Studies of Ephydrinae (Diptera: Ephydridae), I: Revisions of *Parascatella* Cresson and the *triseta* Group of *Scatella* Robineau-Desvoidy

WAYNE N. MATHIS
and
GUY E. SHEWELL

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Studies of Ephydrinae (Diptera: Ephydridae), I: Revisions of *Parascatella* Cresson and the *triseta* Group of *Scatella* Robineau-Desvoidy

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ABSTRACT

Mathis, Wayne N., and Guy E. Shewell. Studies of Ephydrinae (Diptera: Ephydridae), I: Revisions of *Parascatella* Cresson and the *triseta* Group of *Scatella* Robineau-Desvoidy. *Smithsonian Contribution to Zoology,* number 285, 44 pages, 62 figures, 1 table, 1978.—The New World genus *Parascatella* and the *triseta* group of the genus *Scatella* are revised. *Parascatella* is redefined to include species now known only from the temperate regions of South America. Of the 11 species included in *Parascatella,* 10 are newly described. These 11 are arrayed into two species-groups, the *pilifera* and *brunnea* groups. Most specimens of the *pilifera* group were collected at between 3000 and 4500 m elevation in northwestern Argentina and adjacent areas of Chile and Peru. The *brunnea* group is represented by a single species from southern Chile (between 46° and 53° south latitude) at elevations of approximately 400 m. The three species presently comprising the *triseta* group of the genus *Scatella* are also treated. These three species were formerly included in *Parascatella* when the latter was recognized either as a genus or as a subgenus of *Scatella.* All three species of the *triseta* group occur primarily in western North America. Our revised classification is founded on a phylogeny that is proposed using cladistic methods of analysis. The criteria used for recognition of species and of infra- and suprageneric groupings are discussed. Keys to the genera, species-groups, and species based on adult characteristics are provided. Pertinent character states are illustrated using line drawings or scanning electron micrographs. All included taxa are described or redescribed, and appropriate synonymies are listed. Distribution maps are provided for most species. Evolutionary considerations, natural history, and zoogeography are discussed.

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Introduction

Aside from Cresson's review of the Ephydridae of Patagonia and southern Chile (1931) and later synopses of the subfamilies Psilopinae (1946) and Notiphilinae (1947), there are no general studies available for the Neotropical fauna of shore flies. This condition exists despite preliminary indications (Wirth, 1968) suggesting that this fauna will probably be exceedingly rich in species. The present study of the genus *Parascatella* Cresson and of the *triseta* group of the genus *Scatella* Robineau-Desvoidy is the first of several revisions intended to bring our understanding of the Neotropical Ephydriadae into better perspective, especially with regard to the relationships between this fauna and those of other regions.

Parascatella was originally proposed in 1935 by E. T. Cresson, Jr. In the same paper, Cresson also described two Nearctic species, *P melanderi* and *P. marinensis,* and transferred *Scatella triseta* Coquillett and *S. pilifera* Cresson from *Scatella* to *Parascatella*. Cresson designated *S. pilifera* as the type-species of *Parascatella*. To date, no additional species have been described or transferred to the genus, but subsequent synopses of *Parascatella* by Sturtevant and Wheeler (1954, as a subgenus of *Scatella*) and Wirth and Stone (1956) provided keys to the Nearctic species (equals the *triseta* group of *Scatella*) and listed new locality records. In 1965 and 1968, Wirth cataloged the species from North and South America respectively.

Initially, *Parascatella* was recognized largely from chaetotactic characters (Cresson, 1935:357):

> . . . facial bristles are all down-curved, without any strong up-curved bristles in the lower angle of the face; the antesutural dorsocentral is strong and the acrostichal series of setulae setae are more or less complete to base of scutellum, as in *Lamproscatella*; the setulae of the mesofrons are all reclinate; buccal bristle well developed and the lateral scutellar bristle as strong as the apicals.

We concur generally with Cresson's chacterization of *Parascatella,* but in addition, we have noted many new characters, especially in the male terminalia, that provide a basis for further resolution of interspecific relationships. Accordingly, we recognize two species-groups in *Parascatella* and restrict the concept of the latter to include species closely

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related to *P. pilifera,* all of which are Neotropical. We consider the Nearctic species Cresson described in *Parascatella* to be a species-group within the genus *Scatella*. Details relating to these changes are enumerated in the systematic treatment below.

Members of *Parascatella* are presently known only from western South America, where they are typically associated with semiaquatic and aquatic habitats. Specimens are collected infrequently, and prior to the present study, only one species had been described. Virtually nothing is known of the natural history of these species. In this study, we describe ten additional species, all from South America.

The *triseta* group of the genus *Scatella* includes three species, all previously described. Previous authors (Cresson, 1935; Sturtevant and Wheeler, 1954; Wirth, 1965, 1968; Wirth and Stone, 1956) considered these three species to be congeneric with *P. pilifera* and thus were included with the latter under *Parascatella*. We have found that these species are more closely related to *Scatella* (including *Neoscatella* Malloch) species and have transferred them there. Species of the *triseta* group occur throughout most of western North America, primarily west of the Mississippi River.

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For courtesies extended during visits to study types and other collections, we gratefully thank the personnel of the Academy of Natural Sciences of Philadelphia. We also thank Mr. Brian H. Cogan, British Museum (Natural History), for carefully comparing the type of *P. pilifera* (Cresson) with a specimen we sent for his study.

In addition, we thank Mr. George C. Steyskal for assistance with the species etymologies, Mrs. Elaine R. Hodges and L. Michael Druckenbrod for most of the illustrations, Miss Mary Jacque Mann for the scanning electron micrographs, Miss Hollis B. Williams for arranging locality data and making maps, and Miss Anne Halpern for typing the various drafts of this paper. In addition, we thank Drs. Willis W. Wirth, F. Christian Thompson, and Wayne E. Clark for critically reading the manuscript.

Key to Genera Related to *Scatella* Robineau-Desvoidy

1. One pair of lateroclinate fronto-orbital bristles; aedeagal apodeme attached to hypandrium; thorax bi- or tricolored, with each color sharply demarcated from the others 2
   Two pair of lateroclinate fronto-orbital bristles; aedeagal apodeme of male terminalia not attached to hypandrium; coloration of thorax more or less unicolorous or with colors not distinctly contrasting 3
2. Costa extending to R_{4+5} ..... ***Scatophilia*** Becker
   Costa extending to M_{1+2} ..... ***Limnelia*** Malloch
3. Supra-alar bristle reduced, length approximately one-half or less that of postalar bristle; lacking distinctly larger spinelike setae along costal margin; aedeagal apodeme flattened dorsoventrally, frequently L-shaped; surstyli fused indistinguishably with venter of epandrium ..... ***Scatella*** Robineau-Desvoidy
   Supra-alar bristle subequal in length to postalar bristle; costal margin with several interspersed spinelike setae; aedeagal apodeme flattened laterally; surstyli distinct as setulose lobes at venter of epandrium ..... ***Parascatella*** Cresson

Genus *Parascatella* Cresson

Parascatella Cresson, 1935:357 [type-species: *Scatella pilifera* Cresson, by original designation].—Wirth, 1968:26 [catalog of species].

DIAGNOSIS.—Resembling other genera of the *Scatella* complex with spotted wings but differing by the following combination of characters: 2 pair of larger lateroclinate fronto-orbital bristles; lacking an outstanding pair or pairs of distinctly larger upcurved facial bristles, especially toward posteroventral corner of face, and a series of porrect to upcurved bristles extending from interfoveal carina to posteroventral angle of face; 3 pair of dorsocentral bristles (1+2); acrostichal setae seriated into 2 rows and moderately well developed to scutellum, often with a slightly larger pair of setae at level of transverse suture; supra-alar bristle subequal in length to postalar bristle; aedeagal apodeme of male terminalia flattened laterally, teardrop shaped; surstyli evident at venter of epandrium as lobelike setulose processes. Specimens of *Parascatella* are noticeably larger than most of the *Scatella* complex.

DESCRIPTION.—Moderately small to moderately large shore flies, length about 2.5 to 4.9 mm; usually dark colored, with setulose, arched face and patterned wings.

Head: Frons rectangular, wider than long; mesofrons very finely sculptured, shiny metallic reflections, metallic luster weakened anteriorly in specimens of some species, narrowing toward frontal suture; parafrons dull, pollinose, variously colored and usually with discernible fronto-orbits that contrast in color or luster. Ocelli forming isosceles or equilateral triangle, when isosceles, distance between posterior pair shorter than between either posterior ocellus and anterior ocellus; ocellar triangle raised in relief from mesofrons base. One pair of divergent-proclinate ocellar bristles inserted midway between median and posterior ocelli, several smaller setae posterior of larger pair; 2 pair of larger lateroclinate fronto-orbital bristles and several smaller setae interspersed, sometimes 1 pair of smaller setae enlarged; 1 pair each of inner and outer vertical bristles; postocular setae variously developed, often with dorsalmost pair well developed, subequal to ocellar bristles; usually with some scattered, smaller setae in pollinose parafrons, usually somewhat aligned along mesofrons margin. Antenna generally dark; first and second segments concolorous with or darker than face; second segment with distinct, slender seta inserted dorsally and with scattered, smaller setae on median and ventral surfaces; third segment dark brown to black, more pubescent; arista arising from dorsal surface near base of third segment, arista thickened basally, tapering to stylelike tip; macropubescent or micropectinate on basal two-thirds; length various. Face arched, protruding, setulose, usually with distinct interfoveal carina; marginal setae usually larger except dorsally, all setae downcurved; parafacies bare, enlarging gradually posteroventrally along eye margin. Eye bare, obliquely rounded to round; gena high, height at least one-fourth eye height, often one-third to one-half, mostly concolorous with face but often with shinier luster, setulose posteriorly and with 1 larger, prominent genal bristle. Clypeus narrow, a straplike band, usually concealed in cephalic view; maxillary palpus much longer than wide, setulose; prementum bulbous, pollinose, setulose.

Thorax: Mesothorax generally pollinose, dull; mesonotum darker than pleural areas and usually with shiny vittae, which often fuse posteriorly becoming generally shiny; scutellum variously colored and textured, sometimes contrasting with mesonotum, mostly flat to slightly convex, rugose in members of some species. Pleural areas dull, densely pollinose, and lighter in color than mesonotum; color generally subdued, grayish, and more or less uniform, although often darker dorsally. Chaetotaxy as follows: acrostichal setae in 2 rows, extending to scutellum, variously developed but not equaling larger dorsocentral bristles, usually with 1–2 pair of slightly larger setae, 1 pair often at sutural level, usually lacking distinctive, prescutellar acrostichal setae; 3 pair of larger dorsocentral bristles (1+2), last pair displaced laterally, usually with several smaller setae between larger bristles; 1 pair of presutural bristles; 1 pair of well-developed supra-alar bristles, these subequal in length to postalars; 1 pair of postalar bristles; humeral callus lacking macrosetae; 2 pair of notopleural bristles; 1 pair of mesopleural bristles along posterior margin, also with several, smaller setae toward dorsal and posterior margins; 1 pair of sternopleural bristles and several surrounding smaller setae; pteropleuron and hypopleuron bare. Halter pale yellowish. Legs generally more or less concolorous with thoracic pleural areas; tarsomeres often lighter in color ventrally; front coxa with distinctively larger seta laterally near

level of basal one-third; front femur often larger in diameter than other femora and in members of some species with a row of strong, spinelike setae along anteroventral and posteroventral surfaces toward apical half; basal tarsomeres of front legs in males of some species bearing a row of long slender, fringelike hairs; tarsal claws short, slightly curved, pulvillar pads well developed. Wing infuscated, grayish to light brown, and usually with distinct pattern of white spots; costal vein extending to vein M_{1+2}; bearing spinelike setae along costal margin, especially between apices of R_1 and R_{2+3}.

Abdomen: Generally thinly pollinose and usually with subshiny luster; coloration various, unicolorous in most species; generally lacking prominent macrosetae. Males with 5 visible segments dorsally, fifth about twice as long as fourth; segment 1 through 4 more or less subequal; females with 6 to 7 visible segments dorsally, first to sixth subequal, seventh smaller. Male terminalia composed of epandrium, cerci, surstyli, hypandrium, and aedeagus; other segments of terminalia reduced except for spiracle of sixth segment, which is situated in the membrane between the fifth segment and epandrium. Epandrium suboval with medium suture extending from membranous area surrounding cerci to ventral margin; surstylar lobes present, densely setulose, especially long medial surface; hypandrium arched below, forming a continuous process from side to side, attached to epandrium with projecting process; aedeagus with membranous distiphallus basiphallus sclerotized; aedeagal apodeme spatulate, laterally flattened, narrow end slightly curved and attached to the aedeagus.

Discussion.—The male terminalia of *Parascatella* have not been figured previously. Wirth (1948) discussed and illustrated the external male genitalia of representatives of several related genera. Additional figures of genitalic structures of members of the tribe Scatellini are also illustrated in the studies of Malloch (1925), Tonnoir and Malloch (1926), Collin (1930), Tuxen (1944), Harrison (1959), and Andersson (1967, 1971, 1975).

The basic ground plan of *Parascatella* male genitalia closely follows the pattern of other genera as illustrated in the above-cited papers with the exception of *Lamproscatella* Hendel. The genitalic structures of that genus show marked divergence from the general scheme. Within *Lamproscatella,* there is considerable evidence that its various subgroups had independent origins and that at least one assemblage of species has closer affinities to members of genera not closely allied with *Scatella.* In most instances, however, only the external features (epandrium and surstyli) were considered, and we are hesitant at this time to suggest redefining genera based on similar genitalic structures only, without a thorough study of the internal structures throughout the tribe.

Wirth (1948) demonstrated the usefulness of the hypandrial processes (as "gonites") as characters for recognizing species of Hawaiian *Neoscatella.* We have slide-mounted these processes from several specimens of *Parascatella* species but found them to be of little diagnostic value. The overall shape from species to species differs little and the number and position of the setae varies considerably within one species; in many cases, the left process differs from the right process of the same specimen. We have not relied heavily on genitalic characters for delimiting taxa at the species level.

Specimens of many *Parascatella* species exhibit considerable sexual dimorphism in the maculation of the wings and in the chaetotaxy of the face and front legs. Males of *P. apicalis* have a conspicuously large, subquadrate, white spot in cell R_3 and the wing membrane beyond the spot is darker, making the contrast with the white spot more pronounced (Figure 18). The comparable spot of female wings is much smaller, is narrowly subrectangular, and the wing membrane beyond the spot does not appear any darker than elsewhere on the wing (Figure 19). Even though variation of this feature appears more pronounced in specimens of *P. apicalis,* it is also found, though usually to a lesser degree, in specimens of *P. hirticrus, P. semicinerea,* and *P. semipolita.* Sexual dimorphism in the oral margin of the face is characterized well in specimens of *P. lanicrus,* in which setae along the oral margin of females are one-third to one-half again as large as are their homologues in males. In males of *P. pilifera* and *P. lanicrus,* the ventral surface of the basal tarsomeres and apex of the tibiae of the front legs bears long, slender, pale, fringelike hairs (Figures 5, 6), whereas the front legs of females are unmodified.

Age variation is also apparent, particularly in specimens of *P. lanicrus* and *P. semipolita.* Older specimens, which are distinguished by their tattered appearance (torn wings, broken or missing setae,

and rubbed or denuded surface vestiture), take on a rusty brown to rusty coloration, especially the dorsum of the head and thorax. In addition, the luster of surface areas that is typically shining, such as the mesofrons, becomes more brassy or golden in appearance. The occurrence of this type of variation can be confusing, making species recognition difficult.

Key to Species of *Parascatella* Cresson

1. Scutellum with 3 pair of lateral bristles; middle pair weaker, inserted midway between basal and apical pairs 2
   Scutellum with basal and apical pairs of lateral bristles only ....11. ***P. brunnea,*** new species
2. Front femur with row of stout, spinelike setae on apical half along anteroventral and posteroventral surfaces 3
   Front femur lacking rows of stout, spinelike setae, at most with a few stout setae near middle of posteroventral surface 5
3. Acrostichal and dorsalmost postocular setae well developed, much larger than smaller fronto-orbital setae; male front basitarsus lacking fringe of long, pale, slender hairs on ventral surface .....3. ***P. spinicrus,*** new species
   Acrostichal and dorsalmost postocular setae short, weak, subequal to smaller fronto-orbital setae; male front basitarsus with fringe of long pale hairs on posteroventral surface, anteroventral fringe similar but shorter 4
4. Face uniformly pale, whitish gray; interfoveal carina not defined by strong crease above; parafrons gray; mesopleuron entirely pale gray .....1. ***P. pilifera*** (Cresson)
   Face gray below interfoveal carina and antennal foveal brown; interfoveal carina abruptly demarcated above by strong crease; parafrons brown, mesopleuron brown dorsally, gray below .....2. ***P. lanicrus,*** new species
5. Body mostly black, subshiny, sparsely pollinose; femora shiny, abdominal dorsum dull, pollinose, gray; front femur with a few stout setae near middle along posteroventral surface .....4. ***P. glabra,*** new species
   Body greenish gray or brown, mostly dull, thickly pollinose including femora; front femur lacking stout setae near middle of posteroventral surface 6
6. Scutellum densely pollinose, dull, moderately flat with well-defined lateral margins; hind tibia usually with fringe of long hairs along anterodorsal surface nearly twice as long as tibial diameter 7
   Scutellum thinly pollinose, subshiny, mostly convex, lateral margins poorly defined, dorsum sometimes coarsely rugose; hind tibia usually lacking fringe of long hairs along anterodorsal surface, anterodorsal hairs not much longer than tibia diameter 8
7. Mesopleuron mostly gray, nearly concolorous with sternopleuron; mesonotum pale bluish or greenish white pollinose with brown markings; scutellum whitish; wing veins dark brown, base pale yellowish; male wing with large subquadrate white spot in cell R_3 that is not more than its own length from tip of vein R_{2+3}, veins surrounding large spot strongly sinuate, membrane beyond it strongly darkened .....5. ***P. apicalis,*** new species
   Mesopleuron mostly brown, contrasting distinctly with grayer sternopleuron; mesonotum olive green subshiny; scutellum dull, grayish pollinose base of wing light brown; male wing with white spot in cell R_3 at least twice its own length from tip of vein R_{2+3}, veins less sinuate around spot, and wing apex less noticeably clouded .....6. ***P. hirticrus,*** new species
8. Male wing with noticeably large, subquadrate, white spot in apical half of cell R_3; abdominal segments unicolorous, dull in luster, mostly pollinose 9
   Male wing lacking larger, subquadrate, white spot in apical half of cell R_3, if somewhat larger spot is present, it is distinctly longer than wide; apical abdominal segments usually either darker in coloration or appearing less pollinose shinier 10
9. Male wing with larger white spot in cell R_3 situated just beyond alignment of posterior crossvein; apical white spot in cell R_3 and abutting vein R_{4+5} located about its own length from larger white spot in cell R_3; larger species length 3.84 to 4.67 mm .....8. ***P. semicinerea,*** new species
   Male wing with larger white spot in cell R_3 situated distinctly beyond alignment of posterior crossvein; apical white spot in cell R_5 and abutting vein R_{4+5} located much nearer larger white spot in cell R_3; smaller species, length 3.14 to 4.18 mm .....7. ***P. semipolita,*** new species

Key to Species of *Parascatella* Cresson (cont'd)

10. Mesofrons, mesonotal vittae, and scutellum shiny olive green or blue; base of cell M_2 with conspicuous white spot; abdomen slender, male fourth segment two-thirds length of third segment ..... 9. ***P. balioptera,*** new species

Mesofrons, mesonotal vittae, and scutellum shiny dark brown to black; spot at base of cell M_2 not conspicuous; abdomen short and broad, male third and fourth segments subequal ..... 10. ***P. penai,*** new species

The *pilifera* Group

INCLUDED SPECIES.—*Parascatella apicalis,* new species; *P. balioptera,* new species; *P. glabra,* new species; *P. semipolita,* new species; *P. hirticrus,* new species; *P. lanicrus,* new species; *P. penai,* new species; *P. pilifera* Cresson; *P. semicinerea,* new species, and *P. spinicrus,* new species.

DIAGNOSIS.—Species of this group may be recognized by the following combination of characters: ocelli arranged in isosceles triangle; dorsalmost postocular setae often enlarged, nearly equaling length of ocellar bristles; arista short, approximately equal to combined length of antennal segments and at most macropubescent; face more densely setulose but lacking a distinctive row of downcurved to semiporrect, larger setae that extend from interfoveal carina to posteroventral corner of face; acrostichal setae often well developed, but not equaling large dorsocentral bristles and lacking distinctly larger prescutellar bristles; 1 pair of well-developed supra-alar bristles; front femur sometimes bearing partial rows of stout setae along posteroventral and anteroventral margins; scutellum with 3 pair of larger bristles, the middle pair is smaller but at least one-half length of larger pair; and costal margin spinose. The surstyli of males of this group are conspicuous as 2 parallel-sided lobes at the ventral margin of the epandrium. The surface of each lobe, particularly the median facies is densely pilose.

GEOGRAPHIC DISTRIBUTION.—The composite distribution of the included species extends from 12° to 42° south latitude (San Mateo, Lima, Peru to El Maiten, Chubut, Argentina, respectively) along both the east and west slopes of the Andes Mountains. Several species are known to occur only in the region within the provinces of Jujuy and Salta, Argentina. In part, this is probably an artifact, reflecting how poorly the foothills east and west of the Andes Mountains have been collected. By far, most of the specimens upon which this study is based were collected during a single collecting expedition to the provinces of Jujuy and Salta, Argentina, by Luis E. Peña G.

1. *Parascatella pilifera* (Cresson)

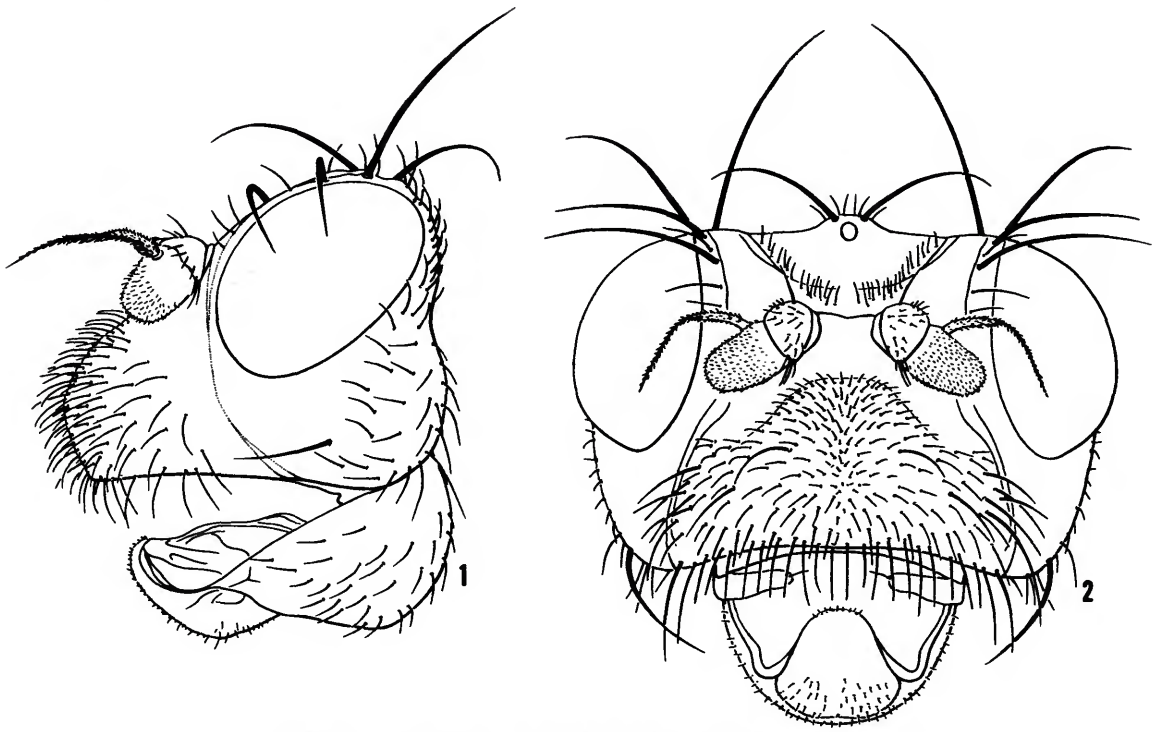
FIGURES 1–10, 14

Scatella pilifera Cresson, 1931:114.
Parascatella pilifera.—Cresson, 1935:357.—Wirth, 1968:26 [catalog].

