# Studies of Ephydrinae (Diptera: Ephydridae), II: Phylogeny, Classification, and Zoogeography of Nearctic *Lamproscatella* Hendel

WAYNE N. MATHIS

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# Studies of Ephydrinae (Diptera: Ephydridae), II: Phylogeny, Classification, and Zoogeography of Nearctic *Lamproscatella* Hendel

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## ABSTRACT

Mathis, Wayne N. Studies of Ephydrinae (Diptera: Ephydridae), II: Phylogeny, Classification, and Zoogeography of Nearctic *Lamproscatella* Hendel. *Smithsonian Contributions to Zoology,* number 295, 41 pages, 52 figures, 1979.—The nearctic species of *Lamproscatella* are revised. Keys to subgenera and species, illustrations, and distribution maps are provided. *Lamproscatella* is divided into three subgenera, each of which is hypothesized to be monophyletic, being based on apotypic character states. The relationships among species within each subgenus are also outlined, again being based on apotypic character states. Assuming, among other assumptions, that the cladograms are reasonably correct, the zoogeography for each subgenus is discussed. I suggest that *Lamproscatella* had its origins in western North America and that through dispersal and subsequent vicariance events, the species of each subgenus differentiated and became more widespread in the Northern Hemisphere. The subgenus *Lamproscatella* eventually dispersed to most of the Old World (including Africa and Asia), where further vicariance events resulted in the species occurring there now. As barriers to partition the range of ancestral species, I propose the existent topography of the Pliocene-Pleistocene coupled with the rather dramatic climatic events of these periods.



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# Contents

# Studies of Ephydrinae (Diptera: Ephydridae), II: Phylogeny, Classification, and Zoogeography of Nearctic *Lamproscatella* Hendel

*Wayne N. Mathis*

## Introduction

Members of the shore fly family Ephydridae are notable because of their ability to successfully inhabit diverse and often inhospitable environments. Frog and spider eggs, snails, human cadavers, salt lakes, crude petroleum or cess pools, and bubbling sulfur springs are among the habitats that are frequented by various species of the family. Within the family, many members of the subfamily Ephydrinae are halophilous and are commonly referred to as brine flies. The genus *Lamproscatella* belongs to this subfamily. Like related taxa, many of the included species have a physiological ability to withstand the osmotic pressure of salty environments. In western North America, these flies are often extremely abundant on the crystaline-mud playas that are exposed to receding water levels of shallow alkaline or saline lakes in late summer. Other species of *Lamproscatella* are usually associated with freshwater systems or with maritime estuaries.

A paucity of natural history data for *Lamproscatella* species precludes a meaningful synthesis at this time. Neither the immature stages nor the life cycle of any species has been described, and what data we do have on their ecology consist of very generalized habitat descriptions. Dahl (1959), Deonier (1965), and Scheiring and Foote (1973) summarize available information for species occurring in the Nearctic Region.

The composite distribution of *Lamproscatella* species ranges nearly worldwide, although most species seem to be limited to one zoogeographic region. The holarctic *Lamproscatella quadrisetosa* (Becker), *L. bimaculata* Hendel, and *L. brunnipennis* (Malloch) are exceptions. No species has been described from the Neotropics or Australia. Becker's (1919) record of *L. sibilans* (Haliday) from Ecuador is an error. Through the kindness of Dr. Loïc Matile, I have examined the specimens Becker studied and found that they represent a species of the genus *Scatophila* Becker.

A detailed historical account of *Lamproscatella* is not within the scope of this paper. Many citations, especially those of the nineteenth century, are simple species lists, published in conjunction with various faunistic studies. For the most part, these references are not cited below, and only papers containing keys, illustrations, or what I consider to be substantial contributions are included.

Hendel proposed *Lamproscatella* in 1917, although two years earlier Becker (1915) recognized

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that the species later included in Hendel's new genus were a separate group but within the genus *Scatella* Robineau-Desvoidy. Indeed, those species described prior to Hendel's proposal of *Lamproscatella* but which were later included, were treated in the genus *Scatella* by most workers (Loew, 1860:40; Schiner, 1863:265–266; Becker, 1896:228–229, 1905: 210–212, 1915:132; Jones, 1906:197; Grunberg, 1910:229–300). However, the type-species of the genus, *L. sibilans* (Haliday), was orginally described in the genus *Ephydra* (Haliday, 1833) and early Scandinavian dipterists continued to follow this precedent (Stenhammar, 1844:180; Zetterstedt, 1846:1832).

Since Hendel's description of *Lamproscatella,* its status has vacillated between generic and subgeneric levels. Becker (1926) treated *Lamproscatella* as a subgenus of *Scatella* in his synopsis of palearctic Ephydridae. This precedent was also followed by Collin (1930) in a review of the *Scatella* species of the British Isles, by Dahl (1959) in a study of Scandinavian Ephydridae, by Sturtevant and Wheeler (1954) when they reviewed the nearctic species, and by Deonier (1964) in a key to the shore flies of Iowa (United States). Cresson (1930), although sympathetic with the subgeneric status given by Becker, kept *Lamproscatella* as a distinct genus. Wirth and Stone (1956) and Wirth (1965) likewise recognized *Lamproscatella* as a distinct genus in treatments of the aquatic Diptera of California and in the recent catalog of North American Diptera respectively. More recently, Andersson (1975) treated *Lamproscatella* as a genus in his synopsis of the northern European species, as did Papp (1975) in an excellent faunistic study of the Ephydridae of Hungary.

The present study was initiated after I discovered that many species are undescribed or difficult to identify from existing literature sources. Names of species occurring in the Palearctic Region have been used for similar species occurring in North America or for nominate taxa which prove to consist of more than one species. The study is based primarily on the morphology of male and female terminalia, together with a reevaluation of other previously used characters. In the resulting classification, *Lamproscatella* is considered a valid genus as characterized by Hendel, by Cresson (1930), and Wirth (1948). In addition, three subgenera are proposed, and five new species are described. The basis for these proposals will be discussed in greater detail under the appropriate taxon.

METHODS.—During the course of this study, nearly 4500 specimens from most major North American collections were examined. Label data for all specimens examined were recorded, organized alphabetically, and presented under the appropriate species. Abbreviations of institutions where specimens are deposited are those cited in the "Acknowledgments" section. Type-specimens of all nominate taxa except for *L. bimaculata* Hendel were studied. Label data accompanying each type are cited as given, with slashes to separate data of one label from another. Clarifying or interpretive comments are included parenthetically.

Cladograms outlining probable phylogenetic relationships have been constructed for subgenera and for species included within each subgenus. The philosophic basis for constructing the cladograms is cladistic (Hennig, 1966). Character states were arranged into transformation series and their relative ancestral or derived conditions were determined, generally by ex-group comparison. Monophyletic sister-group lineages were thus identified. Tables accompanying the cladograms list character state evidence; numbers assigned to characters correspond with those on the cladograms (filled squares = apotypic character states; outlined squares = plesiotypic character states).

Most characters employed in this study need no explanation. The characters listed below, however, are defined to avoid confusion.

*Eye-to-cheek ratio*: Genal height/eye height. Measurements are taken from the head in lateral view.

*Head width-to-height ratio*: Head height/head width as measured from an anterior view.

*Costal vein ratio*: The straight line distance between $R_{2+3}$ and $R_{4+5}$/distance between $R_1$ and $R_{2+3}$.

*$M_{1+2}$ vein ratio*: The straight line distance along $M_{1+2}$ basad of posterior crossvein/distance apicad of posterior crossvein.

The terminology of male and female terminalia is that of Mathis (1975) except for the hypandrial process which I now call the gonite, a more widely used term. These structures were drawn with the aid of a drawing tube attached to a Wild M20 compound microscope.

Measurements or ratios cited in the text are based on an average of six specimens. The specimens were

selected as follows: the largest male and female; the smallest male and female; two other specimens picked randomly.

Descriptions are composite. For the most part, information given in the generic or subgeneric descriptions is not repeated in the species descriptions.

ACKNOWLEDGMENTS.—Without the cooperation and assistance of numerous persons, much of this study could not have been completed. I am grateful to them all for their time, effort, and thoughtful consideration.

I thank the following curators and institutions for loaning specimens (an asterisk indicates collections from which type specimens were borrowed).

| | |
|---|---|
| AMNH | American Museum of Natural History, New York (Dr. Pedro W. Wygodzinsky) |
| ANSP* | Academy of Natural Sciences of Philadelphia (Dr. Daniel Otte) |
| BYU | Brigham Young University (Dr. Stephen L. Wood) |
| CAS | California Academy of Sciences (Dr. Paul H. Arnaud, Jr.) |
| CNC | Canadian National Collection (Mr. Guy E. Shewell) |
| CU | Cornell University (Dr. L. L. Pechuman) |
| FSCA | Florida State Collection of Arthropods (Dr. Howard V. Weems) |
| HU | Museum für Naturkunde, Humbolt Universitat, Berlin (Dr. H. Schumann) |
| ISU | Iowa State University (Dr. Robert E. Lewis) |
| KNSU | Kansas State University (Dr. H. Derrick Blocker) |
| KU* | University of Kansas, Snow Entomological Museum (Dr. George W. Byers) |
| KSU | Kent State University (Dr. Ben. A. Foote) |
| MSU | Michigan State University (Dr. Roland L. Fischer) |
| MCZ | Museum of Comparative Zoology, Harvard University (Margaret Thayer) |
| NMW | Naturhistorisches Museum, Wien (Dr. Ruth Lichtenberg) |
| OSDA | Oregon State Department of Agriculture (Mr. Richard L. Westcott) |
| OSU | Oregon State University (Dr. John D. Lattin) |
| PSU | Pennsylvania State University (Dr. K. C. Kim) |
| UCD | University of California, Davis (Dr. Robert O. Schuster) |
| UCR | University of California, Riverside (Mr. Saul I. Frommer) |
| UMI | University of Michigan (Dr. Thomas E. Moore) |
| UMN | University of Minnesota (Dr. Philip J. Clausen) |
| USNM* | former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution |
| USU | Utah State University (Dr. Wilford J. Hanson) |
| WSU | Washington State University (Dr. William J. Turner) |

Hollis B. Williams prepared all of the maps and organized the locality data; L. Michael Druckenbrod rendered the habitus illustrations; Anne Halpern typed the final draft. An earlier draft of this paper was read and critiqued by Wayne E. Clark and W. W. Wirth.

## Genus *Lamproscatella* Hendel

*Lamproscatella* Hendel, 1917:42 [type-species: *Ephydra sibilans* Haliday, by original designation].—Cresson, 1930:125–126.—Wirth, 1948:278–280; 1965:756.—Wirth and Stone, 1956:474–475.

*Scatella (Lamproscatella)* Becker, 1926:84–86.—Collin, 1930: 133–139.—Dahl, 1959:117–119.—Sturtevant and Wheeler, 1954:175–176.

DIAGNOSIS.—Specimens of *Lamproscatella* are similar to those of several genera of Scatellini but may be distinguished by the following combination of characters: Antennal arista pubescent to bare, not bearing pectinate dorsal branches; genal bristle lacking or reduced, subequal to other genal setae; acrostichal setae in 2 rows, although none well developed except possibly for a prescutellar pair; 3 pair of dorsocentral bristles (1 + 2), hind pair slightly displaced laterally; wings generally immaculate; costal vein extending to apex of vein $M_{1+2}$.

DESCRIPTION.—Small to moderately small shore flies, length 1.25 to 2.90 mm; face arched, protruding; body coloration generally subdued, gray to dark brown.

*Head*: Face prominent, arched, setulose. Frons wider than high, often with distinct, shiny mesofrons that contrasts with duller, pollinose parafrons, frons otherwise uniformly dull colored, mesofrons of some species with small setae along margin or generally scattered over surface. Ocellar triangle raised in relief from mesofrons; dull, pollinose, frequently contrasting with mesofrons if mesofrons shiny; ocelli arranged to form equilateral or isosceles triangle, sometimes brightly colored; 1 pair of large, proclinate, divergent ocellar bristles, 1–3 pair of much smaller, divergent postocellar setae between or posterior of posterior pair of ocelli. Generally only 2 pair of prominent, lateroclinate frontoorbital bristles, although a smaller seta is usually present anterior of and between larger pair; 2 pair of vertical bristles; postocular setae variously developed, usually subequal to postocellar setae. Antenna dark colored, second segment setose, especially toward ventral, median, and dorsal surfaces; arista pubescent; length of arista variable. Marginal

facial setae larger and often with 1–2 pair of dorsally-curved larger setae toward lateral margins. Eye round to oval; eye-to-cheek ratio 1 : 0.17–0.60. Oral opening large; clypeus concealed; maxillary palp small, dark colored; prementum large, bulbous, setose.

*Thorax*: Mesonotum mostly pollinose, dull colored to subshiny, generally unicolorous but usually with faintly evident, dark and light colored vittae, especially along setal tracts; presutural portion often with some partially shiny metallic areas; scutellum either concolorous or slightly lighter in color than mesonotum; pleural areas generally concolorous with mesonotum. Chaetotaxy of thorax as follows: Acrostichal setae in 2 rows, setae generally subequal to each other, small, 1 pair of presutural bristles; 3 pair of dorsocentral bristles (1 + 2), posterior pair inserted laterad of alignment of other dorso-centrals, often with a few smaller setae between larger bristles; 1 pair of postalar bristles; several smaller intra-alar setae generally between larger bristles; 2 pair of lateral scutellar bristles, posterior pair better developed; 2 pair of notopleural bristles; 1 larger mesopleural bristle inserted near posterior margin, several smaller setae, especially toward anterior and posterior margins; 1 larger sterno-pleural bristle, generally 1 smaller bristle anterior of larger one. Legs mostly concolorous with pleural areas, some species with pale basitarsi. Wing mostly immaculate, hyaline to slightly infumated; Setae along costal margin well developed in some species, otherwise normally developed. Costal vein ratio from 1 : 0.14–0.24, with considerable intraspecific variation; costal vein extending to apex of vein $M_{1+2}$. $M_{1+2}$ vein ratio from 1 : 0.54–0.70. Halter pale, yellow to white.

*Abdomen*: Males with 5 visible terga, females with 6–7. Coloration more or less uniform, sometimes slightly darker toward margins; dorsal setae small and scattered. Structures of male terminalia symmetrical, reduced, consisting of andrium only, see subgeneric descriptions for further detail. Female terminalia consisting of terga 6–8 and sterna 6, 7+8, and 9. Sterna 7+8 and 9 paired, symmetrical, setose, but lacking spines. Ninth tergum possibly fused with terminal cerci. Female ventral receptacle variously shaped, see descriptions of subtaxa.

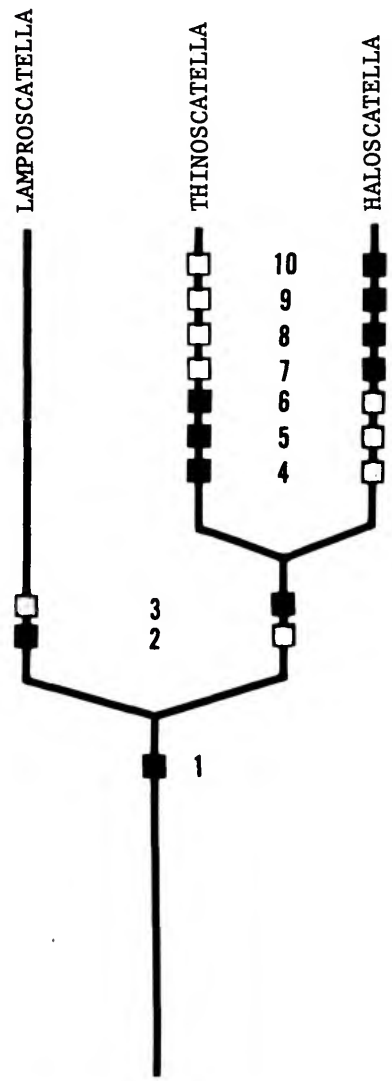



FIGURE 1.—Hypothetical phylogeny for the subgenera of *Lamproscatella*, based on the character states outlined in Table 1. (Solid squares = apotypic character states; open square = plesiotypic character states.)

DISCUSSION.—Within the tribe Scatellini, *Lamproscatella* is one of the more problematic genera. Its relationships with other genera are poorly understood, and its status has been unstable historically. It has been variously treated as a "valid" genus or

TABLE 1.—Characters and character states used in cladistic analysis of the subgenera of *Lamproscatella*

| CHARACTERS | Plesiotypic | Apotypic |
|---|---|---|
| 1. Genal bristle | Present | Absent |
| 2. Vestiture of mesofrons | Lacking | Mostly pollinose, dull |
| 3. Eye-to-cheek ratio | 1 : 0.25 or smaller | 1 : 0.35 or larger |
| 4. Position of posterior fronto-orbital bristle | Inserted closer to anterior bristle than to inclinate vertical bristle | Inserted closer to inclinate vertical bristle than to anterior fronto-orbital bristle |
| 5. Surstyli | Evident as distinct lobes | Fused indistinguishably or lacking |
| 6. Arrangement of ocelli | Isosceles triangle | Equilateral triangle |
| 7. General coloration | Brown to grayish brown | Mostly gray |
| 8. Shape of eye | Round or nearly so | Wider than high |
| 9. Position of posterior notopleural bristle | At same level as anterior bristle | Distinctly raised above level of anterior bristle |
| 10. Habitat | Freshwater | Saline or alkaline water |

as a subgenus of *Scatella*. The latter is clearly untenable. There is now substantial evidence (Mathis and Shewell, 1978) to indicate the monophyly and relationships of *Scatella* and related genera, not to include *Lamproscatella*.

Two general problems are evident. One concerns the monophyly of *Lamproscatella;* the other concerns its relationships within the tribe.

Because convincing evidence is lacking, the hypothesis of monophyly of *Lamproscatella* must be considered provisional. The status and composition of the genus as herein defined are traditional and lack an objective basis. Further resolution of relationships will depend on accumulation of evidence of relationships in related taxa.

The one character state that is possibly apotypic is the traditional "key" character for the genus—a conspicuous genal bristle is either lacking or much reduced (genal setae are present, and one could be the reduced genal bristle). But the apparent loss of a simple structural feature, such as this one, is not convincing evidence of relationship because of the likelihood of its independent occurrence in various lineages. Thus, the possibility that *Lamproscatella* is paraphyletic cannot be discounted.

As for generic relationships, my assessment is that *Lamproscatella* is closely related to *Philotelma* Becker and *Coenia* Robineau-Desvoidy, although these relationships are primarily patristic, being based on plesiotypic character states (see generic diagnosis). Character states distinguishing specimens of these two genera from those of *Lamproscatella* are as follows: Specimens of *Coenia* are generally darker colored, have a pectinate arista, four pair of dorsocentral bristles, a conspicuous genal bristle, parafrons generally concolorous with shiny mesofrons, and have distinct male terminalia (Mathis, 1975); specimens of *Philotelma* are smaller, have a pectinate arista, and distinctive male terminalia.

The preceding problems are further complicated by the relatively large degree of structural diversity exhibited within *Lamproscatella* itself. I have divided *Lamproscatella* into three subgenera, and the distinguishing gap between each is greater than for some so-called genera of the *Scatella*-related complex of genera. The differences between *Neoscatella* Malloch and *Scatella,* for example, are considerably less. The species in each subgenus, however, are fairly uniform, and there is little doubt as to which subgenus a particular species belongs. Similarity or lack thereof, however, is not necessarily an indication of relationship.

The relationships among the subgenera are as outlined in the cladogram (Figure 1) and Table 1. The relationships within each subgenus are discussed separately in their respective discussion sections.

## Key to Subgenera of *Lamproscatella*

1. Posterior notopleural bristle inserted approximately midway between dorsal angle and posterior angle, at distinctly higher level than anterior bristle; eye wider than high, generally oriented at slight oblique angle to oral margin ..... ***Haloscatella,*** new subgenus
   Posterior notopleural bristle closer to posterior angle than to dorsal angle, at approximately same level with anterior bristle; eye slightly higher than wide, appearing round .....2
2. Posterior fronto-orbital bristle inserted closer to inclinate vertical bristle than to anterior fronto-orbital bristle; eye-to-cheek ratio 1 : 0.35 or more; mesofrons shiny ..... ..... ***Thinoscatella,*** new subgenus
   Posterior fronto-orbital bristle inserted closer to anterior fronto-orbital bristle than to inclinate verticle bristle; eye-to-cheek ratio 1 : 0.25 or less; mesofrons at most subshiny..... ..... ***Lamproscatella*** Hendel

### ***Haloscatella,*** new subgenus

TYPE-SPECIES.—*Lamproscatella* (*Haloscatella*) *arichaeta* Mathis, new species, by present designation.

SPECIES INCLUDED.—*Lamproscatella arichaeta,* new species; *L. cephalotes* Cresson; *L. muria,* new species; *L. nivosa* Cresson; *L. salinaria* (Sturtevant and Wheeler).

DIAGNOSIS.—Specimens of this subgenus are very distinctive and may be separated from those of *Thinoscatella* and the nominate subgenus by the following combination of characters: Coloration of most species generally grayer and more pollinose, particularly on face, pleural areas, and abdomen; eye-to-cheek ratio at least 1:0.50; eye obliquely oriented to general plane of head; facial setae gradually becoming longer toward oral margin; setae along oral margin only slightly longer than those above; a distinctive, large, slightly dorsally curved facial bristle near posteroventral angle of face, approximately in line with anterior margin of eye; face in profile more protruding; insertion of posterior notopleural bristle distinctly elevated above level of anterior bristle; a distinct dorsally curved bristle toward anterodorsal corner of mesopleuron; acrostichal setae weak, sparse, seriated into two rows that sometimes converge or overlap each other; prescutellar setae well developed, differing distinctly from other acrostichal setae by being more widely set apart. The male terminalia of the subgenus are morphologically diverse, and in most species, the structures appear to have undergone considerable modification. For species of one lineage, a unique condition exists, wherein secondary extensions of the hypandrium fuse beneath the internal genitalia to form a well sclerotized bridge. The operculum of the female ventral receptacle is broadly fused to the extending process, the latter is wide and rounded; the paired, extending receptacle processes have parallel sides or taper evenly, lacking a median swelling.

ETYMOLOGY.—*Haloscatella* is a combination of the Greek *halo* ("salt") and *scatella,* referring to the brackish-water habitats of these *Scatella*-like flies.

GEOGRAPHIC DISTRIBUTION.—With the exceptions of *L. dichaeta* (Loew) (disjunct Old World distribution) and possibly *L. fluvialis* Miyagi (Japan), members of this subgenus occur only in the Western Hemisphere. Their present center of diversity appears to be western North America, where most species have widespread distributions. Although some species occur along the coasts, they are more abundant inland, especially around the salt-caked shores of shallow saline or alkaline lakes.

NATURAL HISTORY.—Members of this subgenus are distinctly halophilous and seem to proliferate best where saline or alkaline conditions are near saturation. In late summer, when the water level has lowered and exposed more shoreline around many of the shallow lakes of western North America, species of the subgenus are often found in great abundance. As the newly exposed shoreline dries, a white, crystaline layer of salt is formed on the surface, and cracks begin breaking the upper layers of sediment into smaller portions. Within the cracks thousands of flies are frequently encountered. The cracks probably provide protection from heat and the bottoms are the only nearby source of moisture. Scheiring and Foote (1973) also collected *Haloscatella* from small pools of saline water formed from drainage of a larger brine storage and of a salt plant near Rittman, Ohio.

DISCUSSION.—Members of *Haloscatella* are quite homogeneous in overall appearance and are unlikely to be confused with members of the other subgenera. Superficially they are quite similar to

some primitive members of the genus *Scatella* Robineau-Desvoidy, i.e., *S. paludum* (Meigen), *S. favillacea* Loew, and *S. lutosa* (Haliday). The character states that align these species with *Lamproscatella* are primitive (plesiotypic) and an examination of the unique chaetotaxy, structures of the male and female terminalia, and spotted wings (sometimes faint) should quickly eliminate any confusion of generic association.

