York,	Foote *et al*. (1960)
Mesoleptus (declivus ?)	?	*Pteromicra similis*		Michigan, New York	Gower-Teece, unpub.
Mesoleptus n.sp. 1	WRMM	*Pherbellia griseola*	–	–	Bratt *et al*. (1969)
Mesoleptus n.sp. 4	WRMM	*Ditaeniella humilis*	–	–	Bratt *et al*. (1969)

(*Continued*)

Table 3. (Continued).

Mesoleptus n.sp. 5	WRMM	*Ditaeniella humilis*	–	–	Bratt *et al.* (1969)
Mesoleptus n.sp. 5	WRMM	*Pherbellia obscura*	–	–	Bratt *et al.* (1969)
Mesoleptus sp. (misidentified as *Atractodes* sp.)	CFWM	*Atrichomelina pubera*	–	New York, Michigan	Foote *et al.* (1960)
"	JS	*Elgiva cucularia*	(P-1) 26.ix/6.x	S. Moravia	Rozkošný (1967)
"	HKT	*Tetanocera plebeja*	(P-1) 7.iv/?	Idaho	Foote, unpub.
Atractodes sp. A	HKT	*Pherbellia* sp.	(P-1) 14.iv/?	New York	Bratt *et al.*, 1964
Theroscopus sp. A	HKT	*Dictya* sp.	(P-5) 13.iii-30.iv/?	New York	Knutson and Neff, unpub.
"	HKT	*Tetanocera ferruginea*	?	New York	Foote (1961)
"	HKT	*Tetanocera fuscinervis*	(P-1) 5.iv/?	New York	Berg, unpub.
Theroscopus sp. A, B	HKT	*Sepedon fuscipennis*	(L,P) various	New York, Michigan	Neff and Berg (1966)
Theroscopus sp. B	HKT	*Dictya* sp.	13.iii-1.v	New York	Knutson and Neff, unpub.
"	HKT	*Tetanocera ferruginea*	–	New York	Foote (1961)
"	HKT	*Tetanocera fuscinervis*	(P-1) 30.iv/?	New York	Foote, unpub.
"	HKT	*Sepedon* sp.	(P-1) 18.ii/?	New York	Berg, unpub.
Theroscopus sp. C	HKT	*Tetanocera ferruginea*	–	New York	Foote (1961)
Theroscopus sp. E	HKT	*Dictya* sp.	12.iv/?	New York	Berg, unpub.
Theroscopus sp. F	HKT	*Sepedon armipes*	(P-1) 6.xi/?	New York	Neff and Berg (1966)
Theroscopus sp. G	HKT	*Elgiva solicita*	31.v - 7.vi/?	Belgium	Knutson and Berg (1964)
Theroscopus sp. H	HKT	*Anticheta melanosoma*	–	–	Knutson, unpub.
Theroscopus sp. I	HKT	*Dictya* sp.	(P-2) 13.iii/?	New York	Neff, unpub.
Theroscopus sp. J	HKT	*Pherbellia griseola*	(P-1) 26.iv/?	New York	Bratt *et al.* (1969)
Theroscopus sp. K	HKT	*Tetanocera plebeja*	(L-?) 7.iv/?	Idaho	Foote, unpub.
Theroscopus sp. L	HKT	*Tetanocera* sp.	10.v/?	Idaho	Foote, unpub.
Theroscopus sp. M	HKT	*Tetanocera* sp.	10.v/?	Idaho	Foote, unpub.
Theroscopus sp.	HKT	*Sepedon tenuicornis*	10.ii/?	New York	Neff and Berg (1966)
"	HKT	*Tetanocera plebeja*	(L-"few")	–	Trelka and Foote (1970)
Mesoleptus incessor	PL	*Tetanocera arrogans*	(P-1) "spring"	S. Moravia	Rozkošný (1965)
Hemiteles sp. ? (determination not certain)	JS	*Elgiva cucularia*	(P-1) 26.ix/6.x	S. Moravia	Rozkošný (1967)

(*Continued*)

Table 3. (Continued).

Mastrus sp.?	WRMM	*Anticheta melanosoma*	21.iii - 8.iv	New York	Knutson and Abercrombie (1977)
"	WRMM	*Anticheta melanosoma*	27.iv - 12.v	New York	Knutson and Abercrombie (1977)
Orthizema n. sp. ? Possible misidentification	RWC	*Colobaea americana*	(7) 27.iv - 18/21.v	New York	Knutson and Bratt, in prep.
Phygadeuon sp. (misidentified as '*cinctorius*')	A	*Sepedon sphegea*	viii/?	Germany	Gercke (1876)
Phygadeuon elegans	?	*Tetanocera ferruginea*	(P-1) 17.x/xii	England	Disney (1964)
Phygadeuon leucostigmus	HKT	*Pherbina coryleti*	(P-21) 7,9.iv/10.iv-18.v	Italy	Knutson *et al*. (1975)
Phygadeuon trichops	BL	*Sepedon h. hispanica*	(P-1) 7.ii / 19.ii	Spain	Knutson *et al*., 1967
Phygadeuon yonedai	?	*Sepedon aenescens*	–	Japan	Kusigamati (1986)
Phygadeuon sp. A, B	WRMM	*Anticheta borealis*	–	Ohio	Robinson and Foote (1978)
Phygadeuon sp. C	HKT	*Pherbellia dorsata*	(P-2) 27, 28.vi/?	Denmark	Bratt *et al*. (1969) and Bratt, unpub.
Phygadeuon sp. *1* nr. *trichops*	WRMM	*Anticheta melanosoma*	28.iv/8,14.v	New York	Knutson and Abercrombie (1977)
"	WRMM	*Anticheta melanosoma*	14.iv/6.v	New York	Knutson and Abercrombie (1977)
Phygadeuon sp. 2	WRMM	*Anticheta melanosoma*	21.iii-2.iv	New York	Knutson and Abercrombie (1977)
"	WRMM	*Anticheta melanosoma*	14.iv/23.iv	New York	Knutson and Abercrombie (1977)
Phygadeuon sp. 7	WRMM	*Ditaeniella humilis*	–	–	Bratt *et al*. (1969)
"	WRMM	*Anticheta melanosoma*	21.iii, 27.iv - ?	New York	Knutson and Abercrombie (1977)
Phygadeuon sp.	CFWM	*Atrichomelina pubera*	–	New York, Michigan	Foote *et al*. (1960)
"		*Anticheta testacea* [15]	–	California	Fisher and Orth (1964)
"	?	*Sepedon pacifica*		California	Fisher and Orth (1983)
"		*Tetanocera ferruginea*	"spring"	New York	Foote (1999)
Phygadeuontinae sp.		*Pherbellia cinerella*	25.iv - 30.iv	Ireland	Gormally (1987b)
Cylindricomorpha' sp.	RWC	*Colobaea* sp.?	–	Denmark?	Knutson, unpub.
Phygadeuon pumilis	HKT	*Tetanocera ferruginea*	"spring"	New York	Foote (1999)
Phygadeuon pumilis	HKT	*Pherbellia* sp.	(P-1) 8.iv/?	New York	Bratt *et al*. (1969) and Bratt, unpub.

(*Continued*)

Table 3. (Continued).

Phygadeuon pumilis	HKT	*Dictya* sp.	(P-13) 13.iii-7.iv	New York	Knutson and Neff, unpub.
Phygadeuon sp. A, B, C	HKT	*Tetanocera ferruginea*	"spring"	New York	Foote (1999)
Phygadeuon sp.	LMW	*Colobaea americana*	(P) 26.iv-14.v/?	New York	Knutson and Bratt, unpub.
"	LMW	*Tetanocera* sp.	2.v/?	New York	Knutson, unpub.
"	RWC	*Sciomyza varia*	late iv-late v/early vi	New York	Barnes (1990)
'Cryptine'	A	*Colobaea bifasciella*	–	Denmark	Lundbeck (1923)
"	A	*Colobaea punctata*	–	Denmark	Lundbeck (1923)
"	A	*Tetanocera ferruginea*	–	Denmark	Lundbeck (1923)
Unidentified		*Colobaea bifasciella*	9.vi/10.vii	Denmark	Knutson and Bratt, unpub.
"		*Anticheta brevipennis*	(P-3) 18.v/20.v, 6.vi	Denmark	Knutson (1966)
"		*Dictya steyskali*		New York	Valley and Berg (1977)
"		*Elgiva solicita*	10.ii/21.ii	New York	Knutson and Berg (1964)
"		*Elgiva solicita*	"early spring/9.iv"	New York	Knutson and Berg (1964)
"		*Renocera striata* [16]	"spring"	Ohio	Foote (1976)
"		*Pherbina coryleti*	(P-1) 29.iv/9.v	Greece	Knutson *et al.* (1975)
"		*Tetanocera plebeja*	(P-3) 7, 30.iv	New York, Idaho	Foote (1961)
"		*Sciomyza simplex*	(1L) 1.ix(ii.ix)/9.xi	Denmark	Knutson, unpub.
"		*Sepedonea telson*	3.v/16.v	Brazil	Abercrombie (1970)
"		*Tetanocera annae*	(P-1) 2.iv/14.iv	New York	Foote (1999)
"		*Tetanocera fuscinervis*	(P-2) 12.iii/24.iii	New York	Foote (1996a)
Unidentified (2 species)		*Tetanocera rotundicornis*	(P-23) 27.iii-2.iv/?	New York	Foote (1996b)
?		*Sepedon fuscipennis*	"summer"	New York	Eckblad and Berg (1972)
Hymenoptera					
Braconidae					
Aphaereta pallipes	CFWM	*Atrichomelina pubera*	(P-"50") 5.viii/?	Michigan	Foote *et al.* (1960)
Aphaereta sp.	CFWM	*Pherbellia subtilis* (as *obscura*)	(P-1)		Bratt *et al.* (1969)
Panerema inops	RDE	*Pherbellia* sp.	(P-26?)/20.i-11.x	England, Denmark, Finland	Bratt *et al.* (1969)
Phaenocarpa antichaetae		*Anticheta melanosoma*	(P-30) 21.iii/1-6.iv	New York	Fischer (1974), Knutson and Abercrombie (1977)
"		*Anticheta melanosoma*	27.iv/8-11.v	New York	Fischer (1974), Knutson and Abercrombie (1977)

(*Continued*)

Table 3. (Continued).

Phaenocarpa impugnata	JP	*Anticheta brevipennis*	(2 L-3) 25.vi (4.vii)/ 25, 29. vii	Denmark	Knutson (1966), J. Papp (1972)	
"	JP	*Anticheta brevipennis*	(4 L-2) 26.vii (7, 10.viii stet)/30.viii, 4.ix	Denmark	Knutson (1966), J. Papp (1972)	
"	JP	*Anticheta brevipennis*	(1 L) 2.ix (18.ix)/10.x	Denmark	Knutson (1966), J. Papp (1972)	
"	JP	*Anticheta brevipennis*[17]	(1 L?) 2.ix.14.ix/ /3.vii.	Denmark	Knutson (1966), J. Papp (1972)	
"	JP	*Anticheta brevipennis*	3.v/3.vi	Denmark	Knutson (1966), J. Papp (1972)	
Unidentified		*Colobaea americana*	(P-7) ?/18-25.v	New York	Knutson and Bratt, unpub.	
Hymenoptera Pteromalidae						
Trichomalopsis ?dubia	BDB	*Pherbellia n. nana*	(P-1) ?/11.v	New York	Bratt *et al.* (1969) and Bratt, unpub.	
Eupteromalus sp.	BDB	*Colobaea americana*	(2) 14.iv/27.iv, 14.v	New York	Knutson and Bratt, unpub.	
"	BDB	*Colobaea americana*	(1) 28.iv/11.v	New York	Knutson and Bratt, unpub.	
"	BDB	*Pherbellia seticoxa*	(P-1) ?/28.iv	New York	Bratt *et al.* (1969) and Bratt, unpub.	
"	BDB	*Sepedon aenescens*	(P) ? [6-15]	Thailand	Beaver *et al.* (1977)	
"	BDB	*Sepedon ferruginosa*	(P) x/? [6-15]	Thailand	Beaver *et al.* (1977)	
"	BDB	*Dichetophora* sp.	?/5.viii	Australia	Berg, unpub.	
Spalangia nigra	BDB	*Atrichomelina pubera*	?/3.vi	New York	Foote *et al.* (1960)	
Spalangia sp.?		*Atrichomelina pubera*			Universal Chalcidoidea Database	
Trichomalopsis sp.		*Sepedon* sp.			Universal Chalcidoidea Database	
Trichomalopsis dubia		*Pherbellia seticoxa*			Universal Chalcidoidea Database	
"		*Dictya* sp.			Universal Chalcidoidea Database	
Trichomalopsis oryzae	A?	*Sepedon aenescens*	–	Japan	Yoneda (1986)	
Urolepis rufipes	BDB	*Sepedon armipes*	?/20.xi	New York	Neff and Berg (1966)	
"	A	*Atrichomelina pubera*	13.vii.71	New York	Gibson, G. (2000)	USNM
Hymenoptera Chalcididae						
'Chalcid'	A	*Colobaea bifasciella*		Denmark	Lundbeck (1923)	
"	A	*Colobaea punctata*		Denmark	Lundbeck (1923)	
Undetermined (*Cephalobaris eskelundi* Kryger ?)		*Colobaea punctata*	15.ii-20.iii/19.iii-26.v	Spain	Knutson and Bratt, unpub.	
Order Hymenoptera Unidentified Family						
Undetermined		*Ilione albiseta*[18]		Ireland	Gormally, (1987)	
"		*Oidematops ferrugineus*[18]	?/14.ix	Ohio	Foote (1977)	

(*Continued*)

Table 3. (Continued).

Wingless proctotrupid	A	*Tetanocera ferruginea*	–	Denmark	Lundbeck (1923)	
"		*Sciomyza varia*	(P-2) 10.ii.1955 / 3,10.iii	New York	Berg, unpub.	
(B) Predators						
Natural Enemy	**Natural Enemy Identifier**	**Stage Attacked (Number)** [19]	**Sciomyzidae**	**Dates Collected**	**Location**	**Reference**
Hymenoptera						
Sphecidae						
Bembix amoena	A	Adult (1)	*Tetanocera vicina*	vii - viii	Wyoming	Evans (1966)
Bembix spinolae	A	Adult (1)	*Sepedon fuscipennis*	–	Massachusetts	Evans (1966)
Ectemnius paucimaculatus	A	Adult (1)	*Dictya texensis*	–	Maryland	Krombein (1964)
"	A	Adult (4)	*Sepedon armipes*	–	Maryland	Krombein (1964)
"	A	Adult (1)	*Sepedon* sp.	–	Maryland	Krombein (1964)
Crabronidae						
Dasyproctus bipunctatus jucundus	?	Adult (1)	*Ethiolimnia lindneri*	13.x - 7.xi	South Africa	Verbeke (1962)
Crabro hilaris	A	Adult (1)	*Dictya* sp.			Matthews *et al.* (1979)
Crabo sp.		Adult (1)	*Atrichomelina pubera*	ix	Illinois	Specimen in USNM
Formicidae						
Pheidole megacephala	A	Larvae and Puparia (many)	*Sepedomerus macropus*	–	Hawaii	Chock *et al.* (1961)
Odonata						
Anisoptera naiads	A	Larvae (several)	*Sepedomerus macropus*	–	Hawaii	Chock *et al.* (1961)
Zygoptera naiads	A	Larvae (several)	*Sepedomerus macropus*	–	Hawaii	Chock *et al.* (1961)
Coleoptera						
Hydrophilidae						
Tropisternus sp.	A	Larvae (several, in lab)	*Sepedon fuscipennis*	–	New York	Eckblad and Berg (1972)
Hemiptera						
Veliidae						
Mesovelia mulsanti	A	1st instar larvae (several)	*Sepedomerus macropus*	–	Hawaii	Chock *et al.* (1961)
Notonectidae						
Notonecta sp.	A	3rd instar larva (one)	*Sepedon fuscipennis*	–	New York	Eckblad and Berg (1972)
Diptera						
Asilidae						
Andrenosoma atrum	A	Adult	*Pherbellia obtusa*	–	France	Musso (1970)
Dioctria lateralis	?	Adult	*Trypetoptera punctulata*	–	Romania	Weinberg (1973)
Dioctria lateralis	?	Adult	*Coremacera marginata*	–	Romania	Weinberg (1973)
Dysmachus echinurus	?	Adult	*Pherbellia albocostata*	–	USSR (Caucasus)	Richter (1968)
Tolmerus atricapillus	A	Adult (1)	*Dichetophora obliterata*	5.ix	England	Hobby (1933)

(*Continued*)

Table 3. (Continued).

Tolmerus atricapillus	?	Adult	*Pherbina coryleti*	–	Wales	Clements and Skidmore 1998)
Empididae						
Empis opaca	A	Adult (1)	*Tetanocera silvatica*	v	England	Hobby and Smith (1962)
Empis tessalata	A	Adult (1)	*Limnia unguicornis*	–	England	Hobby and Smith (1961)
"	A	Adult (1)	*Renocera pallida*	–	England	Hobby and Smith (1961)
Scathophagidae						
Unidentified species		Adult (several)	*Pherbellia cinerella*	–	Ireland	Gormally, (1987)
Tabanidae						
Hybomitra schineri[20]	LLP	Larvae	*Tetanocera ferruginea*	–	Greece	Knutson (1965)
Orthoptera						
Tettigoniidae						
Conocephalus saltator		Adult ?	*Sepedonea* spp.	27.v	Goias, Brazil	Mello, *in litt.*
Acari						
Argiopidae						
Tetragnatha sternalis		Adult	*Protodictya chilensis*	6.iv	Chile	Abercrombie (1970)
Araneae						
Salticidae		Adult (No?)	*Sepedon plumbella*			Jackson *et al.* (1998)
Aves						
Acarinidae						
Araneus umbraticus		Adult	*Pherbellia pallidiventris*	3.viii	Norway	Greve and Ökland (1989)
Fringillidae						
Leucosticte tephrocotis		Adult (1)	*Pteromicra angustipennis*	6.vi	Amchitka Is., Alaska	Higman, *in litt.*
Caprimulgidae						
Chordeiles minor	?	Adult (1)	Sciomyzidae, undet.	–	U.S.A.	Mosher, *in litt.*
Icteridae						
Euphagus carolinus		Adult (1)	Sciomyzidae, undet.	–	U.S.A.	Orians, *in litt.*
Pisces						
Salmonidae						
Salmo sp.		Larva (1)	*Tetanocera* sp.	v	nr. Fairbanks, Alaska	Loftus, *in litt.*
(C) Pathogens				**Collected / Died**		
Fungi						
Hypocreales						
Hirsutella citriformis	A	Adult	*Sepedon aenescens*[2]	?	Philippines.	Rombach and Roberts (1989)
Entomophthora sp.		Adult (2)	*Dictya pictipes*	12.vii / 13.vii	New York	Valley and Berg (1977)
Nematoda						

(*Continued*)

Table 3. (Continued).