DIAGNOSIS.—Specimens of *P. pilifera* are similar to those of *P. lanicrus* but may be distinguished from the latter by the following combination of characters: face unicolorous, whitish gray; facial setae appearing more pronounced, more uniform in size, setae along oral margin only slightly larger than remaining ones (best seen in profile); interfoveal carina more evenly rounded, not sharply demarcated with a dorsal crease; coloration of parafrons mostly gray, sometimes becoming slightly brownish gray posteriorly; mesopleuron unicolorous whitish gray.

DESCRIPTION.—Medium-sized shore flies, length 3.2 to 3.9 mm; mostly unicolorous, gray, densely pollinose but with some dorsal subshiny to shiny areas.

Head (Figures 1,2): Mesofrons with brassy metallic luster; densely pollinose parafrons charcoal gray anteriorly, sometimes becoming faintly more brownish in coloration posteriorly; fronto-orbits concolorous with face; dorsalmost postocular setae inconspicuous. First and second antennal segments concolorous, gray to brownish gray, slightly darker than facial coloration; third segment dark brown. Face unicolorous, densely pollinose, whitish gray; interfoveal carina more or less evenly rounded, lacking a distinct dorsal crease; facial setae becoming progressively larger ventrally but larger setae along oral margin not obviously larger. Gena concolorous with face, anterior portion with slightly more shiny luster.



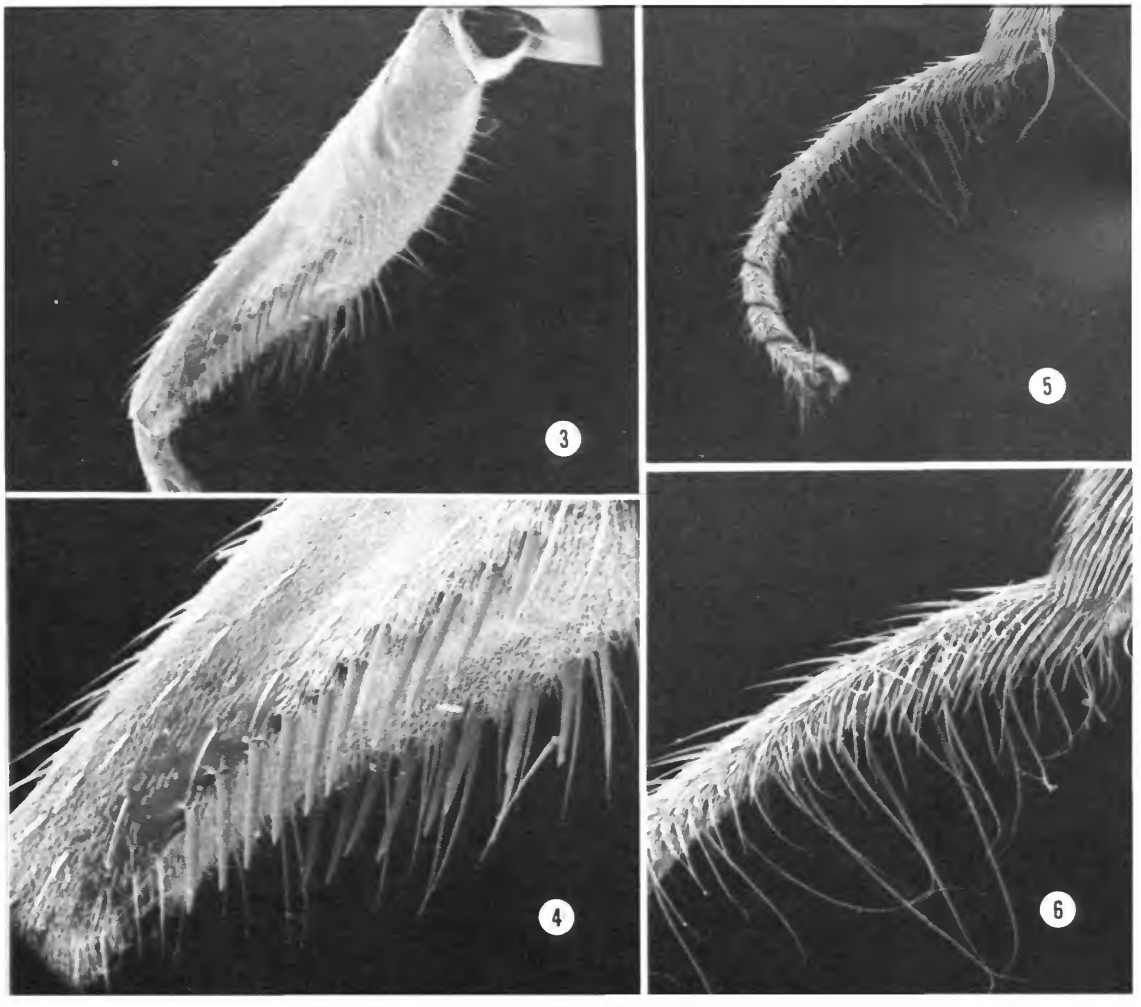
FIGURES 1,2.—*P. pilifera:* 1, head lateral aspect; 2, head, anterior aspect.

Thorax: Except for shiny vittae that are aligned with major setal tracts and a dimly shiny area on the scutellum, thoracic coloration uniform, gray and densely pollinose; shinier areas brassy but coloration less intense than that of mesofrons. Acrostichal setae small, at most equaling larger facial setae. Femora and tibiae mostly concolorous with pleural areas except for some shiny black areas on hind legs; front femur (Figures 3,4) with row of setae along posteroventral and anteroventral surfaces becoming larger, more spinelike apically; apex of tibia and basal tarsomeres of male front leg (Figures 5,6) with distinctive long, pale, fringelike hairs; tarsomeres of front leg pollinose gray dorsally, paler below; tarsomeres of middle and hind legs mostly tawny, becoming darker apically. Wing (Figure 14) hyaline to lightly infumated, grayish brown; wing of male with subrectangular white spot in cell R_3 just beyond alignment of posterior crossvein; smaller, more roundish white spots in cell R_5, apical spot more apicad from posterior crossvein; a single white spot in apical one-fourth of discal cell and abutting vein M_{3+4}. Maculation of female wing not noticeably different from male.

Abdomen: Similar in coloration to pleural areas of thorax but with faint brownish to bluish areas medially and sometimes shinier along anterior margin of each segment; overall, more thinly pollinose than head and thorax. Male terminalia as in Figures 7, 8, and 9.

TYPE-MATERIAL.—Male holotype: (Argentina) Bariloche (San Carlos de), 28 November to 1 December 1926. The holotype is in the British Museum (Natural History). We have not examined the type but have sent a male specimen to Brian H. Cogan, British Museum (Natural History), who kindly compared it with the type. Cogan (in litt.) reports that "the type is *slightly* darker on the head and thorax, probably age; additional small bristles extending laterally over the orbits are *slightly* stronger as are the additional pair between apicals and basals on the scutellum. All-in-all a very good fit" (italics his).

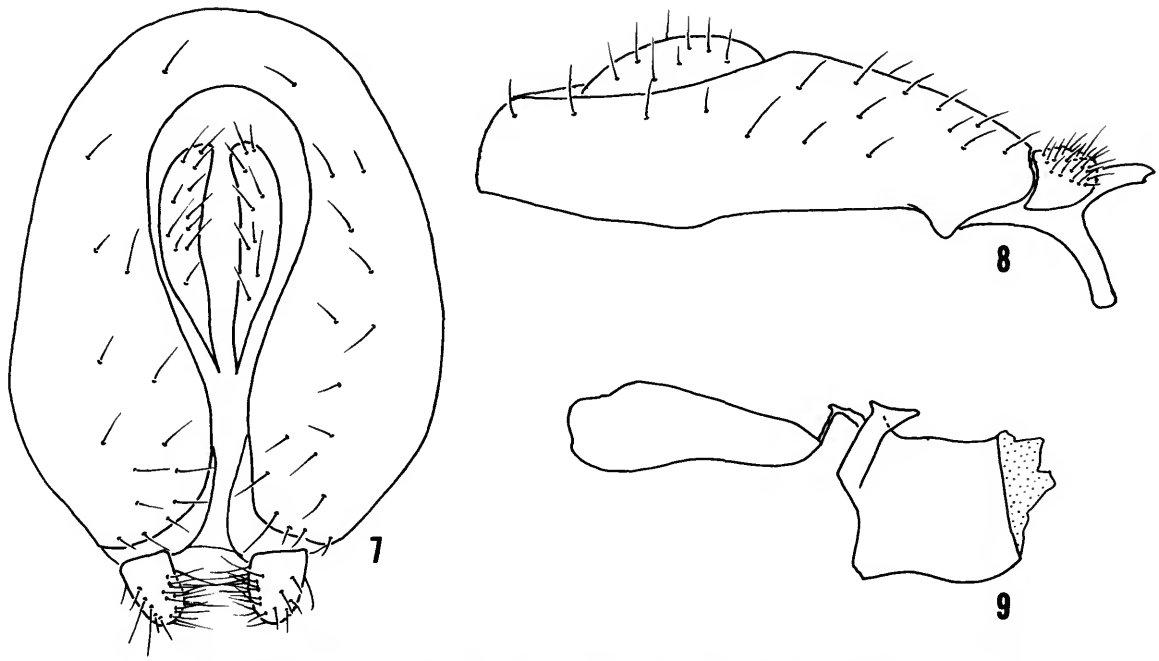
OTHER SPECIMENS EXAMINED.—ARGENTINA. CHUBUT: 1 ♀, 18 km El Maiten, 750 m, 18 Nov 66, E. I. Schlinger and M. E. Irwin. CHILE. MALLECO: 1 ♂, 1 ♀ Angol, 1 Jan 32, D. S. Bullock coll. COQUIMBO: 18 ♂ ♂, 32 ♀ ♀, Hda Illapel, 800 m, 28 Oct 54, L. E. Peña.



FIGURES 3–6.—*P. pilifera:* 3, left front femur, posteroventral aspect; 4, left front femur, enlargement of Figure 3; 5, left front tarsi posterior aspect; 6, left front tarsi, enlargement of Figure 5.

GEOGRAPHIC DISTRIBUTION (Figure 10).—*Parascatella pilifera* ranges from 31° to 42° south latitude along the foothills east and west of the Andes Mountains. This species is the only member of this species-group known to occur at elevations below 1000 m; the highest elevation of record is 800 m, near Hda Illapel, Chile. The type-locality, San Carlos de Bariloche, is located on the south shore of Lake Nahuel Huapi at an elevation of about 772 m. The single female specimen collected near El Maiten, Argentina (750 m), is also the southernmost record for the *pilifera* group (approximately 42° south latitude).

PHYLOGENETIC RELATIONSHIPS.—*Parascatella pilifera* has close affinities with *P. lanicrus*. This relationship is evidenced by the joint possession in male specimens of both species by the following: long, slender, pale hairs along the ventral surface of the basal tarsomeres and tibial apex of the front leg; poorly developed dorsalmost postocular and acro-



FIGURES 7–9.—*P. pilifera:* 7, epandrium, surstyli, and cerci, posterior aspect; 8, epandrium, surstyli, cerci, and gonites, lateral aspect; 9, internal male genitalia, lateral aspect.

stichal setae; and similar pattern of white wing spots. We interpret these character states as synapotypic.

2. *Parascatella lanicrus,* new species

FIGURES 11–13, 15

DIAGNOSIS.—This species is closely related to *P. pilifera* as noted above. Specimens of this species may be distinguished from those of *P. pilifera,* however, by the following combination of characters: face with dorsum of interfoveal carina brown, contrasting with whitish gray coloration below; interfoveal carina more sharply defined with a distinct dorsal crease; facial setae along oral margin distinctly larger than remaining facial setae; pollinose parafrons brown; and mesopleuron grayish brown dorsally, becoming lighter, grayer ventrally.

DESCRIPTION.—Moderately small to medium-sized shore flies, length 2.87 to 3.76 mm; mostly grayish brown to brown above, becoming grayer below; dorsum with considerable subshiny to shiny areas.

Head (Figure 11): Mesofrons with metallic, dark green to greenish blue luster; pollinose parafrons unicolorous, brown, fronto-orbits slightly darker than parafrons, with some very dimly shining patches; dorsalmost postocular setae weak, not subequal with larger ocellars; antenna dark brown, first and second segments darker with some blackish coloration. Face with dorsum of interfoveal carina and space between antennae concolorous, brown, contrasting distinctly with whitish gray coloration on remainder of face; interfoveal carina with distinct dorsal crease; antennal fovea usually slightly less pollinose than face, often with faint subshiny luster that has some weak bluish coloration; setae along oral margin not noticeably larger in males, in female specimens much larger but not to the extent as in *P. balioptera.* Gena concolorous with lower portions of face, anterior portion with more glossy luster.

Thorax (Figure 12): Disc of scutellum and mesonotal vittae subshiny to shiny, concolorous with mesofrons but usually more subdued; pollinose areas between shiny vittae mostly brown or grayish brown, especially anteriorly; acrostichal setae very poorly developed, mostly inconspicuous; upper portion of mesopleuron brown, concolorous with brownish coloration between vittae, lower portion gray, concolorous with pteropleuron; sternopleuron

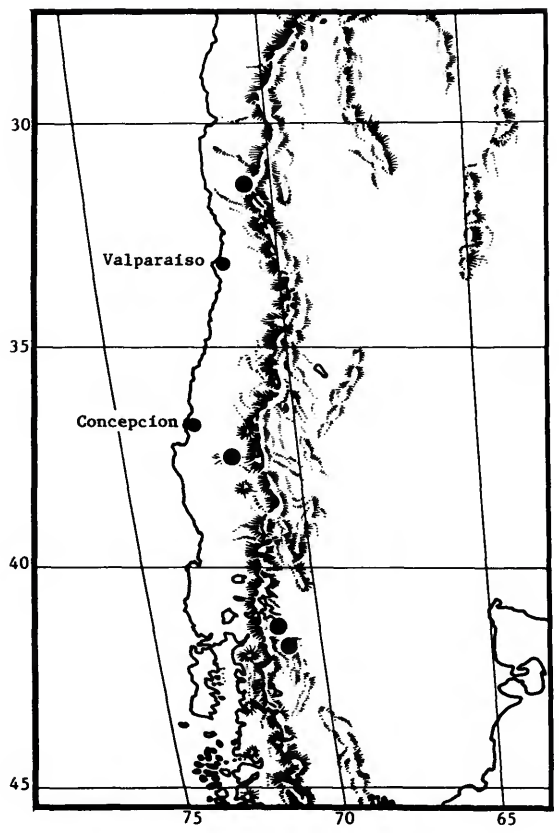


FIGURE 10.—Distribution of *P. pilifera*.

and front coxa concolorous with face. Femora and tibiae mostly concolorous except along dorsal surface of tibiae where there is less pollenosity; tarsi concolorous, blackish brown to tawny on the underside. Front femur with row of setae along the posteroventral and anteroventral surface, becoming larger, spinelike apically; apex of front tibia and basal tarsomeres of male specimens bearing very distinctive, long, pale, fringelike hairs. Wing (Figure 15) hyaline to very lightly infuscated, light brown; wing maculation when evident of male and female similar to that described under *P. pilifera*.

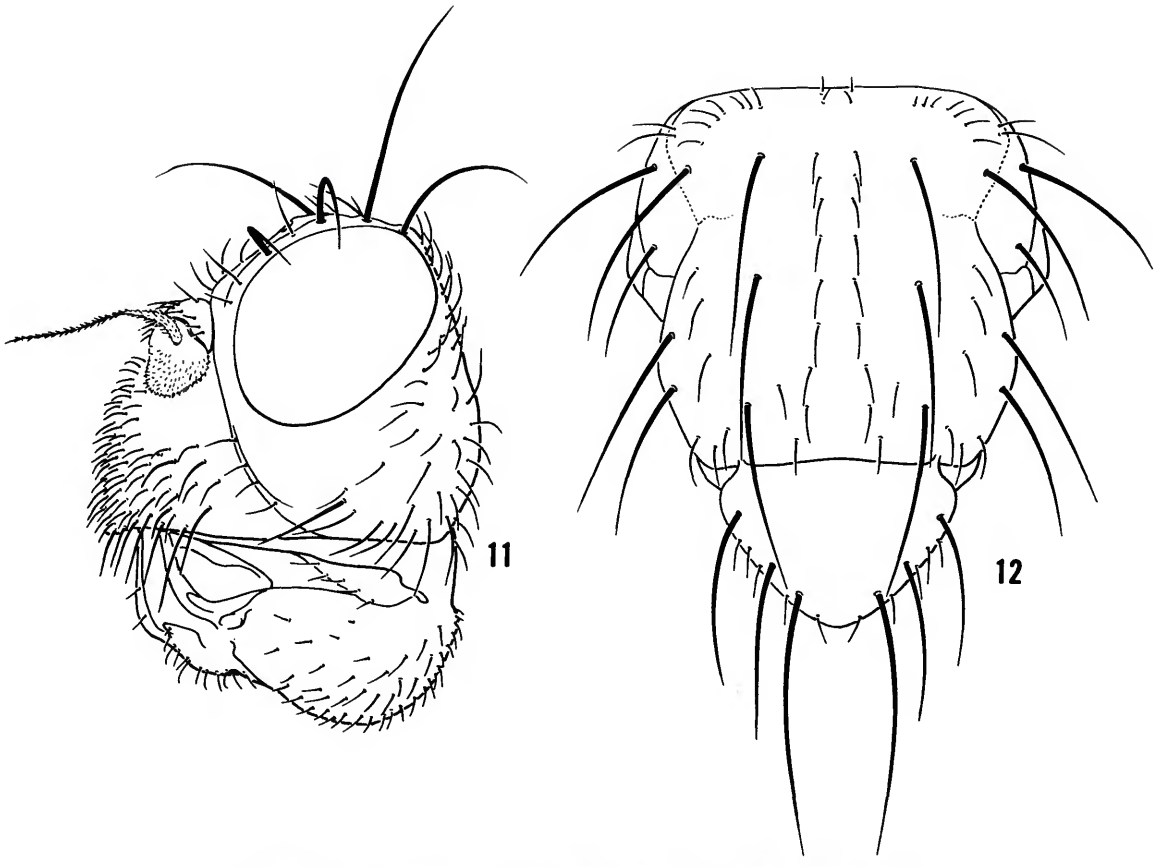
Abdomen: Generally pollinose, although more thinly so than pleural areas of thorax, gray to grayish brown; segments 3–5 of male specimens often mostly olivaceous to brownish gray, contrasting with grayer first and second segments; female abdomen similar but usually with shinier areas toward anterior margin of segments beyond second, shiny area dimly brassy.

TYPE-MATERIAL.—Male holotype: "ARGENT(INA). Jujuy, La Quiaca, 23. X. 68. 3500 m. L. E. Pena." Allotype and 86 paratypes (31♂♂, 55♀♀): same label data as holotype. Other paratypes as follows: ARGENTINA, JUJUY: 18♂♂, 19♀♀, Lecho, 32 km E La Quiaca, 330 m, 24 Oct 68, L. E. Peña; 5♂♂, 16 ♀♀, Yavi-Chico, 2 km E La Quiaca, 3500 m, 24 Oct 68, L. E. Peña; 12♂♂, 10♀♀, Cerrillos, 3600 m, 31 Oct 68, L. E. Peña; 16♂♂, 16♀♀, Rio Orosmayo, 43 km SW Cienaga, 3 Nov 68, L, E. Peña; 4♂♂, 6♀♀, Garrios, S La Quiaca, 3500 m, 31 Oct 68, L. E. Peña; 9♂♂, 3♀♀, Santa Catalina, 3700 m, 25 Oct 68, L. E. Peña; 11♂♂, 16♀♀, 2 km SW Cienaga Rd to Pirquitas, 3900 m, 3 Nov 68, L. E. Peña; 6♂♂, 9♀♀, Rio Seco, 5 km S Sta Catalina, 3500 m, 25 Oct 68, L. E. Peña; 7♂♂, 5♀♀, 3 km N. Humahuaca, 3300 m, 22 Oct 68, L. E. Peña; 1♀, 12 km S of Tilcara, 2000 m, 23 Oct 68, L. E. Peña; 1♂, 1♀. Cangrejillos, S La Quiaca, 3500 m, 28 Oct 68, L. E. Peña, 1♂, 1♀, Coyaguayma, 7 km S Mina Perquitas, 4100 m, 4 Nov 68, L. E. Peña; 2♀♀, Abralaite, 85 km S Abra Pampa, 3650 m, 29 Oct 68, L. E. Peña; 1♂, Suripujio, 3700 m, 24 Oct 68, L. E. Peña; 1♀, 2 km W Yavi, 3400 m, 31 Oct 68, L. E. Peña; 1♀, Cienequillas, 3650 m, 28 Oct 68, L. E. Peña; 2♀♀, Cajas, 35 km E La Quaica, 3800 m, 24 Oct 68, L. E. Peña; 1♂, Cueva Negra, 10 km S Mina Periquitas, 4300 m, 4 Nov 68, L. E. Peña. SALTA: 3♂♂, 1♀, San Antonio de Los Cobres, 3750 m, 6 Nov 68, L. E. Peña; 1♀, Chorillos, 23 km W San Antonio de Los Cobres, 3800 m, 6-7 Nov 68, L. E. Peña. TUCUMAN: 1♀, Tafi Viejo, 13 Oct 46, Coll, Golbech. PERU. LIMA: 7♂♂, 2♀♀, 3 km E San Mateo, 2500 m, 14 Sep 54, E. I. Schlinger and E. S. Ross, collectors. The holotype, allotype, and most paratypes except those from the last 2 localities are in the Canadian National collection, Ottawa, type number 15231.

ETYMOLOGY.—*Lanicrus* is a combination of the Latin nouns *lana,* meaning "wool," and *crus,* meaning "leg" or "shank," in allusion to the wooly appearance of the front legs in specimens of this species. The name stands in apposition to the generic name.

