

Studies of Ephydrinae
(Diptera: Ephydriidae), III:
Revisions of Some Neotropical
Genera and Species

WAYNE N. MATHIS

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ABSTRACT

Mathis, Wayne N. Studies of Ephydrinae (Diptera: Ephydriidae), III: Revisions of Some Neotropical Genera and Species. *Smithsonian Contributions to Zoology*, number 303, 50 pages, 77 figures, 1980.—The systematics phylogeny, classification, and natural history of four genera, three subgenera, and one species of a fourth subgenus of Neotropical Scatellini are revised. Other taxa of Scatellini not known to occur in the Neotropics but whose status is altered as a consequence of this study are diagnosed and discussed. One new genus, *Notiocoenia*, and four new species, *Limnellia itatiaia*, *Notiocoenia acutella*, *N. paniculata*, and *N. pollinosa*, are described. *Calocoenia* Mathis is elevated to generic status as the sister group of *Paracoenia* Cresson, *Thiomyia* Wirth is relegated to subgeneric status as the sister group of *Paracoenia* sensu stricto, *Synhoplos* Lamb and *Teichomyza* Macquart are consigned to subgeneric status in *Scatella* Robineau-Desvoidy, and *Scatophila curtispennis* Becker is placed in the subgenus *Neoscatella* Malloch of *Scatella*. Keys to genera, subgenera, and species, illustrations, and distribution maps are provided.

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Studies of Ephydrinae (Diptera: Ephydridae), III: Revision of Some Neotropical Genera and Species

Wayne N. Mathis

Introduction

This study was undertaken to fulfill two primary objectives. The first, which prompted the study initially, was to revise the Neotropical species of several genera of the tribe Scatellini as part of my ongoing studies of the subfamily Ephydrinae. For the most part, these genera comprise few Neotropical species; many are endemics there; and as a tribe, they have not previously been studied together. There are no available keys, for example, to the known genera and subgenera, nor has a general synthesis been proposed to clarify the relationships among these genera. The second objective is to provide a framework indicating relationships among these taxa, particularly at the generic level. By a framework, I mean a hypothetical reconstruction of the sequence of cladogenetic events. To accomplish this, I have deliberately avoided any attempt to impose an hierarchy, except at the tribal level, that is based on convenience, preconceived notions, or precedent. Rather, I have attempted to unravel the sequence of speciation events from which extant species developed (Griffiths, 1974). To provide perspective for the latter endeavor, it has been necessary to discuss a few taxa that are not known to occur in the Neotropics. Where these taxa have required a change in status, particularly nomencla-

tural, these changes have also been included in the treatment.

The primary objectives, as outlined, are not mutually exclusive, but depend on each other, and I have attempted to treat them together. Their joint consideration, however, has led to uneven coverage of the taxa, which may be confusing without further explanation. Revised taxa are treated more comprehensively, to include complete generic and species descriptions, data on type material, and generally more detailed discussion sections. Extralimital taxa that are included only to facilitate changes I am proposing in the classification are accompanied with a diagnosis, to aid in their recognition, and a discussion section commensurate with any changes made and their implications.

Genera or subgenera that are revised are: *Austrocoenia* Wirth; *Limnellia* Malloch; *Notiocoenia*, new genus; *Paracoenia* (*Paracoenia*) Cresson; *Scatella* (*Synhoplos*) Lamb; *Scatella* (*Teichomyza*) Macquart. Genera, subgenera, or species that are included for changes in classification are: *Calocoenia* Mathis; *Paracoenia* (*Thiomyia*) Wirth; *Scatella* (*Neoscatella*) *curtipennis* (Becker). The geographic scope covered in this study is that used in the catalog of Neotropical Diptera (Papavero, 1966). Essentially, this is the Western Hemisphere south of the United States-Mexico border plus continental and adjacent oceanic islands.

The general methods used in this study were ex-

Wayne N. Mathis, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

plained in parts I and II of this series (Mathis and Shewell, 1978; Mathis, 1979). Except for chaetotaxy characters, I have generally described a feature from one side only. Abbreviations used in the text are those listed in the "Acknowledgments" section. All type specimens were examined except where I have otherwise indicated.

With revision of the genera treated herein and an earlier revision of *Parascatella* (Mathis and Shewell, 1978) all genera of Scatellini from the Neotropics except for *Scatella* and *Scatophila* will have been revised. Revisions of *Scatella* and *Scatophila* are being planned.

HISTORICAL REVIEW.—Relatively few studies have dealt with Neotropical Scatellini, making a review of past workers and their contributions straightforward and simple. Prior to Cresson's review of Ephydriidae (including Canacidae) of Patagonia and southern Chile in 1931, only four other authors treated Neotropical members of the tribe. Bigot (1887) described and figured *Scatella guttipennis* from Orange Bay, Tierra del Fuego. Bigot initially assigned this species to the genus *Palloptera*, but later, Edwards (1933) transferred that species to *Scatella*. Later, Williston (1896) described *Scatella obscura* as part of his faunistic study of the Diptera of St. Vincent Island. In this century, the first to treat Neotropical Scatellini was Becker (1906, 1919). In both of Becker's publications, each Neotropical species of the tribe Scatellini has required nomenclatural changes to correct errors. *Scatophila curtippennis* (Becker, 1906) is not a species of *Scatophila*, as was first pointed out by Wirth (1955); Ecuadorian specimens of *Lamproscatella sibilans* of Becker (1919) represent a species of the genus *Scatophila* (Mathis, 1979); and *Limmellia stenhammari* of Becker (1919), also from Ecuador, is probably conspecific with a new species being described below. In Cresson's report of Costa Rican shore flies (1918), he included three species in two genera of Scatellini. Each of these species was later found to be misidentified and to represent a species that was originally described from North American or European specimens by earlier authors (Wirth, 1968): (*Scatella stagnalis* of Cresson = *S. obscura* Williston; *Scatella nitidifrons* Cresson = *S. favillacea* Loew; and *Scatophila variabilis* of Cresson = *S. despecta* (Haliday)). Finally, Hendel (1930) described two species of the genus *Scatella*, *S. argentea* and *S. obscurella*. Both of Hendel's species remain in their original combination today.

Cresson's (1931) signal study on the shore fly fauna of Patagonia and southern Chile was the first contribution to treat comprehensively all taxa from a particular area of South America. Cresson provided a key to genera, included numerous shore fly species that had been described from other areas but which were discovered to occur in the Neotropics, and described 26 new species of which 12 are members of the tribe Scatellini. Until the present study, the only available generic key of Scatellini was Cresson's, even though numerous deficiencies are now apparent due to additions that have accrued during the last nearly 50 years.

Cresson (1934, 1935) continued his study of Neotropical Scatellini in two additional papers. *Scatella laetifica* and *S. notabilis* were described in 1934 from specimens collected in Buenos Aires. The following year, Cresson (1935) designated *Scatella pilifera* Cresson (Chile) as the type-species of *Parascatella*, a genus he erected in the same paper. Cresson also found that *Scatella laetifica* and *S. obscura* Williston were conspecific, the latter name being the senior synonym, and described *Scatophila parva* from specimens Mr. F. Edwards collected in Buenos Aires. For the next 20 years, no one published on Neotropical Scatellini.

From 1955 to 1970, Wirth contributed four papers that treated various aspects of Neotropical Scatellini. In 1955, Wirth wrote on the Ephydriidae of the Juan Fernandez Islands. In that paper and a later supplement (1957) Wirth described 20 new species in *Scatella* and two new species in *Scatophila*. Wirth's catalog, published in 1968, was the first for the Neotropical fauna of the family. Numerous additions to the fauna were incorporated, and many changes in nomenclature, synonymy, etc. brought the family into better perspective. Over 280 species in 63 genera were included, of which 50 species in 7 genera were listed under the tribe Scatellini. Two years later, Wirth (1970) described *Austrocoenia*, a new and apparently endemic genus from Patagonia.

Within this decade, Mathis (1975) revised *Paracoenia* Cresson, which included one species, *P. wirthi*, that ranges as far south as the Distrito Federal, Mexico. In 1978, Mathis and Shewell revised *Parascatella*, a genus presently known only from South America. They described 10 new species whose composite distribution is centered in the Andes Mountains of northern Chile and Argentina.

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based primarily on specimens in the National Museum of Natural History, numerous others were borrowed, particularly type specimens of previously described species. To my colleagues and their institutions, listed below, who loaned specimens, I express my sincere thanks. Without their cooperation this study could not have been completed.

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BMNH	British Museum (Natural History), London, England; Mr. Brian H. Cogan
CAS	California Academy of Sciences, San Francisco; Dr. Paul H. Arnaud, Jr.
CNC	Canadian National Collection, Entomology Research Institute, Ottawa, Canada; Mr. Guy E. Shewell and Dr. J. Richard Vockeroth
DEI	Deutsche Entomologische Institute, Eberswalde, Germany (DDR); Dr. Gunter Morge
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels; Dr. Georges Demoulin
MZUSP	Museu de Zoologia da Universidade de São Paulo, Brazil; Dr. Nelson Papavero
TUCU	Fundación Miguel Lillo, Tucumán, Argentina; Dr. Mercedes L. Grosso
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution

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Tribe SCATELLINI Wirth and Stone

SCATELLINI Wirth and Stone, 1956:466.

DIAGNOSIS.—Face (prefrons) generally protruding and broadly arched transversely; face setose, particularly along oral margin; at least 1 pair of latero-clinate fronto-orbital bristles; pulvilli well developed; tarsal claws of normal size, conspicuously curved.

DISCUSSION.—In the diagnosis above, I have characterized Scatellini to comply with Wirth and Stone's original diagnosis (diagnosis included in their generic key). With few exceptions, this concept of Scatellini also determined which genera were included in the recent catalogs (Wirth, 1965 (Nearctic), 1968 (Neotropical); Cogan and Wirth, 1977 (Oriental)). Thusly characterized, however, Scatellini is not a monophyletic group. The tribe Ephydrini, for example, is a monophyletic sister group of but one of the included clades of Scatellini (see "Phylogeny," p. 40). Nevertheless, I have not elected to alter the tribal classification here for two primary reasons. First, this paper reports a study of limited geographic scope, the Neotropical fauna, and is not intended to be comprehensive except for taxa known to occur in Middle and South America. Second, a generic and tribal study of Ephydrinae is now in progress. This latter study will be comprehensive, to include all known genera on a world basis.

The Neotropical fauna of Scatellini is by far the richest of the major zoogeographic regions with nearly 65 described species. Numerous undescribed species, particularly in the genera *Scatophila* and *Scatella* (*Scatella*) remain to be described in future revisionary studies.

Key to Genera of Scatellini

1. Paraverticlar seta large, bristlelike, at least one-third length of inner vertical bristle 2
Paraverticlar seta small, generally subequal to setae of postocular row 3
2. Acrostichal setae uniseriate, 4-6 irregular rows; scutellum with dorsum convex; middle femur of male with row of closely-set setae along posteroventral surface; radial stem vein with 1-2 setae above, inserted apicad of transverse septum *Paracoenia* Cresson
Acrostichal setae seriate into 2 rows; scutellum with dorsum subplanate and sparsely setose; middle femur of male lacking row of closely-set setae along posteroventral surface; radial stem vein bare above *Calocoenia* Mathis
3. Four to five pair of dorsocentral bristles (1 + 3; 2 + 3) 4
One to three pair of dorsocentral bristles (1 + 2; 0 + 2; 0 + 1) 6
4. Radial stem vein with 1-2 setae above, inserted apicad of transverse septum; scutellum with dorsum convex; tarsi explanate and densely pubescent; sternopleural bristle reduced or lacking *Paracoenia* Cresson

- Radial stem vein bare above; scutellum with dorsum subplanate; tarsi normal, cylindrical and at most sparsely pubescent; sternopleural bristle well developed5
5. Frons with coloration and vestiture generally uniform pollinose, dull; 1 pair of interalar bristles inserted just posterior of transverse suture.....*Notiocoenia*, new genus
Mesofrons generally distinct from parafrons, shinier, if indistinct, frons uniformly shiny; interalar bristles lacking*Coenia* Robineau-Desvoidy
6. One pair of large laterocline fronto-orbital bristles7
Two pair of large laterocline fronto-orbital bristles9
7. Wing stenopterous*Scatophila* Becker
Wing macropterous, normally developed8
8. Costal vein short, extending to vein R_{4+5} *Scatophila* Becker
Costal vein longer, extending to vein M_{1+2} *Limmellia* Malloch
9. Genal bristle either lacking or much reduced10
Genal bristle normally developed, subequal in length to fronto-orbital bristles13
10. Arista short, subequal to length of third antennal segment; mesofrons conspicuously setose; coloration mostly whitish gray to light brown*Austrocoenia* Wirth
Arista longer, nearly double length of third antennal segment; mesofrons mostly bare except for setulae along margin; coloration variable but generally dark11
11. Wing stenopterous*Amalopteryx* Eaton
Wing macropterous, normally developed12
12. Arista pectinate with dorsally branching rays*Philotelma* Becker
Arista at most macropubescent*Lamproscatella* Hendel
13. Arista short, subequal to length of third antennal segment; mesofrons conspicuously setose; coloration mostly whitish gray to light brown*Austrocoenia* Wirth
Arista longer, nearly double length of third antennal segment; mesofrons mostly bare except for setulae along margin; coloration variable but generally dark14
14. Supra-alar bristle reduced, one-half length of postalar bristle; aedeagal apodeme flattened dorsoventrally, frequently L-shaped; surstyli variously developed, if evident, fused to ventral margin of epandrium*Scatella* Robineau-Desvoidy
Supra-alar bristle subequal in length to postalar bristle; aedeagal apodeme flattened laterally; surstyli distinct as unfused setose lobes at venter of epandrium*Parascatella* Cresson

Genus *Austrocoenia* Wirth

Austrocoenia Wirth, 1970:3 [type-species: *Austrocoenia aczeli* Wirth, by original designation and monotypy].

DIAGNOSIS.—Specimens of *Austrocoenia* do not closely resemble those of any other genus of the tribe Scatellini and are easily distinguished by the following combination of character states: Setae generally reduced; mesofrons uniformly setose, completely pollinose, dull; 2 pair of large laterocline fronto-orbital bristles; inner and outer vertical bristles both well developed; paravertical bristles either reduced or absent; antenna short, third segment subequal to length of second segment from dorsal view; arista short, slightly longer than length of third segment, basal two-thirds thickened; antennal fovea deeply impressed, face long, distinctly protruding anteriorly; facial setae small, hairlike; eye subspherical, slightly higher than wide; gena mostly bare, high, eye-to-check ratio at least 1:0.60; genal bristle poorly developed; acrostichal setae seriated into 2 rows which extend

posteriorly to base of scutellum; 1 pair of large pre-scutellar acrostichal setae, inserted slightly laterad of other acrostichal setae; 1 pair of dorsocentral bristles inserted near base of scutellum and with 3-4 larger setae along dorsocentral tract; 1-2 pair of humeral bristles subequal to presutural bristle; supra-alar bristle either lacking or much reduced, hairlike; disc of scutellum bare; 2 pair of large lateral scutellar bristles; wing normally developed, mostly hyaline; costal margin with short spinelike setae; cercus of male elongate, fused ventrolaterally with epandrium; surstylus evidently fused with ventral margin of epandrium; gonite platelike; aedeagus greatly reduced; female ventral receptacle with operculum subtrapezoidal, asymmetrical, extending process more or less C-shaped.

DESCRIPTION.—Medium-sized to large shore flies, length 3.5 to 5.1 mm; coloration generally gray; wing mostly hyaline.