Gordiacea	Adult (1♀)	*Ilione albiseta*	–	Belgium	Verbeke (1948)
Mermithidae sp.	Adult (1♀)	*Dictya* sp.	?/vii	New York	Knutson, unpub.
Nematoda sp.	Adult (2♀)	*Tetanocera obtusifibula*	26.vi/29,30.vi	Idaho	Foote (1999)
Nematoda sp.	Adult (1♂)	*Dictya steyskali*	9.vi/15.vi	New York	Valley and Berg (1977)
Nematoda sp.	Adult (1♀)	*Dictya steyskali*	(P) 17.v/ 10.vi	New York	Valley and Berg (1977)
Leptosomatidae					
Pseudocella sp.[21]	Adults	'Sciomyzidae' (identification questionable)	–	E. Russia	Platanova (1985) (1988)

[1]as *Sepedon sauteri* Hendel (synonym)
[2]as *Sepedon sphegea* Fabr. (valid species)
[3]The authors cited '*Sepedon angularis* Adams'; this is a nomen nudum, attributed to the authors. They did not indicate who identified the eggs.
[4]Parasitoids emerged from (lab reared? field collected?) eggs of S. aenescens (established in Hawaii from introduction from Japan)then shipped to E. Oatman, University of California, Riverside.
[5]62% 0f 316 eggs collected in nature were parasitised.6 Eggs obtained from lab rearings were placed in clear plastic vials in the field. Among 1005 eggs recovered from 27 vials, only 11 eggs in one vial and 1egg in another had parasitoid emergence holes. Trichogramma sp. were also reared from eggs laid in nature at the same location.
[7]Eggs of Sepedon fuscipennis were successfully parasitised by Trichogramma sp. nr. semblidis in laboratory trials but this host species was notparasitised in nature.
[8]One egg with an emergence hole found on Succinea sp. host snail
[9]13 eggs with emergence holes, photo in Neff and Berg (1966)
[10]Although Diapriidae are known to be pupal parasitoids, Abercrombie (1970) recorded that a S. trichotypa larva collected on 16.iv pupariated 19.iv and*Spilomicrus sp. emerged. The other S. trichotypa that produced Spilomicrus sp. on 16.v was collected as a puparium on 16.iv*
[11]Puparia (<1 day old) of Atrichomelina pubera, reared in the lab, were placed in the field 20-27 vii and left there for 7 days. Sixty-onepuparia in 46 shells of Physa sp. and Lymnaea sp. were recovered. Nine, eleven and eleven T. atrichomelinae emerged from 3 pupariabetween 25-26 August (O'Neill, 1973). O'Neill reared T. atrichomelinae from puparia found in nature "only once" (collection / emergence date not given). Foote *et al.* (1960) recorded "one undetermined Diapriidae" reared from a field-collected puparium, which subsequently was identified by Muesebeck as "Trichopria sp.
[12]These records are from lab rearings. T. popei however was also reared from wild caught (Sarasota County, Florida - 29.iii.1970) Dictya floridensis puparia (Valley & Berg, 1977).
[13]In laboratory rearings both Trichopria popei and T. atrichomelinae oviposited into puparia of Tetanocera plebeja. T. popei emerged from 1 puparium but thepuparia exposed to T. atrichomelinae yielded no adult wasps or flies.
[14]These species oviposit into larvae and the adults emerge from the puparia. Rearings are from field collected puparia unless (L) beforethe first date shown, which indicates larvae were collected. In the latter, the dates in parentheses are the dates of pupariation. Where data are available, the numberof puparia collected are indicated by P-x before the dates of collection / emergence.
[15]The parasitoid wasp was reared out of puparia of Sepedon praemiosa and was exposed to young puparia of A. testacea in the lab.
[16]as Renocera brevis Steyskal (synonym)
[17]Parasitised pupa held at 5°C 1.xi.1964 until 12.vi.1965!
[18]One puparium collected with emergence holes
[19]All records from nature except laboratory rearing observations where indicated.
[20]Mature tabanid larva collected on 29.iv (Corfu, Greece) killed and ate 37 sciomyzid larvae during 21 days.
[21]Identification obviously incorrect. Pseudocella Filipjer is a genus of free living marine nematode
Some dates of collection / emergence, not in the original publication, have been added by our examination of labels on the specimens.
(a) Number and stage of specimens of Sciomyzidae collected (where known) indicated as, e.g. 2L-3 = two third-instar larvae in parentheses before date; P = puparium
(b) For collected larvae, date of pupariation indicated in parentheses (where known). Number in brackets after dates are numbers of parasites that emerged.
(c) Initials of natural enemy identifiers are detailed in Table 7, "A" refers to author of the publication.
(d) Authors of genera and species of natural enemies are given in Table 6 and of Sciomyzidae in Table 5.

Table 4. Summary table of Sciomyzidae (tribes Sciomyzini and Tetanocerini), including their recorded parasitoids, predators, and pathogens; distribution; and phenological and behavioural groups. Taxon authorities for genera and species of natural enemies are given in Table 5, and those for Sciomyzidae are given in Table 6.

Sciomyzidae host/ prey	Natural enemies	Distribution	Behavioural group	Phenological group
Sciomyzini				
Atrichomelina pubera	*Trichopria* sp.	N(NT)	1	1
	Mesoleptus declivus			
	Mesoleptus sp. (misidentified as Atractodes)			
	Aphaereta pallipes			
	Spalangia sp.			
	Urolepis rufipes			
	Crabro sp.			
Colobaea americana	*Orthizema* n. sp.?			
	Theroscopus sp.			
	Eupteromalus sp.			
Colobaea bifasciella	'Cryptine'	P	3	1
	'Chalcid'			
Colobaea punctata	'Chalcid'	P(O)	2	1
	Cephalobaris eskelundi			
Ditaeniella parallela	*Mesoleptus declivus*			
	Mesoleptus n. sp. 4			
	Mesoleptus n. sp. 5			
	Phygadeuon sp.			
Pherbellia albovaria	*Mesoleptus declivus*	N	6	5a
Pherbellia cinerella	*Phygadeuontinae* sp.	P(O)	7	5a,b
	Scathophagidae			
Pherbellia dorsata	*Mesoleptus* sp. C	P	2	1
	Phygadeuon sp. C			
Pherbellia griseola	*Mesoleptus declivus*	H	2	1
	Mesoleptus sp. B			
	Eriplanus sp. J			
Pherbellia n. nana	*Mesoleptus declivus*	H	2	1
	Eupteromalus ? dubius			
Pherbellia obscura	*Mesoleptus* n. sp. 5	H		
	Aphaereta sp.			
Pherbellia obtusa	*Andrenosoma atrum*	P	2	1
Pherbellia pallidiventris	*Araneus umbraticus*	P		
Pherbellia quadrata	*Mesoleptus declivus*	N	2	1?
Pherbellia s. maculata	*Mesoleptus declivus*	N	4	2
Pherbellia s. schoenherri	*Mesoleptus* sp. C	P	4	2
Pherbellia seticoxa	*Mesoleptus* sp. B	N	2	1
	Eupteromalus sp.			
	Trichomalopsis dubia			
Pteromicra angustipennis	*Leucosticte tephrocotis*	H	2	1
Pteromicra pectorosa	*Mesoleptus declivus*	H	2	1
Sciomyza simplex	Unidentified Ichneumonidae	H	2	1
Sciomyza varia	*Mesoleptus declivus*	N	3	5a?
	Theroscopus sp.			
	Wingless proctotrupid			
Tetanocerini				
Anticheta borealis	*Mesoleptus* sp.	N	5	1
	Phygadeuon sp. A, B			
Anticheta brevipennis	Unidentified Ichneumonidae	P	5	5a
Anticheta melanosoma	*Mesoleptus* sp. nr. *declivus*	N	5	5a
	Mesoleptus sp. 3			
	Phygadeuon sp. 1 nr. *trichops*			

(*Continued*)

Table 4. (Continued).

Sciomyzidae host/prey	Natural enemies	Distribution	Behavioural group	Phenological group
	Phygadeuon sp. 2			
	Phygadeuon sp. 7			
	Phaenocarpa antichaetae			
	Phaenocarpa impugnata			
Anticheta testacea	*Phygadeuon* sp.	N	5	1?
Coremacera marginata	*Dioctria lateralis*	P	-	-
Dichetophora obliterata	*Tolmerus atricapillus*	P	7	5b
Dictya floridensis	*Trichopria popei*	N	11	1
Dictya pictipes	*Entomophthora* sp.	N	11	1
Dictya steyskali	Unidentified Ichneumonidae	N	11	1
	Nematoda sp.			
Dictya texensis	*Ectemnius paucimaculatus*	N (NT)	11	1
Elgiva cucularia	*Mesoleptus* sp. (misidentified as *Atractodes* sp.)	P	11	2
	Hemiteles sp. ?			
Elgiva solicita	*Trichogramma julianoi*	H	11	2
	Trichogramma sp.			
	Trichopria atrichomelinae			
	Trichopria popei			
	Theroscopus sp. G			
	Unidentified Ichneumonidae			
Ethiolimnia lindneri	*Dasyproctus bipunctatus*	AF	-	-
Ilione albiseta	*Mesoleptus* sp. 1	P	11	4
	Unidentified Hymenoptera			
	Gordiacea			
Limnia unguicornis	*Empis tessalata*	P	2/8?	5b
Neolimnia tranquilla	*Spilomicrus barnesi*	SA	12c	6
Pherbina coryleti	*Mesoleptus* sp. E	P	2	4
	Phygadeuon leucostigmus			
	Unidentified Ichneumonidae			
	Tolmerus atricapillus			
Protodictya chilensis	*Tetragnatha sternalis*	NT	11	6
Renocera pallida	*Empis tessalata*	P	14	1?
Renocera striata	Unidentified Ichneumonidae	H	14	1
Sepedomerus macropus	*Pheidole megacephala*	NT(N)	11	6
	Anisoptera naiads			
	Zygoptera naiads			
	Mesovelia mulsanti			
Sepedon aenescens	*Trichogramma japonicum*	O(P)	11	6(2)
	Trichogramma sp.			
	Trichogrammatoidea bactrae			
	Trichogrammatoidea nana			
	Phygadeuon yonedai			
	Eupteromalus sp.			
	Trichomalopsis oryzae			
	Hirsutella citriformis			
Sepedon'angularis'	*Trichogramma kalkae*	-	-	-
	Trichogrammatoidea simmondsi			
	Trichogramma pinneyi			
Sepedon armipes	*Mesoleptus declivus*	N(NT)	11	2
	Mesoleptus sp. A			
	Theroscopus sp. F			
	Urolepis rufipes			
	Ectemnius paucimaculatus			
Sepedon ferruginosa	*Trichogramma* sp.	O	11	6
	Eupteromalus sp.			
Sepedon fuscipennis	*Trichogramma julianoi*	N	11	2

(*Continued*)

Table 4. (Continued).

Sciomyzidae host/ prey	Natural enemies	Distribution	Behavioural group	Phenological group
	Trichogramma sp.			
	Trichogramma sp. nr. *californicum*			
	Trichogramma sp. nr. *semblidis*			
	Trichogramma semblidis			
	Trichopria atrichomelinae			
	Trichopria popei			
	Mesoleptus declivus			
	Mesoleptus sp. A			
	Theroscopus sp. A, B			
	Unidentified Ichneumonidae			
	Bembix spinolae			
	Tropisternus sp.			
	Notonecta sp.			
Sepedon h. hispanica	*Phygadeuon trichops*	P	4	6
Sepedon pacifica	*Phygadeuon* sp.	N	11	2?6
Sepedon plumbella	Salticidae	O-OC-A	11	6
Sepedon sphegea	*Trichogramma japonicum*	P(O)	11	2
	Trichogramma semblidis			
	Mesoleptus ripicola			
	Mesoleptus sp.			
	Phygadeuon cinctorius (presumable misidentification)			
Sepedon spinipes	Unidentified Trichogrammatidae	P	11	1?2
Sepedonea telson	Unidentified Ichneumonidae	-	-	-
Sepedon tenuicornis	*Theroscopus* sp.	N	11?	6?
Sepedonea telson	Unidentified Ichneumonidae	NT	11	6
Sepedonea trichotypa	*Spilomicrus* n. sp.	NT	11	6
Sepedonea annulata	*Trichopria* n. sp.	NT	11	6
Sepedonea trichotypa	*Spilomicrus* sp.	NT	11	6
Tetanocera annae	Unidentified Ichneumonidae	N	11	5
Tetanocera arrogans	*Mesoleptus* sp. D	P	4	1
	Mesoleptus sp. 1			
	Mesoleptus incessor			
Tetanocera ferruginea	*Mesoleptu laticinctus*	H	11	1
	Mesoleptus sp.			
	Theroscopus sp. A			
	Theroscopus sp. B			
	Theroscopus sp. C			
	Phygadeuon elegans			
	Phygadeuon sp.			
	Phygadeuon pumilis			
	Theroscopus sp. A, B, C			
	'Cryptine'			
	Wingless proctotrupid diapriid			
	Hybomitra schineri			
Tetanocera fuscinervis	*Theroscopus* sp. A	H	2	1
	Theroscopus sp. B			
	Unidentified Ichneumonidae			
Tetanocera obtusifibula	Nematoda sp.	N	11	4
Tetanocera plebeja	*Trichopria popei*	H	9(8)	1
	Mesoleptus (*Atractodes* sp. – misidentified)			
	Theroscopus sp. K			
	Theroscopus sp.			
	Unidentified Ichneumonidae			
Tetanocera rotundicornis	*Mesoleptus* sp. F	N	4	1
	Unidentified Ichneumonidae – 2 spp.			

(*Continued*)

Table 4. (Continued).

Sciomyzidae host/ prey	Natural enemies	Distribution	Behavioural group	Phenological group
Tetanocera silvatica	*Empis opaca*	H	2	1?
Tetanocera vicina	*Bembix amoena*	N	11	4
Trypetoptera punctulata	*Dioctria lateralis*	P	7	5b

recognised four guilds based on a combination of (1) ovipositing into the egg, larval or pupal stage; (2) idiobionts or koinobionts (ie the former prevent development of the host after immobilising it, whereas the latter feeds on the host as it continues to develop); (3) endo- or ectoparasites; (4) differences in oviposition behaviours; and (5) native or exotic origin. Obviously, this is a very special guild arrangement, quite different from our behavioural groups. In the classification below, where the feeding behaviour is not entirely predaceous, parasitoid, or saprophagous but changes more or less regularly during the course of development, or is variable depending on the presence of intraspecific competition, relative sizes of larva and host/prey, microhabitat conditions, and/or some combination of these, all behaviours are given, the predominant one first. In most such cases, young larvae are more parasitoid and older larvae are more predatory and/or saprophagous. Examples in Sciomyzini genera are in bold face below, Tetanocerini species are given in regular script italics, and Salticellinae in square brackets. Where only one or a few species in a genus are known to exhibit the behaviour, species names are given. Behavioural groups are specified for species associated with natural enemies in Tables 5 and 6. All publications on the biology of Sciomyzidae (as of 2013) are enumerated in the world checklist of Sciomyzidae (Vala *et al*. 2012), and the full literature citations are given in the online Bibliography of Sciomyzidae.

(1) Facultative, opportunistic, predators/parasitoids/saprophages that can feed on dead, moribund, or living snails, eg [*Salticella fasciata* Meigen] and ***Atrichomelina pubera***.
(2) Predators/saprophages of non-operculate, primarily freshwater snails exposed on moist surfaces by seasonal or diel receding or fluctuating water levels or while the snails are foraging or migrating (= most of the 'stranded snail' situations and the 'shoreline' situations mentioned in the literature, eg for *Hydromya dorsalis* Fabricius).
(3) Parasitoids or parasitoids/predators more or less intimately associated with non-operculate freshwater snails aestivating or otherwise exposed for long periods of time in temporary freshwater habitats (eg temporary vernal or autumnal ponds, turloughs, marshes, swamps, playa lakes), eg ***Colobaea bifasciella***.
(4) Parasitoids or parasitoids/predators more or less intimately associated with hygrophilous, semi-terrestrial Succineidae snails, eg ***Pherbellia s. schoenherri***.
(5) Obligate parasitoids/predators of exposed egg masses of freshwater Lymnaeidae, *Aplexa* Fleming, or semi-terrestrial Succineidae snails during early larval life, followed by predation on juvenile to mature snails in damp or vernal situations. Although this niche is dominated by species of *Anticheta*, *H. dorsalis* (group 2) and *Tetanocera ferruginea* (group 11) have been found occasionally in egg masses in

Table 5. Taxon authorities for genera and species of natural enemies of Sciomyzidae, with geographical distributions [A: Australian; AF: Afro tropical; H: Holarctic; N: Nearctic; O: Oriental; OC: Oceanian; P: Palearctic; SA: Sub Antarctic (New Zealand)] of the natural enemies with sciomyzid behavioural groups and phenological groups attacked, and non-sciomyzid host groups (by order, family) attacked.

Natural enemy	Distribution	Scio. behav. grp attacked	Scio. phenol. grp attacked
HYMENOPTERA			
Trichogrammatidae			
Trichogramma japonicum Ashmead		11	6 (2), 2
Trichogramma julianoi Platner and Oatman		11	2
Trichogramma kalkae Schulten and Feijen 1978			
Trichogramma pinneyi Schulten and Feijen			
Trichogramma sp. nr. *californicum* Nagaraja and Nagarkatti		11	2
Trichogramma sp. nr. *semblidis* (Auriv.)		11	2
Trichogramma semblidis (Auriv.)		11	2
Trichogrammatoidea bactrae Nagaraja		11	6 (2)
Trichogrammatoidea nana Zehntner		11	6 (2)
Trichogrammatoidea simondsi			
Diapriidae			
Spilomicrus barnesi Early and Horning		12c	6
Trichopria atrichomelinae Muesebeck		1, 11, 11,	1, 2, 2
Trichopria popei (Muesebeck)		11, 11, 1, 9 (8)	1, 2, 1, 1
Ichneumonidae			
Cephalobaris eskelundi Kryger		2	1
Mesoleptus declivus (Provancher)		1, 6, 2, 4, 3, 11	1, 5(a), 1, 2, 5(a), 2
Mesoleptus sp. nr. *declivus*		5	5(a)
Mesoleptus laticinctus (Walker)		11	1
Mesoleptus vigilatorius (Förster)		11	2
Mesoleptus Gravenhorst sp.		11	2
Atractodes Gravenhorst sp.		1, 11, 9 (8)	1, 2, 1
Mesoleptus incessor (Haliday)		4	1
Phygadeuon sp. (misidentified as '*cinctorius*')		11	2
Phygadeuon elegans (Förster)		11	1
Phygadeuon leucostigmus Gravenhorst		2	4
Phygadeuon trichops Thomson		4	6
Phygadeuon yonedai Kusigemati		11	6(2)
Unidentified Phygadeuontinae		2, 3, 5, 7, 9 (8), 11	1, 2, 5a, b, 6
'Cylindricomorpha' sp.			
Phygadeuon pumilis (Cresson)		11	1
Braconidae			
Aphaereta Förster sp.			
Aphaereta pallipes (Say)		1	1
Phaenocarpa antichaetae Fischer		5	5(a)
Phaenocarpa impugnata Papp		5	5a
Pteromalidae			
Eupteromalus Kurdjumov sp.		2, 11, 11	1, 6 (2), 6
Eupteromalus dubius (Ashmead)		2	1
Spalangia rugosicollis Ashmead		1	1
Spalangia Latreille sp.		1	1
Trichomalopsis Crawford sp.			
Trichomalopsis dubia (Ashmead)		2	1
Trichomalopsis oryzae Kamijo and Grissell		11	6 (2)
Urolepis rufipes (Ashmead)		11, 1	2, 1
Chalcididae			
Cephalobaris eskelundi Kryger (determ. not certain)			
Sphecidae			
Bembix amoena Handlirsch		11	4
Bembix spinolae Lepeletier		11	2
Ectemnius paucimaculatus (Packard)		11, 11	1, 2
Crabronidae			
Dasyproctus bipunctatus Lepeletier and Brulle			
Crabro hilaris Smith			

(*Continued*)

Table 5. (Continued).