GEOGRAPHIC DISTRIBUTION (Figure 13).—The known distribution of *P. lanicrus* extends from the province of Lima, Peru (San Mateo), in the north to the provinces of Jujuy, Salta, and Tucuman, Argentina, in the south. These localities range between approximately 12° and 27° south latitude and 2000 to 4300 m in elevation. Like most members of the *pilifera* group, specimens of *P. lanicrus* occur at high-altitude localities along both the east and west slopes of the Andes Mountains.

VARIATION.—Considerable variation is apparent in this species throughout its distribution. The color of older specimens often appears rusty brown, particularly the wings and dorsal surface of the head



FIGURES 11,12.—*P. lanicrus:* 11, head, lateral aspect; 12, thorax, dorsal aspect.

and thorax; the bristles and wings in these specimens are also usually tattered, torn, or are missing. Sexual dimorphism is also apparent. The facial bristles along the oral margin of males are considerably smaller than homologous bristles in females.

PHYLOGENETIC RELATIONSHIPS.—*Parascatella lanicrus* is the sister-species of *P. pilifera* (see the diagnosis of this species and the discussion under *P. pilifera*).

3. *Parascatella spinicrus,* new species

FIGURES 16, 20

DIAGNOSIS.—Like *P. Pilifera* and *P. lanicrus,* specimens of this species have a row of stout, spinelike setae along the anteroventral and posteroventral surfaces toward the apical half of the front femur. Unlike these congeners, however, members of *P. spinicrus* lack the long, slender, pale fringelike hairs on the ventral surface of the basal tarsomeres of the front leg in males; the dorsalmost postocular and acrostichal setae are well developed, subequal with the ocellar bristles; the face is unicolorous, brown, more or less concolorous with the parafrons and mesopleuron; and the wing of males has a prominent, subquadrate, white spot in cell R_3, slightly more than its width from the apex of vein R_{2+3}.

DESCRIPTION.—Medium-sized to moderately large shore flies, length 3.12 to 4.14 mm; mostly pollinose brown specimens with few subshiny areas on mesonotum.

Head: Mesofrons shining with blackish blue me-

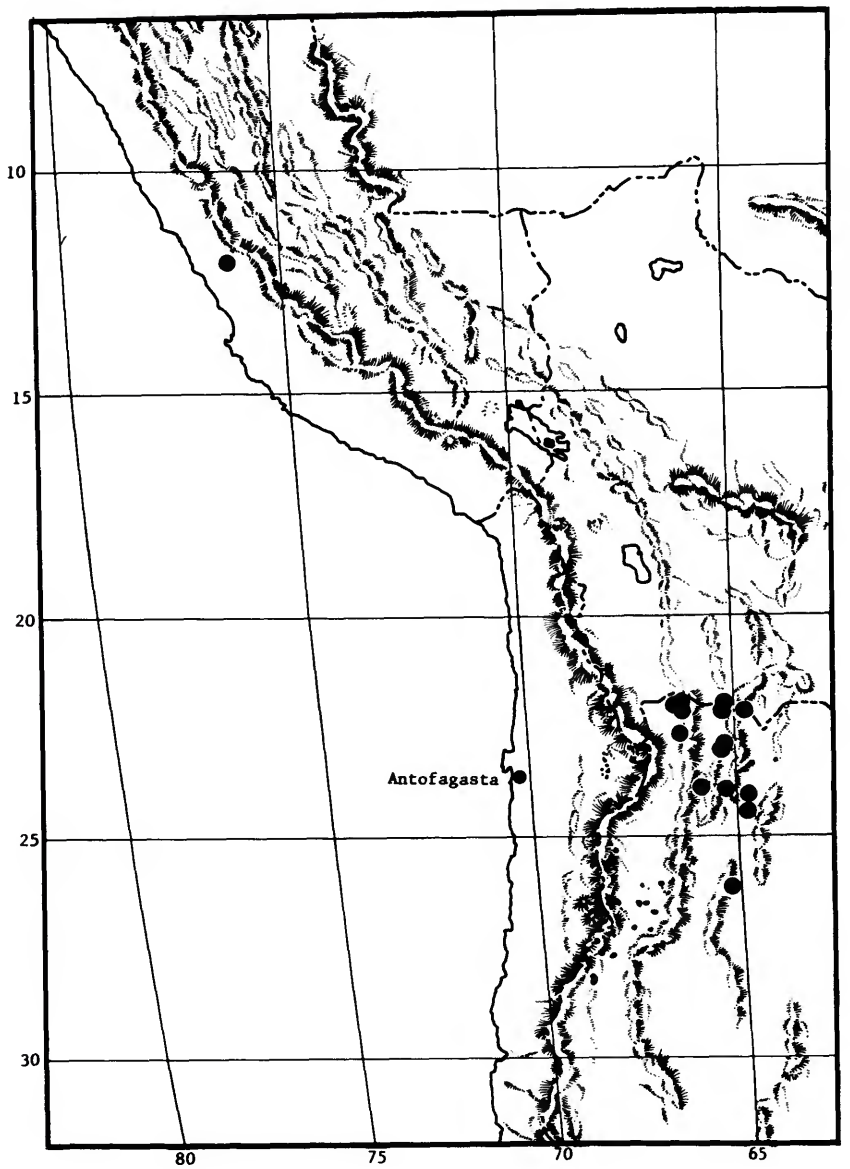


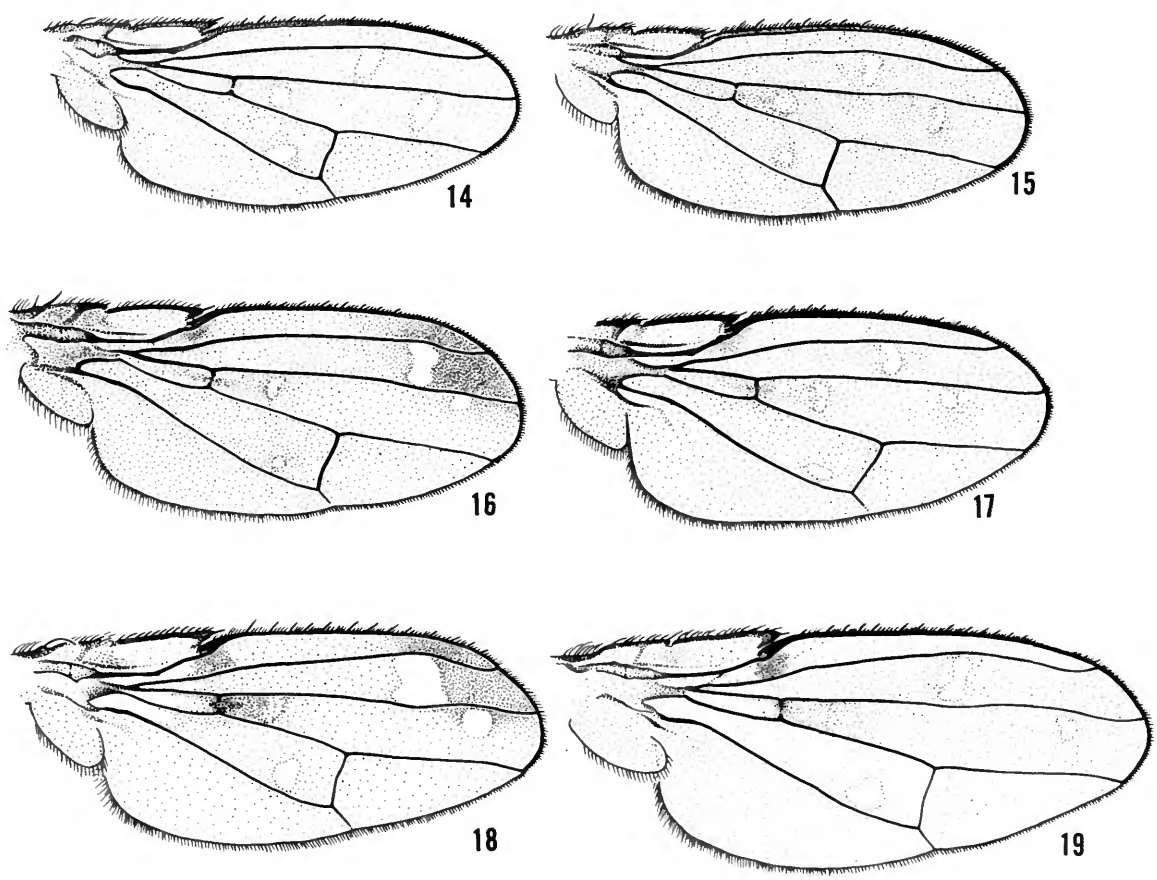
FIGURE 13.—Distribution of *P. lanicrus*.

tallic luster; parafrons pollinose unicolorous, brown; fronto-orbits slightly darker than parafrons, with some weak subshiny blackish blue tinges; dorsalmost postocular setae well developed, subequal to ocellar bristles. Antenna mostly blackish brown and unicolorous. Face unicolorous, brown but with some faint blackish blue metallic coloration dimly shiny through pollinose vestiture; facial setae among oral margin strong, much larger than remaining facial setae; interfoveal carina with distinct crease dorsally. Gena with anterior portion grayish brown, becoming more brownish posteriorly.

Thorax: Generally pollinose, brown. Mesonotal vittae and disc of scutellum concolorous, subshiny to shiny with metallic luster concolorous with mesofrons; acrostichal setae well developed, conspicuous, subequal with dorsalmost postocular setae; mesopleuron, pteropleuron, and dorsal portion of sternopleuron concolorous, brown; remainder of sternopleuron gray; front coxa whitish gray. Legs similar in coloration to each other, mostly gray to brownish gray; front femur with row of progressively stouter, spinelike setae toward apex of posteroventral and anteroventral surfaces. Wing (Figure 16) infumated, light brown; wing of male with large, conspicuous, subquadrate white spot in cell R_3 about its length from apex of vein R_{2+3}; wing membrane beyond large white spot darker, brown; smaller, circular, white spot in cell R_5 abutting vein R_{4+5}; its basal edge aligned with apical margin of larger spot in cell R_3; wing of female with much less conspicuous pattern of white spots; spot in cell R_3 constricted in middle, usually forming 2 smaller spots.

Abdomen: First and second segments of male specimens concolorous, bluish gray; apical segments darker, olivaceous to brownish gray; third and fourth segments subequal in size. Female abdomen more uniformly colored, mostly bluish gray but with some lightly tinged brown areas medially and with subshiny areas along anterior margins of apical segments.

TYPE-MATERIAL.—Male holotype: "Tumbre, E. of Atacama Salt Lk., 3600–3800 m., Antofagasta, CHILE, 6-9. XII. 65, Pena." Allotype: "(Chile) QUEPIACO, Cord. Antof(agasta). 17-May-1952, Coll: L. E. Pena." Other paratypes as follows: CHILE. ANTOFAGASTA: 2♂♂, 1♀, Talabre, 3600 m, 10-12



FIGURES 14–19.—Wing, dorsal aspect: 14, *P. pilifera;* 15, *P. lanicrus;* 16, *P. spinicrus;* 17. *P. glabra;* 18, *P. apicalis,* male; 19. *P. apicalis,* female.

Nov 68, L. E. Peña. The holotype, allotype, and paratypes are in the Canadian National collection, Ottawa, type number 15232.

ETYMOLOGY.—*Spinicrus* is a combination of the Latin nouns *spina,* meaning "spine," or "thorns," plus *crus,* meaning "leg" or "shank," in allusion to the spinelike row of setae on the front femur. The name stands in apposition to the generic name.

GEOGRAPHIC DISTRIBUTION (Figure 20).—The known distribution of *P. spinicrus* is based on five specimens from three localities only. These localities are all in the province of Antofagasta, Chile, near the Chile-Argentine border at elevations of between 3600 and 3800 m.

PHYLOGENETIC RELATIONSHIPS.—*Parascatella spinicrus* is the sister group of the ancestral stem of *P. pilifera* and *P. lanicrus,* as evidenced by the row of spinelike setae along the anteroventral surface of the front femur, which is common to specimens of all three species. This is an apotypic character state, being unique within the genus and related genera.

4. *Parascatella glabra,* new species

FIGURES 17, 21–24

DIAGNOSIS.—Among species of this genus, specimens of *P. glabra* are the most easily recognized. The blackish coloration and metallic luster over

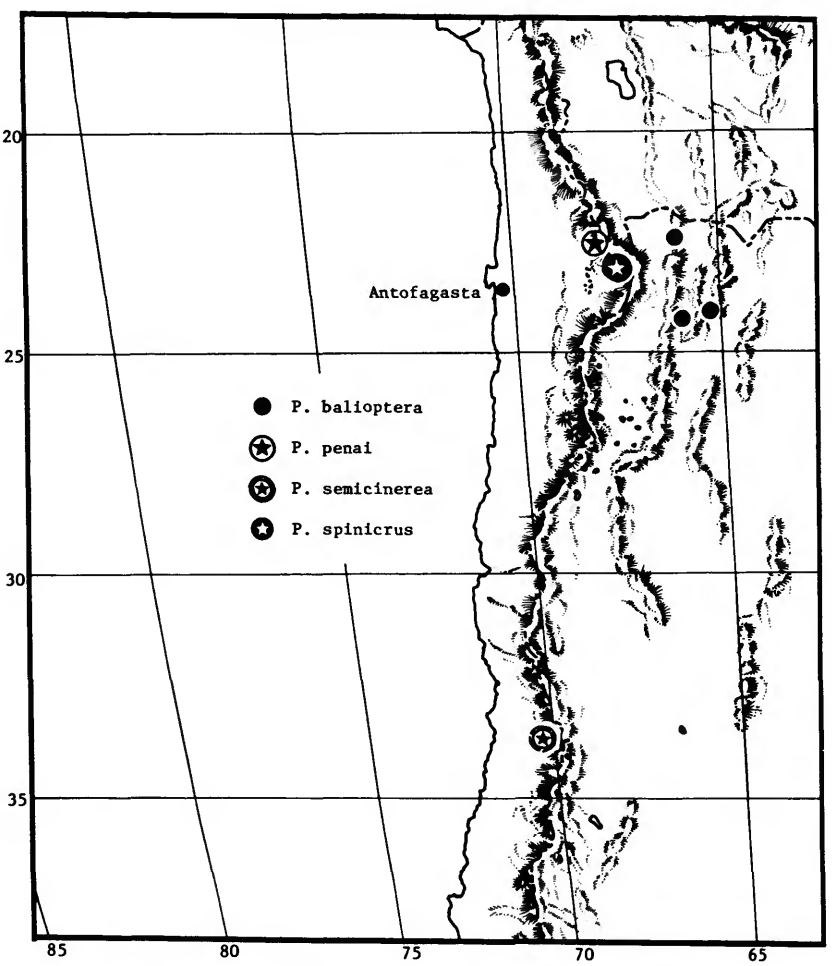


FIGURE 20.—Distribution of *P. balioptera, P. spinicrus, P. penai,* and *P. semicinerea.*

much of the head and thorax are very distinctive and unique to members of this species. The background coloration of the abdomen is also black but is overlaid with a rather thick, whitish gray, lacteous pollinose covering.

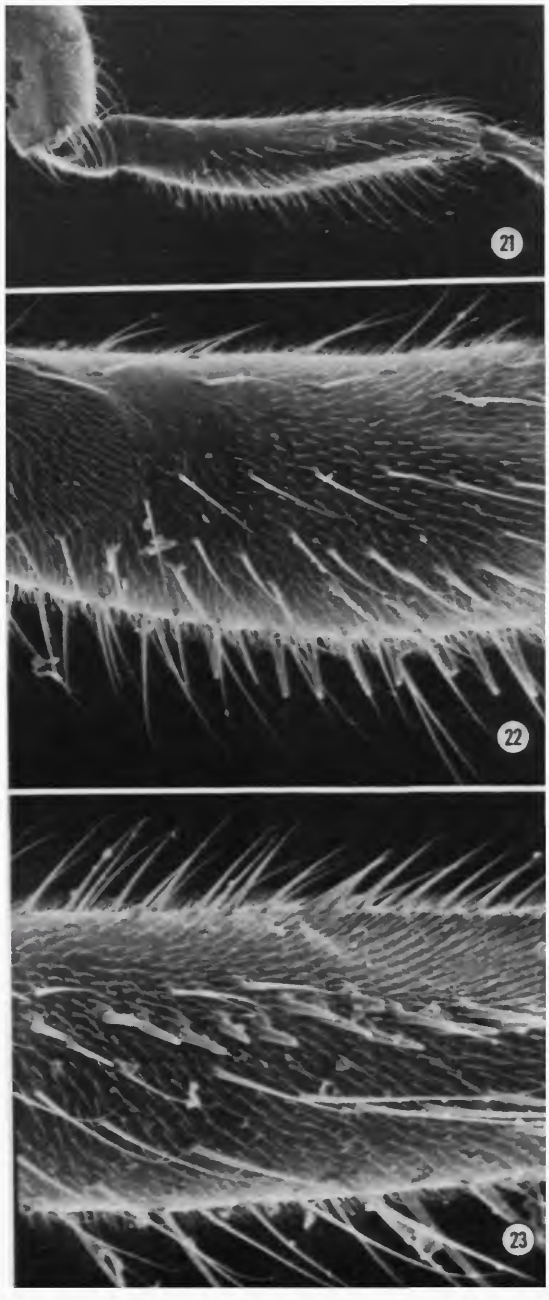
DESCRIPTION.—Medium-sized to moderately large shore flies, length 3.44 to 4.10 mm; mostly black, shiny, but with various degrees of pollinose vestiture, especially on abdomen.

Head: Broad mesofrons and to a degree frontoorbits with metallic luster; pollinose parafrons uniformly charcoal black; dorsalmost postocular setae moderately well developed, equaling larger postocellars. Antenna unicolorous. Face subshiny, becoming duller, more pollinose, and brownish ventrally; facial setae along oral margin distinctly larger than remaining facial setae; interfoveal carina with distinct dorsal crease. Gena black but mostly covered with brownish pollinose vestiture.

Thorax: Generally black and mostly shiny, notably on dorsum, mesopleuron slightly pollinose, appearing very dimly brown from some angles; acrostichal setae moderately well developed. Front coxa shiny black on lateral surface; median surface pollinose, cincereous, concolorous with dorsum of abdomen. Tarsi mostly black, cinereous dorsally, but also with considerable brown to tawny coloration on undersides; front femur (Figures 21–23) with row of rather stout setae along posteroventral surface near middle (difficult to see except in silhouette). Wing (Figure 17) as in *P. pilifera* except for position of white spots; spot in cell R_3 aligned slightly basad of posterior crossvein; basal spot in cell R_5 largest, usually subquadrate, apical spot in same cell closer to posterior crossvein than basal spot.

Abdomen: Uniformly colored, black but with covering of whitish gray, pollinose vestiture; abdominal segments 2 and 4 of male subequal, third segment narrower; all visible female segments more or less equal in length.

TYPE-MATERIAL.—Male holotype: "ARGENT(INA), Jujuy, Cienqguillas, 3650 m., 28. X. 1968. L. Pena." Allotype and 140 paratypes (37 ♂♂, 103 ♀♀): with same label data as holotype. Other paratypes as follows: ARGENTINA. JUJUY: 2 ♀♀, Abralaite, 85 km S Abra Pampa, 3650 m, 29 Oct 68, L. E. Peña; 1 ♀, Cerrillos, 3600 m, 31 Oct 68, L. E. Peña; 4 ♀♀, Rio Cincel S end of L. Pozuelos, 3800 m, 3 Nov 68, L. E. Peña; 2 ♀♀, Cieneguillas, 3650 m, 28 Oct 68, L. E. Peña; 3 ♀♀, Cangrejillos, S La Quiaca, 3500 m, 28 Oct 68, L. E. Peña; 1 ♂, 2 km SW Cienaga, Rd. to Pirquitas, 3900 m,



FIGURES 21–23.—*P. glabra:* 21, right front femur, posterior aspect; 22, right front femur, enlargement of Figure 21; 23, right front femur, enlarged ventral view.

3 Nov 68, L. E. Peña; 1 ♂, Lecho, 32 km E La Quaica, 3300 m, 24 Oct 68, L. E. Peña. The holotype, allotype, and most of the paratypes are in the Canadian National collection, Ottawa, type number 15232. Two pair of male and female paratypes are in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Glabra* is of Latin derivation meaning "smooth" in reference to the extensive, smooth, shining black surface of specimens of this species.

GEOGRAPHIC DISTRIBUTION (Figure 24).—This species is known to occur in the province of Jujuy, Argentina, only. Distributional data are based on eight localities, ranging between 3300 and 3800 m in elevation. This species is broadly sympatric with *P. semipolita* and specimens of both species are frequently collected at the same locality.

PHYLOGENETIC RELATONSHIPS.—The totally black background color of specimens of this species is unique among genera of the tribe Scatellini. The relationship this species has with others of the genus *Parascatella*, however, is somewhat obscure although it is probably the sister species of the ancestral stem of *P. pilifera, P. lanicrus,* and *P. spinicrus*. Specimens of these species are the only members of *Parascatella* that have a single row of rather stout, spine-like setae along the posteroventral margin of the front femur.

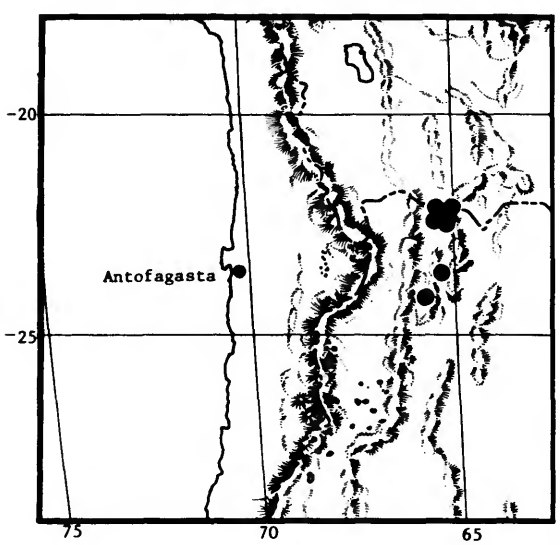


FIGURE 24.—Distribution of *P. glabra*.

5. *Parascatella apicalis*, new species

FIGURES 18, 19, 25

DIAGNOSIS.—Members of this species and *P. hirticrus* are similar in having the characters mentioned in the forepart of key couplet 6. *Parascatella apicalis* specimens, however, may be differentiated by the following combination of characters: face unicolorous, gray; pleural areas mostly concolorous, uniformly whitish gray; mesonotum mostly pollinose, gray but with slight pearly lustered, median area; fifth abdominal segment of male not over twice as long as fourth; and wing of male with a very prominent, large subquadrate white spot in cell R_3, about its width from the apex of vein R_{2+3} and around which veins R_{2+3} and R_{4+5} are distinctly sinuate.

DESCRIPTION.—Medium-sized to moderately large shore flies, length 3.32 to 4.03 mm; mostly pollinose, gray to brown except for shiny mesofrons.

Head: Mesofrons shiny with metallic greenish bronze luster; pollinose parafrons charcoal gray to brownish gray; fronto-orbits mostly grayish pollinose; dorsalmost postocular setae well developed, subequal to ocellars. First and second antennal segments charcoal gray to gray; third segment dark brown. Face mostly gray to lacteous, becoming lighter ventrally; antennal fovea dimly subshiny, mostly gray but with some weak greenish blue coloration; dorsum of interfoveal carina dimly subshiny with bronzish coloration; facial setae along oral margin very well developed, notably longer than remaining facial setae. Gena whitish gray, anterior portion with more glossy luster.