HEAD: Width greater than height in cephalic view. Frons dull, mostly pollinose, generally flat, anterior

portion of mesofrons convex, ocellar triangle and fronto-orbits slightly raised in relief from parafrons; shape of mesofrons subtriangular, anterior angle produced anteriorly, rounded, and broadly reaching ptilinal suture, lateral margins with scattered but conspicuous setae, approximately 8–10 on each side; 2 pair of larger laterocline fronto-orbital bristles, 8–11 smaller setae, frequently 1 larger pair of proclinate to laterocline setae anterior of larger bristles; 1 pair of ocellar bristles, divergent, 3–4 pair of smaller setae posterior of larger bristles; both inner and outer vertical bristles well developed, with posterior inclination; paraverticlar setae not evident; postocular setae becoming slightly larger toward vertex; ocelli arranged to form equilateral triangle. Antenna short, orientation generally lateral; third antennal segment with greatest width larger than its length; arista shorter than combined length of first 3 segments, thickened along basal three-fourths, apical one-fourth stylelike; second segment with small setae, generally inconspicuous, except for 1 larger dorsally erect seta inserted dorsally. Face protruding, broadly arched; generally setose but lacking larger marginal setae, none dorsally curved; interfoveal hump broadly formed dorsally but lacking a distinct dorsal crease; antennal fovea deeply impressed. Eye nearly round, bare. Parafacies with 3–5 prominent setae. Gena high, at least one-half eye height. Mouthparts generally retracted into oral cavity; clypeus exposed as a narrow transverse band.

Thorax: Relatively long and narrow; rather densely pollinose, appearing dull. Chaetotaxy of thorax as follows: Acrostichal setae seriated into 2 rows, setae becoming larger and rows slightly more divergent posteriorly, 1 pair of larger prescutellar setae; 2–5 large dorsocentral bristles but only last 2 pair obviously larger, postermost pair distinctly larger and slightly displaced laterally from alignment of others; interalar setae in a row, postermost seta largest; 2–4 humeral setae; 1 pair of presutural bristles, these not much larger than surrounding setae; a row of supra-alar setae, 2 posterior pair larger but neither greater than one-half length of postalar bristle that is well developed; 2 pair of lateral scutellar bristles, otherwise scutellum bare except for an apical pair of setae, these frequently cruciate; 2 pair of notopleural bristles, one near each ventral corner, remainder of notopleuron bare; 1 mesopleural bristle, inserted near middle along posterior margin, several scattered setae, particularly toward dorsal and posterior margins;

1 sternopleural bristle and a small row of setae just anterior of larger bristle. Wing mostly hyaline to very lightly milky; costal vein reaching tip of vein M_{1+2} ; coastal margin with several evenly spaced spinelike larger setae. Legs normally developed; tarsal claws moderately curved; pulvilli well developed.

Abdomen: Generally setose, setae along margins larger. Males with 5 visible segments, with fifth tergum longest, shape trapezoidal, broadly truncate posteriorly; females with 7. Male terminalia as in diagnosis.

GEOGRAPHIC DISTRIBUTION.—*Austrocoenia* is a monotypic genus that is endemic to southern South America, Patagonia, between 49° and 52° south latitude.

DISCUSSION.—*Austrocoenia* is an anomaly. Due to the autapotypic condition of most of its character states, I have not succeeded in discovering evidence that would indicate a phylogenetic relationship with other generic level taxa of Ephydrinae. I have tentatively placed it near the *Paracoenia-Calocoenia* lineage because adults have five pair of dorsocentral bristles. But even this character state is autapotypic, as the anterior pairs of bristles are reduced and are only slightly larger than surrounding setae.

Wirth (1970) was also perplexed by his new genus. He stated that although the *Austrocoenia* is clearly a member of the subfamily Ephydrinae,

... it is not closely allied with any known genus. It appears to be closest to *Coenia* Robineau-Desvoidy, a Holarctic genus, which it resembles to a slight extent in the presence of four pairs of dorsocentrals and curved tarsal claws. Otherwise, its similarities are diverse and rather remote . . . *Austrocoenia* is doubtless an annectant form surviving and modified from a very early offshoot of the Ephydrinae.

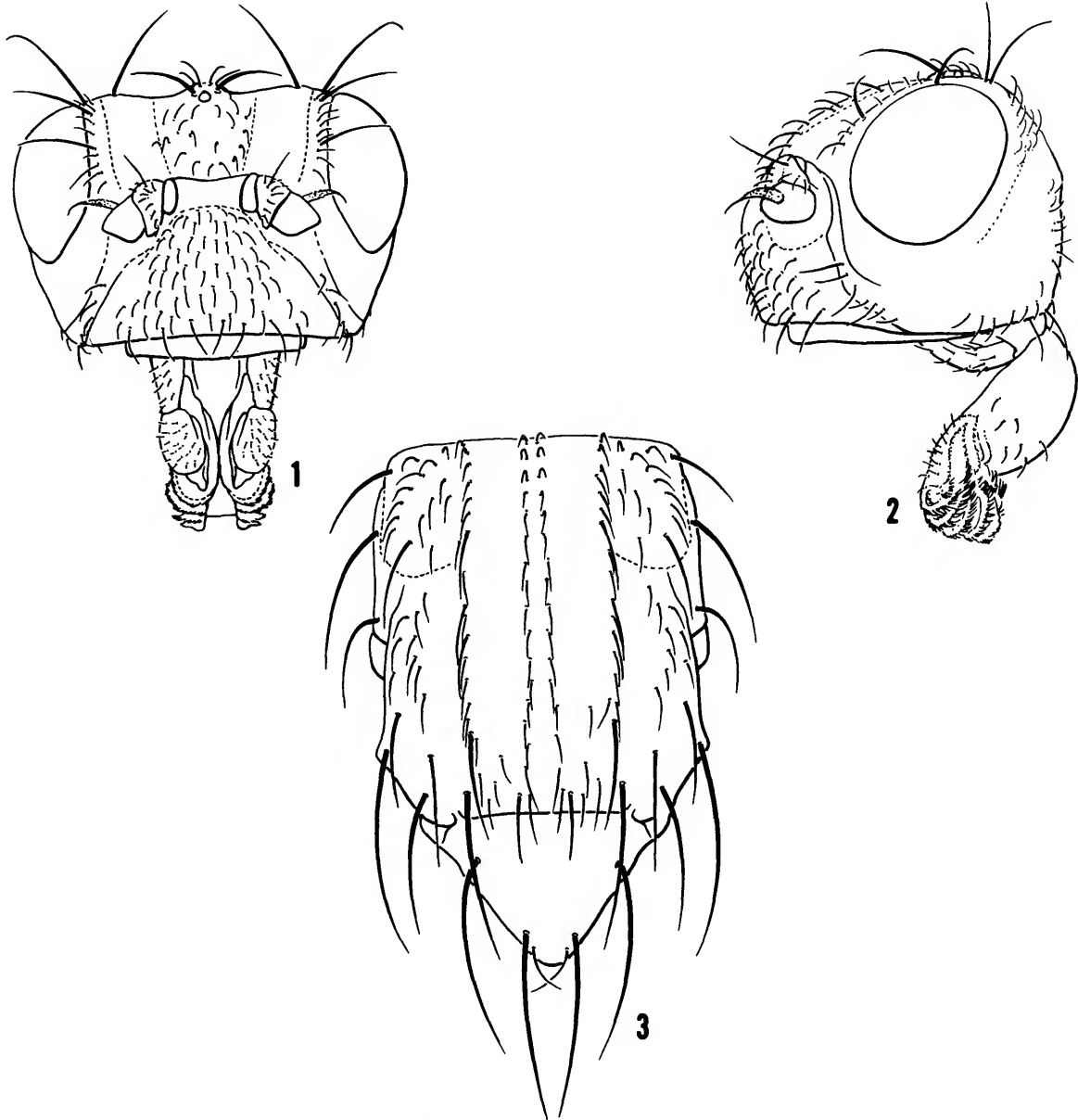
1. *Austrocoenia aczeli* Wirth

FIGURES 1–6

Austrocoenia aczeli Wirth, 1970:8

DIAGNOSIS.—Generally pollinose, whitish gray to gray but with some brown coloration dorsally; ocelli arranged in equilateral triangle; tarsi with venter yellowish, hind basitarsus mostly yellowish except for thin linear dorsal gray stripe; wing mostly hyaline, veins brown except for yellowish costa, subcosta, and basal portions of other veins; structures of male and female terminalia as in Figures 4–6.

DESCRIPTION.—Medium-sized to large shore flies, length 3.67 to 5.08 mm; generally gray.



FIGURES 1-3.—*Austrocoenia aczeli*: 1, head, anterior aspect; 2, head, lateral aspect; 3, thorax, dorsal aspect.

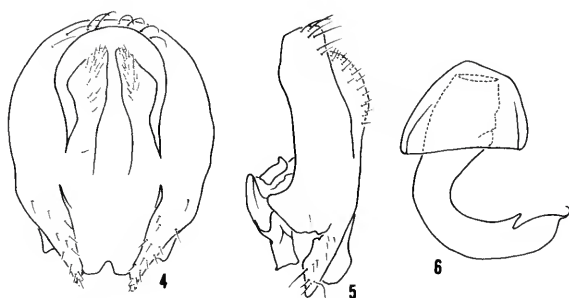
Head (Figures 1, 2): Head width-to-height ratio averaging 1:0.73. Mesofrons generally gray to grayish brown but frequently with some bluish, greenish, or charcoalish coloration immediately around ocelli;

parafrons generally darker in coloration than mesofrons, more bluish to charcoalish fronto-orbits nearly concolorous with mesofrons. Antenna mostly gray but with small patches blackish gray or whitish gray.

Facial unicolorous, whitish gray, becoming slightly darker dorsally. Eye-to-cheek ratio averaging 1:0.65. Gena concolorous with face. Maxillary palp blackish gray.

Thorax (Figure 3): Mesonotum dark bluish gray to whitish gray but mostly grayish brown to brown; 2 darker stripes on either side of acrostichal setae extending posteriorly no further than level of transverse suture; acrostichal track mostly brownish, frequently with whitish stripe between; scutellum with disc mostly grayish brown to brown; pleural areas distinctly lighter in color than mesonotum, becoming whitish gray to white ventrally. Femora and tibiae concolorous, whitish gray; basal 2 tarsomeres pale, rufous to yellowish orange; apical tarsomeres becoming darker, grayer. Wing (Figure 66) veins yellowish brown to yellowish anterobasally, otherwise brownish; membrane mostly hyaline, occasionally lightly infuscated, brownish, or slightly milky; costal vein index averaging 1:0.18; M_{1+2} vein index averaging 1:0.88. Halter yellowish.

Abdomen: Generally unicolorous, gray. Male and female terminalia as in generic diagnosis and Figures 4-6.



FIGURES 4-6.—*Austrocoenia aczeli*: 4, epandrium, cerci, and surstyli, posterior aspect; 5, male terminalia, lateral aspect; 6, female ventral receptacle, lateral aspect.

TYPE MATERIAL.—Holotype male, labeled: "[republica] A[rgentina]. SANTA CRUZ Cabo Buen Tiempo Gallegos 29-II-(1) 953 Coll: Biraben." Allotype female and 31 paratypes (7 ♂, 24 ♀; TUCU, BM(NH), USNM): with same label data as the holotype. The holotype, allotype, and several paratypes are in the Instituto Miguel Lillo, Tucumán, Argentina. The holotype specimen is double mounted (minute nadel in cork base) and is in good condition.

OTHER SPECIMENS EXAMINED.—ARGENTINA: Santa Cruz Province: Piedrabuena, 5 km NW, 130 m elevation, 25 Nov 1966, M. Irwin and E. I. Schlinger (11 ♂, 4 ♀; USNM). CHILE: Magallanes Province: Laguna Amarga, 4 km W, 51°00'S, 72°48'W, 300 m elevation, 7 Dec 1966, M. E. Irwin and E. I. Schlinger (1 ♀; USNM).

Genus *Calocoenia* Mathis, new status

Calocoenia Mathis, 1975:78 [type-species: *Paracoenia platypelta* Cresson, original designation and monotypy].

DIAGNOSIS.—Specimens of *Calocoenia* closely resemble those of *Paracoenia* but may be distinguished from the latter and other genera of Scatellini by the following combination of character states: Generally dark colored; mesofrons subshiny to shiny, inconspicuously setulose; 2 pair of large laterocline fronto-orbital bristles; inner and outer vertical bristles both well developed; paraverticilar seta well developed, about one-half length of cruciate vertical bristle; arista pectinatè, dorsally branching rays subequal to one-half width of third antennal segment; face with interfoveolar carina, but dorsal crease not as distinct as in specimens of *Paracoenia*; eye subspherical to subelliptical, oriented at slight oblique angle to general plane of head; acrostichal setae uniformly small, hair-like, seriated into 2 rows that extend to base of scutellum; 5 pair of dorsocentral bristles (2 + 3); humeral callus with 2-3 larger setae, bristlelike; supra-alar bristle well developed, subequal to anterolateral postalar bristle; scutellum setose dorsally, with 2 pair of lateral bristles; with dorsum subplanate; costal margin with evenly spaced spinelike setae distinct from remaining setae; radial stem vein bare; male fifth abdominal tergum slightly wider than long; terga generally unicolorous; surstylus as angulate processes extending from ventral margin of epandrium, contiguous medially; aedeagus well developed, acutely pointed apically; female ventral receptacle with small operculum, conformation subtrapezoidal in lateral view, extending process much longer than width of operculum.

DISCUSSION.—In 1975 I described *Calocoenia* as a subgenus of *Paracoenia*, but because I now show that *Calocoenia* is the sister group of the *Paracoenia-Thiomyia* lineage, it has been accorded generic status. As characterized, only two described species, each in a separate subgenus, are included: *Calocoenia* (*Calocoenia*) *platypelta* (Cresson), new combination;

and *Calocoenia* (*Leptocoenia*) *paurosoma* (Sturtevant and Wheeler), new combination. The evidence I used to establish the cladogram, which prompted the change in classification, is elaborated under "Phylogeny."

Genus *Paracoenia* Cresson

Paracoenia Cresson, 1935:356 [type-species: *Coenia bisetosa* Coquillett, by original designation].—Mathis, 1975:65–85 [review].

DIAGNOSIS.—Specimens of *Paracoenia* are similar to those of *Coenia* and *Notiocoenia* but may be distinguished from either by the following combination of character states: Generally dark colored, subshiny to shiny dorsally; mesofrons subshiny to shiny, contrasting distinctly with duller parafrons; 2 pair of large laterocline fronto-orbital bristles; inner and outer vertical bristles both well developed; paravertical seta well developed, about one-half length of cruciate vertical bristles; arista with pectinate, dorsally branching rays; eye subspherical to subelliptical, oriented at oblique angle to general plane of head, acrostichal setae uniformly small, hairlike uniseriate, 4–5 irregular rows; 4–5 pair or dorsocentral bristles (2 + 3; 2 + 2); humeral callus with 2–3 larger setae; supra-alar bristle variously developed; scutellum setose dorsally, with 2 pair of lateral bristles; wing normally developed; radial stem vein with setae inserted anterior of transverse septum; fifth abdominal tergum longer than either the third or fourth tergum; surstylus evident as lobelike ventral extension separated by a median triangular process; aedeagus well developed, acutely pointed apically; female ventral receptacle with operculum helmet-shaped, extending process short.

DESCRIPTION.—Moderately small to large shore flies, length 3.0 to 5.2 mm; generally dark colored, dull to shiny.