Natural enemy	Distribution	Scio. behav. grp attacked	Scio. phenol. grp attacked
Crabro sp.		1	1
Formicidae			
Pheidole megacephala (Fabricius)		11	6
ODONATA			
Anisoptera sp.		11	6
Zygoptera sp.		11	6
COLEOPTERA			
Hydrophilidae			
Tropisternus sp.		11	2
HEMIPTERA			
Veliidae			
Mesovelia mulsanti White		11	6
Notonectidae			
Notonecta L. sp.		11	2
DIPTERA			
Asilidae			
Andrenosoma atrum (L.)		2	1
Dioctria lateralis Meigen		7	5b
Dysmachus echinurus Richter		6	5a
Tolmerus atricapillus (Fallén)		7, 2	5b, 4
Empididae			
Empis opaca Meigen		2	1
Empis tessellate Fabricius		2/8, 14	5b, 1
Scathophagidae undet.		7	5a,b
Tabanidae			
Hybomitra schineri Lyneborg		11	1
ORTHOPTERA			
Tettigoniidae			
Conocephalus saltator Saussure			
ACARI			
Argiopidae			
Tetragnatha sternalis Nicolet		11	6
ARANEAE			
Salticidae undet.		11	6
AVES			
Acarinidae			
Araneus umbraticus Clerck			
Fringillidae			
Leucosticte tephrocotis (Swainson)		2	1
Caprimulgidae			
Chordeiles minor Forster			
Icteridae			
Euphagus carolinus Muller			
PISCES			
Salmonidae			
Salmo (L.) sp.			
FUNGI			
Hypocreales			
Hirsutella citriformis Speare		11	6 (2)
Entomophthora sp.		11	1
NEMATODA			
Gordiacea undet.		11	4
Mermithidae sp.			
Nematoda sp.		11	4
Leptosomatidae			
Pseudocella Filipjev sp.			

Table 6. Taxon authorities for genera and species of Sciomyzidae, arranged taxonomically, attacked by natural enemies (see Table 3), with geographical distribution, behavioural group, and phenological group. EP: egg parasitoid; L-PP: larval-pupal parasitoid; PP: pupal parasitoid; PA: pathogen; PR: predator.

Sciomyzinae	Geographical distribution	Behavioural group	Phenological group	Attacked by
Sciomyzini				
Atrichomelina Cresson				
A. pubera (Loew)	N(NT)	1	1	L-PP, PP, PR
Colobaea Zetterstedt				
C. americana Steyskal	N	2	1	L-PP
C. bifasciella (Fallén)	P	3	1	L-PP
C. punctata (Lundbeck)	P(O)	2	1	L-PP
Ditaeniella Sack				
D. parallela (Walker)	N(NT)	2	1	L-PP
Oidematops Cresson				
O. ferrugineus Cresson	N	6	5a	L-PP
Pherbellia Robineau-Desvoidy				
P. albocostata (Fallén)	H	6	5a	PR
P. albovaria (Coquillett)	N	6	5a	L-PP
P. cinerella (Fallén)	P (O)	7	5a,b	PR
P. dorsata (Zetterstedt)	P	2	1	L-PP
P. griseola (Fallén)	H	2	1	L-PP
P. nana nana (Fallén)	H	2	1	L-PP
P. obscura (Ringdahl)	H	?	?	L-PP
P. obtusa (Fallén)	P	2	1	PR
P. pallidiventris (Fallén)	P	?	?	PR
P. quadrata Steyskal	N	2	?1	L-PP
P. schoenherri maculata (Cresson)	N	4	2	L-PP
P. seticoxa Steyskal	N	2	1	L-PP
P. sp. 1	?	?	?	L-PP
P. sp. 2	N	?	?	L-PP
P. sp. 3	P	?	?	L-PP
Pteromicra Lioy				
P. angustipennis (Staeger)	H	2	1	PR
P. similis Steyskal	N	?	?	L-PP
Sciomyza Fallén				
S. varia (Coquillett)	N	3	?5a	L-PP
Tetanura Fallén				
T. pallidiventris Fallén	P	6	5a	
Tetanocerini				
Anticheta Haliday				
A. borealis Foote	N	5	1	L-PP
A. brevipennis (Zetterstedt)	P	5	?5a	L-PP, PP
A. melanosoma Melander	N	5	5a	L-PP
A. testacea Melander	N	5	?1	L-PP
Coremacera				
C. marginata (Fabricius)	P	7	5a,b	PR
Dichetophora Rondani				
D. obliterata (Fabricius)	P	7	5b	PR
Dictya Meigen				
D. floridensis Steyskal	N	11	1	PP
D. pictipes (Loew)	N	11	1	PA
D. steyskali Valley	N	11	1	L-PP, PA
D. texensis (Curran)	N (NT)	11	1	PR
D. spp.	N	?	?	L-PP, PP, PA, PR
Elgiva Meigen				
E. cucularia (L.)	P	11	2	L-PP
E. solicita (Harris)	H	11	2	EP, L-PP, PP
Ethiolimnia Verbeke				
E. lindneri Verbeke	AF	?	?	PR
Ilione Haliday				
I. albiseta (Scopoli)	P	11	4	L-PP, PA

(*Continued*)

Table 6. (Continued).

Sciomyzinae	Geographical distribution	Behavioural group	Phenological group	Attacked by
Limnia Robineau-Desvoidy				
L. unguicornis (Scopoli)	P	?2/8	5b	PR
Neolimnia Tonnoir and Malloch				
N. tranquilla (Hutton)	SA	12c	6	PP
Pherbina Robineau-Desvoidy				
P. coryleti (Scopoli)	P	2	4	L-PP, PR
Protodictya Malloch				
P. chilensis Malloch	NT	11	6	PR
Renocera				
R. pallida (Fallén)	P	14	?1	PR
R. striata (Meigen)	H	14	1	L-PP
Sepedomerus Steyskal				
S. macropus (Walker)	NT (N)	11	6	PR
Sepedon Latreille				
S. aenescens Wiedemann	O (P)	11	6 (2)	EP, L-PP, PA
S. armipes Loew	N (NT)	11	2	L-PP, PR
S. ferruginosa Wiedemann	O	11	6	EP, L-PP
S. fuscipennis Loew	N	11	2	EP, L-PP, PP, PR
S. h. hispanica Loew	P	4	6	L-PP
S. praemiosa Giglio-Tos	N (NT)	11	2	
S. senex Wiedemann	O	11	6	
S. sphegea (Fabricius)	P (O)	11	2	EP, L-PP
S. tenuicornis Cresson	N	?11	?6	L-PP
Sepedonea Steyskal				
S. telson (Steyskal)	NT	11	6	L-PP
S. trichotypa Freidberg *et al.*	NT	11	6	PP
S. spp.	NT	?	?	PR
Tetanocera Duméril				
T. annae Steyskal	N	11	5a	L-PP
T. arrogans Meigen	P	4	1	L-PP
T. ferruginea Fallén	H	11	1	L-PP, PR
T. fuscinervis (Zetterstedt)	H	2	1	L-PP
T. obtusifibula Melander	N	11	1	PA
T. plebeja Loew	H	9 (8)	1	L-PP, PA
T. rotundicornis Loew	N	4	1	L-PP
T. silvatica Meigen	H	2	?1	PR
T. vicina Macquart	N	11	4	PR

Table 7. Identifiers of natural enemies, museum affiliation (where some retained specimens might be situated).

Initials	Original identifier	Collection
BDB	B.D. Burks	USNM
BL	B. Llopis	
CFWM	C.F.W. Muesebeck	USNM
GHO	G.H. Orians	
GOP	G.O. Poinar	UCB
GP	G. Platner	UCR
HEE	H.E. Evans	CU
HKT	H.K. Townes, Jr.	FDA
SN and HN	S. Nagarhatti and H. Nagaraja	CIBC-B
JCM	J.C. Mosher	
JFA	J.F. Aubert	
JFP	J.F. Perkins	
JS	J. Šedivý	
JP	J. Papp	
JWE and DSH	J.W. Early and D.S. Horning, Jr.	
KVK	K.V. Krombein	USNM

(*Continued*)

Table 7. (Continued).

Initials	Original identifier	Collection
KY	K. Yasumutsu	CNC
LLP	L.L. Pechuman	CU
LMW	L.M. Walkley	USNM
MCR	M.C. Rombach	ARSEF
MGF	M.G. Fitton	BM (NH)
MJG	M.J. Gates	USNM
PL	P. Laska	
RDE	R.D. Eady	
RM	R. Miller	
RWC	R.W. Carlson	USNM
WHA	W.H. Ashmead	
WRMM	W.R.M. Mason	CNC

Collection abbreviations: ARSEF: USDA-ARS Entomopathogenic fungal cultures, Cornell University, Ithaca; BM(NH): British Museum of Natural History, London; CNC: Canadian National Collection, Ottawa; CU: Cornell University, Ithaca; FDA: Florida Department of Agriculture and Consumer Services, Gainesville; UCB: University of California, Berkeley; UCR: University of California, Riverside; USNM: United States National Museum, Washington, DC

nature. In laboratory studies larvae of 10 species in groups 2 and 11 fed on eggs of freshwater snails (Knutson and Vala 2011).

(6) Parasitoids intimately associated with non-operculate, terrestrial snails, eg *Oidematops ferrugineus*.

(7) Predators/saprophages of non-operculate terrestrial snails. Some species have some parasitoid aspects of behaviour during early larval life, eg ***Pherbellia cinerella***.

(8) Predators/saprophages opportunistic on both terrestrial snails and slugs, eg *Euthycera cribrata* (Rondani).

(9) Obligate ectoparasitoids/predators of slugs. Ectoparasitoid slug feeders keep at least their posterior spiracles exposed, eg *Tetanocera elata*.

(10) Obligate mesoparasitoids of slugs that live completely within the slugs, eg *Euthycera chaerophylli* (Fabricius).

(11) Predators of non-operculate snails at or just below the water surface, just above the surface on emergent vegetation, and occasionally those exposed on moist surfaces, eg *Sepedon spinipes* (Scopoli). Most larvae live at the water surface, with their posterior spiracles exposed most of the time. Several freshwater predators habitually leave the water for moist surfaces when mature. Larvae of some species in this group often have labile feeding behaviour and might be placed as well in group 2.

(12) Predators and predators/parasitoids of exposed and neustonic (surface dwelling) operculate (prosobranch) aquatic snails.
  (a) *Littorina littoria* (L.) in strandline debris on Nearctic Atlantic Ocean beaches, eg *Hoplodictya setosa* (Coquillett).
  (b) Salt marsh operculates, eg *Dictya lobifera* (Curran).
  (c) *Valvata* Müller spp. exposed in freshwater marshes, eg ***Pherbellia prefixa*** Steyskal.
  (d) Freshwater operculate snails, eg *Dictya fontinalis* (Fisher and Orth).

  Note: The two species of Sciomyzidae in 12*a* and *b* above, along with two species of Sarcophagidae (McKillup *et al*. 2000), are the only Insecta known or very likely to be restricted to marine Gastropoda.

(13) Predators of non-operculate snails under the water surface, at least during the first part of larval life, eg *Ilione albiseta*.

(14) Predators/parasitoids of fingernail clams. All except *Renocera pallida* feed beneath the water surface, at least during the first part of larval life.
Note: These six species in three genera of Sciomyzidae (one species of *Eulimnia* Tonnoir and Malloch, one species of *Ilione* and four species of *Renocera*) are the only members of the Class Insecta that are well documented as obligate natural enemies of any species of the Class Bivalvia.
(15) Predators of freshwater oligochaete worms, eg *Sepedonella nana* Verbeke.

Microhabitats. The microhabitats of the immature stages of Sciomyzidae, especially of the larvae, have been rather well defined. Characterisation of the microhabitats is important in helping to determine the range of sciomyzid natural enemies, especially parasitoid Hymenoptera, known or yet to be discovered, and thus in the application of sciomyzid species to specific biocontrol target sites. See also the discussion of behavioural groups, above.

Eggs of Sciomyzidae generally are dispersed in the microhabitats of the Mollusca and are rather difficult to find, except those of most *Sepedon* species and a few other genera that are laid in groups of 30 or more on emergent vegetation. They are usually laid on vegetation, but the females of some species in freshwater habitats (eg *Ilione albiseta*) have a preference for ovipositing onto dead or dying plants (Lindsay *et al*. 2011). A few other sciomyzids [eg *Pherbellia schoenherri schoenherri* (Fallén)] oviposit directly onto suitable food snails for the larvae; these are usually the more parasitoid members of the Sciomyzini (Vala and Ghamizi 1992).

The microhabitats (aquatic, semi-aquatic, terrestrial) of sciomyzid larvae are primarily dependent on some portion of the arena of their mollusc hosts/prey and to the searching arena of the ovipositing female flies. The larvae are quite mobile, but their searching arenas have not been determined. They seem to be particularly vulnerable to natural enemies, the predacious larvae being exposed between their attacks on a series of snails or slugs, and the predacious/saprophagous and parasitoid/saprophagous larvae feeding within dead, malodourous, decaying snails. The latter situations also likely provide olfactory cues to parasitoids and predators, but this has not been studied.

At the end of the third-instar stadium, sciomyzid larvae contract and form a more or less barrel-shaped, more or less strongly sclerotised puparium on or slightly below the substrate of the larva, or for some species, in the shell of the host/prey (semi-terrestrial and terrestrial species) or floating in the water (aquatic species). Puparia formed in shoreline situations and in the water may be carried long distances by diel/seasonal/temporary flood waters and become congregated around emergent vegetation or at out-flow locations where perhaps they are more subject to parasitism/predation pressures. Only a few species, for example *Elgiva* species, have a lightly pigmented puparium, but there have been no studies to show whether these are more susceptible than the others to parasitism/predation. The duration of the fourth larval (or prepupal) stadium is not well known for most species but apparently lasts only a few hours. The pupal period, *per se*, lasts only a few days for multivoltine species but may persist for weeks or a few months for univoltine species overwintering in the puparium. The latter stage and the unsclerotised pharate adult stage are perhaps particularly vulnerable to attack by parasitoid wasp larvae. The duration of the unsclerotised to sclerotised pharate adult stage is not well known for most species but in over-wintering *Dictya* species can be quite variable (Berg *et al*. 1982). The stage of development of the contents of the puparium probably is of little concern to predators but perhaps is important to parasitoids. The remaining contents of puparia from which parasitoids have emerged – whether fourth larval, pupal, or pharate adult integuments – have not been examined.

Phenological groups. Phenological groups 1–5a were proposed by Berg *et al*. (1982), group 5b by Vala (1984) and group 6 by Knutson and Vala (2002, 2011) based primarily on number of generations per year, flight period, overwintering stage, and presence/absence of diapause/quiescence. The representative species included by them are summarised below. Phenological groups are specified for species associated with natural enemies in Tables 4 and 5.

Group 1: multivoltine species overwintering in the puparium as diapausing or quiescent pupae or pharate adults. The puparial stage is found throughout the year. The overwintering stage ranges from very young, unpigmented pupae to pharate adults in the puparium. Pupae or pharate adults of some species are in diapause; those of other species are simply quiescent. In temperate areas, adults emerge during early spring and produce 3–5 successive generations until the onset of cold temperatures. Larval stages are present from spring to autumn. The first generation is often concomitant with the beginning of reproduction of gastropods in the habitat. Included are many freshwater and terrestrial species of both tribes of Sciomyzinae.

Group 2: multivoltine species overwintering as diapausing adults. Adults overwinter. Reproductive diapause, at least in some species, is corroborated in the female with reduced ovaries and accessory glands and hypertrophied fat bodies, and in the male with slightly developed testes. The generations succeed one another during spring and summer as in group 1 with the egg, larval and pupal stages being of relatively short duration. Included are many freshwater predators in the genera *Sepedon* and *Elgiva*, the terrestrial parasitoid *Pherbellia schoenherri*, the terrestrial predator *P. cinerella* in southern parts of its range, and possibly *Psacadina* Enderlein species. *Sepedon spinipes* possibly overwinters as a quiescent larva, pupa or adult. Adults of three sciomyzids have been collected on snow: *Pherbellia schoenherri maculata*, *P. s. schoenherri*, and *P. cinerella*.

Group 3: univoltine species overwintering within egg membranes. The first larval stadium, within the egg membrane, undergoes diapause, extending this stage to several months. There is also a reproductive diapause of adults during spring and early summer. Included are *Tetanocera latifibula* Frey, *T. montana* Day, *T. loewi* Steyskal, *T. soror* Melander, and *Hedria mixta* Steyskal, except the latter lacks aestival diapause of adults.

Group 4: univoltine species overwintering primarily in the larval stage. Adults have an aestival diapause, eggs are then laid and hatch promptly, and larvae begin to develop before winter – based primarily on *Tetanocera vicina* along with *T. plumosa* Loew and *T. obtusifibula*. Some other species in this group, such as *Ilione albiseta* and *I. lineata* Fallén, show minor variations or have group 3 or 4 features depending on the availability of food and water. *Pherbina coryleti* adults mate during spring and early summer, but oviposition is delayed for several months. *Eulimnia philpotti* Tonnoir and Malloch mate and oviposit during spring and early summer, and the incubation period is short.

Group 5a: univoltine species overwintering as pupae. Puparia are formed from early summer until autumn depending on the species; most have a pupal diapause lasting until the following spring. Adults are active and oviposit from spring to late summer. Included are many species of *Anticheta*, *Renocera* and *Pherbellia* living in seasonally freshwater sites and feeding on snail eggs, fingernail clams or freshwater snails, respectively, and six species of *Pherbellia*, *Oidematops*, and *Tetanura* attacking terrestrial snails. Berg *et al*. (1982) referred to this group as a group that had evolved a univoltine lifestyle under quite different evolutionary pressures. Instead of as temporary wetland specialists. Berg suggested it was availability of prey that was key to the evolution of univoltinism in this group. The terrestrial species in this group are better placed in group 5b.

Group 5b: univoltine species overwintering as larvae, then in the puparium. Several univoltine, Palaearctic, parasitoids/predators/saprophages of terrestrial snails do not fit well into group 5 of Berg *et al*. (1982). These are *Coremacera marginata*, *Dichetophora obliterata*, *Euthycera cribrata* (Rondani), *E. stichospila* (Czerny), and *Trypetoptera punctulata*. They are univoltine with exceptionally long pre-oviposition periods, larval life from late summer or early autumn to mid winter, and overwintering completed as diapausing pupae. Vala (1984) proposed group 5a for the Nearctic and northern Palearctic species originally included by Berg *et al*. (1982) in group 5, and group 5b for southern Palearctic species having phenologies like the five species noted above. Knutson and Vala (2002, 2011) also included the six terrestrial Nearctic and Palearctic species in group 5 of Berg *et al*. (1982) in group 5b, and possibly *Salticella fasciata*, placed in group 1 by Berg *et al*. (1982).

Group 6: tropical species breeding continuously. Stereotyped phenology appears to characterise aquatic and semi-aquatic predators in tropical zones. They seem to be multivoltine, breeding more or less continuously, with a variable number of generations per year (perhaps 4–12) which are not discrete but are successive, spread temporally, and overlap. During laboratory rearings, these species showed no indication of diapause, developed promptly, had a short pre-oviposition period, a long oviposition period, and short egg, larval, and pupal periods.

Some Nearctic, Neotropical and Oriental species that are distributed primarily in temperate areas have broad latitudinal ranges. Populations in warmer areas probably have the characteristics of group 6, with those at higher elevations the characteristics of group 1. Examples are *Dictya montana* Steyskal in the Nearctic, extending from Saskatchewan, Canada, to Baja California, Mexico (Mc Donnell *et al*. 2007); the Neotropical *Perilimnia albifacies* Becker, extending from southernmost Argentina to central Colombia (Kaczynski *et al*. 1969); and the Oriental-Palearctic *Sepedon aenescens*, extending from 10 to 50°N latitude.