Thorax: Mostly pollinose and generally lacking subshiny areas; dorsum bluish gray or greenish gray to gray but with brownish maculation over much of median area; scutellum whitish gray; acrostichal setae well developed; mesopleuron lightly brownish gray; other pleural areas mostly gray. Femora and tibiae mostly concolorous, gray; tarsi slightly darker, somewhat blackish. Wing (Figures 18,19) very lightly infumated, grayish brown; male wing with very large, subquadrate white spot in cell R_3 approximately its own width from apex of vein R_{2+3}; veins R_{2+3} and R_{4+5} strongly sinuate around this spot and wing membrane apicad to spot noticeably darker brown; apical spot in cell R_5 abutting vein R_{4+5} and about its width from alignment of apical margin of larger spot in

cell R_3; other spots as in *P. pilifera;* female wing with white spot in cell R_3 not nearly as large and surrounding veins not sinuate.

Abdomen: Generally unicolorous and not as densely pollinose as pleural areas of thorax, mostly gray to very faintly brownish gray; fifth tergum of male approximately as wide as second or third segment; fourth segment shorter, slightly more than half the length of third and usually subshiny along anterior margins.

TYPE-MATERIAL.—Male holotype: "ARG(ENTINA), Juj(uy), 4100 m., Coyaquayma, 7 km S Mina Perquitas, 4. XI. 68. Pena." Allotype and 28 paratypes (8♂♂, 20♀♀) with same label data as holotype. Other paratypes as follows: ARGENTINA. JUJUY: 1♀, 6 km NW Turilari (Turi Tari ?), 4000 m, 5 Nov 68, L. E. Peña. SALTA: 1♂, 1♀, Chorillos, 23 km W San Antonio de Los Cobres, 3800 m, 6-7 Nov 68, L. E. Peña. TUCUMAN: 1♀, El Banado, 1700 m, 5 Oct 68, L. E. Peña. CHILE. ATACAMA: 4♀♀, Vegas de San Andres, 2250 m, 28 Sep 52, P. G. Kuschel. The holotype, allotype, and most paratypes are in the Canadian National collection, Ottawa, type number 15234. Two pair of male and female paratypes are in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Apicalis* is derived from the Latin masculine noun *apex,* meaning "apex," "summit," or "tip," in allusion to the large white spot near the wing apex in male specimens of this species.

GEOGRAPHIC DISTRIBUTION (Figure 25).—*Parascatella apicalis* is known to occur from about 22° to 26° south latitude along the east and west slopes of the Andes Mountains. Elevations of these localities are from between 1700 and 4100 m.

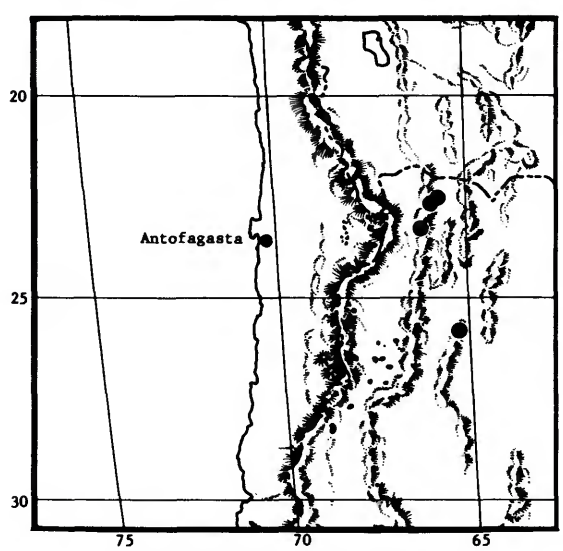


FIGURE 25.—Distribution of *P. apicalis.*

VARIATION.—Considerable sexual dimorphism is evident in specimens of this species. The apical white spot in wing cell R_3 of males is markedly larger, more prominent, and more subquadrate than in females. Moreover, the wing membrane apicad of this spot is distinctly darker in males (Figures 18,19).

PHYLOGENETIC RELATIONSHIPS.—Apparently this species and *P. hirticrus* are closely related. Specimens of both species have the enlarged spot in wing cell R_3 of males and the scutellum is flat, rather densely pollinose, and lacteous in color. The latter character states are unique to these two species.

6. *Parascatella hirticrus,* new species

FIGURES 26–28, 32

DIAGNOSIS.—Members of this species are similar to those of *P. apicalis* (see diagnosis of *P. apicalis)* but differ by the following combination of characters: face unicolorous, brown and with slight metallic luster; mesofrons grayish brown, contrasting distinctly with whitish gray coloration of front coxa; mesonotum mostly dark, weakly shiny, olive green to bluish green but with some more densely pollinose brown areas. Abdominal segments with considerable light brownish gray coloration, especially along anterior margins; fifth abdominal segment of males usually twice as long as fourth segment; and wing of male with smaller, subquadrate white spot in cell R_{2+3} around which veins R_{2+3} and R_{4+5} are less sinuate.

DESCRIPTION.—Medium-sized to moderately large shore flies, length 3.68 to 4.86 mm; mostly pollinose, grayish brown to blackish brown on head and thorax; abdomen lighter, gray.

Head: Shining mesofrons with metallic brassy, dark green luster; pollinose parafrons unicolorous, charcoal brown; fronto-orbits largely undifferentiated or but slightly more shiny; dorsalmost postocular moderately well developed but not subequal with ocellar bristles. Antenna mostly unicolorous or with third segment more brownish. Face unicolorous, brown, dimly shiny dorsally; facial setae along oral margin well developed, larger than remaining facial setae; interfoveal carina with dis-

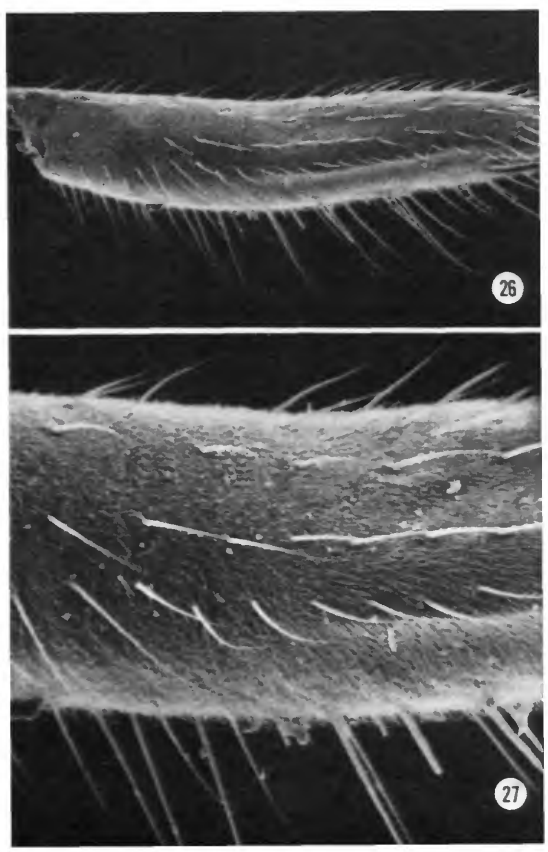
tinct crease dorsally. Gena gray to whitish gray, distinctly contrasting with facial coloration.

Thorax: Mesonotum overlaid with thin pollinose covering of whitish-gray vestiture; when viewed from posteroblique angle appearing somewhat subshiny with blackish mesonotal vittae; disc of scutellum distinctly flat and covered with whitish pollinose vestiture; mesopleuron mostly brown; pteropleuron grayer than mesopleuron but with some brownish coloration anteriorly; sternopleuron and front coxa nearly concolorous, although the former is slightly darker. Legs (Figures 26,27) more or less equal to each other in coloration; pollinose, gray although considerably darker than front coxa; tarsi of hind leg slightly darker dorsally, blackish. Wing (Figure 32) very lightly infuscated, light brown; wing of male and female resembling each other and with conspicuous pattern of large white spots; apical white spot in cell R_{4+5} usually triangular; general pattern similar to that of *P. pilifera.*

Abdomen: Each abdominal segment more or less concolorous with others, more thinly pollinose than pleural areas of thorax and with considerable bluish tinges and some faint brown areas, especially medially and along anterior margin of each segment; segments 2, 3, and 4 of male specimens subequal in length; fifth segment much broader than long although about twice the length of fourth.

TYPE-MATERIAL.—Male holotype: "ARG(ENTINA), SALTA, 3800 m. Chorillos, 23 km. S. S(an) Ant(onio) (de) Los Cobres, 6-7. XI. 68. Pena." Allotype and 7 paratypes (2♂♂, 5♀♀): with same label data as holotype. Other paratypes as follows: ARGENTINA. JUJUY: 1♂, E Mina Perquitas, 4200–4500 m, 4 Nov 68, L. E. Peña; 2♀♀, 6 km, NW Turilari (Turi Tari ?), 4000 m, 5 Nov 68, L. E. Peña. SALTA: 1♂, 4♀♀, San Antonio de Los Cobres, 3700 m, 6 Nov 68, L. E. Peña. CHILE. ANTOFAGASTA: 1♂, 2♀♀, Mucar, 23°23′ S on Argentina border, 4000–4100 m, 12-16 Dec 65, L. E. Peña. ATACAMA: 3♂♂, Vegas de San Andres, 2250 m, 28 Sep 52, P. G. Kuschel. The holotype, allotype, and most of the paratypes are in the Canadian National collection, Ottawa, type number I5235. A male and female pair of paratypes are in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Hirticrus* is a combination of the Latin adjective *hirtus,* meaning "hairy," plus the noun *crus,* meaning "leg" or "shank," in allusion



FIGURES 26,27.—*P. hirticrus:* 26, right front femur, posterior aspect; 27, right front femur, enlargement of Figure 26.

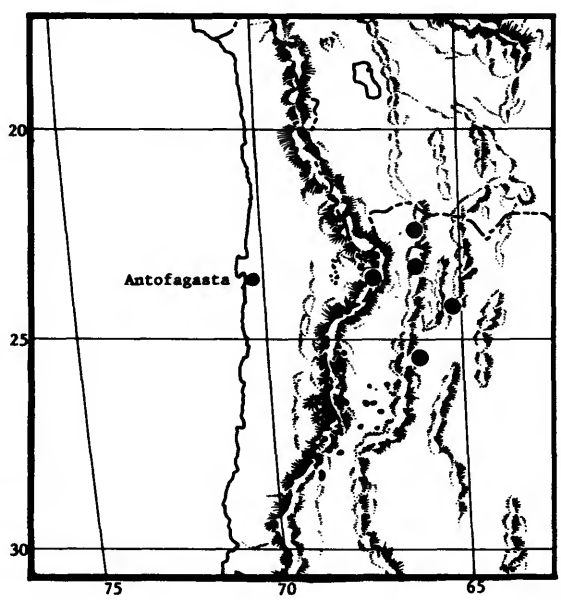


FIGURE 28.—Distribution of *P. hirticrus.*

to the hairy legs of specimens of this species. The name stands in apposition to the generic name.

GEOGRAPHIC DISTRIBUTION (Figure 28).—*Parascatella hirticrus* is known to occur to the provinces of Jujuy and Salta, Argentina, and Antofagasta and Atacama, Chile. These localities are distributed from about 22° to 26° south latitude and have elevations ranging from between 2250 and 4500 m. This distribution broadly overlaps those of several species assigned to the *pilifera* group.

PHYLOGENETIC RELATIONSHIPS.—Members of this species are fairly distinctive and could only be confused with those of *P. apicalis,* which is evidently the sister species of *P. hirticrus.* The latter relationship is demonstrated by the joint possession of the characters cited in the forepart of key couplet 6.

7. *Parascatella semipolita,* new species

FIGURES 29, 33

DIAGNOSIS.—Specimens of this species resemble those of *P. semicinerea* but are distinguished by the following combination of characters: mesonotal vittae more pollinose, much lighter in coloration and luster than mesofrons; white spot in cell R_3 of males usually smaller, often somewhat circular; apical white spot in cell R_5 little evident or lacking, if present aligned with apical margin of larger white spot in cell R_3; overall size smaller, averaging 3.21 mm; usually lighter appearing specimens, more pollinose dorsally.

DESCRIPTION.—Medium-sized to moderately large shore flies, length 3.14 to 4.18 mm; mostly grayish brown to brown on head and thorax, abdomen gray.

Head: Shiny mesofrons with metallic dark green to dark bluish green luster; pollinose parafrons mostly unicolorous, brown or with some grayish charcoal tinges anteriorly; fronto-orbits only slightly darker than parafrons, more charcoal colored and with some faint subshiny appearance; dorsalmost postocular setae strong, almost equal with ocellar bristles. Antenna dark brown; first and second segments with more blackish appearance. Face unicolorous, brown, pollinose, but with some faint subshiny green tinges; interfoveal carina with distinct dorsal crease; facial setae along oral margin larger than remaining facial setae but not markedly so. Gena grayish brown, mostly unicolorous.

Thorax: Mesonotal vittae and disc of scuttelum subshiny, brassy to concolorous with mesofrons; pollinose areas between vittae grayish brown; acrostichal setae well developed, subequal with dorsalmost postocular setae; scutellum slightly convex and generally shinier than mesonotum; mesopleuron and anterior portion of pteropleuron concolorous, grayish brown; sternopleuron and front coxa lighter, mostly gray, contrasting with mesopleural coloration. Legs similar in color with each other; femora and tibiae mostly gray, more or less concolorous with sides of abdomen; tarsi of hind leg darker dorsally, blackish but becoming brown to tawny on underside. Wing (Figure 33) lightly infuscated, light grayish brown; wing of male with white spot in cell R_3 enlarged, more or less subquadrate to subtriangular, usually wider anteriorly, and situated its own length from alignment of posterior crossvein, membrane beyond spot with darker infuscation; small white spot in cell R_5 abutting vein R_{4+5}; wing of female with pattern of white spots less conspicuous; larger spot in cell R_{2+3} more rectangular and situated closer to alignment of posterior crossvein, otherwise pattern of both sexes similar.

Abdomen: Generally pollinose, segments concolorous, lightly bluish gray to lacteous gray but often with some very faint brownish coloration on lateral margins of basal segments. Third and fourth abdominal segments of male subequal to length, both shorter than second; female abdominal segments all more or less subequal.

TYPE-MATERIAL.—Male holotype: "ARGENT(INA), Jujuy, Cerrillos, 31. X. 68, 3600 m., L. E. Pena." Allotype and 49 paratypes (30 ♂♂, 19 ♀♀): with same label data as holotype. Other paratypes as follows: ARGENTINA. JUJUY: 10 ♂♂, 20 ♀♀, 2 km SW Clenage Rd. to Pirquitas, 3900 m, 3 Nov 68, L. E. Peña; 7 ♂♂, 7 ♀♀, La Quiaca, 3500 m, 23 Oct 68, L. E. Peña; 1 ♀, La Quiaca, 3500 m, 30 Oct 68, L. E. Peña; 3 ♂♂, 1 ♀, Cangrejillos, S La Quiaca, 3500 m, 28 Oct 68, L. E. Peña; 1 ♂, Cieneguillas, 3650 m, 28 Oct 68, L. E. Peña; 2 ♀♀, 3 km N Humahuaca, 3300 m, 22 Oct 68, L. E. Peña; 4 ♂♂, 3 ♀♀, 2 km SW Cienaga Rd. to Pirquitas, 3900 m, 3 Nov 68, L. E. Peña; 5 ♂♂, 8 ♀♀, Coyaquayma, 7 km S. Mina Perquitas, 4100 m, 4 Nov 68, L. E. Peña; 5 ♂♂, 3 ♀♀, Rio Seco, 5 km S Sta Catalina, 3500 m, 25 Oct 68, L. E. Peña; 2 ♀♀, Rio Orosmayo, 43 km SW Cienaga, 3 Nov 68, L. E. Peña; 2 ♀♀, Santa Catalina, 3700 m, 25 Oct 68, L. E. Peña; 2 ♀♀, Cajas, 35 km E La Quiaca, 3800 m, 24 Oct 68, L. E. Peña; 3 ♂♂, 8 ♀♀, E Mina Perquitas, 4200–4500 m, 4 Nov 68, L. E. Peña; 2 ♀♀, Cueva Negra, 10 km S Mina Perquitas, 4300 m, 4 Nov 68, L. E. Peña; 2 ♀♀, Abralaite, 85 km S Abra Pampa, 3650 m, 29 Oct 68, L. E. Peña. SALTA: 6 ♂♂, 3 ♀♀, San Antonio de Los Cobres, 3750 m, 6 Nov 68, L. E. Peña; 9 ♂♂, 17 ♀♀, Chorillos, 23 km W San Antonio de Los

Cobres, 3800 m, 6-7 Nov 68, L. E. Peña. The holotype, allotype, and most of the paratypes are in the Canadian National collection, Ottawa, type 15236. Two pair of male and female paratypes are in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Semipolita* is a combination of the Latin noun *semis*, meaning "half," and the Latin adjective *politius*, meaning "polished," in allusion to the appearance of specimens of this species.

GEOGRAPHIC DISTRIBUTION (Figure 29).—The distribution of *P. semipolita* is based on 19 localities in the provinces of Jujuy and Salta, Argentina. These sites are arrayed between approximately 22° and 25° south latitude, with elevations ranging from between 3300 and 42–4500 m.

VARIATION.—Sexual dimorphism in members of this species is quite apparent. Males characteristically have a larger and more prominent white spot in wing cell R_3. The comparable spot in females is considerably smaller, linear, and not as conspicuous.

PHYLOGENETIC RELATIONSHIPS.—Evidently this species and *P. semicincerea* are closely related. Specimens of both species are large, males of both have an enlarged white spot in cell R_3, and the segments of the abdomen are more or less unicolorous, dull, and pollinose. The male genitalia of both species are virtually identical.

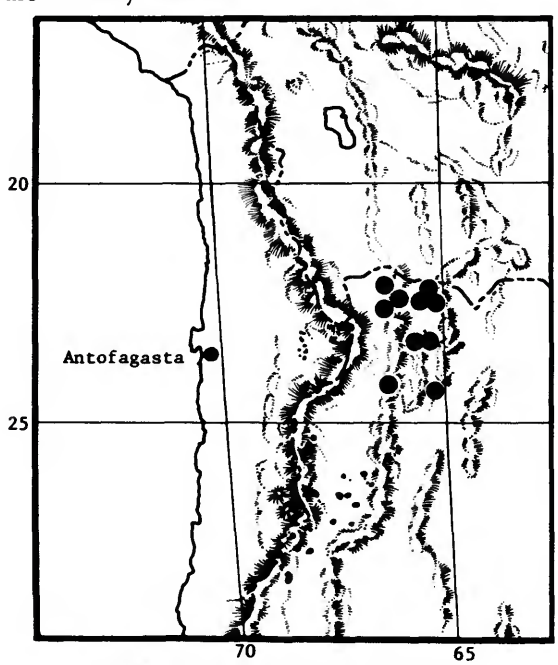


FIGURE 29.—Distribution of *P. semipolita*.

8. *Parascatella semicinerea*, new species

FIGURES 30, 31, 34

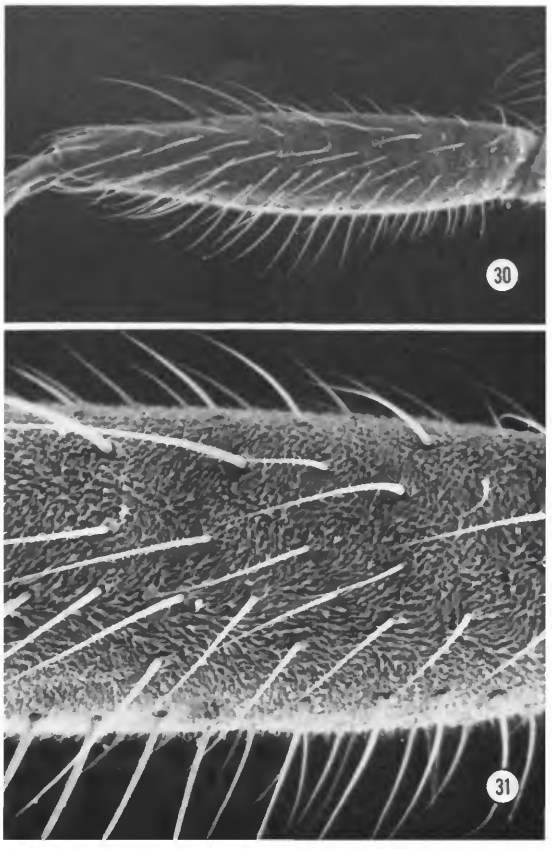
DIAGNOSIS.—Specimens of this species and *P. semipolita* very closely resemble each other and both are distinguished from related congeners as noted in the key (first half of couplet 8). Specimens of *P. semicinerea* are distinguished most readily from those of *P. semipolita* by the following characters: mesonotal vittae similar in luster and almost concolorous with mesofrons; white spot in apical half of cell R_3 in males larger, subquadrate, and well over twice its width from apex of vein R_{2+3}; apical white spot in cell R_5 usually prominent and located its own width from alignment of large spot in cell R_3; overall size larger, length averaging 4.29 mm; usually darker appearing specimens.

DESCRIPTION.—Medium-sized to moderately large shore flies, length 3.84 to 4.67 mm; mostly dark brown to blackish brown on head and thorax; abdomen more pollinose, gray.

Head: Shiny mesofrons with dark blackish brown metallic luster; pollinose parafrons unicolorous, charcoal brown; fronto-orbits darker than parafrons, blackish and slightly subshiny; dorsalmost postocular setae well developed. Antenna brown to blackish brown; first and second segments darker. Face unicolorous, brown; interfoveal carina with distinct dorsal crease; facial setae along oral margin much larger than remaining setae. Gena grayish brown, becoming slightly bluish gray posteriorly.

Thorax: Mesonotal vittae and disc of scutellum blackish brown to black, subshiny; pollinose areas between vittae more pollinose, brown; acrostichal setae well developed, subequal to dorsalmost postocular setae. Mesopleuron and pteropleuron concolorous, grayish brown, contrasting with lighter colored, grayer sternopleuron and front coxa. Legs (Figures 30,31) unicolorous with each other, pollinose, gray; tarsi slightly darker in coloration dorsally, becoming brownish below. Wing (Figure 34) very lightly infuscated, light brown; wing of male with larger white spot in cell R_{2+3} more or less subquadrate; spot in cell R_{4+5} abutting vein R_{4+5} and slightly more than its width apicad from larger spot in cell R_{2+3}; wing of female with less conspicuous pattern of white spots but with more spots than male, pattern similar to that of *P. pilifera*.

Abdomen: Generally unicolorous, gray to bluish gray and with slight subshiny appearance; second



FIGURES 30,31.—*P. semicinerea:* 30, left front femur, anterior aspect; 31, left front femur, enlargement of Figure 30.

and fourth segments of male subequal in length; third segment shorter; female abdomen with all segments more or less subequal.

