# The snail-killing flies of Alaska (Diptera: Sciomyzidae)

B. A. Foote

Department of Biological Sciences Kent State University, Kent, OH 44242 USA

> L. V. Knutson 4 Rue des Erables Clapiers 34830, France

> > J. B. Keiper

Department of Entomology University of California at Riverside Riverside, CA 92521, USA.

**Abstract:** Information is given on the geographic distribution, habitat preferences, larval foods, and immature stages for 57 species of 9 genera of Sciomyzidae known to occur in Alaska. An illustrated key to adults is included. Alaska as a habitat for sciomyzid flies is discussed, and information on feeding habits of the larvae is summarized.

# Introduction

Steyskal (1954) listed 30 species of Sciomyzidae from Alaska. In the summer of 1971, the senior author spent approximately four weeks in the southeastern, southcentral, and central areas of the state investigating the sciomyzid fauna. Additional records for the state have accumulated since 1971, and it is desirable to update our knowledge of the Alaskan Sciomyzidae. It is particularly timely now, as Alaska is undergoing rapid development and undoubtedly will lose many habitats currently supporting large and diverse sciomyzid populations.

This paper lists 57 species, in nine genera, of Sciomyzidae known to occur in Alaska, presents an illustrated key to the genera and species, gives general distributional information and specific Alaska records, and summarizes biological information for each species. A discussion of Alaska as an environment for Sciomyzidae is presented as well as a summary of the feeding habits of the larvae.

#### Physiography and Climate of Alaska

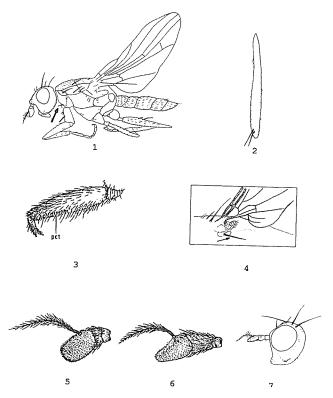
Occupying the great northwestern peninsula of the North American continent, Alaska is nearly 600,000 square miles in extent. It is highly diverse topographically, with 12 physiographic provinces recognized (Wahrhaftig, 1965). Much of Alaska is hilly or mountainous, although several low-lying plains, 32-160 km in width, also occur. The interior, bordered on the north and south by rugged mountain ranges, consists of a diverse mixture of low mountain masses, plains, and plateaus. North of this vast central area is the Brooks Range and several lesser ranges whose summits reach 1829-2438 m. Along the Arctic Ocean, the North Slope, a low-lying coastal plain, interdigitates with the Brooks Range through a zone of foothills. The mountain barrier lying south of the huge central region consists of a pair of ridges separated by disconnected lowland areas. The highest peaks of North America, rising to more than 6096 m, occur in the Alaskan Range of this region, and mountains reaching elevations of 2438-3658 m are common.

The physiographic features of Alaska have their counterparts farther south in western Canada and the United States (Fenneman, 1942). Almost the entire state is included in the North American Cordillera, a great mountainous area that forms the backbone of western America. The mountain ranges of southeastern Alaska are the topographical equivalents of the Coastal Ranges of British Columbia, Washington, and Oregon. The Alaska Range and the Aleutian Range correspond with the Cascade and Sierra Nevada Ranges. The relatively lowlying central area between the Alaska Range and the Brooks Range is comparable to the Basin and Range and Colorado Plateau Provinces. The northern mountain area, dominated by the Brooks Range,

is a continuation of the Rocky Mountain System. The North Slope is the northern extension of the Interior Plains, a second major physiographic realm of western North America.

Most of the mountain masses bordering the interior were extensively glaciated during the Pleistocene and many still support extensive icecaps and valley glaciers. In contrast, much of the central intermontane plateau area and the North Slope were never glaciated. The mountainous areas that were buried by icecaps consist today of blocklike groups of mountains having rounded summits that are separated from each other by a network of broad, steep-sided, U-shaped valleys. In contrast, mountain masses that rose above the icecaps are jagged and knife-like. Glaciated lowland areas consist of end and ground moraines, drumlins, kames, eskers, and glacial lake plains. Large lakes are present around the margins of the glaciated lowlands, and marshy situations and muskegs are abundant. Unglaciated lowlands are mostly broad silt plains bordering widely meandering streams. Thaw lakes and sinks are abundant. The topography of these lowlands has been largely determined by the deposition of material brought in from adjacent highlands (Wahrhaftig, 1965).

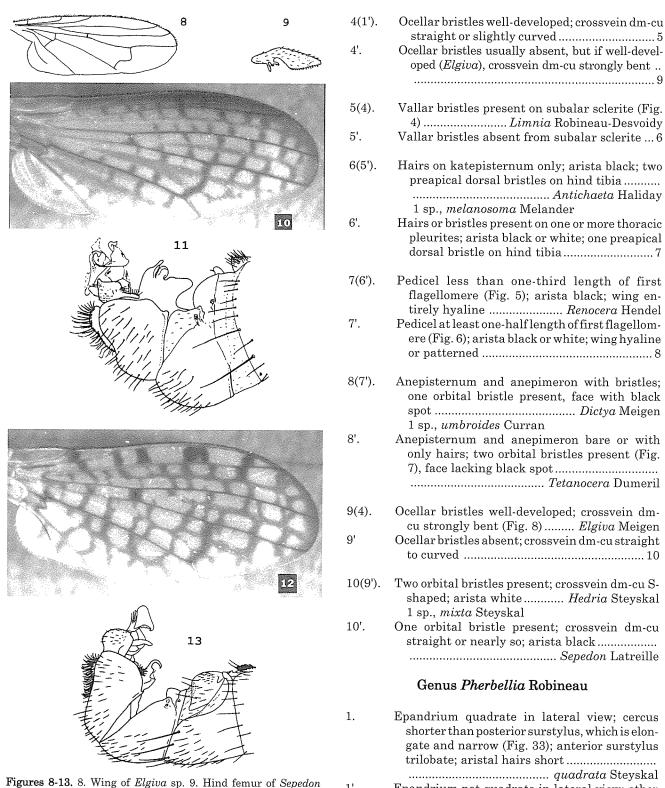
Climatically, Alaska is surprisingly diverse, with four climatic zones being recognized in the state (Hulten, 1968). The southern coastal areas, particularly in the Panhandle Region, are relatively mild and exhibit an oceanic climate. Inland areas have a modified continental climate that is transitional between the maritime and true continental types. The North Slope supports the fourth climatic zone, with an arctic weather pattern. The mean annual air temperature ranges from 2° to 4° C along the southern coast, from -2° to -35° C along the western coast, between -50° and -55° C on the North Slope, and temperatures can fall to -63° C in the interior. The mean daily temperature in July is around 13° C in the southern coastal areas, 7° C on the North Slope, and 16° C in the interior. The length of the frost free period ranges from 40 days in the lowlands bordering the Arctic Ocean and in the higher mountains, to around 60 days in the interior, and to over 200 days in the Panhandle Area. Annual precipitation can exceed 2500 mm in the Panhandle, ranges between 250 and 300 mm in the interior, and varies from 200 to 250 mm on the North Slope. There are some 240 rainy days annually along the southern coast, but only about 120 days with precipitation in the interior areas (Hulten, 1968).



Figures 1-7. 1. Habitus of *Sciomyza* sp. showing proepisternal bristle. 2. Fore tibia of *Sciomyza* sp. 3. Fore femur of *Pteromicra* sp. showing pecten (pct). 4. Wing base of *Limnia* sp. showing vallar bristles. 5. Antenna of *Renocera* sp. 6. Head of *Tetanocera* sp. 7. Head of *Tetanocera* sp., sinestral view. (1, modified from Foote, 1961; 2, modified from Steyskal *et al.*, 1978; 3, modified from Orth and Knutson, 1987; 4, modified from Rozko√ nΩ and Knutson, 1970; 5, modified from Steyskal, 1959; 6, modified from Vala and Brunel, 1987; 7, modified from Steyskal, 1961.) (Abbreviations appearing on figures: ap, process of posterior surstylus; as, anterior surstylus; b, protandrial sternite; ep, epandrium; ce, cercus; hy, hypandrium; pra, protandrium; ps, posterior surstylus; s6, spiracle of segment six; s7, spiracle of segment seven.)

#### Key to Alaskan Species

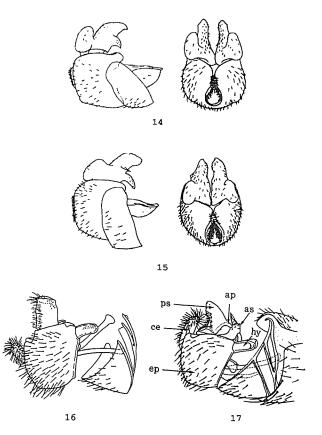
1.	Proepisternal bristle well-developed (Fig. 1) Sciomyzini
1'.	No proepisternal Bristle Tetanocerini 4
2(1).	Two preapical dorsal bristles on fore tibia (Fig. 2)
2',	One preapical dorsal bristle on fore tibia 3
3(2').	Frons and thorax shiny; row of anteromedial spinules on fore femur (Fig. 3)
3'.	Frons and thorax not shiny; anteromedial spinules absent from fore femur



anchista. 10. Wing of Limnia lindbergi. 11. Male genitalia of L. lindbergi. 13. Male genitalia of L. sandovalensis. 12. Wing of L. sandovalensis. (8, modified from Rosko  $n\Omega$ , 1966; 9, modified from Steyskal, 1966; 10, modified from Bratt et al., 1969; 11, modified from Steyskal, 1967; 12, modified from Orth, 1987; 13, modified from Rosko $\sqrt{n\Omega}$ , 1982.)

- shorter than posterior surstylus, which is elongate and narrow (Fig. 33); anterior surstylus trilobate; aristal hairs short ..... ...... quadrata Steyskal 1'. Epandrium not quadrate in lateral view; other characters variable ......2
- 2(1'). Anterior part of frons silvery or white pruinose, midfrontal stripe reaching approximately half-

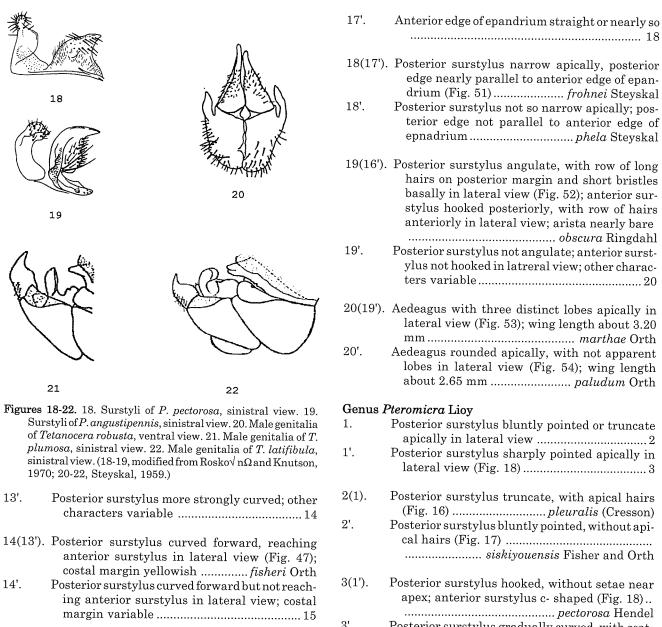
	way to anterior margin; aristal hairs short plumose; mesopleuron bare; gonostylus as in Fig. 34argyra Verbeke
2'.	Anterior part of frons not silvery or white pruinose; other characters variable
3(2').	Abdomen and thorax yellowish in color; anepisternum with short, black hairs along posterior border; posterior surstylus slightly curved in lateral view (Fig. 35)
3'	albocostata (Fallén) Abdomen and thorax dark; other characters variable4
4(3').	Midfrontal stripe extending more than half-way to anterior margin of frons5
4'.	Midfrontal stripe extending less than or equal to half-way to anterior margin of frons 7
5(4).	Wing darkly patterned with spots forming rows in cells schoenherri maculata (Cresson)
5'	Wing hyaline except for cross-vein infuscations
6(5').	Midfrontal stripe narrowly reaching anterior margin; mesonotum uniformly gray with faint longitudinal brown stripes; distal portion of vein M lacking stump vein; male genitalia as in Fig. 36
6'	Midfrontal stripe extending approximately 2/3 to anterior margin; mesonotum gray pruinose with brown longitudinal stripes; distal portion of vein M with stump vein on posterior side; male genitalia as in Fig. 3
7(4').	First posterior cell with three transverse dark bars (Fig. 38)nana (Fallén)
7'.	First posterior cell without dark transverse bars; wing hyaline except for cross-vein infuscation
8(7').	Posterior surstylus truncate in lateral view (Fig. 39); fore legs extensively black vitalis (Cresson)
8'	Posterior surstylus not truncate in lateral view; fore legs variable in color
9(8').	Posterior surstylus much broader basally than apically in lateral view10
9'.	Posterior surstylus only slightly broader basally than apically
10(9).	Third antennal segment dark yellow, elongate, and oval; coxa yellow with silver plumosity; front tibia black with some yellow basally; posterior surstylus as in Fig. 40
10'.	Not with above combination of characters 11



Figures 14-17. 14. Male genitalia of *Elgiva connexa*, ventral and sinistral views. 15. Male genitalia of *E. divisa*, ventral and sinistral views. 16. Male genitalia of *Pteromicra pleuralis*. 17. Male genitalia of *P. sishiyouensis*, sinistral view. (14, modified from Orth, 1983; 15, modified from Orth *et al.*, 1980; 16, modified from Steyskal, 1963.)