Berg *et al*. (1982) noted that although the Sciomyzidae are so heavily attacked by parasitoid Hymenoptera that collections of puparia formed during late spring, summer and autumn often yielded more wasps than flies, the authors never reared a parasitoid wasp from any puparium of species in phenological groups 3 and 4 (univoltine, overwintering within egg membranes or as partly grown larvae). In fact, seasonality of development of sciomyzid larvae may be related, in part, to parasite pressure, with those species whose larvae develop during the late autumn to early spring escaping attack. The current paper presents eight records of parasitoids of group 4 phenology, but none from group 3.

Sciomyzid defence mechanisms against and vulnerability to natural enemies. The apparent paucity of defence mechanisms of Sciomyzidae might be related to the facts that (1) host/prey mollusc populations are invariably enormously greater than sciomyzid populations, (2) most adult sciomyzids produce many progeny, and (3) the larvae seem to have little competition among the relatively few other insect natural enemies of molluscs (except possibly other Diptera larvae feeding saprophagously in rotting snails). These features would seem to result in little evolutionary pressure to produce in sciomyzid defence mechanisms. Most morphological features of sciomyzid larvae seem to be adaptations to a predaceous or parasitoid lifestyle, to their feeding site, and to their microhabitat, not to defence. Also, the often patchy distribution of their food resources has likely contributed to the evolution of short life cycles, thus decreasing the exposure of larvae in search of food to parasitoids, predators and inimical conditions.

Sciomyzid adults are probably particularly vulnerable to predaceous insects and foliage-gleaning birds; they are solitary, slow-flying and prone to rest on upper surfaces of exposed vegetation. Most are dull brownish-greyish but some are brightly coloured and others have strongly patterned wings, which might attract predators. The terrestrial *Trypetoptera punctulata* has been considered a mimic of a spider, and species of *Thecomyia* are obvious mimics of some predatory wasps. At least in laboratory rearings, pairs remain *in copula* for up to an hour or more and are obviously less agile then. The unique, very strong labellar hooks of species of *Sepedon* and related genera perhaps afford some protection against small insect predators.

Eggs of the many species of the aquatic predators *Sepedomerus*, *Sepedon* and *Sepedonea* that are placed side by side in masses (Figure 1) and of *Protodictya*, placed end to end, and of a few species of Sciomyzini laid only on the shells of snail prey, are probably especially vulnerable to parasitoid Hymenoptera. However, many of these sciomyzid species are eminently successful, being widespread and abundant. Notably, even the most intimately associated, specialised, true-parasitoid sciomyzids that lay their eggs on exposed '*Lymnaea*' spp. snails, although not common, are widespread; an example is *Sciomyza varia*, which is transcontinental in North America, and its ecological equivalent, *Colobaea bifasciella*, widespread in the western Palearctic (Williams *et al*. 2013; Bratt *et al*. 2020). The fact that these unique biological entities, seemingly the most vulnerable to parasitoid biological pressures, survive despite cryptine ichneumonid parasitoids (Table 3), indicates that parasitoid pressure, in some cases, has not been important in the evolution of some Sciomyzidae. This might be related to the fecundity of the female flies, ie far more eggs are produced than necessary for the survival of the species. The majority of species of Sciomyzidae, which scatter their eggs individually on the substrate, low-growing mosses, etc., perhaps limit parasitism to some extent by this behaviour. However, some parasitoid Hymenoptera are probably sensitive to olfactory cues provided by the living and decaying snails which are often abundant in such situations.

Larvae of Sciomyzini, except *Ditaeniella*, which have encircling spinule bands, and terrestrial Tetanocerini, are essentially naked except for a few rows of ventral spinules, whereas most aquatic larvae are replete with minute integumentary scales and hairlike structures. Surprisingly, the larvae with the strongest integumentary structures (*Perilimnia*

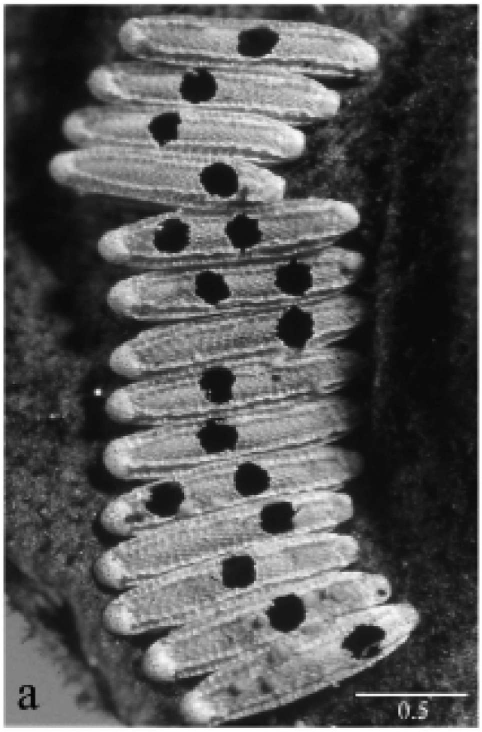


Figure 1. Eggs of *Sepedon americana* parasitised by *Trichogramma* sp. (from Neff and Berg 1966). Permission granted by the Verginia Agricultural Experimental Station Bulletin.

and *Shannonia*, Figure 2(a,b); also see Kacynski *et al*. 1969) tend to remain buried up to the posterior spiracles in their snail prey. Species of *Anticheta* and *Renocera* have a dense coat of fuzzy to spicule-like integumentary processes at least ventrally and on the posterior spiracular disk. The strongly toothed mouthhooks (and accessory teeth in Tetanocerini), the ventral arch, and the postoral spinule band perhaps are used to ward off small predators, but this has not been observed. The unique, bright green fat bodies of the translucent larvae of some species of aquatic, predacious *Elgiva* species probably provide protective colouration. Larvae of aquatic predators feed for only a few minutes up to about an hour or a day in the snail prey, then rest away from the prey, then forage for additional prey and, thus, are exposed to natural enemies. Larvae of semi-terrestrial ('shoreline' predators) and terrestrial species that remain for long periods feeding in the shell of the prey are probably somewhat protected, but their posterior spiracles are exposed. Those that feed on more than one snail are exposed during foraging, as are some terrestrial third-instar larvae that 'wander' after feeding, searching for a pupariation site. Larvae pupariating in shells generally clean the shell and push remaining snail tissue out of the shell, perhaps thus removing olfactory cues for natural enemies. This could also be important in removing rotting tissue that could be a source of bacterial or fungal infection.

Puparia of Sciomyzini are only moderately well sclerotised, whereas those of Tetanocerini (except the translucent puparia of *Elgiva* species) are sclerotised to the a.

b

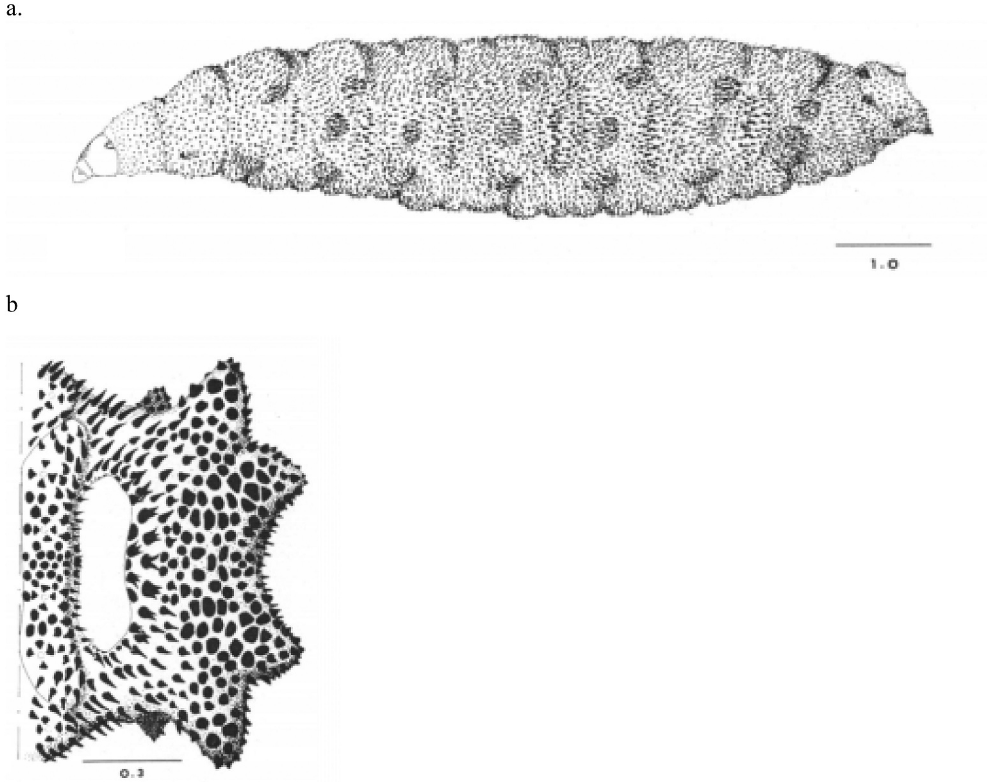


Figure 2. *Shannonia meridionalis* Zuska, third-instar larva. (a), lateral view; (b), ventral view of posterior end. as: anterior spiracle; ps: posterior spiracle (from Kaczynski *et al*. 1969).

point of being brownish black; however, even these do not deter ovipositing Diapriidae (Figure 3). Thirty-six species of Sciomyzini, in eight genera, routinely pupariate in snail shells (Knutson and Vala 2011, table 15.1), the anterior segments of some species occluding the shell opening like a snail operculum (Figure 4). Pupariating larvae of some species of *Colobaea*, *Ditaeniella* and *Pherbellia* produce a calcareous substance in their malpighian tubules, which is excreted and moved to the anterior end by peristaltic body movements and, in some species, is fashioned into one or two septa that occlude the aperture, thus obviously deterring some natural enemies (Figure 5). Pupariating larvae of *Sciomyza varia* (Sciomyzini) produce a unique, anterior empty chamber by subtending a wall of chitin before the posterior chamber containing the pupa (Figure 6). The developmental process of erecting an interior wall of chitin (formed by the last (fourth-stage) larva, which takes place inside the puparium) is unknown. The floating puparia of freshwater Tetanocerini (often congregated by wave and outflow action, and therefore more vulnerable) seem especially vulnerable to small predators (especially fish) and parasitoids that oviposit into puparia. Puparia of both semi-terrestrial and terrestrial species (both Sciomyzini and Tetanocerini) are formed on/in the substrate, with pupariating larvae of some burying themselves just below friable surfaces.

Of course, in eutrophic and mesotrophic microhabitats there can be high populations of many species of polyphagous, predatory, aquatic and semi-aquatic insects, whose

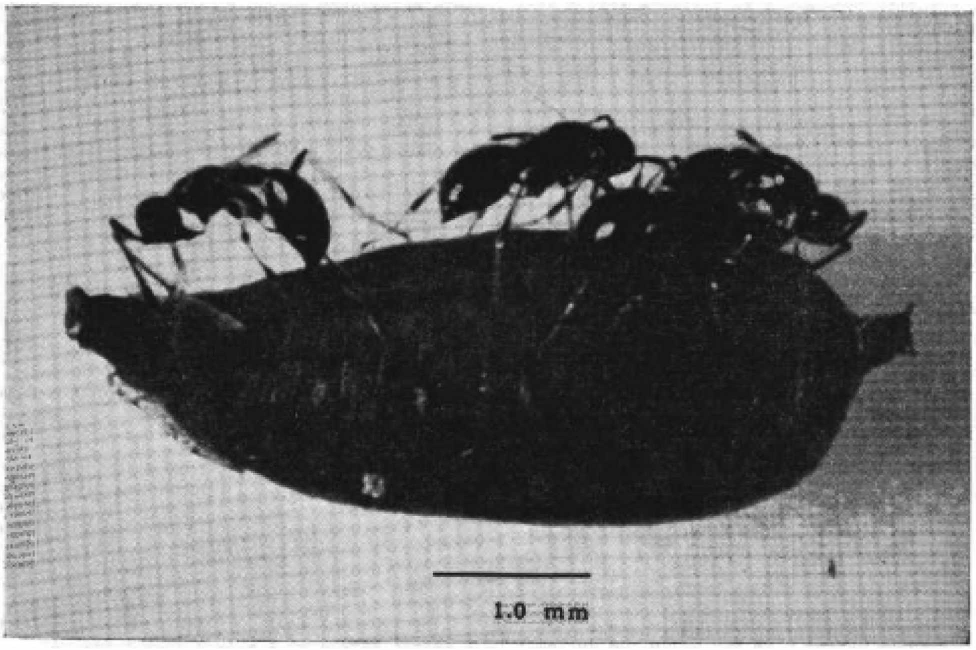


Figure 3. *Phaenopria popei* (Diapriidae) ovipositing into a puparium of a *Dictya* species from the Ithaca, New York, area (from Knutson and Berg 1963).

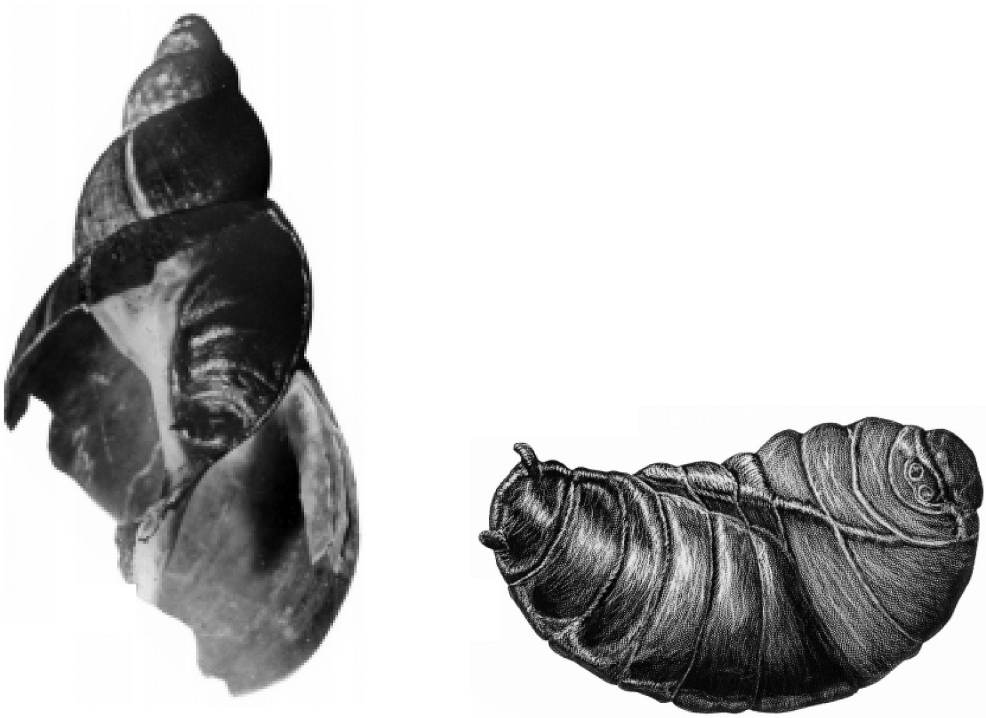


Figure 4. (Left) Puparium of *Colobaea bifasciella* at beginning of second whorl in shell of *Stagnicola* sp.; (Right) puparium removed from shell of *Stagnicola* sp. (from Knutson and Bratt unpublished data).

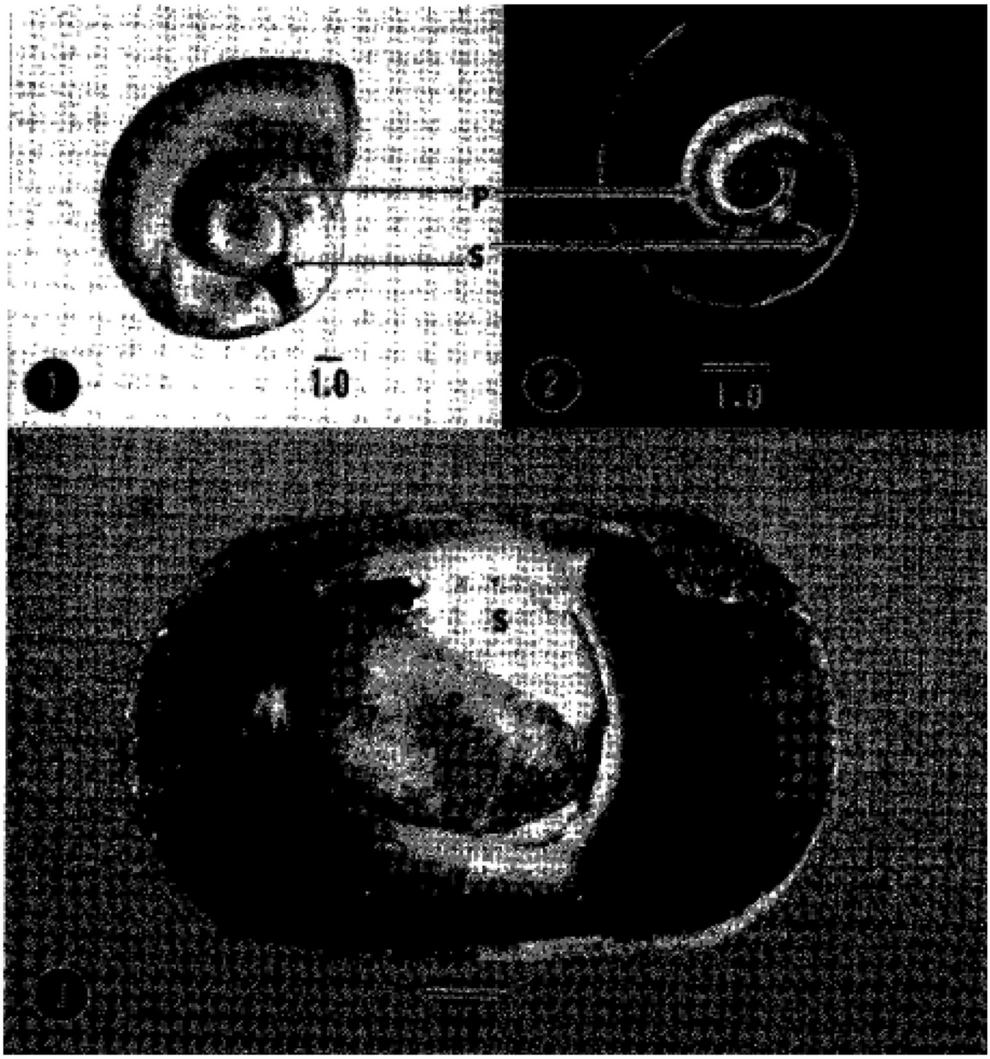


Figure 5. Septa and puparia of *Pherbellia*. (1) *P. seticoxa* in shell of *Helisoma trivolvis*. (2) *P. trabeculata* in shell of *Biomphalaria glabrata*, x-ray photograph. (3) *P. dorsata* in shell of *H. trivolvis*. A: anterior end of puparium; O: slit-like opening in septum made by pupariating larva; P: puparium; S: septum (modified from Knutson L.V., Berg C.O. *et al*. 1967).

populations could result in enhanced depredation of sciomyzids. This aspect of sciomyzid/natural enemy population dynamics, obviously important to biocontrol, has not been examined. In fact, polyphagous natural enemies of potential biocontrol agents is, in general, a neglected area of research.

Snail and slug defence mechanisms against Sciomyzidae are discussed by Knutson and Vala (2011) and therefore are not detailed herein. Quicke (1997) provides excellent general information on defence mechanisms of host insects against parasitoid wasps.