TYPE-MATERIAL.—Male holotype: "Sud-Chile, Banos Morales, 18. 12. 40, 539, leg. G. H. Schwabe." Allotype and 9 paratypes (5♂♂, 4♀♀) with same label data as holotype. The holotype, allotype, and most of the paratypes are in the "Deutschen Entomologischen Institutes," (DEI) Eberswalde, Germany. One male and one female paratype are in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Semicinerea* is a combination of the Latin noun *semis,* meaning "half," and the adjective *cinereus,* meaning "ash-colored," in allusion to the ash coloration of specimens of this species.

GEOGRAPHIC DISTRIBUTION (Figure 20).—This species is known only from the type-locality.

PHYLOGENETIC RELATIONSHIPS.—Specimens of *P. semicinerea* are among the largest of the genus. Their large size coupled with the characters cited in the diagnosis are the only features for distinguishing between specimens of this species and those of *P. semipolita.* The latter is probably the sister species of *P. semicinerea,* but we have not identified an apotypic character state that confirms this relationship.

9. *Parascatella balioptera,* new species

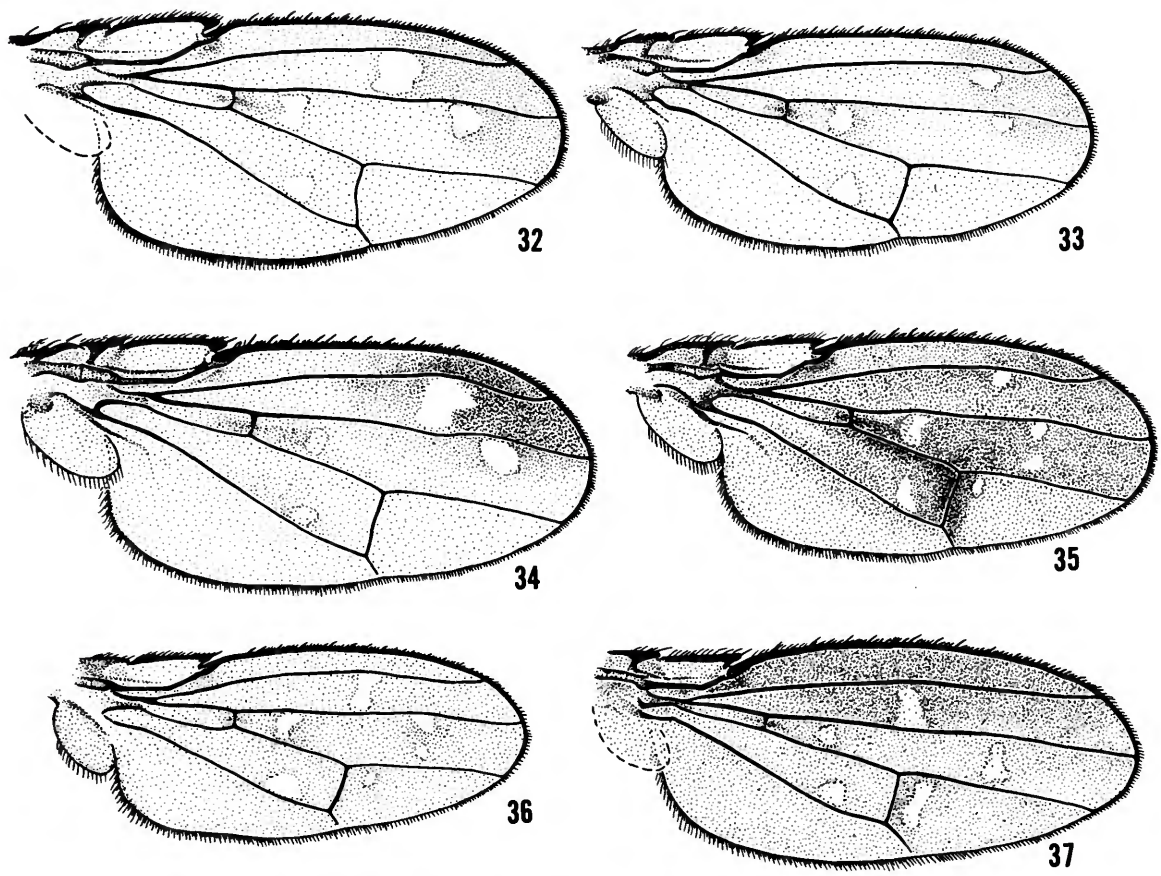
FIGURES 20, 35, 38–41

DIAGNOSIS.—Specimens of this species are similar to those of *P. penai* but are distinguished by the following combination of characters: color of shiny mesofrons dark blue, contrasting distinctly with brown, pollinose parafrons; mesonotal vittae and scutellar disc nearly concolorous with mesofrons although more pollinose; abdomen more slender; apical abdominal segments distinctly shinier than basal ones; fourth abdominal segment of male specimens two-thirds length of more pollinose third segment; white spot in base of cell M_2 conspicuous.

DESCRIPTION.—Medium-sized shore flies, length 3.32 to 3.86 mm; mostly brown especially head, becoming olivaceous gray to bluish gray posteriorly, especially on abdomen and with some faintly subshiny to shiny darker blue areas.

Head (Figure 38): Shiny mesofrons with dark, metallic blue luster; pollinose parafrons mostly dull charcoal brown; fronto-orbits mostly concolorous with parafrons but with faint tinges of dark blue luster; dorsalmost postocular setae well developed, subequal with ocellar bristles; some specimens with a third pair of larger fronto-orbital bristles anterior of other pairs. Antenna brown, first and second segments darker with charcoal tinges; face more or less unicolorous, pollinose, grayish brown, sometimes becoming slightly grayer ventrally and dimly subshiny along slope of interfoveal carina; interfoveal carina with distinct crease dorsally; facial setae along oral margin many times longer than remaining facial setae, as long as combined length of antennal segments. Gena grayer than face and with faint subshiny bluish tinges.

Thorax: Generally pollinose, gray to brown.

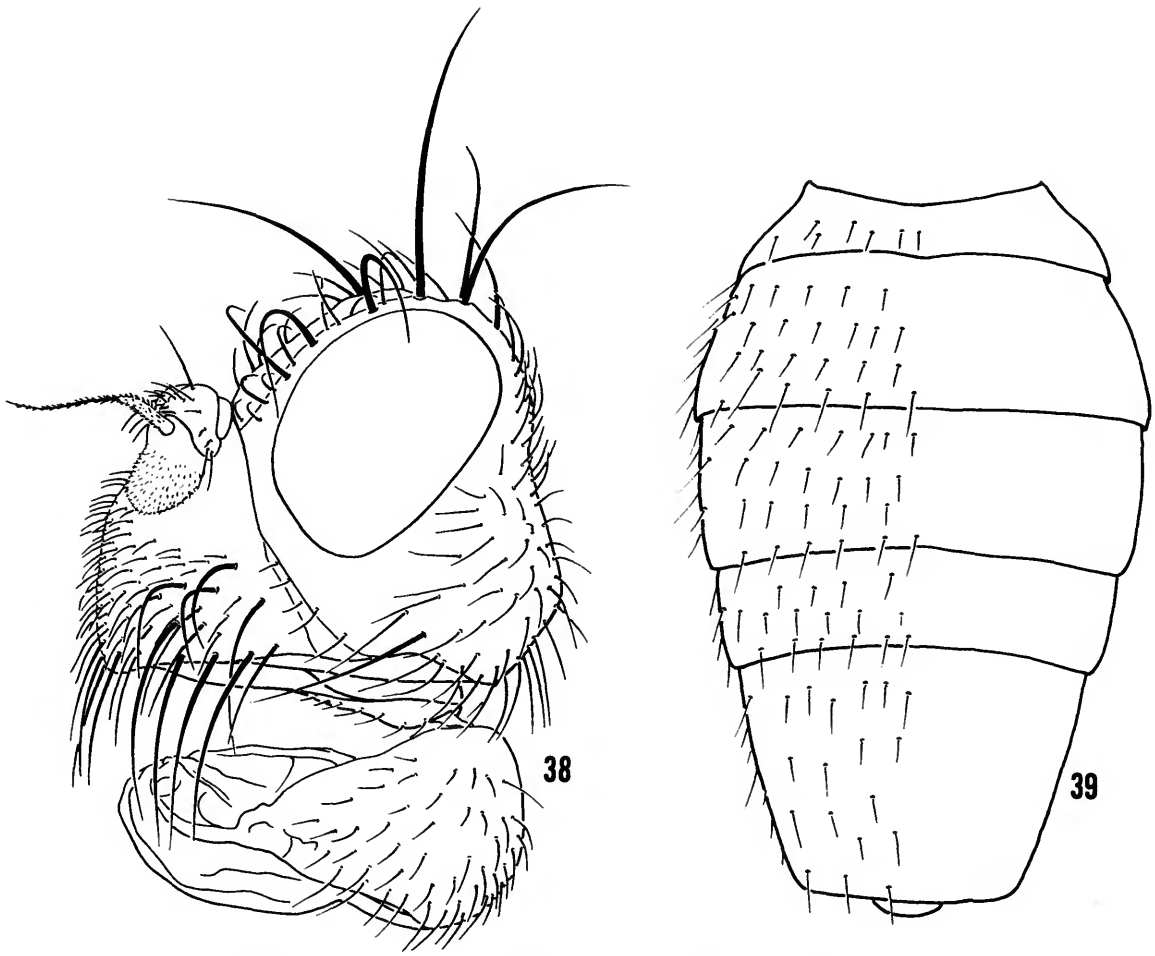


FIGURES 32-37.—Wing dorsal aspect: 32, *P. hirticrus;* 33, *P. semipolita;* 34, *P. semicinerea;* 35, *P. balioptera;* 36, *P. penai;* 37, *P. brunnea.*

Mesonotal vittae and disc of scutellum subshiny to shiny, color and luster similar to mesofrons but to lesser degree; between vittae mostly brown; acrostichal setae well developed, subequal to dorsalmost postocular setae; mesopleuron and pteropleuron concolorous, faintly olivaceous gray, mesopleuron with some weak bluish tinges around larger mesopleural bristle; sternopleuron, front coxa and extreme anterior portion of mesonotum gray. Femora (Figures 40,41) mostly concolorous with pleural areas of thorax; tibiae and tarsi darker with faint tinges of charcoal coloration. Wing (Figure 35) infumated, brown; male and female wing similar; whitish spot in cell R_3 narrowly rectangular, usually constricted medially and often appearing as 2 spots; basal white spot in cell R_5 largest; apical spot in same cell equidistant from alignment of posterior crossvein as basal spot; apical spot usually divided; white spot in discal cell abutting vein M_{3+4} and irregular in shape; usually with conspicuous although small white spot in cell M_2 near mergence of posterior crossvein and vein M_{1+2}.

Abdomen (Figure 39): Basal 2 abdominal segments densely pollinose, grayish blue; apical segments becoming shiner, more bluish and with some brownish coloration; second and third abdominal segments of male specimens very long, subequal, and approximately twice the length of the smaller fourth segment, male abdomen appearing quite long; female abdominal segments more or less subequal.

TYPE-MATERIAL.—Male holotype: "ARG(ENTINA), Juj(uy), 4200 m., Aguas Cal(ientes), 10 km., Ros(ario) d(e) Coyaguayma, 5. XI. 68. Pena." Allotype and 40 paratypes (29 ♂ ♂, 11 ♀ ♀): with same label data as holotype. Other paratypes



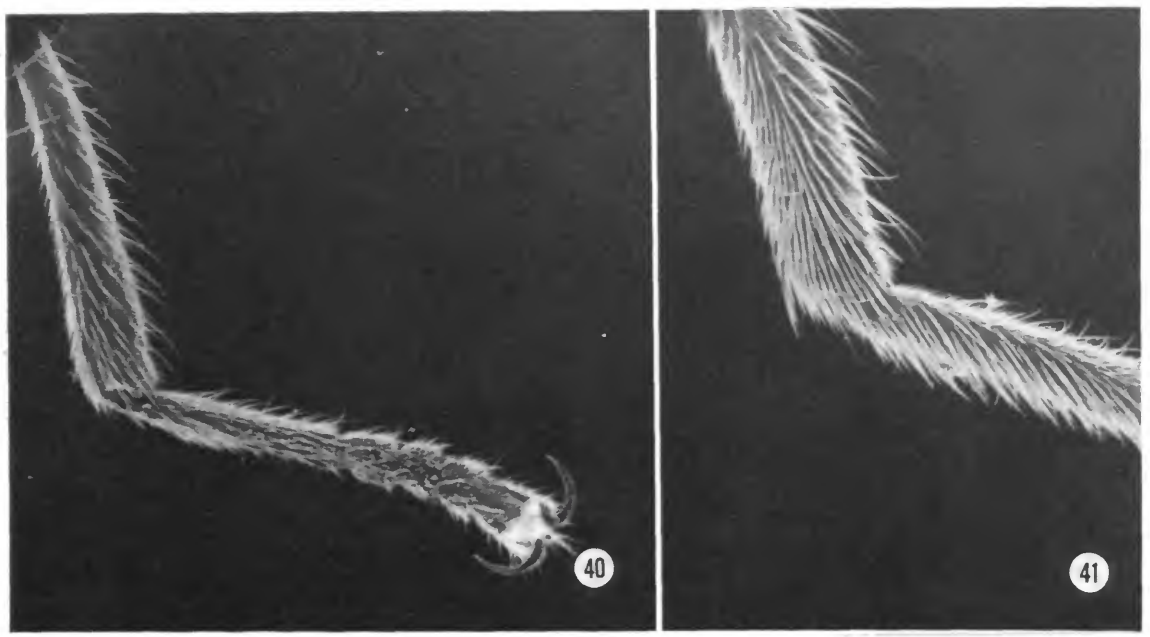
FIGURES 38,39.—*P. balioptera:* 38, head, lateral aspect; 39, abdomen, dorsal aspect.

as follows: ARGENTINA. SALTA: 1 ♂, San Antonio de Los Cobres, 3750 m, 6 Nov 68, L. E. Peña; 2 ♂ ♂, 1 ♀, Chorillos, 23 km W San Antonio de Los Cobres, 3800 m, 6-7 Nov 68, L. E. Peña. The holotype, allotype, and most of the paratypes are in the Canadian National collection, Ottawa, type number 15237. Two pairs of male and female paratypes are in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Balioptera* is a combination of the Greek adjective *balios,* meaning "spotted," plus the noun *pteron,* meaning "wing," in allusion to the spotted wing in specimens of this species.

GEOGRAPHIC DISTRIBUTION. (Figure 30).—The known distribution of this species is based on data from three localities only. The type-locality is in the province of Jujuy, the other two are in the province of Salta, Argentina. These localities range in elevation from 3700 to 4200 m.

PHYLOGENETIC RELATIONSHIPS.—Specimens of *P. balioptera* are very distinctive and could only be confused with those of *P. penai;* they are distinguished from the latter as outlined in the diagnosis. Whether *P. penai* is the sister species of *P. balioptera* is as yet unconfirmed, although their joint, overall similarity is probably a good indication. No apotypic character state has been found, however, to corroborate this relationship.



FIGURES 40,41.—*P. balioptera:* 40 left front tibia and tarsus, anterior aspect; 41, left front tibia and basitarsus, enlarged posterior aspect.

10. *Parascatella penai*, new species

FIGURES 20, 36

DIAGNOSIS.—Specimens of *P. penai* are similar to those of *P. balioptera* but are distinguished by the following combination of characters: mesofrons, mesonotal vittae, and disc of scutellum concolorous, dark brown to black; abdomen wider; apical abdominal segments brownish, contrasting with grayer basal ones; fourth abdominal segment of males subequal in length to third; spot at base of second M_2 cell conspicuous.

DESCRIPTION.—Medium-sized shore flies, length 3.03 to 3.76 mm; head and thorax mostly dark brown, shiny dorsally, becoming lighter below; abdomen mostly pollinose, gray to brownish gray.

Head: Shiny mesofrons with metallic, brassy dark green to dark blue luster; pollinose parafrons unicolorous, brown, some specimens with charcoal brown coloration anteriorly; fronto-orbits brown, only slightly darker than parafrons, usually with more charcoal tinges; dorsalmost postocular setae moderately well developed, not subequal with ocellar bristles. Antenna more or less unicolorous, concolorous with parafrons. Face unicolorous, brown, but lighter in coloration than parafrons; interfoveal carina with distinct dorsal crease; facial setae along oral margin distinctly larger than remaining setae. Gena grayish brown, slightly lighter in coloration anteriorly than posterior portion.

Thorax: Dorsum, particularly mesonotal vittae and disc of scutellum subshiny to shiny, brassy to dark green, more pollinose areas between mesonotal vittae dark brown; acrostichal setae well developed, conspicuous, subequal with dorsalmost postocular setae; mesonotum, pteropleuron, and very dorsal portion of sternopleuron concolorous, olivaceous to light brownish gray; most of sternopleuron, femora, and tibiae more or less concolorous, brown contrasting distinctly with grayer front coxa; tarsi darker gray, dorsal surface of hind leg darker with blackish coloration. Wing (Figure 36) infuscated, brown; male and female wing similar, resembling wing of *P. balioptera* but with white spots less conspicuous.

Abdomen: Generally pollinose, bluish gray, becoming grayer posteriorly and usually shinier, with some faint light greenish coloration; abdominal seg-

ments 2–4 of male becoming progressively slightly shorter in size, fifth segment often distinct in coloration; female abdominal segment more or less equal in length and coloration except for darker trend on posterior segments.

TYPE-MATERIAL.—Male holotype: "Puritama, Antofagasta, CHILE, 14. x., L. E. Pena, 1955." Allotype and 8 paratypes (1 ♂, 7 ♀ ♀): with same label data as holotype. The holotype, allotype, and most of the paratypes are in the Canadian National collection, Ottawa, type number 15238. One female paratype is in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—We take pleasure in naming this species for Sr. Luis E. Peña, the well-known Chilean biologist and collector.

REMARKS.—Our comments under *P. balioptera* also apply to this species.

The *brunnea* Group

INCLUDED SPECIES.—*Parascatella brunnea,* new species.

DIAGNOSIS.—Members of the *brunnea* group are recognized by the following combination of characters: ocelli arranged in equilateral triangle; dorsalmost postocular setae weakly developed, approximately equal to postocellar setae; face appearing less setulose; facial setae extending from interfoveal carina more or less equal with those along oral margin, often semiporrect but not upcurved; acrostichal setae conspicuous but not equaling larger dorsocentral bristles and usually with a distinct, larger pair of prescutellar setae; 1 pair of well-developed, supra-alar bristles; scutellum with only 2 pair of larger, lateral setae; costal margin spinose; and the surstyli of the male genitalia are evident as 2 triangular-shaped lobes at the ventral margin of the epandrium. The surstyli are not as conspicuous as those of the *pilifera* group and probably represent an intermediate stage between the *pilifera* group and *scatella.* In other respects, this species-group is intermediate between the *pilifera* group and *scatella* (see diagnosis above).

GEOGRAPHIC DISTRIBUTION.—The distribution of the only included species presently known ranges on either side of the southern Andes from approximately 46° to 53° south latitude. This area is within the Patagonia and Subantarctic biogeographic provinces as described by Cabrera and Willink (1973).

NATURAL HISTORY.—Virtually nothing is known about the natural history of the included species. Label data accompanying specimens collected at 4.8 km W Chile Chico indicate that they were collected from a meadow-associated habitat at 400-m elevation.

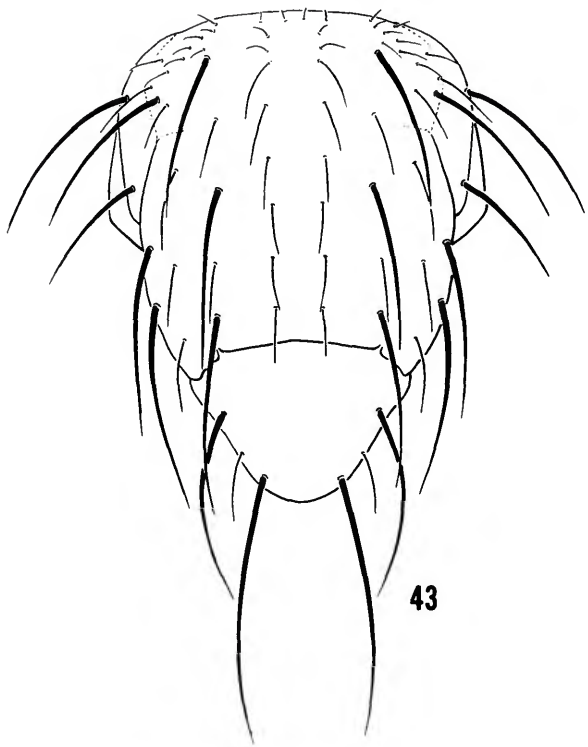
11. *Parascatella brunnea,* new species

FIGURES 37, 42–47

DIAGNOSIS.—Specimens of *P. brunnea* are the only Neotropical species known to have 2 pairs of lateral scutellar bristles similar to the Nearctic species. Specimens of this species may be further distinguished from those of similar congeners, especially the Nearctic species, by the following combination of characters: facial interfoveal carina unicolorous with remainder of face below carina; arista short, subequal to combined length of antennal segments; dorsalmost postocular setae small; and wing with evenly spaced, spinelike bristles along costal margin.

DESCRIPTION.—Moderately small to medium-sized shore flies, length 2.58 to 3.17 mm; generally dark brown to black with head and thorax subshining dorsally.