- 11(10'). Anterior margin of posterior surstylus angled near apex creating a narrow point in lateral view; setae present near apex (Fig. 41); ejaculatory apodeme notched apically (Fig. 42) ...... bryanti Steyskal
- 11'. Anterior margin of posterior surstylus nearly straight in lateral view; setae absent near apex (Fig. 43); ejaculatory apodeme without notch apically (Fig.44) .... propages Steyskal

- 13(12). Posterior surstylus slightly curved in lateral view (Fig. 45), subtriangular with apical ends overlapping or nearly so in posterior view (Fig. 46); arista relatively long plumose; fore femur and tibia usually dark brown; crossveins infuscated ...... griseola (Fallén)



15(14'). Anterior margin of posterior surstylus strongly

16(12'). Posterior surstylus pointed apically in lateral

17(16'). Anterior edge of epandrium with a short protru-

15'.

16'.

concave in lateral view (Fig. 48); cross-veins infuscated ..... griseicollis (Becker)

Anterior margin of posterior surstylus curved but not concave (Fig. 49); cross-veins infuscated, but darker than in griseicollis..... ...... hackmani Rozko√nΩ

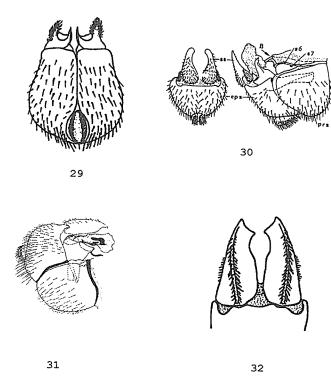
view .......17

sion; surstylus as in Fig. 50 ...... aloea Orth

Posterior surstylus rounded apically in lateral 

18(17').	Posterior surstylus narrow apically, posterior edge nearly parallel to anterior edge of epan-
18'.	drium (Fig. 51)
19(16').	Posterior surstylus angulate, with row of long hairs on posterior margin and short bristles basally in lateral view (Fig. 52); anterior surstylus hooked posteriorly, with row of hairs anteriorly in lateral view; arista nearly bare
19'.	Posterior surstylus not angulate; anterior surstylus not hooked in latreral view; other characters variable
20(19').	Aedeagus with three distinct lobes apically in lateral view (Fig. 53); wing length about 3.20
20'.	mm
Genus I	Pteromicra Lioy
1.	Posterior surstylus bluntly pointed or truncate
1'.	apically in lateral view
2(1).	Posterior surstylus truncate, with apical hairs (Fig. 16) pleuralis (Cresson)
2'.	Posterior surstylus bluntly pointed, without api- cal hairs (Fig. 17)siskiyouensis Fisher and Orth
	stantyouensis Pisher and Orth
3(1').	Posterior surstylus hooked, without setae near apex; anterior surstylus c- shaped (Fig. 18)
3'.	Posterior surstylus gradually curved, with scattered setae near apex; anterior surstylus broadest medially, not c-shaped (Fig. 19)
Genus $S$	ciomyza Fallén
	Mesopleuron with at least two strong bristles
	posteriorly in addition to numerous shorter bristly hairs; ventral half of pleura pruinose, dorsum of mesonotum grayish with dark stripes; fore femora usually entirely yellowsimplex Fallén
1'.	Mesopleuron with only a few short, fine hairs; ventral half of pleura not prunose, dorsum of mesonotum shining reddish-brown; fore femora usually blackened on at least apical half

Genus	Elgiva Meigen	1			
1.	Wing with apical dark spot in r <sub>2+3</sub> ; fore femur with well-developed bristles along distal half of ventral marginsolicita (Harris)				
1'.	Wing lacking apical dark spot in r <sub>2+3</sub> ; fore femur usually lacking well developed bristles along distal half of ventral margin2				
2(1').	Epandrium with ventral swelling on each side (Fig. 14) connexa (Steyskal)	23	3	24	25
2'.	Epandrium without ventral swellings (Fig. 15) divisa (Loew)		۸,	A.a.	(20)
O	Limnia Robineau-Desvoidy	11	J1		
1.	Costal margin of wing infuscated from R <sub>1</sub> to M <sub>1+2</sub> (Fig. 10); ventral process of hypandrium with posterior outline straight, broad basally, and suddenly constricted to large round apical hook (Fig. 11)		26		
1'.	Costal margin of wing usually infuscated only between $R_{2+3}$ and $M_{1+2}$ (Fig. 12); hypandrium hooked (Fig. 13)				
	sandovalensis Fisher and Orth				
	Renocera Hendel				THE THE WAY
1. 1'.	Two fronto-orbital bristles johnsoni Cresson Usually one fronto-orbital bristle; if an anterior bristle is present it is always distinctly small-			27	28
	er than posterior bristlebrevis (Cresson)				erteszi, sinistral view. 24. le genitalia of <i>T. montana</i> ,
Canne	Sepedon Latreille				lus of $T$ . rotundicornis. 27.
1.	Katatergite bare fuscipennis Loew				T. silvatica. 28. Posterior
1'.	Katatergite with numerous black hairs2	and anterior surstyle of <i>T. freyi.</i> (23-26, Steyskal, 1959; 27-28, modified from Vala and Brunel, 1987.)			
2(1')	Middle of face bare, only parafacies with black				
	hairs spinipes americana Steyskal	3(2').			dle femur with single
2'.	Middle of face with black hairs3			bristle near tip; scutellum somewhat flattene dorsally, with slight anterior ridge	
3(2).	Hind femur of male with deep indentation on	3'.			6
	ventral surface (Fig. 9), female without indenta- tion; abdomen brown, often with slight indica-	4(3).	Posterior :	surstylus hooke	ed in lateral view with
	tion of bluish color anchista Steyskal	1(0).	scattered hairs basally (Fig. 19); blackish or-		
3'.	Hind femur of both sexes without indentation on ventral surface; abdomen dark colored with		bitoante	ennal spot prese	ent; aristal hairs dense plumosa Loew
	distinct bluish reflection	4'.			ooked in lateral view;
	borealis Steyskal				d aristal hairs variable
Ganne	Tetanocera Dumeril		***************************************	•••••	
1.	Prosternum setose; epandrium asymmetrical in	5(4').			genitalia as in Fig. 22
	ventral view (Fig. 18) robusta Loew				latifibula Frey
1'.	Prosternum not setose; epandrium symmetrical in ventral view2	5'.			mm. Male genitalia as <i>kertezsi</i> Hendel
2(1').	Aristal hairs very short, broadest part of plu-	6(3').			dorsal bristle, opposite
	mosity much narrower than third antennal				ical anterodorsal bris- mosity long but sparse
2'.	segment brevisetosa Frey Aristal hairs long, broadest part of plumosity at				7
<b>-</b> .	least half as broad as width of third antennal	6'.	Hind fem	ur without post	terodorsal bristle; ari-
	segment3		stal plu	mosity variable	e8



Figures 29-32. 29. Male genitalia of *T. ferruginea*, ventral view. 30. Male genitalia of *T. plebeja*, ventral and sinistral views. 31. Male genitalia of *T. stricklandi*, sinistral view. 32. Posterior surstyli of *T. phyllophora*, ventral view. (29-32, modified from Steyskal, 1959.)

Posterior surstylus slightly curved apically with

7(6).

scattered hairs basally (Fig. 23); large species. wing 7.2 - 9.0 mm long ..... montana Day 7'. Posterior surstylus not curved apically and lacking hairs basally (Fig. 24); small species, wing 5.0 - 6.6 mm long ..... rotundicornis Loew 8(6'). Interfrontal stripe not sharply demarcated but consisting of broad, triangular, dully shining area anterior to ocelli; costal margin hyaline; crossveins margined with brown ..... ..... fuscinervis (Zetterstedt) 8'. Interfrontal stripe more or less parallel-sided; if stripe indistinct, then no dully shining area anterior to ocelli; wing variable ......9 9(8'). Anterior margin of frons slightly inflated, shining, and connecting interfrontal and parafrontal shining stripes ......10 9'. Anterior margin of frons dull......11 10(9). Posterior surstylus with an apical notch (Fig. 25) ..... silvatica Meigen 10' Posterior surstylus without an apical notch (Fig.

26) ..... freyi Stackelberg

- 11(9'). Midfrontal stripe narrow, ending well before anterior margin of frons or indistinct ....... 12
  11'. Midfrontal stripe well developed, extending to or nearly to anterior margin of frons ........ 13
- 12(11). Hairs of anterior front longer than diameter of ocellus; arista with long, loose, and sparse hairs; surstylus with thin, erect, mediobasal laminae (Fig. 27); fourth abdominal sternite lacking papilla ...... ferruginea Fallén

We list below the 57 species, in 9 genera, of Sciomyzidae presently known to occur in Alaska, but it is safe to assume that additional taxa will be recorded as collecting efforts continue.

In the listing of larval foods, prey records from nature are listed first, when available; records from laboratory rearings are then given in parentheses.

Abbreviations used in the list are given below.

E: Egg

L: Larva;  $L_1 = first instar$ ,  $L_2 = second instar$ ,  $L_3$ 

= third instar

P: Puparium

CNC: Canadian National Collection

CU: Cornell University

FSCA: Florida State Collection of Arthropods

ISU: Iowa State University
KSU: Kent State University
MSU: Michigan State University
OSU: Ohio State University

UCD: University of California at Davis

UK: University of Kansas

UMA: University of MassachusettsUSNM: United State National MuseumWSU: Washington State University

#### Tribe Sciomyzini

#### Pherbellia Robineau-Desvoidy

1. Pherbellia albocostata (Fallén)

Distribution: Holarctic. In the Nearctic Region, from western Alaska to Newfoundland southward to southern Colorado and New England (map: Bratt et al. 1969, fig. 179).

Alaskan Records (fig. 55): Anchorage, VII-21-1921, J. M. Aldrich (USNM); Holy Cross, Lower Yukon River (Steyskal 1954, p. 55); Valdez Glacier Campground #2, VII-31-1971, BAF (KSU); mile 10, Haines Highway, VIII-6-1971, BAF (KSU); Chilkoot Campground, 15.7 km south Haines, VII-13-1971, BAF (KSU); Moon Lake, 24 km west Tok, VII-15-1971, BAF (KSU).

Biology, immature stages: Bratt et al. 1969 (E,  $L_1$ . ,, P).

Habitat: Mesic deciduous and coniferous woodlands.

Larval food: Terrestrial snails; Discus rotundatus (Muller), Balea, Cochlicopa, Discus, Euconulus, Retinella, Zonitoides).

#### 2. Pherbellia aloea Orth

Distribution: Nearctic. Southern Alaska to Yukon and southward to Washington and Idaho (map: Orth 1983, fig. 7).

Alaskan Records (fig. 55): Anchorage, VII-1960, M. R. Wheeler (Orth 1987).

Biology, immature stages: Unknown.

Habitat: Unknown.

Larval food: Unknown

# 3. Pherbellia anubis Knutson

**Distribution:** Nearctic. Northern Alaska to western New Brunswick, southward to Montana, central Michigan and northern New York (map: Bratt *et al.* 1969, fig. 169).

Alaskan Records (fig. 55): Umiat (Bratt et al. 1969, p. 32).

Biology, immature stages: Bratt et al. 1969 (E, L<sub>1</sub>, P).

**Habitat:** Open to partly shaded *Carex* marshes, marshy borders of permanent ponds.

Larval food: Shoreline and stranded aquatic snails; (Aplexa, Australorbis, Gyraulus, Helisoma, Lymnaea, Physa, Planorbula, Zonitoides, Discus).

#### 4. Pherbellia argyra Verbeke

Distribution: Holarctic. In North America, from western Alaska to eastern Massachusetts, southward to western Nevada and northern Illinois (map: Bratt et al. 1969, fig. 175).

Alaskan Records (fig. 56): Unalakleet (Bratt et al. 1969, p. 64); Matanuska; Nenana, VI-28-2921, J. M. Aldrich (USNM); Fairbanks, VII-1-1921, J. M. Aldrich (USNM); Mile 1316.5 Alaskan Highway, VI-25-1954, R. Coleman (USNM); Goldstream River Valley, 13.6 km north Fairbanks, VII-28-1971, BAF (KSU); 32 km east Fairbanks, VII-28-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Bratt *et al.* 1969 (E,  $L_{1.}$  3, P).

Habitat: Marshy borders of permanent ponds and lakes, rush and sedge marshes and other aquatic situations, particularly those in which water levels drop as summer progresses. Larvae were found in *Lymnaea* snails that had been stranded in a drying roadside ditch in the Goldstream River valley a few kilometers north of Fairbanks.





33

Figures 33-34. 33. Male genitalia of *Pherbellia quadrata*, sinistral view. 34. Gonostylus of *P. argyra*, sinistral view. (33, modified from Steyskal, 1961.)