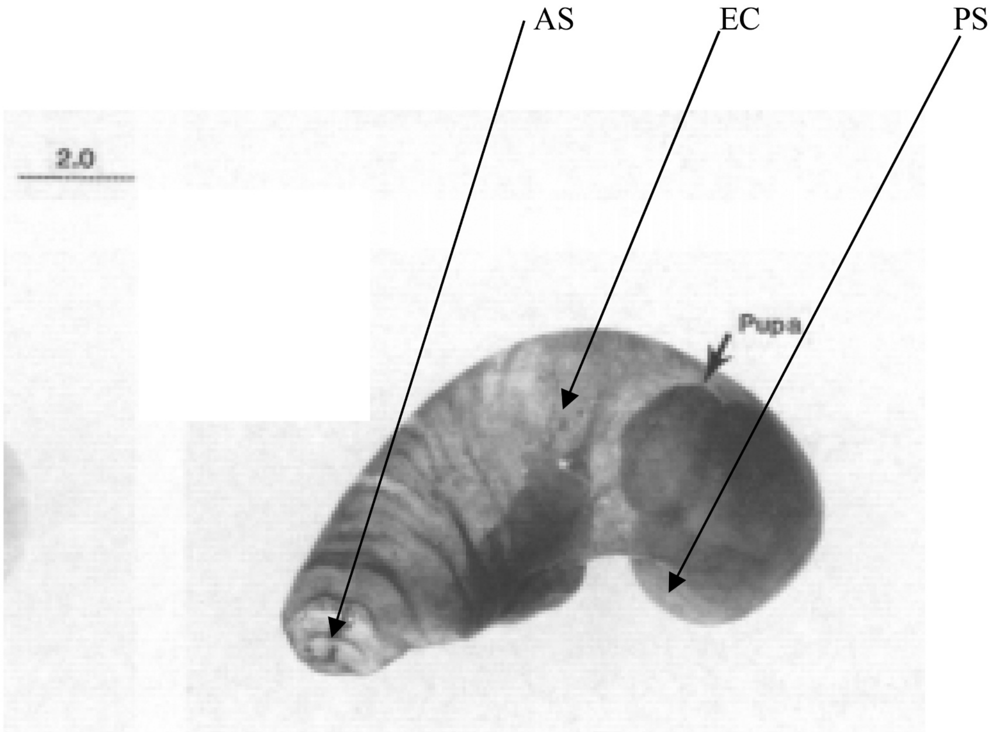


Figure 6. *Sciomyza varia*, puparium. AS: anterior spiracle; EC: empty chamber; PS: posterior spiracle (from Barnes 1990).

Background information on major groups of natural enemies of Sciomyzidae

General, in regard to Sciomyzidae

Interest in natural enemies of Sciomyzidae emerged early during research on biology of the family (eg Foote *et al*. 1960 on biology of *Atrichomelina pubera*). The first, but brief, overview of natural enemies (particularly in regard to natural enemies of species of *Sepedon*) was presented by Neff and Berg (1966). Specific detail on natural enemies has been routinely included in many of the publications on life cycles of Sciomyzidae (these publications on the world species are tabulated, by species, in Vala *et al*. 2012). In most of these references the pervading theme is relating the natural enemies to the biology of the host/prey flies, especially in the context of the fly/gastropod ecological relationships. Summaries of thesis research specifically on natural enemies (Diapriidae by O'Neill 1973 and Trichogrammatidae by Juliano 1981, 1982) are major contributions. The film on Sciomyzidae produced by C.O. Berg in 1973 at Cornell University, Ithaca, New York, USA, includes remarkable footage of parasitoid Hymenoptera ovipositing into and emerging from sciomyzid puparia, aquatic insect natural enemies attacking sciomyzid larvae, and a discussion of the impacts of natural enemies of Sciomyzidae in relation to the potential of using these flies as biological control agents. That classic 14-min colour film is included in the supplementary online material of Knutson and Vala (2011) and Murphy *et al*. (2012). The most recent summaries are the four pages in Knutson and Vala (2011).

Review of the literature

General, with regard to Sciomyzidae

The genera and species of Sciomyzidae, with taxon authorities, that are associated with natural enemies as presented in the text and Table 3 are listed taxonomically in Table 5; taxon authorities for other sciomyzid species and genera are given in the text. The genera and species of natural enemies, along with their taxon authorities, are presented in Table 4.

Egg parasitoids

The roughly 1.0 mm long eggs of most species of Sciomyzidae (Sciomyzini and Tetanocerini) are scattered individually on the substrate or onto very low vegetation, and hatch within a few days except for those few species that overwinter in the egg membranes. Thus, they are difficult to find, at least by entomologists; perhaps parasitoid wasps find eggs (and larvae and puparia) by chemical cues as in parasitoids of leaf beetles (Chrysomelidae) (Meiners *et al*. 2000). However, eggs of most of the 40 reared species of *Sepedomerus*, *Sepedon* and *Sepedonea* are laid in side-by-side masses of up to 25 eggs, and thus, it is these species of *Sepedon* for which most records of egg parasitoids have been made. Note that this behavioural feature lends itself to quantitative evaluation of parasitoid pressure on *Sepedon* species, the most obvious candidates as biocontrol agents of non-operculate snail intermediate hosts of *Schistosoma* Weinland and *Fasciola* L. parasites of humans and livestock. A few species of Sciomyzini (in the genera *Atrichomelina*, *Colobaea*, *Pherbellia* and *Sciomyza*) and *Salticella fasciata* (Salticellinae) lay one or a few eggs onto the shell of the host/prey snail. Some *Anticheta* (Tetanocerini) oviposit only onto egg masses of freshwater or semi-terrestrial snails, and *Pelidnoptera nigripennis* Fabricius oviposits onto its millipede host, *Ommatoiulus moreletii* (Lucas). There are a few records of hymenopterous parasitoids from some species of *Anticheta*, *Colobaea, Pherbellia* and *Sciomyza* which also could be considered biocontrol agents of *Lymnaea* Lamarck hosts of *Fasciola*, but there are no records of parasitoids of *S. fasciata* (which has been considered a biocontrol agent of agriculturally important pests in Australia; see Coupland *et al*. 1994) or *P. nigripennis* as a biocontrol agent of millipede house-hold pests in Australia (Baker 1985; Bailey 1989).

Trichogrammatidae. Eggs of *Sepedon* species are attacked in nature by several Trichogrammatidae (Figure 1). Barnes (1976) found an average of 62% of 316 eggs of *Sepedon fuscipennis* collected from four habitats near Ithaca, New York, to be parasitised by *Trichogramma* sp.

The first of the few attempts to sample egg parasitism in nature by placing laboratory-reared eggs of Sciomyzidae in their natural habitats (a generally neglected procedure) were conducted by Arnold (1978, p. 126, 127, 139, 150). As the several key points in Arnold's thesis are not reported in publications by Arnold, nor in the two major publications on Trichogrammatidae parasitising Sciomyzidae (Juliano 1981, 1982), nor in other publications, we present the major points below (with permission of S.L. Arnold).

Arnold (1978) placed eggs of *Sepedon fuscipennis*, laid by field-collected females, mainly on the inside surface of plastic rearing vials in the laboratory on 18–19 July 1976 in the man-made experimental marshes near Ithaca, New York, where he conducted

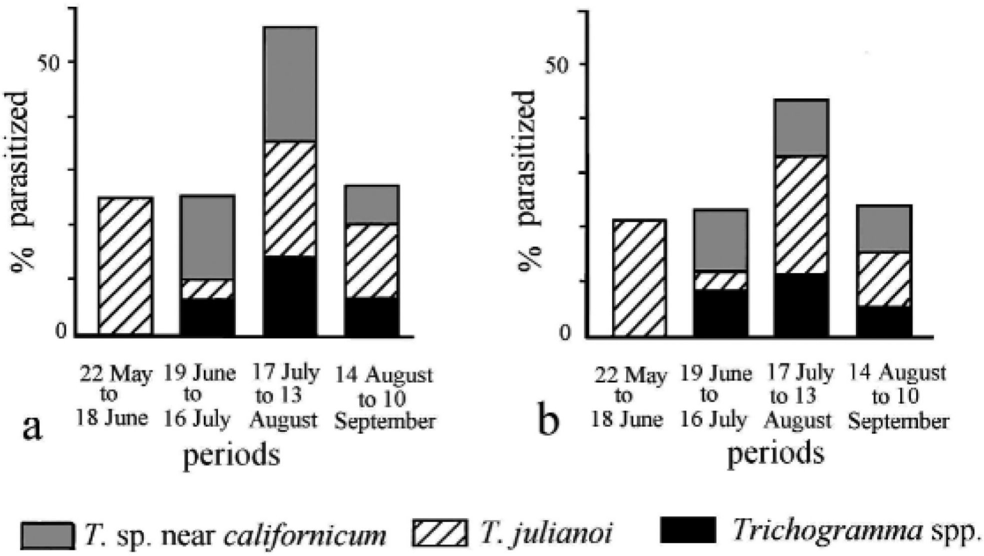


Figure 7. Percent parasitisation of eggs of *Sepedon fuscipennis* by *Trichogramma* spp. during four periods. Data from nine sites. (a) egg masses; (b) individual eggs (from Juliano 1981).

extensive field sampling of Sciomyzidae populations (1972–1977). The vials were propped obliquely, bottom up, without lids, in clumps of emergent vegetation, then returned to the laboratory after one week. Arnold noted parasitisation by the presence of wasp emergence holes in otherwise intact eggs. Arnold had reared *Trichogramma* sp. from *S. fuscipennis* eggs during 1975, and he obviously assumed that the 1976 eggs also were parasitised by *Trichogramma* sp. He noted that of the 1005 eggs recovered from the marshes (in 27 rearing vials), only 12 eggs had parasitoid emergence holes. This equates to a a parasitism rate of 1.19 ± 1.10%. Arnold further notes that it is likely that Barnes's (1976) estimation of rates of parasitism are more realistic than those found through Arnold's experiments (ie by placing eggs in the field).

Juliano (1981) studied *Trichogramma julianoi* in nature at four sites near Ithaca, New York. He found that it parasitises *Sepedon fuscipennis* and *Elgiva solicita*, and that *Trichogramma* sp. nr. *californicum* parasitises *S. fuscipennis*, *E. solicita*, *Tetanocera* spp. (the latter two genera deposit eggs individually), and pyralid moths. *Trichogramma julianoi* was most active during early and late summer; *Trichogramma* sp. nr. *californicum* was most active during mid and late summer. Another undescribed species, similar to *Trichogramma semblidisi* Aurivillus, occurred in the same habitats but was not found to parasitise *S. fuscipennis*; its primary hosts were Stratiomyidae flies. Mortality of *S. fuscipennis* eggs due to *Trichogramma* spp. varied significantly over the summer and peaked at 43.6% during late July and early August (Figure 7). Eggs of Sciomyzidae (up to 31.4% parasitisation) and Stratiomyidae (at least 30% parasitisation) were the most heavily parasitised by *Trichogramma* spp. of the various freshwater insects included in this study (Diptera: Ephydridae, Sciomyzidae, Stratiomyidae, Syrphidae, Tabanidae; Lepidoptera: Pyralidae (probably Crambidae); Megaloptera: Corydalidae, Sialidae; Coleoptera: Chrysomelidae, Coccinellidae, and Dytiscidae).

In laboratory trials, *Trichogramma* sp. nr. *californicum* parasitised all of these taxa. Juliano (1982), in the laboratory, offered eggs of *S. fuscipennis* (<1, 1–2, 2–3, and 3–4 days old) to inexperienced female *Trichogramma* sp. nr. *californicum*. He noted that when an exposure period of 2 h and the number of host eggs offered were kept constant – host eggs were offered one at a time on 10 occasions – percentage parasitism and survivorship of parasitoids all decreased with increased host age. Furthermore, he noted that over 50% of the adult parasiotoids emerging from hosts <1 or 1–2 days old were female, while hosts 2–3 days old produced only males.

Some *Sepedon* species have been suggested as important alternate hosts of *Trichogramma* parasites of rice stem borers in Southeast Asia (Nagatomi and Kushigemachi 1965; Yano 1968, 1975, 1984) as they seem to sustain their populations on sciomyzids when egg masses of the borers are absent. Of 134 egg masses of *S. aenescens*, containing 2123 eggs collected on 3 June in Kyushu, Japan, 117 masses (87.3%) and 1395 eggs (65.8%) were parasitised by *Trichogramma japonicum* (Nagatomi and Kushigemachi 1965).

Larval/pupal parasitoids

Ichneumonidae. Although the Ichneumonidae represent, by far, the greatest number and diversity of species/genera attacking many species/genera of Sciomyzidae, the main results are from the emergence of these parasitoids from field-collected larvae or puparia. Notably, there are few detailed, laboratory experimental studies on development and behaviour, as there are for Trichogrammatidae and Diapriidae, and few quantitative field data.

Neff and Berg (1966), in their study of 16 species of aquatic, predaceous multivoltine *Sepedomerus*, *Sepedon* and *Sepedonea* (Tetanocerini), concluded Ichneumonidae were the most frequently reared hymenopteran parasitoids of sciomyzid larvae and puparia: Gelinae, 23 species belonging to the genera *Eriplanus* [=*Theroscopus*] (12), *Mesoleptus* (7) and *Phygadeuon* (4) (Townes, *in litt*.). They noted that they obtained some of these from *Sepedon* collected as larvae and held in closed containers. The parasitised larvae attacked snails in the usual way and formed apparently normal puparia from which the parasitoid wasps emerged. Berg *et al*. (1982) noted that over 50% of 110 puparia of four species of *Dictya* (*D. atlantica* Steyskal, *D. expansa* Steyskal, *D. pictipes* and *D. texensis*) collected in central Pennsylvania, USA, on 21 December and 1 January had been killed by parasitoids.

We note that the population dynamic effects of early season larvae of multivoltine Sciomyzidae which deplete, to some extent, early season snail and snail-egg populations, are not compromised by the fact that many of those predaceous sciomyzid larvae are destined, upon pupariation in a few weeks, to produce ichneumonid wasps. However, those wasps could, predictably, reduce populations of late generation sciomyzids. But their impact on the totality of, for example, *Sepedon* populations, which over-winter as adults and whose first-/second-generation larvae attack snail eggs and snails during the 'spring' (or on set of cooler weather in tropical areas) is questionable. The phenology/population dynamics of Ichneumonidae populations vs sciomyzid phenology/population dynamics requires further study. The caveat is to acquire those data for biocontrol purposes before man-made extension of snail populations overwhelms any attempts at biocontrol.

The Ichneumonidae now known to have been reared from Sciomyzidae puparia of both aquatic and terrestrial species (collected either as puparia or as larvae that pupariated in the laboratory) amount to ±40 species and morphospecies in at least four genera (see Tables 3–5). The wasps have been reared from 17 species in six genera of Sciomyzini and 24 species in nine genera of Tetanocerini. As noted in the sections 'Materials and methods' and 'Discussion', the significant impact of Ichneumonidae on populations of Sciomyzidae requires further taxonomic studies of the wasps, determination of the oligophagous/polyphagous nature of the parasitoids, clarification of which species are acting as primary vs secondary parasitoids, and quantitative field studies before or concordant with biological control attempts.

Foote *et al*. (1960) reared Ichneumonidae (*Mesoleptus declivus*, *Mesoleptus* sp., *Atractodes* sp. and *Phygadeuon* sp.) and one species each of Braconidae, Diapriidae and Pteromalidae from field-collected puparia of the multivoltine 'shoreline' predator/parasitoid/saprophage *Atrichomelina pubera* (Sciomyzini) in North America. They collected 76 shells of *Helisoma anceps* (Menke) during August in Michigan, estimating that these shells contained at least 152 puparia. Sixty-three puparia produced adult flies and 73 produced parasitoid wasps (23 producing one ichneumonid each and the remaining 50 producing 151 Braconidae: two to five braconids from each puparium). From two collections of *Physa* sp. shells made during the summer of 1957, containing 59 sciomyzid puparia, 19 failed to open, 12 produced adult sciomyzids, and 28 produced parasitoid wasps, of which 24 were Ichneumonidae. Also, the authors made the first attempts at quantitative analyses of parasitoid impact by comparing two square-metre quadrats of 'stranded', freshwater *Aplexa hypnorum* (L.) collected at the lowest point and at a higher point of a vernal pond, during September near Ithaca, New York. They did not distinguish the families of parasitoid wasps reared from these samples. However, they noted that of the 349 shells collected in the lower quadrat, 34 contained puparia, no adult flies emerged, but 19 parasitoid wasps were produced. Surprisingly, only two puparia were found in the 176 shells collected in the higher quadrat, and they both produced adult flies. Their rationale for these disparate results from a rather simple, but innovative, attempt will be instructive to more sophisticated studies.

Fisher and Orth (1964) found that *Phygadeuon* sp. reared from puparia of the freshwater predator *Sepedon praemiosa* and exposed to young pupae of the egg-feeder *Anticheta testacea* readily oviposited into and completed development on the latter.

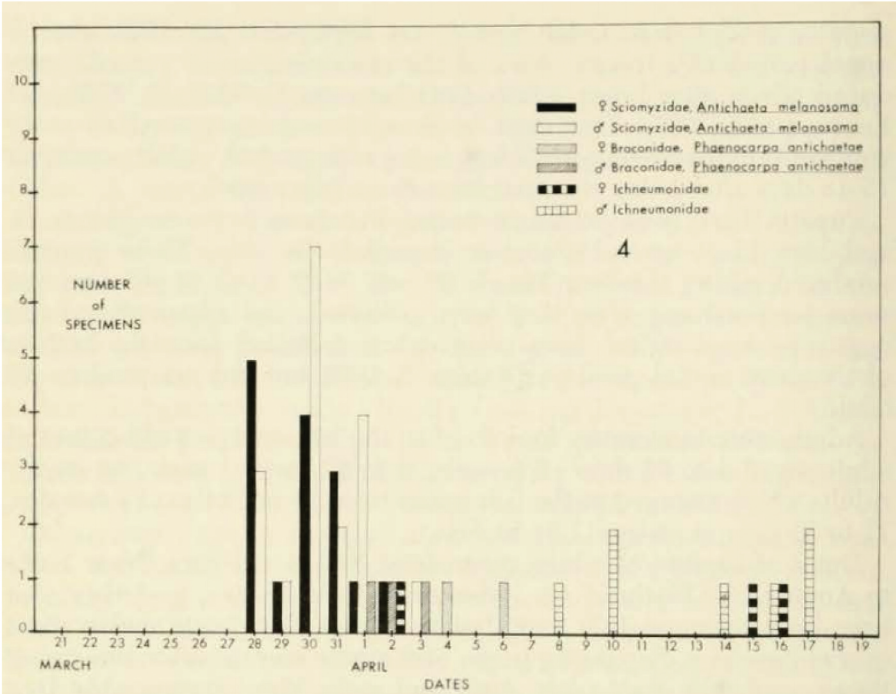
Bratt *et al*. (1969) recorded 15 species of parasitoid Hymenoptera (two Braconidae species, 11 Ichneumonidae species, and two Pteromalidae species) reared from field-collected larvae and/or puparia of nine northern Hemisphere species of *Pherbellia* and one *Ditaeniella* species. However, except for detail on parasitoids of *P. albovaria* (p. 32) and a few incomplete notes on *P. seticoxa* (p. 50) and *P. dorsata* (p. 85), they did not provide details on dates of collection of larvae and puparia, pupariation, or emergence of wasps; in Table 3 we have added some of these details (as Bratt, unpub.) from our review of specimens in the Cornell University pinned collection of wasps reared from Sciomyzidae. The authors noted (p. 32) that 15 puparia of the univoltine, terrestrial *P. albovaria* collected in New York between 25 April and 29 November produced *Mesoleptus declivus* and *Mesoleptus* sp. (det. H. K. Townes). Their data show that puparia collected during spring and early summer can produce wasps within about 1 month. However, their experiments of holding other puparia collected during May, October and November at room temperature or 5°C for as long as 6 months produced wasps. These results indicate that these wasps can undergo diapause, as was shown for the sciomyzid host.