Head: Head wider than high in cephalic view. Frons rectangular, wider than long; mesofrons subtrapazoidal to subquadrate, if subtrapazoidal, narrower anteriorly, subshiny to shiny, setose, although setae mostly inconspicuous; parafrons and fronto-orbits mostly appearing dull, more pollinose, fronto-orbits slightly more subshiny; ocelli and to a less extent the fronto-orbits slightly raised in relief from level of mesofrons or parafrons. One pair of proclinate divergent ocellar bristles and 2–3 pair of divergent setae posterior of

larger bristles; 2 pair of large laterocline fronto-orbital bristles, several smaller, generally inconspicuous setae along fronto-orbits; 1 pair of well developed inner and outer vertical bristles; 1 pair of larger paravertical bristles, subequal to ocellar bristles; post-ocular setae becoming larger toward vertex, dorsalmost 1–2 pair distinctly larger; ocelli arranged to form equilateral triangle. Antenna brownish black to black, unicolorous; third segment densely pubescent to tomentose; second segment setose, particularly along median and ventral surfaces; arista variously developed. Face broadly arched, setose, setae along margins larger; interfoveal carina distinct with prominent dorsal crease, vestiture densely pollinose to tomentose, coloration mostly unicolorous. Eye obliquely oval to nearly round, bare. Gena high, eye-to-cheek ratio 1:0.22 or greater; generally setose and with 1 larger genal bristle; coloration generally concolorous with face. Mouthparts generally retracted into oral cavity; clypeus not exposed; prementum bulbous, setose; maxillary palp dark colored.

Thorax: Generally dark colored, dull to subshiny dorsally, becoming duller and lighter colored ventrally, particularly pleural areas. Mesonotum mostly unicolorous, dull, but becoming shinier posteriorly, some faint indications of vittae, especially anteriorly; scutellum convex, generally setose. Chaetotaxy of thorax as follows: Acrostichal setae uniformly sized, uniseriate 4–6 irregular rows; 4–5 pair of dorsocentral bristles (2 + 2; 2 + 3), postermost pair displaced laterally from alignment of others; 2–4 pair of humeral setae; 1 pair of presutural interalar bristles; supra-alar bristles variable, if present subequal to postalar bristles; 2 pair of postalar bristles, anterolateral pair stronger; 2 pair of lateral scutellar bristles; 2 pair of notopleural bristles, 1 pair near each ventral corner; 1 mesopleural bristle near middle along posterior margin, several scattered smaller setae toward dorsal and posterior margins, usually 1–2 larger setae next to larger bristle; sternopleural bristle variable, with some setae surrounding larger bristle or where larger bristle would be absent; middle coxa with 1 larger seta near middle. Wing nearly hyaline to infuscated; costal vein extending to tip of vein M_{1+2} ; radial stem vein with setae inserted anterior to transverse septum. Legs generally dark colored, shape and vestiture variable. Halter whitish yellow to brownish.

Abdomen: Generally more or less concolorous with posterior portion of thorax, particularly scutellum; setose, sometimes weakly so, setae toward margins

larger. Male and female terminalia as in diagnosis.

GEOGRAPHIC DISTRIBUTION.—*Paracoenia* occurs only in northern temperate region (Mathis, 1975). No species are known from the Afrotropical, Oriental, Australian, or Neotropical regions.

NATURAL HISTORY.—The algal herbivore *P. bisetosa* (Coquillett) is the only species of this genus whose life history, ecology, etc. has been studied extensively (Brock and Brock, 1968; Brock, et al, 1969; Wiegert and Mitchell, 1973; Collins, et al, 1976). Unfortunately, nearly all available information has been published under the name *P. turbida* (Curran). Although *P. turbida* does occur in Yellowstone National Park, which in fact is its type locality, *P. bisetosa* is more abundant there, and the voucher specimens I examined that were collected in conjunction with the research conducted at Yellowstone are of *P. bisetosa*. My recent revision of *Paracoenia* (Mathis, 1975) gives distinguishing character states for *P. turbida* and *P. bisetosa*.

DISCUSSION.—In 1975, when I reviewed *Paracoenia*, three subgenera were proposed for that genus, namely *Paracoenia* sensu stricto, *Calocoenia* Mathis,

and *Leptocoenia* Mathis. This study was completed and published before specimens of *Thiomyia* were available for study; consequently it was not considered. Since then, however, I have made detailed studies of *Thiomyia* and have concluded that *Thiomyia* and *Paracoenia* sensu stricto are sister groups. The evidence for this relationship is primarily from character states of the male and female terminalia and of the wing. Externally, the members of these two taxa are quite dissimilar and are easily identified. These differences, which for the most part are unique (apotypic), are attributed to anagenetic evolution occurring subsequent to the separation of the two groups. The many unique character states of *Paracoenia* sensu stricto or *Thiomyia* clearly establish their monophyly, and based on the number of synapotypies of both taxa, there is likewise little doubt regarding their sister group relationship. Because specimens of both taxa are quite distinct, I have given each group the rank of subgenus. As noted previously *Calocoenia* is elevated to generic status with *Calocoenia* sensu stricto and *Leptocoenia* as included subgenera. These relationships are diagrammed in Figure 77.

Key to Subgenera of *Paracoenia*

- Both supra-alar and sternopleural bristles either lacking or much reduced; middle femur of male lacking row of closely-set setae along posteroventral surface; apical 4 tarsomeres explanate and short; pulvilli lacking; third antenna segment short, less than length of second segment; general coloration black *Thiomyia* Wirth
- Both supra-alar and sternopleural bristles well developed; middle femur of male with row of closely-set setae along posteroventral surface; apical tarsomeres normally developed, cylindrical; pulvilli evident; third antennal segment longer than second; general coloration olivaceous gray to dark green or bluish green *Paracoenia* Cresson

Subgenus *Paracoenia* Cresson

DIAGNOSIS.—General body coloration olivaceous gray to dark green or bluish green; setae and bristles generally well developed; frons short, not projecting as far as face; antenna more slender, third segment longer than wide; arista with dorsal rays about equal in length to width of third antennal segment; face high, more than twice length of largest setae along oral margin; face generally and conspicuously setose; antennal fovea evident but not as deeply impressed; 5 pair of dorsocentral bristles (2 + 3); supra-alar bristle well developed, subequal to length of anterolateral postalar bristle; sternopleural bristle well developed; wing generally hyaline to very lightly infuscated; femora more swollen, nearly twice width

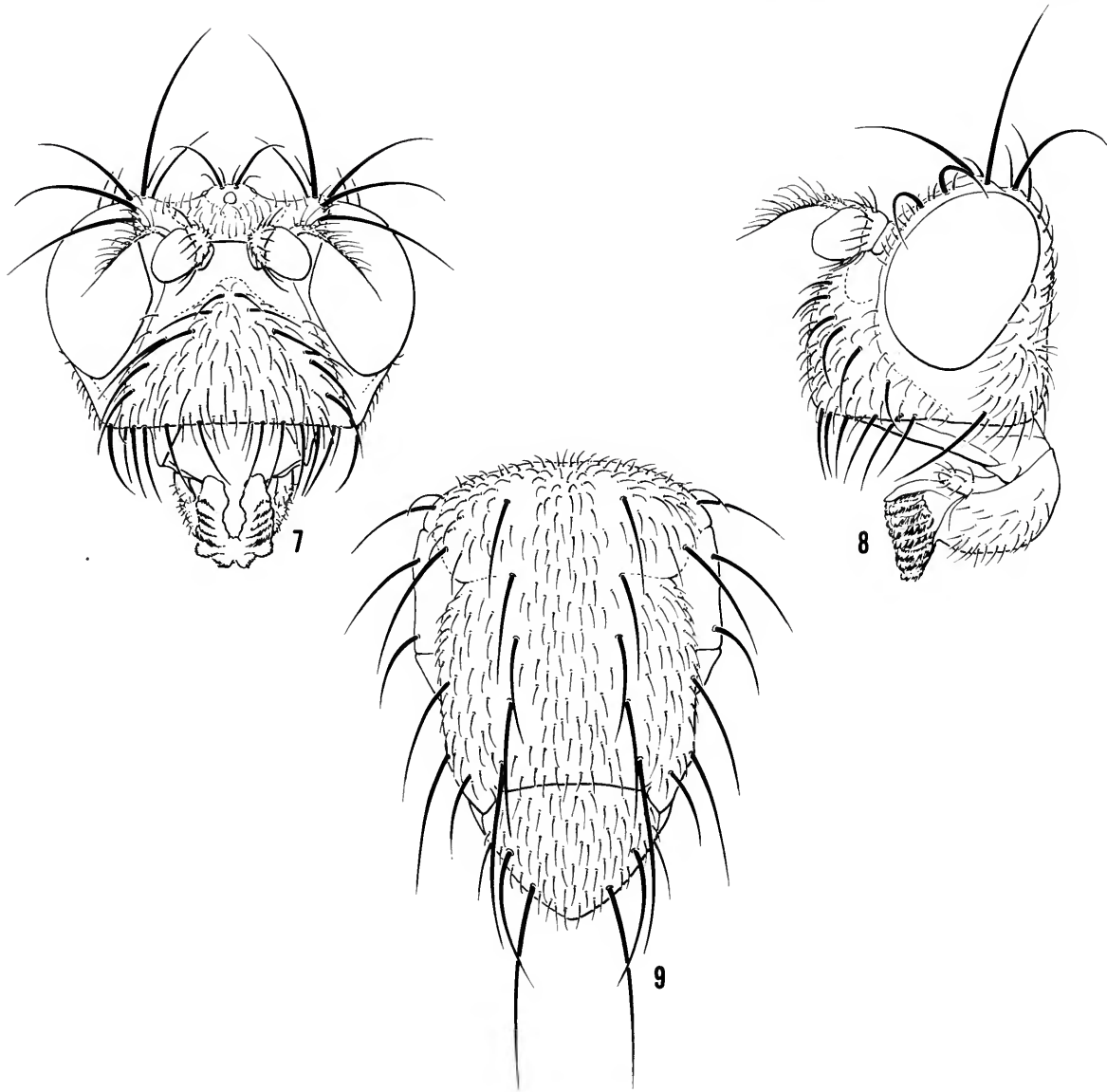
of tibiae; middle femur of male with comblike row of setae along posteroventral surface; tarsomeres normally developed, cylindrical, pulvilli evident, well developed; halter whitish yellow to yellow; abdominal terga wide, particularly second and third, each more than 3 times wider than long; fifth tergum of male generally with ventral prong oriented with general plane of body.

2. *Paracoenia (Paracoenia) wirthi* Mathis

FIGURES 7–14, 67

Paracoenia wirthi Mathis, 1975:78.

DIAGNOSIS.—Specimens of this species are similar to those of *P. bisetosa* (Coquillett) and *P. turbida* Curran but may be distinguished by the following

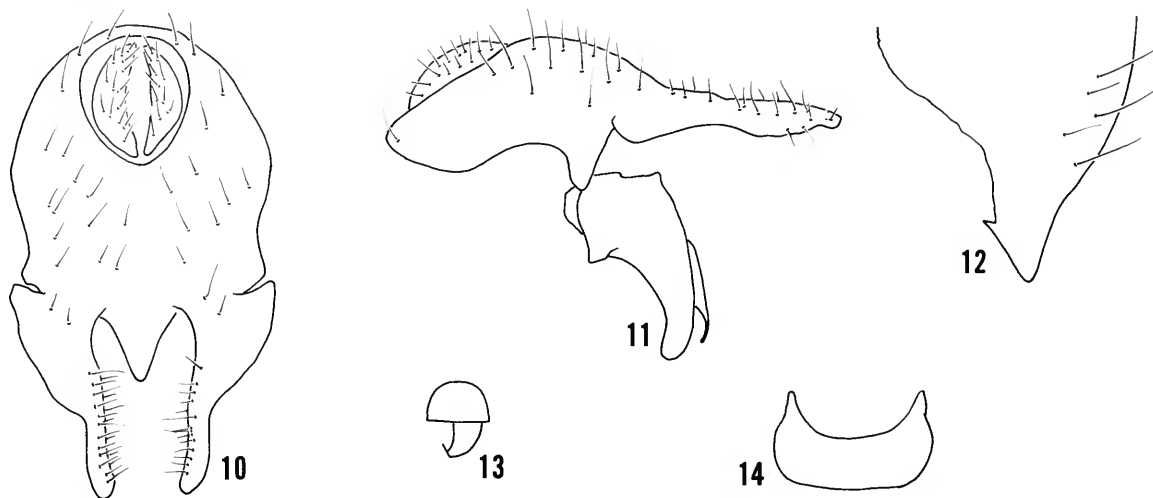


FIGURES 7-9.—*Paracoenia wirthi*: 7, head, anterior aspect; 8, head, lateral aspect; 9, thorax, dorsal aspect.

combination of character states: Specimens smaller and less setose than those of *P. bisetosa*; ventral margin of male fifth abdominal tergum produced into acutely pointed process; male fifth abdominal sternum broadly U-shaped, connecting portion wide; surstyli thickened along basal one-half; gonite with apex digitiform, broadly rounded.

DESCRIPTION.—Medium-sized shore flies, length 3.12 to 3.64 mm; subshiny with bluish green to green metallic luster.

Head (Figures 7, 8): Mesofrons greenish blue, shiny; face pollinose, grayish tan. Eye-to-cheek ratio averaging 1:0.22; Head width-to-height ratio averaging 1:0.6.



FIGURES 10-14.—*Paracoenia wirthi*: 10, epandrium, cerci, and surstyli, posterior aspect; 11, male terminalia, lateral aspect; 12, ventral apex of fifth tergum of male, ventral aspect; 13, female ventral receptacle, lateral aspect; 14, fourth sternum of male, ventral aspect.

Thorax (Figure 9): Acrostichal setae in 3-4 rows anteriorly, becoming irregular, 5-6 rows posteriorly. Pleural areas with more subdued coloration than mesonotum, most olivaceous gray. Wing (Figure 67) hyaline to lightly infumated.

Abdomen: Metallic luster green to olive green. Male terminalia as in diagnosis and Figures 10-12, 14.

TYPE MATERIAL.—Holotype male, labeled: "CALIF Inyo Co 1 mi N Tecopa Hot Spg 24 June 1974 Wayne N. Mathis." Allotype and 21 paratypes (7♂, 14♀; CAS, USNM): with same label data as the holotype. Other paratypes as listed in Mathis (1975:78). The holotype and allotype are in the California Academy of Sciences, San Francisco, California, type number 12033. The holotype specimen is double mounted (minute nadel) and is in good condition.

GEOGRAPHIC DISTRIBUTION.—This species occurs in the Sonoran desert from southern California and northern Baja California eastward to Arizona. Its extension south is known to reach the Distrito Federal (Mixquic), Mexico.

NATURAL HISTORY.—Like many *Paracoenia* species *P. wirthi* is sometimes associated with the effluent of hot springs, where the larvae feed on thermophilous

algae. The type-locality is a hot spring in southern California.

DISCUSSION.—This species is closely allied to *P. bisetosa* (Coquillett) and *P. turbida* (Curran) and is very similar to specimens of both species. Specimens are distinguished from either congener as outlined in the diagnosis, but since most of the distinguishing character states are for males only, unassociated females can only be tentatively identified.

Subgenus *Thiomyia* Wirth, new status

Thiomyia Wirth, 1954:196 [type-species: *Thiomyia quatei* Wirth, by original designation and monotypy].

DIAGNOSIS.—General body coloration dark blackish brown to black; setation generally weakly developed, particularly on abdomen; frons protruding anteriorly nearly to level of face; antenna short, third segment as wide as long; length of dorsal rays of arista short, approximately equal to one-half width of third antennal segment; face short, subequal to length of longer facial setae along oral margin; face with much longer setae along margin, remainder of face at most setulose; antennal fovea well developed, deeply impressed; 4-5 pair of dorsocentral bristles (2 + 2; 2 + 3); supra-alar bristle lacking or hairlike, sterno-

pleural bristle lacking; wing generally infuscated, brownish; femora slender, subequal to tibiae; middle femur of male lacking comblike row of setae along posteroventral surface; tarsomeres explanate and short; pulvilli lacking; halter brownish, abdominal terga narrower, width of second and third terga at most twice length; male fifth tergum with ventral margin lacking any pronglike process.

DISCUSSION.—I have changed the status of *Thiomyia* to the subgeneric level because it is the sister group of *Paracoenia* sensu stricto (see generic discussion and "Phylogeny," p. 40).