Larval food: Stranded aquatic snails; Aplexa hypnorum L., Lymnaea sp. Planorbis planorbis (L.), (Aplexa, Australorbis, Lymnaea, Helisoma, Physa, Planorbula, Planorbis). Laboratory-reared larvae also attacked terrestrial snails of the genera Clausilia, Cochlicopa, Discus, Euconulus, Helix, Hygromia, Oxychilus, and Zonitoides.

# 5. Pherbellia bryanti Steyskal

**Distribution:** Nearctic. Known only from Saskatchewan, Alberta, Northwest Territories, and Alaska.

Alaskan Records (fig. 56): Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Unknown.

Habitat: Equisetum - Eleocharis marshes.

Larval food: Unknown.

# 6. Pherbellia fisheri Orth

**Distribution:** Nearctic. Northern Alaska to Manitoba and southward to southern Alberta (map: Orth 1987, fig. 8).

Alaskan Records (fig. 56): Umiat, VII-03-1959, J. E. H. Martin (Orth 1987).

Biology, immature stages: Unknown.

Habitat: Unknown.

Larval food: Unknown.

#### 7. Pherbellia frohnei Steyskal

**Distribution:** Nearctic. Known only from southwestern Alaska.

Alaskan Records (fig. 57): Naknek (Steyskal 1963, p. 114); King Salmon, Naknek River, VII-06-1952, W. R. Mason (CU); Unalakleet, VII-10-1962, B. S. Heming (CU).

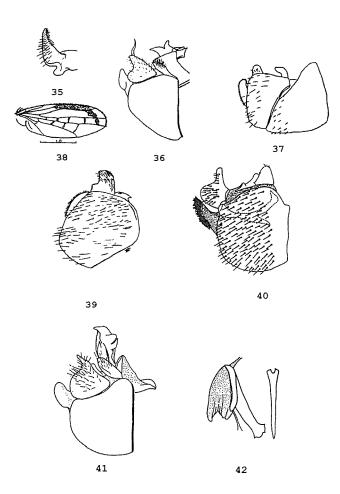
Biology, immature stages: Unknown.

Habitat: Unknown.

Larval food: Unknown.

# 8. Pherbellia griseicollis (Becker)

Distribution: Holarctic. In the Nearctic Region, known only from northern Alaska (map: Orth 1987, fig. 8).



Figures 35-42. 35. Posterior surstylus of P. albocostata, sinistral view. 36. Male genitalia of P. prefixa, sinistral view. 37. Male genitalia of P. tenuipes, sinistral view. 38. Wing of P. nana (bar = 1.0 mm). 39. Male genitalia of P. vitalis, sinistral view. 40. Male genitalia of P. anubis, sinistral view. 41. Male genitalia of P. bryanti, sinistral view. 42. Ejaculatory apodeme of P. bryanti. (35, modified from Rosko $\sqrt{n\Omega}$ , 1966; 36, modified from Steyskal, 1966; 40, modified from Bratt et al., 1969; 41-42, modified from Steyskal, 1967.)

Alaskan Records (fig. 57): Prudhoe Bay, VI-08, VI-20-, VII-4-1971, M. Deyrup (USNM); Umiat, VIII-07-1959, R. Madge; Circle, VII-26-1971, BAF (Orth 1987).

Biology, immature stages: Knutson 1987. Habitat: Open sedge marshes.

Larval food: Aquatic pulmonate snails that have been stranded by dropping water levels (*Helisoma trivolvis*, *Lymnaea palustris*).

9. Pherbellia griseola (Fallén)

Distribution: Holarctic. In North America, from southern Alaska to eastern Labrador, southward to California, northern Ohio, and central New York (map: Bratt et al. 1969, fig. 177, 178).

Alaskan Records (fig. 57): Anchorage, Big Delta (Bratt et al. 1969, p. 67); Eagle River Flats near Anchorage, V-9-1948, F. S. Blanton (USNM); Matanuska, IV-29-, V-10-, V-31-1944, J. C. Chamberlin (USNM); Otter Lake near Anchorage, V-29-1948, R. I. Sailer (USNM); Fairbanks, VII-2-1921, J. M. Aldrich (USNM); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); Shaw Creek, mile 289 on Richardson Highway, W. R. M. Mason and J. R. McGillis (CNC).

Biology, immature stages: Bratt *et al.* 1969 (E,  $L_{1.}$  3, P.).

Habitat: Open or shaded marshy borders of permanent or vernal ponds, sedge and rush marshes, and vernal woodland pools. Particularly abundant in aquatic habitats in which the water level drops as summer progresses.

Larval food: Shoreline and stranded aquatic snails; Lymnaea palustris (Muller), (Australorbis, Helisoma, Lymnaea humilus Say, L. sp., Oxyloma, Physa, Pomacea, Succinea).

10. Pherbellia hackmani Rozko $\sqrt{n\Omega}$ 

Distribution: Holarctic. In the Nearctic Region, this species is known only from northern Alaska and the Northwest Territories (map: Orth 1987, fig. 8).

Alaskan Records (fig. 58): Cape Thompson, VI-10-1960, W. C. Hanson; Cape Thompson, Crowbill Mountain, VI-06-1960, W. C. Hanson; Gulkana, Paxton Lodge, VIII-04-1951, W. R. M. Mason; Isabella Pass, mile 206 on Richardson Highway, 2900 ft., VII-17, 1962, P. J. Skitsko: Isabella Pass, Summit Lake, VII-09-1951, P. J. Skitsko; Isabella Pass, Summit Lake, VIII-03-1951, Mason-McGillis; King Salmon, Naknek River, VII-09-1952, J. B. Hartley, VII-13-1952, VIII-04-1952, W. R. Mason; Kotzebue, VI-24-1951, R. I. Sailer; Nome, VII-09-1951, D. P. Williams; Umiat, VI-10-1951, C. Smith, VII-03-1959, VII-10-1959, J. E. H. Martin, VII-10-1959, VII-23-1959, VIII-03- 1959, VIII-07-1959, VIII-12-1959, R. Madge; Unalakleet, VI-11-1961, VI-18-1961, R. Madge (Orth 1987).

Biology, immature stages: Unknown.

Habitat: Unknown. Larval food: Unknown.

11. Pherbellia marthae Orth

Distribution: Nearctic. Recorded from Alaska and western Canada south to Montana and North Dakota (map: Orth 1982, fig. 33).

Alaskan Records (fig.58): Fairbanks, VI-07-1971, R. Sailer; Goldstream River Valley 13.6 km north of Fairbanks, VII-29-1971, B. A. Foote; Wonder Lake, McKinley National Park, VII-25-1965, D. Chant (Orth 1982).

Biology, immature stages: Unknown.

Habitat: Unknown.

Larval food: Unknown.

12. Pherbellia nana (Fallén)

Distribution: Holarctic. Ranges in the Nearctic Region from western Alaska, southward to central Mexico and southern Florida and eastward to eastern Quebec (map: Bratt *et al.* 1969, fig. 176, 182).

Alaskan Records (fig. 58): Anchorage, Matanuska Valley, mile 154 on Glenn Highway (Steyskal 1954, p. 56); Cape Thompson, Unalakleet (Bratt et al. 1969, p. 70); Fish Creek flats near Anchorage, VII-27-1948, R. I. Sailer (USNM); mile 10, Haines Highway, VIII-6-1971, BAF (KSU); Fairbanks, VII-02-1921, J. M. Aldrich (USNM); Goldstream River Valley 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); Circle, VIII-26-1971, BAF (KSU).

Biology, immature stages: Bratt *et al.* 1969 (E,  $L_1$ . 3, P.).

Habitat: Lake margins, open marshes, vernal ponds, and swampy woods.

Larval food: Shoreline and stranded aquatic snails; Lymnaea palustris, L. humilis, Gyraulus parvus, Physa sp., (Aplexa, Australorbis, Eulota, Gyraulus, Helicella, Hygromia, Lymnaea, Planorbis, Physa, Segmentina, Succinea).

13. Pherbellia obscura (Ringdahl)

Distribution: Holarctic. Recorded in the Nearctic Region from eastern Alaska and northern Yukon Territory, eastward to Ontario and Quebec and southward to Alberta (map: Bratt et al. 1969, fig. 169).

Alaskan Records (fig. 59): Naknek (Bratt et al. 1969, p. 73); Anchorage, VII-1-1921, J. M. Aldrich (USNM), VI-13-1921, J. M. Aldrich (USNM), VI-8-1948, C. O. Esselbaugh (USNM), V-28-1948, F. S. Blanton (USNM); Ft. Richardson near Anchorage, V-25-1948, E. Lepage (USNM); mile 173, Glenn Highway, V-27-1951, R. I. Sailer (USNM); Fairbanks, VII-1-1921, J. M. Aldrich (USNM); Matanuska, V-25-1944, V-18-, V-21-IX-13-1945, J. C. Chamberlin (USNM); Palmer, V-1-1951, R. H. Washburn (USNM); Circle, VII-26-1971, BAF (KSU).

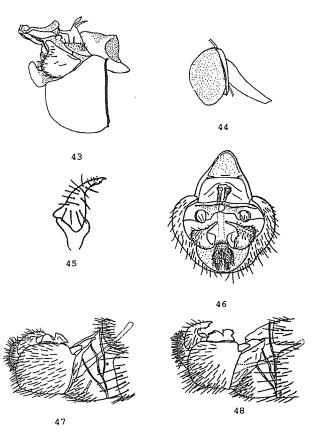
Biology, immature stages: Unknown. Biological information supplied for *P. obscura* by Bratt *et al.* 1969 must be assigned to *P. subtilis* Orth and Steyskal (Orth et al. 1980).

**Habitat:** Muddy shores of lakes, grassy borders of sluggish streams, unshaded seepage areas.

Larval food: Shoreline snails: Lymnaea humilis, (Lymnaea, Oxyloma).

14. Pherbellia paludum Orth

Distribution: Nearctic. Transcontinental in Canada and the northern United States (map: Orth 1982, fig. 33).



Figures 43-48. 43. Male genitalia of *P. propages*, sinistral view. 44. Ejaculatory apodeme of *P. propages*. 45. Posterior surstylus of *P. griseola*. 46. Male genitalia of *P. griseola*, ventral view. 47. Male genitalia of *P. fisheri*, sinistral view. 48. Male genitalia of *P. griseicollis*, sinistral view. (43-44, modified from Steyskal, 1967; 45-46, modified from Rozko√nΩ, 1966; 47-48, modified from Orth, 1987.)

Alaskan Records (fig. 59): Fort Richardson, Eagle River Flats, V-25-1948, E. Lepage; Matanuska, VIII-14-1952, C. O. Berg (Orth 1982).

Biology, immature stages: Unknown.

Habitat: Unknown. Larval food: Unkown.

15. Pherbellia phela Steyskal

Distribution: Nearctic. Recorded only from south central Alaska, Northwest Territories, and northwestern Montana.

Alaskan Records (fig. 59): Eagle River Flats near Anchorage, Matanuska, Tonsina (Steyskal 1963, p. 116); Nome, VI-21-1951, D. P. Williams (CU).

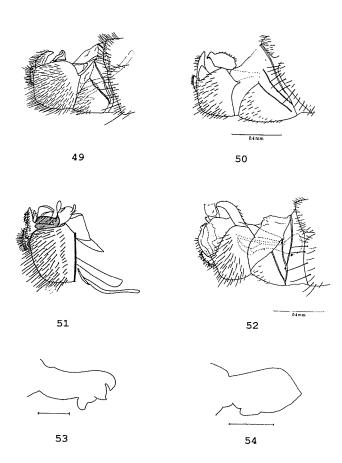
Biology, immature stages: Unknown.

Habitat: Unshaded grass-sedge-rush marshes in which water levels drop as summer advances.

Larval food: Unknown.

16. Pherbellia prefixa Steyskal

**Distribution:** Nearctic. Western Alaska to southern Idaho and western Montana.



Figures 49-54. 49. Male genitalia of P. hackmani, sinistral view. 50. Male genitalia of P. aloea, sinistral view. 51. Male genitalia of P. frohnei, sinistral view. 52. Male genitalia of P. obscura, sinistral view. 53. Apex of aedeagus of P. marthae (bar = 1.0 mm), 54. Apex of aedeagus of P. paludum (bar = 1.0 mm). (49, modified from Rosko $\sqrt{n}\Omega$ , 1982; 50, modified from Orth et al., 1980; 51, modified from Steyskal, 1963; 52, modified from Orth et al., 1980; 53-54, modified from Orth, 1982.

Alaskan Records (fig. 60): Lower Yukon River, (Steyskal 1966, p. 37), Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); 32 km east Fairbanks, VII-28-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Foote, 1973.

Habitat: Unshaded sedge marshes.

Larval food: Parasitoid on stranded aquatic operculate snails; *Valvata sincera* Say.

17. Pherbellia propages Steyskal

Distribution: Nearctic. Southern Alaska and MacKenzie Delta, eastward to northeastern Quebec and southward to northern California, southern Idaho, northern Ohio, and northern New York (map: Bratt et al. 1969, fig. 170).