A suggested phylogeny of the species included in

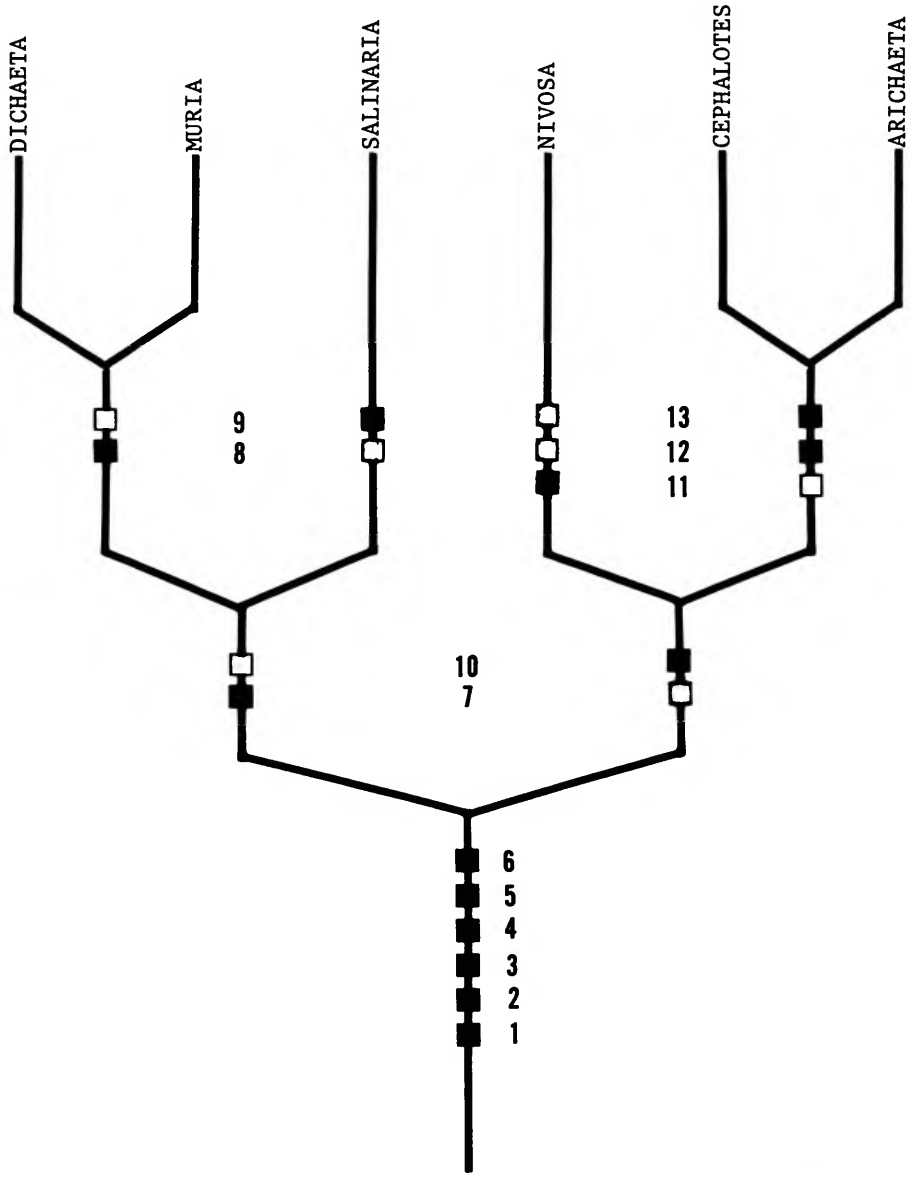



FIGURE 2.—Hypothetical phylogeny for the species of the subgenus *Haloscatella*, based on the character states outlined in Table 2. (Solid squares = apotypic character states; open squares = plesiotypic character states.)

TABLE 2.—Characters and character states used in cladistic analysis of the species of the subgenus *Haloscatella*

| CHARACTERS | Plesiotypic | Apotypic |
|---|---|---|
| 1. Position of posterior notopleural bristle | At same level as anterior bristle | At distinctly higher level than anterior bristle |
| 2. Shape of eye | Round or nearly so | Wider than high |
| 3. Small, distinct ventrally-curved mesopleural seta near anterodorsal corner | Absent | Present |
| 4. General coloration | Brown or grayish brown | Mostly gray |
| 5. Habitat preference | Freshwater | Saline or alkaline water |
| 6. Operculum of female ventral receptacle | Distinct from female ventral receptacle | Fused with female ventral receptacle |
| 7. Size of cercal cavity | Small | Large |
| 8. Shape of ventral margin of epandrium | Parallel sided | Narrowing abruptly at ventral apex |
| 9. Color of hind basitarsi | Concolorous with tibiae | Yellowish |
| 10. Lateral margins of epandrium | Ending at juncture of gonite | A process continuing from each side which is fused anteromedially |
| 11. Vestiture of mesofrons | Mostly lacking, shiny | Densely pollinose, dull |
| 12. Orientation of third fronto-orbital bristle | Lateroclinate | With posteroblique orientation |
| 13. Development of setae | Normally developed | Setae generally stronger, longer and wider |

*Haloscatella* is proposed as outlined in Figure 2, and Table 2, which lists character states. The monophyly of *Haloscatella* is well established as indicated by the number of autapotypies.

In addition to species of the Nearctic fauna, two others are included in this subgenus: *L. dichaeta* (Loew, 1860; Europe and South Africa) and *L. fluvialis* Miyagi (1977; Japan). Specimens of *L. dichaeta* are very similar to those of *L. muria,* and except for structures of the male terminalia, cannot be distinguished. I have not examined specimens of *L. fluvialis,* but Miyagi (1977) compared *L. fluvialis* with *L. dichaeta* in his diagnosis of the former, so I suspect the two are closely related.

## Key to Species of the Subgenus *Haloscatella*

1. Mesofrons dull, mostly pollinose, not distinctly contrasting in color or texture with parafrons, blending gradually with parafrons ..... 4. ***L. nivosa*** Cresson
   Mesofrons usually subshiny to shiny, distinctly contrasting with parafrons ..... 2
2. Third fronto-orbital seta much reduced, length less than half that of first, inserted mesad of alignment of other fronto-orbitals, much closer to second than to fourth, orientation nearly reclinate ..... 3
   Third fronto-orbital seta larger, at least one-half length of first, inserted only slightly closer to second fronto-orbital than to fourth, orientation lateroclinate ..... 4
3. Mesonotum with considerable gray coloration; dorsum of scutellum mostly gray; each surstylus more or less parallel-sided, fingerlike, densely setose along median surface; width of gap between surstyli less than width of surstylus ..... 2. ***L. cephalotes*** Cresson
   Mesonotum and scutellum mostly brown; surstylus gradually tapering from base to apex; width of gap between surstyli about equal to length of surstylus, much greater than width of surstylus ..... 1. ***L. arichaeta,*** new species
4. Mesofrons shiny, subquadrate, broadly reaching frontal suture; basitarsi pale, yellowish; disc of mesonotum generally gray; larger species, length generally greater than 1.75 mm.... ..... 5. ***L. salinaria*** (Sturtevant and Wheeler)
   Mesofrons subshiny to shiny, lateral margins distinctly narrowing anteriorly, shiny area often weak anteromedially, dull; smaller species, length generally less than 1.65 mm ..... ..... 3. ***L. muria,*** new species

### 1. *Lamproscatella (Haloscatella) arichaeta*, new species

FIGURES 3–6

DIAGNOSIS.—Although specimens of *L. arichaeta* appear to be very similar to those of *L. cephalotes*, they may be distinguished from the latter by the following combination of characters: Specimens averaging smaller in overall size; setal development much less pronounced; mesonotum generally more brownish. The male terminalia of *L. arichaeta* males differ markedly from those of *L. cephalotes* males, being smaller and of a unique conformation, particularly the shape of the surstyli (Figures 3–5).

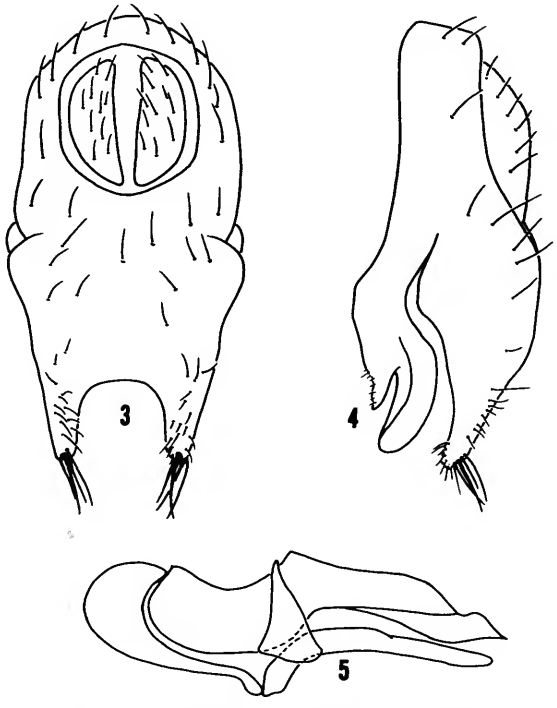
DESCRIPTION.—Small to moderately small shore flies, length 1.70 to 2.45 mm (averaging 2.00 mm); generally brownish gray, with some extensive brown colored areas.

*Head:* Head width-to-height ratio averaging 1:0.74; coloration whitish gray to brown. Mesofrons subshiny to shiny with metallic brown to bluish green luster, subtriangular, rounded anteriorly, with 1–2 pair of small setae marginally; parafrons mostly charcoal gray, ocellar triangle pollinose, brown. Anterior fronto-orbital seta large, length at least one-half that of larger, posterior bristles; third fronto-orbital seta much reduced, inserted mesad of line of other bristles, very close to second bristle, oriented at posteroblique angle to other fronto-orbitals. Dorsalmost postocular seta more strongly developed than remaining postoculars, inserted posterolaterad of divergent vertical bristle. Antennal segments dark colored, mostly blackish, pollinose; arista slightly longer than combined length of second and third segments. Face whitish gray, densely pollinose to tomentose, protruding and arched; lateral facial setae larger than median ones, becoming larger toward posteroventral angle of face; setae along oral margin only slightly larger than median facial setae. Eye-to-cheek ratio averaging 1 : 0.47; gena concolorous with face; 2–3 parafacial setae.

*Thorax:* Dorsum mostly light brown, becoming grayer on pleural areas, especially toward venter. Scutellum lighter brown in coloration than disc of mesonotum. Setation quite pronounced and well developed. Legs becoming darker toward apices; apical tarsomeres mostly black. Wing hyaline to faintly infumated with grayish brown coloration: costal margin only slightly setose; costal vein ratio averaging 1 : 0.17; $M_{1+2}$ vein ratio averaging 1 : 0.55; posterior crossvein with posterior half slightly angulate laterally, wrinkled in middle.

*Abdomen:* Generally grayer than dorsum of thorax, but also with considerable brown coloration. Male terminalia with surstyli fused to epandrium and forming open triangle with pocket formed by paired arms U-shaped and shallow (Figures 3–5).

TYPE MATERIAL.—Holotype male is labeled: "WASH Grant Co Soap Lake 5 August 1973 Wayne Mathis/HOLOTYPE Lamproscatella arichaeta W N Mathis (red)." Allotype female and 46 paratypes (10♂, 36♀; USNM) have the same locality data as the holotype. Other paratypes are as follows: Oregon, Harney Co., Borax Lake, 7.2 km NE Fields, 29 Jul 1975, W. N. Mathis (1♂, 1♀; USNM); Malheur Co., 24.2 km NW Yale, 28 Aug 1965, Kenneth Goeden (1♀; USNM); Lake Co., Goose Lake State Park, 23 Aug 1970, Karl W. Simpson (1♂, 3♀; CU). The holotype is in the National




FIGURES 3–5.—*L. arichaeta:* 3, epandrium, surstyli, and cerci, posterior aspect; 4, epandrium, surstyli, and cerci, lateral aspect; 5, internal male terminalia, lateral aspect.

Museum of Natural History, Smithsonian Institution, Washington, D. C., type number 75956.

OTHER SPECIMENS EXAMINED.—UNITED STATES: CALIFORNIA: Kern Co., Onyx, 23 Jul 1940, D. E. Hardy (1 ♂, 2 ♀; KU, USNM); Lassen Co., Hallelujah Junction, 4 Jul 1949, P. D. Hurd (1 ♀; USNM). Spauldings, 27 Jul 1949, P. D. Hurd (2 ♀; USNM); Mono Co., Mammoth Lakes, 29 July 1949, L. J. Lipovsky (4 ♂; KU); Riverside Co., Palm Springs, 24–26 Mar 1918, J. C. Bradley (1 ♀; CU). MONTANA: Fire Hole River, 27 Aug 1940, A. L. Melander (1 ♂, USNM). NEBRASKA: Cherry Co., Big Alkali Lake, 2 Jun 1969, W. W. Wirth (1 ♂, USNM), Twin Lake, 2 Jun 1969, W. W. Wirth (3 ♂, 11 ♀; USNM). NEVADA: Churchill Co., Soda Lakes near Hazen, 13 Jul 1911 (1 ♀; USNM). OREGON: Union Co., North Powder, 13 Jun 1971, R. H. Beamer (1 ♂; USNM). SOUTH DAKOTA: Yankton Co., Gavins Point, 17 Jun 1969, W. W. Wirth (1 ♂; USNM). WASHINGTON: Grant Co., O'Sullivan Dam, 23 May 1954, 19 Jul 1955, M. T. James (3 ♂; WSU), Soap Lake, 24 July 1919, A. L. Melander (1 ♂, 2 ♀; USNM), Soda Lake near O'Sullivan Dam, Columbia National Wildlife Refuge, W. L. Turner (1 ♀; WSU), Warden Lake, Columbia National Wildlife Refuge, 16 Aug 1977, R. S. and V. L. Zack (2 ♀; WSU); Stevens Co., Evans, 13 June 1930, R. C. Shannon (1 ♂, 1 ♀; USNM). WYOMING: Hot Springs Co., Thermopolis, 13 Jun 1969, W. W. Wirth (2 ♀; USNM); Teton Co., Yellowstone National Park, U Geyser Basin, 7 Aug 1916, A. L. Melander (3 ♀; USNM).

GEOGRAPHIC DISTRIBUTION. (Figure 6).—This species occurs mainly west of the 100th meridian between 32° and 49° north latitude.

ETYMOLOGY.—The epithet *arichaeta* is a combination of the Greek *ari* ("very" or "much") plus *chaeta* ("bristle"), in allusion to the pronounced setation of specimens of this species.

REMARKS.—Specimens of *L. arichaeta* were confused with those of *L. cephalotes*. Like the latter, they are associated with aquatic systems that have an unusually high salt content. The type-locality, Soap Lake, is a popular recreational area in central Washington because of its dry, sunny climate, and because the lake water contains a variety of dissolved salts that are reputed to endow frequent bathers with improved health. The water margin is generally outlined with an accumulation of foam, hence the name for the lake. The sandy banks are an ideal habitat for tiger beetles (Cicindelidae) and other shore fly species. Specimens of *L. muria* also occur in abundance along the banks.

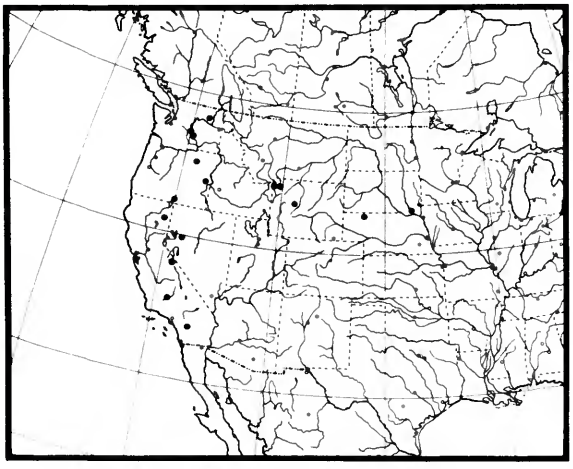


FIGURE 6.—Distribution map of *L. arichaeta*.

The extent and degree of brown coloration on the dorsum of specimens of this species, particularly on the mesonotum, displays considerable variability. In general, however, the brown coloration is better developed than in specimens of *L. cephalotes*. Care should be exercised in emphasizing either of these characters and if there is doubt, reference to the characters of the male terminalia should eliminate confusion.

## 2. *Lamproscatella (Haloscatella) cephalotes* Cresson

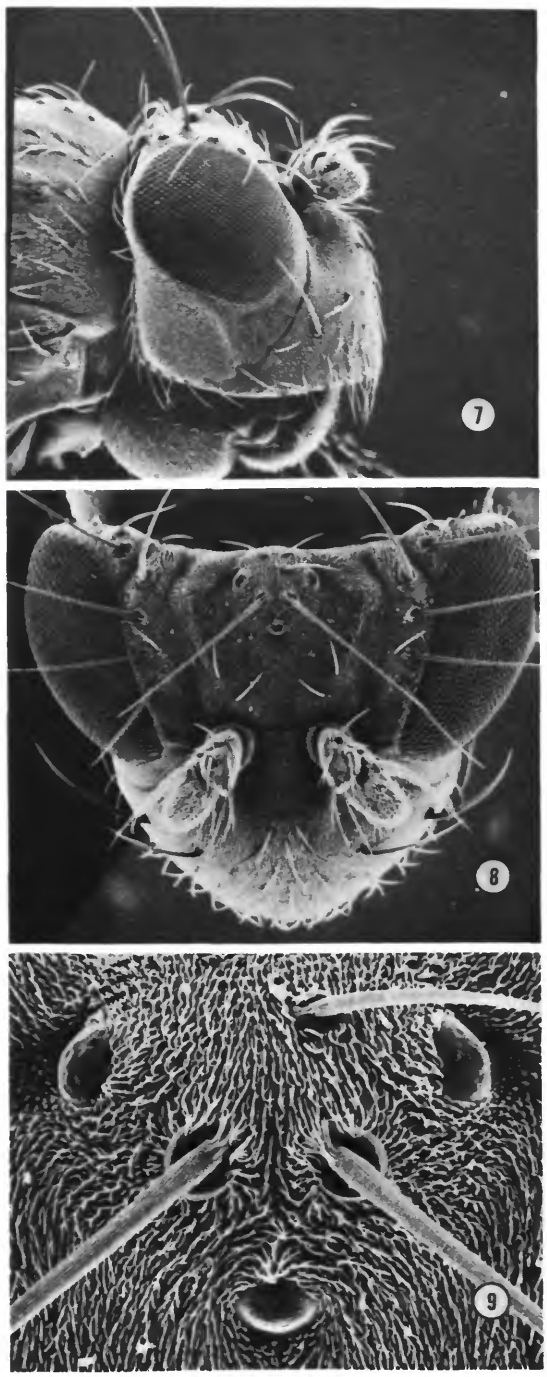
FIGURES 7–13

*Lamproscatella cephalotes* Cresson, 1935:360.—Wirth and Stone, 1956:475 [key, distribution in California].—Wirth, 1965:756 [catalog].

DIAGNOSIS.—This species and *L. arichaeta* are closely related as evidenced by their overall similarity. However, specimens of *L. cephalotes* may be distinguished from those of *L. arichaeta* and other congeners by the following combination of characters: Setal development more pronounced, appearing exaggerated; length of specimens averaging larger; mesonotum grayer in color. The structures of the male terminalia are larger, especially the surstyli which are fingerlike and densely setose along median surface (Figures 10–12).

DESCRIPTION.—Moderately small shore flies, length 2.05 to 2.90 mm (averaging 2.64 mm); coloration generally grey, often tinged with light blue or faint green, some brown colored areas on dorsum.

*Head* (Figures 7–9): Head width-to-height ratio averaging 1:0.7; mesofrons subtriangular, subshiny to shiny with metallic bluish green luster, contrasting with gray to charcoal gray parafrons, anterior margin with 1–3 setae. Ocellar triangle raised in relief from mesofrons, pollinose, brownish gray.




FIGURES 7–9.—*L. cephalotes:* 7, head, lateral aspect; 8, head, dorsal aspect, 9, ocelli, dorsal aspect.

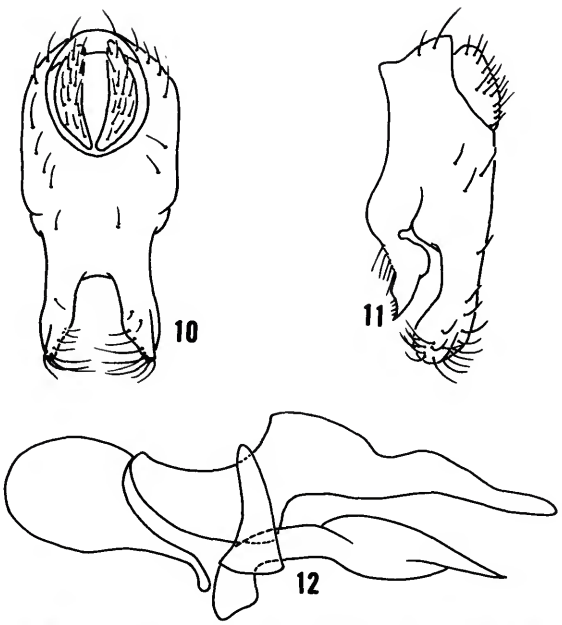
Anterior fronto-orbital seta well developed, length over one-half that of larger fronto-orbital bristles; third fronto-orbital seta much reduced, situated mesad of alignment of other setae. Postocular bristle inserted posterolaterad of divergent vertical bristle, length approximately double that of other postocular setae. Antenna dark, brownish black, pollinose, with some gray pollinose areas; arista short, subequal to length of second and third segments. Face distinctly protruding, arched, pollinose, generally gray but usually with faint brown coloration toward interfoveal carina; 2 larger facial setae inserted just below interfoveal carina, oriented obliquely, lateroventrad; second pair of larger, lateral setae oriented almost directly laterad; third pair of setae largest, inserted near posteroventral angle of face, slightly dorsally-curved; other facial setae subequal to each other, small; oral setae only slightly larger than facial setae. Eye-to-cheek ratio averaging 1:0.60; gena concolorous with face or lighter.

*Thorax:* Dorsum pollinose, generally gray, especially scutellum but with light brown areas of variable size. Setae appearing exaggerated, very well developed. Legs gray but with considerable darker appearing areas; basitarsi sometimes appearing amber colored, terminal tarsomeres charcoal gray. Wing hyaline to brownish tinged; costal margin distinctly setose; costal vein ratio averaging 1:0.15; $M_{1+2}$ vein ratio averaging 1:0.61, posterior crossvein often wrinkled, posterior half slightly angulate laterally.

*Abdomen:* Generally concolorous with thorax, with varying degrees of faint brown coloration, especially toward margins. Structures of male terminalia as in diagnosis and Figures 10–12.

TYPE MATERIAL.—Holotype male is labeled: "Salt Lake 26•6 Ut/H S Barber Collector/♂/Type No. 21844 U.S.N.M. [red]/Holo-TYPE 1 Scatella CEPHALOTES E. T. Cresson Jr. [red]/Type No. 51102 U.S.N.M. [red]." Allotype female has same label data as holotype. The holotype and allotype are in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., type number 51102.

SPECIMENS EXAMINED.—UNITED STATES: CALIFORNIA: Mono Co., Mono Lake, 2.4 km NE Mono Inn, 29 Feb 1964, J. D. Birchim (2♂; CAS), west shore Mono Lake, 22 Jun 1974, W. N. Mathis (17♂, 28♀; USNM). IDAHO: Elmore Co., 22 May 1938, H. S. Telford (1♂; UMN). NEVADA: Washoe




FIGURES 10–12.—*L. cephalotes:* 10, epandrium, surstyli, and cerci, posterior aspect; 11, epandrium, surstyli, and cerci, lateral aspect; 12, internal male terminalia, lateral aspect.

Co., Pyramid Lake, 24 Jun 1964, J. A. Miller (5♂, 3♀; UCD, USNM). OREGON: Lake Co., Abert Lake, 6.4 km N Valley Lake, 2 Jul 1964, J. D. Lattin (1♂; USNM). UTAH: Cache Co., Logan, 27 Jun 1960, G. F. Knowlton (1♂; UCD); Salt Lake Co., Salt Lake, 26 Jun, H. S. Barber (1♂, 1♀; ANSP).

GEOGRAPHIC DISTRIBUTION (Figure 13).—This species occurs in the Great Basin of the western United States from the area between 37° and 43° north latitude and west of 110° west longitude.

REMARKS.—Specimens of *L. cephalotes* are the largest of the subgenus. They also have the most pronounced features, particularly chaetotaxal. This species should only be confused with *L. arichaeta,* which has uniquely shaped male terminalia.

The type-locality, Great Salt Lake, is a well-known saline lake in western North America where several other species of shore flies also occur. The extreme saline conditions of this lake are inimical to most forms of life and except for brine shrimp, shore flies, and algae, few other living organisms are known to exist there. Despite the harsh environmental conditions, shore flies proliferate in great abundance (Wirth, 1971), posing a nuisance to

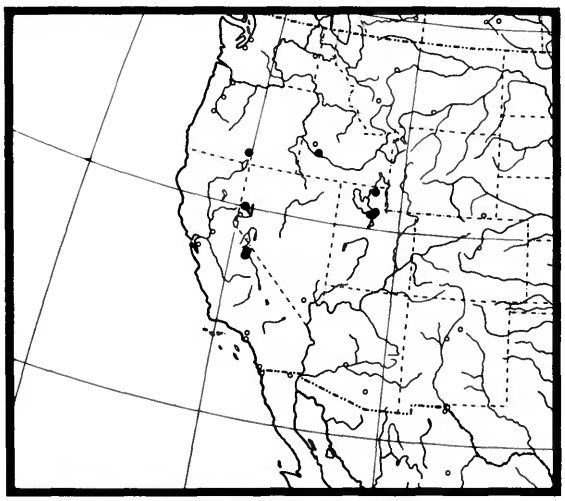


FIGURE 13.—Distribution map of *L. cephalotes.*

bathers (Hansen, 1969; Jorgensen, 1969) and consequently to the local tourist business.