Head (Figure 42): Subshiny to shiny mesofrons with blackish brown luster, mesofrons of some specimens becoming distinctly pollinose anteriorly and poorly differentiated from pollinose parafrons; parafrons mostly dull, charcoal brown; frontoorbits concolorous with anterior portion of mesofrons or slightly duller; dorsalmost postocular setae weakly developed, only slightly larger than postocellars and many times smaller than ocellars. Antennal segments mostly unicolorous but third segment more micropubescent, appearing blacker and more velvety. Facial color from interfoveal carina to oral margin unicolorous, brown to lightly grayish brown; antennal fovea and space between antennae much lighter appearing, gray to lacteous in color, especially from frontal view; interfoveal carina with distinct dorsal crease; facial setae along oral margin and lateroblique margin extending from facial carina to posteroventral corner of face with well-developed setae; remaining facial setae much smaller; some specimens with 1 pair of larger setae with semiporrect orientation but not curved upward. Gena more or less concolorous with face



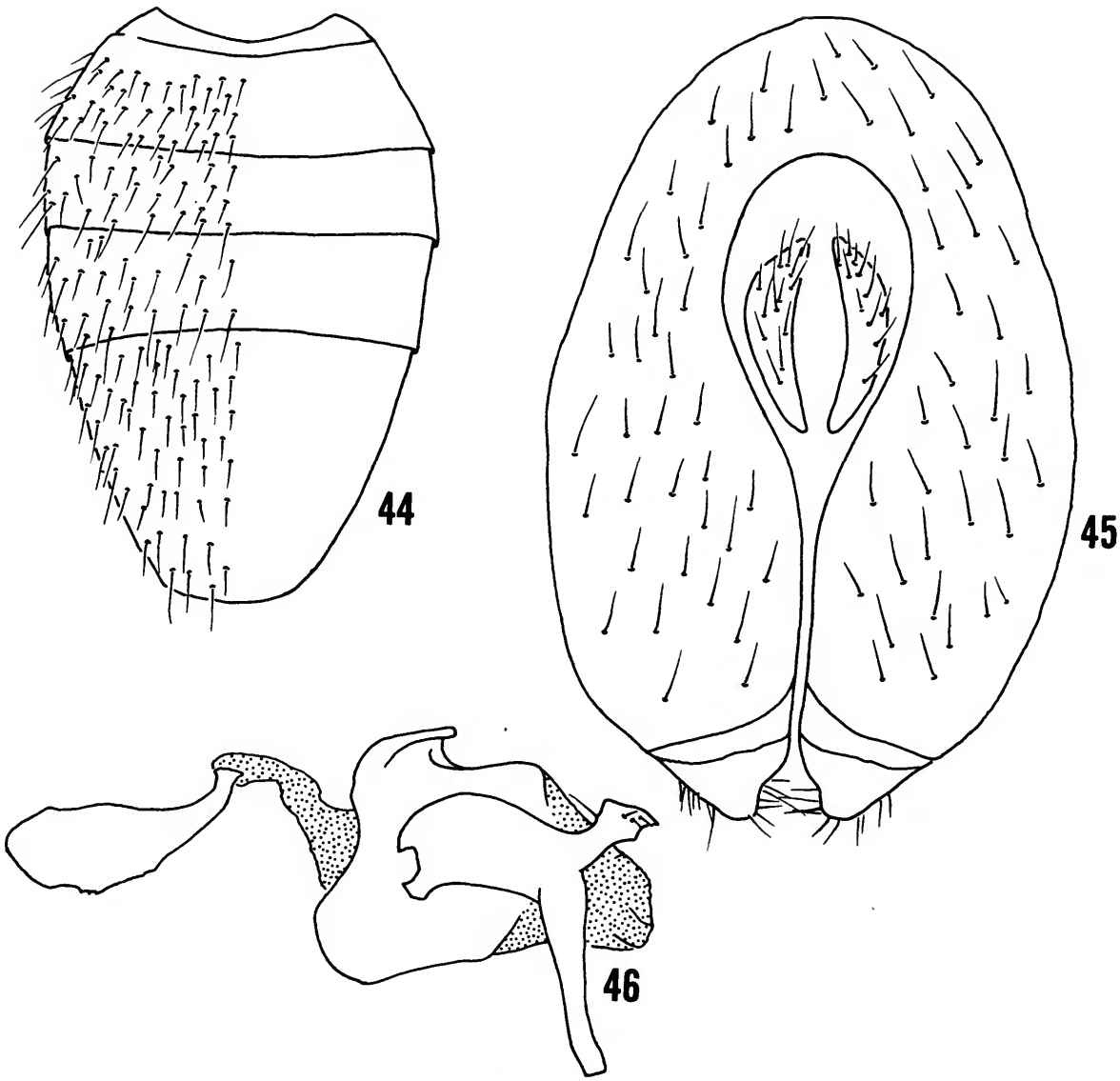
FIGURES 42,43.—*P. brunnea:* 42, head, lateral aspect; 43, thorax, dorsal aspect.

but slightly duller and with some greenish tinges posteriorly.

Thorax (Figure 43): Generally brown in color; mesonotum shinier and darker blue largely to shiny black color of background; usually with 2 and occasionally with 3 pair of larger acrostichal setae, anterior pair approximately aligned with transverse "suture," posterior pair are prescutellars; mesopleuron, pteropleuron, and dorsal portion of sternopleuron unicolorous, dull, brown; lower portion of sternopleuron becoming grayer and lightly greenish; front coxa mostly gray, contrasting distinctly with pleural areas. Legs brownish black to black, becoming less pollinose and darker toward apices; tarsi entirely black. Wing (Figure 37) infuscated brown; white spot in cell R_5 quite faint, often linear; both spots in cell R_5 about equidistant from posterior crossvein.

Abdomen (Figure 44): Unicolorous, blackish brown, appearing slightly greenish from posteroblique angle; fifth abdominal segment of male appearing swollen in lateral view; third segment of male shorter than second or fourth, the latter segments more or less subequal in length. Male terminalia as in Figures 45 and 46.

TYPE-MATERIAL.—Male holotype: "CHILE, Magallanes, Laguna Azul, I-II-956 (1956?)." Allotype and 32 paratypes (6 ♂♂, 26 ♀♀): with same label data as holotype. Other paratypes as follows: CHILE. MAGALLANES: 1 ♂, 2 ♀♀, Ultima Esperanza, Laguna Azul, 1 Feb 52, T. Cekalovick; 1 ♂, Cameron, S Bahia Inutio, Tierra del Fuego, 14-17 Nov 60, L. E. Peña; 1 ♀, Lab. Amarga, Natales E of Mt. Payne, 200 m, 14-20 Dec 60, L. E. Peña (CNC). AISEN (Aysen): 3 ♂♂,



FIGURES 44–46.—*P. brunnea:* 44 abdomen, dorsal aspect; 45, epandrium, cerci, and surstyli, posterior aspect; 46, internal male genitalia, lateral aspect.

4♀♀, 4.8 km W Chile Chico, 400 m, 22 Nov 66, E. I. Schlinger and M. E. Irwin, Meadow Assoc. (UCR, USNM). The holotype, allotype, and most of the paratypes are in the Instituto Miguel Lillo, Tucuman, Argentina; male and female paratypes are also deposited in the National Museum of Natural History, Smithsonian Institution.

ETYMOLOGY.—*Brunnea* is derived from the Medieval Latin adjective *brunneus,* meaning "brown," in allusion to the dark brown appearance of specimens of this species.

GEOGRAPHIC DISTRIBUTION AND NATURAL HISTORY (Figure 47).—See species-group discussion.

PHYLOGENETIC RELATIONSHIPS.—*Parascatella*

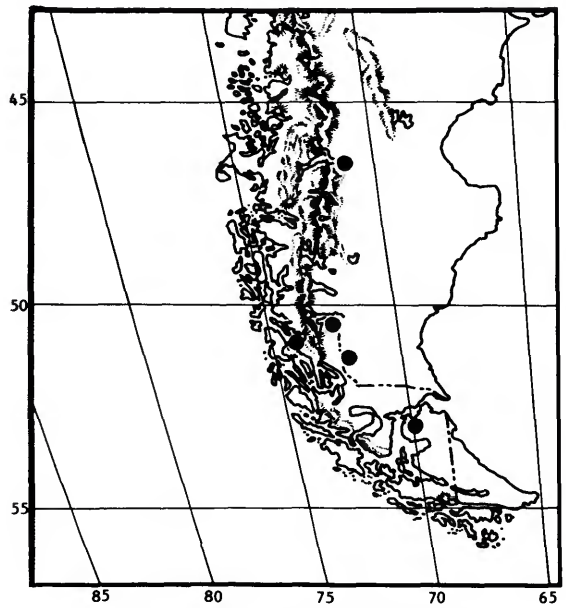


FIGURE 47.—Distribution of *P. brunnea*.

brunnea is the most plesiotypic of the South American species; specimens retain many character states that we consider to be part of the generalized ground plan for the genus, i.e., there are only two pairs of larger, lateral scutellar setae; the dorsalmost postocular setae are poorly developed; the acrostichal setae are well developed, although smaller than the larger dorsocentral bristles. Furthermore, the surstyli of the male genitalia remain differentiated from the ventral margin of the epandrium as distinct lobes. Like members of the *pilifera* group, however, specimens of *P. brunnea* have well-developed, spinelike setae along the coastal margin of the wing, a condition unique to members of these two species-groups.

Genus *Scatella* Robineau-Desvoidy

Scatella Robineau-Desvoidy, 1830:801 [type-species: *Scatella buccata* Robineau-Desvoidy (= *S. stagnalis* (Fallén)), by subsequent designation, Coquillett, 1910:603].—Aldrich, 1905:630–631 [catalog of North American species].—Deonier, 1964:108–109 [key to Iowan species].

Parascatella of authors, and of Cresson [in part], 1935:357–358 [review].—Wirth and Stone, 1956:474 [review of California species].—Wirth, 1965:747 [catalog of North American species].

Scatella (Parascatella) Cresson.—Sturtevant and Wheeler, 1954:172, 178–179 [review of North American species].

DIAGNOSIS.—Specimens of most species with an outstanding pair or pairs of larger, dorsally curved facial setae; 2 pair of larger lateroclinate frontoorbital setae; either with 3 (1+2) or 2 (0+2) pair of dorsocentral bristles; acrostichal setae seriated into 2 rows anteriorly, setae posterior of suture becoming weak or lacking, but most specimens with a distinctly larger pair of setae at sutural level; supra-alar seta weak, length one-half or less that of postalar seta; costa vein extending to apex of vein M_{1+2}; aedeagal apodeme of male terminalia flattened dorsoventrally, often angulate, L-shaped; surstyli fused indistinguishably to venter of epandrium.

DISCUSSION.—We have deliberately limited the synonymic citations listed under *Scatella* to those directly relating to the *triseta* group. It is not our intention here to present a definitive treatment of *Scatella* and all of its subtaxa. A colleague, Erling Olafsson, Lund, Sweden, is now conducting a study of this complex. We are only concerned with our conclusion that the North American species that were included in *Parascatella* are best treated as a species-group of *Scatella*.

The *triseta* Group

INCLUDED SPECIES.—*Scatella marinensis* (Cresson), *S. melanderi* (Cresson), *S. triseta* Coquillett.

DIAGNOSIS.—Members of the *triseta* group are recognized by the following combination of characters: ocelli arranged in equilateral triangle; dorsalmost postocular setae poorly developed, subequal to postocellar setae; arista longer than combined length of first three antennal segments, micropectinate dorsally: facial setae extending from interfoveal carina to posteroventral corner of face, well developed, subequal to setae along oral margin, often semiporrect; acrostichal setae small, hairlike, lacking distinctly larger pair at transverse suture; 3 pair of dorsocentral bristles (1+2); supra-alar bristle rudimentary, at most one-half length of postalar bristles; scutellum with only 2 pair of larger, lateral bristles; costal margin of wing with interspersed, slightly larger setae, these not more than width of costal vein; aedeagal apodeme flattened dorsoventrally; surstyli fused indistinguishably with venter of epandrium, or they are lacking.

GEOGRAPHIC DISTRIBUTION.—The combined distribution of the included species ranges throughout western North America, extending from Anchorage, Alaska, to San Cristobal, Chiapas, Mexico. The distribution eastward extends to the Mississippi River, although most specimens were collected considerably farther west. The distribution of these species broadly overlap each other, adequately confirming their reproductive isolation.

NATURAL HISTORY.—Very little is known about the natural history of any of the included species. To date, neither the life history nor the immature stages of any of the species have been discovered and described. Deonier (1965) did describe briefly the habitat of *S. triseta* in Iowa (see "Natural History" under that species).

Key to Species of the *triseta Group*

1. Face unicolorous, dark brown; 2 pair of larger, lateroclinate, fronto-orbital bristles; wing distinctly infuscated, with white spots contrasting distinctly .....3. ***S. melanderi*** (Cresson)
   Face bicolored, dorsal portion of interfoveal carina brown, contrasting with grayer ventral portion; 2–3 pair of larger, lateroclinate, fronto-orbital bristles, if 3, middle pair smaller but frequently one-half length of either larger bristle; wing hyaline to very light infuscated, white spots weakly evident. 2
2. Mesonotum and scutellum dull, pollinose, brown with some weak gold-colored tomentosity; dorsum of scutellum flat .....1. ***S. triseta*** Coquillett
   Mesonotum and scutellum subshiny to shiny, very thinly pollinose, dark brown; scutellum weakly convex .....2. ***S. marinensis*** (Cresson)

1. *Scatella triseta* Coquillett

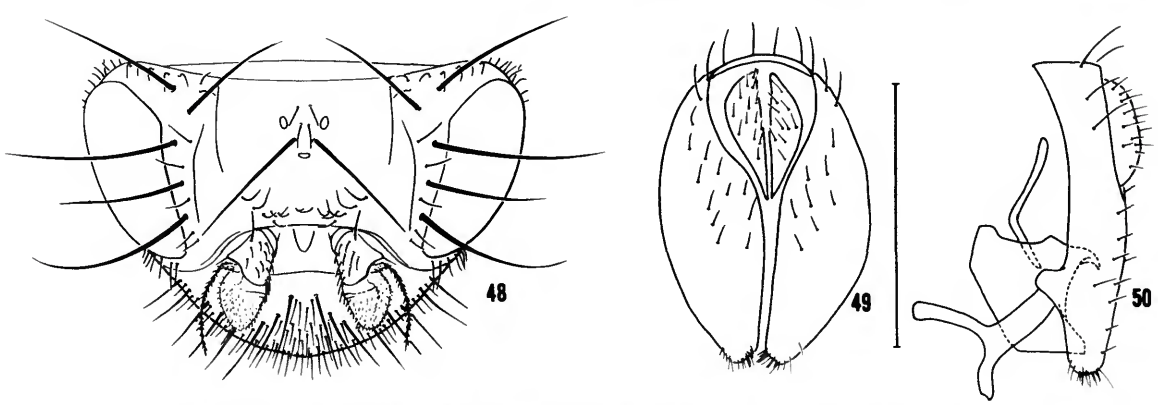
FIGURES 48–52

Scatella triseta Coquillett, 1902:184.
Parascatella triseta.—Cresson, 1935:358.—Wirth, 1965:757 [catalog].
Scatella (Parascatella) triseta.—Sturtevant and Wheeler, 1954:179.

DIAGNOSIS.—Specimens of this species are closely related to those of *S. marinensis* as evidenced by their close resemblance, but may be distinguished from the latter and all similar congeners by the following combination of characters: 3 pair of larger fronto-orbital setae, middle pair smaller but at least one-half the length of larger, outer pairs; interfoveal carina brown, contrasting distinctly with grayish white, lower portion of face; mesonotum dull, grayish brown; scutellar disc flat; wing hyaline to very lightly infuscated, white spots inconspicuous.

DESCRIPTION.—Moderately small to medium-sized shore flies, length 2.50 to 3.74 mm; generally dull, pollinose mostly brown but becoming distinctly grayer ventrally and along posterior margins of abdominal segments.

Head (Figure 48): Mesofrons shiny with metallic brown to brassy luster, becoming weakly differentiated anteriorly, equaling parafrons in color and



FIGURES 48–50.—*S. triseta:* 48, head, dorsal aspect; 49, epandrium and cerci, posterior aspect; 50, epandrium, cerci, internal male genitalia, lateral aspect.

vestiture; parafrons dull, pollinose brown; dorsalmost postocular setae very poorly developed, at most equaling length of postocellars; 3 pair of larger, lateroclinate fronto-orbital bristles, middle much smaller but equal to, or larger than, one-half length of larger, outer pairs. Antennal segments more or less unicolorous; third segment more pubescent; arista approximately equal to combined length of other antennal segments, micropectinate above over most of length. Dorsum of interfoveal carina brown, contrasting distinctly with lower portion that is lacteous to argenteous; facial setae extending ventrad from interfoveal carina to posteroventral corner of face and those along oral margin well developed, obviously larger than remaining facial setae that are uniformly smaller; interfoveal carina with distinct dorsal carina. Gena mostly concolorous with face.

Thorax: Generally dull, pollinose, brown to gray, dorsum darker. Mesonotum gray to grayish brown, becoming darker and browner posteriorly; scutellum concolorous with disc of mesonotum, flat; acrostichal setae sparse and weakly developed. Dorsal portion of mesopleuron and notopleuron concolorous, light brown; lower portion of mesopleuron, pteropleuron, and sternopleuron mostly gray; front coxa silvery gray not contrasting distinctly with sternopleuron. Femora and tibiae more or less concolorous, pollinose, gray to bluish gray; tarsi dark, black dorsally, ventral surfaces paler, often tawny. Wing (Figure 52) mostly hyaline or but slightly infuscated, white spots usually inconspicuous, small, roundish.

Abdomen: Generally dull, gray to brown. Anterior portion of each segment brown, bordered posteriorly with gray band, gray on ventral surface also; segments 2–4 of male specimens more or less subequal in length. Male terminalia as in Figures 49 and 50.

TYPE-MATERIAL.—Female lectotype (here designated): "Williams, 6, 6 Ariz; HBarber, Collector." One male and 2 female paralectotypes (here designated): with the same label data as the lectotype. The lectotype and paralectotypes are in the National Museum of Natural History, Smithsonian Institution, type number 6646. Cresson's original description lists one additional female specimen, which we have not been able to locate in the collection at the USNM.

SPECIMENS EXAMINED.—404 specimens (133 ♂ ♂, 271 ♀ ♀). CANADA. ALBERTA Norton, 49°52'N, 10°24'W (CNC). MEXICO. BAJA CALIFORNIA: Sierra San Pedro Martir–La Grulla, 6900' (CA, USNM). UNITED STATES. ARIZONA: Cochise Co., Chiricahua Mtns (USNM), Chiricahua Mtns–Rustlers Park, 8200' (USNM), Douglas (USNM), Herb Martyr Park (WNM), Huachuca Mtns (AMNH), SW Research Sta–5 mi W Portal, 5400' (WNM); Coconino Co., Grand Canyon, S Rim (USNM), Williams ANSP, USNM); Pima Co., Greaterville (CA), Tucson–Saguaro Nat'l. Mon. (USNM); Pinal Co., Superior (USNM); Santa Cruz Co. Sycamore Canyon–Yank's Spring–Tumacacori. CALIFORNIA: Andrea Canyon (USNM); Coachella Valley (CA); Green Valley (USNM); Monarch Pass, 8000' (USNM); Morongo Valley (USNM); Scotland (USNM); Sentence Canyon (USNM): Stoddard Well (USNM); Alameda Co., Berkeley Hills (ANSP); Inyo Co., Big Pines (USNM); Los Angeles Co., Claremont, near mountains (USNM), Los Angeles (CA), Los Cerritos (ANSP), Mojave Desert–Lovejoy Springs (USNM), Pasadena (USNM), Rosemead (USNM), Valyermo (USNM): Mono Co., Mono Lake (CA, USNM), Topaz Lake (CA, USNM): Monterey Co., Asilomar (USNM); Riverside Co., Cathedral Canyon (USNM), Cathedral City (USNM), Indio (CNC), Mag. Spring Canyon (USNM), Mag. Spring near Indio (USNM), Palm Springs (USNM), Whitewater Canyon (USNM); San Bernardino Co., Barton Flat, E of (USNM), Barton Flat, S Fork Camp (USNM), Crestline (USNM), Helendale (CNC), Herkey Camp (USNM), San Bernardino Mtns–Sugarloaf (USNM), South Fork Santa Ana River (USNM), Upper Santa Ana River (USNM), Upper Santa Ana River–Lost Creek (USNM), Wrightwood (USNM); San Diego Co., Agua Caliente (CNC), Borego Desert–Tubb Canyon (USNM), Desert Edge (ANSP, CA); San Mateo Co., Corte de Madera vic Portola (CA), Redwood City (USNM); Santa Barbara Co., Sant Cruz Island (USNM); Tulare Co., Sequoia Park, 6200' (USNM); Tuolumne Co., Yosemite (USNM); Ventura Co., Santa Paula (USNM). COLORADO: (USNM); Mt Evans–timberline, 11,600' (CNC); Clear Creek Co., Idaho Springs, 6 mi SW (CNC); Eagle Co., Tennessee Pass, 10,240' (ANSP, USNM); El Paso Co., Colorado Springs (ANSP, CA). IDAHO: Lake Vaha (USNM). KNASAS: Douglas Co., Lawrence Nat. Hist. Res (WNM). NEBRASKA: Cherry Co., Pelican Lake (USNM), Snake River (USNM). NEW MEXICO: Dartford (USNM); Catron Co., Glenwood, 32 mi E (WNM); Grant Co., Cherry Creek–Pinos Altos (USNM); Otero Co., Alamogordo (ANSP), Cloudcroft (CNC), Cloudcroft, 2.5 mi E (WNM), Penasco River–Mayhill (USNM); Sandoval Co., Cuba, 11 mi SE (WNM), Jemez Springs, 7.5 mi N (WNM), Rabbit Mnt (USNM), 7 Springs Ranger Sta (WNM); San Miguel Co., Las Vegas, 6400' (USNM); Socorro Co., Bear Trap Camp, 28 mi SW Magdelena (AMNH), Magdelena Mtns (AMNH), Magdelena (AMNH); Torrance Co., Tajique (USNM). NORTH DAKOTA: Mountrail Co., White Lake (UNSM). OKLAHOMA: Alfalfa Co., Gt. Salt Plains (USNM). SOUTH DAKOTA: Custer Co., Custer, 7 mi W (WNM) Lawrence Co., Savoy, 2 mi W (WNM). TEXAS: (USNM); Brewster Co., Big Bend Nat'l. Park–Pulliman Canyon; Gillespie Co., Pedernales River (USNM); Presidio Co., Shafter near old silver mine (USNM); Randall Co., Palo Duro Canyon (USNM); Sonora Co., Sonora (USNM), Sonora Exp. Sta (USNM); Travis Co., Austin (ANSP, USNM). UTAH: Utah Co., Goshen Pond (WNM); Washington Co., Santa Clara, 6 mi W (WNM), Zion Park (USNM). WASHING-

TON: Okanogan Co., Brewster (USNM); Walla Walla Co., Walla Walla (USNM); Whitman Co., Almota (ANSP). WYOMING: Teton Co., Yellowstone Lake (USNM), Yellowstone Park Falls (USNM), Yellowstone Park, U Geyser Basin (USNM).

GEOGRAPHIC DISTRIBUTION. (Figure 51).—*Scatella triseta* occurs in most states west of the Mississippi River, as far north as Norton, Alberta, and southward to Big Bend National Park (Brewster County), Texas. It is likely that this species also occurs throughout the high plateau region of northern Mexico.

NATURAL HISTORY.—Deonier (1965) collected specimens of this species commonly in stream rock and freshet-seep habitats in Boone County, Iowa. He characterized the stream-rock habitat as the moss- and alga-covered shoal or riffle rocks that project above the surface of shallow riffles. The exposed rocks are covered with bryophytes and diatoms, the latter being very abundant and constituting most of the microflora. Deonier found that this habitat is restricted to forested areas and that is one of the most stable shore fly habitats in Iowa. The freshet-seep habitat is more ephemeral, depending on seepage that is governed by rainfall. Deonier described it as a microhabitat, consisting of small seepage areas on embankments. The flora includes species of *Nostoc* and other Cynophyta plus mosses; these grew on the seepage areas and around small pools at the bases of embankments.

PHYLOGENETIC RELATIONSHIPS.—*Scatella triseta* is the sister species of *S. marinensis*. This relationship is established by the joint possession of acrostichal setae that are reduced in size and by the color of the interfoveal carina that is brown to golden brown, contrasting distinctly with the bottom portion of the face. Both of these character states are synapomorphous.