Wirth's (1954) description of *Thiomyia* also included figures and descriptions of the third instar larva and puparium. He also provided observations on the natural history of the only included species, *P. quatei* (Wirth).

Notiocoenia, new genus

TYPE-SPECIES.—*Notiocoenia paniculata* Mathis, new species, by present designation.

DIAGNOSIS.—Specimens of *Notiocoenia* are similar to those of *Coenia* Robineau-Desvoidy but are distinguished from the latter and other genera of Scatellini by the following combination of character states: Frons mostly unicolorous, vestiture uniform, dull, pollinose, lacking a distinctly colored mesofrons; 2 pair of large laterocline fronto-orbital bristles and 1 pair of much smaller procline setae anterior of larger bristles; paraverticilar bristle small, inconspicuous, none one-half length of vertical bristle; shape of eye subspherical, slightly higher than wide; gena short, eye-to-cheek ratio 1:0.20 or less; acrostichal setae seriated into 2 rows; 4 larger dorsocentral bristles (1 + 3), rarely with a fifth (2 + 3) bristle; 1 pair of interalar bristles inserted just posterior of transverse suture; wing normally developed, hyaline to lightly infuscated; male terminalia as in species-group diagnoses.

DESCRIPTION.—Small to moderately large shore flies, length 1.90 to 4.20 mm; mostly grayish brown to brown, generally appearing dull but subshiny to shiny over much of dorsum.

Head: Wider than high from cephalic views; frons mostly level and bare, wider than long, vestiture more or less uniform, dull, pollinose, coloration brown, margins of mesofrons indicated by shallowly impressed furrow, otherwise undifferentiated from parafrons;

ocelli arranged to form isosceles triangle, distance between posterior ocelli larger than distance between either posterior ocellus and median one; ocellar triangle only slightly raised in relief from level of mesofrons; 2 pair of large laterocline fronto-orbital bristles, some smaller setae, mostly inconspicuous, fronto-orbital setae; paraverticilar bristles small, subequal to postocular setae; 1 pair of slightly divergent well-developed ocellar bristles; 2-3 pair of small postocellar setae; inner vertical bristles well developed, outer vertical bristle variable. Antenna dark colored; third segment rounded apically, slightly longer than wide, tomentose to pubescent; second segment with several setae, especially along median and ventral surfaces; with one large, dorsally erect seta. Face protruding, broadly arched, setulose to setose; interfoveal carina evident but variously developed; vestiture densely pollinose. Eye slightly higher than wide but nearly round, bare; gena short, eye-to-cheek ratio 1:0.20 or less; 1 large genal bristle. Mouthparts generally retracted into oral opening, clypeus not exposed; maxillary palp dark; prementum longer than wide; pollinose to tomentose, setose.

Thorax: Vestiture variable, dull to shiny, generally becoming shinier posteriorly; coloration grayish brown to blackish brown. Pleural areas generally becoming lighter colored ventrally; humeral callus, part of mesopleuron, and sternopleuron grayish tan to whitish tan, otherwise pleural areas darker brown; front coxa gray to silvery gray, contrasting with remainder of pleural areas. Chaetotaxy of thorax as follows: Acrostichal setae seriated into 2 rows, larger setae mostly anterior of transverse suture; 4-5 pair of large dorsocentral bristles (1 + 3; 2 + 3), anterior 1-2 pair of bristles smaller, several smaller setae anterior of larger bristles; 1 pair of presutural interalar bristles; 1 pair of interalar bristles inserted just posterior of transverse suture; supra-alar bristle variable; postalar bristle well developed; 2 pair of lateral scutellar bristles; 2 pair of notopleural bristles, inserted near each ventral corner; 1 pair of mesopleural bristles, inserted near middle of posterior edge, numerous smaller setae, particularly toward dorsal and posterior margins; 1 pair of larger sternopleural bristles and 1-2 smaller setae around larger bristle; middle coxa with 1 larger bristle. Wing variable, mostly hyaline to lightly infuscated, generally lacking distinct pattern of spots. Legs variable, femora swollen to slender; coloration rufous to black. Halter yellowish to light brown.

Abdomen: Generally darker and shinier than thorax; otherwise quite variable, see species-group diagnoses.

GEOGRAPHIC DISTRIBUTION.—The composite distribution of this genus extends from 24° to over 53° south latitude along the east and west slopes of the Andes Mountains.

DISCUSSION.—Although the monophyly of *Notio-coenia* appears to be well established (Figure 76), its relationship within Scatellini is not as evident. In Figure 76, I have indicated a sister group relationship with *Coenia*, which I think is correct, but the evidence to support this alliance is not altogether convincing (character state number 9).

Key to Species-Groups and Species of *Notiocoenia*

- 1. Outer vertical bristle subequal to inner vertical bristle; supra-alar bristle either lacking or much reduced; arista at most macropubescent; humeral callus setose; wing appearing dull, lightly infuscated, 2 white spots on either side of posterior crossvein (the *pollinosa* group)5. *N. pollinosa*, new species
- Outer vertical bristle lacking; supra-alar bristle subequal to postalar bristle; arista micropectinate; wing appearing shiny, mostly hyaline, lacking white spots as above (the *paniculata* group)2
- 2. Male fourth abdominal sternum subrectangular, posterior margin truncate, setae at posterior margin slightly larger but not clumped; ventral margin of epandrium with conspicuous U-shaped median emargination in posterior view; aedeagus more slender and with more distinct taper toward apex; gonite with acutely pointed process posteriorly ... 3 *N. acutella*, new species
- Male fourth abdominal sternum pentagonal, posterior margin shallowly pointed, with distinct clump of 15 or more larger setae near apex; ventral margin of epandrium lacking U-shaped median emargination in posterior view; aedeagus with gradual taper throughout its length; gonite lacking pointed process along posterior margin 4 *N. paniculata*, new species

The *paniculata* Group

DIAGNOSIS.—Although similar to the *pollinosa* group, specimens of this species-group may be distinguished by the following combination of character states: Frons wider, width at level of median ocellus about 3 times distance between ptilinal suture and median ocellus; arrangement of ocelli nearly forming equilateral triangle, distance between posterior pair only slightly longer than between either posterior ocellus and median one; outer vertical bristle lacking; 1 pair of smaller proclinate fronto-orbital bristles inserted anterior of larger latero-clinate bristles, size about one-third larger bristles; arista pectinate with dorsal branches along basal two-thirds, longest rays subequal to one-half width of third antennal segment; interfoveal carina with distinct dorsal crease; face from oral margin to dorsum of interfoveal carina higher, length much longer than longest facial bristle along oral margin; coloration of face grayish brown to brown, not contrasting distinctly with coloration of frons; vestiture of mesonotum appearing duller, more densely pollinose, disc of scutellum much shinier;

larger acrostichal setae extending posteriorly beyond level of transverse suture; humeral callus completely bare; scutellum slightly convex, bare dorsally; 4 pair of dorsocentral bristles (1 + 3), anterior pair weaker; supra-alar bristle subequal to postalar bristle; coloration of pleural areas with contrasting brown and slightly brownish gray areas, especially evident on mesopleuron; wing appearing shiny, mostly hyaline but with slight brownish infuscation, posterior crossvein with darker brown infuscation; coloration of legs mostly rufous but variable; femora mostly subequal in size, slender; coloration of abdomen darker brown, with some bluish coloration, subshiny to shiny; fifth abdominal tergum short, approximately one-third length of fourth; surstylus of male terminalia lost or fused indistinguishably with ventral margin of epandrium; ventral margin of epandrium truncate; aedeagus a long slender tapering process, apex slightly corniform; female ventral receptacle with small operculum and large roughly C-shaped extending process in lateral view.

NATURAL HISTORY.—I have collected specimens of both described species of this species group from the

Lake District of southern Chile (Osorno Province). Although an occasional specimen was encountered in other habitats, most were collected at one site near Aguas Calientes, Parque Nacional Puyehue. This site was a densely shaded seepage area, approximately 2 by 10 m, alongside a narrow path used by grazing stock. A densely vegetated, steep bank paralleled its length to the south; the path marked its northern limit. The seepage area was muddy, highly organic, and relatively undisturbed. A dense overhang of brush from the adjacent bank shaded the area at all times and probably provided most of the organic debris. The brush also protected the area, acting as a barrier to stock animals. Most specimens were collected by sweeping under the overhang and just over the muddy seepage area. The surrounding vegetation was typical of a Southern Beech (*Nothofagus*) forest. The day on which I collected the majority of specimens, 8 February 1978, was overcast and with occasional light showers. Both species occur sympatrically at this locality.

3. *Notiocoenia acutella*, new species

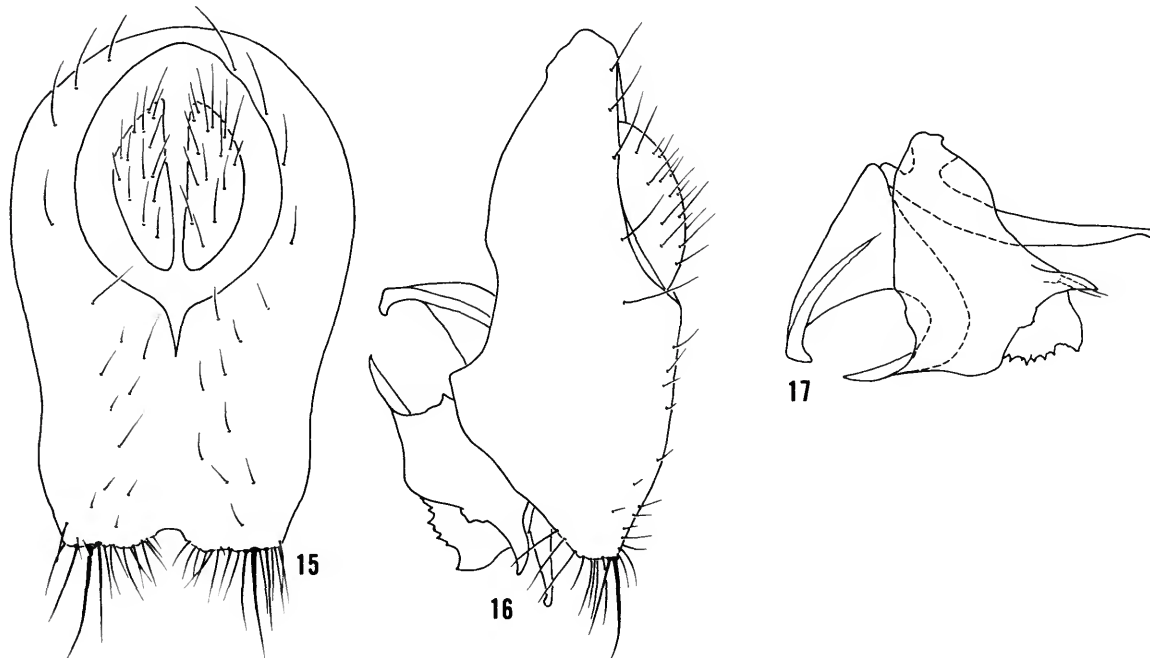
FIGURES 15–18

DIAGNOSIS.—Although very similar to specimens of *P. paniculata*, specimens of this species may be distinguished by the following character states of the male terminalia: Fourth abdominal sternum subrectangular, posterior margin truncate, setae at posterior margin slightly larger but not clumped; ventral margin of epandrium with conspicuous U-shaped median emargination in posterior aspect; aedeagus more slender and with more distinct taper toward apex; gonite with acutely pointed process posteriorly.

DESCRIPTION.—As in description of *N. paniculata* except as follows: Moderately small to medium-sized shore flies, length 2.78 to 3.93 mm.

Head: Eye-to-cheek ratio averaging 1:0.17; eye height-to-width ratio averaging 1:0.87.

Thorax: Legs tending to consistently be more yellowish orange, with little or no blackish coloration.



FIGURES 15–17.—*Notiocoenia acutella*: 15, epandrium and cerci, posterior aspect; 16, male terminalia, lateral aspect; internal male genitalia, lateral aspect.

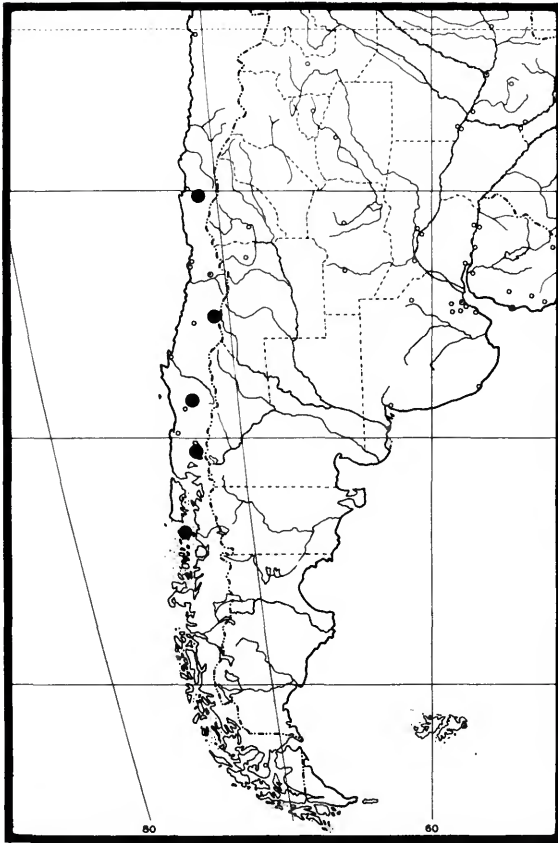


FIGURE 18.—Distribution map of *Notiocoenia acutella*.

Abdomen: Male terminalia as in diagnosis and Figures 15–17.

TYPE MATERIAL. — Holotype male, labeled: "CHILE: Osorno Prov. Aguas Calientes (1 km SE) 530 m. elev. 7–8 Feb. 1978 WNMathis/HOLOTYPE *Notiocoenia acutella* Mathis [handwritten, red]." Allotype female and 10 paratypes (6 ♂, 4 ♀; DEI), labeled: "Sud. Chile 14. 4. 40. (14 Apr 1940) Puerto Puyuguapi leg. G. H. Schwabe 201." Other paratypes as follows: CHILE: Coquimbo Province, El Pangue, 1 Nov 1954, P. G. Kuschel (1 ♂; USNM). Malleco Province, 16.1 km N of Perquenco, 1 Jun 1951, E. Ross and Michelbacher (1 ♂; CAS). Osorno Province, Anticura (1 km W) 430 m. elevation, 1–3 Feb 1978, W. N. Mathis (1 ♂; USNM). The holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., type number

76067. The holotype specimen is double mounted (minute nadel) and is in good condition.

GEOGRAPHIC DISTRIBUTION. (Figure 18).—This species is largely sympatric with *N. paniculata*, being known from the west slope of the Andes between 32° and 44° south latitude.

ETYMOLOGY.—The species epithet, *acutella*, is derived from the Latin *acutus* ("sharp"), referring to the sharp-pointed aedeagus.