Alaskan Records (fig. 60): Matanuska Valley (Steyskal 1966, p. 37); Ft. Richardson on Eagle River Flats near Anchorage, V-25-1948, E. Lep-

age (USNM); Fairbanks, VI-07-1948 (USNM); Meander Lake, Mt. McKinley National Park, VII-23-1965, D. Chant (USNM); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU).

Biology, immature stages: Bratt et al. 1969 (E,  $L_3$ ,).

**Habitat:** Wet tundra, open *Equisetum* and grass-sedge-rush meadows in which water levels drop as summer advances.

Larval food: Stranded aquatic snails; (Gyraulus, Helisoma, Lymnaea, Planorbula). Laboratory-reared larvae completed development only on species of Lymnaea.

18. Pherbellia quadrata Steyskal

Distribution: Nearctic. Central Alaska southward and eastward to southern Idaho, southern Quebec, and southcentral New York (map: Bratt et al. 1969, fig. 173).

Alaskan Records (fig. 60): Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU).

Biology, immature stages: Bratt et al. 1969 (E, L<sub>1</sub>., P).

**Habitat:** Open marshes, partially shaded borders of marshy streams, and lowland woods containing vernal pools.

Larval food: Stranded aquatic snails; Lymnaea palustris, (Aplexa, Australorbis, Helisoma, Lymnaea, Physa, Planorbula).

19. Pherbellia schoenherri maculata (Cresson) Distribution: Nearctic. Western Alaska and the MacKenzie Delta to eastern Newfoundland, southward to central California, northern Ohio, and southeastern Massachusetts (map: Bratt et al. 1969, fig. 171).

Alaskan Records (fig. 61): Anchorage: Matanuska Valley: Fairbanks; Healy; Lower Yukon River; Mile 16 on Palmer Highway (Steyskal 1954, p. 56); Russian Mission, Unalakleet (Bratt et al. 1969, p. 44); Tonsina, V-18-1954, (WSU); mile 15, Haines Highway, VII-14-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Bratt *et al.* 1969 (E, L<sub>1</sub>. , P).

**Habitat:** Relatively dry *Equisetum*, sedge-grass-rush marshes containing large populations of succineid snails.

Larval food: Hygrophilous succineid snails; Oxyloma retusa Lea, (Catinella, Oxyloma, Succinea)

20. Pherbellia tenuipes (Loew)

Distribution: Nearctic. Alaska to Maine, southward to British Columbia, South Dakota, Michigan, and Virginia.

Alaskan Records (fig. 61): Anchorage, VII-20-1948, G. E. Nielsen (USNM); College, D. D. Miller (M. Wheeler).

Biology, immature stages: Unknown

Habitat: Mesic coniferous-deciduous forests, shaded seepage areas and roadside ditches.

Larval food: Unknown.

21. Pherbellia vitalis (Cresson)

Distribution: Nearctic. Western Alaska, Mackenzie Delta to northern Quebec and eastern Massachusetts, southward to southern California, New Mexico and southern New Jersey (map: Bratt et al. 1969, fig. 174).

Alaskan Records (fig. 61): Russian Mission; Unalakleet (Bratt et al 1969, p. 57); Bethel (M. Wheeler); Fairbanks, VII-2-1921, J. M. Aldrich (USNM); Big Delta, VII-03-1951, W. R. M. Mason and J. R. McGillis (CNC).

Biology, immature stages: Bratt et al. 1969 (E, L<sub>1.</sub> P.).

Habitat: Open shoreline or marshy situations in which water levels drop as summer progresses.

Larval food: Helisoma trivolvis (Say), L. humilis, Physa sp., Planorbula armigera (Say), P. jenksii (Carpenter), (Helisoma, Lymnaea, Oxyloma, Physa, Planorbula, Succinea).

# Pteromicra Lioy

22. Pteromicra angustipennis (Staeger)

Distribution: Holarctic. Recorded in North America only from Alaska, British Columbia, Alberta, and Manitoba

Alaskan Records (fig. 62): Popoff Island; Amchitka Island (Knutson 1970, p. 249).

Biology, immature stages: Rozko $\sqrt{n\Omega}$  and Knutson 1970 (E, L<sub>1.3</sub>, P).

Habitat: Vernal ponds and woodland pools having marshy borders.

Larval food: Shoreline and stranded aquatic snails; (Aplexa, Australorbis, Gyraulus, Helisoma, Lymnaea, Physa, Planorbis, Segmentina, Succinea).

23. Pteromicra pectorosa (Hendel)

Distribution: Holarctic. In North America, from western Alaska, to Quebec and New York, and southward to California and Montana.

Alaskan Records (fig. 62): Cape Thompson (Rozko $\sqrt{n\Omega}$  and Knutson 1970, p. 1439); 32 km east Fairbanks. VII-28-1971, BAF (KSU).

Biology, immature stages: Rozko $\sqrt{n\Omega}$  and Knutson 1970 (E, L<sub>1,3</sub>, P).

Habitat: Vernal ponds and woodland pools having marshy borders.

Larval food: Shoreline and stranded aquatic snails; (Aplexa, Australorbis, Gyraulus, Helisoma, Lymnaea, Physa, Planorbis, Segmentina, Succinea).

24. Pteromicra pleuralis (Cresson)

**Distribution:** Nearctic. Ranges from southcentral Alaska to eastern Canada and south to Wyoming and Pennsylvania.

Alaskan Records (fig. 62): Mile 289, Richardson Highway (Fisher and Orth 1966).

Biology, immature stages: Parasitoid on pulmonate aquatic and hygrophilous snails stranded by dropping water levels.

**Habitat:** Unshaded marshes and marshy borders of lakes in which water levels drop as summer progresses.

Larval food: Wide variety of pulmonate aquatic snails.

25. Pteromicra siskiyouensis Fisher and Orth

Distribution: Nearctic. Alaska to northern California and east to western Alberta and Wyoming (map, Knutson 1970, fig. 1).

Alaskan Records (fig. 63): mile 10, Haines Highway, VIII-06-1971, BAF (KSU).

Biology, immature stages: Parasitoid on hygrophilous and stranded pumonate aquatic snails.

Habitat: Open marshes, woodland ponds, and marshy margins of shallow lakes in which water levels fluctuate.

Larval food: Wide variety of pulmonate aquatic

# Sciomyza Fallén

26. Sciomyza dryomyzina Zetterstedt

Distribution: Holarctic. In North America, from southcentral Alaska to Newfoundland, southward to central Idaho and northwestern Montana.

Alaskan Records (fig. 63): Mantanuska Valley, mile 16, Palmer Highway (Steyskal 1954, p. 57); mile 10, Haines Highway, VIII-06-1971, BAF (KSU).

Biology, immature stages: Berg 1953, Foote 1959 (P), Knutson 1987.

Habitat: Unshaded *Equisetum*, sedge, and rush marshes.

Larval food: Hygrophilous succineid snails: Oxyloma decampi gouldi (Tryon), (Oxyloma).

27. Sciomyza simplex Fallén

**Distribution:** Holarctic. In North America from Alaska to Manitoba and Michigan, southward to California and Idaho.

Alaskan Records (fig. 63): Kotzebue; Matanuska Valley (Steyskal 1954, p. 58); Silver Fox, VIII-5-1945 (USNM); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU); Umiat, VII-15-1959, J. E. H. Martin (CNC); Unalakleet, VIII-07-1961, B. S. Heming (CNC).

Biology, immature stages: Predator of exposed aquatic and shoreline snails. Foote 1959 (E,  $L_3$ , P).

Habitat: Open sedge-grass marshes, unshaded margins of small ponds and lakes.

Larval food: Lymnaea palustris, Oxyloma sp., (Bathyomphalus, Helix, Lymnaea, Oxyloma, Physa, Retinella).

#### Tribe Tetanocerini

# Antichaeta Haliday

28. Antichaeta melanosoma Melander

**Distribution:** Nearctic. Alaska east to Quebec and south to Utah and New Jersey (map: Knutson and Abercrombie 1977, fig. 1).

Alaskan Records (fig. 64): Shaw Creek, mile 289, Richardson Highway, VII-11-1951, W. R. M. Mason and J. R. McGillis (CNC); west of Fairbanks; Umiat (Knutson and Abercrombie 1977).

Biology, immature stages: Knutson and Abercrombie 1977.

Habitat: Shaded and unshaded wetlands in which water levels drop as summer progresses.

Larval food: Eggs of pulmonate aquatic snail Aplexa hypnorum.

# Dictya Meigen

29. Dictya umbroides Curran

**Distribution:** Nearctic. Alaska to Newfoundland, southward to New Mexico and Michigan (map: Valley and Berg 1977, fig. 48).

Alaskan Records (fig. 64): Matanuska Valley (Steyskal 1954, p. 58); Haines, VII-17-1954, W. C. Frohne (WSU); Amura Lake, Kodiak Island, VI-23-25-1962, G. E. Ball (USNM); mile 19, Haines Highway, VII-30-1971, BAF (KSU); 32 km west Glenallen, VII-16-1971, BAF (KSU); Robe Lake near Valdez, VII-3-1971, BAF (KSU); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU).

Biology, immature stages: Berg 1953, Valley and Berg 1977 (E,  $L_{1.3}$ , P).

Habitat: Wide variety of marshy freshwater situations.

Larval food: Pulmonate aquatic snails (Aplexa, Biomphalaria, Gyraulus, Helisoma, Lymnaea, Physa).

#### Elgiva Meigen

30. Elgiva connexa (Steyskal)

Distribution: Nearctic. Western Alaska to Ontario, southward to California, Colorado, and North Dakota (map: Orth and Knutson 1987, fig. 17).

Alaskan Records (fig. 64): Anchorage; Matanuska Valley; Holy Cross on the Lower Yukon River; Tanana (Steyskal 1954, p. 60); Tonsina (Orth and Knutson 1987, p. 832); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); 32 km east Fairbanks, VII-28-1971; BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Knutson and Berg 1964 (E, L<sub>1.3</sub>, P).

Habitat: Open marshes, margins of ponds and shallow lakes.

Larval food: Pulmonate aquatic snails; (Australorbis, Gyraulus, Helisoma, Lymnaea, Physa).

31. Elgiva divisa (Loew)

Distribution: Holarctic. In North America recorded from northwestern Canada (Yukon, Northwest Territories) and Alaska (Map: Orth and Knutson 1987, fig. 17)

Alaskan Records (fig. 65): Beaver Mts., VI-31-1920, A. H. Twitchell (CNC); Prudhoe Bay, VIII-06-1971, M. Deyrup (CU); Umiat, VII-12-1950, R. Madge (CNC), VII-10-1950, J. E. H. Martin (CNC).

Biology, immature stages: Unknown.

Habitat: Unknown.

Larval food: Unknown.

32. Elgiva solicita (Harris)

Distribution: Holarctic. In North America, from northwestern Alaska to Newfoundland, southward to California, Colorado, and Virginia (map: Orth and Knutson 1987, fig. 16).

Alaskan Records (fig. 65): Anchorage; Matanuska Valley; Holy Cross on the Lower Yukon River; Kotzebue; Nenana; Tanana (Steyskal 1954, p. 63); Tonsina, V-18-1957, W. C. Frohne (USNM); near Teklanika campground, Mt. McKinley Nat. Park, G. W. Byers (UK); mile 10, Haines Highway, VIII-06-1971, BAF (KSU); 32 km west Glenallen, VII-16-1971, BAF (KSU); Goldstream River Valley, 13.6 km north Fairbanks, VII-28-1971, BAF (KSU); 32 km east Fairbanks, VII-28-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Berg 1953; Hennig 1952 (L); Smith (1959) (P); Knutson and Berg (1964) (E, L<sub>1,2</sub>, P).

Habitat: Wide variety of freshwater situations, including open and partly shaded marshes, margins of ponds and lakes, and woodland pools.

Larval food: Pulmonate aquatic snails; (Australorbis, Gyraulus, Helisoma, Lymnaea, Physa, Planorbis).

#### Hedria Steyskal

33. Hedria mixta Steyskal

Distribution: Nearctic. Central Alaska to Maine, southward to Montana and southern Michigan (map: Foote 1971, fig. 25).

Alaskan Records (fig. 65): Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Foote 1971 (E,  $L_{1-3}$ , P).

Habitat: Open sedge marshes, *Equisetum* meadows near sloughs.

Larval food: Submerged non-operculate, aquatic snails; (Aplexa, Gyraulus, Helisoma, Lymnaea, Physa, Planorbula).

# Limnia Robineau-Desvoidy

34. Limnia lindbergi Steyskal

**Distribution:** Nearctic. Alaska to Newfoundland, south to Colorado and New York (map: Steyskal *et al.* 1978, map 4).

Alaskan Records (fig. 66): Big Delta (Steyskal *et al.* 1978, p. 20).

Biology, immature stages: Unknown.

Habitat: Marshy borders of lakes and ponds.

Larval food: Unknown.

35. Limnia sandovalensis Fisher and Orth

Distribution: Nearctic. Alaska to Newfoundland, south to New Mexico, Ohio, and District of Columbia (map: Steyskal *et al.* 1978, map 7).

Alaskan Records (fig. 66): Holy Cross on the Lower Yukon River, Matanuska Valley (Steyskal 1954, p. 64, as *L. boscii* Robineau-Desvoidy); Anchorage; Big Delta; Matanuska (Steyskal *et al.* 1978, p. 28); mile 15, Haines Highway, VII-14-1971, BAF (KSU); mile 150, Richardson Highway, VII-30-1971, BAF (KSU); Circle, VI-26-1971, BAF (KSU).