Nemenz (1960) studied the osmotic regulatory mechanism of *Ephydra cinerea* Jones, a species of the same subfamily that also occurs in the lake. He found that it could withstand pressures of over 250 atmospheres and attributed this to the resistant cuticle and probably to an active osmotic regulation system. *Lamproscatella cephalotes* and other shore flies that inhabit the shoreline of this and similar lakes have probably developed similar mechanisms to overcome the extremely saline ambient conditions. I have also collected specimens of *L. cephalotes* along the shoreline of Mono Lake, California, and have examined a large series from Pyramid Lake, Nevada. Both of these lakes are highly saline.

### 3. *Lamproscatella (Haloscatella) muria,* new species

FIGURES 14–17

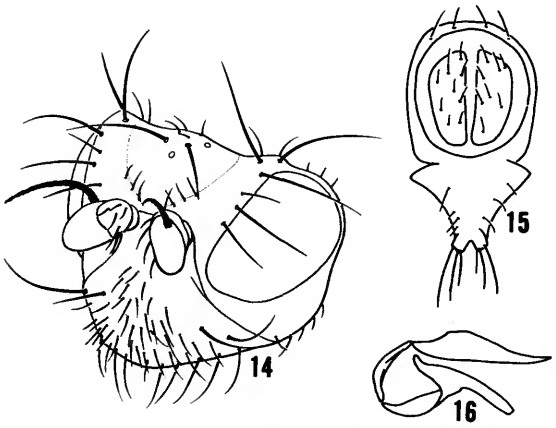
*Lamproscatella dichaeta* of American authors [misidentification, not Loew, 1860:40].—Sturtevant and Wheeler, 1954:175 [review as species of *Scatella*].—Wirth and Stone, 1956:475 [key, distribution in California].—Deonier, 1964:108 [key as species of *Scatella*].—Wirth, 1965:756 [catalog].

DIAGNOSIS.—Although specimens of this species are similar externally to those of *L. dichaeta,* they may be distinguished from the latter by the following combination of characters: Surstyli more elon-

gate and more narrowly produced, slightly bifurcate apically, apices bearing approximately 4 longer setae; aedeagal apodeme narrower; aedeagus more slender (Figures 15–16).

DESCRIPTION.—Small shore flies, length 1.27 to 1.97 mm (averaging 1.61 mm); coloration mostly tannish brown dorsally, becoming distinctly lighter, grayer on sides.

*Head* (Figure 14): Head width-to-height ratio averaging 1:0.76; mesofrons shiny with metallic bluish green to gold luster, shiny area often weakened toward anterior margin, usually with 2–3 small setae along anterolateral margin; ocellar triangle and posteromedian portion of parafrons concolorous, pollinose, brown; otherwise coloration of parafrons mostly gray to charcoal gray and distinctly contrasting with mesofrons. First and third fronto-orbital setae considerably smaller than second and fourth; first slightly longer than third; third generally aligned and oriented with other fronto-orbital setae. Postocular setae subequal to each other except for 1–2 pair of larger setae just posterolaterad of divergent vertical bristle. Antenna dark, mostly grayish black; arista pubescent to macropubescent, subequal to combined length of second and third segments. Face generally whitish silver, but varying considerably from faint tannish dorsally to distinctly grayish white, often with darker coloration toward interfoveal carina, otherwise unicolorous; generally only 2 pair of larger, lateral facial setae; 1 large slightly dorsally curved bristle toward posteroventral angle of face; usually 1–3 setae along lower parafrons. Eye-to-cheek ratio averaging 1:0.48; eye ratio averaging 1:0.79; gena generally concolorous with face.




FIGURES 14–16.—*L. muria:* 14, head, lateroblique aspect; 15, epandrium, surstyli, and cerci, posterior aspect; 16, internal male terminalia, lateral aspect.

*Thorax:* Mesonotum light brown with some grayer areas toward margins, especially above dorsal angle of notopleuron; scutellum grayer, terminal portion usually distinctly lighter gray to whitish gray; pleural areas contrastingly grayer, but often with some areas appearing discolored, faint brown; legs gray to black, pollinose; basitarsi sometimes with some pale, amber coloration, especially along ventral surfaces; apical tarsomeres mostly black. Wing hyaline; costal margin only slightly setose; costal vein ratio averaging 1:0.20; $M_{1+2}$ vein ratio averaging 1:0.54; posterior crossvein with slight median wrinkle, posterior portion slightly angulate laterally.

*Abdomen:* Dorsum mostly gray, darker than pleural areas, usually with some faint metallic bluish green luster and light brownish coloration toward anterior and posterior margins. Structures of male terminalia as in diagnosis and Figures 15–16.

TYPE MATERIAL.—Male holotype is labeled: "Thermopolis Wyo. Hot Spng. 13 June 1969 W. W. Wirth hot spring/HOLOTYPE Lamproscatella muria W. N. Mathis [red, handwritten]." Allotype female and 33 paratypes (7♂, 26♀; USNM) have same label data as the holotype. Other paratypes are as follows: Colorado, Archuleta Co., Pagosa Springs, 27 May 1969, W. W. Wirth (8♂, 9♀; USNM). Missouri, Howard Co., Booneslick Salt Spring, 17 May 1969, W. W. Wirth (2♂, 3♀; USNM). Montana, Roosevelt Co., Bainville, 9 Jun 1969, W. W. Wirth (1♂; USNM). Nebraska, Cherry Co., Big Alkali Lake, 2 Jun 1969, W. W. Wirth (1♀; USNM), Twin Lake, 2 Jun 1969, W. W. Wirth (5♂, 5♀; USNM); Lancaster Co., Lincoln, 19 Jun 1969, W. W. Wirth (1♂, 6♀; USNM). North Dakota, Benson Co., Leeds, 5 Jul 1969, W. W. Wirth (5♂, 11♀; USNM); Mountrail Co., White Lake, 8 Jun 1969, W. W. Wirth (2♂, 1♀; USNM). The holotype and paratypes are in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., type number 75955.

OTHER SPECIMENS EXAMINED.—CANADA: ALBERTA: Coden, 22 Oct 1916, A. H. Sturtevant (4♂, 5♀; USNM); Edmonton, 1932, O. Bryant (1♂; USNM); Leroy, 11–12 Jun 1917 (2♀; USNM); Okotoks, Sheep River, 27 Jun 1968, W. W. Wirth (1♀; USNM). MANITOBA: Baldur, 23 Jun 1924, R. D. Bird

(1♀; CNC); Churchill, 22 Jun–30 Aug 1948, G. E. Shewell, W. R. Richards (1♂, 1♀; CNC); Forrest, 6.4 km N, 29 Jul 1958, N. B. Chillcott (2♂, 4♀; CNC); Whitewater Lake, 6.4 km N Whitewater, 17 Jul 1958, N. B. Chillcott (3♀; CNC). NOVA SCOTIA: Baddeck, 15 Jul 1936, T. N. Freeman (1♂, 1♀; CNC). MEXICO: BAJA CALIFORNIA: Agua Caliente, San Carlos, 18.5 km E Maneadero, 6 Jul 1973, P. H. Arnaud, Jr. (2♂, 1♀; CAS); Cabo Calnette, 24 Mar 1950, A. H. Sturtevant (1♂; USNM); Ensenada, 80.5 km S, 12 Mar 1950, A. H. Sturtevant (1♂; USNM). JALISCO: Ajijic, 11 Sep 1964, W. L. Nutting, (1♂, 3♀; USNM). MEXICO: Lago Texcoco, 7340 feet, 1 Nov 1963, B. Krogstad (1♂; USNM). UNITED STATES: ALABAMA: Mobile Co., Theodore, 10 Jun 1917 (1♂; CU); Washington Co., Leroy, 11–12 Jun 1917 (10♂, 12♀; CU); Wilcox Co., Flatwood, 12 Jun 1917 (1♂, 3♀; CU). ARIZONA: Coconino Co., Happyjack, 9.7 km N, 13 Jun 1971, B. A. Foote (1♀; KSU), Sedona, Oak Creek Canyon, 29 Jun 1953, W. W. Wirth (1♂; USNM), The Gap, 17 Jun 1950, A. H. Sturtevant (1♂, 2♀; USNM); Graham Co., Fort Thomas, 18 May 1950, A. H. Sturtevant (1♀; USNM), Geronimo, 17 May 1950, A. H. Sturtevant (1♂, 6♀; USNM); Maricopa Co., Buckeye, 4.8 km S Apr 1969, W. N. Mathis (2♀; USNM), Tempe, 11 May 1942, A. L. Melander (2♀; USNM); Pima Co., Organ Pipe Cactus National Monument, Williams Spring, 16 Feb 1970, P. H. Arnaud, Jr. (1♀; CAS), Upper Sabino Canyon, Santa Catalina Mountains, 24 May 1971, B. A. Foote (1♂; KSU); Yavapai Co., Prescott, 15 June 1950, A. H. Sturtevant (1♀; USNM). CALIFORNIA: Alameda Co., Berkeley, 11 Apr–4 Oct, 1908–1947, W. W. Wirth (9♂, 1♀; ANSP, USNM), Jewell Lake, 4 Oct 1947, W. W. Wirth (4♂, 3♀; USNM); Contra Costa Co., Antioch, 5 Apr 1952, P. D. Hurd (2♂, 1♀; USNM), Jewell Lake, 4 Oct 1947, W. W. Wirth (8♂, 8♀; USNM), Richmond, 28 Dec 1947, W. W. Wirth (1♀; USNM), Humboldt Co., Trinidad, 18 Sep 1934, A. L. Melander (1♀; USNM); Imperial Co., Salton Sea, 9 Mar 1950 (1♂, 3♀; USNM); Inyo Co., Deep Spring, 16 Jul 1953, E. I. Schlinger (1♀; UCD); Lake Co., Butts Creek, 0.8 km SE Black Oak, 250 m, 11 Oct 1971, H. B. Leech (1♀; CAS), Clear Lake, 19 Apr–11 Oct, 1935–1954, A. L. Melander, W. W. Wirth, E. I. Schlinger (4♂, 4♀; UCD, USNM), North Fork Cache Creek, highway 20, 14 May 1961, F. D. Parker (1♂; USNM); Los Angeles Co., Long Beach, Los Angeles River, 26 Jun 1954, M. T. James (3♂, 2♀; USNM, WSU), Los Angeles, 29 Jul 1897, A. P. Morse (1♀; MCZ); Love Joy Spring, Mojave Desert, 10 May 1944, A. L. Melander (1♂, 2♀; USNM), Saugus, 8.1 km E, 10 Apr 1953, A. H. Sturtevant (1♀; USNM), Whittier, 5 Oct 1960, A. L. Melander (2♀; USNM); Madera Co., San Joquin Experiment Station, 22 Feb 1953, P. D. Hurd (1♀; USNM); Mono Co., Bridgeport, 7000 feet, 7–18 Jun, 1948–1954, A. H. Sturtevant, W. W. Wirth (1♂, 5♀; USNM), Mono Lake, 29 Feb 1964, J. D. Birchim (1♀; CAS), Topaz Lake, Jul 1948, W. W. Wirth (1♀; USNM); Monterey Co., Pacific Grove, upper beach, 6 May 1906, J. M. Aldrich (1♀; USNM); Napa Co., Knoxville, 26 Oct 1952, J. C. Hall (1♀; UCR); Orange Co., Corona del Mar, 15 Feb–22 Mar, 1946–1950, A. H. Sturtevant, A. L. Melander (4♀; USNM), Dana Point, 25 Mar 1953, A. H. Sturtevant (1♂, 1♀; USNM), Laguna Beach, 25 Mar–5 Apr, 1945–1953, A. H. Sturtevant, A. L. Melander (3♂, 6♀; USNM), La Jolla, 22 Jun 1950, A. L. Melander (1♀; USNM); Riverside Co., Agua Caliente Indian Reservoir, Palm Canyon, 25 Feb 1970, P. H. Arnaud, Jr. (1♀; CAS), Deep Canyon, 3 May 1963, E. I. Schlinger (1♀; UCR), Deep Creek, 25 Oct 1953, A. L. Melander (1♂; USNM), Lake Elsinore, 4 Jan–21 Nov, 1911–1950, A. H. Sturtevant, A. L. Melander, J. M. Aldrich (19♂, 66♀; ANSP USNM), Palm Springs, 24–26 Mar 1918, J. C. Bradley (1♀; CU), Pushawalla Palms, Indio Hills, 20 May 1965, M. E. Irwin (1♀; UCR), Riverside, 6 Jan–29 Sep, 1934–1935, A. L. Melander (2♂; USNM); San Bernardino Co., Chino, 6 Sep 1925 (1♀; USNM), Helendale, 18 May 1955 (1♂; CNC), Salt Wells, 30 Mar 1951, P. D. Hurd (1♂, 2♀; USNM), Trona, 31 Mar 1953, A. H. Sturtevant (4♀; USNM), Trona, 19.3 km S, 31 Mar 1953, A. H. Sturtevant (1♂, 4♀; USNM), Vidal, Apr 1948, R. Coleman (1♀; USNM); San Diego Co., Agua Caliente, 5 Apr 1967, D. M. Wood (2♂, 3♀; CNC), Del Mar, 15 Sep 1955, A. L. Melander (4♂, 7♀; USNM); San Luis Obispo Co., Oso Flaco Lake, 15–23 Jun, 1948–1965, W. W. Wirth, R. Orth (1♂, 6♀; UCR, USNM); San Mateo Co., Dumbarton Bridge, 30 Jul 1947, W. W. Wirth (1♂; USNM); Redwood City, 4 May 1947, P. H. Arnaud, Jr. (1♂, 1♀; CAS); Santa Barbara Co., Carpinteria, 2–11 Aug 1950, A. L. Melander (1♂, 19♀; USNM), Cuyler, Harbor San Miguel Island, 11 Jul 1970, R. O. Schuster (1♂, 1♀; USNM), Santa Ynez River, 23 Jun 1965, M. E. Irwin (1♀; UCR); Santa Clara Co., Palo Alto, salt marshes, 20 Apr 1906, J. M. Aldrich (3♀; USNM); Santa Cruz Co., Santa Cruz, 1 Sep 1953, P. H. Arnaud, Jr. (1♂, 2♀; CAS); Solano Co., Cordelia Road, 0.8 km E Pittman Road, 24 Aug 1970, K. W. Simpson (1♂, 2♀; CU); Ventura Co., Rincon Beach or Point, Ventura, 28 Aug–9 Sep. 1945–1946, A. L. Melander (4♂, 12♀; USNM), Santa Paula, 8 May 1952, A. H. Sturtevant (1♀; USNM); Wheeler Canyon, 13 Apr 1954, J. C. Hall (3♀; UCD, USNM); Yolo Co., Davis, 4 Apr–13 Aug, 1952–1967, E. I. Schlinger, J. C. Hall, C. R. Kovacic (3♀; UCD, USNM), Winters, 1 May–19 Jun, 1940–1966, G. E. Bohart, R. O. Schuster (3♂; CAS, UCD, USNM). COLORADO: Archuleta Co., Pagosa Springs hot springs, 27 May 1969, W. W. Wirth (8♂, 9♀; USNM); Larimer Co., Fort Collins, 10 Aug 1937, M. T. James (1♂; ANSP). CONNECTICUT: Fairfield Co., Redding, 12 Aug 1939, A. L. Melander (1♀; USNM). DELAWARE: Sussex Co., Rehoboth, 25 Jun 1939, A. L. Melander (1♂, 8♀; USNM). FLORIDA: Gulf Co., Beach at McNeil's, 25 Mar 1954, G. C. Steyskal (1♀; MCZ), St. Joseph State Park, 1–3 May 1970, W. W. Wirth (2♀; USNM); Lee Co., Bonita Beach seashore, 17 Apr 1970, W. W. Wirth (1♂, 4♀; USNM), Sanibel Island, 11 May 1973, W. W. Wirth (3♂, 6♀; USNM); Levy Co., Cedar Key, 25 Apr 1970, W. W. Wirth (1♀; USNM); Monroe Co., Everglades National Park, 8 Apr 1970, W. W. Wirth (1♀; USNM); Pinellas Co., St. Petersburg, 16 Feb–12 Aug, 1910–1932, J. C. Bradley, E. T. Cresson, A. L. Melander (2♂, 7♀; ANSP, CU, USNM). GEORGIA: Chatham Co., Tybee Island, 31 Jan 1971, J. R. Vockeroth (2♂, 5♀; CNC). IDAHO: Kootenai Co., Fernan Lake, 15 Jul 1968, W. N. Mathis (1♂; USNM); Latah Co., Potlach, 21 Sep 1918 (2♂; USNM). KANSAS: Barton Co., Great Bend, 5 June 1939, R. H. Beamer (1♂; USNM). MAINE: Chebrag, 3 Sep 1952, A. H. Sturtevant (1♂; USNM). MASSACHUSETTS: Barnstable Co., Woodshole, 6 Jun–3 Aug, 1922–1952, A. H. Sturtevant (2♂, 4♀; USNM), Falmouth Hts, 13 Aug 1924 (1♂; USNM), South Yarmouth, 1 Aug 1939 (1♂, 5♀; USNM); Dukes Co., Naushon Island, 9–16 July 1922, A. H.

Sturtevant (2♂, 1♀; USNM), Nonomesset Island, 28 Jun 1923, A. H. Sturtevant (2♂, 3♀; USNM), Pasque Island, 15 Aug 1923, A. H. Sturtevant (4♂, 1♀; USNM). MICHIGAN: Wayne Co., Detroit, 13 May 1939, G. C. Steyskal (1♀; USNM). MINNESOTA: Dakota Co., Mendota, 14 Oct 1923, W.N.E. Hoffman (1♀; UMN). MISSISSIPPI: Harrison Co., Biloxi, 13 Jun 1917 (2♀; CU), Pass Christian, 6 Aug 1917, J. M. Aldrich (6♀; USNM). MISSOURI: Howard Co., Boonesboro, 17–23 May, 1954–1969, D. L. Lindsley, W. W. Wirth (3♂, 4♀; USNM). MONTANA: Gallatin Co., Firehole River, 27 Aug 1940, A. L. Melander (1♂; USNM); Lake Co., Ronan, 5.2 km S, 8 Aug 1972, W. N. Mathis (1♂; USNM), Ronan, 8.1 km S, 15 Jul–8 Aug, B. A. Foote (10♂, 22♀; KSU); Roosevelt Co., Bainville, 9 Jun 1969, W. W. Wirth (1♂; USNM); Sheridan Co. Medicine Lake, 9 Jun 1969, W. W. Wirth (1♂, 1♀; USNM). NEW JERSEY: Cape May Co., Cape May, 3 Jun, H. S. Vierick (2♂; ANSP, MCZ), Wildwood, 18 Jul 1908 (6♂, 7♀; ANSP); Ocean Co., Seaside, 16 May, H. S. Vierick (1♀; ANSP), Tuckerton, 8.1 km S, 21 May 1974, G. C. Steyskal (1♂; USNM). NEW MEXICO: Catron Co., Zuni Salt Lake, Quemado, 32.2 km W, 2 Jul 1953, W. W. Wirth (5♂, 14♀; USNM). NEW YORK: Richmond Co., Staten Island, south beach, 25 Jul–7 Sep 1917, A. H. Sturtevant (4♂, 2♀; USNM); Suffolk Co., Cold Spring Harbor, 19–21 July 1927, A. L. Melander (3♂, 2♀; USNM), Long Island, Jul (2♀; USNM); Tompkins Co., Ithaca (4♀; ANSP, CU). NORTH CAROLINA: Brunswick Co., Wilmington, 1 Jul 1935 (1♀; USNM); Dare Co., Nags Head, 15 May 1954, W. W. Wirth (7♂, 7♀; USNM). NORTH DAKOTA: Barnes Co., Eckelson Lake, 8 Sep 1951, A. H. Sturtevant (2♀; USNM); Benson Co., Leeds alkali lake, 5 Jul 1969, W. W. Wirth (5♂, 11♀; USNM), Pleasant Lake, alkali lake, Jun 1969, W. W. Wirth (1♂, 1♀; USNM); Burleigh Co., Long Lake, 4 Jun 1969, W. W. Wirth (1♀; USNM); Mountrail Co., White Lake, 8 Jun 1969, W. W. Wirth (2♂, 1♀; USNM). OHIO: Portage Co., Kent, 25 Aug 1969, J. Scheiring (1♂; KSU), Kent, 1.6 km E, 23 Sep 1973, B. A. Foote (2♂, 4♀; KSU), Ravenna, 24.2 km E., 11 Oct 1971, B. A. Foote (1♀; KSU); Summit Co., Barberton, 14 Oct 1969, W. Eastin (3♂; KSU); Wayne Co., Rittman, 8.1 km S, 18 Nov 1969, B. A. Foote (1♂; KSU). OREGON: Grant Co., Dayville, 2 Sep 1950, A. H. Sturtevant (2♀; USNM); Harney Co., Borax Lake, 7.2 km NE Fields, 29 Jul 1975, W. N. Mathis (1♀; USNM), Burns 12.9 km N, K. Goeden (1♂; USNM), Crane Hot Spring, 30 Jul 1975, W. N. Mathis (3♀; USNM), Harney Lake, hot spring, 7 Mar–25 May, 1969–1975, K. Goeden, W. N. Mathis (11♂, 42♀; OSDA, USNM), 00 Ranch, 7 Mar 1975, W. N. Mathis (1♂, 4♀; USNM); Jackson Co., Mt. Ashland, 5500 feet, 24 Sep 1968, P. Oman (1♂; USNM); Lake Co., Summer Lake, 7.7 km N, 11 July 1974, W. N. Mathis (1♂; USNM); Malheur Co., Adrian, 32.2 km S, 1 Oct 1964, K. Goeden (4♂; OSDA, USNM), Andrews, 12.9 km N, 1 Oct 1972, J. D. Lattin (1♀; USNM). RHODE ISLAND: Washington Co., Watch Hill, 5 Aug 1939, A. L. Melander (2♂, 2♀; USNM). UTAH: Utah Co., Utah Lake, 3 Oct 1968, W. N. Mathis (3♂, 12♀; USNM); Weber Co., Kanesville, 21 Nov 1937, D. Hardy (1♀; ANSP). VIRGINIA: Accomack Co., Assateague Island, 18 May–22 Jul 1967–1968, G. C. Steyskal, W. W. Wirth (4♂, 3♀; USNM); Smythe Co., Saltville, 4 May 1962, W. W. Wirth (10♂, 7♀; USNM); Portsmouth (independent city), 10 Jun 1973, Laist (2♂, 2♀; USNM); Virginia Beach (independent city), 22 Jun 1933, J. M. Aldrich (1♀; USNM). WASHINGTON: Benton Co., Rattlesnake Springs, 17 Oct 1955, J. J. Davis (1♂; WSU), West Richland, 24 Feb 1974, N. E. Woodley (1♂; WSU); Clallam Co., Sequim, 25 Aug–3 Sep, 1934–1951, A. H. Sturtevant, A. L. Melander (1♂, 1♀; USNM); Franklin Co., Pasco, 3.2 km E, 8 Aug 1975, W. N. Mathis (12♂, 3♀; USNM); Grant Co., Coulee City, 3 Sep 1920, R. C. Shannon (2♀; USNM), Soap Lake, 17 Jul–20 Aug, 1922–1972, A. L. Melander, M. T. James, W. N. Mathis (5♂, 10♀; USNM), Stratford, 4 Jul 1920, R. C. Shannon (1♂; USNM); King Co., Seattle, 2 Aug 1908 (1♂, 3♀; USNM); Lincoln Co., Davenport to Wilbur, 19 Jun 1950, R. B. Spurnier (1♂; WSU); Mason Co., Lilliwaup, 23 Jul 1917, A. L. Melander (1♀; USNM); Pierce Co., Tacoma, 18 May 1971, W. N. Mathis (1♀; USNM); San Juan Co., Olga, 20 Jun–20 Jul, 1909–1919 (3♂, 5♀; USNM), Orcas Island, 19 Aug 1925, A. L. Melander (2♀; USNM), Friday Harbor, 30 Jun–7 Jul, 1905–1909, J. M. Aldrich (8♂, 3♀; ANSP, USNM); Snohomish Co., Everett, 20 Jun 1920, A. Spuler (1♀; WSU); Stevens Co., Evans, 13 Jun 1920, R. C. Shannon (♀; WSU); Wahkiakum Co., Puget, 4 Jul 1925, A. L. Melander (2♂, 1♀; USNM); Whatcom Co., Birch Bay, 13 Jun 1945, R. D. Shanefelt (1♂; WSU); Whitman Co., Almota, 2 Jun 1918, A. L. Melander (1♂; USNM); Yakima Co., Selah, 8 Jul 1941, Brookman Reeves (1♀; USNM); Zillah, 17 Aug 1941, Brookman and Reeves (1♀; USNM). WYOMING: Hot Spring Co., Thermopolis, 13 Jun–30 Aug, 1940–1969, A. L. Melander, W. W. Wirth (12♂, 28♀; USNM); Niobrara Co., Lusk, 64.4 km N, Jul 1895 (2♀; ANSP); Teton Co., Old Faithful, 1 Aug 1934, A. L. Melander (1♀; USNM).