4. *Notiocoenia paniculata*, new species

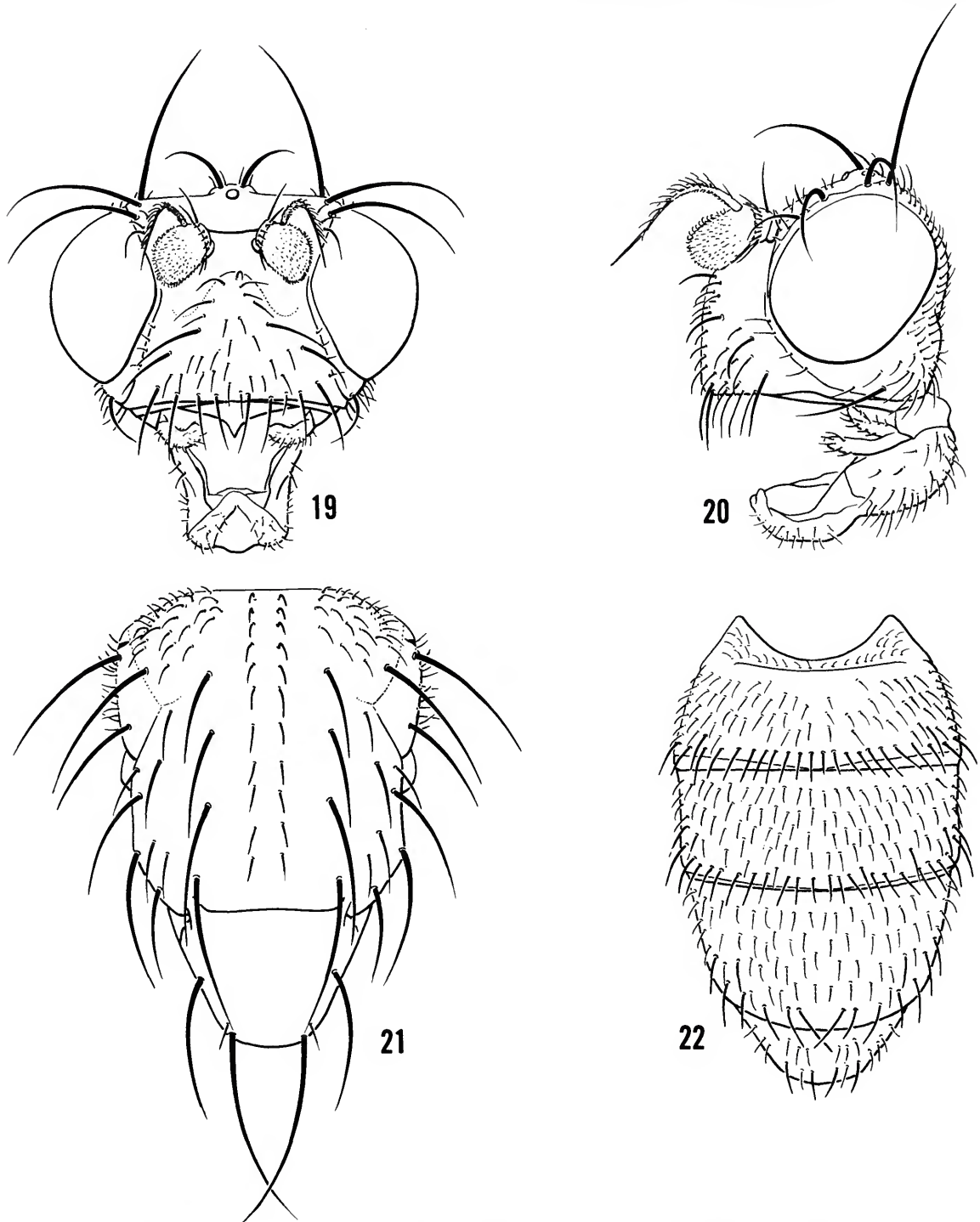
FIGURES 19–28, 68

DIAGNOSIS.—Specimens of this species very closely resemble those of *N. acutella*, and I can distinguish them confidently only by comparing structures of the male terminalia. The latter differ as follows: Fourth abdominal sternum pentagonal, posterior margin shallowly pointed and with distinct clump of 15 or more larger setae near apex; ventral margin of epandrium lacking U-shaped median emargination in posterior aspect; aedeagus with gradual taper throughout its length; gonite lacking pointed process along posterior margin.

DESCRIPTION.—Moderately small to moderately large shore flies, length 2.91 to 4.17 mm; appearing dull, pollinose; coloration mostly light brown to brown; wing hyaline.

Head (Figures 19, 20): Frons width-to-length ratio averaging 1:0.33; coloration of frons uniform, slightly charcoalish brown. Antenna mostly brownish black to black, third segment of some specimens with rufous coloration posteroventrally along median surface. Coloration of face nearly concolorous with mesonotum, slightly lighter brown than frons; antennal fovea more grayish and with some greenish tinges. Eye height-to-width ratio averaging 1:0.95; eye-to-cheek ratio averaging 1:0.19. Gena unicolorous, whitish gray.

Thorax (Figure 21): Mesonotum dull, rather densely pollinose, light brown anteriorly, becoming darker and shinier posteriorly, with a pair of whitish brown vittae laterad of acrostichal setae, extending posteriorly no further than transverse suture, distinctiveness of vittae variable. Scutellum subshiny to shiny, darker colored than mesonotum, more blackish. Pleural areas lighter brown than mesonotum, becoming generally lighter ventrally; humeral callus, pro-



FIGURES 19-22.—*Notiocoenia paniculata*: 19, head, anterior aspect; 20, head, lateral aspect; 21, thorax, dorsal aspect; 22, abdomen, dorsal aspect.

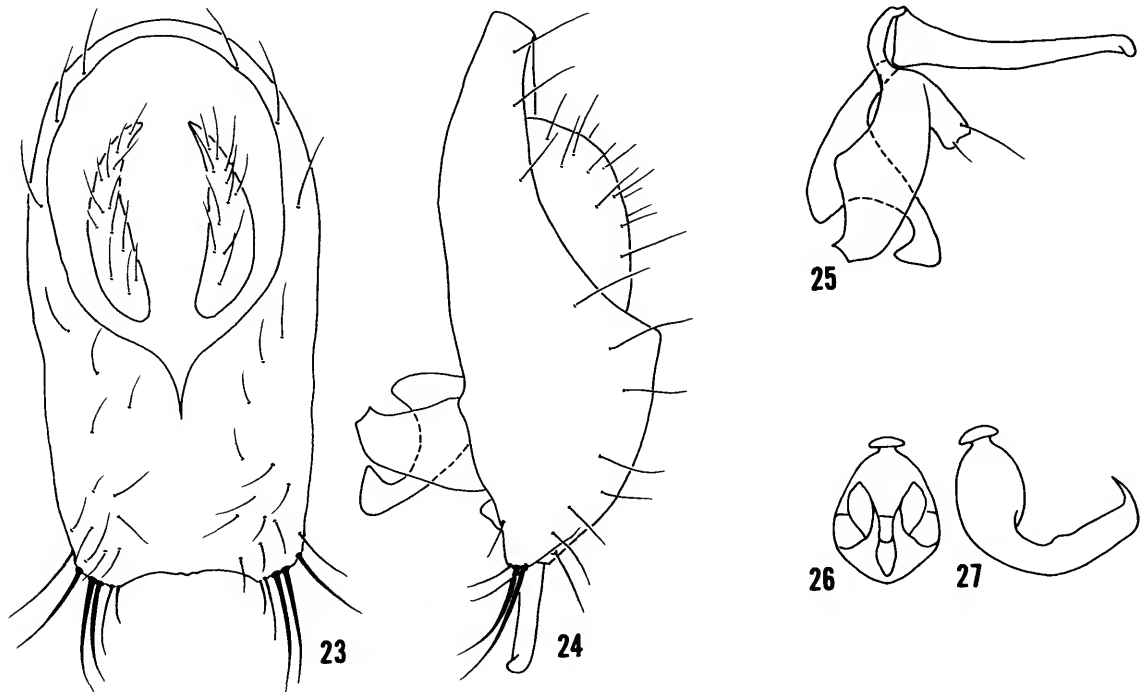
pleuron, part of mesopleuron, front coxa, and sternopleuron distinctly lighter colored, brownish gray to whitish gray, otherwise pleural areas mostly unicolorous, brown to light brown. Wing (Figure 68) mostly hyaline, shiny; slight infuscation anteriorly and particularly around posterior crossvein; costal vein index averaging 1:0.14; M_{1+2} vein index averaging 1:0.66. Legs rufous to orange, frequently with some infuscation; tarsi becoming darker, blackish, toward apical tarsomere. Halter yellowish to yellowish orange, unicolorous.

Abdomen (Figure 22): Coloration nearly unicolorous, brownish black with some bluish hues, subshiny to shiny. Male terminalia as in diagnosis and Figures 23–25; female ventral receptacle as in Figures 26, 27.

TYPE MATERIAL. — Holotype male, labeled: "CHILE: Osorno Prov. Aguas Calientes (1 km SE) 530 m. elev. 7–8 Feb. 1978 WNMathis/HOLOTYPE

Notiocoenia paniculata Mathis [handwritten, red]." Allotype female and 16 paratypes (4♂, 12♀; USNM): with same label data as the holotype. Other paratypes as follows: CHILE: Antofagasta Province: Rincon El Arbol, Oct. 1969, L. E. Peña (1♀; MZUSP). Concepción Province: Concepción, Parque Botanico Hualpen, Jan 1970, L. E. Peña (1♀; MZUSP). Coquimbo Province: Tilama, El Naranjo, Oct 1967, L. E. Peña (16♂, 22♀; MZUSP). The holotype, allotype, and paratypes from the type-locality are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., type 76068. The holotype specimen is double mounted (minute nadel) and is in good condition.

GEOGRAPHIC DISTRIBUTION. (Figure 28).—This species occurs along the western slope of the Andes, mostly in the foothills, between 24° and 41° south latitude.



FIGURES 23–27.—*Notiocoenia paniculata*: 23, epandrium and cerci, posterior aspect; 24, male terminalia, lateral aspect; 25, internal male genitalia, lateral aspect; 26, female ventral receptacle, anterior aspect; 27, female ventral receptacle, lateral aspect.

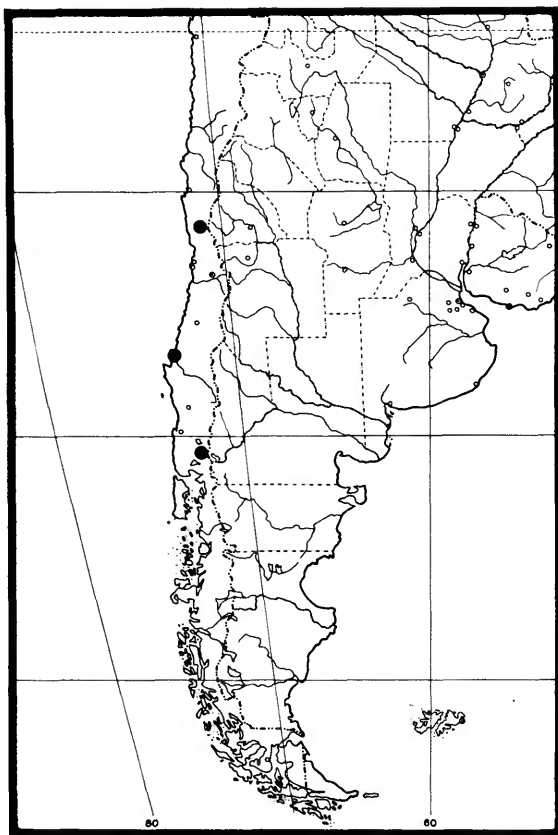


FIGURE 28.—Distribution map of *Notiocoenia paniculata*.

ETYMOLOGY.—The species epithet, *paniculata*, is the diminutive form of *panus* ("ear of millet"), referring to the tuft of setae on the fourth sternum of males.

The *pollinosa* Group

DIAGNOSIS.—Specimens of this species-group are similar to those of the *paniculata* group but may be distinguished by the following combination of character states: Frons narrower, width at level of median ocellus about 2 times distance between ptilinal suture and median ocellus; arrangement of ocelli distinctly forming isosceles triangle, distance between posterior pair much larger than between either posterior ocellus and median one; outer vertical bristle well developed, subequal to inner vertical bristle; smaller fronto-orbital setae much less than one-fourth larger latero-

clinate bristles, lacking a larger anterior pair of setae; arista macropubescent along most of length; interfoveal carina poorly developed, lacking a distinct dorsal crease; face between oral margin and dorsum of interfoveal carina shorter, length about equal to larger bristles along oral margin; coloration of face whitish gray, contrasting distinctly with brownish coloration of frons; mesonotum subshiny to shiny, pollinose vestiture sparse, not contrasting distinctly with appearance of scutellum; larger acrostichal setae not extending posteriorly much past level of transverse suture; humeral callus with 2–3 setae; scutellum flat and very sparsely setulose; 4–5 pair of dorsocentral bristles (1 + 3; 2 + 3); supra-alar bristle either lacking or much reduced; coloration of pleural areas becoming gradually grayer toward venter, but lacking patches of contrasting coloration; wing appearing dull, infuscated; 2 white spots on either side of posterior crossvein; legs black; front and hind femur swollen; coloration of abdomen blackish, shiny; fifth abdominal tergum as long or longer than fourth; male fourth tergum subequal to combined length of second and third terga; surstylus of male terminalia fused to ventral margin of epandrium but distinct, setose; aedeagus produced ventrally as 2 symmetrical narrow processes; gonite produced anteroventrally as curved parallel-sided slender process.

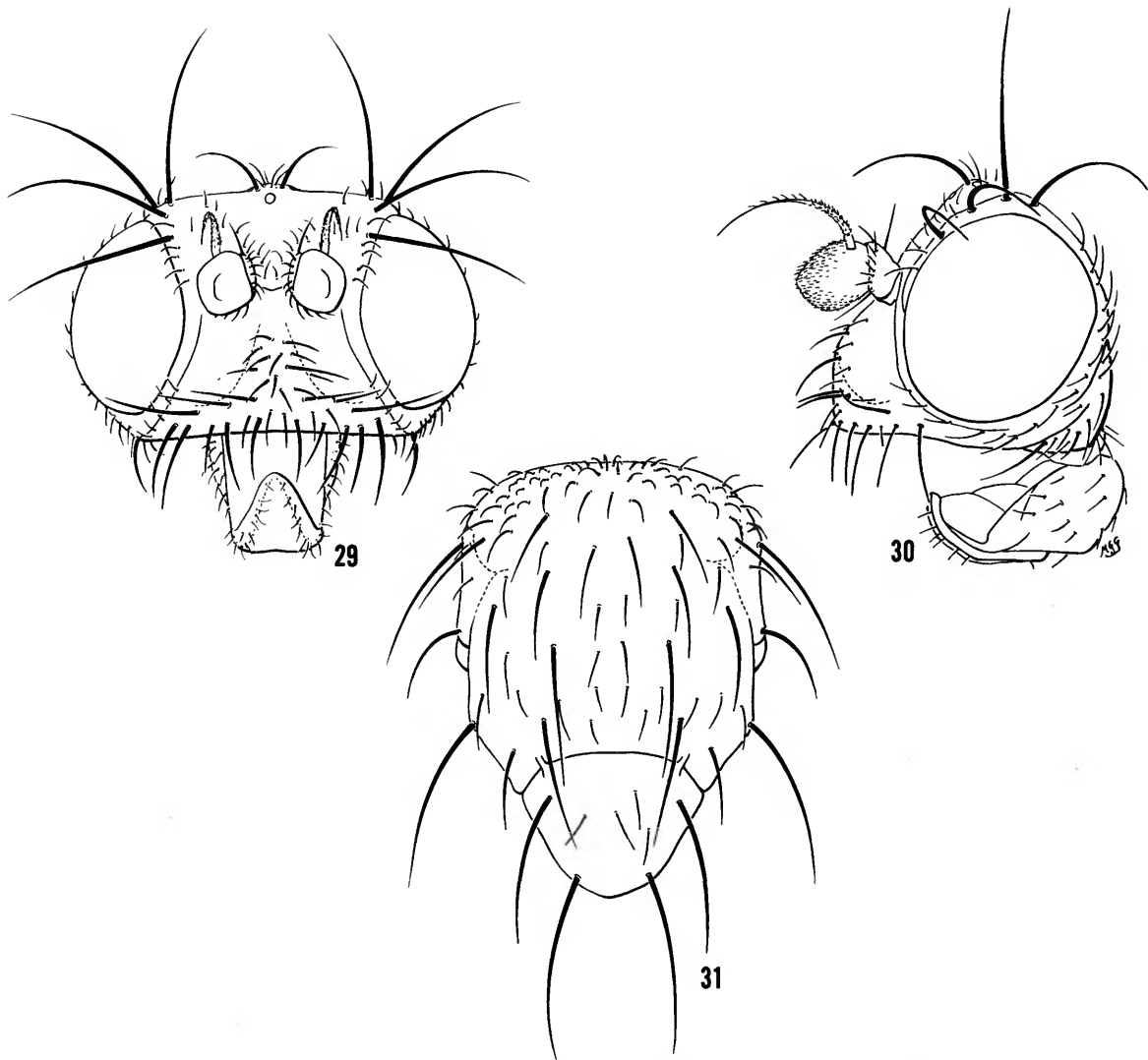
5. *Notiocoenia pollinosa*, new species

FIGURES 29–35, 69

DIAGNOSIS.—Because this is the only known species of the *pollinosa* group, the diagnosis of the latter, as cited previously, will adequately serve to distinguish specimens of this species. Should additional species of this species-group be discovered, character states of the male terminalia will undoubtedly distinguish them from the present species.