Biology, immature stages: Unknown.

Habitat: Marshy borders of lakes and ponds.

Larval food: Unknown.

#### Renocera Hendel

36. Renocera brevis (Cresson)

Distribution: Nearctic. Alaska to Newfoundland, southward to California, New Mexico, and Pennsylvania. (map: Foote 1976, fig. 1).

Alaskan Records (fig. 66): Matanuska Valley (Steyskal 1954, p. 64, as *R. bergi*)

Biology, immature stages: Foote and Knutson 1970, Foote 1976.

**Habitat:** Open and partly shaded sedge and cattail marshes, marshy borders of shallow ponds and lakes.

Larval food: Fingernail clams of the family Sphaeriidae; (Sphaerium, Musculium, Pisidium).

37. Renocera johnsoni Cresson

**Distribution:** Nearctic. Alaska to Newfoundland, southward to Idaho, Colorado, and Massachusetts. (map: Foote 1976, fig. 1).

Alaskan Records (fig. 66): Fairbanks; Matanuska Valley (Steyskal 1954, p. 65); Summit Lake on Isabella Pass, VIII-3-1951, W. R. M. Mason (CNC); Igloock, VI-24-1954, W. C. Frohne (CU); Northway Airport, VI-25-1954, R. Coleman (USNM); 32 km east Fairbanks, VII-28-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Unknown. In contrast to other species of *Renocera*, larvae of *R*.

*johnsoni* will not attack fingernail clams (Foote 1976).

**Habitat:** Drying roadside drainage ditches, vernal grass-sedge marshes, marshy borders of sluggish streams.

Larval food: Unknown.

# Sepedon Latreille

38. Sepedon anchista Steyskal

Distribution: Nearctic. Central Alaska to Maine, southward to Montana and southern Michigan.

Alaskan Records (fig. 67): Circle, VII-26-1971, BAF (KSU), Goldstream River Valley, 13.6 km north of Fairbanks, VII-29-1971, BAF (KSU).

Biology, immature stages: Neff and Berg (1966) (E, L<sub>1.3</sub>, P).

Habitat: Open marshes, roadside drainage ditches, marshy borders of small lakes.

Larval food: Pulmonate aquatic snails; (Australorbis, Helisoma, Physa).

39. Sepedon borealis Steyskal

Distribution: Nearctic. Southern Alaska to Newfoundland, southward to California, Colorado, and North Carolina (map: Neff and Berg 1966, map F).

Alaskan Records (fig. 67): Matanuska, mile 16 on the Palmer Highway (Steyskal 1954, p. 66).

Biology, immature stages: Neff and Berg 1966 (E, L<sub>1,3</sub>, P).

**Habitat:** Open and partly shaded sedge marshes, roadside drainage ditches, borders of ponds and shallow lakes.

Larval food: Pulmonate aquatic snails; (Australorbis, Helisoma, Lymnaea, Physa).

40. Sepedon fuscipennis nobilis Orth

Distribution: Nearctic. Central Alaska to Newfoundland southward to southern Oregon, Texas and Florida (map: Neff and Berg 1966, map R)

Alaskan Records (fig. 67): Matanuska Valley (Steyskal 1954, p. 66); Goldstream River Valley, 13.6 km north of Fairbanks, VII-29-1971, BAF (KSU).

Biology, immature stages: Berg 1953, Neff and Berg 1966 (E, L<sub>1.3</sub>, P); Eckblad 1973.

Habitat: Unshaded cattail marshes, borders of lakes and ponds, roadside drainage ditches.

Larval food: Pulmonate aquatic snails; Lymnaea emarginata Say, (Australorbis, Helisoma, Lymnaea, Oxyloma, Physa).

41. Sepedon spinipes americana Steyskal

Distribution: Nearctic. Central Alaska to Maine, southward to California, northern Utah, and Connecticut (map: Neff and Berg 1966, map C).

Alaskan Records (fig. 67): Matanuska; Nenana (Steyskal 1954, p. 66).

Biology, immature stages: Neff and Berg 1966 (E, L<sub>1,3</sub>, P).

**Habitat:** Marshy borders of ponds and shallow lakes, *Equisetum* meadows bordering slough.

Larval food: Aquatic pulmonate snails; (Australorbis, Helisoma, Physa).

#### Tetanocera Dumeril

42. Tetanocera bergi Steyskal

**Distribution:** Nearctic. Recorded only from Alaska, British Columbia, Alberta, Manitoba, Washington, and Oregon.

Alaskan Records (fig. 68): Matanuska Valley; Auke Bay (Steyskal 1954, p. 67); King Salmon on Naknek River, VIII-11-1952, J. B. Hartley (CNC); Amara Lake, Kodiak Island, VI-23-25-1962, G. E. Ball (USNM); near Teklanika campground in Mt. McKinley Nat. Park, VI-23-1957, G. W. Byers (UK); Summit Lake on Isabella Pass, VIII-3-1951, W. R. M. Mason (CNC); mile 10, Haines Highway, VII-14-1971, BAF (KSU); 32 km west Glenallen, VII-16-1971, BAF (KSU); Robe Lake near Valdez, VII-3-1971, BAF (KSU).

Biology, immature stages: Numerous puparia were found in a roadside drainage ditch near Valdez by the senior author. Laboratory-reared larvae fed predaciously on pulmonate aquatic snails. The immature stages are undescribed.

Habitat: Open sedge-rush-grass marshes, roadside drainage ditches and marshy borders of shallow lakes, ponds, and sloughs.

Larval food: Aquatic pulmonate snails; (Gyraulus, Helisoma, Lymnaea, Physa).

43. Tetanocera brevisetosa Frey

**Distribution:** Holarctic. Recorded only from Alaska in the Nearctic Region.

Alaskan Records (fig. 68): Fairbanks (Steyskal 1959, p. 77); King Salmon on Naknek River, VIII-11-1952, J. B. Hartley (CNC); Matanuska Flats near Palmer, VII-17-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Unknown. Five first-instar larvae fed for a few days on succineid snails, but none reached the second instar.

Habitat: *Equisetum* meadows, sedge marshes, and unshaded margins of small lakes and sloughs.

**Larval food:** Possibly shoreline snails; (Oxyloma).

44. Tetanocera ferruginea Fallén

**Distribution:** Holarctic. In North America, it has been recorded from Alaska to Newfoundland, southward to California, Colorado, Ohio, and New Jersey.

Alaskan Records (fig. 68): Matanuska Valley (Steyskal 1954, p. 67), Anchorage; King Salmon on Naknek River (Steyskal 1959, p. 83); Isabella Pass, VIII-3-1951, W. R. M. Mason (CNC); Palmer, C. O. Berg (CU); Horseshoe Lake in Mt. McKinley Nat. Park, VI-20-1957, G. W. Byers (UK); Robe Lake near Valdez, VIII-3-1971, BAF

(KSU); 32 km east Fairbanks, VII-28-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Beaver 1972, Disney 1964, Foote 1961 (E, L<sub>1.3</sub>, P), Rozko√nΩ 1965, 1967 (L<sub>3</sub>, P), Manguin and Hung 1991, Manguin and Vala 1989, Manguin et al. 1986, 1988a, 1988b.

Habitat: Wide variety of ponds, marshes, swamps, and other freshwater situations, particularly those containing water throughout the summer.

Larval food: Aquatic pulmonate snails, Planorbis sp., Lymnaea palustris, (Gyraulus, Helisoma, Lymnaea, Physa, Planorbis, Succinea).

45. Tetanocera freyi Stackelberg

**Distribution:** Holarctic. In North America, known only from southern Alaska and Alberta.

Alaskan Records (fig. 69): Matanuska Valley,
 VII-01-, VII-08-1950, VI-27-, VIII-02-1952, C.
 O. Berg (USNM) (Knutson 1981).

Biology, immature stages: Unknown.

Habitat: Open, marshy floodplains.

Larval food: Unknown.

46. Tetanocera fuscinervis (Zetterstedt)

Distribution: Holarctic. In North America, from Alaska to Newfoundland, southward to California, Arizona, Iowa, and New York (map: Foote, 1996a, fig. 1).

Alaskan Records (fig. 69): 25.6 km northeast of Anchorage; Eagle River; Matanuska Valley; mile 16 on the Palmer Highway; Popoff Island; Tanana; Thane (Steyskal 1959, p. 81); Healy, VI-26-1921, J. M. Aldrich (USNM); Fairbanks, VII-02-1921, J. M. Aldrich (USNM); Amara Lake, Kodiak Island, VI-23-1962, G. E. Ball (USNM); Kodiak Island, VI-17-1962, C. Lindroth (USNM); Haines, VII-17-1954, W. C. Frohne (USNM); Gulkana River (UMA); Igitkin Island in the Aleutians, VII-06-1936, C. S. Williams (USNM); Unalakleet, VIII-09-1961, B. S. Heming (CNC); Naknek River (CNC); mile 10, Haines Highway, VIII-6-1971, BAF (KSU); mile 15, Haines Highway, VII-15-1971, BAF (KSU); Chilkoot Campground, 15.7 km south Haines, VII-13-1971, BAF (KSU); Moon Lake, 24 km west Tok, VII-15-1971, BAF (KSU); Robe Lake near Valdez, VIII-3-1971, BAF (KSU); Goldstream River Valley, 13.6 km north Fairbanks, VIII-29-1971, BAF (KSU); 32 km east Fairbanks, VII-28-1971, BAF (KSU); Circle VII-26-1971, BAF (KSU).

Biology, immature stages: Beaver 1972; Foote 1961 (as T.unicolor) (E,  $L_{1-3}$ , P), Rozko $\sqrt{n\Omega}$  1967.

Habitat: Great variety of freshwater situations. Larval food: Shoreline and aquatic pulmonate snails, (Anisus, Bathyompholus, Cochlicopa, Discus, Eulota, Gyraulus, Helisoma, Helix, Hygromia, Lymnaea, Physa, Planorbis, Succinea).

47. Tetanocera kerteszi Hendel

**Distribution:** Holarctic. In North America, known from Alaska to Labrador, and south to Colorado and New Hampshire.

Alaskan Records (fig. 69): King Salmon; Naknek River; Nabesna; mile 183 on Richardson Highway (Steyskal 1959, p. 77, as *T. mallochi*); 24 km west Nabesna, VII-03-1948, R. I. Sailer (USNM); Polychrome Pass, VII-03-1954, W. C. Frohne (USNM); Gulkana, VII-04-1951, W. R. M. Mason (CNC); Isabella Pass, Summit Lake, VII-03-1951, W. R. M. Mason and J. R. McGillis (CNC); 32 km west Glenallen, VII-16-1971, BAF (KSU).

Biology, immature stages: Unknown.

Habitat: Unknown.

Larval food: Unknown.

48. Tetanocera latifibula Frey

**Distribution:** Holarctic. In North America, from Alaska to Alberta, southward to California, New Mexico, and South Dakota.

Alaskan Records (fig. 70): Anchorage; Lower Tonsina in the Matanuska Valley; Palmer (Steyskal 1959, p. 71, as *T. hespera*); Shaw Creek on Richardson Highway, VII-11-1951, W. R. M. Mason and J. R. McGillis (CNC); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Foote 1961 (E,  $L_{1.3}$ , P)

Habitat: Open sedge and rush marshes, roadside drainage ditches, and marshy borders of shallow lakes and ponds. Particularly common in those freshwater situations in which standing water disappears as summer progresses.

Larval food: Aquatic pulmonate snails, (Gyraulus, Physa, Planorbula).

49. Tetanocera montana Day

Distribution: Holarctic. In North America, from Alaska to Ontario, south to Wyoming and New York.

Alaskan Records (fig. 70): Eklutna; Matanuska Valley (Steyskal 1954, p. 67); Camp Eielson in McKinley National Park (Steyskal, 1959, p. 75); Gulkana, VIII-04-1951, W. R. M. Mason (CNC); Shaw Creek on Richardson Highway, VII-11-1951, W. R. M. Mason and J. R. McGillis (CNC); Eagle Trail Campground, 39.6 km south Tok, VII-15-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Foote 1961 (E,  $L_{1.3}$ , P).

**Habitat:** Permanent and seasonal swamps and marshes.

Larval food: Aquatic pulmonate snails.

50. Tetanocera phyllophora Melander

**Distribution:** Holarctic. In North America, from Alaska to Nova Scotia, southward to New Mexico, Michigan, and New York.

Alaskan Records (fig. 70): Anchorage; Matanuska Valley; Fairbanks, Holy Cross on the Lower Yukon River (Steyskal 1954, p. 68); King Salmon on the Naknek River (Steyskal 1959, p. 82); Curry, VI-29-1951, W. R. M. Mason (CNC); Big Delta, VII-14-1951, J. R. McGillis (CNC); Blair Lakes, VI-21-1954, G. D. Gill (KSU); mile 10, Haines Highway, VIII-6-1971, BAF (KSU); Valdez Glacier Campground #2, VII-31-1971, BAF (KSU).

Biology, immature stages: Bhatia and Keilin 1973 (L). Larvae prey on a wide variety of terrestrial pulmonate snails.