GEOGRAPHIC DISTRIBUTION (Figure 17).—This species is widespread in North America between 18° and 55° north latitude.

ETYMOLOGY.—The feminine Latin noun *muria* ("brine") refers to the brackish water habitat of this species.

REMARKS.—Like its closely related congener *L. dichaeta,* this species is primarily halophilous in habitat preference, although it has occasionally been found around freshwater environments (Sturtevant and Wheeler, 1954:175). Scheiring and Foote (1973) have records of this species from salt-pool habitats formed by drainage from a large brine storage pond associated with a salt plant near Rittman, Wayne County, Ohio. Dr. B. A. Foote (pers. comm.) has also successfully reared specimens from puparia collected in algae-coated mud bordering an alkaline pond at the Ninepipes Wildlife Refuge approximately 8.1 km south of Ronan, Montana.

The pattern and intensity of brown coloration on the mesonotum varies considerably. This is particularly evident on the scutellum, where the brown pattern varies from total coverage to a small subrectangular area at the anterior margin. The intensity of coloration is partially a consequence of

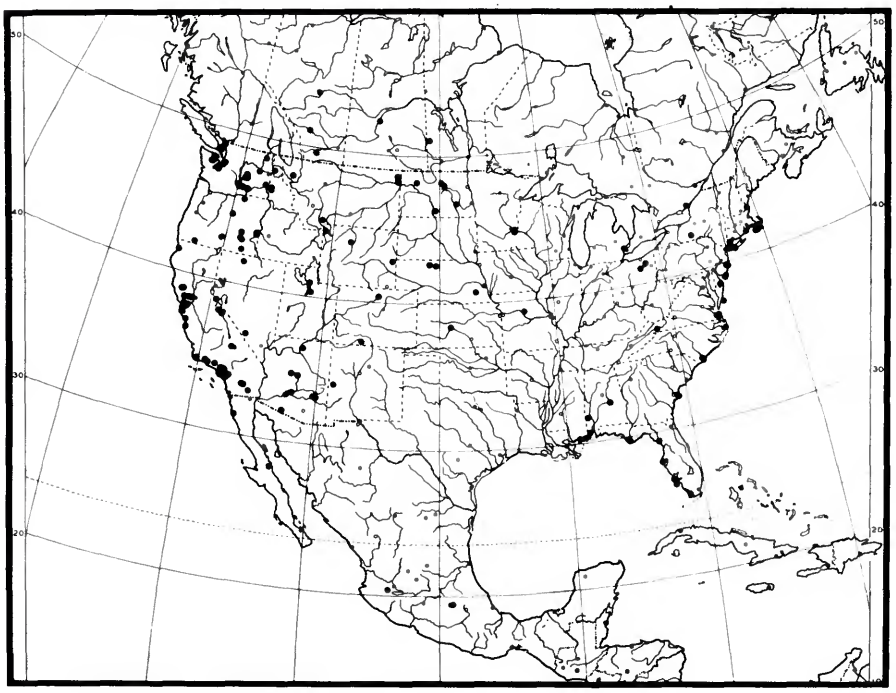


FIGURE 17.—Distribution map of *L. muria*.

age polymorphism. The more pollinose, less tattered specimens are nearly always younger.

A second obvious polymorphism is the degree of shiny, metallic luster on the mesofrons. A few specimens were examined in which the mesofrons was entirely dull, pollinose, as in specimens of *L. nivosa*. Specimens with the dull appearance were collected with others that had the mesofrons subshiny to shiny.

### 4. *Lamproscatella (Haloscatella) nivosa* Cresson

FIGURES 18–21

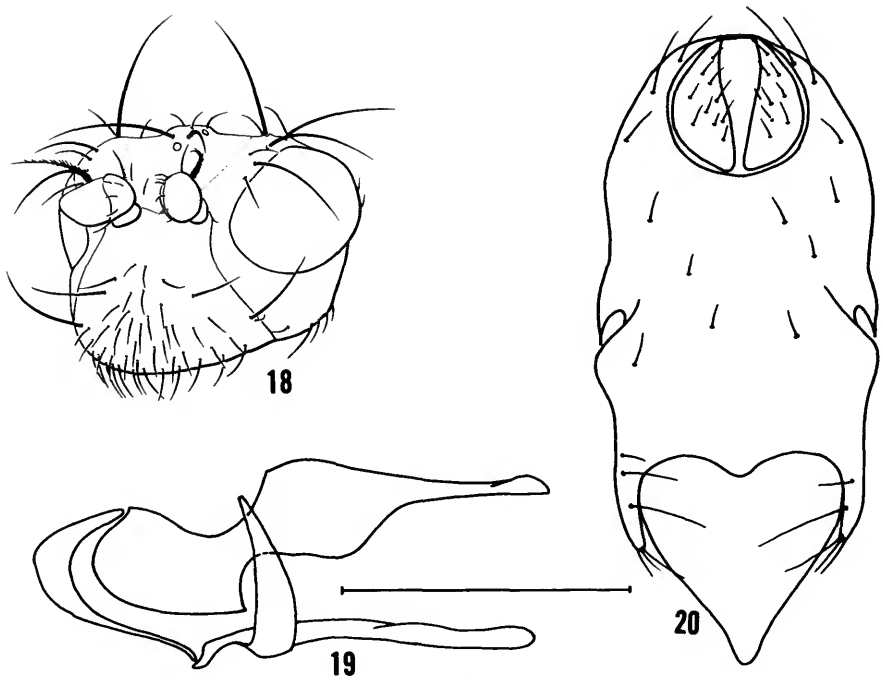
*Lamproscatella nivosa* Cresson, 1935:361.—Wirth and Stone, 1956:475 [key, distribution in California].—Wirth, 1965:756 [catalog].

*Scatella (Lamproscatella) nivosa* Sturtevant and Wheeler, 1954:175.

DIAGNOSIS.—*Lamproscatella nivosa* is allied with *L. arichaeta* and *L. cephalotes* but may be distinguished from these and other congeners by the following combination of characters: Mesofrons dull, generally completely pollinose, contrasting little from parafrons in texture, although often slightly more brownish in coloration; conformation of structures of male terminalia unique (Figures 19–20).

DESCRIPTION.—Small to moderately small shore flies, length 1.60 to 2.26 mm (averaging 1.95 mm); mostly pollinose, coloration gray but with faint brownish gray areas on dorsum.

*Head* (Figure 18): Head width-to-height ratio averaging 1:0.76; coloration generally charcoal gray to faintly brownish white. Mesofrons dull, pollinose, broadly rounded anteriorly, usually light brownish gray, contrasting with paler whitish gray parafrons; 3–4 small setae along anterior margin. First and third fronto-orbital setae much reduced, first seta slightly larger; third inserted approximately in line with other fronto-orbital setae, much closer to second than to fourth. Postocular seta just posterolaterad of divergent vertical bristle; 1–3 pair of divergent postocellar setae. Antenna dark, mostly black, pollinose; arista approximately equal to combined length of second and third antennal segments, pubescent to macropubescent. Face light brownish gray, distinctly protruding and arched,




FIGURES 18–20.—L. *nivosa:* 18, head, lateroblique aspect; 19 internal male terminalia, lateral aspect; 20, epandrium, surstyli, and cerci, posterior aspect (scale equals 0.25 mm).

setose. Usually 3 pair of larger lateral facial setae, these becoming larger and more dorsally-curved toward posteroventral angle of face. Eye-to-cheek ratio averaging 1:0.55; gena generally concolorous with face or slightly lighter in color.

*Thorax:* Mesonotum light brown, pollinose, grayer toward lateral margins; scutellum generally lighter gray; setation moderately well developed. Pleural areas and legs grayer than dorsum; basitarsi often pale, yellowish orange; apical tarsomeres darker, mostly blackish: Wing slightly opaque, lacteous; costal margin only slightly setose; costal vein ratio averaging 1:0.16; $M_{1+2}$ vein ratio averaging 1:0.54; posterior crossvein slightly angulate laterally, appearing wrinkled near middle.

*Abdomen*: Dorsum grayer than that of thorax, but with some brownish coloration toward anterior and posterior margins. Structures of male terminalia very distinctive; cerci and cercal cavity small, situated toward dorsal margin; fused surstyli widely separated, narrowly fingerlike, setulose, and with small emarginate bump between; aedeagus large, broad, extending from ventral margin of epandrium (Figures 19–20).

TYPE MATERIAL.—Holotype male is labeled: "♂/40 m N of Lusk, Wyo Jul, '95./Property of U of K [Snow Entomological Museum] On Deposit [pink]/269/Presumed HOLOTYPE Lamproscatella nivosa Cresson by W. N. Mathis [red]." The specimen is double mounted and the abdomen has been removed and dissected; the structures are in an attached microvial. The holotype will be deposited in the Snow Entomological Museum, The University of Kansas, Lawrence.

SPECIMENS EXAMINED.—CANADA: ALBERTA: Okotoks, Sheep River, 27 Jun 1968, W. W. Wirth (1♂; USNM). MANITOBA: Ninette, 16 May 1958, J. F. McAlpine (1♀; CNC), Russell, 1 Aug 1937, R. H. Beamer (KU). UNITED STATES: CALIFORNIA: Modoc Co., Jul 1948, 13 Aug 1948, W. W. Wirth (1♂, 6♀; USNM), Lake City, 11 Oct 1952, E. I. Schlinger and J. Hall (1♂; UCR), Topaz Lake, 18 Aug, W. W. Wirth (1♀; USNM). NEVADA: Elko Co., Elko, 19 May 1926, M. C. VanDuzee (1♀; CAS); Humboldt Co., Denio, 11.3 km W, 23 Jun 1971, G. Steyskal (3♂, 4♀; USNM); Lander Co., Austin, 8.1 km ESE, 5 Aug 1964, H. B. Leech (1♂; USNM); Washoe Co., Pyramid Lake, 28 Mar 1952, I. LaRivers (2♂, 1♀; USNM). NORTH DAKOTA: Mountrail Co., White Lake, 8 Jun 1969, W. W. Wirth (5♂, 6♀; USNM); Pierce Co., Pleasant Lake, Jun 1969, W. W. Wirth (4♂, 14♀; USNM); Ramsey Co., Devil's Lake, 30 Jun 1921, C. K. Sibley (1♀;

USNM). OREGON: Baker Co., Anthony Lake, 8 Jul 1977, R. S. and V. L. Zack (1♂; WSU); Harney Co., Borax Lake, 7.2 km NE Fields, 29 Jul 1975, W. N. Mathis (2♂, 13♀; USNM), Harney Lake, hot spring, 25 May 1969, 16 Jun 1972, K. Goeden, W. N. Mathis (4♂, 3♀; OSDA, USNM); Lake Co., Lake Abert, 19 Jun 1954, A. H. Sturtevant (1♀; USNM), Goose Lake State Park, 23 Aug 1970, K. W. Simpson (5♂, 16♀; CU, USNM), Summer Lake, 25 Sep 1971, W. N. Mathis (31♂, 114♀; USNM). UTAH: Tooele Co., Blue Lake, 27.4 km S Wendover, 26 Aug 1970 (1♀; CU). WASHINGTON: Grant Co., Soap Lake, 20 Aug 1922, A. L. Melander (2♂, 1♀; USNM).

GEOGRAPHIC DISTRIBUTION (Figure 21).—This species occurs in western North America, primarily west of the 100th meridian between 38° and 52° north latitude.

REMARKS.—I collected *L. nivosa* in large numbers in eastern Oregon, around shallow alkaline lakes. Specimens are particularly abundant in late summer on the partially dried mud shores where the water level has receded and cracks have begun to form on the surface.

Cresson's original description was based on a unique male, stated to be in the "Kansas Univ. Colln." In a more recent paper, cataloging the names Cresson proposed, Roback (1969) also listed "KU" as the depository for the type. However, Byers, et al. (1962), in a catalog of the Diptera types in the Snow Entomological Museum, University of Kansas does not list this type, and in subsequent correspondence, Dr. Byers confirmed that the type of *L. nivosa* was not there. Among specimens loaned to me from the Academy of Natural Sciences at Philadelphia, a single male specimen of *L. nivosa* bearing the label data Cresson cited in his original description was found. This specimen agrees with Cresson's description, including the reference to missing antennae, and I concluded that it is the type, although mislabeled. Accordingly, I attached a label to this specimen, as cited above, and after conferring with Dr. S. S. Roback (ANSP), sent it to the Snow Entomological Museum, The University of Kansas, Lawrence.

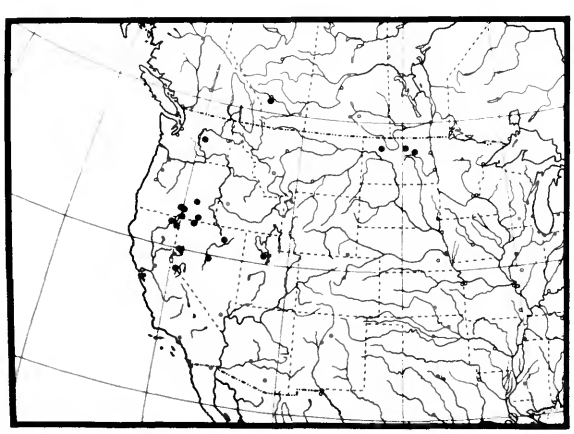


FIGURE 21.—Distribution map of *L. nivosa*.

Color tends to vary in specimens of this species according to geographic locality. West of the Rocky Mountains, most specimens have some brownish coloration dorsally, especially on the mesonotum, which varies from very faint, grayish tan, to distinctly light brown. East of the Rockies, many specimens lack any indication of brown coloration and are entirely grayish to silvery white. The type is included in the latter category. Because the male terminalia in all color morphs are virtually identical, all specimens I have examined are recognized as one species.

Some color polymorphism is also evident within populations. This seems to be particularly evident in coloration of tarsomeres. In the majority of specimens from a given locality, the tarsi are dark, usually black, or in some cases with sparse gray pollinosity, although never obscuring the dark background color. Occasional specimens are encountered, however, that have much paler tarsomeres, especially the basal ones, and these are usually yellow orange. When the basitarsi are pale, the apical tarsomeres are dark colored.

### 5. *Lamproscatella (Haloscatella) salinaria* (Sturtevant and Wheeler)

FIGURES 22–25

*Scatella (Lamproscatella) salinaria* Sturtevant and Wheeler, 1954:176.

*Lamproscatella salinaria*.—Wirth and Stone, 1956:475 [key, distribution in California].—Wirth, 1965:756 [catalog].

DIAGNOSIS.—Specimens of *L. salinaria* closely resemble those of both *L. dichaeta* and *L. muria* but may be distinguished by the following combination of characters: Specimens averaging larger; conformation of mesofrons subrectangular, parallel sided, completely shiny; tarsi paler, mostly yellow but becoming darker apically. The structures of the male terminalia are diagnostic, although they are similar to those of *L. dichaeta;* the surstyli are more

divergent and the V-shaped pocket formed between them is proportionately larger. Further, the surstyli do not bear large, apical setae that are subequal to the surstylar length. Several smaller setae, however, are evident along the apex of each surstylus (Figures 23–24).

DESCRIPTION.—Small to moderately small shore flies, length 1.77 to 2.47 mm (averaging 2.25 mm); mostly gray but with some slightly brownish coloration.

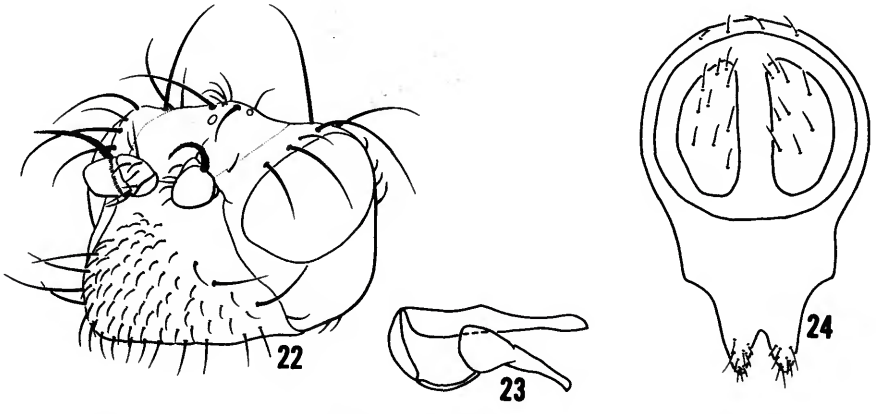
*Head* (Figure 22): Wider than high. Mesofrons shiny with bluish green metallic luster, broadly attaining anterior margin of frons, contrasting with pollinose, gray parafrons; ocellar triangle pollinose, gray, 1–3 pair of small setae toward anterolateral margins of shiny area. First and third fronto-orbital setae much reduced; first larger than third; postocular seta poorly developed, only 1–2 dorsal pair evident. Antenna dark, pollinose; arista pubescent to macropubescent, subequal to combined length of second and third segments. Face silvery white, sometimes with slight brownish discoloration toward interfoveal carina; 2 larger, lateral pair of setae toward posterolateral corner of face, more lateral pair larger. Eye-to-cheek ratio averaging 1:0.56; gena concolorous with face, becoming grayer posteriorly.

*Thorax:* Mesonotum mostly gray but often with some brownish colored areas or with faint metallic patches anteriorly; scutellum lighter in color; setation moderately well developed; pleural areas gray. Legs mostly gray; basitarsi of middle and hind legs pale, yellowish to amber colored, basitarsus of front leg usually darker; apical tarsomeres becoming darker, mostly blackish. Wings hyaline but slightly opaque basally; costal margin only slightly setose; costal vein ratio averaging 1:0.24; $M_{1+2}$ vein ratio averaging 1:0.59, posterior crossvein slightly angulate.

*Abdomen:* Mostly gray dorsally, generally concolorous with mesonotum but with more faint metallic green or blue luster. Structures of male terminalia as follows: Cerci and cercal cavity large, approximately half total length of epandrium; surstyli closely apposed medially and fused basally; pocket formed by surstylar arms more or less V-shaped; each surstylus diffusely setulose apically (Figures 23–24).

TYPE MATERIAL.—Holotype male is labeled: "Trona, Cal. Ap. 29. 50/HOLOTYPE Scatella salinaria Stvt & Whlr/6690 TYPE." The holotype is in the Academy of Natural Sciences of Philadelphia, type number 6690.

OTHER SPECIMENS EXAMINED.—UNITED STATES: CALIFORNIA: Inyo Co., Death Valley, 9.2 km N Furnace Creek, 24 Jun 1974, W. N. Mathis (7♂, 4♀; USNM), Death Valley, Wildrose Campground, 4000 feet, 6 Nov 1968, P. H. Arnaud, Jr. (1♀; CAS), Owens Lake, Columbia Southern, 23 Feb 1963, J. D. Birchim (4♂, 1♀; CAS), Tecopa Hot Spring, 1.6 km N, 24 Jun 1974, W. N. Mathis (4♂, 5♀; USNM); San Bernardino Co., Trona, 29 Apr 1950 (1♀; ANSP). NEVADA: Washoe




FIGURES 22–24.—*L. salinaria:* 22, head, lateroblique aspect; 23, internal male terminalia, lateral aspect; 24, epandrium, surstyli, and cerci, posterior aspect.

Co., Pyramid Lake, 24 Jun 1964, J. A. Miller (1♂, 1♀; UCD, USNM). OREGON: Harney Co., Harney Lake, hot spring, 23 Feb 1963, 23 May 1975, K. Goeden, W. N. Mathis (1♂, 5♀; OSDA, USNM); Lake Co., Summer Lake, 25 Sep 1971, W. N. Mathis (2♀; USNM). UTAH: Box Elder Co., Bear River Refuge, 5 Jul 1949 (1♀; ISU); Salt Lake Co., Saltair, 1 Jul 1942, D. T. Jones 1♂, 1♀; ISU).

GEOGRAPHIC DISTRIBUTION (Figure 25).—This species occurs in the Great Basin of western United States between 35° and 43° north latitude west of 110° west longitude.

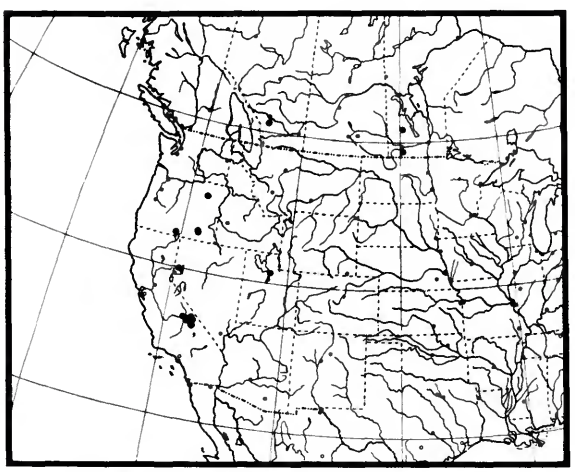


FIGURE. 25.—Distribution map of *L. salinaria*.

### *Thinoscatella*, new subgenus

TYPE-SPECIES.—*Lamproscatella* (*Thinoscatella*) *lattini* Mathis, new species, by present designation.

SPECIES INCLUDED.—*Lamproscatella lattini*, new species; *L. quadrisetosa* (Becker).

DIAGNOSIS.—This subgenus is closely allied to *Lamproscatella*, sensu stricto, but specimens may be distinguished by the following combination of characters: Coloration generally brownish; mesofrons shiny, distinctly contrasting with dull, pollinose vestiture of dorsum of scutellum; eye-to-cheek ratio 1:0.35 or larger; 2 larger pair of lateroclinate fronto-orbital bristles, orientation parallel to each other or diverging slightly; posterior fronto-orbital bristle inserted closer to inclinate vertical bristle than to anterior fronto-orbital; 2 pair of much smaller fronto-orbital setae also evident, alternating with larger bristles, length of smaller setae less than half that of larger bristles; ocelli arranged to form isosceles triangle, distance between posterior pair shorter than distance between anterior ocellus and either posterior ocellus; basal pair of lateral scutellar bristles well developed, length usually over half that of larger, apical pair. Structures of male terminalia also diagnostic: Surstyli either lacking or fused indistinguishably with ventral margin of epandrium; aedeagus tubelike, slender, gradually tapering toward apex; aedeagal apodeme narrow, nearing straight to slightly curved; gonite projecting ventrally as a narrow process, shape of process various.

ETYMOLOGY.—*Thinoscatella*, a combination of the Greek *thinos* ("beach" or "shore") and *scatella*, alluding to the coastal distribution of these *Scatella*-like flies.

GEOGRAPHIC DISTRIBUTION.—Both species of this subgenus are known to occur only along the coasts of the temperate and arctic Holarctic Region. *Lamproscatella quadrisetosa* is found in both the Palearctic and Nearctic Regions, whereas *L. lattini* is somewhat more restricted, occurring along the coast of western North America where there is exposure to the Pacific or Arctic Oceans. The range of the species apparently do not overlap, however.

NATURAL HISTORY.—The ecology, life cycle, and natural history of the species of *Thinoscatella* are not well known; neither have the immature stages of either species been described. Adults are common inhabitants of mud-sand beaches and at low tide they can be observed in considerable numbers among seaweed that has washed ashore. Adults also seem to prefer the mud-sand beaches of embayments or other protected estuary-like areas and are not found commonly where the tidal zone has direct exposure to the ocean and the constant churning action of large ocean waves. The maritime biotope has been called "the watt" by Dahl (1959:13), which he defines as follows:

> Of biotopes belonging to the tidal zone of the sea, *the watt* may be characterized as a biotope regularly inundated by flood, consisting of a flat, silt-impregnated sand area, often crossed by waterfilled erosion grooves during low water. Bluegreen algae dominate the vegetation, further [sic] almost exclusively may consist of *Salicornia*.

DISCUSSION.—*Thinoscatella* differs markedly from the other subgenera of *Lamproscatella* and the distinguishing gap between it and the other subgenera is more than between the *Scatella*-related "genera."