DESCRIPTION.—Small to moderately small shore flies, length 1.98 to 2.56 mm; generally shiny, dark brown dorsally.

Head (Figures 29, 30): Frons width-to-length ratio averaging 1:0.37; coloration of frons mostly light brown with some faintly olivaceous to greenish tinges. Antenna unicolorous, black. Coloration of face unicolorous, whitish gray to silvery gray; antennal fovea shallowly impressed. Eye height-to-width ratio averaging 1:0.87; eye-to-cheek ratio averaging 1:0.12; coloration of gena light brown; 1 large genal bristle.



FIGURES 29-31.—*Noticoenia pollinosa*: 29, head, anterior aspect; 30, head, lateral aspect; 31, thorax, dorsal aspect.

Thorax (Figure 31): Mesonotum and scutellum concolorous, shiny, bronzish brown, except extreme anterior margin of mesonotum dull, grayish. Pleural areas gradually becoming lighter brown ventrally, grayer, particularly front coxa and sternopleuron. Wing (Figure 69) lightly infuscated, light brown, appearing dull; with 2 white spots on either side of posterior crossvein; costal vein index averaging 1:

0.15; M_{1+2} vein index averaging 1:0.59. Legs unicolorous, black; front and hind femur appearing swollen. Halter brownish yellow, unicolorous.

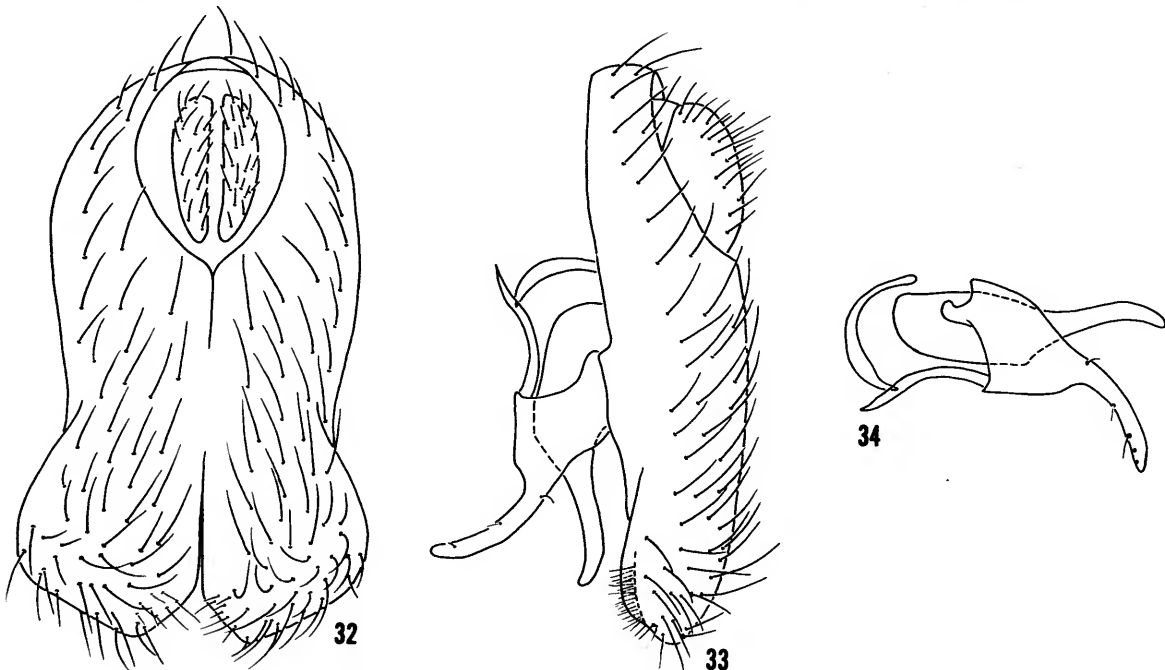
Abdomen: Subshiny anteriorly, becoming distinctly shiny posteriorly; coloration grayish black anteriorly, becoming very dark greenish black posteriorly; female terga becoming progressively longer posteriorly, also narrowing with gradual taper toward posterior end;

male fourth tergum subequal to combined length of second and third terga; male fifth tergum subtrapezoidal, bluntly rounded apically, length about equal to length of fourth tergum; male fourth tergum produced ventrally to acutely pointed apex; male fourth sternum subquadrate, becoming densely setose medio-posteriorly; male terminalia as in Figures 32-34.

TYPE MATERIAL.—Holotype male, labeled: "CHILE: Prov. Magallanes Rio Verde 12 Jan. 1966 Flint & Cekalovic/HOLOTYPE *Notiocoenia pollinosa* Mathis [handwritten, red]." Allotype female and four paratypes (2♂, 2♀; USNM), labeled: "CHILE Chanillo Esperanza 25-II-1962 T. Cekalovic." Other paratypes as follows: ARGENTINA: Rio Negro Province: Bariloche, Nov 1926, R. and E. Shannon (1♂; USNM); Llao Llao, 11.4 km E, 760 m elevation, 16 Nov 1966, M. E. Irwin and E. I. Schlinger (2♂, 3♀; CAS); Puerto Moreno, 3.7 km S, 800 m elevation, 17 Nov 1966, M. E. Irwin and E. I. Schlinger (1♀; CAS). Santa Cruz Province: Lago Argentino, 26 Feb 1953, Willink (1♂, 1♀; TUCU). CHILE: Aisen Province: Chile Chico, 4.8 km W,

400 m elevation, 22 Nov 1966, meadow association, M. E. Irwin and E. I. Schlinger (1♂, 1♀; CAS). Magallanes Province: Rio Verde, 12 Jan 1966, Flint and Cekalovic (1♂, 2♀; USNM); Rio Tres Brazos 9-13 Jan 1966, Flint and Cekalovic (4♀; USNM); Punta Arenas, 9-15 Jan 1966, Flint and Cekalovic, 22 Feb 1962, T. Cekalovic (3♀; USNM); Laguna Amarga, 4 km W, 7 Dec 1966 (50°59'S, 72°45' W), M. E. Irwin and E. I. Schlinger (4♂, 4♀; CAS); Laguna Amarga, 4 km W, 300 m elevation, 7 Dec 1966 (51°00' S, 72°48' W), M. E. Irwin and E. I. Schlinger (3♀; CAS); Laguna Azul, 1 Feb 1952, (2♂, 1♀; TUCU); Cerro Mina Rica, 13 Jan 1952 (1♀; TUCU); Dos Lagunas, 27 Jan 1957, T. Cekalovic (1♀; USNM). The holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., type number 76069. The holotype specimen is double mounted (glued to a paper point) and is in good condition, although both third antennal segments are missing.

GEOGRAPHIC DISTRIBUTION. (Figure 35).—*Notiocoenia pollinosa* occurs in southern South America



FIGURES 32-34.—*Notiocoenia pollinosa*: 32, epandrium and cerci, posterior aspect; 33, male terminalia, lateral aspect; 34, internal male genitalia, lateral aspect.

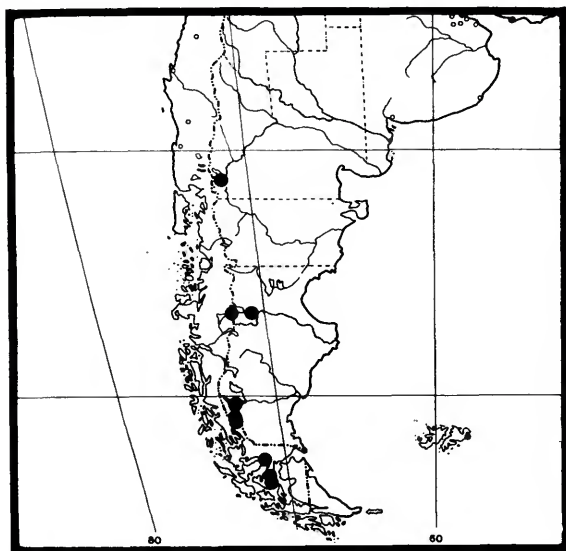


FIGURE 35.—Distribution map of *Notiocoenia pollinosa*.

along the Andes Mountains between 41° and 55° south latitude.

ETYMOLOGY.—The species epithet, *pollinosa*, is derived from the Latin *pollen* (“fine flour or meal”), referring to the pollinose vestiture of the frons in specimens of this species.

Genus *Limnellia* Malloch

Limnellia Malloch, 1925:331 [type-species: *Limnellia maculipennis* Malloch, by original designation and monotypy].—Anderson, 1971:53–59 [review of European species].—Mathis, 1978:250–293 [review of nearctic species].

Eustigoptera Cresson, 1930:126 [type-species: *Notiphila quadrata* Fallén, by original designation. Synonymy by Cresson, 1935:362].

Stictoscatella Collin, 1930:133 [type-species: *Notiphila quadrata* Fallén, by original designation; synonymy by Cresson, 1935:362].

Stranditela Duda, 1942:30 [as subgenus of *Scatella*; type-species: *Notiphila quadrata* Fallén, by original designation; synonymy by Dahl, 1959:126].

DIAGNOSIS.—Specimens of *Limnellia* are similar to those of *Scatophila* but are distinguished by the following combination of character states: One pair of large laterocline fronto-orbital bristles; inner and outer vertical bristles both well developed; paraverti-

cal bristles either reduced or absent; arista at most macropubescent; antennal fovea shallowly impressed; interfoveal carina not projecting or creased dorsally; facial setae mostly small, hairlike; eye nearly round; gena short; 1 genal bristle well developed; acrostichal setae uniform in size, small, seriated into 2 rows which extend posteriorly to base of scutellum; 2 pair of dorsocentral bristles (0 + 2); supra-alar bristle either reduced or lacking; disc of scutellum bare; 2 pair of large lateral scutellar bristles; wing maculate, mostly dark brown with white, generally guttate markings; abdominal terga black, becoming polished and shiny posteriorly; surstylus well developed as unfused processes at ventral margin of epandrium; aedeagal apodeme rudimentary.

DESCRIPTION.—Small to moderately small shore flies, length 1.24–2.47 mm; mostly dark brown to black, pollinose to shiny, frequently with cinerous guttate and vittate maculae; wings maculate.

Head: Wider than high from cephalic view; frons wider than long, vestiture more or less uniformly pollinose, dull, coloration varying, brown to charcoal brown, frequently with cinerous areas; mesofrons broadly triangular, narrowing anteriorly, forming an obtuse rounded angle, not differentiated from parafrons generally similar to mesofrons, occasionally slightly darker, more charcoal colored, narrowing posteriorly, forming an acute angle between convergence of fronto-orbital plate and mesofrons; fronto-orbital plate distinct only by differences in conformational relief, paralleling dorsal margin of eye. Ocelli arranged in equilateral triangle, on suboval plate which is slightly raised in relief. Two pairs of fronto-orbital bristles, anterior pair much smaller, proclinate; posterior pair of fronto-orbital bristles laterocline; 1 pair each of inner and outer vertical bristles, distance between them less than between inner vertical and postermost fronto-orbital bristle; 1 pair of large, proclinate, divergent ocellar bristles, insertions aligned with median margin of posterior ocelli; 1–2 pair of much smaller postocellar setae. Antenna generally dark, black, occasionally with pale areas; third segment macropubescent to tomentose, longer than combined length of first and second segments, broadly rounded apically; arista inserted dorsally near postero-dorsal corner of third segment, thickened basally, tapering gradually to stylelike tip, with short, micropectinate branching above. Face generally pollinose

to tomentose; antennal fovea shallowly impressed; interfoveal carina not projecting as in other Scatellini; portion of face below antennal fovea setose; with 2-3 pair of posterolaterocline, larger setae dorsally and several ventrocline setae along oral margin, these becoming larger toward lateral margins; 2-3 indistinct, small, parafacial setae. Eye nearly round, oriented at slight oblique angle to plane of epistoma, bare; gena very narrow, postgena widening setose, with 1 large bristle. Mouthparts generally retracted into oral opening, clypeus not exposed; maxillary palp dark colored; prementum longer than wide; pollinose to tomentose.

Thorax: Generally pollinose, dull, dark brown, with cinerous guttate or vittate maculae. Mesonotum dull to slightly subshiny, generally pollinose, anterior portion duller, more densely pollinose, usually with paired, guttate to vittate cinerous areas just laterad of acrostichal tract, cinerous color weakening abruptly to form a faintly, lighter colored vitta that gradually blends with surrounding color posteriorly; color of acrostichal track generally brown with distinct cinerous vitta developing posteriorly between setae, evident for about posterior two-thirds of mesonotal length, becoming stronger posteriorly; humeral callus cinerous dorsally, 1-2 pair of additional cinerous guttate to vittate areas laterad and paralleling dorsocentral tract; scutellum generally flat, subshiny. Chaetotaxy of thorax as follows: acrostichal setae arranged in 2 rows that extend to base of scutellum, no setae prominently larger than others; 2 pair of larger dorsocentral bristles (0 + 2) and 3-4 setae, especially anteriorly; postermost dorsocentral slightly displaced laterally; 1 pair of presutural bristles; 2 pair of notopleural bristles, both near ventral margin of notopleuron; 1 pair of posterior supra-alar bristles; 2 pair of lateral scutellar bristles, anterior pair less than one-third length of posterior pair; 1 pair of large mesopleural bristles near posterior margin at middle; 1 pair of sternopleural bristles; mesopleuron and sternopleuron usually more pollinose, cinerous for the most part. Legs generally dark, tending to be subshiny to shiny; femora and tibiae dark, brownish black to black; color of tarsi variable, apical tarsomeres generally dark regardless of color of basitarsi; front femur with row of setae along posteroventral margin; middle femur with row of setae along anterior surface, becom-

ing stronger apically. Prosternum bare. Wing maculate, mostly dark brown with white or hyaline markings, these mainly guttate; maculation pattern variable but generally recognizable for each species. Halter color variable, yellowish to dark brown.

Abdomen: Generally black, anterior terga with pollinose, brownish black vestiture, posterior segments becoming polished, shiny; both sexes with 5 terga exposed, occasionally females with posterior portion of sixth exposed; fifth tergum generally truncate posteriorly. Male terminalia as follows: symmetrical; surstylus well developed as unfused process at ventral margin of epandrium, shape of epandrium and surstylus diagnostic at species level; aedeagal apodeme generally reduced, broadly Y-shaped, with each arm attached to posterodorsal corners of aedeagus; gonite with larger process oriented ventrally and the second, smaller and thinner process more or less fused apically with similar process from opposite side, forming an irregularly shaped loop through which the aedeagus projects; aedeagus with sclerotized and membranous areas, usually longer than high, frequently with V-shaped notch dorsally.

GEOGRAPHIC DISTRIBUTION.—The genus occurs worldwide with the exception of the Arctic and Antarctic regions (Mathis, 1978). Eleven of the seventeen described species are from the New World.