Habitat: Mesic deciduous and coniferous wood-

Larval food: Terrestrial snails, Euconulus fulvus Muller, Vertigo genesii Gredler, (Clausilia, Cochlicopa, Discus, Helix, Hygromia, Lymnaea, Oxyloma, Succinea, Zonitoides).

51. Tetanocera plebeja Loew

Distribution: Holarctic. In North America, recorded from southwestern Alaska to Newfoundland, southward to northern California, New Mexico, and North Carolina. (map: Trelka and Foote 1970, fig. 51).

Alaskan Records (fig. 71): Anchorage; Eagle River near Anchorage; Matanuska Valley; Nabesna; Nushagak (Steyskal 1954, p. 68); Goose Bay; King Salmon on the Naknek River (Steyskal 1959, p. 85); Shaw Creek on Richardson Highway, VI-27-28, VII-11-1951, W. R. M. Mason and J.R. McGillis (CNC); Curry, VI-3-1952, J. B. Hartley (CNC); Fairbanks, VI-25-1952, W. R. M. Mason (CNC); mile 315 on the Richardson Highway, VI-28-1951, W. R. M. Mason (CNC); 14.4 km east Kenai, VI-26, VII-13-1957, W. Bryant (MSU); 4.8 km south Tok, VII-14-1948, R. I. Sailer (USNM); 51.2 km north Seward, VII-1-1957, G. W. Byers (UK); Salcha River at mile 1481 on the Alaskan Highway, VI-17-1957, G. W. Byers (UK); Brooks Lake in Katmai Nat. Mon, VI-19-1960, D. T. Hoopes (ISU), VII-03-1961, M. A. Trautman (FSCA); Whale Pass, 72 km south Petersburg, VII-02-1962 (UCD); mile 10, Haines Highway, VIII-6-1971, BAF (KSU); Eagle Trail Campground, 28.8 km south Tok, VII-15-1971, BAF (KSU); Robe Lake near Valdez, VIII-03-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Foote 1961 (E,  $L_1$ , P), Trelka and Foote 1970 (E,  $L_{1\cdot3}$ , P), Trelka and Berg (1977).

Habitat: A wide variety of marshy situations and wet to mesic woodlands.

Larval food: Slugs; Deroceras laeve Muller, (Deroceras, Philomycus). Older larvae will also attack land snails; Oxyloma sp., (Oxyloma, Ventridens, Zonitoides).

52. Tetanocera plumosa Loew

Distribution: Holarctic. In North America, from Alaska to Newfoundland, and south to California, New Mexico, and North Carolina.

Alaskan Records (fig. 71): Anchorage; Eagle River; Kodiak Bay; Matanuska Valley; Nenana; Valdez (Steyskal 1954, p. 68); Teklanika River in Mt. McKinley National Park, VI-21-1957, G. W. Byers (UK); Shaw Creek at mile 289 on Richardson Highway, VI-28-, VII-11-1951, W. R. M. Mason (CNC); Curry VI-28-1952, J. B. Hartley (CNC); Palmer, VII-11-1950, R. H. Washburn (USNM); northeast corner of Brooks Lake on Dumpling Mountain, VII-04-1960, D. T. Hoopes (ISU); mile 15, Haines Highway, VII-14-1971, BAF (KSU); Eagle Trail Campground, 39.6 km south Tok, VII-15-1971, BAF (KSU); Moon Lake, 24 km west Tok, VII-15-1971, BAF (KSU); Robe Lake, near Valdez, VIII-03-1971, BAF (KSU); salt marsh near Valdez, VII-03-1971, BAF (KSU); Matanuska Flats near Palmer, VII-17-1971, BAF (KSU); Goldstream River Valley, 13.6 km north Fairbanks, VII-29-1971, BAF (KSU); Circle Hot Springs, VII-24-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Foote 1961 (as T. nan-ciae) (E, L<sub>3</sub>, P).

Habitat: Marshy shorelines of lakes and ponds, vernal marshes and swamps, roadside drainage ditches, and other freshwater situations in which water levels drop as summer progresses.

Larval food: Exposed aquatic and shoreline pulmonate snails, (Gyraulus, Helisoma, Lymnaea, Planorbula, Succinea).

53. Tetanocera robusta Loew

**Distribution:** Holarctic. In North America, from Alaska to Newfoundland, and south to California, New Mexico, and Michigan.

Alaskan Records (fig. 71): 25.6 km northeast Anchorage; Savonoski on Naknek Lake (Steyskal 1954, p. 69); Nome (Steyskal 1959, p. 62); Dutch Harbor, VII-15-1944, H. H. Stage (USNM); mile 242 on the Richardson Highway, VII-04-1951, W. R. M. Mason (CNC); mile 250 on the Richardson Highway, VII-27-1951, W. R. M. Mason (CNC); near Teklanika campground in Mt. McKinley National Park, VI-23-1957, G. W. Byers (UK); Katmai, VII-1927, J. Hine (OSU); Umiat, VII-08-1959, R. Madge (CNC).

Biology, immature stages: Foote 1961 (E,  $L_{1.3}$ , P).

Habitat: Marshy borders of lakes and ponds, permanent marshes.

Larval food: Aquatic pulmonate snails; (Gyraulus, Helisoma, Lymnaea, Physa, Planorbis).

54. Tetanocera rotundicornis Loew

**Distribution:** Nearctic. Alaska to Newfoundland southward to Oregon, Illinois, and North Carolina.

Alaskan Records (fig. 72): Matanuska Valley; Palmer; Tanana (Steyskal 1954, p. 69); Lower Yukon River; Naknek River; mile 40 on the Palmer Highway (Steyskal 1959, p. 78); King Salmon on Naknek River (CNC); Haines, VII-17-1954, W. C. Frohne (USNM); Shaw Creek on Richardson Highway, VII-11-1951, W. R. M. Mason and J. R. McGillis (CNC); Fairbanks, VI-25-1952, W. R. M. Mason (CNC); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Berg 1953, Foote 1961 (E, L<sub>1.2</sub>, P), Foote 1996b.

Habitat: Open *Equisetum* and sedge meadows, roadside drainage ditches.

Larval food: Shoreline snails of the family Succineidae; Oxyloma decampi gouldi, O. effusa (Pfeiffer), (Oxyloma, Succinea).

55. Tetanocera silvatica Meigen.

Distribution: Holarctic. In North America, from Alaska to Labrador, and south to British Columbia, Arizona, and South Dakota (map: Foote 1996a, fig. 2).

Alaskan Records (fig. 72): Matanuska Valley; Palmer; Tanana (Steyskal 1954, p. 69); Anchorage; King Salmon on Naknek River (Steyskal 1959, p. 90); Seward, (CNC); Big Delta, V-24-, VII-3-1951, W. R. M. Mason (CNC); 14.4 km east Kenai, VII-23-1957, W. Bryant (MSU); near Teklanika campground in Mt. Mckinley National Park, VI-23-1957, G. W. Byers (UK); Brooks Lake, VI-19-1960, D. T. Hoopes (ISU); mile 10, Haines Highway, VIII-6-1971, BAF (KSU); Circle, VII-26-1971, BAF (KSU).

Biology, immature stages: Beaver 1972, Rozko- $\sqrt{n\Omega}$  1967 (E, L<sub>1.3</sub>, P), Foote 1996a.

Habitat: Marshy shorelines of ponds and lakes, roadside drainage ditches.

Larval food: Terrestrial, shoreline, and stranded aquatic pulmonate snails, *Discus rotundatus*, (*Discus, Gyraulus, Helisoma, Lymnaea, Oxyloma, Physa, Planorbis, Succinea*).

56. Tetanocera spirifera Melander

Distribution: Nearctic: Alaska to Manitoba southward to Idaho, Wyoming, and South Dakota.

Alaskan Records (fig. 72): Shaw Creek, VI-28-, VII-11-1951, W. R. M. Mason and J. R. McGillis (CNC); Nome, VI-10-1951, D. P. Whillaus (CNC).

Biology, immature stages: (Foote 1996b).

Larval food: Shoreline snails of the family Succineidae; (Catinella, Oxyloma).

57. Tetanocera stricklandi Steyskal

Distribution: Nearctic: Known only from southern Alaska and western Alberta.

Alaskan Records (fig. 72): Nome, VII-09-1951, D. P. Williams (CNC).

Biology, immature stages: Larvae prey on aquatic pulmonate snails. The immature stages are undescribed.

Habitat: Permanent open to partly shaded marshes.

Larval food: Aquatic pulmonate snails; (Gyraulus, Lymnaea).

#### Discussion

Biogeography of the Alaskan Sciomyzidae

Alaska is of considerable importance biogeographically as it lies on the broad pathway that once led from Asia into northwestern North America via the Bering Land Bridge. A land connection between the two continents existed throughout the early and middle parts of the Tertiary Periods and periodically during both the Illinoian and Wisconsin Glaciations (Hopkins, 1959), although there is some question as to its extent during the Illinoian (Sainsbury, 1967).

Sea levels fell during the Quaternary Period, and a broad land bridge connecting Alaska and Asia appeared, although the connection was broken several times by rising sea levels caused by meltwater from the periodically retreating continental glaciers (Hopkins, 1967). Certainly there was ample opportunity for Palearctic species of plants and animals, including Sciomyzidae, to cross from Asia into North America and become established in Alaska, and vice versa.

Somewhat surprisingly, much of central Alaska was ice-free even during periods of maximum glaciation and may have served as a refugium for a variety of northern plants and animals. Although there was an ice-free corridor between Asia and North America during much of the Quaternary, there was for extended periods in northwestern Canada an impassible ice barrier that prevented movement of animals from Alaska into other areas of western North America. The continental glacier in western Canada, the Laurentide ice sheet, fused with various cordilleran glaciers to form a massive ice cap that extended from the Arctic to the Pacific Oceans. However, during interglacial times this ice cap retreated, and organisms undoubtedly could have moved from the Alaskan area into Alberta and thence into other regions of North America during periods of more equitable climate (Hopkins, 1967).

Dice (1943) recognized four biotic provinces in Alaska. The Sitkan Province covers the mostly mountainous, heavily forested, well-watered Panhandle and the southern coast west to about Kodiak Island. Dense coniferous forest, dominated by Alaska cypress (*Chamaecyparis nootkatensis* (Lamb.) Spach), western hemlock (*Tsuga heterophylla* (Raf.) Sargent), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.), is typical of this province except in those areas that rise above timberline. In such areas alpine tundra dominates the landscape. Thirty-six species of Sciomyzidae have been collected in the Sitkan Province.

The Aleutian Province includes the Aleutian Island chain, part of the Alaska Peninsula, and the Pribilof Islands. This is a treeless area for the most part, although scattered stands of low shrubs occur. Grasses, forbs, and ferns dominate the lowlands, whereas a heath type of vegetation clothes the higher elevations. Only two species of Sciomyzidae have been reported from this province, a situation that is probably due to lack of collecting effort rather than a reflection of an unfavorable environment.

The Eskimoan Province comprises the North Slope and most of the coastal areas fronting the Bering Sea. Low tundra vegetation is typical of this province, although some tree growth can be found on the Yukon River delta and in sheltered areas elsewhere. Eight species of Sciomyzidae have been reported from this province.

The Hudsonian Province includes the huge landscapes of central Alaska between the Alaska and Brooks mountain ranges. Spruces, particularly black spruce (*Picea mariana* (Britt.) Sterns and Pogg.), dominate this province along with scattered stands of paper birch (*Betula papyrifera* Marsh), tamarack (*Larix laricina* (DuRoi) K. Koch), shrubby willows (*Salix* spp.), and alders (*Alnus* spp.). Sphagnum moss carpets much of the land surface, and muskegs are abundant. Few localities within this province have been collected, and the small list of 13 species of Sciomyzidae recorded from the region probably is not representative of the diversity that exists in this vast area.

Larval feeding habits of Alaskan Sciomyzidae:

Over 200 species of Sciomyzidae from nearly all of the major biogeographic realms have now been reared (Knutson and Berg, 1978). All have larvae that prey exclusively on members of the molluscan classes Gastropoda and Pelecypoda. Although the trophic spectrum represented by the feeding habits of the larvae is relatively narrow, a considerable amount of adaptive radiation with respect to larval food preference has occurred. Seven trophic guilds can be recognized in the sciomyzid fauna of Alaska:

(1) predators of aquatic snails, (2) predators of shoreline and stranded aquatic snails, (3) predators of terrestrial snails, (4) parasitoids of terrestrial snails, (5) predators of slugs, (6) predators of snail eggs, and (7) predators of fingernail clams.

# Predators of Aquatic Snails

The aquatic predators form a distinctive group of species having larvae that attack pulmonate snails of the families Lymnaeidae, Physidae, and Planorbidae. Larvae of all species but *Hedria mixta* are not truly aquatic in that they remain in contact with the water surface and breathe atmospheric air. In general, they prey on aquatic snails that glide along the under side of the surface film. In contrast, larvae of H. mixta actively seek out submerged prey. The larvae seemingly are nonselective in their choice of prey species except that they seem unable to attack operculate snails. Each larva can kill between 10 and 35 snails depending on the size of prey available. Younger larvae are restricted to prey measuring only a few millimeters in size, but older larvae can overcome snails measuring 10-20 mm in greatest diameter. The following 15 species of Alaskan Sciomyzidae are known to be predators of aquatic snails: Dictya umbroides, Elgiva connexa, E. solicita, Hedria mixta, Sepedon anchista, S. borealis, S. fuscipennis nobilis, S. spinipes americana, Tetanocera bergi, T. ferruginea, T. fuscinervis, T. latifibula, T. montana, T. robusta, and T. stricklandi.