Trelka and Foote (1970) reared *Theroscopus* sp. (as *Eriplanus*) from puparia of the slug-killing *Tetanocera plebeja* collected in the USA. They noted that the female wasp oviposited into the larva of the fly, but that the wasp larva did not become active until after the fly's puparium had been formed. They further note some *T. plebeja* larvae (collected in nature) fed readily on *Deroceras laeve* (Müller) in the laboratory, then formed normal puparia, but failed to transform into pupae. In all of these puparia, wasp larvae subsequently were seen. In each case, the wasp larva completely destroyed the prepupa of the fly before pupating itself within the fly's puparium. Adult wasps emerged 15–20 days later. Each parasitised puparium produced only one adult wasp.

Eckblad and Berg (1972) studied the population ecology of adult and larval *Sepedon fuscipennis* and their snail prey in a freshwater habitat near Ithaca, New York, over two years. Their methods included placing unfed and fed first-instar larvae in floating mesh cylinders, open at the top and bottom. Two cohorts of 300 larvae (25 in each of 12 cylinders) were followed in the periods 17 June–5 July 1969 and 24 August–11 September 1969, and three cohorts of 25, 25 and 50 larvae in each of 12 cylinders were followed from about 6 July for 3 weeks in 1970. Their results from the cylinders focused on survival (ie in terms of puparia formed and larvae recovered). They concluded that survival was due to population density of snails in the cylinders, whether or not first-instar larvae were fed before being released, and predation (but the latter could not be determined). They noted that 3.9% of the field-collected puparia produced adult Ichneumonidae wasps after being kept under laboratory conditions. They noted that the total observed mortality in field-collected puparia was 13.0% (for two summers); the cause of the mortality of the additional 9.1% was not identified. J.W. Eckblad (*in litt* 13 April 2013) noted that 'field-collected puparia' refers to puparia recovered from the cylinders, and the Ichneumonidae were not further identified.

Fisher and Orth (1983, p. 8) reared *Phygadeoun* sp. from several field-collected puparia of the freshwater predator *Sepedon pacifica* from southern California and cultured 'several successive all-female generations … on house fly puparia in the laboratory'.

In southern France, Vala and Manguin (1987) showed that mortality of *Sepedon sphegea* was significant in the spring generation of the flies, with 34 of 38 puparia collected in a temporary aquatic habitat on May 10 parasitised by *Mesoleptus vigilatorius* (as *ripicola*). Close correlations in seasonal activity of (1) seven parasitoid wasp species (Ichneumonidae: *Mastrus* (?) sp., *Mesoleptus* spp., *Phygadeuon* spp.; Braconidae: *Phaenocarpa antichaetae*), reared from puparia of the snail-egg feeding *Anticheta melanosoma*, collected near Ithaca, New York; (2) the sciomyzid; and (3) the food snail [*Aplexa hypnorum* (L.)] were described by Knutson and Abercrombie (1977) (Figure 8). All were associated with seasonal changes in the water level of their ephemeral, vernal pond habitat. From the overwintered puparia there was sequential emergence; first the flies, then the braconids, then the ichneumonids. From a total of 161 overwintering puparia of *Tetanocera ferruginea* collected between 28 February and 5 April on five occasions at two sites near Ithaca, New York, 108 flies and ichneumonids of six species (four *Theroscopus* spp., one *Mesoleptus* sp., and one *Phygadeuon* sp.) emerged (21% parasitisation), with a.



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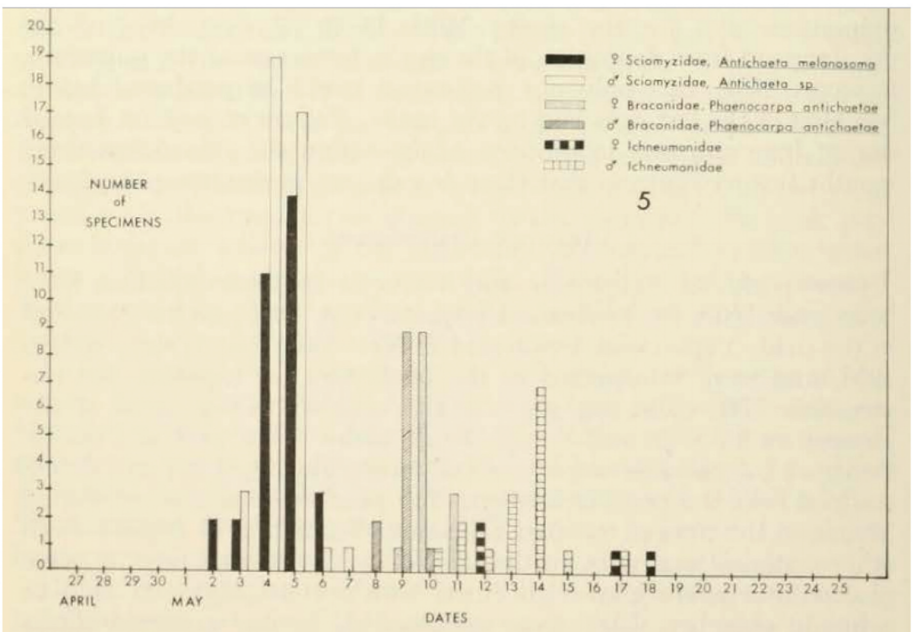

Figure 8. (a) Emergence patterns of Sciomyzidae, Braconidae and Ichneumonidae from 56 overwintering puparia of *Anticheta melanosoma* collected 21 March 1966. (b) Emergence patterns from 134 overwintering puparia collected 27 April 1966. Both collections made at Geneva, New York. Male fly that emerged 7 May was *Anticheta borealis*; all other flies and puparia were *Anticheta melanosoma* (from Knutson and Abercrombie 1977).

Table 8. Emergence of flies and Ichneumonidae spp. from puparia of *Tetanocera ferruginea* collected near Ithaca, New York (from Foote 1999).

No. of puparia collected	Date (in 1958)	No. of flies emerged	No. of wasps emerged
45	28 February	33	7
15	30 March	7	5
21	2 April	11	7
18	3 April	12	3
62	5 April	45	13
TOTAL: 161		108	35

parasitisation of the individual collections (Table 8) ranging from 16 to 33% (Foote 1999). In each sample, the wasps emerged 2–6 days after the last emergence of the flies.

Only four species of Ichneumonidae have previously been recorded as parasitoids of Sciomyzidae: the European *Phygadeuon elegans* from *Tetanocera ferruginea* (Horstmann, 1993); *Phygadeuon yonedai* from *Sepedon aenescens* (Kusigemati 1986) in Japan; the North American *Mesoleptus declivus* from *Atrichomelina pubera* (Foote *et al*. 1960), *Pherbellia schoenherri* (Carlson, 1979), and *Sepedon fuscipennis* (Ashmead, 1901); and *Mesoleptus incessor* from *Tetanocera arrogans* (Šedivý, 1965) in Europe. Both *Mesoleptus* and *Phygadeuon* as a whole have wider host ranges, encompassing Sarcophagidae in the case of *Mesoleptus* and a range of families for *Phygadeuon*. *Mesoleptus*, along with *Atractodes* and *Stilpnus* species, are unusual within the subfamily Phygadeuontinae in being koinobiont endoparasitoids (ie they are internal parasitoids and allow the host to develop further post-oviposition). The biology of *Phygadeuon* is generally poorly known, although where known species seem to be endoparasitoids and koinobionts.

Although several studies (as described above) have named parasitoids of sciomyzids as *Theroscopus* species, these have sometimes been under the synonymous name *Eriplanus*. *Theroscopus* is a variable genus and the distinctions between *Theroscopus* and *Phygadeuon* are unclear, with a few species being assigned to one or the other genus mainly on the basis of biology (Schwarz and Shaw 2011): where known, *Phygadeuon* are parasitoids of brachyceran Diptera whereas *Theroscopus* are parasitoids of various insect cocoons, often including Ichneumonoidea cocoons. There are a few possible explanations for *Theroscopus* species being involved in this complex of sciomyzid parasitoids: specimens identified as *Theroscopus* might be better classified in *Phygadeuon*; *Theroscopus* are more biologically varied than previously reported (or should be synonymised under *Phygadeuon*); *Theroscopus* are acting as (pseudo-)hyperparasitoids of *Phygadeuon* or *Mesoleptus* primary parasitoids; or, in the case of specimens not reared from isolated hosts, species of *Sulcarius* or *Oecotelma* (some species have previously been ascribed to *Eriplanus*) have been reared from pupae of other aquatic insects. If *Cephalobaris eskelundi* is confirmed as a parasitoid of Sciomyzidae, this would be the first host record for this poorly known and rarely collected genus.

Braconidae. Four species of Braconidae, *Aphaereta pallipes* (Say), *Phaenocarpa antichaeta* Fischer, *Phaenocarpa impugnata* Papp, and *Panerema inops* Förster, have been reported as parasitoids of Sciomyzidae (Bratt *et al*. 1969; Yu *et al*. 2016). The aforementioned species belong to Alysiinae, a subfamily consisting exclusively of koinobiont endoparasitoids of cyclorrhaphous flies that emerge from the host puparium (Wharton

1997). *Aphaereta pallipes* is a gregarious parasitoid of *Atrichomelina pubera* (Loew), a sciomyzid with larvae that feed on various freshwater snails and can also successfully develop on terrestrial snails in laboratory assays (Foote *et al*. 1960). The record of *A. pallipes* was from *A. pubera* likely feeding on *Helisoma anaceps* (Menke), but *A. pallipes* successfully utilises many dipteran hosts and has been reported from 28 fly species in nine families and found in the Nearctic, Neotropical and Palearctic regions (Yu *et al*. 2016). It is possible, however, that specimens regarded as *A. pallipes* are a complex of cryptic species given their collectively wide geographic distribution, broad host range, and perceived intraspecific morphological variation (Wharton 1977, R. Kula, pers. obs.). This has also been observed in species of *Asobara* (Abram *et al*. 2020), an alysiine genus recovered as sister to *Aphaereta* (Jasso-Martínez *et al*. 2022). *Phaenocarpa antichaeta* was reported as a parasitoid of *Antichaeta melanosoma* Melander (Fischer 1974) via wasps reared from host puparia collected on 'floating litter and debris' in a vernal pond (Knutson and Abercrombie 1977). The authors did not indicate whether the reared *P. antichaeta* specimens were solitary or gregarious. The larval food source of its host, *A. melanosoma*, was eggs of *Aplexa hypnorum* (L.), although in laboratory assays *A. melanosoma* was also able to complete development on the eggs of an undetermined *Physa* species (Knutson and Abercrombie 1977). Similarly, *P. impugnata* has been reared from *Antichaeta brevipennis* (Zett.), the larvae of which fed on the eggs of an unspecified snail species (Papp 1972). The specimens of *P. impugnata* were initially identified as a species of *Phaenocarpa* near *conspurcator* Haliday. While it was not stated explicitly, descriptions of field collections suggest that collected snail egg masses with fly host larvae were unidentified *Succinea* species (Knutson 1966). Notes about the rearings also imply that *P. impugnata* is a solitary parasitoid, with one wasp emerging per host puparium (Knutson 1966; Papp 1972). In addition to feeding on eggs of *Succinea* species, *A. brevipennis* larvae fed in egg capsules of *Galba truncatula* (Müller) in laboratory assays, but it is unclear whether those larvae completed development to the adult stage (Knutson 1966). *Panerema inops* Förster was reported as a parasitoid of unidentified *Pherbellia*, and an unidentified species of *Aphaereta* has been reported from *Pherbellia subtilis* Orth and Steyskal (as *Pherbellia obscura* in Bratt *et al*. 1969; see Orth *et al*. 1980). The food sources were not specified for the *Pherbellia* host flies from those parasitoid rearings (Bratt *et al*. 1969), although species of *Lymnaea* were indicated as preferred hosts for *P. subtilis*, notably *Lymnaea humilis* Say (Bratt *et al*. 1969; Orth *et al*. 1980). *Panerema inops* has also been reported as a solitary parasitoid of the phorid fly *Megaselia fuscinervis* (Wood) feeding on the terrestrial snail *Vitrea crystallina* (Müller) (Disney 1982).

In addition of the Braconidae listed above, several species of Ichneumonidae reared from sciomyzid puparia have also been reared from puparia of other families of Diptera. Presumably polyphagous species of parasitoids are indicated by an asterisk in Table 3. These and polyphagous parasitoids reared from fly larvae in dead snails are pertinent to our new recommendation that this reservoir of natural enemies of Sciomyzidae be determined in pre-biocontrol attempts.

Pteromalidae. The first larval/pupal Pteromalidae parasitoids were reported by Bratt *et al*. (1969) and in unpublished reports of Bratt. These were from the Sciomyzini species *Pherbellia* and *Colobaea*. Beaver *et al*. (1977), from Thailand, reared the family from *Sepedon* spp. and Yoneda (1986) reared a pteromalid from a species of *Sepedon*. Berg (unpublished) reared a pteromalid from an Australian species of *Dichetophora*. There are also several records from the Universal Chalcidoidea Database.

Chalcidoidae. Likewise, a search of the Universal Chalcidoidea Database (http://www.nhm.ac.uk/research-curation/projects/chalcidoids/) yielded some new records (Table 3).

Unidentified family. There are four as yet unidentified Hymenoptera that are parasitoidal on both Tetanocerini and Sciomyzini.

Pupal parasitoids

Diapriidae. The first record of Diapriidae reared from a puparium of a sciomyzid was in the description of *Phaenopria* (= *Trichopria*) *popei* by Muesebeck (1949) based on 30 parasitoids reared from one *Sepedon fuscipennis* puparium collected by C.O. Berg in Michigan in 1949; these specimens, along with holotype and paratypes, are in the United States National Museum. Berg's Michigan collections were clarified in Knutson and Berg (1963). The latter authors presented additional records of *T. popei* reared from field-collected sciomyzid puparia (see Table 3) and their results on rearing the parasitoid to the F1 generation. They also presented laboratory observations on mating and oviposition behaviour and duration of the life cycle of *T. popei* reared from a puparium of a *Dictya* species collected near Ithaca, New York, on 29 October 1960. Notably, they exposed laboratory *T. popei* to laboratory-reared puparia of other sciomyzids and other families of Diptera. They concluded that *P. popei* adults have been reared in July, August and November. Reared adults attempted to mate in small rearing boxes, and viable eggs were laid in a 1-day-old puparium of a *Dictya* sp. Thirty adults were reared from the single puparium. The host range includes *Dictya*, *Elgiva* and *Sepedon* (Sciomyzidae) and probably other genera in this family. Some years later, O'Neill sent specimens of *Trichopria* reared as a pupal parasitoid of *Atrichomelina pubera* from Ithaca, New York; this species was described by Muesebeck as *Trichopria atrichomelinae* (holotype and paratypes in the USNM). While researching the specimens of these species listed above, an undescribed species of *Trichopria* was found in the USNM collection, reared from *Sepedonea annulata* in Colombia. These were determined by P. Marsh (Systematic Entomology Laboratory - United States Department of Agriculture) as *Trichopria* sp. at an undetermined date. The species will be described in a subsequent paper.

The most detailed laboratory studies of Diapriidae (*T. popei* and *T. atrichomelinae*) reared from puparia of Sciomyzidae are from O'Neill's MS thesis research (1973). His abstract notes *Trichopria popei* and *T. atrichomelinae* are gregarious internal parasitoids of the pupae of some Sciomyzidae. He further notes that in nature *T. popei* parasitises aquatic Sciomyzidae whereas *T. atrichomelinae* attacks a terrestrial species, but, in the laboratory, both wasps readily parasitise aquatic and terrestrial hosts. At 24°C *T. popei* emerged 19 days after oviposition and *T. atrichomelinae* required 26 days.

O'Neill then began PhD thesis research on Diapriidae parasitoids of Sciomyzidae, but his notes have been lost. However, the very extensive material of Diapriidae from field collections and laboratory rearings made by W.L. O'Neill are included in the Cornell material on loan to the USNM. Importantly, the specimens are pinned in trays as he left them. This valuable material will be difficult to work with because for most of it there are only his handwritten date–locality labels on the first specimen of field-collected or laboratory-reared series, but often a Biological Note Number label is included, the latter primarily for laboratory-reared specimens. Although O'Neill's manuscript detailing Biological Note Numbered material is lost, the numbers will be useful in associating specimens of a series and in some cases their specific origin, mainly around Ithaca. Obviously, the specimens should not be re-arranged until they can be examined and labelled by a specialist in Diapriidae. Negatives (35 mm) of photographs made by O'Neill of his research subjects are included with his specimens.

Barnes (1979, p. 567) reared a new species of Diapriidae, *Spilomicrus barnesi*, from puparia of *Neolimnia tranquilla*, an unusual predator of small, operculate freshwater snails in New Zealand. He found that these wasps attacked an unusually large proportion of the sciomyzid population, noting,

These wasps emerged from 29 of the 86 puparia collected in winter (20 July 1976) at the Rimutaka Forest Park. Adult flies emerged from 24 of the puparia 5–21 days after collection. The other 33 puparia were dissected; 6 of them contained dead wasps, 22 contained dead flies, and 5 contained unidentifiable dead tissue.

These specimens were not examined for the present study.

Early and Horning (1978, p. 234), in their description of *Spilomicrus barnesi*, cited Barnes's unpublished details on his rearings and the wasp's ecology as follows with elegant, specific, additional details: '

Mr Jeffrey K. Barnes kindly provided information (*in litt*.) on the habitats in which *Neolimnia tranquilla* puparia were found. The Rimutaka Forest Park, Wellington, collections site is less than 30 m altitude. Puparia were found on the water surface of a stagnant, unshaded, backwater area of Catchpool Stream. The water was up to 1 m deep and the aquatic vegetation included *Lemna*, *Juncus* and *Carex*. *Ulex* and grasses were the principal components of the shoreline vegetation. Wasps emerged from 29 of the 86 puparia collected. Thirty-three puparia were dissected and six contained dead Hymenoptera, probably *Spilomicrus barnesi*.

While researching the specimens of Barnes's species, an undescribed species of *Spilomicris* was found in the USNM collection, reared from *Sepedonea trichotypa* in Argentina. These were determined by C.F. Muesebeck (Smithsonian Institute Entomology) as *Spilomicris* sp. on an undetermined date. The species will be described in a subsequent paper.

Superparasitism. Superparasitism, where more than one parasitoid emerges from the host, appears to occur with some regularity among the Diapriidae parasitoids of Sciomyzidae pupae. Barnes (1979) and Early and Horning (1978) recorded the emergence of 333 *Spilomicris barnesi* from 35 puparia of *Neolimnia tranquilla* (Table 3). *Trichopria popei* also appears to superparasitise Sciomyzidae (Table 3). Amongst the other families of parasitoids, there is no evidence of superparasitism.

Invertebrate predators of larvae

There are no known specialised predators of Sciomyzidae; the recorded predators are probably all opportunistic. During mass rearings of the aquatic predator *Sepedon macropus* in containers outdoors in Hawaii, predators of the fly 'exacted a heavy toll' (Chock *et al*. 1961, p. 3). The authors noted that odonate naiads accidentally introduced into the containers attacked larvae, *Pheidole megacephala* ants robbed the containers of larvae and puparia, and the hemipteran *Mesovelia mulsanti* preyed heavily on first-instar larvae. In a study of survivorship of *S. fuscipennis* larvae in the field over a 2-year period in Ithaca, New York, 1000 larvae were kept in floating cylinders in a typical freshwater habitat of the species (Eckblad and Berg 1972). Only one instance of predation was observed: an immature *Notonecta* sp. (Hemiptera: Notonectidae) attacked and fed on a third-instar larva. Nymphs of various Odonata and larvae of *Tropisternus* Solier sp. (Coleoptera: Hydrophilidae) collected in the same study area were successful predators of *S. fuscipennis* under laboratory conditions. *Tetanocera* species, abundant in a nature preserve near Rome, Italy, were absent in areas where *Gambusia* spp. fish had been introduced for control of mosquito larvae (Rivosecchi 1992). O. Beaver (1989) noted that in laboratory trials when predaceous Odonata nymphs and four species of fish were kept overnight with larvae of *Sepedon senex*, all of the larvae were consumed. A mature larva of the tabanid *Hybomitra schineri* killed and ate 37 second- and third-instar larvae of *T. ferruginea* in a laboratory rearing during 21 days before pupating (Knutson 1965).