This is particularly evident in characters of the male terminalia. The surstyli of the male terminalia are apparently fused to the ventral margin of the epandrium as in many males of *Scatella*-related genera, and indeed, there is some similarity in the overall facies of all of these taxa, although superficial for the most part. The internal structures of the male terminalia of *Thinoscatella* do not resemble those of Scatella-related genera and obviously reflect a different lineage of descent. These differences are also evident in the shape of the female ventral receptacle, which is unlike any of the *Scatella*-related genera or of the other subgenera of *Lamproscatella*.

Apotypic character states establishing the monophyly of this subgenus are as follows: Position of fronto-orbital bristles (see diagnosis); surstyli lacking or fused indistinguishably with ventral margin of epandrium; unique conformation of male terminalia; ocelli arranged to form isosceles triangle. I believe this subgenus is the sister-group of *Haloscatella* (Figure 1).

### Key to Males in Species of the Subgenus *Thinoscatella*

Gonite tapering gradually to apex; apex gently rounded (Palearctic and east coast of North America) ..... ***L. quadrisetosa*** (Becker)

Gonite recurved toward apex; apex slightly expanded (west coast of North America) ..... ***L. lattini***, new species

### 6. *Lamproscatella (Thinoscatella) lattini*, new species

FIGURES 26–30, 33

*Scatella (Lamproscatella) quadrisetosa*.—Sturtevant and Wheeler, 1954:176 [review, misidentification in part].—not Becker, 1896:229.

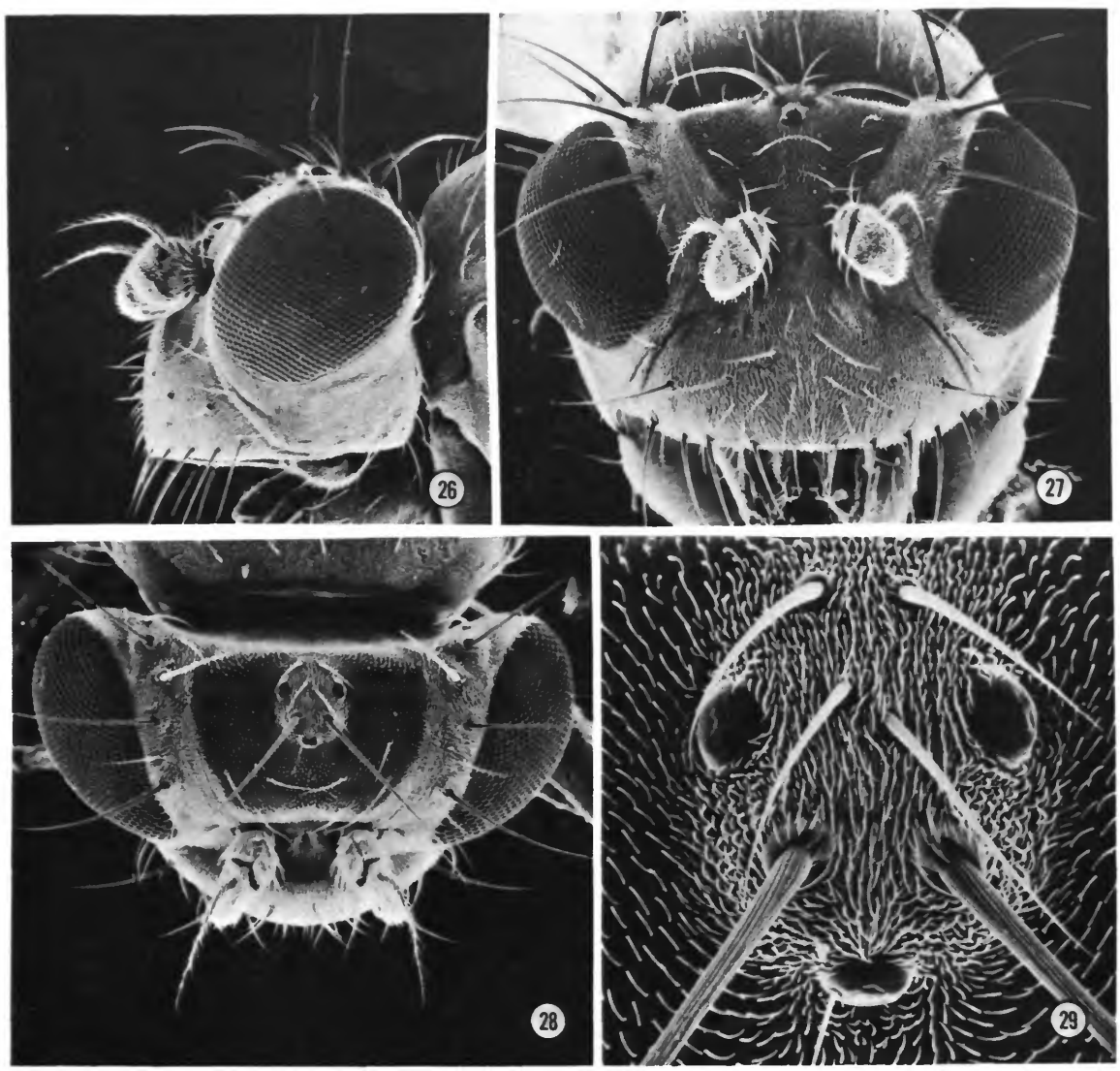
*Lamproscatella quadrisetosa*.—Wirth and Stone, 1956:475 [key, distribution in California, misidentification].—Wirth, 1965: 756 [catalog, misidentification in part].—not Becker, 1896: 229.

DIAGNOSIS.—Structures of the internal male terminalia are the only characters I have discovered to distinguish specimens of this species from its congener *L. quadrisetosa*. The ventral extension of the gonite is concave apically, appearing as a shallow bowl, and the apex is slightly swollen (Figure 33).

DESCRIPTION.—Small to moderately small shore flies, length 1.86 to 2.85 mm (averaging 2.43 mm); generally olivaceous brown to dark brown, but with some faintly gray areas, particularly on head.

*Head* (Figures 26–29): Head width-to-height ratio averaging 1:0.60; conformation of mesofrons trapezoidal, lateral margins narrowing anteriorly, shiny with metallic bronze luster, bearing 2–3 small, generally inconspicuous setae anterior of ocellar triangle; ocellar triangle and fronto-orbital plate concolorous, pollinose to subshiny, brownish; remainder of parafrons mostly charcoal gray. First and third fronto-orbital setae much reduced, subequal in length to each other; second and fourth bristles well developed; all fronto-orbital setae aligned with each other and oriented in same direction. Antenna pubescent, coloration brown to black; arista subequal in length to combined length of first 3 segments, micropubescent to bare. Face subshiny to pollinose, becoming more pollinose ventrally, coloration mostly olivaceous brown, but becoming grayer toward venter and in antennal fovae; 3–4 marginal facial setae in line decending from interfoveal carina, length of these approximately equal to setae along oral margin, several smaller setae on centralized portion of face which extend ventrally and laterally from interfoveal carina. Eye width-to-height ratio averaging 1:0.94; eye-to-cheek ratio averaging 1:0.42; anterior portion of gena and parafacial areas unicolorous, distinctly lighter in color than face, grayish white, becoming darker posteriorly; mouthparts pollinose, brown, with several evenly distributed small setae.

*Thorax:* Mesonotum pollinose to subshiny, mostly unicolorous, olivaceous brown to grayish brown, more pollinose toward anterior margin; scutellum shinier than mesonotum and slightly darker in color. Pleural areas mostly unicolorous, olivaceous brown but with some lighter colored areas around margins. Femora greenish brown, concolorous, tibiae and tarsi dark brown to black, becoming darker




FIGURES 26–29.—*L. lattini:* 26, head, lateral aspect; 27, head, anterior aspect; 28, head, dorsal aspect; 29, ocelli, dorsal aspect.

toward apices. Halter pale yellow apically. Costal vein ratio averaging 1:0.16; $M_{1+2}$ vein ratio averaging 1:0.70.

*Abdomen:* Dorsum mostly unicolorous, subshiny, olivaceous brown, but slightly lighter colored than mesonotum. Structures of male terminalia as in diagnosis and Figure 33.

TYPE MATERIAL—Holotype male is labeled: "WASH, Pierce Co. Tacoma Environs 25 May 1971 Wayne N. Mathis/HOLOTYPE Lamproscatella lattini W. N. Mathis [red, handwritten]." Allotype female and 38 paratypes (21 ♂, 17 ♀; USNM) have same label data as holotype. The holotype and paratypes are in the National Museum of Natural

History, Smithsonian Institution, Washington, D. C., type number 75957.

OTHER SPECIMENS EXAMINED.—CANADA: BRITISH COLUMBIA: Comox, 24 Jun 1933, J. McDunnough (1♂, 1♀; CNC), Vancouver, 8 Aug 1917, A. L. Melander (4♀; USNM); Vancouver Island, Cowichan Bay, 11–12 July 1924, A. L. Melander (5♂, 5♀; USNM), Deep Bay, 16 Jun 1955, R. Coyles, (1♀; CNC), Elk Lake, 11 Jul 1924, A. L. Melander (1♀; USNM), Ladysmith, 13 Jul 1924, A. L. Melander (1♂; USNM), Mill Bay, 11 Jul 1924, A. L. Melander (2♂; USNM). UNITED STATES: ALASKA: Anchorage, 20 Jul 1921, J. M. Aldrich (3♂; ANSP, USNM); Cape Thompson, 29 Jul 1961, B. S. Hemming (1♀; CNC); Haines, 14 Jul 1971, B. A. Foote (4♂, 2♀; KSU, USNM); Homer, 31 Jul 1954, C. P. Alexander (5♂, 1♀; USNM); Hukok Bay, 10 Jul 1953, W. C. F. (1♀; WSU); Kotzebue, 26 Jun 1951, R. I. Sailer (3♂, 1♀; USNM); Matanuska, 7 Jun 1944, J. C. Chamberlain (1♂; USNM); Seward, 24 Jul 1921, J. M. Aldrich (4♂ 6♀; USNM); Unakleet, 7 Aug 1951 (1♀; USNM); Valdez, 3–4 Jul, 14 Jul, 3 Aug, 1947–48, 1971, A. H. Storm, R. I. Sailer, B. A. Foote (22♂, 18♀; KSU, USNM). CALIFORNIA: Alameda Co., Alameda, 26 May 1915, M. C. VanDuzee (1♂, 4♀; CAS), Albany Bay, 26 Sep 1947, Albany Bay, 26 Sep 1947, W. W. Wirth (2♂, 4♀; CAS, USNM), Berkeley, 12 May–22 Nov, 1915–1968, M. C. VanDuzee, R. S. Lane (4♂, 5♀; CAS); Contra Costa Co., Richmond, 28 Dec 1947, W. W. Wirth (1♀; USNM); Los Angeles Co., Los Angeles, 28 Feb 1915, M. C. VanDuzee (2♂; CAS); Marin Co., Bolinas, 1971, G. Page (1♂, 1♀; USNM), Muir Beach, 6 Aug 1950, A. L. Melander (2♀; USNM), Point Reyes, 2 Oct–21 Nov, 1947–1957, W. W. Wirth (4♀; CAS, USNM), Tomales, 19 Oct 1947, W. W. Wirth (3♂, 3♀; CAS, USNM); Monterey Co., Asilomar, 4 Aug 1950, A. L. Melander (1♂; USNM); Orange Co., Corona del Mar, 2 Mar–11 Jun, 1944–1950, A. L. Melander, A. H. Sturtevant (2♂, 8♀; USNM), Dana Point, 25 Mar 1953, A. H. Sturtevant (2♂; USNM), Morro Bay, 29–30 Aug 1945, A. L. Melander (36♂, 34♀; USNM), Newport Beach, 27 Oct 1928, A. H. Sturtevant (1♂, 1♀; USNM), Sunset Beach, 12 Jun 1948, A. L. Melander (2♂, 2♀; USNM); San Diego Co., Palm City, 19 Jul 1940, D. E. Hardy (3♂; KU), San Diego, 5 Apr 1915, M. C. VanDuzee (1♂, 3♀; CAS); San Luis Obispo Co., Laguna Beach 25 Mar-15 May, 1946–1947, A. L. Melander (4♂, 1♀; USNM), Morro Dunes, 6 Sep 1945, A. L. Melander (1♂; USNM); San Mateo Co., Dumbarton Bridge, 30 Jul 1947, W. W. Wirth (2♂, 3♀; USNM); Santa Barbara Co., Carpinteria, 9 Oct 1946, A. L. Melander (1♂, 1♀; USNM); Santa Clara Co., Palo Alto, 10 Jul–11 Aug, 1911–1917, J. M. Aldrich (1♂, 3♀; USNM); Santa Cruz Co., Big Basin, 18 Jul 1954, A. L. Melander (4♂, 5♀; USNM), Capitola, 7 Apr 1956, P. H. Arnaud (1♂, 1♀; CAS), Santa Cruz, 3 Jan 1948, W. W. Wirth (1♀; USNM); Sonoma Co., Bodega Bay, 16 Apr–19 Oct, 1947–1964, W. W. Wirth, J. D. Birchim (7♀; CAS, USNM); Ventura Co., Hueneme, 17 Jun 1948, W. W. Wirth (6♀; USNM), Point Mugu, 20 Jul 1962, R. R. Saunders (7♂, 5♀; ISU, USNM). OREGON: Clatsop Co., Fort Stevens State Park, 26 Jun 1963, R. C. Dickson (1♀; UCR), Seaside, 23 Aug 1951, A. H. Sturtevant (1♂, 7♀; USNM); Coos Co., Coos Bay, 8 Aug 1940, A. L. Melander (1♀; USNM); Lincoln Co., Boiler Bay, 9 Mar 1930, J. Wilcox, (4♂, 5♀; ANSP), Lincoln Beach, 26 Jun 1971, G. Steyskal (1♂; USNM), Waldport, Alsea Bay, 9 Oct 1971, W. N. Mathis (14♂, 25♀; USNM); Tillamook Co., Neskowin, 10–17 Aug 1948, M. T. James (2♂, 1♀; WSU), Sand Lake, 3.2 km S, 13 Jun 1972, W. N. Mathis (1♂; USNM). WASHINGTON: Clallam Co., Blyn, 10–24 Jul, 1917–1921, A. L. Melander (13♂, 13♀; USNM), Crescent Bay, 26 Jul 1917, A. L. Melander (1♂, 1♀; USNM), Sequim, 25 Aug 1951, A. H. Sturtevant (1♀; USNM); Grays Harbor Co., Copalis, 25 Aug 1951, A. H. Sturtevant (1♀; USNM), Hoquiam, 26 Aug 1951, A. H. Sturtevant (1♂, 1♀; USNM); Jefferson Co., Brinnon, 11 Aug 1921, A. L. Melander (3♂; USNM), Fort Warden near Point Townsend, 15 Jun 1971 (1♂, 1♀; WSU); King Co., Seattle, 2 Aug 1908 (2♂; ANSP, USNM); Mason Co., Dewatto, 15 Aug 1910 (1♂, 2♀; USNM), Shelton, Walkers Park, 21 Jul 1917, A. L. Melander (1♂; USNM); Pacific Co., Fort Canby, 8 Aug 1975, W. N. Mathis (1♀; USNM), Ilwaco, 28 Jun–12 Jul, 1922–1924, A. L. Melander (6♂; 7♀; USNM), Kickerville, gulf, 5 Sep 1954, J. J. Davis (2♂; WSU), Nahcotta, 14 Jul–24 Aug, 1953–1960, M. T. James (37♂, 40♀; USNM, WSU), Naselle, 13 Jul 1922, A. L. Melander (5♂, 5♀; USNM), Ocean Park, 23 Jul–18 Aug, 1950–1961, M. T. James (9♂ 11♀; WSU), Raymond, 15 Feb 1971, W. N. Mathis (1♂, 7♀; USNM), South Bend, 23 May 1917, A. L. Melander (1♀; USNM), Tokeland, 18 Jul 1917, A. L. Melander (9♂, 5♀; USNM); Pierce Co., Gig Harbor, 17 May–26 Jul 1971, W. N. Mathis (35♂, 44♀; USNM), Tacoma, 18 May–27 Aug 1971, W. N. Mathis (39♂, 41♀; USNM); San Juan Co., Friday Harbor, 25 Jun–1 Aug, 1909–1930, A. C. Hodson (36♂, 72♀; ANSP, MCZ, UMN, USNM); Snohomish Co., Everett, 20 Jun 1920, A Spuler (1♂; WSU); Thurston Co., Olympia, South Bay, 3 Jul 1925, A. L. Melander (1♂, 4♀; USNM); Whatcom Co., Birch Bay, 11–15 Jul 1949, M. T. James (31♂, 14♀; WSU), Larabee State Park, Bellingham, 17 Jul 1949, M. T. James (10♂, 5♀; WSU).

GEOGRAPHIC DISTRIBUTION (Figure 30).–The species occur along the west coast of North America between 32° and 67° north latitude.

ETYMOLOGY.—The Latinized genitive patronym *lattini* honors Dr. John D. Lattin, who furthered my interest in entomology and made its study pleasant.

REMARKS.—Until the present study, this species was confused with *L. quadrisetosa*. There are no known external characters that may be used to distinguish between these two species, and reliance on characters of the male terminalia and on the distribution are necessary to separate these two.

Like specimens of *L. quadrisetosa*, those of *L. lattini* are restricted to coastal habitats, where they are often common on the intertidal wrack zone of embayments and estuaries. I have not collected specimens of *L. lattini* from sandy ocean shores where wave action disturbs the habitat.

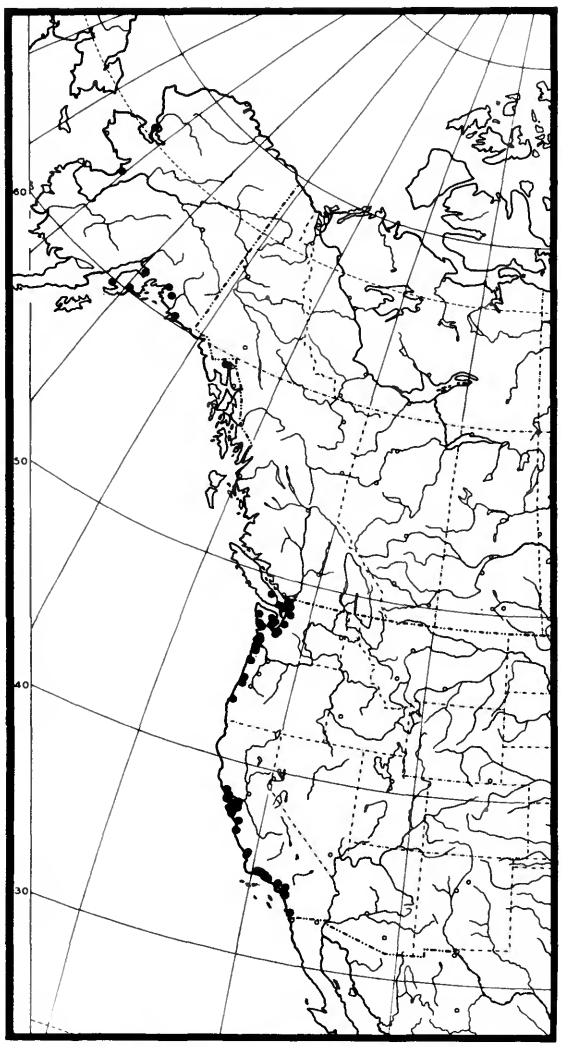


FIGURE 30.—Distribution map of *L. lattini*.

### 7. *Lamproscatella (Thinoscatella) quadrisetosa* (Becker)

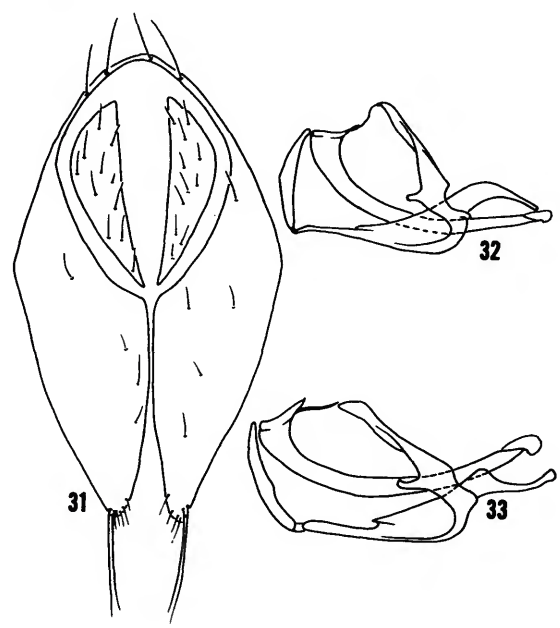
FIGURES 31–32, 38

*Scatella quadrisetosa* Becker, 1896:229.
*Scatella (Lamproscatella) quadrisetosa*.—Becker, 1926:85.—Sturtevant and Wheeler, 1954:176 [review, in part].
*Lamproscatella quadrisetosa*.—Cresson, 1930:126.—Wirth, 1965: 756 [catalog, in part].

DIAGNOSIS.—Specimens of this species and *L. lattini* very closely resemble each other and on the basis of external morphology alone, cannot be consistently distinguished. Structures of the male terminalia, however, may be used to reliably characterize the species. Males of *L. quadrisetosa* have the ventral extension of the gonite gently rounded throughout its length, without recurving or expanding apically (Figures 31–32).

DESCRIPTION.—Small to moderately small shore flies, length 1.87 to 2.76 mm (averaging 2.46 mm); otherwise similar to description of *L. lattini* except for the following specific details: eye-to-cheek ratio averaging 1 : 0.47; costal vein ratio averaging 1 : 0.17; $M_{1+2}$ vein ratio averaging 1 : 0.64.

TYPE MATERIAL.—Lectotype male (here designated) is labeled: "Norwegen, 8/8 36219/quadrisetosa [handwritten]/Typus [red]/LECTOTYPE Scatella quadrisetosa Becker ♂ by W. N. Mathis [red bordered]." A female specimen with the same label data as the lectotype is herein designated as paralectotype. The lectotype and paralectotype are in the Humbolt University insect collection, Berlin, D. D. R. In the original description, Becker (1896) also stated that these specimens were collected on the beach at "Molde Fjorder in Norwegen."




FIGURES 31–33.—*L. quadrisetosa:* 31, epandrium, surstyli (?), and cerci, posterior aspect; 32, internal male terminalia, lateral aspect. *L. lattini:* 33, internal male terminalia, lateral aspect.

OTHER SPECIMENS EXAMINED.—CANADA: MANITOBA: Churchill, 16 Jun–9 Aug, 1930–1948, O. Bryant, D. G. Denning, G. E. Shewell (8♂, 21♀; CAS, CNC, UMN). NEW BRUNSWICK: Tabusintac, 4 Aug 1939, J. McDunnough (4♂, 3♀; CNC). NORTHWEST TERRITORIES: Eskimo Point, 28 Jun–29 Jul, 1948–1950, J. R. Vockeroth, G. R. Roberts (17♂, 14♀; CNC). NOVA SCOTIA: Petpeswick, 29 Jul 1971, B. Wright (1♂, 1♀; CNC). UNITED STATES: MASSACHUSETTS: Essex Co., Gloucester, 20 Jun 1924, C. W. Johnson (1♂; ANSP).

GEOGRAPHIC DISTRIBUTION (Figure 38).—This species has a transboreal, Holarctic distribution. In North America it occurs mainly along the coasts of northern Canada and the east coast as far south as Massachusetts.

REMARKS.—Specimens demonstrate considerable age-related variation, especially with respect to color. Older specimens often tend to be lighter in overall appearance, less shiny, and with some broken or missing setae. The face is lighter in color, more grayish white as opposed to olivaceous brown, and the wings appear to be light reddish brown rather than hyaline to slightly infuscated. The male terminalia of these color morphs, however, are virturally identical to those of the more typical morph and are clearly within the variation of the latter.

Color variation of this sort is not an uncommon phenomenon in the subfamily Ephydrinae and has been observed in species of several genera. Wirth (1971:359), for example, in a study of the North American *Ephydra* commented that

> freshly emerged specimens tend to be brighter metallic colored than older flies; as the flies mature their body surfaces tend to grow duller with an accumulation of brownish dusting, until flies at the end of their adult life span appear quite brownish, dull, and ragged.

Dahl (1959) reported that this species is eucoenic within the watt biotope, where it is the dominant shore fly species, accounting for 37 percent of the ephydrid fauna. Dahl also collected specimens of *L. quadrisetosa* in the maritime sand high beach biotope in northern Norway (Norrland), where it replaces *Scatella (Neoscatella) subguttata* (Meigen), a species found commonly within the biotope in southern Sweden.

Like specimens of *L. lattini* in western North America, specimens of this species are frequently very abundant. Dahl (1959:82) stated the *L. quadrisetosa* has

> the greatest abundance, taken as a whole, within any biotope investigated. In the watt biotope on several North-Norwegian fjord shores an individual density of about 40 individuals per 10 cm² was recorded, an abundance certainly connected to the green coloration of the substrate by sand algae.