Predators of Shoreline and Stranded Aquatic Snails

The habit of utilizing stranded or exposed aquatic and hygrophilous shoreline snails is well developed among the North American Sciomyzidae. In fact, it is the largest trophic guild and includes species of both Sciomyzini and Tetanocerini. Nearly all species prey on pulmonate snails, but Pherbellia prefixa attacks the operculate species Valvata sincera Say. The guild is not as uniform behaviorly as that of the aquatic predators, and a broad amplitude exists with respect to habitat selection, food snail preference, and larval feeding habits. Morphologically, larvae of many species are intermediate between those of the aquatic and terrestrial species. Species belonging to this group usually are found in shoreline situations, produce large number of eggs that are scattered over the surface litter, and feed as larvae mainly on Lymnaea, Helisoma, Physella. and Oxyloma snails. The larvae may act as predators or parasitoids; in either case they are able to

complete their development on only one or a very few snails. Pupation habits vary, as some species regularly form puparia within cleaned-out shells of food snails, whereas others normally pupate in surface litter. Most species have two or more generations a year. The 19 Alaskan species in this guild are Pherbellia anubis, P. argyra, P. griseicollis, P. nana, P. obscura, P. prefixa, P. propages, P. quadrata, P. vitalis, Pteromicra angustipennis, P. pectorosa, P. pleuralis, P. siskiyouensis, Sciomyza simplex, Tetanocera plumosa, T. silvatica, and T. spirifera.

# Predators of Terrestrial Snails

A small group of the North American sciomyzid species occur in terrestrial habitats where their larvae prey on land snails. Females of species belonging to this category lay eggs on low vegetation or surface litter in habitats harboring food snails. Younger larvae typically feed singly within one snail for several days to a week or more, but then abandon the snail after killing it and seek out additional prey. Usually two to five snails satisfy the nutritional needs of each larva. Pupation usually occurs in surface litter outside of the shell of the food snail. Only *Pherbellia albocostata* and *Tetanocera phyllophora* are known to belong to this guild.

# Parasitoids of Terrestrial Snails

The habit of utilizing terrestrial snails in a more parasitoid manner is not well developed in the Sciomyzidae, and only a few North American species fall into this category. An adult female usually deposits her eggs only on or very close to the larval host, and each larva typically completes its entire life within one snail. Furthermore, the puparium may be formed within the cleaned-out shell. The terrestrial parasitoids are highly host specific, and the two Alaskan species that are placed in this group, *Pherbellia schoenherri maculata* and *Sciomyza dryomyzina*, are restricted to snails of the family Succineidae.

#### Predators of Slugs

As far as the North American sciomyzid fauna is concerned, only three species of *Tetanocera* are known to have an obligatory trophic relationship with slugs. Eggs of all three species are placed on vegetation or litter in marshy or wooded habitats, and the newly hatched larvae must seek out prey. Younger larvae have a rather parasitoid relationship with the prey animal and frequently remain with a slug for several days before killing it. In contrast, older larvae are more predatory and quickly

overcome and consume their victims. Two to four slugs are needed to complete larval development. Pupation occurs in surface litter. Only *T. plebeja* is known to be a slug-killer in Alaska.

# Predators of Snail Eggs

Species of Antichaeta are the only Sciomyzidae known to have larvae that prey on snail eggs. In Alaska, adults of A. melanosoma place their eggs directly on the egg masses of Physella sp. that have been exposed by dropping water levels. Larvae hatching from these eggs invade the gelatinous matrix of the mass and soon begin attacking the developing eggs. Larvae can move from one egg mass to another, and puparia are formed away from the larval food source.

# Predators of Fingernail Clams

In North America, larvae of only three species of *Renocera* are known to prey on fingernail clams of the family Sphaeriidae. Eggs are laid on shoreline vegetation and litter. In contrast to nearly all other aquatic Sciomyzidae, newly hatched larvae of *Renocera* leave the surface film and seek out completely submerged prey. The first-instar larva usually remains within the mantle cavity of a clam for 4-6 days before killing it. Older larvae are more predacious and can kill up to 25 prey before pupating. In Alaska, only *R. brevis* is known to belong to this trophic guild.

Practically nothing is known of the life histories, larval feeding habits, and immature stages of the following 10 species of Alaskan Sciomyzidae: Pherbellia aloea, P. bryanti, P. frohnei, P. phela, P. tenuipes, Limnia boscii, Renocera johnsoni, Tetanocera brevisetosa, T. freyi, and T. kerteszi. This list represents nearly 20% of the fauna of the state; obviously much more work is needed before a clear picture of adaptive radiation in the Alaskan Sciomyzidae can be ascertained.

# Acknowledgments

Research supported by grants from the National Science Foundation, National Institute of Allergy and Infectious Disease, National Geographic Society, and the American Philosophical Society. We express deep appreciation to George C. Steyskal, formerly of Gainesville, Florida, for his expert help in determining species of Sciomyzidae, and to John P. Keiper of Polk City, Florida, for his help in preparation of the illustrations.

Specimens representing the Alaskan species of Sciomyzidae have been deposited in the insect collections at the Carnegie Museum of Natural History. Appreciation is expressed to Chen Young and John Rawlins of that institution and Karl Valley of the Pennsylvania Department of Agriculture for their reviews of the manuscript and suggestions for its improvement.

This paper is dedicated to the fond memory of Dr. C. O. Berg, formerly of the Department of Entomology at Cornell University in Ithaca, New York, who stimulated many students throughout the world to initiate biological studies of the family Sciomyzidae.

#### References

- Beaver, O. 1972. Notes on the biology of British sciomyzid flies (Diptera: Sciomyzidae). II. Tribe Tetanocerini. Entomologist 105:284-299.
- Berg, C.O. 1953. Sciomyzid larvae (Diptera) that feed on snails. Journal of Parasitology 39:630-639.
- Bhatia, M. L., and D. Keilin. 1937. On a new case of parasitism of a snail (*Vertigo genesii* Gredl.) by a dipterous larva. Parasitology 29:399-407.
- Bratt, A. D., L. V. Knutson, B. A. Foote, and C. O. Berg. 1969. Biology of *Pherbellia* (Diptera: Sciomyzidae). Memoir of Cornell University Agricultural Experiment Station 404:1-247.
- Dice, L. R. 1943. The Biotic Provinces of North America. University of Michigan Press, Ann Arbor. viii+78p.
- Disney, R. H. L. 1964. A note on the diet and habitats of the larva and an ichneumonid parasitoid of the pupa of *Tetanocera ferruginea* Fall. (Dipt., Sciomyzidae). Entomologist's Monthly Magazine 100:88-90.
- Eckblad, J. W. 1973. Experimental predation studies of malacophagous larvae of *Sepedon fuscipennis* (Diptera: Sciomyzidae) and aquatic snails. Experimental Parasitology 33:331-342.
- Fenneman, N. M. 1942. Physiography of Western United States. McGraw Hill, New York City. x+534p.
- Fisher, T. W., and R. E. Orth. 1966. A new species of *Pteromicra* from western North America and resurrection of *Pteromicra pleuralis* (Cresson). Pan-Pacific Entomologist 42:307-318.
- Foote, B. A. 1959. Biology and immature stages of the snail-killing flies belonging to the genus *Sciomyza* Fallén (Diptera: Sciomyzidae). Annals of the Entomological Society of America 52:31-43.

- Foote, B. A. 1961. Biology and immature stages of the snail-killing flies belonging to the genus *Tetanocera* (Diptera: Sciomyzidae). Ph. D. Thesis. Cornell University. 190 pp. Order Number 62-105. University Microfilms, Ann Arbor, Michigan (Dissertation Abstracts 22:3302-3303).
- **Foote, B. A.** 1971. Biology of *Hedria mixta* (Diptera: Sciomyzidae). Annals of the Entomological Society of America 64:931-941.
- Foote, B.A. 1973. Biology of *Pherbellia prefixa* (Diptera: Sciomyzidae), a parasitoid- predator of the operculate snail *Valvata sincera* (Gastropoda: Valvatidae). Proceedings of the Entomological Society of Washington 75:141-149.
- **Foote, B. A.** 1976. Biology and larval feeding habits of three species of *Renocera* (Diptera: Sciomyzidae) that prey on fingernail clams (Mollusca: Sphaeridae). Annals of the Entomological Society of America 69:121-133.
- **Foote, B. A.** 1996a. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Insecta: Diptera: Sciomyzidae). I. Introduction and life histories of predators of shoreline snails. Annals of Carnegie Museum 65:1-12.
- **Foote, B. A.** 1996b. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Insecta: Diptera: Sciomyzidae). II. Life histories of predators of snails of the family Succineidae. Annals of Carnegie Museum 65:153-166.
- Foote, B. A., and L. V. Knutson. 1970. Clam-killing fly larvae. Nature 226:466.
- Hennig, W. 1952. Die Larvenformen der Dipteren. Part 3. Akademie Verlag, Berlin. 628pp.
- Hopkins, D. M. 1959. Cenozoic history of the Bering Sea land bridge. Science 129:1519-1528.
- Hopkins, D. M. 1967. The Cenozoic history of Beringia a synthesis, pp. 451-484. *In* D. M. Hopkins, ed., The Bering Land Bridge. Stanford Univ. Press, Stanford. ix+459pp.
- Hulten, E. 1972. Outline of the history of arctic and boreal biota during the Quaternary Period. Wheldon and Wesley, Ltd, New York. 168pp
- **Hulten, E.** 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford. xx+1008pp.
- Knutson, L. V. 1970. Biology of snail-killing flies in Sweden (Dipt., Sciomyzidae). Entomologica Scandinavia I 4:307-314.
- Knutson, L. V. 1981. New combinations and synonymies in Palearctic and Nearctic Sciomyzidae (Diptera). Proceedings of the Entomological Society of Washington 83:332-338.

- Knutson, L. V. 1987. Life cycles of snail-killing flies: Pherbellia griseicollis, Sciomyza dryomyzina, and Sciomyza testacea (Diptera: Sciomyzidae). Entomologica Scandinavia 18:383-391.
- Knutson, L. V., and J. Abercrombie. 1977. Biology of *Antichaeta melanosoma* (Diptera: Sciomyzidae), with notes on parasitoid Braconidae and Ichneumonidae (Hymenoptera). Proceedings of the Entomological Society of Washington 79: 111-125.
- Knutson, L. V., and C. O. Berg. 1964. Biology and immature stages of snail-killing flies: The genus *Elgiva* (Diptera: Sciomyzidae). Annals of the Entomological Society of America 57:173-192.
- Knutson, L. V., and C. O. Berg. 1973. Biology and systematics of Sciomyzidae (Diptera). Annual Review of Entomology 23:239-258.
- Manguin, S., and J.-C. Vala. 1989. Prey consumption by larvae of *Tetanocera ferruginea* (Diptera: Sciomyzidae) in relation to number of snail prey available. Annals of the Entomological Society of America 82:588-592.
- Manguin, S., J.-C. Vala, and J. M. Reidenbach. 1986. Predation de mollusques dulcaquicoles par les larves malacophages de *Tetanocera ferruginea* Fallén, 1820 (Diptera, Sciomyzidae. Canadian Journal of Zoology 64:2832-2836.
- Manguin, S., J.-C. Vala, and J. M. Reidenbach. 1988. Determination des preferences alimentaires des larves de *Tetanocera ferruginea* (Diptera: Sciomyzidae), predateur de mollusques dulcaquicoles. Acta Oecologica/Oecologica Applicata 9:353-370.
- Neff, S. E., and C. O. Berg. 1966. Biology and immature stages of malacophagous Diptera of the genus *Sepedon* (Sciomyzidae). Virginia Agricultural Experiment Station Bulletin 566:1-113.
- Orth, R. E. 1982. Five new species of *Pherbellia* Robineau-Desvoidy, subgenus *Oxytaenia* Sack, from North America. Proceedings of the Entomological Society of Washington 84:23-37.
- Orth, R. E. 1983. Two new species of *Pherbellia* from North America (Diptera: Sciomyzidae). Proceedings of the Entomological Society of Washington 85:537-542.
- Orth, R. E. 1986. Taxonomy of the Sepedon fuscipennis group (Diptera: Sciomyzidae). Proceedings of the Entomological Society of Washington 88:63-76.
- Orth, R. E. 1987. A new species of *Pherbellia* from North America with range extensions for *P. hackmani* and *P. griseicollis* (Diptera: Sciomyzidae). Proceedings of the Entomological Society of Washington 89:344-350.