Invertebrate and vertebrate predators of adults

Fifteen species of Hymenoptera, Diptera and Orthoptera have been recorded as predators of adult Sciomyzidae (Table 3). Surveys of museum collections of predaceous odonates, wasps, Asilidae and Empididae for specimens with sciomyzids as prey would be of interest. A database on the prey of Asilidae (http://www.geller-grimm.de/catalog/lavigne.htm) recorded six species of Sciomyzidae (*Pherbellia albocostata*, *P. obtusa*, *Coremacera marginata*, *Dichetophora obliterata*, *Pherbina coryleti* and *Trypetoptera punctulata*) as prey of four species of Asilidae (*Adrenosoma atrum*, *Dioctria lateralis*, *Dysmachus echinurus* and *Tolmerus atricapillus*). Whereas Sciomyzidae obviously are preyed upon by birds, bats, and fish, there are only three actual records of this (Table 3).

Pathogens

The adults of many Sciomyzidae are restricted to damp, shady situations which are ideal for the development of many pathogens. Diseased adults or immatures rarely have been collected in nature although the larvae of many species, especially terrestrial snail feeders in the second and third stadia, spend several days to a month or more inside the shells of their host, feeding on decaying tissue. Mechanisms for avoiding disease in such a favourable nutrient for pathogens seem likely. In rearing *Salticella fasciata* on terrestrial snails, Knutson *et al*. (1970) noted that a thick, white film of bacteria, characteristically covering the exposed tissues of dead and decaying snails within several hours, does not develop in snails that have larvae feeding in them.

When small rearing containers of larvae of freshwater sciomyzids are not changed daily or when dead snails are not removed and the containers not flushed with clean water, an apparent viral disease may develop, resulting in bright red Malpighian tubules, a flaccid body with bulging weak spots in the cuticle, and death of the larvae.

The only records of fungal pathogens of adults are *Hirsutella citriformis* (Hypocreales) attacking *Sepedon aenescens* (as '*Sepedon sphegea*'); the fungus also attacked a delphacid and a psyllid (Homoptera) (Romback and Roberts 1989). Valley and Berg (1977) noted that

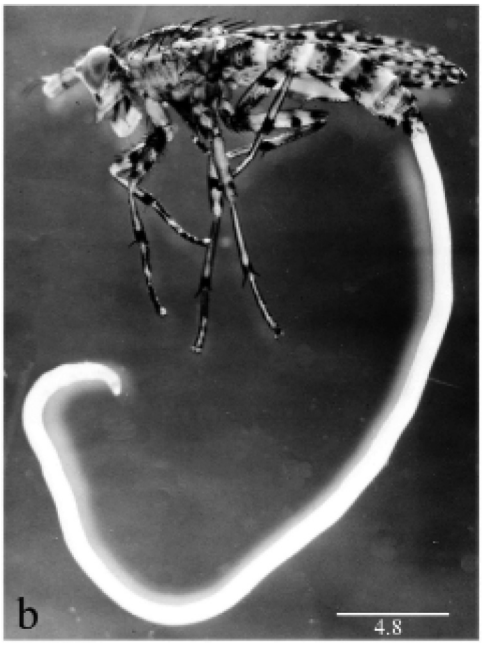

Figure 9. Emergence of adult nematode from anal aperture of *Dictya* sp. female (from Knutson and Vala 2011).

a pair of *Dictya pictipes* collected on 12 July in north-eastern USA died a day later due to *Entomophthora* Cohn sp.

Saprophagous nematodes often are seen in terrestrial snails in which mature terrestrial, primarily parasitoid–predatory sciomyzid larvae are feeding in a saprophagous manner, apparently unimpeded by the nematodes as the larvae complete development. Entomopathogenic nematodes have emerged from a few field collected adults (Figure 9). Verbeke (1948) recorded a species of Gordidae reared from a female *Ilione albiseta* in Belgium. 'Sciomyzidae' (determinations questionable) were recorded as hosts of marine nematodes of the genus *Pseudocella* Filipjev (Leptosomatidae) on the coast of Kamchatka and from the Kara Sea by Platanova (1985, 1988). Valley and Berg (1977) reared one nematode from a male *Dictya steyskali* collected in New York on 9 June; the male died on 15 June when the worm emerged from his posterior end. A second rearing of a nematode from *D. steyskali* by the authors (our notes combined from data in Valley 1974 and Valley and Berg 1977) show that at least this worm reared from an adult fly actually began its parasitisation of the individual in its larval or puparial stage. Of 10 puparia of *D. steyskali* collected on 17 May, one female was placed in a breeding jar with a male, 2 days after emerging on 19 May. The pair mated at least three times during the following few days. When 17 days old the female's abdomen was greatly expanded, and a worm could be seen through her abdominal wall. The 51.0 mm long worm emerged 8 days later by penetrating between her fifth and sixth abdominal sternites, killing the female. During her 22 days of life, the female never oviposited nor were eggs ever seen in her abdomen. None of the other nine adults reared from puparia collected with that of this female produced nematodes. Parasitism by unidentified Nematoda was noted in two females of *Tetanocera* *obtusifibula* collected on 26 June in Idaho; four worms emerged from one female on 29 June and two from the other on 30 June; both females died 1 day after emergence of the worms (Foote 1999).

Many minute, round, brownish 'sacs' occasionally have been found in the abdomen of some adult sciomyzids during the course of macerating the abdomen in potassium hydroxide (KOH) for study of the genitalia. These are resistant to strong caustic solution. They might be microsporidia, or there is the unlikely possibility that parasitoid eggs have not hatched in the larva and stayed until the adult stage (but no parasitoid Hymenoptera have been reared from adult Sciomyzidae); they have not been identified.

Materials and methods for data in Tables 3 and 4

Collection of eggs, larvae and puparia of Sciomyzidae in nature, and holding them in the laboratory for emergence of parasitoids, were extensively carried out, primarily by C.O. Berg and his students at Cornell University during the late 1950s to the early 1970s, which is the original source of much of the unpublished detail in this paper. Most of these collections at Cornell were recorded on handwritten 3 × 5 inch cards by Knutson during 1967 and are preserved in his files in The Smithsonian Institution (USNM).

Many parasitoid Hymenoptera specimens, especially Ichneumonidae and Braconidae, via rearings by C.O. Berg and his students from field-collected larvae and puparia, especially in North America and Europe, have not been identified, and the records remain unpublished as they belong to genera in need of taxonomic revision. Most of the large amount of dry reared material from the sciomyzid collections at Cornell University is on loan to the USNM. The alcohol material at Cornell, dispersed amongst some 69 jars, has not been surveyed or tabulated since it was deposited.

Larvae and puparia of Sciomyzidae are replete with distinguishing morphological features, and it is possible to identify those species that have been described (and especially figured) but for which keys are unavailable. Examination of the third-instar cephalopharyngeal skeleton (on the ventral 'cephalic' cap of the puparium) and other larval vestiges on the puparium will be especially useful in identifying the hosts/prey of unidentified parasitoids pinned with puparia. We caution that even in the best-studied genera of Sciomyzidae, the immature stages of some species have not been described. Further details on habitats, collection, rearing and identification can be found in Knutson and Vala (2011).

More than 20 taxonomists during the late 1950s, 1960s, and early 1970s spent considerable time and effort identifying reared natural enemies sent to them by C.O. Berg and his students at Cornell University. The identifiers' initials are entered in Table 3 and are detailed in Table 7. Further review of specimens identified only as morphogenera or morphospecies (Genus A, B, 1, 2, etc.) is needed. It is likely that some of the identifiers retained some specimens, and thus, we have included the 'Location/collection' with which the identifier was associated in Table 3. For example, our colleague W.L. Murphy recently discovered several specimens of Braconidae, labelled *Phygadeuon* sp., reared by C.O. Berg and students from Sciomyzidae, in the Canadian National Collection. We realise a criticism of this paper could be that some of the essential raw data are based upon identifications made many years ago. However, (1) our data are the most extensive on the natural enemies of any group of Diptera, and (2) our comprehensive documentation will allow the next several generations of parasitoid wasp taxonomists to find the appropriate specimens for corrections and additional identifications. The identifications of the host/prey Sciomyzidae were made by the sciomyzid specialists indicated; all were re-examined and confirmed or newly identified by L. Knutson. From that point of view, the association of species of Sciomyzidae, and at least genera/morphospecies of their hymenopterous parasitoids, is more certain than for any other such data on natural enemies of a family of flies.

In Table 3 where it is obvious that the author of the publication identified the natural enemy, 'A' is entered in the identifier column. Unpublished information is attributed to the collectors as 'unpub.' in the reference column in Table 3. The museums where some specimens of unpublished records might have been kept by identifiers are noted in Table 7. The dry, pinned material in the Cornell collection (but not the probably extensive alcoholic material) was transferred as a long-term loan to the USNM in October 2009. The Cornell and USNM collections of pinned hymenopterous parasitoids of Sciomyzidae are separately identified as to museum collection but placed together in seven drawers at the end of the Sciomyzidae in the USNM Diptera collection, along with the above-mentioned cards.

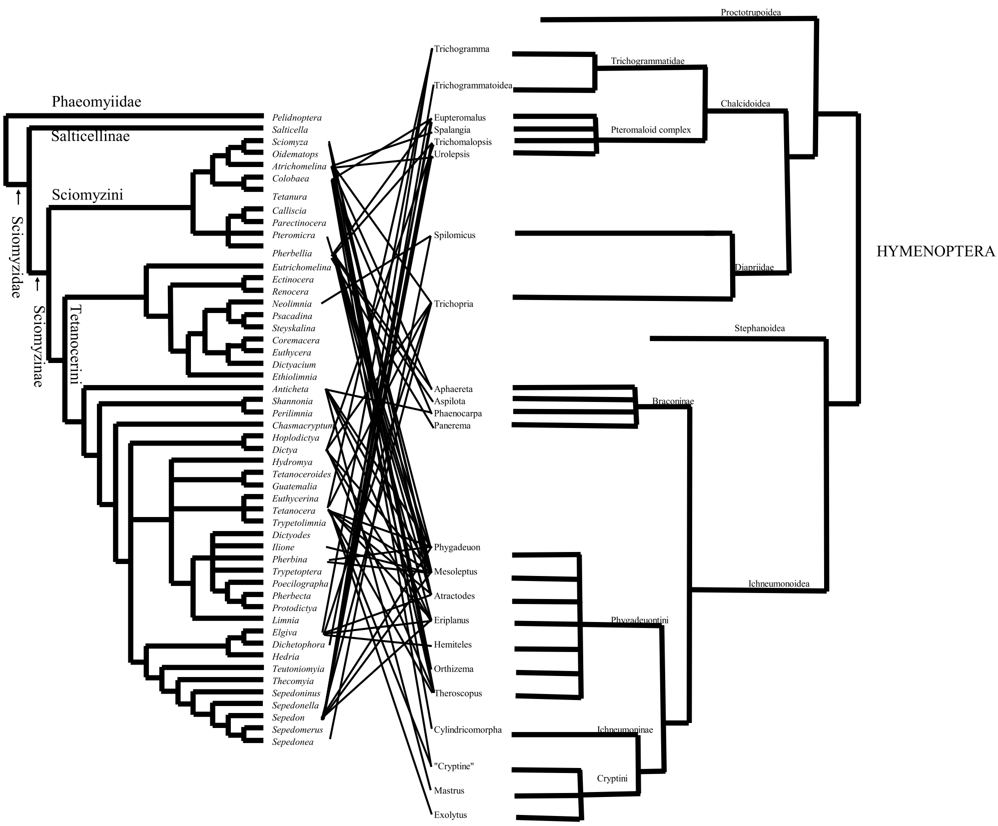

Figure 10. Pattern of utilisation of genera of Sciomyzidae by parasitoid Hymenoptera.

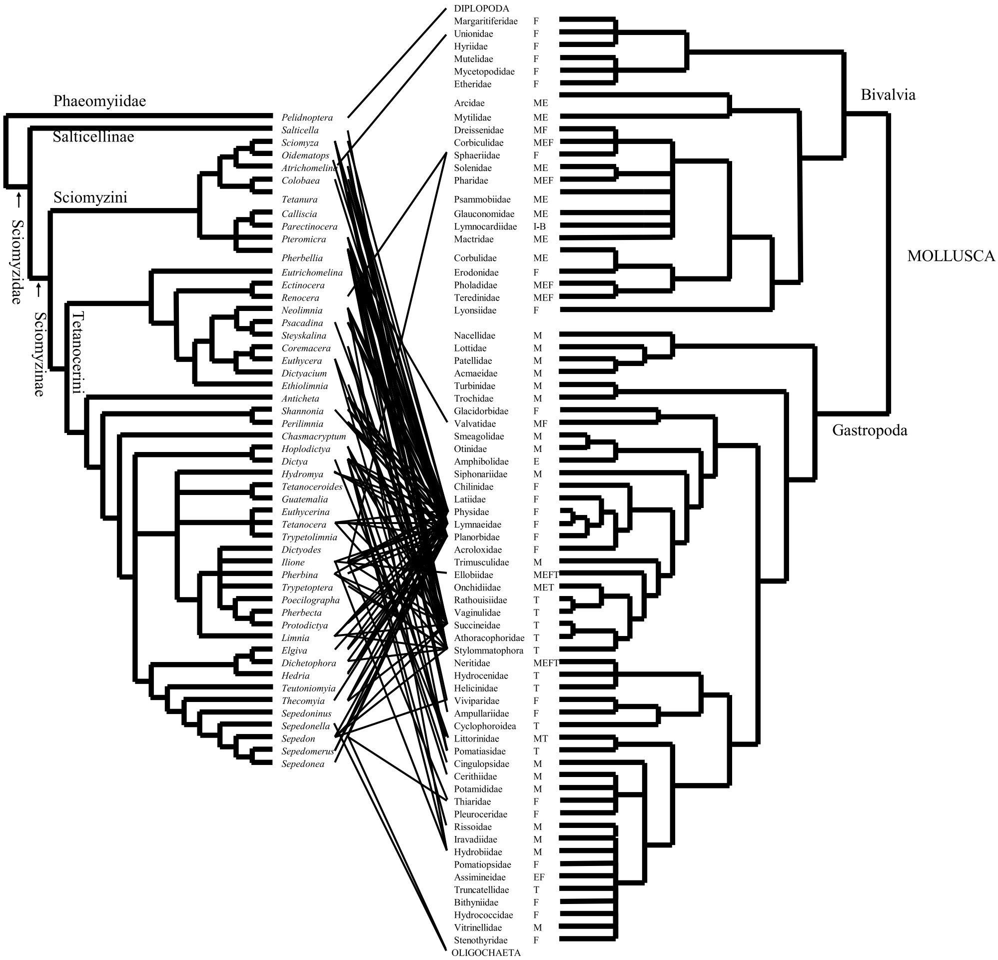

Figure 11. Pattern of utilisation of families of Mollusca by Sciomyzidae (suppl. fig. 3 from Murphy *et al.* 2012).

Analyses

Our basic data are presented primarily in Table 3 and are also summarised in Tables 4–6. We present the following analyses in regard to several aspects of natural enemy, sciomyzid and mollusc relationships.

Taxonomic classification, phylogeny and host ranges

Whereas Barker *et al*. (2004) noted that the Mollusca–Sciomyzidae phylogenies were somewhat congruent with the Sciomyzidae being linked with the freshwater pulmonate families Lymnaeidae, Planorbidae and Physidae (see Figure 11), no such biases are present in the Hymenoptera–Sciomyzidae dendrograms (Figure 10). However, it should be noted that the Phygodeuontini (seven genera) have a wide host range among the Sciomyzidae including both Sciomyzini and Tetanocerini but not Pelidnoptera or Salticella.

Biogeography

It is instructive to compare the zoogeography of the Sciomyzidae in general (see Table 1) with that of their natural enemies (see Table 4). For the 26 species of Holarctic Sciomyzidae, there are 37 records of parasitoids (142%). For the 197 Nearctic species of Sciomyzidae, there are 93 records of parasitoids (47%). For the 184 Palearctic sciomyzids, there are 38 records of parasitoids (21%). For the 114 Neotropical sciomyzids, there are 25 records of parasitoids (22%). For the 67 Afrotropical Sciomyzidae, there are only 3 records of parasitoid species (4%). Of the 27 Oriental sciomyzids, there are 14 (52%) records of parasitoids. Of the 12 Australian sciomyzids, only 1 (8%) has a parasitoid record. Likewise, Oceania, with 4 sciomyzids, and Subantarctic (New Zealand), with 16 sciomyzids, have just 1 parasitoid record each – amounting to 25% (Oceania) and 6% (Subantarctic). The reasons for the differences in proportions of recorded cases of parasitism among zoogeographic realms is uncertain. Certainly, the avid recording of these details by Berg's students (who mainly worked in the USA and Europe) probably increased the number of records seen in both the Holarctic and Nearctic. Nevertheless, Neotropical records appear to be relatively high. Afrotropical, Australian, Oceania and Subantarctic (New Zealand) are all very poorly represented by parasitoids of Sciomyzidae. Whether this is a consequence of under-recording or a genuine lack of hymenopterous natural enemies in these zoogeographic realms remains to be seen.

Host range

From Table 4 it can be seen that the majority of Sciomyzidae, here recorded, hosted only one natural enemy (35 species). However, some hosted more – most notably *Sepedon fuscipennis* with 13 natural enemies recorded and *Tetanocera ferruginea* with 11. It is noticeable from these data (Table 4) that there is a greater prevalence of natural enemies hosted per species in the Tetanocerini than the Sciomyzini. For Sciomyzini (n = 20 species) the mean number of natural enemies recorded per species = 2.0 standard deviation (SD) = 1.34; for Tetanocerini (n = 43) the mean number of natural enemies recorded per species = 2.56 SD = 2.71. The variation is therefore higher in the Tetanocerini as is the number of natural enemies per species, though given the sparsity of the data it is unlikely to be statistically significantly different. This difference, however, is probably due to the larger size of the Tetanocerini with respect to the Sciomyzini, which are diminutive. Also, the Sciomyzini may be less exposed to parasitoid natural enemies, being more likely to be parasitoidal themselves (Berg and Knutson 1978) with the added protection of the shell of the host and, in some cases, a calcareous septa (Knutson L.V., Berg C.O. *et al*. 1967) – see Figure 5.

Macro- and microhabitats (Tables 5 and 6)

Knutson and Vala (2011) extensively reviewed the macrohabitat of adults and the microhabitats of immatures with regards to guild (*sensu* Root 1967). Although the macrohabitats are wide-ranging and diverse, Maher *et al*. (2014) quantified the fine-scale hydrological niches of 22 species of Sciomyzidae in terms of adult collections, showing that although each species had a distinct optimum (median) hydroperiod, there were numerous overlapping occurrences. Knutson and Vala (2011, p. 172) note:

Although the niches occupied by Sciomyzidae are diverse in terms of macro- and microhabitat, seasonality, taxonomic complement of hosts/prey, larval feeding site, and nutritional state of food resource, relatively few other Insecta occupy these niches … Surprisingly, the niches where most competition likely occurs (predation of non-operculate snails in open water and predation/saprophagy of exposed aquatic and semi-aquatic snails) are those niches where, in terms of diversity of species and genera and in terms of individuals, the Sciomyzidae have been most successful, worldwide.