NATURAL HISTORY.—Specimens are not generally found abundantly and no life history studies have been conducted for any species. Dahl (1959) stated that in Scandinavia, specimens of *L. stenhammari* exhibit weak xerophilous tendencies, preferring drier meadow and dune heath habitats. Sturtevant and Wheeler (1954) noted that *Limnellia* specimens are frequently collected from tree trunks and flowers. I have found adults by sweeping through emergent vegetation from wet meadow habitats and similar situations along lotic and lentic aquatic systems.

DISCUSSION.—In my revision of Nearctic species of *Limnellia* (Mathis, 1978), I included a world checklist of species, which then numbered 16, although I did not examine types of non-Nearctic species. With the description of *L. itatiaia*, the genus now numbers 17 species.

The sister group of *Limnellia* is *Scatophila* as demonstrated in my earlier revision (Mathis, 1978) and again in the "Phylogeny" section (p. 40).

Key to Neotropical *Limnellia*

- Tarsi mostly pale, yellowish, contrasting with darker tibiae; cell R_5 of wing with 2 brown spots closely appressed against vein R_{4+5} 6. *L. huachuca* Mathis
 Tarsi blackish brown, concolorous with tibiae; cell R_5 with 3 dark brown spots closely appressed against vein R_{4+5} 7. *L. itatiaia*, new species

6. *Limnellia huachuca* Mathis

FIGURES 36-39, 70

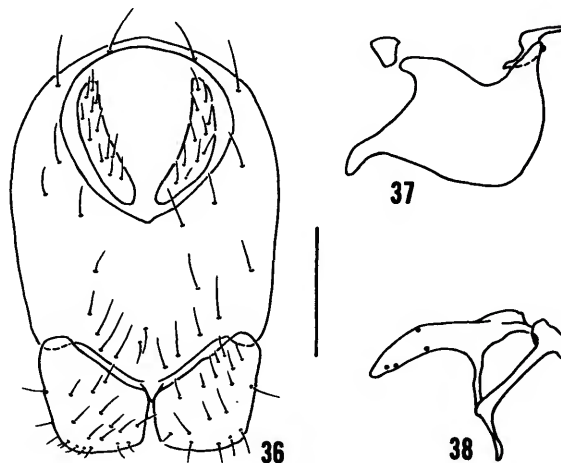
Limnellia huachuca Mathis, 1978:270.

DIAGNOSIS.—Specimens of *L. huachuca* are similar to those of *L. sejuncta* (Loew) and *L. turneri* Mathis but may be distinguished from them and other congeners by the following combination of character states: Setose portion of face mostly unicolorous; antennal fovea shallowly impressed; wing with 2 brown spots in cell R_5 , both closely appressed against vein R_{4+5} , neither spot much darker than brown coloration in remainder of cell; second basal white spot with large brown spot in center, sometimes brown spot with unicolorous pedicle reaching vein M_{1+2} ; halter mostly brown; tarsi mostly pale, yellowish; surstylus truncate ventrally, shape unevenly pentagonal, median surface shortest, lateral and mediodorsal surfaces longest.

DESCRIPTION.—Small shore flies, length 1.24 to 1.93 mm.

Head: Head width-to-height ratio averaging 1:0.62. Frons generally brown to charcoal brown; mesofrons with faintly evident, vertical, cinereous vitta; parafrons with anterior margin cinereous, becoming more brownish in color posteriorly. Face in profile nearly flat, very slightly arched; interfoveal carina not evident; antennal fovea evident but shallowly impressed; ventral margin of face slightly cinereous, remaining area brownish gray, becoming more cinereous dorsally, lacking distinct banding sequence. Eye height-to-width ratio averaging 1:0.83; eye-to-cheek ratio averaging 1:0.11.

Thorax: Basitarsi plus second and third tarsomeres pale, yellowish, contrasting distinctly with black tibiae. Maculation pattern of wing (Figure 70) as follows: cell R_1 with 6-7 white spots; cell R_3 with 4-5 white spots, frequently basal spot weakly developed; cell R_5 with 4 white spots, second basal white spot largest, with brown spot in center; discal cell with 3 white spots; cell M_2 with 2 white spots; cell M_4 with 2



FIGURES 36-38.—*Limnellia huachuca*: 36, epandrium, cerci, and surstyli, posterior aspect; 37, aedeagus, lateral aspect; 38, gonite, lateral aspect.

spots, one or the other frequently weakly developed. Wing length-to-width ratio averaging 1:0.46; costal vein index averaging 1:0.25; M_{1+2} vein index averaging 1:0.53. Halter brownish yellow.

Abdomen: Male terminalia (Figures 36-38) as follows: epandrium (Figure 36) in caudal view oval dorsally, becoming subtruncate ventrally, forming a broadly based triangular process between attachments of surstyli; surstylus truncate ventrally, quadrate except for lateral margin which extends dorsally further than median margin, setose; aedeagus (Figure 37) generally subquadrate but with extending anterior and posterior processes; aedeagal apodeme indistinguishable from aedeagus.

TYPE MATERIAL.—Holotype male, labeled: "Ramsey Cyn. 6000' 15 mi. S. Sierra Vista Huachuca Mts. ARIZ. Sternitsky 18. V. 67." Allotype female and 18 paratypes (9 ♂, 9 ♀; CNC, USNM): with same label data as the holotype except for dates, which are from 13 Apr to 13 Aug, 1967. Other paratypes as follows: Arizona: Cochise Co., Chiricahua Mountains (1 ♂, 2 ♀; USNM). The holotype, allotype, and



FIGURE 39.—Distribution map of *Limnellia huachuca*.

most of the paratypes are in the Canadian National Collection, Ottawa, Canada, type number 15433.

OTHER SPECIMENS EXAMINED.—COLOMBIA. Boyaca, Tunja, 2690 m elev., R. V. Ruiz (1♂; USNM). JAMAICA. Hardwar Gap, 10 Mar 1970, W. W. Wirth (1♂; USNM). MEXICO. Michoacan: El Pueblito, 9 Aug 1954, Rykman Christenson, light trap (1♀; USNM). PUERTO RICO. Yauco-Lares Road, km 22, 18 Jul 1953, J. A. Ramos and J. Maldonado (1♀; USNM). UNITED STATES: ARIZONA: Cochise Co., Herb Matyr Park (1♂; USNM); Pima Co., Greaterville (1♀; CAS).

GEOGRAPHIC DISTRIBUTION. (Figure 39).—Since discovering this species (Mathis, 1978), I have examined specimens from four countries in Middle or South America, and I suspect that additional localities beyond the presently known distribution will be discovered in South America. This is the only species known from the West Indies.

RELATIONSHIP.—*Limnellia huachuca* is apparently closely allied with *L. turneri*, a Nearctic species. The

surstyli of males of both species are wider than long, the conformation of the aedeagus of both is similar, and the whole genital complex of both is relatively small.

7. *Limnellia itatiaia*, new species

FIGURES 40–42

DIAGNOSIS.—Externally, specimens of this species appear similar to those of *L. stenhammari* but may be distinguished from the latter and other congeners by the following combination of character states: Coloration of setose portion of face mostly cinereous, some specimens with faintly evident brown transverse band toward ventral margin just dorsad of cinereous ventral margin; antennal fovea shallowly impressed; wing with 3 darker brown spots in cell R_5 closely appressed against vein R_{4+5} ; halter and tarsi dark brown; length of surstylus not greater than width;

more or less subtriangular, with ventrolateral surface shallowly emarginate.

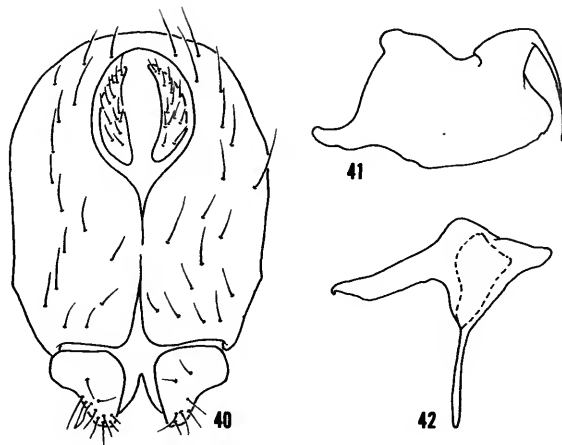
DESCRIPTION.—Small shore flies, length of allotype 1.72 mm (abdomen of holotype removed before it was measured).

Head: Head width-to-height ratio averaging 1:0.69. Frons mostly dark golden brown to blackish brown with faint metallic luster; parafrons wedge-shaped anteriorly, coloration gray to brownish gray; narrowly gray colored also along posterolateral margins of mesofrons. Face grayish to brownish, thin stripe along oral margin and to a lesser extent antennal fovea grayish, nearly flat, very slightly arched transversely; interfoveal carina brownish; interfoveal carina evident but not distinctly protruding; antennal fovea distinctly impressed but shallow. Eye height-to-width ratio averaging 1:0.91; eye-to-cheek ratio averaging 1:0.08.

Thorax: Legs entirely dark, blackish brown, unicolorous. Maculation pattern of wing as follows: Cell R_1 with 4–5 white spots, if apical one present not as evident; cell R_3 with 4 white spots, each well developed and evenly spaced along cell; cell R_5 with 5–6 poorly defined white spots, each small, apical ones frequently abutting; discal cell with 2–3 white spots, apical one better developed; cell M_2 with 2 white spots; cell M_4 with 2–3 white areas, generally guttate. Wing length-to-width ratio averaging 1:0.47; costal vein index averaging 1:0.22; M_{1+2} vein index averaging 1:0.72. Halter blackish.

Abdomen: Male terminalia (Figures 40–42) as follows: Epandrium (Figure 40) higher than wide in caudal view, rounded dorsally, more or less truncate ventrally; surstylus (Figure 40) subtriangular in caudal view, centrolateral margins emarginate, generally setose; aedeagus (Figure 41) in lateral view longer than wide, with shallowly V-shaped notch along dorsum; aedeagal apodeme attached to posterior portion of aedeagus and extending ventrally.

TYPE MATERIAL.—Holotype male, labeled: "Alto Itatiaia (Rio de Janeiro) Serra do Itatiaia S E Brazil Feb 21 1922/Alt 7150 [handwritten]/E G Holt Collector/HOLOTYPE *Limnellia itatiaia* Mathis [handwritten, red]." Allotype female, labeled: "S[ao]. PAULO Capital Forattini Col IV-60 [handwritten]/COLECAO J. LANE [black bordered pink label]/ALLOTYPE *Limnellia itatiaia* Mathis [handwritten, red]." The holotype is in the National Museum of Natural History, Smithsonian Institution, Washington,



FIGURES 40–42.—*Limnellia itatiaia*: 40, epandrium, cerci, and surstyli, posterior aspect; 41, aedeagus, lateral aspect; 42, gonite, lateral aspect.

D.C., type number 76066. The allotype is in the Museu de Zoologia da Universidade de São Paulo, Brazil. The holotype specimen is double mounted (glued to a paper point) and is in fair condition. One wing is missing, and the abdomen has been removed and dissected; the structures are in an attached microvial.

GEOGRAPHIC DISTRIBUTION.—This species is known only from the two localities from southeastern Brazil as listed previously.

RELATIONSHIP.—Because specimens of this species closely resemble those of *L. stenhammari*, I suspect that these two species are related, at least patristically.

DISCUSSION.—This species might possibly be the same that Becker (1919) reported from Ecuador. I have not examined the specimens Becker studied.

Genus *Scatella* Robineau-Desvoidy

Scatella Robineau-Desvoidy, 1830:801 [type-species: *Scatella buccata* Robineau-Desvoidy (= *Scatella stagnalis* (Fallén), by subsequent designation, Coquillett, 1910:603].—Cresson, 1931:108 [review of species from southern South America].—Wirth, 1955:55–68 [review of species from Juan Fernandez Islands]; 1957:403–408 [supplementary report on species from Juan Fernandez Islands]; 1968:24–26 [catalog].

DIAGNOSIS.—Specimens of *Scatella* are similar to those of *Parascatella* but may be distinguished from the latter or those of other genera of Scatellini by the

following combination of character states: Mesofrons dull to shiny, if subshiny or shiny, contrasting distinctly with duller more pollinose parafrons; 2 pair of large laterocline fronto-orbital bristles; inner and outer vertical bristles both well developed; paravertic bristles either reduced or absent; conformation and vestiture of antenna, arista, face, and eye various; genal bristle generally well developed; acrostichal setae seriated into 2 rows, frequently poorly developed or lacking posterior of transverse suture; 2-3 pair of dorsocentral bristles (0 + 2; 1 + 1; 1 + 2); 1-2 pair of humeral setae, frequently quite small, hairlike; supra-alar bristle either lacking or reduced, if evident, smaller than postalar bristle; wing variously developed, micropterous to normally developed, generally with pattern of white spots against infuscated brownish black background color, infuscation sometimes faintly developed; surstylus either appearing to be absent (probably fused indistinguishably to the ventral margin of the epandrium) or evident as fused epandrial lobes, generally setose; aedeagal apodeme attached to aedeagus only, attachment to hypandrium lost, conformation flattened dorsoventrally and frequently L-shaped, angle sometimes quite obtuse; gonite with ventral and anterior projection, anterior projections from each side united anteriorly to form a loop through which the aedeagus can project, ventral projections generally acutely corniform.

Discussion.—I have broadened the concept of

Scatella to include a number of taxa as subgenera that had been given generic status previously. Included are: *Teichomyza* Macquart, *Synhoplos* Lamb, *Neoscatella* Malloch, and *Apulvillus* Malloch. This might appear to be a brash departure, particularly in view of the divergent nature of some external characters within *Synhoplos* and *Teichomyza*. When the male terminalia are examined carefully, however, it is quite evident that all of the taxa listed are closely related. In fact, I have some reservations regarding the merits of even subgeneric status for *Neoscatella* and possibly *Apulvillus*. In the case of *Neoscatella*, the only distinguishing character state is the presence of an antesutural dorsocentral bristle, a plesiotypic character state that renders the whole concept of *Neoscatella* to ambiguity with regard to its monophyly. It is a convenient character for separating a large assemblage of species, however, and has merit on that basis.

The principal character state for recognizing *Scatella* is in the male terminalia. The aedeagal apodeme has only one point of attachment or articulation, that with the base of the aedeagus, and it is dorsoventrally flattened and generally angulate. The degree of angulation is subject to considerable variation, and the shape ranges from distinctly L-shaped to nearly flat. A second character state is the reduced or absent supra-alar bristle. Both of these character states are apotypic to this lineage and indicate its monophyly.

Key to Subgenera of *Scatella*

1. Two pair of larger dorsocentral bristles (0 + 2), anterior bristle posterior of transverse suture 2
Two to three pair of larger dorsocentral bristles (1 + 1; 1 + 2), anterior bristle antesutural 3
2. Wing lightly infuscated, light brown, but lacking pattern of white spots; dorsum of scutellum setose, more so toward lateral margins; middle coxa with row of long setae along anteroventral surface; male middle femur with row of 7-10 long stout setae near middle of posteroventral surface, setae longer than width of femur *Teichomyza* Macquart
Wing generally darkly infuscated and with evident pattern of white spots; dorsum of scutellum bare; setae of middle coxa shorter; male middle femur lacking row of setae as above *Scatella* Robineau-Desvoidy
3. Wing micropterous, subequal to length of hind basitarsus; second antennal segment with spinelike, dorsal seta subequal to length of arista *Synhoplos* Lamb
Wing stenopterous to macropterous, if reduced, much longer than length of hind basitarsus; seta of second antennal segment, if present, much shorter, not more than one-half length of arista 4
4. Pulvilli rudimentary or lacking; tarsal claws large *Apulvillus* Malloch
Pulvilli evident, normally developed; tarsal claws of normal size *Neoscatella* Malloch

Subgenus *Neoscatella* Malloch

Neoscatella Malloch, 1933:9 [type-species: *Neoscatella atra* Malloch, by original designation and monotypy].—Cresson, 1935:360 [transferring previously described species to *Neoscatella*].—Wirth, 1948:281 [review]; 1968:26 [catalog citation].