- Orth, R. E., and L. V. Knutson. 1987. Systematics of snail-killing flies of the genus *Elgiva* in North America and biology of *E. divisa* (Diptera: Sciomyzidae). Annals of the Entomological Society of America 80:829-840.
- Orth, R. E., G. C. Steyskal, and T. W. Fisher. 1980. A new species of *Pherbellia* Robineau-Desvoidy with notes on the *P. ventralis* group (Diptera: Sciomyzidae). Proceedings of the Entomological Society of Washington 82:284-292.
- Rosko√nΩ, R. 1965. Neue Metamorphosestadien mancher *Tetanocera*-arten (Diptera, Sciomyzidae). Zoologicke Listy 14:367-370.
- Rosko√nΩ, R. 1966. Ceskoslovenské druhy malakofagni celedi Sciomyzidae (Diptera). Folia Prirodovedecke Eak. J. E. Purkyne Brno 7:1-111.
- Rosko√nΩ, R. 1967. Zur Morphologie und Biologie der Metamorphosestadien mitteleuropaischer Sciomyziden (Diptera). Acta Sciences Natural Brno 1:117-160.
- Rosko√nΩ, R. 1982. Three new species of *Pherbellia* Robineau-Desvoidy and new synonyms of Holarctic and Palaearctic Sciomyzidae (Diptera). Annals of the Entomological Society of Fenn. 48:51-56.
- Rosko√nΩ, R. 1990. Additions to the taxonomy, morphology and distribution of Palaearctic Sciomyzidae (Diptera). Scripta (Brno) Biologia 21:37-46.
- Rosko√nΩ, R., and L. V. Knutson. 1970. Taxonomy, biology, and immature stages of Palaearctic *Pteromicra*, snail-killing Diptera (Sciomyzidae). Annals of the Entomological Society of America 63:1434-1459.
- Sainsbury, C. L. 1967. Quaternary geology of Western Seward Peninsula, Alaska, pp. 121-143. *In D. M. Hopkins*, ed., The Bering Land Bridge. Stanford Univ. Press, Stanford. xiii+495pp.
- Smith, K. V. G. 1959. A note on the floating puparium of *Elgiva sundewalli* (Fries) (=*Hedroneura rufa* Panz.) (Dipt., Sciomyzidae. Entomologists Monthly Magazine 95:67-68.
- Steyskal, G. C. 1949. New Diptera from Michigan (Stratiomyidae, Sarcophagidae, Sciomyzidae). Papers of the Michigan Academy of Science, Arts and Letters 33: 173-180.
- Steyskal, G. C. 1954a. The Sciomyzidae of Alaska (Diptera). Proceedings of the Entomological Society of Washington 56:54-71.
- Steyskal, G. C. 1954b. The American species of the genus Dictya Meigen (Diptera: Sciomyzidae). Annals of the Entomological Society of America 47:511-539. Steyskal, G. C. 1959. The American species of the genus Tetanocera Dumeril (Diptera). Papers of the Michigan Academy of Sciences, Arts, and Letters 44:55-91.

- Steyskal, G. C. 1960. The genus *Antichaeta* Haliday, with special reference to the American species (Diptera, Sciomyzidae). Papers of the Michigan Academy of Science, Arts and Letters, 45:17-26.
- Steyskal, G. C. 1961. The North American Sciomyzidae related to *Pherbellia fuscipes* (Macquart) (Diptera Acalyptratae). Papers of the Michigan Academy of Science, Arts, and Letters 46:405-415.
- Steyskal, G. C. 1963. Taxonomic notes on Sciomyzidae (Diptera, Acalyptratae). Papers of the Michigan Academy of Science, Arts, and Letters 48:113-125.
- Steyskal, G. C. 1966. The Nearctic species of *Pherbellia* Robineau-Desvoidy, subgenus *Oxytaenia* Sack (Diptera, Sciomyzidae). Papers of the Michigan Academy of Science, Arts, and Letters 51:31-38.
- Steyskal, G. C. 1967. The Nearctic species of *Pherbellia* Robineau-Desvoidy, subgenus *Oxytaenia* Sack (Diptera: Sciomyzidae). Papers of the Michigan Academy of Science, Arts, and Letters 51:31-36.
- Steyskal, G. C., T. W. Fisher, L. Knutson, and R. E. Orth. 1978. Taxonomy of North American flies of the genus *Limnia* (Diptera: Sciomyzidae). University of California Publications in Entomology 83:1-48.
- Trelka, D. G., and C. O. Berg. 1977. Behavioral studies of the slug-killing larvae of two species of *Tetanocera* (Diptera: Sciomyzidae). Proceedings of the Entomological Socety of Washington 79:475-486.
- Trelka, D. G., and B. A. Foote. 1970. Biology of slugkilling *Tetanocera*. Annals of the Entomological Society of America 63:877-895.
- Vala, J.-C., and C. Brunel. 1987. Le genre *Tetanocera* en France et premiere mention de *Tetanocera freyi* (Diptera, Sciomyzidae). L'Entomologiste 43:149-154.
- Valley, K. R., and C. O. Berg. 1977. Biology and immature stages of snail-killing Diptera of the genus *Dictya* (Sciomyzidae). Search Agriculture (Geneva, New York) 7:1-44.
- Wahrhaftig, C. 1965. Physiographic divisions of Alaska. Geological Survey Professional Paper 482:1-52.

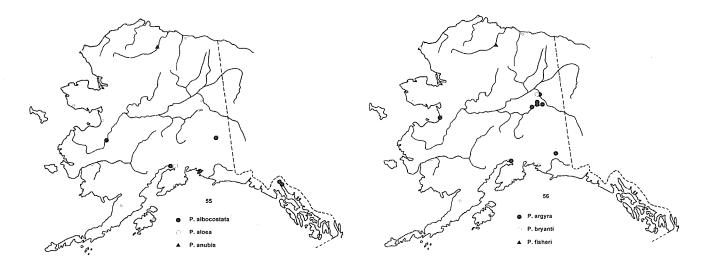


Figure 55. Distribution of Alaskan Species of Sciomyzidae: *Pherbellia albocostata*, *P. aloea*, *P. anubis*.

Figure 56. Distribution of Alaskan Species of Sciomyzidae: *Pherbellia argyra*, *P. bryanti*, *P. fisheri*.

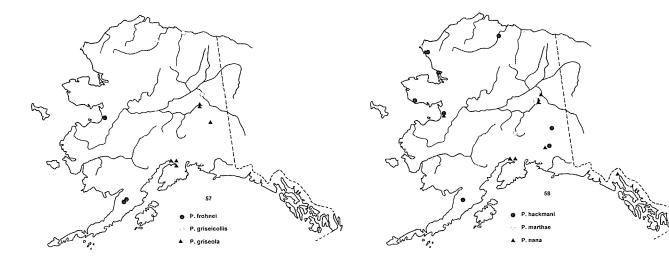


Figure 57. Distribution of Alaskan Species of Sciomyzidae: *Pherbellia frohnei, P. griseicollis, P. griseola.* 

Figure 58. Distribution of Alaskan Species of Sciomyzidae: Pherbellia hackmani, P. marthae, P. nana.

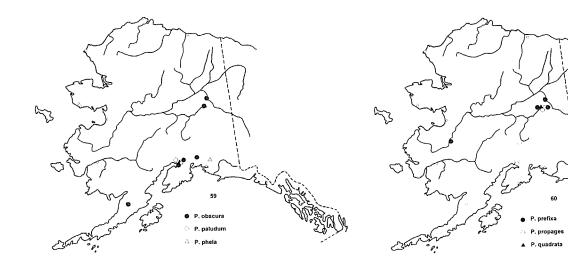


Figure 59. Distribution of Alaskan Species of Sciomyzidae: Pherbellia obscura, P. paludum, P. phela,

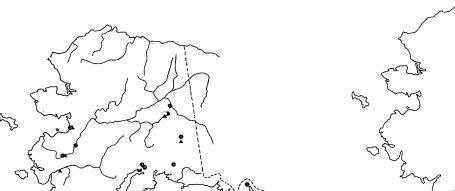


Figure 61. Distribution of Alaskan Species of Sciomyzidae: P.  $schoenherri\ maculata,\ P.\ tenuipes,\ P.\ vitalis.$ 

Figure 60. Distribution of Alaskan Species of Sciomyzidae: Pherbellia prefixa, P. propages, P. quadrata.

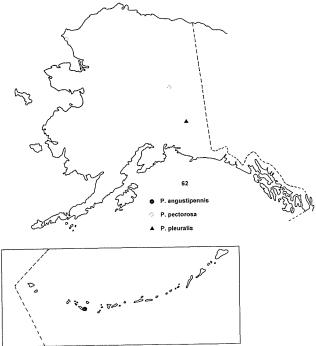


Figure 62. Distribution of Alaskan Species of Sciomyzidae: Pteromicra angustipennis, P. pectorosa, P. pleuralis.

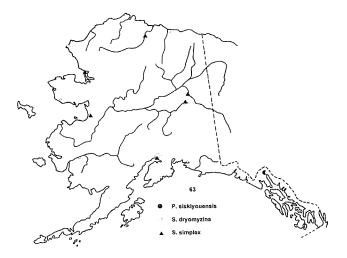


Figure 63. Distribution of Alaskan Species of Sciomyzidae: Pteromicra siskiyouensis, Sciomyza dryomyzina, S.simplex.

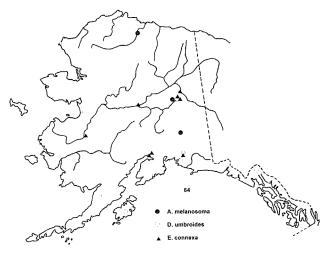


Figure 64. Distribution of Alaskan Species of Sciomyzidae: Antichaeta melanosoma, Dictya umbroides, Elgiva connexa.

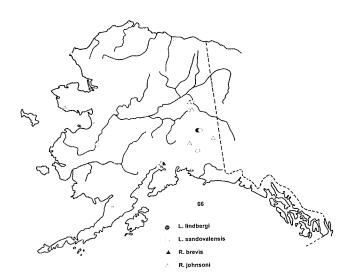


Figure 65. Distribution of Alaskan Species of Sciomyzidae: Elgiva divisa, E. solicita, Hedria mixta.

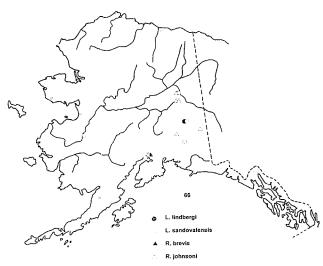


Figure 66. Distribution of Alaskan Species of Sciomyzidae: Limnia lindbergi, L. sandovalensis, Renocera brevis, R. johnsoni.

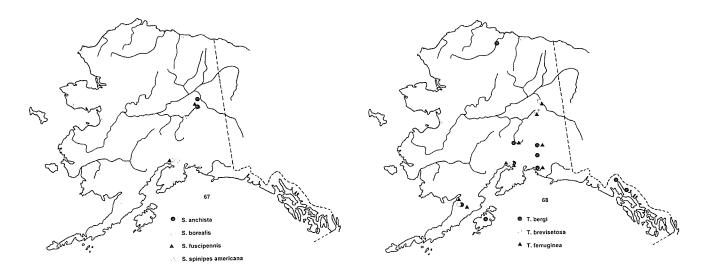


Figure 67. Distribution of Alaskan Species of Sciomyzidae: Sepedon anchista, S. borealis, S, fuscipennis nobilis, S. spinipes americana.

Figure 68. Distribution of Alaskan Species of Sciomyzidae: Tetanocera bergi, T. brevisetosa, T. ferruginea.

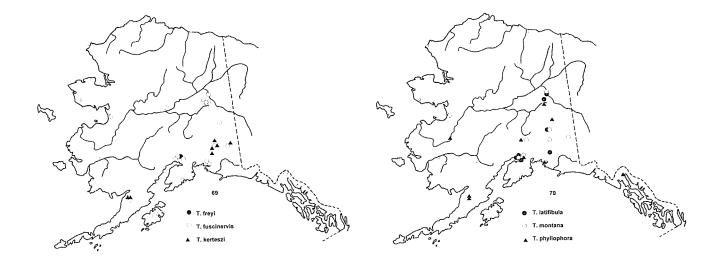
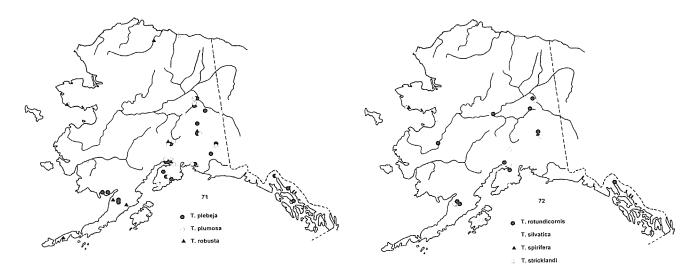


Figure 69. Distribution of Alaskan Species of Sciomyzidae: Tetanocera freyi, T. fuscinervis, T. kerteszi.

Figure 70. Distribution of Alaskan Species of Sciomyzidae: Tetanocera latifibula, T. montana, T. phyllophora.



**Figure 71.** Distribution of Alaskan Species of Sciomyzidae: *Tetanocera plebeja, T.* plumosa, *T. robusta*.

Figure 72. Distribution of Alaskan Species of Sciomyzidae:

Tetanocera rotundicornis, T. silvatica, T. spirifera, T. stricklandi.