### Subgenus *Lamproscatella*, sensu stricto

For the synonymy of the subgenus, see the generic synonymy.

SPECIES INCLUDED.—*Lamproscatella aklavik*, new species; *L. bimaculata* Hendel; *L. brunnipennis* (Malloch); *L. occidentalis*, new species.

DIAGNOSIS.—Specimens of this subgenus are quite similar to those of *Thinoscatella* but may be distinguished by the following combination of characters: General coloration brownish; mesofrons generally dull, subequal or but slightly shinier than dorsum of scutellum; eye-to-cheek ratio 1 : 0.25 or less; both lateroclinate fronto-orbital bristles distinctly divergent; posterior fronto-orbital bristle inserted approximately midway between anterior fronto-orbital bristle and inclinate vertical bristle, or it is closer to anterior fronto-orbital; smaller fronto-orbital setae very weakly developed, not generally evident; acrostichal setae stronger than in subgenus *Haloscatella*, more numerous, rows not converging or overlapping; prescutellar pair inconspicuous, not readily distinguished from remaining acrostichal setae; basal pair of lateral scutellar bristles not more than half length of apical pair; wing mostly hyaline, posterior crossvein very slightly infuscated in some species. Structures of male terminalia as follows: Surstyli generally evident, basally fused indistinguishably to ventral margin of epandrium; cercal cavity generally small, usually not longer than combined length of epandrium plus surstyli; aedeagal apodeme generally slender, curved, C- to J-shaped; gonite in lateral view generally projecting ventrally, shape variable, broadly V-shaped in anterior view; operculum of female ventral receptacle flat, extending process much wider near operculum, becoming considerably narrower and curving more abruptly away from operculum.

GEOGRAPHIC DISTRIBUTION.—Members of this subgenus are the most widespread of the genus, occurring in all major faunal realms except for the

Neotropical and Australian. In North America, their distribution is almost exclusively western, where several of the species occur in sympatry. There are a few collection records east of the 100th meridian.

NATURAL HISTORY.—Very little is known concerning the habitat preferences of members of this subgenus. North American species generally occur in freshwater environments, but specimens are occasionally collected near saline or alkaline water systems. In particular, most collections of *L. brunnipennis* are from coastal areas with exposure to the Arctic Ocean.

DISCUSSION.—Members of the subgenus *Lamproscatella* exhibit more characteristics of the hypothetical *Lamproscatella* ancestor than the other two subgenera. Consequently, specimens are generally quite similar to those of *Coenia* and *Philotelma* except as noted in the generic diagnosis and discussion. Within the genus, I suggest that *Lamproscatella,* is the sister-group of the lineage from which the other two subgenera arose as outlined in Figure 1.

Only four North American species are known to belong to this subgenus. Elsewhere, particularly in Africa and Asia, there are several undescribed species that are closely related to *L. sibilans* (Haliday), the type-species of *Lamproscatella.* The hypothetical relationships are as outlined in Figure 34 and Table 3.

The basic dichotomy is the split between species whose males have retained evident surstyli and those where the surstyli are either lost or are fused indistinguishably with the ventral margin of the epandrium. The more plesiotypic condition is their retention, similar to males in related genera such as *Coenia.*

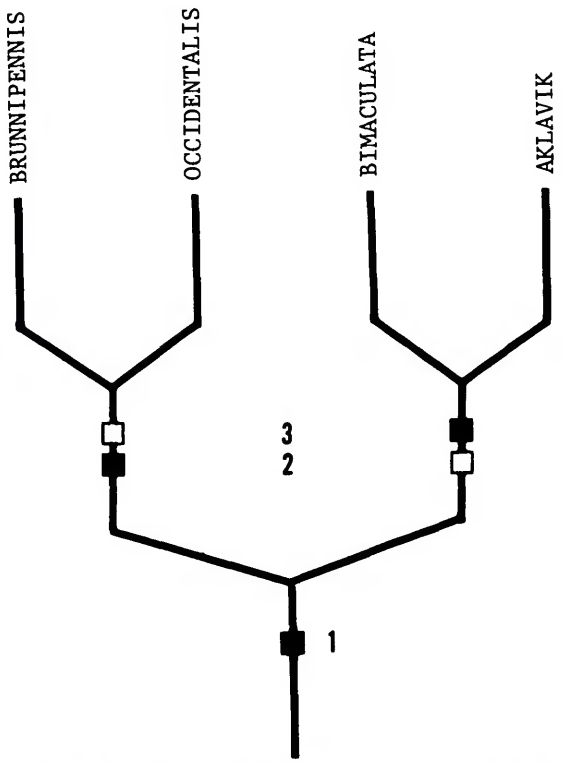



FIGURE 34.—Hypothetical phylogeny for the Nearctic species of the subgenus *Lamproscatella,* based on the character states outlined in Table 3 (Solid squares = apotypic character states; open squares = plesiotypic character states.)

TABLE 3.—Characters and character states used in cladistic analysis of the species of the subgenus *Lamproscatella*

| CHARACTERS | Plesiotypic | Apotypic |
|---|---|---|
| 1. Vestiture of mesofrons | Lacking, shiny | Mostly pollinose, dull |
| 2. Shape of fifth abdominal tergum of male | Subtriangular | Subtrapezoidal |
| 3. Condition of surstyli | Evident as distinct lobes | Either lost or fused indistinguishably with ventral margin of epandrium |

**Key to Males in Species of the Subgenus *Lamproscatella,* sensu stricto**

1. Shape of fifth tergum in dorsal view subtriangular, apex pointed or acutely rounded .....2
   Shape of fifth tergum in dorsal view subtrapezoidal, apex broadly rounded or truncate .....3
2. Length of cercal cavity about one-half that of combined epandrium and surstyli; lateral

margin of epandrium narrowing gradually, merger with fused surstylus inconspicuous; ventral margin of surstylus at most setulose .....9. *L. bimaculata* Hendel

Length of cercal cavity about one-third that of combined epandrium and surstyli; lateral margin of epandrium narrowing abruptly just before merger of fused surstylus; ventral margin of surstylus with approximately 4 very stout bristles .....8. *L. aklavik*, new species

3. Epandrium gradually narrowing ventrally to merger of surstyli; shape of surstyli digitiform, straight; aedeagal apodeme wide, greatest width equal to width of gonite ..... ..... 10. *L. brunnipennis* (Malloch)

Epandrium abruptly rounded at merger of surstyli; shape of surstyli reniform curved; aedeagal apodeme narrow, much less than width of gonite ....11. *L. occidentalis*, new species

## 8. *Lamproscatella (Lamproscatella) aklavik*, new species

FIGURES 35–38

DIAGNOSIS.—Specimens of this species closely resemble those of *L. bimaculata* but may be distinguished from the latter and other congeners by the following combination of characters: Size of specimens averaging smaller than those of *L. brunnipennis* and *L. occidentalis*; shape of fifth tergum of males subtriangular; epandrium becoming gradually wider ventrally; apex of surstyli bluntly rounded, bearing 4–5 stout, broad, spinelike bristles; gonite produced ventrally, acutely rounded in lateral view.

DESCRIPTION.—Small to moderately small shore flies, length 1.62 to 2.16 mm (averaging 1.90 mm); description generally as for specimens of *L. occidentalis* except as follows.

*Head:* Head width-to-height ratio averaging 1:0.66; eye-width-to-height ratio averaging 1:1.04; eye-to-cheek ratio averaging 1:0.23.

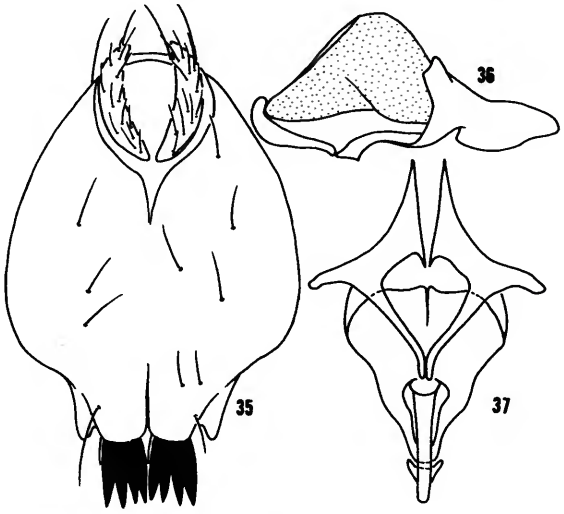
*Thorax:* Coloration of mesonotum mostly grayish brown, pollinose, dull. Wing length-to-width ratio averaging 1:0.39; costal vein ratio averaging 1:0.165; $M_{1+2}$ vein ratio averaging 1:0.69.

*Abdomen:* Epandrium (Figure 35) widest near ventral margin, narrowing abruptly at merger with surstyli; surstyli closely appressed medially; each surstylus bluntly rounded apically, subrectangular, bearing 4–5 stout, spinelike bristles at apex; aedeagal apodeme (Figure 36) shallowly J-shaped, apex of curved portion attached to base of aedeagus; gonite (Figure 37) projecting ventrally, acutely rounded apically in lateral view, broadly V-shaped basally in anterior view; fifth sternum a broadly U-shaped narrow band.

TYPE MATERIAL.—Holotype male is labeled "Aklavik, N.W.T. Aug. 25 1930 O. Bryant/HOLOTYPE Lamproscatella aklavik W. N. Mathis [red; handwritten]." Allotype female and 10 paratypes (4♂, 6♀; CAS, CNC, USNM) have the same locality data as the holotype. Other paratypes are as follows: Canada, Northwest Territories, Fort McPherson, 17–24 Jul 1957, R. Hurley (2♂, 3♀; CNC). The holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., type number 75958.

GEOGRAPHIC DISTRIBUTION. (Figure 38).—The distribution of *L. aklavik* appears to be the most restricted of the genus, being known, as cited above, from only two sites within the delta of the Mackenzie River, Northwest Territories. Both localities are north of the Arctic Circle.

ETYMOLOGY.—The epithet *aklavik* is the name of the type-locality in the Northwest territories of




FIGURES 35–37.—*L. aklavik:* 35, epandrium, surstyli, and cerci, posterior aspect; 36, internal male terminalia, lateral aspect; 37, gonites and aedeagus, anterior aspect.

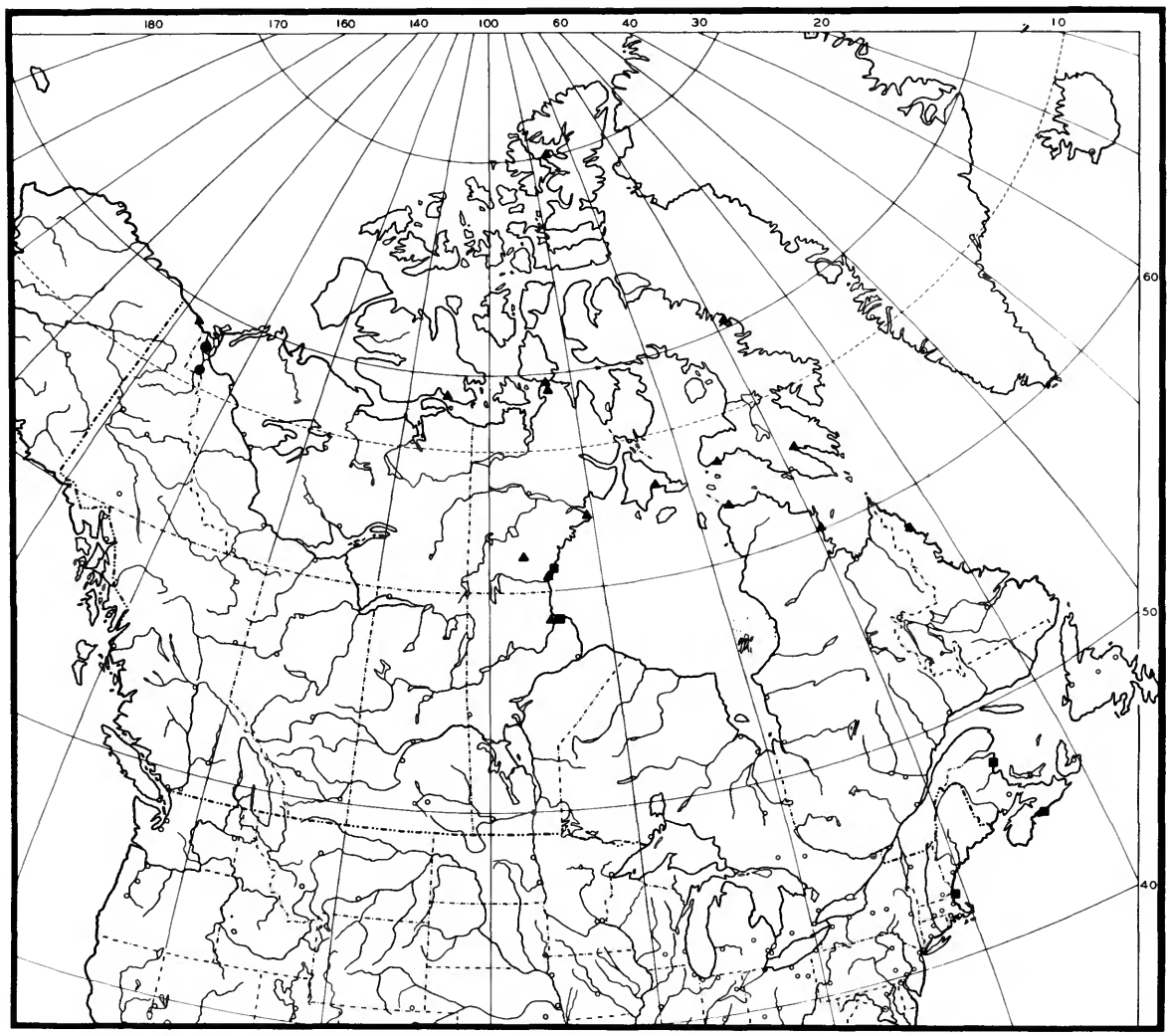



FIGURE 38.—Distribution map of *L. aklavik* (filled circles); *L. brunnipennis* (filled triangles); and *L. quadrisetosa* (filled squares).

Canada; it stands in apposition to the generic name.

REMARKS.—Within the small sample examined, coloration of facial pollenosity seemed less variable in specimens of other species of this subgenus. Generally, the coloration in these is light grayish brown with slight shade differences in some specimens.

### 9. *Lamproscatella (Lamproscatella) bimaculata* Hendel

FIGURES 39–41

*Lamproscatella sibilans* (in part) of American authors [misidentification; not Haliday, 1833:175].—Sturtevant and Wheeler, 1954:176 [review, as species of *Scatella*].—Wirth and Stone, 1956:475 [key, distribution in California].—Wirth, 1965:756 [catalog].

*Lamproscatella bimaculata* Hendel, 1933:53.—Papp, 1975:115 [review, figures of head, wing, male terminalia].

DIAGNOSIS.—Specimens of this species are distinguished from those of similar congeners by the following combination of characters: Specimens averaging smaller than those of *L. brunnipennis* or *L. occidentalis,* coloration of facial pollenosity appearing white (white appearance becomes discolored, light golden brown in older and worn specimens); shape of fifth tergum of males subtriangular; merger of surstyli with ventral margin of epandrium indistinguishable; cercal cavity large; posteroventral surface of surstyli with secondary lobe; gonite slender, not produced ventrally.

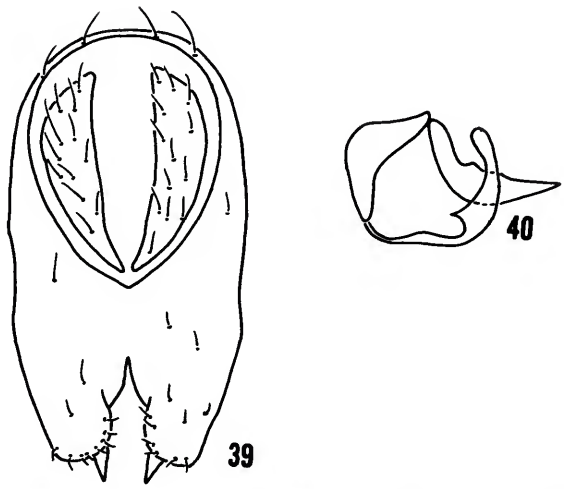
DESCRIPTION.—Small to moderately small shore flies, length 1.72 to 2.07 mm (averaging 1.85 mm); description generally as for specimens of *L. occidentalis* except as follows.

*Head:* Head width-to-height ratio averaging 1:0.69; eye width-to-height ratio averaging 1:1.05; eye-to-cheek ratio averaging 1:0.17. Face tending to be whitish gray, but coloration variable.

*Thorax:* Coloration of mesonotum mostly grayish brown, slightly subshiny, thinly pollinose. Wing length-to-width ratio averaging 1:0.49; costal vein ratio averaging 1:0.155; $M_{1+2}$ vein ratio averaging 1:0.63.

*Abdomen:* Fifth tergum of male subtriangular in dorsal view, apex distinctly pointed or acutely rounded; cercal cavity (Figure 39) large, subequal to one-half length of combined epandrium and fused surstyli; surstyli in posterior view broadly produced as subtruncate ventral processes, each bearing a secondary, acutely pointed anteromedial lobe; gap between surstyli about one-half width of surstylus near apex; aedeagus (Figure 40) acutely pointed apically; aedeagal apodeme sublunate in lateral view; gonite not produced ventrally.

TYPE MATERIAL.—Two syntype males. According to Hendel (1933:54), both males were collected from "Donau-Auen der Lobau bei Wien, Juni." Hendel also stated that the types were in his collection which was later given to the Naturhistorisches Museum Wien. Through Dr. Ruth Lichtenberg, I was sent the specimens of *L. bimaculata* from the Wien collection, but none could be identified as either of the two syntype males. One male specimen did bear a single label indicating that it was from the Hendel collection but lacked a locality label.




FIGURES 39–40.—*L. bimaculata:* 39, epandrium, surstyli, and cerci, posterior view; 40, internal male terminalia, lateral aspect.

OTHER SPECIMENS EXAMINED.—CANADA: ALBERTA: Lethbridge, 27 Jun 1968, W. W. Wirth (1♂; USNM). UNITED STATES: ARIZONA: Coconino Co., Happy Jack, 9.7 km N, 13 Jun 1971, B. A. Foote (1♂; KSU). CALIFORNIA: Alpine Co., Forestdale Meadow, 17 Jul 1960, G. G. Moore (1♂; UCD); Inyo Co., Bishop, 28 Jul 1940, D. E. Hardy (1♀; USNM); Kern Co., Onyx, 11.2 km E, 12 Jun 1961, H. F. Howden (1♀; CNC), Tehachapi, 14 Sep 1898 (1♀; ANSP); Los Angeles Co., Lovejoy Lake, Mojave Desert, 10 Oct 1934, A. L. Melander (2♂; USNM); Mono Co., Sardine Creek, 6 Jul 1951, A. T. McClay (1♀; UCD), Sonora Pass, 13 Aug 1960 (1♀; CAS); Nevada Co., Hobart Mills, 1.6 km NW, 20 Jun 1974, W. N. Mathis (1♂; USNM), Hobart Mills, 8.1 km NW Sage Hen, 20 Jun 1954, H. B. James (1♀; WSU), Sage Hen Creek, 20 Jun–15 Jul, 1954–1970, M. T. James, D. S. Chandler, E. C. Sickels, S. F. Casey, C. Goodpasture, E. C. Sickels (3♂, 5♀; UCD, USNM); Placer Co., Lake Tahoe, 6300–7000 feet, 30 Aug 1910 (1♂; USNM); Riverside Co., Palm Springs, 14–28 Dec, 1917–1947, J. C. Bradley, R. Coleman (4♂; CU, USNM), Riverside, 11 Apr 1951, A. L. Melander (1♀; USNM), Temecula, 10 May 1945, A. L. Melander (2♂, 1♀; USNM); San Bernardino Co., Barton Store, 3 Sep 1950, A. L. Melander (1♂; USNM), Jenks Lake, 18 Aug 1950, A. L. Melander (2♂; USNM), 1000 Springs, 24 Oct 1946, A. L. Melander (1♂; USNM), Victorville, 16 May 1955, W. R. Richards (1♀; CNC); Santa Barbara Co., Santa Barbara, 16 Apr 1951, K. W. Tucker (1♂; UCD); Sierra Co., Webber Lake, 3 Jul 1964, M. E. Irwin (1♂; UCR), Yuba Pass, 7 Jul 1964, M. E. Irwin (1♂; UCR); Sonoma Co., Cloverdale, J. C. Bradley (2♂; CU); Stanislaus Co., Adobe Creek, 19.3 km W Patterson, 25 Apr 1948, H. B. Leech (1♀; CAS); Tulare Co., Crabtree Meadow, 10,550 feet, 29 Jul 1915 (1♀; ANSP), Siberian Outpost, 9,500–10,500 feet, 31 Jul 1915 (1♀; CAS), Tulare, 9 Sep 1898 (1♀; USNM). COLORADO:

Clear Creek Co., Mt. Evans, Echo Lake, 10,600 feet, 20 Jul 1961, B. H. Poole (1♂; CNC); Gunnison Co., Monarch Pass, 21 Jun 1940, A. L. Melander (2♀; USNM); Jackson Co., Cameron Pass, 11 Aug 1955, M. T. James (1♂; WSU); Logan Co., Crook, 15 Jun 1940, A. L. Melander (1♀; USNM); Saguache Co., John Smith Ranger Station, Cochetopa National Forest, 3 Jul 1913, A. K. Fischer (1♂; CAS). IDAHO: Gem Co., Emmett, 15 Apr 1938, H. S. Telford (1♀; USNM). NEVADA: Elko Co., Harrison Pass, 25 Jun 1953, A. B. Gurney (1♂, 1♀; USNM), Thomas Creek, Ruby Mountains, 21 Aug 1958, E. Mezger (1♀; USNM); Lander Co., Austin, 12 Aug 1940, D. E. Hardy (1♂; KU); Washoe Co., Mt. Rose, 6000 feet, 7 Jul 1972, C. Goodpasture (2♀; UCD), Pyramid Lake, 27 Jun 1972, C. Goodpasture (1♀; UCD). OREGON: Baker Co., Anthony Lake, 21 Jul 1964, K. Goeden (4♂; OSDA); Harney Co., 29 Jun 1953, A. B. Gurney (5♂, 3♀; USNM), Idlewild Campground, 25.8 km N Burns 15 Jun–30 Jul, 1972–1975, W. N. Mathis (6♂, 3♀; USNM); Lake Co., Ana Reservoir, 24 Sep 1971, W. N. Mathis (1♂; USNM); Umatilla Co., Tollgate, 3.2 km E, 6 Jul 1954, J. J. Davis (1♂; WSU). UTAH: Box Elder Co., Bear River City, 14 Oct 1953, G. F. Knowlton (1♀; USNM); Davis Co., Farmington, 8 Oct 1950, G. F. Knowlton (1♂; USNM), Syracuse, 10 Sep 1933, J. A. Rowe (2♂, 4♀; ANSP); Duchesne Co., Neola, 12 Jun 1962, G. F. Knowlton (1♀; UMN); Salt Lake Co., Little Cottonwood Canyon, 8000 feet, 23 Jun 1940, A. L. Melander (2♂, 2♀; USNM); Utah Co., Goshen Pond, 2 Mar 1968, W. N. Mathis (1♂; USNM); Weber Co., Hooper, 20 Sep 1933, J. A. Rowe (1♂; ANSP). WASHINGTON: Grant Co., O'Sullivan Dam, 22 May–30 Oct, 1953–1955, M. T. James, H. G. Davis (22♂, 21♀; WSU); Kittitas Co., American River, Hell's Crossing, 14 Jul 1954, M. T. James (1♂; WSU); Klickitat Co., Willow Creek, La Crosse-Hooper, 13 May 1951, J. J. Davis (1♂; WSU); Okanogan Co., Boiling Lake, 6000 feet, 27 Jul 1950, C. L. Cooper (1♂, 1♀; WSU); Pierce Co., Mt. Rainier, Berkeley Park, 23 Aug 1934 (1♂; USNM), Mt. Rainier, Paradise Park, Aug 1917, A. L. Melander (1♂; USNM), Mt. Rainier, Yakima Park, 14–19 Aug, 1934–1940, A. L. Melander (2♂; USNM). WYOMING: Albany Co., Snowy Range Mountains, Lake Marie, 13 Aug 1957, G. F. Knowlton (1♀; WSU), Snowy Range Mountains, Libby Flats, 13 Jul–13 Aug 1957, G. F. Knowlton (72♂, 60♀; UMN, USNM, WSU), Mirror Lake, 13 Aug 1957, G. F. Knowlton (14♂, 8♀; WSU), Silver Lake, 10,000 feet, 13 Aug 1957, G. F. Knowlton (1♀; UMN), Laramie, 8 Aug 1947, P. B. Lawson (9♂, 8♀; KU).