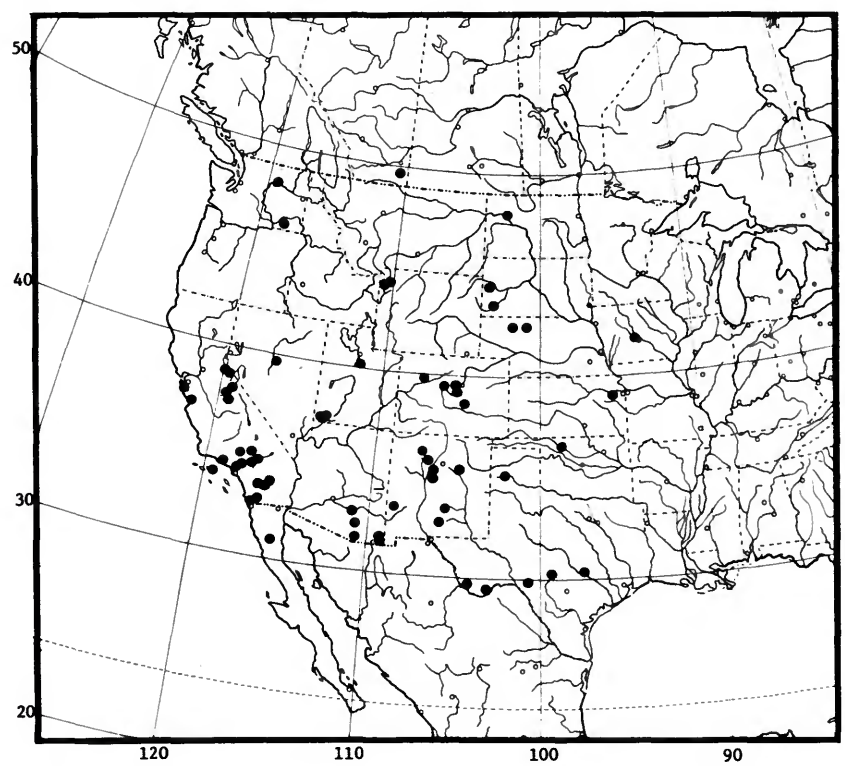


FIGURE 51.—Distribution of *S. triseta*.

2. *Scatella marinensis* (Cresson)

FIGURES 53, 55–57

Parascatella marinensis Cresson, 1935:358.—Wirth, 1965:757 [catalog].

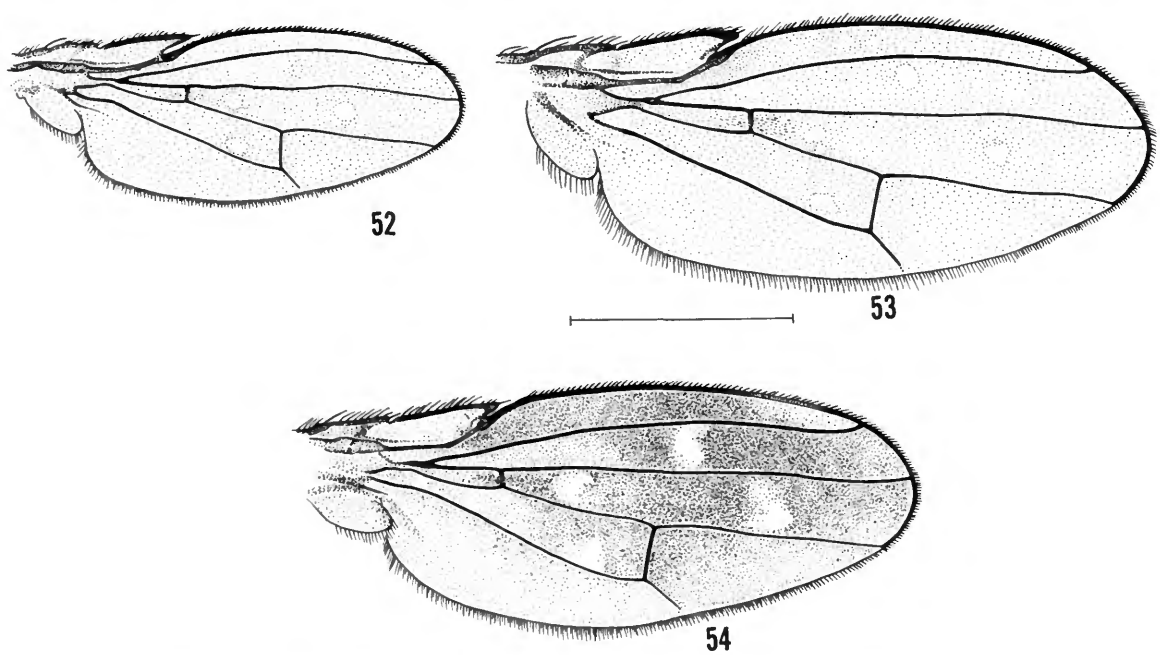
Scatella (Parascatella) marinensis.—Sturtevant and Wheeler, 1954:178.

DIAGNOSIS.—Members of this species and *S. triseta* very closely resemble each other and care must be exercised in distinguishing between them. *Scatella marinensis* specimens are recognized by the following combination of characters: 2 pair of larger, lateroclinate fronto-orbital setae, between larger pairs there is a smaller pair, always less than one-half the length of larger setae; mesonotum and scutellum darker brown and becoming shinier posteriorly; disc of scutellum slightly convex, not distinctly flattened.

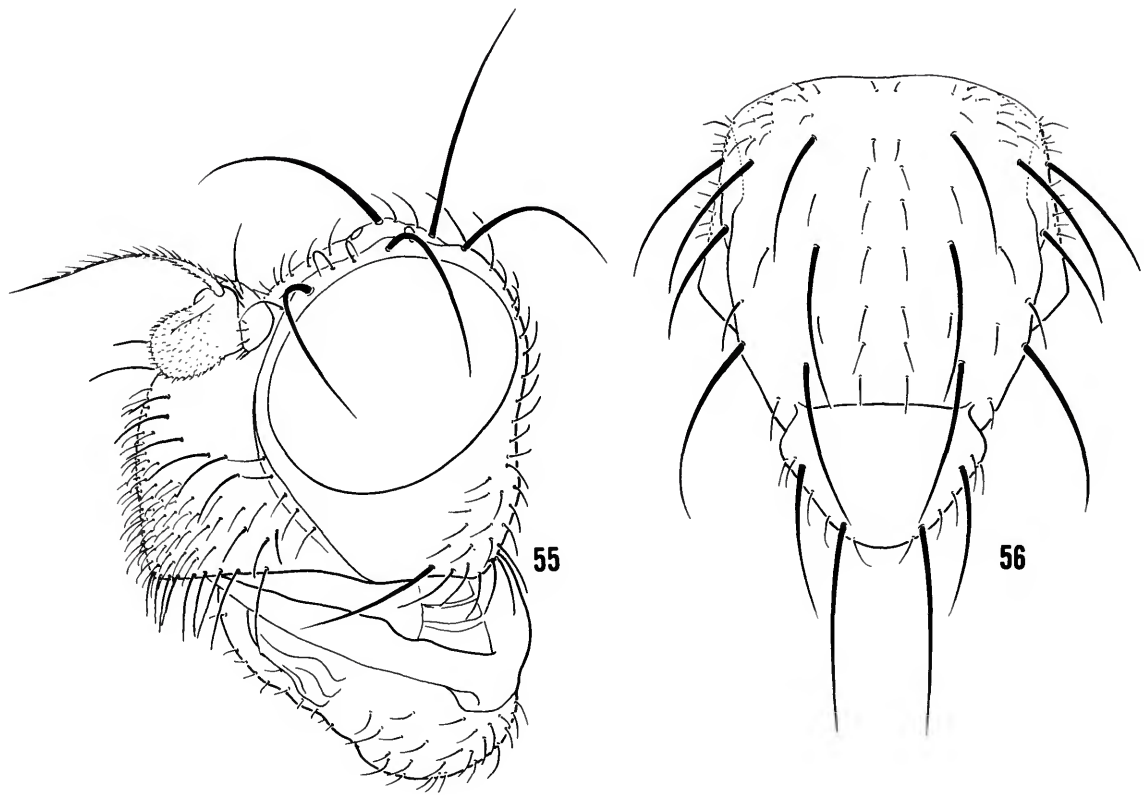
DESCRIPTION.—Moderately small to medium-sized shore flies, length 2.72 to 3.56 mm; generally subshiny dorsally, brown to dark brown, becoming duller and more pollinose ventrally.

HEAD (Figure 55): Mesofrons mostly shiny, appearing brassy in luster, background color black but overlaid with sparse brown pollinose vestiture, giving brassy appearance, anterior portion bordering frontal suture generally dull, pollinose, at most weakly subshiny; parafrons densely pollinose, brown; dorsalmost postocular setae weakly developed, less than one-third length of ocellar bristles; 2 pair of strong, lateroclinate fronto-orbital bristles, between larger pairs is a smaller pair of setae much less than one-half length of either larger pair. Antenna mostly unicolorous; third segment more pubescent; arista slightly longer than combined length of antenal segments, micropectinate above over most of length. Color of dorsal portion of interfoveal carina brown, concolorous with parafrons, contrasting distinctly with silvery white color over lower three-fourths of face; space between antennal bases charcoal black in color; dorsum of interfoveal carina with distinct crease; facial setae extending from interfoveal carina toward posteroventral corner of face and those along oral margin much larger than remaining facial setae, the latter setae uniformly smaller. Gena concolorous with face or slightly less silvery.

Thorax (Figure 56): Brown to gray, darker dorsally. Mesonotum dull and pollinose anteriorly, becoming darker and shinier posteriorly and with very



FIGURES 52–54.—Wing, dorsal aspect: 52, *S. triseta;* 53, *S. marinensis;* 54, *S. melanderi.*



FIGURES 55,56.—*S. marinensis:* 55 head, lateral aspect; 56, thorax, dorsal aspect.

faint indication of a vitta along acrostichal setal tract; acrostichal setae weakly developed, often with a slightly larger pair of setae where transverse suture would cross mesonotum; scutellum concolorous with posterior portion of mesonotum, slightly convex. Notopleuron and posterodorsal portion of mesonotum concolorous, brown; remaining areas of mesopleuron lighter, becoming grayer, especially ventrally, and concolorous with sternopleuron and front coxa; pteropleuron grayish brown, intermediate between brown and gray color of mesopleuron. Legs concolorous, femora densely pollinose, mostly gray but with some faint greenish tinges; tibiae less pollinose than femora, becoming black ventrally; tarsi mostly black but paler ventrally, tawny in some specimens. Wing (Figure 53) mostly hyaline or very lightly infuscated, light brown; pattern of white spots similar to *P. triseta,* often not very evident.

Abdomen: Generally brown or blackish brown dorsally, becoming grayer on venter; posterior margins of posterior segments often banded with grayer border; segments 2 to 4 of male specimens more or less subequal in length, fifth segment about twice the length of fourth.

TYPE-MATERIAL.—Holotype male, labeled: "Redwood Canon [sic] Marin Co., V, 17, '08 Cal./♂/ TYPE Parascatella MARINENSIS E. T. Cresson, Jr. 6525 (red)." The holotype is in good condition and is double mounted. Cresson's original description also lists 4 male and 4 female paratopotypes. The type series is in the Academy of Natural Sciences of Philadelphia, type number 6525.

SPECIMENS EXAMINED.—286 specimens (87 ♂♂, 199 ♀♀). CANADA. BRITISH COLUMBIA: Fairmont Hot Springs (CA). MEXICO. CHIAPAS: San Cristobal (CNC). UNITED STATES. ALASKA: Anchorage–Eagle River Flats (USNM). ARIZONA: Cochise Co., Chiricahua Mtns, 8500′ (USNM), Huachuca Mtns–Miller Canyon (USNM), Huachuca Mtns–Ramsey Canyon, 15 mi S Sierra Vista, 6000′ (CNC), Portal–SW Research Sta (USNM); Pima Co., Organ Pipe Cactus Nat. Mon.–Dripping

Spring (WNM), Santa Rita Range Res.–Florida Canyon (WNM); Santa Cruz Co., Tumacacori Mtns.–Sycamore Canyon–Yanks Spring (CA, USNM). CALIFORNIA: Live Oak Park (USNM); Mountain Home (USNM); Ortega Hwy–El Cariso Camp (USNM); Alameda Co., Berkeley (CA, USNM), Berkeley Hill (ANSP); Contra Costa Co., Danville (CA), Mt. Diablo (USNM), San Ramon Creek–Danville (USNM); Imperial Co., Salton Beach (USNM); Los Angeles Co., Los Angeles (ANSP), Saugus, 10 mi NE (USNM); Marin Co., Lagunitas Canyon (ANSP), Mill Valley (CA), Muir Woods (USNM), Redwood Canyon (ANSP); Mariposa Co., Big Creek–Summerdale Forest Camp (CA); Monterey Co., Big Sur (USNM), Big Sur State Park–Pfeiffer (CA), Carmel (USNM), San Simeon (AMNH); Placer Co., Bear Valley, E end (CA); Riverside Co., Agua Caliente Indian Res.–Palm Canyon (CA), Cathedral Canyon (USNM), Cathedral City (USNM), Mag. Spring Canyon, near Indio (USNM), Palm Canyon (USNM), Palm Canyon–Palm Springs (USNM); San Benito Co., Pinnacles (USNM); San Bernardino Co., Big Pines (USNM), E Fork Devils Canyon, San Bernardino, 8 mi N (USNM); San Diego Co., Cuyamaca Park (USNM); San Francisco Co., San Francisco (CA); San Luis Obispo Co., Morro Bay (USNM), Pozo (USNM); San Mateo Co., Corte de Madera Creek (CA), Palo Alto (CA, USNM), Redwood City (USNM); Santa Clara Co., San Jose (CA), Stanford University (CA); Shasta Co., Bondary Campground (CA); Stanislaus Co., Del Puerto Canyon–Frank Raines Park–Del Puerto Creek, 335 m (CA); Tuolumne Co., Pinecrest (CA), Yosemite (USNM); Ventura Co., Santa Paula (USNM). IDAHO: Nez Perce Co., Culdesac (USNM). MONTANA: Thompson (USNM); Gallatin Co., Firehole River (USNM). NEW MEXICO: Catron Co., Whitewater Canyon (USNM). OREGON: Benton Co., Cary's Grove (WNM), Clackamas Co., Eagle Creek (USNM); Crook Co., Marks Creek–Cougar Campground (CA); Curry Co., Humbug Mtn State Park (USNM); Harney Co., Crane Hot Spring (WNM), Umatilla (USNM). TEXAS: Brewster Co., Big Bend Nat'l. Park–Pulliman Canyon (CNC). UTAH: Utah Co., Goshen Pond (WNM). WASHINGTON: Husam (WNM); Adams Co., Lind (WNM); Asotin Co., Asotin (WNM); Chelan Co., Entiat (WNM); Clallam Co., Sol Duc Hot Spring (WNM); Garfield Co., Central Ferry (WNM); Mason Co., Lilliwaup (WNM); Pierce Co., Ft. Lewis (WNM), Mt Rainier–Ohanapechosh (WNM); Walla Walla Co., Walla Walla (WNM).

GEOGRAPHIC DISTRIBUTION (Figure 57).—*Scatella marinensis* occurs primarily in the Rocky Mountains and westward, although we have examined specimens from Big Bend National Park (Brewster County), Texas. We have also seen specimens from as far north as Anchorage, Alaska, and as far south as 3 miles northeast of San Cristobal, Chiapas, Mexico. This species is sympatric over much of its range with *S. triseta* and it is not uncommon to collect specimens of both species at the same locality.

NATURAL HISTORY.—No detailed study on the natural history of this species is available and we can only offer the following descriptive data summarized from collecting notes. Mathis has collected specimens of this species from protected areas along the banks of small streams in Utah and Oregon. Specimens were taken while sweeping through emergent vegetation that consisted mainly of grasses and sedges. Backwater areas or pools left in alternative, high-water channels were especially fruitful collecting areas, although specimens were not encountered commonly anywhere.

PHYLOGENETIC RELATIONSHIPS.—Our remarks under *S. triseta* regarding the relationship of this species with the former also apply here.

3. *Scatella melanderi* (Cresson)

FIGURES 54, 58–60

Parascatella melanderi Cresson, 1935:358.—Wirth, 1965:757 [catalog].

Scatella (Parascatella) melanderi.—Sturtevant and Wheeler, 1954:179.

DIAGNOSIS.—Specimens of this species are easily distinguished from those of similar congeners by the following combination of characters: mesofrons mostly dull, pollinose, weakly differentiated from surrounding parafrons; antennal arista very long, almost equal to twice the combined length of other antennal segments; face from interfoveal carina to oral margin unicolorous, pollinose, grayish brown; wing distinctly infuscated, brown; white spots in wing membrane contrasting distinctly; general coloration of abdomen grayish brown to blackish brown.

DESCRIPTION.—Medium-sized shore flies, length 3.07 to 3.91 mm; generally dull, pollinose, grayish brown to grayish blue, abdomen darker in color and shinier.

Head (Figure 59): Mesofrons brown, more or less concolorous with disc of mesonotum, at most subshiny, usually heavily pollinose, vestiture weakly differentiated from parafrons; parafrons pollinose, usually darker in color than mesofrons, grayish charcoal or slightly blackish blue anteriorly; frontoorbits brown, pollinose; dorsalmost postocular setae weakly developed, at most slightly larger than postocellar setae and much smaller than ocellars; 2 pair of large, lateroclinate fronto-orbital setae. Antennal segments mostly unicolorous, brownish black to black; third segment more pubescent, appearing darker from some angles; arista long (Fig-

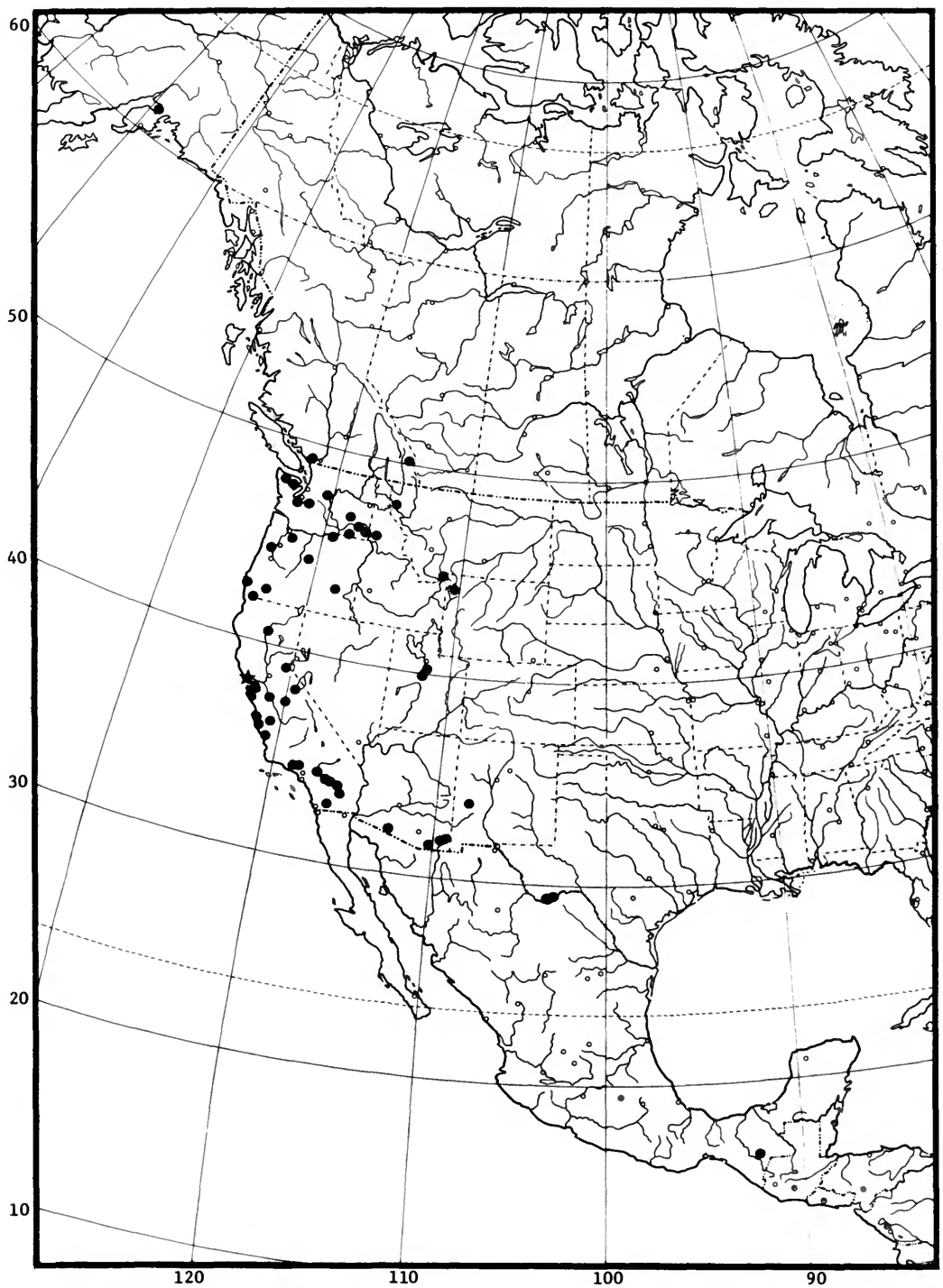


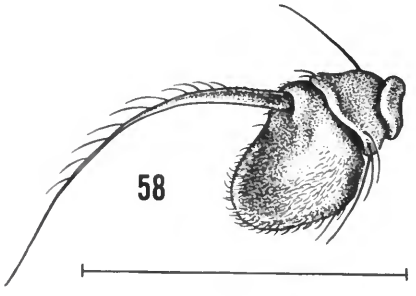
FIGURE 57.—Distribution of *S. marinensis*.

ure 58), length subequal to twice the combined length of first 3 antennal segments, micropectinate above on basal two-thirds. Face except for antennal fovea mostly unicolorous, grayish brown; antennal fovea lighter in color, whitish gray; facial setae extending obliquely ventrad from interfoveal carina to posteroventral corner of face and those along oral margin distinctly larger, remaining facial setae uniformly smaller; interfoveal carina with distinct dorsal carina. Gena lighter in color than face, with distinct greenish tinges but also with light tan areas.

Thorax: Generally grayish brown to gray, mostly pollinose, dull, darker dorsally; mesonotum with faint indication of vittae along major setal tracts, slightly darker brown; scutellum more or less concolorous with mesonotum or slightly darker. Mesonotum and pteropleuron mostly concolorous, both more or less concolorous with gena; lower portion of sternopleuron grayer and front coxa distinctly grayer, contrasting with rest of pleural areas. Legs generally dark, grayish black; femora with slight greenish color; tibiae and tarsi darker, especially dorsally; ventral surface of tarsi often quite pale, tawny. Wing (Figure 54) infuscated, brown; larger white spots subrectangular and very distinct from surrounding infuscation; white areas in cell R_3 slightly apicad of alignment of posterior crossvein.

Abdomen: Generally unicolorous, dark, greenish brown, but overlaid with grayish pollinose vestiture; posterior segments tending to become darker and less pollinose; often subshiny; abdominal segments 2–4 more or less subequal in length in male specimens.

TYPE-MATERIAL.—Holotype male, labeled: "Tacoma, Wash./TYPE Parascatella MELANDERI ♂ E. T. Cresson, Jr. 6526 (red)." The holotype is in good condition, is pinned directly, and is in the Academy of Natural Sciences of Philadelphia, type number 6526. Cresson's original description also



FIGURES 58,59.—*P. melanderi:* 58, antenna, lateral aspect (line equals 0.5 mm); 59, head, lateral aspect.

lists 4 male paratopotypes, all collected by A. L. Melander.