Vegetation structure is also important for Sciomyzidae. Williams, Sheahan *et al*. (2009) showed that the diminutive Sciomyzini (*Pherbellia nana*) was a significant indicator of vegetation zones with short vegetation lengths, and larger Tetanocerini (eg *Ilione albiseta*) were significant indicators of zones with taller vegetation.

Behavioural groups of Sciomyzidae (Tables 5 and 6)

With 90 records (52%) of parasitoids from Sciomyzidae matching behavioural group 11, and 33 records (19%) from group 2, it is worth noting that there is somewhat of an overlap between these two groups. As noted above: group 11 are predators of non-operculate snails at or just below the water surface, just above the surface on emergent vegetation, and occasionally those exposed on moist surfaces, such as *Sepedon spinipes* (Scopoli). Most larvae live at the water surface, with their posterior spiracles exposed most of the time. Several freshwater predators habitually leave the water for moist surfaces when mature. Larvae of some species in this group often have labile feeding behaviour and might be placed as well in group 2. On the other hand, group 2 species are predators/saprophages of non-operculate, primarily freshwater snails exposed on moist surfaces by seasonal or diel receding or fluctuating water levels or while the snails are foraging or migrating (= most of the 'stranded snail' situations and the 'shoreline' situations mentioned in the literature, eg for *Hydromya dorsalis* Fabricius). Thus, it appears from the present review that the Sciomyzidae most vulnerable to hymenopterous parasitoids are those foraging as larvae on the shoreline during fluctuating water levels.

Phenological groups of Sciomyzidae

Fifty percent of parasitoids recorded attacking Sciomyzidae (90 records) attack those from phenological group 1. These are multivoltine species overwintering in the puparium as a diapausing or quiescent pupa or pharate adult. The fact that the puparia are found throughout the year may be the reason for the propensity of this phenological group to host hymenopterous parasitoids. Those sciomyzids of phenological group 2 account for 33 records of parasitism (18%). Although members of this group overwinter as adults, they are multivoltine and all life stages are found throughout the year. The species range, like group 1 phenology, from terrestrial to aquatic and are included in both the Tribe Sciomyzini and Tetanocerini. The next most-frequent choice for parasitoids is phenology group 5(a), with 23 records (13%) – these flies are univoltine and overwinter in the puparium. In contrast, those of phenology group 5b make up only 3 records (2%). This group overwinters as a larva and then in the puparium. This is possible evidence that parasitoids attack the puparium, although it should be noted that parasitoids could possibly be attacking larvae and then completing development as the host pupates. Further support for this is that there are no records of parasitoids emerging from those sciomyzids of phenology group 3 (univoltine overwintering in the egg membrane) and only eight records of parasitoids (4%) emerging from group 4 (univoltine overwintering as a larva). The remaining 24 cases of parasitoids come from group 6 phenology sciomyzids, accounting for 13% of cases. These flies have overlapping generations and no diapause and are multivoltine.

The Trichogrammatidae appear to be somewhat unique in their preference for Sciomyzidae from only behavioural group 11. Although this is the most popular prey behavioural group, all other hymenopterous parasitoid families include species that attack other behavioural groups. Interestingly, the Trichogrammatidae also primarily attack phenology group 2 – again, the most popular phenology.

Most vulnerable stages of Sciomyzidae

We hypothesise, according to the analysis above (see behavioural groups of Sciomyzidae), that 'wandering' larvae are in the microhabitat most susceptible to attack by larval parasitoidal natural enemies, especially parasitic Hymenoptera. Also, the other susceptible microhabitat appears to be floating puparia (see analysis under phenological groups of Sciomyzidae above). Under macro- and microhabitats above, it is noted that diminutive Sciomyzini are significant indicators of zones with short vegetation, while larger ones (mainly Tetanocerini) are indicators of taller vegetation. Williams, Sheahan *et al.* (2009) supposed that this is a consequence of apparent competition (Holt 1977) whereby only diminutive species can survive in short turf due to exposure to natural enemies.

Discussion

Adult sciomyzids are relatively solitary and inconspicuous, do not congregate, and are not often collected on flowers – but see a reference to them on *Caltha palustris* (Judd 1964). It is also worth noting that Bistline-East *et al.* (2018) showed that Sciomyzidae will feed on aphid honey dew. This suite of features, except their slow flying, would seem to protect them from many opportunistic predators (Knutson and Vala 2011). As noted, Sciomyzidae are slow fliers, so it is quite probable that they are prey to robber flies (Asilidae) – more so than recorded. Table 3 includes six records of four Asilidae preying upon six Sciomzidae species (two Sciomyzini and four Tetanocerini). It is often observed that if an adult Sciomyzidae is collected in the same net as an adult Scathophagidae, the scathophagid will decapitate the sciomyzid (Gormally, pers. comm.). Table 3 lists only one case of this, where a scathophagid preyed upon *Pherbellia cinerella*.

Alternate hosts/prey of natural enemies of Sciomyzidae, with special reference to Diptera feeding in dead snails

Studies of parasites and predators of Diptera larvae feeding in dead snails is of interest in regard to Sciomyzidae for theoretical and practical reasons. Not discussed here but discussed extensively by Knutson and Vala (2011) is the theory that the primitive species of the monophyletic family Sciomyzidae arose from dipterous larvae feeding in dead snails. Pertinent to the present paper are the natural enemies of Diptera larvae feeding saprophagously in dead snails, especially polyphagous parasitoids and opportunistic predators, because these will likely affect the use of Sciomyzidae as biological control agents. Larvae of many sciomyzid species, including *Pherbellia* spp., *Pteromicra* spp., *Coremacera marginata* and *A. pubera*, feed in the decaying tissues of snails long after their hosts/prey have died. The macro- and microhabitat conditions of the snails recorded in studies of saprophagous Diptera are similar to those of the food snails of many Sciomyzidae. Their likely interaction has not been previously noted in the literature. There has been no overall review of natural enemies of fly larvae feeding in dead snails. However, the species of such Diptera have been rather well documented; thus, a search of the literature for their natural enemies is possible.

We present here notes on some of the most recent and comprehensive publications on Diptera larvae feeding in dead snails. R.A. Beaver (1972, 1977) made seven collections of dead *Cepaea nemoralis* (L.), a terrestrial snail, from 16 May to 3 March among dune slacks in Wales and reared adults of eight species of saprophagous Diptera from these collections. He reared two dipterous opportunistic predators from the larvae of *Muscina assimilis* Fallén (Muscidae) from three of the seven collections, and he reared the dipteran *Hydrotaea occulta* (Meigen) (Muscidae) from one collection. R.A. Beaver (1977) made a few 'casual observations' of some coleopterous opportunistic predators of fly larvae in dead snails: one Silphidae, six Carabidae, and four Staphylinidae species. None of the above predators have been recorded as preying on Sciomyzidae but they, and/or their congeners, probably do so.

R.A. Beaver (1977) reared *Mesoleptus* sp. (Ichneumonidae) frequently from one (*Sarcophaga nigripennis* Meigen) of three species of *Sarcophaga* Meigen and *Trybliographa* Förster sp. (Cynipoidea) from two specimens of the anthomyiid *Subhylemyia longula* (Fallén) from the snails he studied. The percentage parasitised by *Mesoleptus* sp. was 0–100% in individual snails; 0–44.7% of snails in his seven collections produced this wasp. Many *Mesoleptus* species but no *Trybliographa* have been reared from Sciomyzidae.

Chandler *et al.* (1978) noted that some dipterous larvae reared from dead snails [the sphaerocerid *Copromyza pedestris* (Meigen), the ephydrid *Discomyza incurva* (Fallén) and the phorid *Spinophora maculata* (Meigen)] appear to be obligatory feeders on dead snails. This obligatory behaviour is probably true of some other dipterous larvae, and such species probably are major reservoir hosts of polyphagous parasitoids that also attack Sciomyzidae.

L. Papp (2002) included 'dead snails' along with droppings of forest animals, decaying fungi, *Vespa* wasp nests, etc., in his study of the Diptera and Coleoptera guilds on 'very small-sized feeding resources' in low montane forests in Hungary. He trapped adult flies on dead *Helix pomatia* L. and reared flies from traps baited with *H. pomatia* set out for 48-hour periods. Twenty traps of each type were set up at identical places on the same three days of July and August in three consecutive years (1995–1997). Of the 20,500 flies collected from 10 types of feeding resources, 5013 individuals of 91 species were obtained from dead *H. pomatia*; in one series a maximum of 37 species were collected. Analysis of these data was not presented in that paper and the list of fly species apparently is not yet published.

Knutson and Vala (2011) listed 14 families of acalyptrate Diptera, including 29 species, plus species in the families Empididae, Sciadoceridae and Syrphidae, as having been reared from dead snails. Also of interest here is the detailed review of the biology of dipterous larvae primarily associated with terrestrial snails by Coupland and Barker (2004, p. 106), emphasising the families Calliphoridae (11 species), Fanniidae (2), Muscidae (6), Phoridae (15) and Sarcophagidae (42) (these are all calyptrate Diptera except the Aschiza Phoridae). Their emphasis is on parasitoids, facultative parasitoids and possible parasitoids, but as they noted,

That both saprophagous and parasitoid sarcophagids utilise gastropods has frequently led to uncertainty of the true nature of association for species reared from gastropod cadavers. This uncertainty is accentuated by the facultative interchange of necrophagous and parasitoid life strategies in many species.

Although there is an extensive literature on the biology of malacophagy in these dipterans, Coupland and Barker (2004, p. 106) regarded it as bothf ragmentary and, indeed, provisional.

Role of Sciomyzidae in biocontrol and evaluation of biocontrol implications of natural enemies of Sciomyzidae

Other than data on percentages of field collections of Sciomyzidae eggs and larvae/puparia parasitised by some Hymenoptera reviewed above, there is little quantitative information on the impact of natural enemies on sciomyzid populations. Obviously, the impact of, at least, Trichogrammatidae on egg populations and of Braconidae and Ichneumonidae on emergence of adults from puparia might be significant. However, the impact of the latter two families on the standing crop of larvae feeding in/on snails may be low, because the larvae continue to feed and develop to pupariation even when parasitised by these wasps. It should be noted that physiological reactions of hosts and death of larvae as a result of parasitoid feeding may be non-negligible.

About 240 of the 548 valid, described species of Sciomyzidae, worldwide have been well documented (in most cases including complete life cycles) as obligate parasitoids/predators of Mollusca (except two predators of oligochaete and one parasitoid of millipedes). Thus, Sciomyzidae are well recognised as potential biocontrol agents of disease-carrying freshwater snails and terrestrial snails and slugs of agricultural importance. Their potential has been reviewed by WHO (1961), Berg (1964), Greathead (1981), Appleton *et al*. (1993), Coupland and Barker (2004), Knutson and Vala (2011), Murphy *et al*. (2012), and others. Knutson and Vala (2011) extensively reviewed the field trials and laboratory experiments to date against freshwater *Biomphalaria* snails that are obligate intermediate hosts of *Schistosoma* spp. worms affecting man [in Iran (Tirgari and Massoud 1981) and South Africa (Appleton *et al*. 1993)] and against *Lymnaea* freshwater snails that are obligate intermediate hosts of *Fasciola* spp. worms affecting livestock [in Hawaii (Chock *et al*. 1961) and Ireland (Gormally 1988a, 1988b; McDonnell 2004)]. Research results and reviews of Sciomyzidae that are natural enemies of terrestrial snails and slugs that are agricultural pests are presented by Coupland (1996), Coupland *et al*. (1994), and Coupland and Barker (2004). Baker (1985) and Bailey (1989) presented the life cycle and biology of *Pelidnoptera nigripennis* (Fabricius) as a potential biocontrol agent of millipede household pests in Australia. PhD thesis research on *Tetanocera* spp. as biocontrol agents of slugs in greenhouses in Ireland has been conducted at the National University of Ireland, Galway [see papers from The Applied Ecology Unit (Gormally's lab) by Hynes *et al*. (2014a, 2014b), Bistline-East *et al*. (2018, 2020a, 2020b) and D'Ahmed *et al*. (2019)].

There are studies underway on the role of natural populations of Sciomyzidae in providing ecosystem services (ie their effects on natural populations of pest molluscs and as bioindicators). Some earlier population studies (eg Eckblad and Berg 1972; Arnold 1978) and more recent studies (eg Williams, Moran *et al*. 2009, Williams, Sheahan 2009, 2010; D'Ahmed 2021) give some indications of the value of data on Sciomyzidae in those regards.

In terms of modern ecological and biocontrol theory, the most comprehensive analysis of Sciomyzidae is that by Barker in Coupland and Barker (2004). In reviewing the requirements for successful biocontrol agents, Barker detailed that Sciomyzidae meet, or potentially meet, some of these requirements. More research is needed in some areas.

Ease of laboratory rearing

McLaughlin and Dame (1989) reared the endemic North American freshwater predator *Dictya floridensis* Steyskal on a large scale, continuously through the F8 generation, availability of snails and manpower being the limiting factors. Appleton *et al*. (1993) demonstrated that production of large numbers of endemic South African freshwater *Sepedon* spp. predators could be achieved with relatively modest investment and non-specialised workers in laboratory rearings.

Successful long-distance transport

Sciomyzidae adults, eggs and pupae are very generally robust animals, with viable cultures being easily transported (eg the freshwater predator *Sepedomerus macropus* (Walker) from Nicaragua reared at Cornell University and shipped to the Department of Agriculture, Hawaii Chock *et al*. 1961). Knutson successfully carried many rearing containers of studies in progress on several species, 2–7 January 1964, from Harpenden, England, to Almeria, Spain, under less-than-ideal conditions.

Favourable recipient environment

Sciomyzidae exploit most freshwater and terrestrial snail habitats (eg Speight and Knutson 2012). Also, many species reproduce continuously at favourable temperatures, having several generations per year; many species have a broad north–south range which allows for selection of natural enemies from a range of climatic/environmental conditions.

Pest suppression

There have been no studies on Sciomyzidae (and few on gastropods) using the procedures and criteria proposed by Waage and Mills (1992), Kidd and Jervis (1997), or Jaenike (1998). Such studies – especially highlighting polyphagous parasitoids of Diptera – are essential.

Stability of pest suppression

Barker *et al.* (2004) commented extensively on the plethora of features of Sciomyzidae and their potential freshwater and terrestrial gastropod target prey. He noted that some research has been conducted on some aspects – this is a particularly important aspect of his analysis.

Minimal adverse impacts on biodiversity

While information on Sciomyzidae meets requirements 1–3, there is insufficient information concerning pest suppression (4) and pest suppression stability (5) and the impact of natural enemies (that attack sciomyzids?) on those aspects. Requirement 6 is discussed by Barker *et al*. (2004) and extensively by Knutson and Vala (2011). Barker *et al*. (2004) discussed the potential impact of Sciomyzidae on non-target gastropods in relation to four scenarios proposed by Hopper (1995). He concluded that no sciomyzid could be guaranteed to have no direct non-target effects (his scenario 1) and that many might have considerable impact on biodiversity (his scenario 4). However, with careful selection of sciomyzid species for introduction based on niche requirements and prey preferences, scenario 3 (some small but generally unpredictable mortality if the natural enemy also utilises one or more co-occurring species in addition to its normal hosts/prey) or even scenario 2 (no impact if the natural enemy utilises other hosts/prey but is temporally or spatially isolated from them) may be the expected outcome. The methods, protocols and facilities for testing the safety of introduced agents have improved greatly over the past few decades; if these are followed we can be assured of the safety of introduced agents (Knutson and Coulson 1997). Van Driesch and Hoddle (2017) further outline the possible direct and indirect impacts of introduced biological control agents. They list the following potential impacts: (1) direct attacks on native insects; (2) negative foodweb effects, such as competition for prey, apparent competition, or displacement of native species; (3) positive foodweb effects that benefit non-target species; (4) hybridisation of native species with introduced natural enemies; and (5) attacks on introduced weed biocontrol agents. All these need to be considered before Sciomyzidae are introduced as classical biological control agents of molluscs.

Barker emphasised the need for six kinds of information to estimate levels of gastropod mortality caused by the larvae, (1) the average level of predation or parasitism per host/prey generation, (2) its variability from generation to generation and whether or not this source of host/prey mortality is a key factor, (3) the extent to which predation or parasitism tends to act as a density-dependent factor, (4) other prey mortalities that combine with that caused by the sciomyzid larvae to counter the host/prey's potential rate of increase, (5) any important mortalities suffered by the sciomyzids that reduce their effectiveness, and (6) the density of searching sciomyzid adults.

Research needs for further understanding the impact of natural enemies in the use of Sciomyzidae as biocontrol agents

- Other than the publications on Trichogrammatidae (Juliano 1981, 1982), Diapriidae (Knutson and Berg 1963; O'Neill 1973) and parasitoids of *Anticheta melanosoma* (Knutson and Abercrombie 1977), there is essentially no quantitative data or information on populations of natural enemies of Sciomyzidae.

- The internal pathogens of adult and immature Sciomyzidae are essentially unknown; larvae, pupae and adults should be examined for pathogens, for example *Wolbachia* (Proteobacteria: Rickettsiales: Rickettsiaceae).
- An investigation of potential endosymbionts which are known to occur in other Diptera (eg Sciaridae) might also yield useful results.
- Review of museum collections of pinned adults such as Asilidae, Empididae, Scathophagidae and some predatory wasps holding adult prey will provide information on sciomyzid species that are preyed upon by such predators.
- The major advance in knowledge of parasitoid natural enemies of Sciomyzidae will come from further collecting immature stages in nature and holding them in the laboratory for the emergence of natural enemies. Methods for collecting larvae and puparia of Sciomyzidae are detailed by Knutson and Vala (2011). Larvae are held with food snails, until pupariation, in containers simulating the conditions where they were found. Puparia are held individually in vials with a slightly moist substrate until emergence of the parasitoids or adult flies. The hosts of many of these parasitoids could be identified, especially by study of the third-instar cephalopharyngeal skeleton and other larval vestiges, as well molecular methods such as DNA barcoding.
- Egg, larval and pupal parasitoids could be obtained by exposing laboratory-reared stages in small containers in the precise sciomyzid micro-habitats in nature, then retrieving and holding them for emergence of parasitoids. This technique was successfully used by O'Neill (1973), who obtained the new species *Trichopria atrichomelinae* (Diapriidae) from puparia of *Atrichomelina pubera* reared in the laboratory and exposed for seven days in *A. pubera* habitats.
- Laboratory tests of the host range of the more common, polyphagous parasitoids, including appropriate stages of potential sciomyzid biocontrol agents, should be carried out in areas where biological control projects are planned. Techniques as described in the 'Review of the literature' section above could be used to monitor natural enemy impact on sciomyzid biocontrol agents during such projects.
- Preliminary to introduction/augmentation of Sciomyzidae for biocontrol purposes, assessments of the impact of endemic parasitoids (especially polyphagous species) on Sciomyzidae should be made by rearing parasitoids from fly larvae/puparia found in dead snails and from eggs of insects in the target microhabitats, as described in our Section "Behavioural groups and microhabitats" - see above. Rearing of parasitoids from other Diptera in the biocontrol target area will help to reveal the potential extent of impacts of polyphagous parasitoids.
- A review of the super-parasites that attack parasitoids of Sciomyzidae is needed.

Notes

1. Taxon authorities for genera and species not included in Tables 5 or 6 are included at first mention in the text.
2. Pupariation is the formation of the puparium in cyclorrhaphous flies, which occurs many hours before that of the pupa. Formation of the pupa is termed pupation.

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