GEOGRAPHIC DISTRIBUTION (Figure 41).—This species has a transboreal, Holarctic distribution. In North America, it occurs west of 103° west longitude between 33° and 49° north latitude.

REMARKS.—Hendel (1933) described this species from specimens collected in Austria (see "Type Material"). Through the kindness of Dr. L. Papp, Hungarian Natural History Museum, and Dr. Ruth Lichtenberg Naturhistorisches Museum Wien, I have been able to compare European exemplars with specimens from North America to confirm

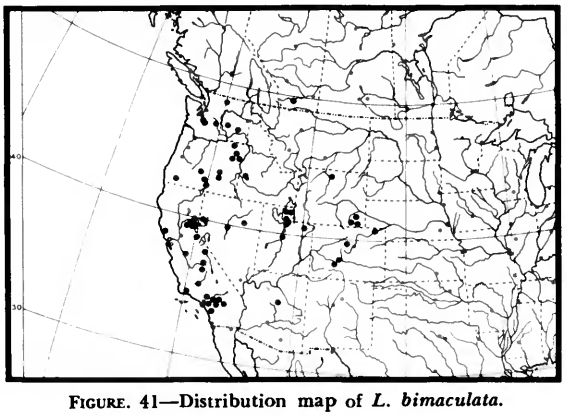


FIGURE. 41—Distribution map of *L. bimaculata*.

their conspecificity. The male terminalia of specimens from the two continents differ only in minor respects. In European specimens, the cleft between the surstyli is slightly more divergent, and the secondary, anteromedial lobe of each surstylus is not as pointed from a posterior view. In comparison with the degree of structural divergence of other species of this subgenus, these differences are not of consequence at the species level.

This species often occurs in sympatry with *L. occidentalis* in western North America. It is commonly found in freshwater habitats, particularly alpine meadows.

## 10. *Lamproscatella (Lamproscatella) brunnipennis* (Malloch)

FIGURES 38, 42–46

*Scatella brunnipennis* Malloch, 1923:221.—Scheiring, 1975: 297–298 [lectotype designation].

*Lamproscatella brunnipennis* Vibe, 1950:420.—Wirth, 1965: 756 [catalog].

*Lamproscatella brunneipennis* [sic] *norvegica* Andersson, 1975: 165 [new synonym].

DIAGNOSIS.—Specimens of this species are similar to those of *L. occidentalis* but may be distinguished from the latter and other congeners by the following combination of characters: Size of specimens averaging larger than those of *L. aklavik* or *L. bimaculata;* coloration of facial pollinosity golden brown, sometimes with some grayish or olivaceous coloration; shape of fifth tergum of male subtrapezoidal, posterior margin broadly rounded to subtruncate, orientation of fifth tergum in lateral view sometimes at ventro-oblique angle to general

body plane (this could be an artifact of how the specimens were preserved); shape of surstyli digitiform, straight; epandrium narrowing gradually to merge with surstyli, in lateral view with posterior surface undulate, distinctly swelling near merger with surstyli; gonite produced ventrally, rounded, with submucronate lateral projection in anterior view.

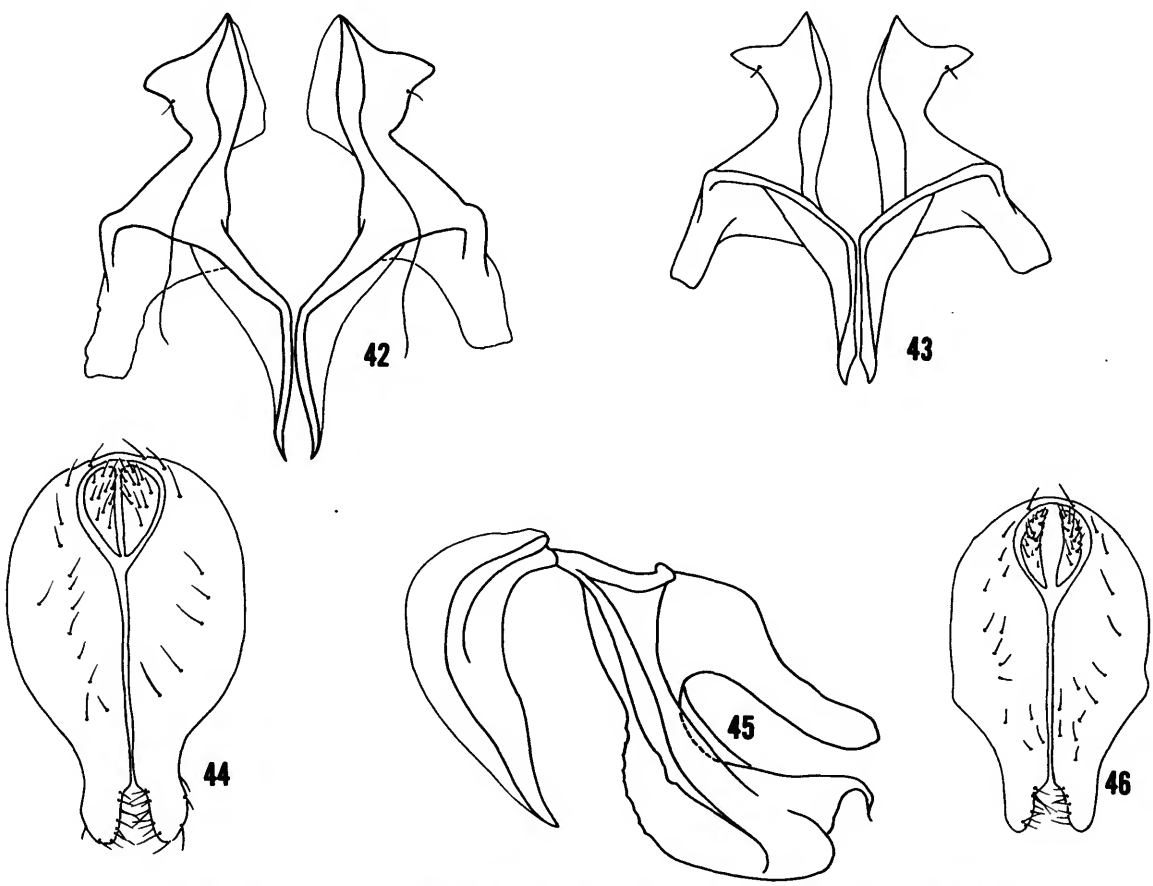
DESCRIPTION.—Small to moderately small shore flies, length 1.58 to 2.57 mm (averaging 2.07 mm); description generally as for specimens of *L. occidentalis* except as follows.

*Head:* Head width-to-height ratio averaging 1:0.64; eye width-to-height ratio averaging 1:1.10; eye-to-cheek ratio averaging 1:0.25. Coloration of face not as variable as in specimens of *L. occidentalis,* see above.

*Thorax:* Coloration generally duller than abdomen, vestiture more pollinose, grayer. Wing length-to-width ratio averaging 1:0.45; costal vein ratio 1:0.175; $M_{1+2}$ vein ratio averaging 1:0.63.

*Abdomen:* As described in diagnosis and in Figures 42–46.

TYPE MATERIAL.—Lectotype male (designated by Scheiring, 1975:297–298) is labeled: "St. Paul Id Bering Sea Aug. 16, 1915/G Dallas Hanna Collector/Paratype No. 26462 U.S.N.M. [red]/LECTOTYPE Scatella brunnipennis Malloch 1923 J. F. Scheiring, 1975 [red, handwritten]." Seventy paralectotypes were also designated by Scheiring. The




FIGURES 42–46.—*L. brunnipennis:* 42–43, gonites, anterior aspect; 44, 46, epandrium, surstyli, and cerci, posterior aspect; 45, internal male terminalia, lateral aspect. (42, 44–45, St. Paul Island; 43, 46, Southhampton Island, Northwest Territories.)

lectotype and most of the paralectotypes are in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., type number 26462. Four paralectotypes are in the California Academy of Sciences. Locality data for the type of *L. brunnipennis norvegica* are as follows (extracted from Andersson, 1975): "Norway, Finnmark, Lakselv, 5. VII. 1956, leg. R. Dahl. The holotype is a male and is deposited in the Zoological Museum, Lund, Sweden."

OTHER SPECIMENS EXAMINED.—CANADA: MANITOBA: Churchill, 14 Jun–28 Aug, 1930–1952, D. G. Denning, P. R. Ehrlich, B. Hocking, L. A. Miller, W. R. Richards, G. E. Shewell (11♂, 22♀; CAS, CNC, UMN, USNM). NEWFOUNDLAND: Hebron, 4–5 Aug 1954, J. F. McAlpine, E. E. Sterns (2♂, 1♀; CNC). NORTHWEST TERRITORIES: Baffin Island, Head of Clyde, 7 Aug 1958, G. E. Shewell (26♂, 18♀; CNC); Cambridge Bay, 30 Jun–28 Jul 1950, E.H.N. Smith, D. K. Sweetman (79♂, 32♀; CNC); Cape Dorset, 26 Aug 1954, H. Huckel (2♀; CNC); Chesterfield, 28 Jun 1950, J. R. Vockeroth (1♂, 4♀; CNC); Coral Harbor, Southhampton Island, 7 Jun–30 Aug, 1948–1954, P. R. Ehrlich, H. Huckel, G. E. Shewell (64♂, 48♀; CNC); Eskimo Point, 28 Jun 1950 (4♂, 4♀; CNC); Eureka, Ellesmere Island, 19 Aug 1953, P. F. Bruggemann (4♂, 15♀; CNC); Frobisher Bay, Baffin Island, 9 Aug 1948, G. F. Dilabio (6♂; CNC); Kidluit Bay, Richards Island, 29–30 Jul 1948, J. R. Vockeroth (1♂, 2♀; CNC); Lady Melville Lake, 3 Jul 1951, J. G. Chillcott (1♂; CNC); Masik Riv Banks, 18–31 Jul 1968, W.R.M. Mason, G. E. Shewell (2♂, 2♀; CNC); Padlei, 30 Jun 1950, R. A. Hennigar (1♀; CNC); Spence Bay, 10 Jun–14 Aug 1951, J. C. Chillcott (13♂, 17♀; CNC). QUEBEC: Sugluk, 2–30 Aug 1954, H. Huckel (20♂, 36♀; CNC). YUKON TERRITORY: 28 Jun–20 Jul, 1930–1971, C. D. Bird, O. Bryant, J. S. Waterhouse, D. M. Wood (14♂, 26♀; CAS, CNC, USNM); Shingle Point, Mackenzie River, 29 Aug 1929, O. Bryant (5♂, 9♀; CAS, USNM). UNITED STATES: ALASKA: St. George Island, Bering Sea, 4 Jun 1914, G. D. Hanna (1♂, 5♀; USNM); St. Paul Island, Bering Sea, 20 Jun–19 Aug, 1897–1921, Kincaid, E. A. Preble, G. D. Hanna, A. Christofson (35♂, 24♀; ANSP, CAS, USNM).

GEOGRAPHIC DISTRIBUTION (Figure 38).—This species has a Holarctic, transarctic distribution. In North America, it occurs along the northern coasts of Canada between 58° and 80° (the most northern locality of any known shore fly) north latitude from Labrador to the Yukon Territory. The type-locality is in the Bering Sea, southwest of the Alaska mainland.

REMARKS.—This species was initially described from island populations in the Bering Sea (Malloch, 1923). Some years later, Vibe (1950) reported its occurrence in Greenland (species determination by W. W. Wirth), and more recently, Andersson (1975) described a subspecies, *L. brunnipennis norvegica,* from northern Europe. Andersson based this subspecies on differences in the form and size of the male terminalia. Specimens of *L. brunnipennis norvegica* were characterized by the smaller combined length of the fused surstyli plus epandrium, the more undulating ventral surface of the epandrium, and the less acutely pointed, submucronate lateral projection of the gonite. Andersson also mentioned that the facial coloration was more golden brown.

I have now examined over 600 specimens (mostly in the Canadian National Collection) of this species from several localities along the coasts of northern Canada, Greenland, and the type-localities of both described subspecies. The latter two localities represent the extremes in the known distribution. I elect not to recognize subspecies. Several of the populations could be uniquely characterized, although none of these differences is of a magnitude comparable to that used to distinguish other species of this subgenus. Furthermore, the differences evident in specimens from the geographic extremes tend to be clinal when interlocular populations are examined. Differences in the Bering Sea populations are more distinctive, but this could simply reflect the larger geographic gap between them and the next closest populations I sampled. No specimens were available from the mainland of Alaska.

## 11. *Lamproscatella (Lamproscatella) occidentalis,* new species

FIGURE 47–52

*Lamproscatella sibilans* [in part] of American authors [misidentification; not Haliday, 1833:175].—Sturtevant and Wheeler, 1954:176 [review, as species of *Scatella*].—Wirth and Stone, 1956:475 [key, distribution in California].—Wirth, 1965:756 [catalog].

DIAGNOSIS.—Specimens of this species are very similar to those of *L. brunnipennis* but may be distinguished from the latter or other congeners by the following combination of characters: Specimens averaging larger than those of *L. aklavik* and *L. bimaculata;* coloration of facial pollinosity variable but frequently golden brown; shape of fifth tergum of males subtrapezoidal, posterior margin broadly rounded to subtruncate; shape of surstyli reniform, curved inward; epandrium more or less parallel sided, abruptly narrowing at merger of surstyli;

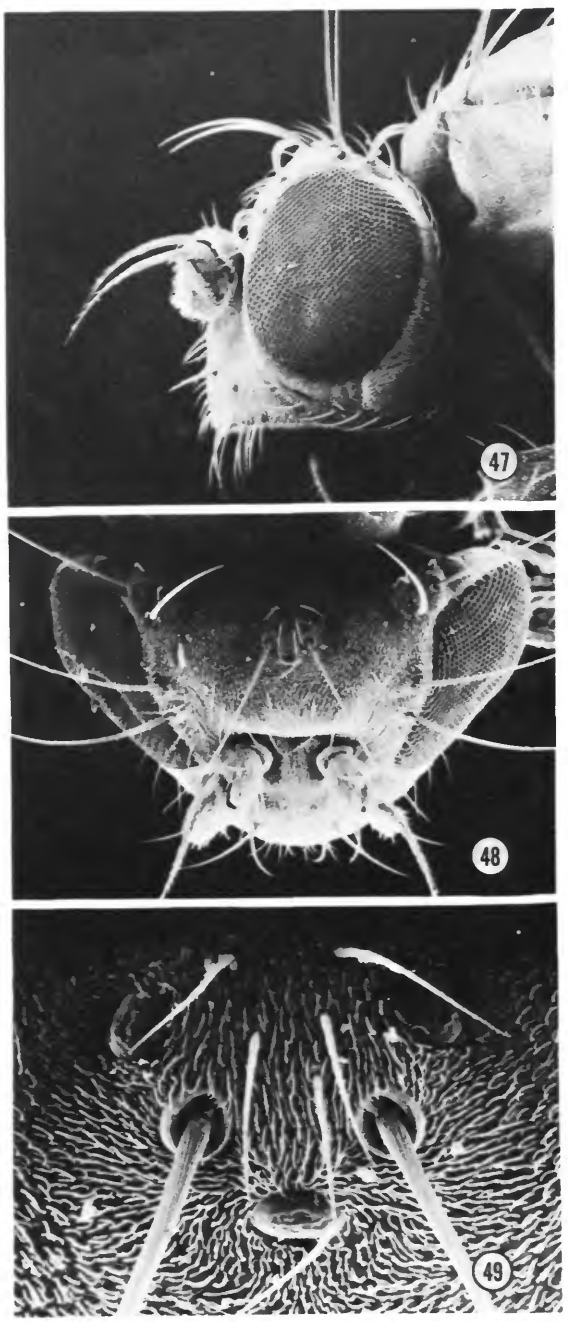
shape of aedeagal apodeme lunate; gonite produced ventrally, broadly rounded in lateral view.

DESCRIPTION.—Small to moderately small shore flies, length 1.85 to 2.55 (averaging 2.20 mm); coloration generally brown to tannish with few speckles of faintly metallic bluish green luster.

*Head* (Figures 47–49): Head width-to-height ratio averaging 1:0.66; vestiture of mesofrons thinly pollinose with some faintly subshiny, metallic golden brown to bronzish luster reflecting through; coloration of mesofrons contrasting distinctly with dull colored, charcoal gray parafrons; several small setae on mesofrons anterior of median ocellus, setae generally scattered; fronto-orbital plate concolorous with mesofrons. Only 2 larger fronto-orbital bristles, first and third setae much reduced, not generally discernible from surrounding, smaller setae. Postocular setae becoming slightly larger toward dorsum, none well developed. Antenna dark, pollinose, brownish black; arista usually longer than combined length of second and third segments, micropubescent to bare. Face wider than high, not protruding greatly, interfoveal facial carina lacking distinct crease; without distinct, large, dorsally-curved bristle toward posteroventral angle of face, but with several larger setae along oral margin and descending from facial carina to posteroventral angle to face; other facial setae subequal to each other, smaller than marginal ones; facial color variable, from very light grayish white to golden brown; 4–7 parafacial-genal setae. Eye nearly round; eye-to-cheek ratio averaging 1:0.21; gena narrow, generally concolorous with facial color anteriorly, becoming lighter, more whitish gray posteriorly.

*Thorax*: Mesonotum mostly brown but varying in shade, blackish brown to light tan, generally with sparse, scattered, faint metallic speckles, especially anteriorly; development of setae relatively moderate. Coloration of pleural areas tannish brown, generally lighter in color than mesonotum, becoming lighter anteroventrally. Coloration of legs from olivaceous gray to black, becoming darker toward apices. Wing hyaline; costal margin normally setulose; costal vein ratio averaging 1:0.145; $M_{1+2}$ vein ratio averaging 1:0.64.

*Abdomen*: Dorsum generally concolorous with mesonotum, becoming darker and subshiny posteriorly; ventral portion of anterior terga lighter in color, grayish, more pollinose. Structures of male terminalia as follows: Cerci and cercal cavity small,

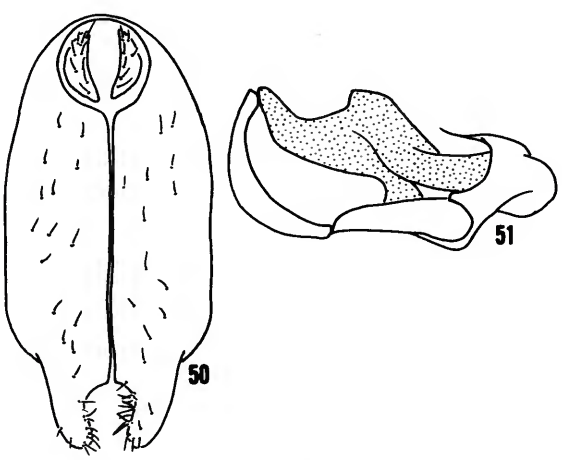



FIGURES 47–49.—*L. occidentalis:* 47, head, lateral aspect; 48, head dorsal aspect; 49, ocelli, dorsal aspect.

positioned in dorsal one-third of epandrium; shape of surstyli reniform, gently curved inwardly, setose; lateral margins of epandrium more or less parallel sided but curving medially abruptly at merger of surstyli; aedeagal apodeme lunate in lateral view; gonite projecting ventrally, broadly rounded in lateral view (see Figures 50–51).

TYPE MATERIAL.—Holotype male is labeled: "NEW MEXICO Rabbit Mtn. Sandoval Co. 25 May 1969 W. W. Wirth/HOLOTYPE Lamproscatella occidentalis W. N. Mathis [red, handwritten]." Allotype female and seven paratypes (5♂, 2♀; USNM) have the same label data as the holotype. Other paratypes are as follows: New Mexico, Wheeler Peak, Taos, 12,500 feet, 15–25 Jun 1960, Burks and Kinzer (4♂, 3♀; USNM). The holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., type number 75959.

OTHER SPECIMENS EXAMINED.—CANADA: ALBERTA: Banff National Park, Sunwapta Pass, 6700 feet, 9 Jul 1955, G. E. Shewell, (2♂, 2♀; CNC). Banff National Park, Victoria Glacier, 6000–6500 feet, 18 Jul 1955, R. Coyles (1♀; CNC); Chin, 7 Jun 1923, H. L. Seamans (1♂, 2♀; CNC); Edmonton, 26 Apr 1924, O. Bryant (16♂, 22♀; CAS, USNM); Elkwater Lake, 9–10 Jun 1956, O. Peck, E. E. Sterns (3♂, 2♀; CNC); Lake Newel, 9 Jun 1923, W. Carter (3♂, 2♀; CNC); Lethbridge, 7 Jun–5 Jul 1956, O. Peck, E. E. Sterns, W. W. Wirth (9♂, 3♀; CNC, USNM); Norton, 31 May 1955, J. R. Vockeroth (1♂; CNC); Okotoks, Sheep River, 27 Jun 1968, W. W. Wirth (3♂, 1♀; USNM); Onefour, 1–13 Jun 1956, O. Peck, E. E. Sterns (5♀; USNM); Scandia, 26 Jun 1956, E. E. Sterns (1♂, 1♀; CNC); Sunwapta Pass, 5 Jul 1955, J. R. McGillis (1♂; CNC). BRITISH COLUMBIA: Chilcotin, 26 Apr-11 Jun 1920, E. R. Buckell (2♀; CNC, USNM); Kamloops, alkali lake, 2 Jul 1968, W. W. Wirth (2♂, 1♀; USNM). MANITOBA: Churchill, 2–9 Aug 1937, D. G. Denning (1♂, 1♀; USNM). SASKATCHEWAN: Atton Lake, Cut Knife, 11 Jun 1940, A. R. Brooks (1♂; CNC); Dundurn, 23 Apr 1923, K. M. King (1♂, 2♀; CNC); Eaglehill Creek, 31 May 1939, A. R. Brooks (1♂, 1♀; CNC); Swift Creek, 15 May 1938, A. R. Brooks (3♂, 2♀; CNC). MEXICO: BAJA CALIFORNIA: Ensenada, 40.3 km N, 22 Mar 1950 (1♀; USNM); Ensenada, 80.5 km S (1♂; USNM); San Jose, Rose, 23 Mar 1950 (1♀; USNM); Sierra San Pedro Martir, Rancho Viejo, 7000 feet, 13 June 1953, P. H. Arnaud, Jr. (1♂, 1♀; CAS). UNITED STATES: ALASKA: Ketchikan, 24 Jul 1954, F. Baker (1♀; WSU); Willow, 40.3 km E, 18 Jul 1948, F. S. Blanton (1♂; USNM); Matanuska, 15 May 1944, J. C. Chamberlain (2♂, 4♀; USNM). ARIZONA: Coconino Co., Williams, 27 May (1♀; USNM); Apache Co., Springerville, 32.2 km S, 30 May 1972, W. W. Wirth (1♂, 1♀; USNM). CALIFORNIA: Alameda Co. Berkeley Hills, 11 Apr 1908 (8♂, 6♀; USNM); Butte Co., Manzanita, 21 Aug 1957, A. L. Melander (1♀; USNM); Colusa Co., Maxwell, 22 Mar 1953, J. C. Hall (2♂, 1♀; UCD); Contra Costa Co., Richmond, 16 Feb 1948, W. W. Wirth (2♀; USNM); El Dorado Co., Lake Fontanillis, 21 Aug 1955, E. I. Schlinger (2♀; UCD); Fresno Co., Dunlap, 9 Apr 1953, J. C. Hall (1♂; UCD), Heart Lake, 10,500 feet, 1 Sep 1952, E. I. Schlinger (1♂; UCD), Mammoth Lake, 29 Jul 1940, D. E. Hardy (2♂, 2♀; KU); Inyo Co., Bishop, 20 May–28 Jul 1940–1951, D. E. Hardy, E. I. Schlinger (6♂, 7♀; KU, UCD), Deep Springs Lake, 5000 feet, 9 Mar 1966, R. E. Orth (1♀; UCR), Independence, 3.2 km NW, 1 Mar 1964, J. D. Bircham (1♂, 3♀; CAS), Independence, 20.9 km NE, 10 Mar 1964, J. D. Bircham (10♂, 13♀; CAS); Kern Co., Arvin, 14 Mar 1935, A. L. Melander (1♂, 2♀; USNM), Bakersfield, 17.7 km SW, 7 Mar 1957, E. I. Schlinger (1♀; UCD), Bakersfield, 43.5 km SE, 2725 feet, 23 Mar 1971, P. Oman (1♂; USNM), Kernville, 30 Mar 1952, E. I. Schlinger (3♀; UCD, USNM), Park, 5 Feb 1948, R. Coleman (3♂, 5♀; USNM); Kings Co., Lemore, 8.1 km W, 6 Mar 1953, J. C. Hall (1♂; UCD), McClure Valley, 6 Mar 1953, J. C. Hall (11♂, 21♀; UCD); Lassen Co., Hallelujah Junction, 22 Jun 1964, M. Irwin (1♀; UCR); Los Angeles Co., Love Joy Spring, Mojave Desert, 10 May 1944, A. L. Melander (1♂, 1♀; USNM), Montebello, 30 Jan 1950, A. L. Melander (3♂, 1♀; USNM), Palos Verdes, 24 Dec 1944, A. L. Melander (1♀; USNM), Pasadena, 15 Mar 1950, A. L. Melander (1♀; USNM), San Gabriel River, 21 Jan 1950, A. L. Melander (1♀; USNM); Mono Co., Bridgeport, 7 Jun 1948, W. W. Wirth (3♀; USNM), Mono Lake, 7 Jun–31 Jul, 1940–1948, E. E. Kenaga, W. W. Wirth (2♂; KU, USNM), seepage of Mono Lake, 29 Feb 1964, J. D. Bircham (1♂, 4♀; CAS), Mono Lake, 2.4 km NE, 29 Feb 1964, J. D. Bircham (1♀; CAS), Sonora Pass, 9624 feet, 27 Jun 1951, A. T. McClay (1♀; UCD), Tioga Pass, 31 Jul 1940, A. L. Melander (4♂; KU, USNM), Whitman Hot Springs, 29 Feb 1964, J. D. Bircham (1♀; CAS); Nevada Co., near Hobart Mills, 10 Oct 1952, E. I. Schlinger (1♂; USNM), Sage Hen Creek, 23 Jun 1972, C. Goodpasture (1♀; UCD); Orange Co., Balboa, 5 Jan 1929, A. H. Sturtevant (1♀;




FIGURES 50–51.—*L. occidentalis:* 50, epandrium, surstyli, and cerci, posterior aspect; 51, internal male terminalia, lateral aspect.