SPECIMENS EXAMINED.—158 specimens (79♂♂, 79♀♀). CANADA. BRITISH COLUMBIA: Vancouver, Point Grey (CNC, USNM). UNITED STATES. CALIFORNIA: San Mateo Co., Memorial Park USNM); Santa Cruz Co., Capitola (CA), Davenport (CA, USNM), Santa Cruz (CA, USNM); Sonoma Co., Stillwater Cove (USNM). OREGON: Marion Co., Silver Falls State Park–South Silver Creek Falls (CA); Tillamook Co., Neskowin (WNM). WASHINGTON: Clallam Co., Sequim (USNM), Sequim Bay (USNM); Grays Harbor Co., Hoquiam (USNM); Lewis Co., Chehalis (ANSP); Mason Co., Lake Cushman (USNM); Pacific Co., Ilwaco (ANSP, USNM); Pierce Co., La Grande, 3 mi N (WNM), Tacoma (ANSP, USNM).

GEOGRAPHIC DISTRIBUTION (Figure 60).—*Scatella melanderi* occurs along the coast of the Pacific Northwest from Vancouver, British Columbia, in the north to Santa Cruz County, California, in the south. This distribution pattern overlaps that of *S. marinensis,* although we do not have specific collecting records of *S. melanderi* occurring with that species.

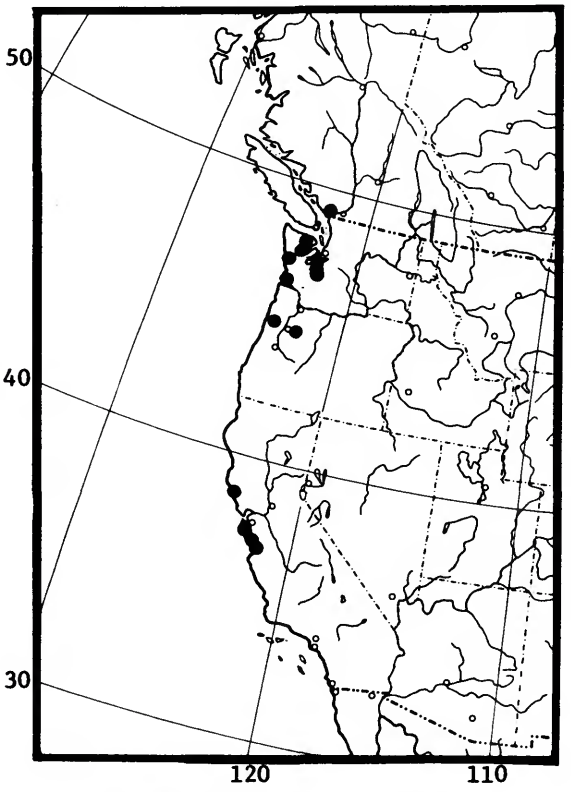


FIGURE 60.—Distribution of *S. melanderi.*

NATURAL HISTORY.—Mathis has collected specimens of this species along freshwater streams that eventually drain into the Pacific Ocean. Sweeping through grasses and other emergent vegetation associated with protected, moist areas, especially near embankments, yielded better catches, although specimens were not collected commonly anywhere. The specimens from Vancouver, British Columbia, were collected by Dr. J. R. Vockeroth at Point Grey and were labeled with a habitat description as follows: "On seepage on earth cliff."

PHYLOGENETIC RELATIONSHIP.—*Scatella melanderi* is apparently the sister species to *S. triseta* and *S. marinensis;* however, no apotypic character state has been discovered to establish this relationship.

Evolutionary Considerations

Most recent classifications divide the subfamily Ephydrinae into two tribes: Ephydrini and Scatellini (Wirth, 1965, 1968). Ephydrini is characterized by several synapotypies (Mathis, in preparation) and is undoubtedly monophyletic. Scatellini, however, as presently recognized, is an assemblage of convenience. Genera included are largely the residue of the subfamily Ephydrinae that cannot be placed in Ephydrini. It is likely that these will be arrayed into several tribes once their relationships are clarified, which is beyond the scope of the present paper.

Various apparently monophyletic assemblages of genera can be recognized, however, within the tribe Scatellini. One such group, comprising genera that are similar in appearance to the genus *Scatella* Robineau-Desvoidy, include (besides the latter) *Limnellia* Malloch, *Neoscatella* Malloch (here treated as part of *Scatella*), *Parascatella* Cresson, and *Scatophila* Becker (and perhaps *Apulvillus* Malloch, not studied). With the exception of *Scatophila,* these genera plus *Lamproscatella* Hendel were previously treated as an informal group (Wirth, 1948) and a key was provided for their identification. We are excluding *Lamproscatella* from further consideration here because it appears to be more closely related to another assemblage of genera (Mathis, in prep.).

The assemblage related to *Scatella* is characterized as follows.

1. *Wing pattern:* The wing pattern appears to be a simple morphocline in which the plesiotypic

state is a hyaline wing, characteristic of most members of Ephydrinae. At the next level, the wing becomes lightly infuscated, grayish to tan, with a pattern of white areas arranged as follows: cell R_1 with one white spot, sometimes subquadrate, more or less aligned or slightly apicad of posterior crossvein; cell R_3 with two white spots on either side of posterior crossvein; discal cell with one white spot, often subdivided, near the apical end; cell M_2 with one basal white area, frequently large and irregular in shape and/or subdivided; cell M_4 with one to two white areas, usually in apical one-half. Some inter- and intraspecific variation occurs, usually by the addition of white spots.

2. *Gonite shape:* Typically the gonites are paired structures extending from the sides of the aedeagus, connecting the latter with the hypandrium. In the *Scatella* assemblage, the hypandrium becomes rudimentary or is lacking, and the gonite is modified to form an angulate structure with a stout "arm" that extends along the same plane as the aedeagus and a simpler, narrow ventral process. The apices of each ventral, gonal process fuse, to form a loop through which the aedeagus projects. This condition becomes more pronounced in the genera immediately related to *Scatella,* such as *Parascatella.*

3. *Aedeagal apodeme:* The shape and attachments of this structure appear to form a duo morphocline. The generalized condition in Ephydrinae and throughout most of the family is for the aedeagal apodeme to be attached basally to the hypandrium as in *Ephydra* (Wirth, 1971) and *Paracoenia* (Mathis, 1975), and for the structure to be well developed but laterally flattened. From this condition, the structure becomes rudimentary. In males of *Scatophila* and *Limnellia,* the aedeagal apodeme still remains attached to the base of the aedeagus and to the rudimentary hypandrium or to the fused apices of the ventral gonal processes. But in males of *Scatella* and *Parascatella,* the apodeme is detached from the hypandrium or ventral gonal processes and is only loosely attached to the base of the aedeagus.

The cladogram (Figure 61) plus the accompanying list of supportive character evidence (Table 1) summarizes the relationships among the species and species-groups of *Parascatella* and *Scatella* herein treated as we understand them at present.

Our concept of *Parascatella,* as characterized above, is a conveniently recognized, monophyletic group. The species and species-groups comprising the genus are closely related as evidenced by the synapotypic character states that establish the monophyly of the genus (characters 1–2). Additionally, the species and species-groups are very similar to each other, making the genus an easily recognizable taxon.

Using these criteria, we are excluding from *Parascatella* the species included in what we are designating as the *triseta* group, preferring to include them in *Scatella* sensu lato. We suggest that the latter genus is also monophyletic as recognized by the character states indicated on the cladogram (characters 1′, 3–4). We are treating the *triseta* group as an informal species-group because its basis is patristic, lacking characterization by an apotypic character state. The monophyly of the remaining species of *Scatella* (including *Neoscatella*) is clearly evident, however, being established by three synapotypies (characters 24–26).

The reason we are treating the species of the *triseta* group here is because they have been included in *Parascatella* by most students of the family, either when *Parascatella* was a distinct genus (Cresson, 1935; Wirth, 1965, 1968) or a subgenus of *Scatella* (Sturtevant and Wheeler, 1954). Also, the *triseta* group is closely related to *Parascatella,* and we had already gathered the basic data pursuant to a taxonomic treatment and did not feel a second paper would be any more effective in communicating our results of that group.

The first major dichotomy in the phylogeny of *Parascatella* is the differentiation of the *brunnea* and *pilifera* groups. The monophyly of the *pilifera* group is indicated by many synapotypies (characters 6–8), while the *brunnea* group is defined by only one, subjectively determined apotypic character state (character 5).

Within the *pilifera* group, the major weakness in the proposed phylogeny is the suggested relationship between *P. balioptera* and *P. penai* and the remaining species. We suspect these two species are closely related and that they are more closely related to those species having a setal comb along the posteroventral margin of the front leg (*P. glabra, P. spinicrus, P. lanicrus,* and *P. pilifera*) than to the species with a large white spot in cell R_3 of male specimens (*P. apicalis, P. hirticrus, P. semicinerea,* and *P. semipolita*). A second lineage, that of *P. semicinerea* and *P. semipolita,* lacks char-

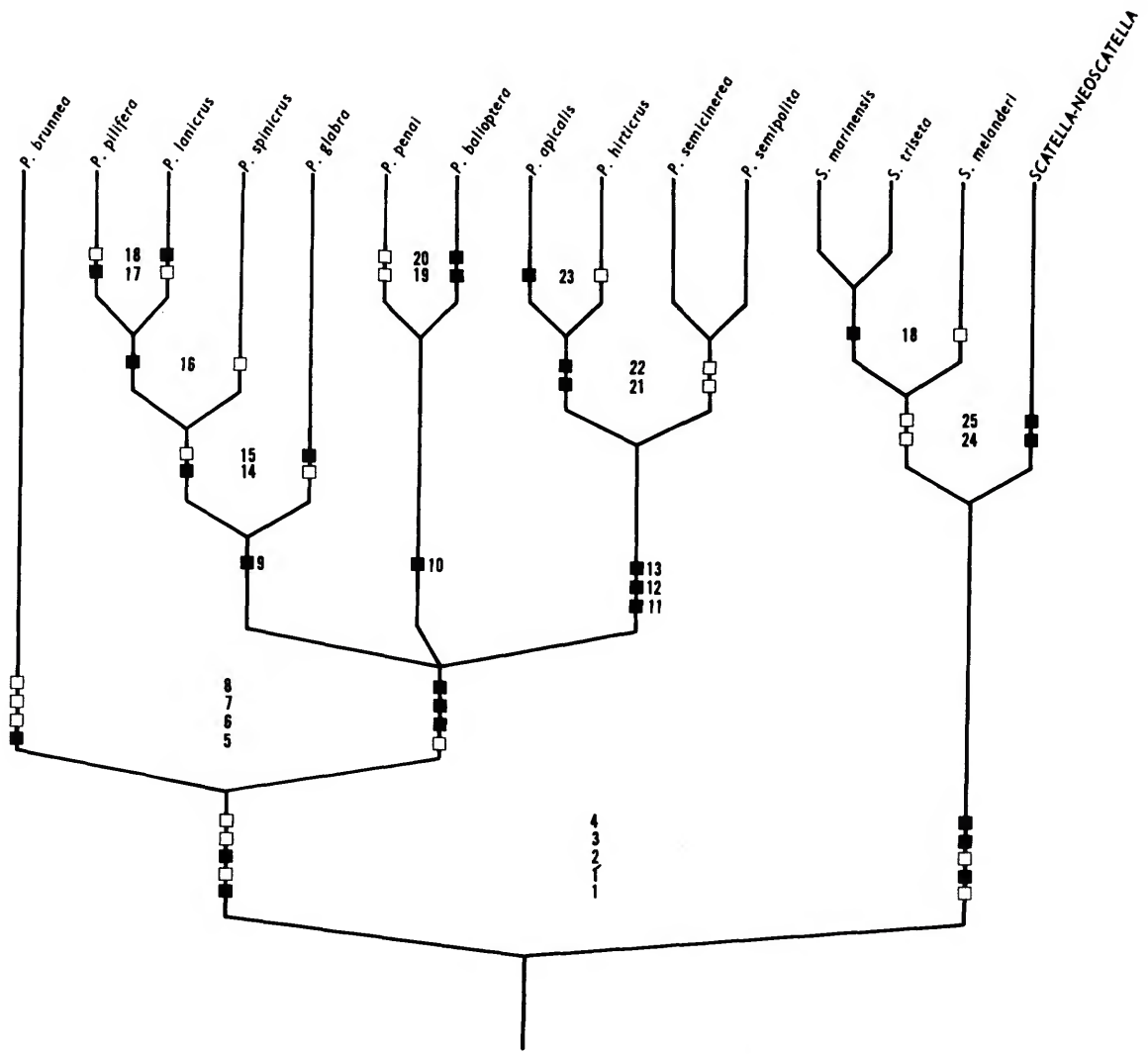


FIGURE 61.—Hypothetical phylogeny for the species-group and species of *Parascatella* and for the species of the *triseta* group of the genus *Scatella*, based on the character states outlined in Table 1. (Solid squares = apotypic character states; open squares = plesiotypic character states.)

acterization by apotypic character states, but the large size of specimens of these species may be synapotypic.

Because species of *Parascatella* reproduce sexually, speciation is likely to occur only when populations are isolated. Accordingly, where species are now sympatric, we assume that they were once disjunct and that the zone of overlap is secondary. Of the ten species presently comprising the *pilifera* group, eight frequent similar aquatic habitats in the provinces of Jujuy and Salta in northwestern Argentina and adjacent areas of Chile (Figure 62). It is not uncommon to collect several species, including sister species at the same locality. For example, the sister species *P. apicalis* and *P. hirticrus* are known from collection data to frequently

Character	Plesiotypic	Apotypic
1. Shape of aedeagal apodeme	crescent-shaped to triangular	obclavate with basal curve
1' " " " "	laterally flattened	dorsoventrally flattened
2. Setae along costal margin	all subequal in size	several interspersed spinelike setae
3. Surstyli	well developed, lobelike	fused indistinguishably to ventral margin of epandrium
4. Supra-alar seta	subequal to postalar seta	reduced, usually less than ½ length of postalar seta
5. Prescutellar acrostichal setae	weak if at all evident	well developed
6. Marginal facial setae extending from facial carina to posteroventral corner of face	2-3 very large setae	setae gradually enlarging
7. Lateral scutellar setae	2 large pairs	3 large pairs
8. Ocellar triangle	equilateral	isosceles
9. Setal comb along posteroventral margin of front femur	absent	present
10. Color of male abdomen	unicolorous	multicolorous
11. White spot in cell R_3 of male	small	large
12. Wing membrane color beyond spot of number 11	pale	dark
13. Size and pattern of wing spots	similar in both sexes	sexually dimorphic
14. Setal comb along anteroventral margin of front femur	absent	present
15. Body vestiture	pollinose	mostly shiny
16. Fringelike hair on ventral surface of front tarsi and tibial apex of male	absent	present
17. Facial carina	distinctly carinate	gently rounded
18. Facial coloration	unicolorous	bicolored
19. Maculation of wing	with normal pattern	with many additional spots
20. Male abdominal ratios	3rd and 4th segments subequal in length	4th segment much shorter than 3rd
21. Scutellar surface	slightly convex	flat
22. Scutellar coloration	concolorous with posterior portion of mesonotum	white pollinose
23. Wing vein R_{2+3} and R_{4+5}	straight	sinuate
24. Orientation of facial setae along margins toward posteroventral corners	ventrally curved or semi-porrect	distinctly dorsally curved
25. Acrostichal setae	2 rows extending to scutellum	usually lacking setae posterior of enlarged sutural pair

TABLE 1.—Plesiotypic and apotypic character states used in Figure 61

occur together. We can speculate, therefore, that during the recent past the parent populations of these two species were separated by a barrier, allowing differentiation (vicariance), and that the present extensions of their overlapping distributions developed subsequently (dispersal). During the differentiation of the *pilifera* group, these events apparently occurred repeatedly, some undoubtedly concurrently, to result in the speciation pattern now evident for the group.

According to Simpson (1975), the region now occupied by these species, the Altiplano, is "a broad relatively flat high plateau stretching from southern Peru to northern Argentina." The following historical description of the plateau, summarized largely from Simpson (1975), provides a basis for further discussion.

The plateau arose initially from the sea during the Cretaceous but remained low throughout much of the Tertiary. During the Miocene, the plateau was raised further, but not until the mid-Pliocene to possibly the Pleistocene did significant uplift occur. Deep surface deposits now covering the Altiplano are from lacustrine sediments that were

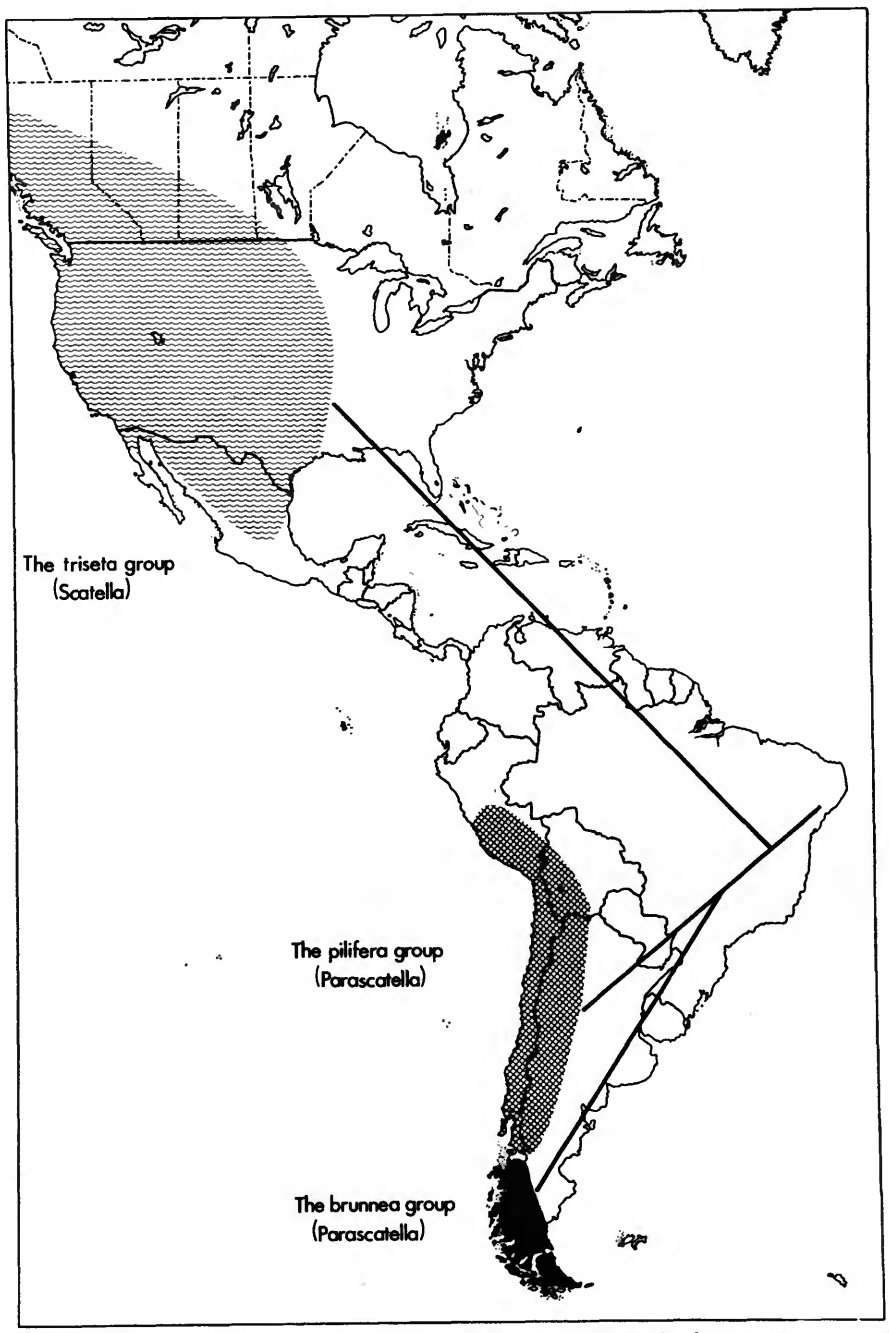


FIGURE 62.—Composite distribution of species-groups. (Stippling = the *brunnea* group; cross hatching = the *pilifera* group; wavy lines = the *triseta* group.)

probably deposited during the Pleistocene when large lakes covered the area. Today, the Altiplano is a dry, barren steppe with characteristic nonarborescent vegetation known as puna. There is, however, a slight but noticeable transition in the vegetation from open tussock grass shrubland in the dryer west to meadowlike grass scrub formations in the wetter east.

Despite the apparent uniformity of the area now, several studies (F. Vuilleumier, 1968, 1969, 1971) have documented the occurrence of many plant and animal genera with several sympatric species or taxa that have distributional boundries at the same specific localities within this region. Simpson (1975) suggested that during the recent past, populations of many taxa were isolated in at least three major areas and possibly several minor ones. The third major area Simpson discussed is located south of glacial Lago Michin, where the distributions of eight species of *Parascatella* appear to be centered (Figure 62).

During the Pleistocene, this area was subject to glacial climates (summarized in Vuilleumier, 1971) that lowered both the snowline and timberline and resulted in increased opportunities for migration and contact for organisms inhabiting high-altitude environments along the eastern and western slopes. During the interglacial periods, like the present, however, the climate was considerably dryer. Intermontane valleys lying in the rainshadow would act as barriers due to the drying up and partitioning of aquatic habitats. Ecological barriers as described coupled with physiographic ones, such as the paralleling mountain ranges of this region, would be particularly effective in isolating populations of aquatic organisms, such as *Parascatella* members.

Dating these events presents difficulties, especially as greater precision is sought. For our purposes, it is sufficient to establish rough estimates. Because the final uplift of the Altiplano dates to the end of the Tertiary, the age of the high plateau habitats and their endemic biotas is limited to the late Tertiary and Quaternary. From this, we suggest that the *pilifera* group arose and differentiated within the last ten million years.

The zoogeography of *Parascatella* can be explained satisfactorily by reference to Figure 62, without recourse to a complicated exposition. Perhaps this simple pattern is an artifact of our data base, our interpretation, or is due to the relative recency of the genus.

Evidence for our explanation is as follows. *Parascatella* is known to occur only along the western cordilleran system of South America below 10° south latitude, where present-day climatic conditions are temperate. The distribution of the genus is fairly continuous along this system, where they have apparently differentiated. Differentiation can be explained by vicariating events accompanying the changing geography and climate of the Altiplano during the ebb and flow of glaciation and the general uplift of the area in general.

We speculate that the ancestral stock, from which *Parascatella* arose, originated in South America. The South American fauna is by far more diverse (Wirth, 1968) and all genera closely related to *Parascatella* except *Apulvillus* are represented there. The latter genus probably arose more recently in the Pacific Islands.

Following differentiation of *Parascatella* from the ancestral lineage, which also gave rise to the *Scatella-Neoscatella* complex, two further radiations occurred, both in the Neotropics. The *brunnea* group, presently known from only *P. brunnea,* developed in the Tierra del Fuego region of the southern Andes. Radiation in the higher elevation habitats of the Andes Mountains produced most of the known species of *Parascatella.*

In summary, we suggest that *Parascatella* arose in South America from an ancestor that was common to it and to the genus *Scatella. Parascatella* then underwent two major radiations: the *brunnea* group developing in the Tierra del Fuego region and the *pilifera* group radiating in the Altiplano from southern Peru to northern Argentina and Chile.

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Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9b." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9b." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.