USNM), Buena Park, 23 Dec 1944, A. L. Melander (6♂, 11♀; USNM), Corona del Mar, 15 Feb 1950, A. L. Melander (6♀; USNM); Plumas Co., Johnsville, 28 Jun 1964, M. E. Irwin (1♀; UCR), Mt. Ingalls, 11 Jul 1964, J. C. Buckett (3♂, 1♀; UCD); Riverside Co., Cathedral Canyon, 31 Dec 1945, A. L. Melander (1♂, 1♀; USNM), Helmet Lake, 19 May 1965, T. W. Fisher (1♀; UCR), Elsinore Lake, 25 Jan 1935, A. L. Melander (1♂, 1♀; USNM), Magnesium Spring Canyon near Indio, 5 Apr 1945, A. L. Melander (1♂, 1♀; USNM), Mt. San Jacinto, 19 May 1935, A. L. Melander (1♂; USNM), Palm Canyon, Agua Caliente Indian Reservation, 25 Feb 1970, P. H. Arnaud, Jr. (1♂; CAS), Palm Springs, 6 Jan–17 Dec, 1917–1944, J. C. Bradley, A. L. Melander (8♂, 5♀; CU, USNM), Riverside 23 Feb 1935, A. L. Melander, (3♂, 4♀; USNM), Santa Rosa Pass, 24 Apr 1951, E. I. Schlinger (37♂, 26♀; UCD); Sacramento Co., Elk Grove, 15 Apr 1952, E. C. Carlson (2♂; UCD); San Bernardino Co., Barton Flat, 20 Jul 1950, A. L. Melander (1♂, 7♀; USNM), Barton Store, 3 Sep 1950, A. L. Melander (3♂; USNM), Cucamonga, 21 Dec 1917, J. C. Bradley (1♀; CU), Jenks Lake, 18 Aug 1950, A. L. Melander (18♂, 13♀; USNM), Lost Creek, 27 Jul 1953, A. L. Melander (1♂; USNM), 1000 Springs, 31 Aug 1953, A. L. Melander (9♂, 3♀; USNM), South Fork Santa Ana, 18 Jun 1945, A. L. Melander (1♂; USNM), Sugar Loaf Mountain, 22 Jul 1953, A. L. Melander (1♂; USNM), Upper Santa Ana, A. L. Melander (18♂, 13♀; USNM), Victorville, 13 Dec 1917, J. C. Bradley (1♀; CU); San Diego Co., Cuyamaca Lake, 4600 feet, 21 Apr 1955, W. R. Richards (1♂; CNC), Lake Henshaw, 10 Mar 1950, A. L. Melander (1♂, 2♀; USNM), La Pasta Creek, 10 Apr 1950, L. W. Quate (1♂; USNM), San Diego, 8 Mar–30 Dec, 1934–1953, A. L. Melander, P. H. Arnaud, Jr. (3♂, 1♀; CAS, USNM); San Luis Obispo Co., south end, Soda Lake, 24.2 km SE Simmler, 2 Apr 1969, H. B. Leech (1♂, 1♀; CAS); San Mateo Co., Redwood City, 19–26 Apr 1906 (3♂, 1♀; ANSP, USNM); Santa Barbara Co., Carpinteria, 24 Feb 1950, A. L. Melander (1♂; USNM); Santa Clara Co., Palo Alto, 2 Apr 1906 (1♂; USNM); Siskiyou Co., Panther Meadows, 22.5 km E Shasta, 8 Apr 1966, E. L. Smith (1♀; UCD); Solano Co., Benicia, 12 Apr 1952, E. I. Schlinger (1♀; UCD); Stanislaus Co., Del Puerto Canyon (1♀; USNM), Qdoal Creek, 17 Mar 1948, P. D. Hurd (1♂; USNM); Sutter Co., Sutter Buttes, 2 Apr 1953, J. C. Hall (2♂; UCD), Yuba City, 26 Nov 1937, Christenson (1♀; USNM); Tulare Co., Crabtree Meadow, 10,550 feet, 23–29 Jul 1915 (2♂; CAS, CU), Idlewild, 14 May 1950, A. L. Melander (3♂, 2♀; USNM), Siberian Outpost, 10,500 feet, 31 Jul 1915 (1♂; ANSP); Tuolumne Co., Dardanelles, 26 Jun 1951, A. T. McClay (1♂; UCD); Ventura Co., Sulfur Springs, Angeles Forest, 3 Mar 1953, A. H. Sturtevant (1♂; USNM); Yolo Co., Elkton Ferry, 16 Apr 1952, E. I. Schlinger (1♂, 1♀; UCD). COLORADO: Archuleta Co., Pagosa Springs hot spring, 27 May 1969, W. W. Wirth (4♀; USNM); Baca Co., Walsh, 4.8 km S, 23 May 1947, M. T. James (1♂; WSU); Boulder Co., Corona Pass, 10,600 feet, 6 Jul 1961, J. G. Chillcott (3♂, 1♀; CNC); Dolores Co., Dove Creek, 10.5 km W, 23 Jun 1973, W. N. Mathis (1♀; USNM); Jackson Co., Cameron, 10,500–11,000 feet, 20 Aug 1940, H. E. Milliron (6♂, 8♀; CNC, UMN, USNM), Lake Agnes, 19–21 Aug, 1940–1947, G. F. Knowlton, M. T. James (3♂; CNC, WSU), Rabbit Ear Pass, 13 Jul 1949, R. H. Beamer (1♀; KU), Phillipsburg, 3 Jul 1947, M. T. James (1♀; WSU); Larimer Co., Fort Collins, 6 Jun 1937, M. and H. James (1♂, 1♀; ANSP); Logan Co., Crook, 15 Jun 1940, A. L. Melander (1♀; USNM); Park Co., Alma, Mt. Lincoln, 10 Aug 1945, I. H. Blake (1♂; USNM); Rio Grande Co., South Fork, 8000 feet, 20 Jun 1972, W. W. Wirth (1♂, 1♀; USNM). IDAHO: Franklin Co., Camp Wilderness, 26 Aug 1967, G. F. Knowlton (1♂; UCD); Latah Co., Bovill, 18 Jun 1911 (1♀; ANSP), Moscow, 2–11 Jun, 1908–1912 (1♂, 3♀; ANSP, USNM). KANSAS: Riley Co., Manhattan, 5–28 Mar 1932, C. W. Sabrosky (1♂, 1♀; ANSP, KNSU). MONTANA: Flathead Co., Bigfork, 12.9 km E, 1 Aug 1969, B. A. Foote (1♂; KSU); Glacier Co., Glacier National Park, Logan Pass, 18 Jul 1935 (1♂; USNM), Monida, Alaska Basin, Jun 1957, H. R. Dodge (1♀; WSU). NEW MEXICO: Sandoval Co., Jemez Springs, 12.8 km N, 25 Jun 1973, W. N. Mathis (2♀; USNM), Rabbit Mountain, 25 May 1969, W. W. Wirth (8♂, 2♀; USNM); San Miguel Co., Montezuma Hot Springs, Las Vegas, 24 May 1969, W. W. Wirth (1♂, 1♀; USNM); Taos Co., Taos, Wheeler Peak, 12,500 feet, 15–25 June 1960, Burks and Kinzer (4♂, 3♀; USNM). NEBRASKA: Cherry Co., Snake River, 2 Jun 1969, W. W. Wirth (2♀; USNM). NEVADA: Carson City (independent city), 25 May 1956, E. I. Schlinger (1♂, 1♀; UCD, USNM); Washoe Co., Reno, 16 Nov 1915 (1♀; USNM). NORTH DAKOTA: Emmons Co., Linton, 23 May 1940, D. G. Denning (1♀; UMN); Mountrail Co., White Lake, 8 Jun 1969, W. W. Wirth (2♂, 3♀; USNM); McHenry Co., Upham, 6.4 km N, 5 Jun 1969, W. W. Wirth (1♂; USNM). OREGON: Deschutes Co., Paulina Creek, 9.7 km NE LaPine, 20 May 1966 (1♂; USNM), Paulina Lake, 10 Jul 1972, W. N. Mathis (2♀; USNM), Sisters, 24.2 km S, 10 Jul–23 Aug, 1972–1974, W. N. Mathis (5♂, 2♀; USNM); Harney Co., Crane Hot Springs, 40.3 km SE Burns, 23 Feb–8 Mar, 1963–1975, K. Goeden, W. N. Mathis (4♂, 1♀; OSDA, USNM), Harney Lake, 25 May 1969, K. Goeden (1♀; OSDA); Hood River Co., Mt. Hood, 3000–6000 feet, 7 Aug 1925, C. L. Fox (1♀; CAS); Klamath Co., Crater Lake, 22 Jun–16 Sep 1924–1934, C. L. Fox (4♂, 5♀; CAS, USNM), Klamath Falls, 35.4 km NE, 10 Aug 1973, W. N. Mathis (3♂, 1♀; USNM); Malheur Co., Andrews, 12.9 km N, 1 Oct 1972, J. D. Lattin (1♀; USNM); Umatilla Co., Cold Springs, 11 Apr 1954, M. T. James (1♀; WSU); Wallowa Co., Mira Lake, 6000 feet, 30 Jul 1950, J. J. Davis (1♀; WSU). UTAH: Beaver Co., Beaver Mountain, 13 Jul 1945, G. F. Knowlton (1♀; UMN); Cache Co., Mendon, 17 May 1968, G. F. Knowlton (1♀; UCD); Davis Co., Woods Cross, 5 Oct 1933, J. A. Rowe (2♀; ANSP); Duchesne Co., Hanna, 24 Jul 1945, G. F. Knowlton (1♂, UMN); Kane Co., Kanab Canyon, 5 May 1943, G. F. Knowlton (1♀; UMN); Millard Co., Fillmore, 30 May 1945, G. F. Knowlton (1♂, 3♀; UMN); Uintah Co., Vernal, 13 Jun 1962, G. F. Knowlton (2♀; UMN); Utah Co., Aspen Grove, 11 May 1968, W. N. Mathis (4♂, 16♀; USNM), Goshen Pond, 2 Mar 1968, W. N. Mathis (4♂, 13♀; USNM), Payson, 2 Jun 1945, P. E. Telford (1♀; UMN), Provo, 23 Mar–7 Nov, 1944–1968, G. F. Knowlton, W. N. Mathis (3♀; UMN, USNM); Wasatch Co., Lost Lake Camp, Uintah Mountains, 9800 feet, 21 Jun–28 Aug 1940, C. Hayward (2♂, 3♀; ANSP); Weber Co., Hooper, 28 May 1943, G. F. Knowlton (1♂; UMN). WASHINGTON: Chelan Co., Chelan, 9 Apr 1921 (1♀; USNM); Franklin Co.,

Basin City, 8.1 km N, 19 May 1973, W. N. Mathis, (1♂, 2♀; USNM), Eltopia, 11.3 km WSW, 22 May 1971, W. N. Mathis (2♀; USNM); Grant Co., Ephrata, 22 Apr 1916 (1♀; USNM), O'Sullivan Dam, 1 May–30 Oct, 1954–1956, H. G. Davis, M. T. James (11♂; 33♀; WSU); Jefferson Co., Port Townsend, 18 May, A. Seaton (1♂; ANSP); Okanogan Co., Omak, 19 May 1916, A. L. Melander (2♂; USNM); Pierce Co., Mt. Rainier National Park, Berkeley Park, 22–23 Aug 1934, A. L. Melander (4♂, 6♀; USNM), Mt. Rainier National Park, Yakima Pass, 19 Aug 1934, A. L. Melander (7♂, 5♀; USNM); San Juan Co., Olga, 17 May 1910 (1♂; ANSP); Whitman Co., Chambers, south of Pullman, 30 Jun 1953, M. T. James (1♂; USNM), Pullman, 21 Mar–15 Jun, 1909–1971, A. L. Melander, W. Turner (8♂, 17♀; USNM, WSU), Rock Lake, 29 Mar 1902, Snodgrass (1♂; WSU), Wawawai, 2 Apr 1950, R. Spurrier (1♀; WSU); Yakima Co., Yakima, 22 May 1917, A. L. Melander (2♀; ANSP, USNM). WYOMING: Albany Co., Lake Marie, 13 Aug 1957, G. F. Knowlton (2♂, 3♀; WSU), Libby Flats, 13 Aug 1957, G. F. Knowlton (2♂; WSU), Mirror Lake, 13 Aug 1957, G. F. Knowlton (1♂, 5♀; WSU); Fremont Co., Atlantic City, 3.2 km E, 21 Jun 1968, S. Wood (3♂, 5♀; USNM).

GEOGRAPHIC DISTRIBUTION (Figure 52).—This species occurs primarily in western North America. Most records are west of the 100th meridian between 31° and 63° north latitude.

ETYMOLOGY.—The neuter Latin adjective *occidentalis* ("in the direction of the setting sun") refers to the western distribution of this species.

REMARKS.—In North America, this is one of the commonest and most widespread species in the genus, although both it and *L. bimaculata* have been misidentified by American workers as *L. sibilans*. Based on material at hand, *L. sibilans* occurs only from the Palearctic Region. Andersson's (1975) figures of the male terminalia of *L. sibilans* should be consulted should questionable specimens be discovered.

Considerable color variation is evident in the face. Coloration of facial pollinosity of most specimens is dull, grayish brown, but extremes from nearly pure white to golden and various shades between are not uncommon, frequently within specimens of the same population. Because facial coloration is so variable, overlapping the color within species that are relatively constant, I cannot generally recommend it as a reliable distinguishing character for this species.

Specimens of *L. occidentalis* are generally collected from emergent vegetation associated with freshwater habitats.

## Zoogeography

Assuming that the cladograms (discussion for *Thinoscatella*) represent reasonable constructions of the relationships between the species and that available locality data fairly accurately portray the actual species distributions, several hypotheses can be generated to explain existing distribution patterns.

Origins are a frequent topic in biogeographic considerations, although of late their prominence has been questioned (Croizat, et al., 1974). Regardless of our widened, perhaps enlightened perspective, however, the subject is neither dead nor moot.

For *Haloscatella,* it appears likely that its ancestor had its origin in western North America. I suggest western North America as the *terra originis* because of the relationships indicated within the cladogram (Figure 2). The first dichotomy produced two ancestral stem species from which all present-day species are believed to have originated. All existing species from one of these stems are endemic to the West, and *L. muria,* from the other lineage, likewise occurs in the West in addition to elsewhere. Because one lineage is exclusively western and the other has at least one species occurring there, it is reasonable that the stem species also occurred there. In the West, the ancestral stem species became widespread, and with the onset of vicariance events, the species now existent resulted. The fact that distributions of many present-day species are now sympatric simply indicates subsequent dispersal.

Two generalized patterns (tracks) are evident in *Haloscatella.* The first resulted from short-range dispersal, the other from long-range dispersal. With the exception of *L. dichaeta, L. muria,* and *L. fluvialis* (if indeed the latter is a member of this subgenus), the species of this subgenus occur in western North America only. Without fossil evidence to suggest extinction elsewhere, I assume that these species are the products of repeated vicariance events in the general area where they now occur. Because geographic features now existent in western North America do not appear to prevent dispersal, fragmentation of the ancestral species distributions must be attributable to barriers that are now ineffective or have disappeared. It is now well known that during the Pleistocene, western North America south of the larger ice sheets was partitioned by generally north-south bands of glaciation, particularly along the mountain ranges (Howden,

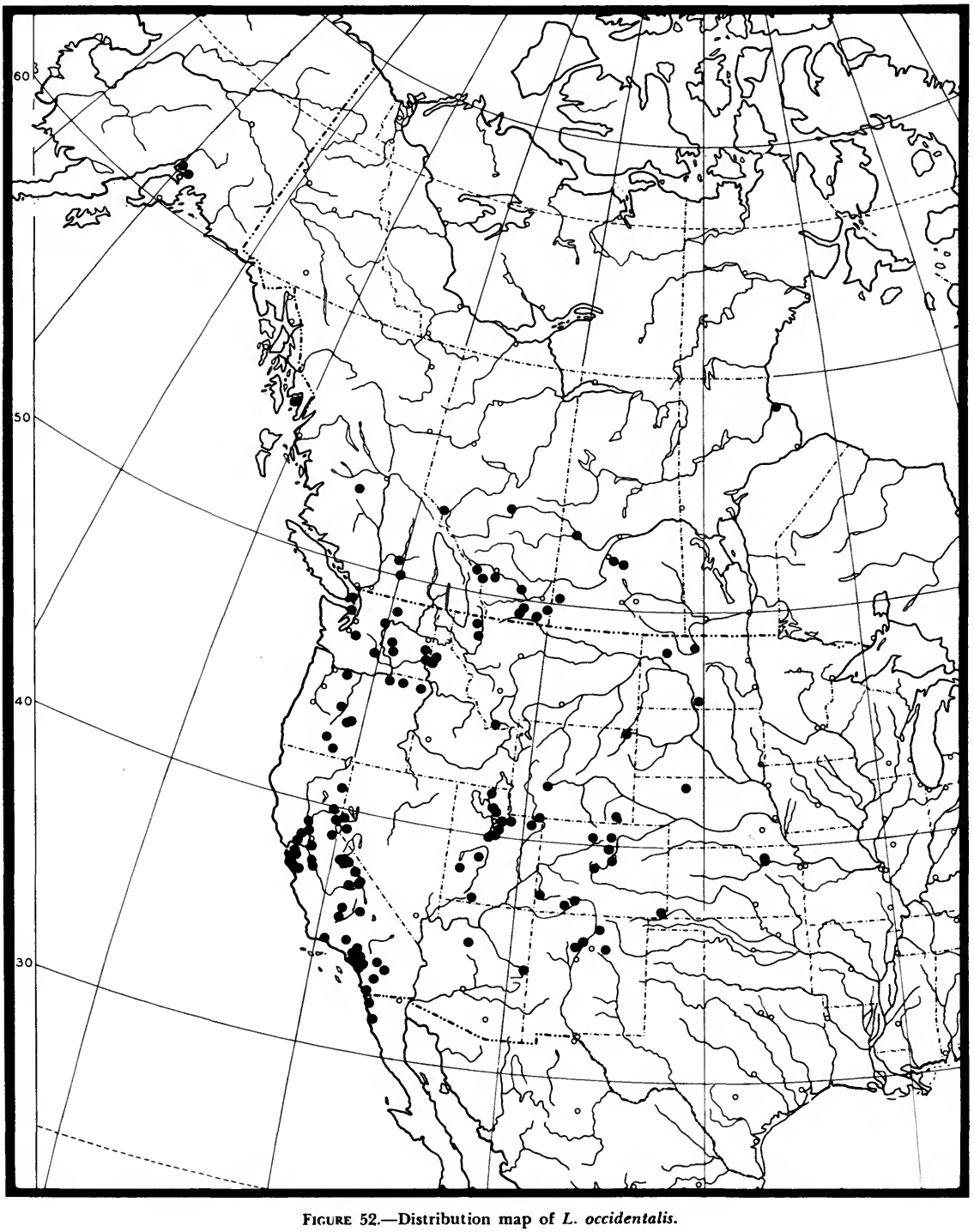



FIGURE 52.—Distribution map of *L. occidentalis*.

1969). During this period of glaciation, larger ice sheets covered most of northern North America above the United States-Canadian border. This information seems to provide a basis for a simple explanation of how the species of this subgenus arose and why they now occur where they do. The distributions of none of the species of this group extend much beyond the United States-Canadian border, and the few localities above the border are easily explained by immigration after the last glacial period. Barriers necessary to fragment the distribution of the species from which the present species were derived are likewise explained by the bands of glaciation extending south along the mountain ranges. These glacial bands would partition the species range, permitting speciation to occur. With the ebb of glaciation during warmer interglacial periods, the range of the newly formed species could be expanded through subsequent dispersal.

The ancestor of *L. dichaeta, L. muria,* and possibly *L. fluvialis* apparently dispersed widely throughout much of the Northern Hemisphere. Subsequently a barrier arose, followed by speciation that eventually resulted in these three species. The route of dispersal is difficult to determine because our knowledge of Siberian Ephydridae is virtually nonexistent. It seems likely that the last large ice sheet in northeastern North America was the barrier to separate the populations of northern Europe from those of North America. Should specimens of *L. dichaeta* be discovered in Siberia, Beringia would be another possible route of dispersal, although glaciation would again seem to offer the best possibility as a barrier.

The vagility of these species and probably their stem ancestor is inferred from their present-day distributions and what appear to be new range extentions. Presently, *L. muria* is the most widespread species in North America, as is *L. dichaeta* in the Old World. Specimens of the latter were discovered in South Africa, thousands of miles south of its known palearctic distribution. The presence of *L. dichaeta* in South Africa must be the result of a recent introduction.

*Thinoscatella* occurs principally along the Northern Hemisphere coasts with secondary exposure to cold-water oceans. Of the two known species, *L. quadrisetosa* is more widespread, occurring in northern Europe and northern North America as far west as Alaska. The second species, *L. lattini,* ranges from Alaska to southern California. The distributions of the two species apparently do not overlap. As with *Haloscatella,* our lack of knowledge concerning the Siberian fauna of *Thinoscatella* is critical, limiting discussion to incomplete data. It is not known whether or not *L. lattini* occurs in Siberia. Should *L. lattini* be found in Siberia, and I think it will, the vicariance event that produced the two species may have occurred there. Through subsequent dispersal, the ranges of the two species could have attained their present-day distributions. Otherwise, I would suggest that the vicariance event took place somewhere in northern Alaska, an area that presently divides the distributions of the two species.

In North America, the distributions of species of *Lamproscatella,* sensu stricto, are primarily western, and I suggest that the events leading to species formation among members of this subgenus were similar to those leading to speciation in *Haloscatella. Lamproscatella bimaculata* is widespread in northern Europe, Asia, and western North America, and *L. brunnipennis* occurs in the Arctic Regions of North America and northern Europe (Andersson, 1975). The other North American species are endemic to the Western Hemisphere.

From the standpoint of historical zoogeography, perhaps the most interesting distribution of a member of this subgenus is that of *L. aklavik.* This species is known only from the delta of the Mackenzie River in northern Yukon Territory. This area has been considered a refugium (Ball, 1963) because of the high degree of endemics found there. The distribution of *L. aklavik* corroborates this hypothesis.

As for the origins of *Lamproscatella,* sensu stricto, I suggest western North America, as suggested for *Haloscatella* earlier. Males of *L. occidentalis* and *L. brunnipennis* have very evident surstyli, a condition I interpret as plesiotypic. Assuming that these two species are the most primitive extant species of the subgenus, and because both species occur in western North America, one being endemic there, the simplest explanation is that the subgenus had its origins there also. From there, the subgenus radiated into the Old World, where a second major radiation gave rise to the numerous species related to *L. sibilans.* The route of dispersal was probably through Beringia, although again, this is highly

speculative without confirming evidence from the fauna of Siberia.

The distributions of all three subgenera are similar in many respects. In North America, most species are confined to the West and Arctic north. Species retaining more plesiotypic character states specifically occur in the West, all of which suggest that the species ancestral to present-day taxa had their origins in the West and then dispersed along northern routes.

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