Scatella (*Neoscatella*).—Sturtevant and Wheeler, 1954:174.

DIAGNOSIS.—Specimens of *Neoscatella* are similar to those of *Scatella*, sensu stricto, but may be distinguished from the latter and other subgenera of *Scatella* by the following combination of character states: Frons nearly flat, fronto-orbits and ocellar triangle only slightly raised in relief from mesofrons; mesofrons generally subshiny, at least partially so, remaining area of frons mostly pollinose, appearing dull; largest dorsal seta of second antennal segment not more than one-half length of arista; face with interfoveal carina only moderately well developed, dorsal crease present but not conspicuously evident; antennal fovea shallowly impressed; marginal facial setae larger than anteromedian ones but not stoutly developed; eye subglobose, about as wide as high, bare; gena moderately high, about one-fourth to one-third eye height; mesonotum moderately arched to arched; acrostichal setae seriated into 2 rows, generally not extending posteriorly past level of transverse suture, 1 pair at level of transverse suture well developed, bristlelike; 3 pair of dorsocentral bristles (1 + 2); humeral callus nearly bare except for 1–2 smaller setae; scutellum as long as wide, bare dorsally, with 2 pair of lateral bristles; wing normally developed to stenopterous, if normally developed, with pattern of white spots against infuscated background; legs normal, femora not unusually turgid.

DISCUSSION.—*Neoscatella* includes about 25 described species whose composite distribution comprises most of the world except for the Oriental, eastern Palearctic, and Antarctic regions. Ten of these species were described from the Hawaiian Islands (Wirth, 1948).

I have not discovered an apotypic character state to establish the monophyly of this subgenus, and it could be paraphyletic.

8. *Scatella* (*Neoscatella*) *curtipennis* (Becker), new combination

FIGURES 43–47, 71

Scatophila curtipennis Becker, 1905b:192; 1906:73 [verbatim repeat of original description].—Bezzi, 1916:177

[list].—Cresson, 1931:86 [discussion].—Wirth, 1955:56 [discussion]; 1968:27 [catalog citation].—Hackman, 1964:81 [discussion].

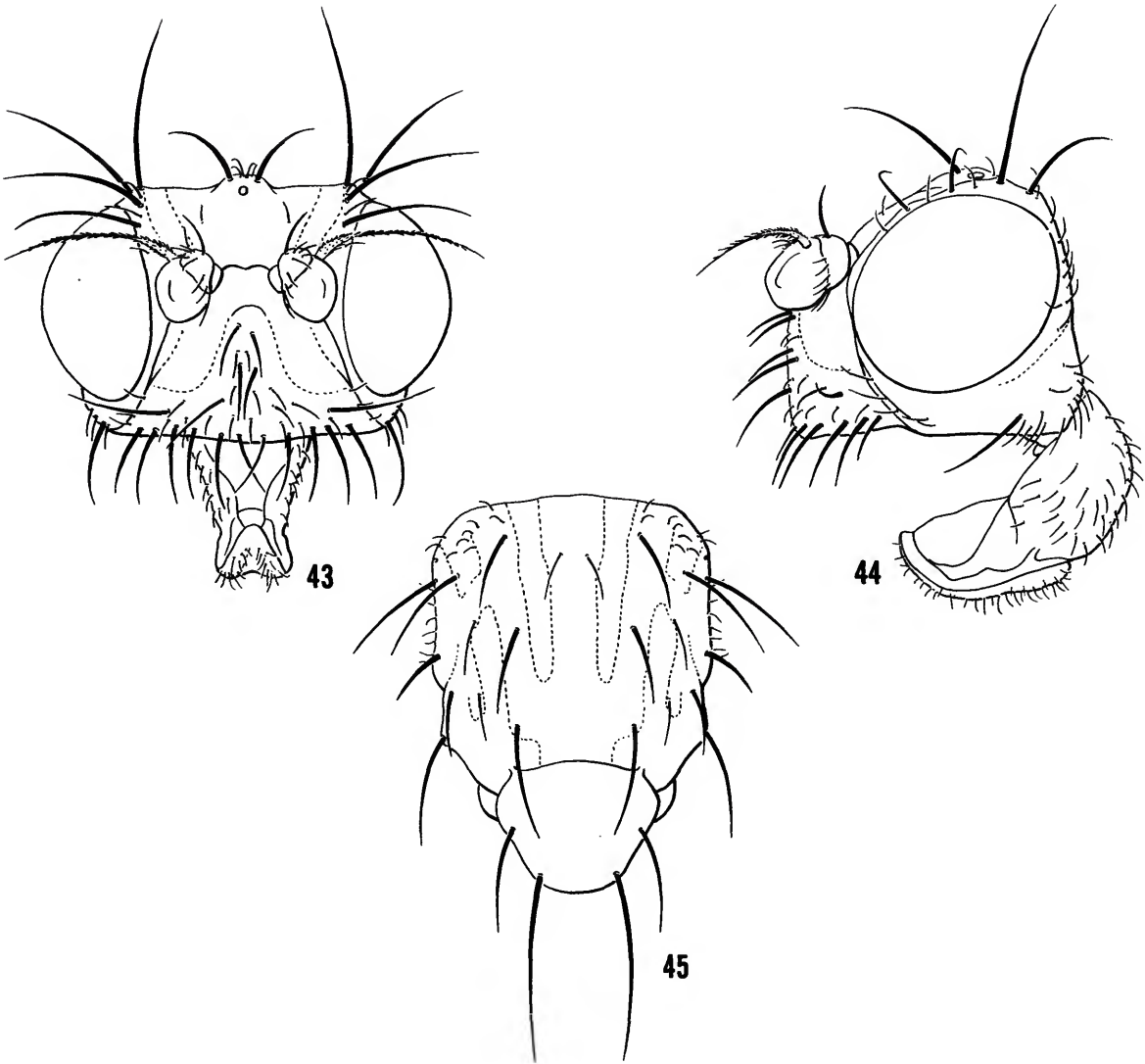
DIAGNOSIS.—Specimens of *S. curtipennis* are easily distinguished from those of any described *Scatella* species by the following combination of character states: Wing brachypterous, but longer than hind basitarsus; 1 pair of strong antesutural dorsocentral bristles; 1 pair of strong acrostichal bristles at or near level of transverse suture; mesonotum with dark brown W-shaped pattern; male terminalia as in Figures 46–47.

DESCRIPTION.—Moderately small shore flies, length 2.05 to 2.75 mm; mostly pollinose, brown, but with considerable grayish areas.

Head (Figures 43, 44): Mesofrons partially subshiny, particularly anterior and laterad of ocellar triangle, becoming gradually more pollinose anteriorly; coloration of frons mostly brown to lightly blackish brown, subshiny area with brassy luster. Antenna velvety, mostly black, some specimens faintly rufous along median posteroventral surface of third segment; arista macropubescent along basal three-fourths. Facial coloration mostly gray to whitish gray, dorsum of interfoveal carina darker, more brownish, brownish coloration extending into antennal fovea in some specimens; eye height-to-width ratio averaging 1:0.96; gena only moderately high, eye-to-cheek ratio averaging 1:0.20, nearly concolorous with face but appearing less densely pollinose.

Thorax (Figure 45): Mesonotum mostly brown, 2 gray vittae between acrostichal and dorsocentral tracts that extend posteriorly for three-fourths mesonotal length; 2 vittae also laterad of dorsocentral tract along posterior three-fourths of mesonotum; combination of vittae making a narrow W-shaped pattern of brown coloration; humeral callus mostly gray to whitish gray; notopleuron, mesopleuron, and pteropleuron concolorous, mostly brown to grayish brown; sternopleuron and front coxa brownish gray to gray. Wing (Figure 71) stenopterous, as long as middle tibia, costa appearing to extend only to R_{4+5} but beyond this point there is no free costal margin. Front femur slightly more turgid than other femora, with 3–4 irregular rows of short, spinelike setae along venter; legs more or less unicolorous and concolorous, grayish black, becoming slightly more brownish toward apices; halter yellowish.

Abdomen: Mostly subshiny but with pollinose me-

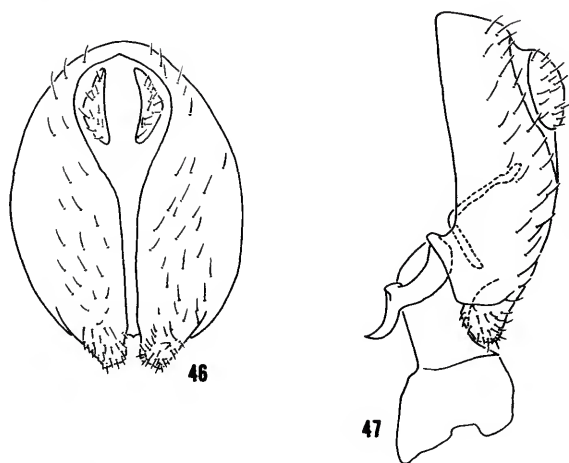


FIGURES 43-45.—*Scatella* (*Neoscatella*) *curtipennis*: 43, head, anterior aspect; 44, head, lateral aspect; 45, thorax, dorsal aspect.

dian stripe and to a lesser degree along lateral margins; coloration mostly brown with some grayish areas. Male fifth tergum as long as combined length of third and fourth terga. Male terminalia as in Figures 46, 47.

TYPE MATERIAL.—Lectotype female (herein designated), labeled: “♀ /192 [handwritten]/Iles des Etats Argentine 8. I. 1898 [8 Jan 1898] [handwritten]/

Scatophila curtipennis det. Becker [handwritten]/*Scatophila curtipennis* det. Becker [scientific name handwritten]/**TYPE** [pink]/cf. Exped. Antardt. Belg. [Belgica] Zool. [Ins.] 1906 p. 73-74/Reg. Mus. Hist. Nat. Belg. I. G. 10.131/**LECTOTYPE** *Scatophila curtipennis* Becker by W. N. Mathis [handwritten, red].” The lectotype is in the Institut Royal des



FIGURES 46-47.—*Scatella* (*Neoscatella*) *curtipennis*: 46, epandrium and cerci, posterior aspect; 47, male terminalia, lateral aspect.

Sciences Naturelles de Belgique, Brussels, Belgium. The specimen is double mounted (minute nadel in foam block) and is in fairly good condition. In general, the specimen appears to be grayer than most recently collected material that I have examined, particularly the face and abdomen, and many of the abdominal segments have small patches of parasitic ascomycete fungi (*Laboulbeniales*).

OTHER SPECIMENS EXAMINED.—ARGENTINA. Tierra del Fuego National Territory: Isla de los Estados: Puerto Cook, 16-19 May 1971, O. S. Flint and G. F. Hevel (7♂, 6♀; USNM); Puerto San Juan, 12-15 May 1971, O. S. Flint and G. F. Hevel (8♂, 49♀; USNM); Puerto Vancouver, 7-9 May 1971, O. S. Flint and G. F. Hevel (1♂, 1♀; USNM).

DISCUSSION.—The species was originally described in the genus *Scatophila*, but it is now clear that this was an error. Becker (1905b) seemed to prefer *Scatophila* largely because the costal vein appeared to end near the third vein (R_{4+5}), which is one of the principal identifying character states of that genus. As noted by Cresson (1931:86), however, the costa cannot extend beyond the third vein as there is no free margin of the wing beyond that vein. Cresson, although making no formal change, seemed to favor *Scatella* as the genus under which this species should be placed, especially because specimens of *S. curtipennis*, like those of *Scatella*, have two pair of fronto-

orbital bristles and those of *Scatophila* have but one pair. Wirth (1955:56) stated that the combination of two pair of fronto-orbital bristles and three pair of strong dorsocentral bristles precludes assignment in either *Scatophila* or *Scatella*, as the latter genus was then characterized. Wirth eliminated *Scatella*, sensu stricto, as a possibility because members of that subgenus have only two pair ($0+2$) of strong dorsocentral bristles. The combination of three strong dorsocentral bristles and a strong sutural or antesutural pair of acrostichal bristles is characteristic only of *Neoscatella*, which I consider to be a subgenus of *Scatella*.

Subgenus *Synhoplos* Lamb, new status

Synhoplos Lamb, 1917:390 [type-species: *Synhoplos sturdeanus* Lamb, by subsequent designation, Wirth, 1968:27 (catalog)].

DIAGNOSIS.—Specimens of *Synhoplos* are most similar to those of some brachypterous *Scatophila* and *Scatella*, sensu stricto, but may be distinguished from them and other members of Scatellini by the following combination of character states: Frons generally flat, vestiture mostly uniform, pollinose appearing dull; paraverticlar seta small, subequal to postocular setae; 1 long dorsal seta of second antennal segment, subequal to length of arista; marginal facial setae larger, stoutly developed; eye subglobose-quadrate, curvature decidedly more abrupt, almost angulate at "corners," oriented at oblique angle to general plane of head; eye-to-cheek ratio large, at least 1:0.5; mesonotum flat; acrostichal setae seriated into 2 rows, extending one-half to two-thirds length of mesonotum, size of setae uniform; 2-3 pair of dorsocentral bristles ($1+1$; $1+2$) plus several larger setae; humeral callus setose; wing strongly subapterous, micropterous, subequal to length of basitarsus of middle leg; halter short, about three-fourths length of maxillary palp, capitillum poorly developed; scutellum short, nearly twice as wide as long, dorsum bare with apical pair of scutellar bristles upturned and usually cruciate; surstylus well developed but fused to ventral margin of epandrium, setose; aedeagal apodeme dorsoventrally flattened, more or less L-shaped; gonites well developed, with anterior process that fuses with same process from opposite side to form a loop through which the aedeagus projects.

DESCRIPTION.—Small to medium-sized shore flies, length about 1.8 to 3.1 mm; micropterous, mostly pollinose, appearing dull colored.

Head: Head wider than high from anterior view. Frons nearly flat, neither fronto-orbits nor ocellar triangle raised in relief from mesofrons, vestiture mostly pollinose, appearing dull; ocelli arranged generally to form isosceles triangle, occasionally forming equilateral triangle, anterior ocellus generally smaller than posterior ones; mesofrons more or less triangular, lateral margins indicated by coloration change and 7–10 small setae, broadly reaching ptilinal suture; 1 pair of slightly divergent ocellar bristles, 2–4 pair of much smaller setae posterior of larger bristles; both inner and outer vertical bristles well developed; paraverticilar bristle either lacking or much reduced, not conspicuous; 2 pair of large laterocline fronto-orbital bristles, orientation nearly parallel to each other, 1–2 smaller setae anterior and inbetween larger bristles. Antenna moderately developed; second and third segments about equal in length; second segment with numerous short setae along median and ventral surfaces, those along venter slightly larger, 1 slender long seta inserted dorsally and with anterodorsal orientation, length subequal to arista length; third segment about as long as wide, broadly rounded apically; arista subpectinate along dorsal two-thirds, longest rays slightly greater than arista width at base. Face distinctly protruding, arched; interfoveal carina well developed, conspicuously creased dorsally; antennal fovea deeply impressed, extending for approximately two-thirds facial height; facial setae along margins, especially oral margin well developed, 3–4 times longer than setae on anteromedian surface of face; vestiture, other than setae, densely pollinose to nearly tomentose. Eye subglobose-quadrangle except for posteroventral plane, which is markedly more angulate, about as high as wide, bare. Gena high, over one-half eye height, bare anteriorly, becoming obviously setose posteriorly, with 1 larger genal bristle. Clypeus concealed within oral cavity; prementum large, bulbous, uniformly setose.

Thorax: Pollinose generally, appearing dull. Mesonotum relatively flat, notopleuron in particular nearly flat. Scutellum about twice as wide as long, broadly rounded. Chaetotaxy of thorax as follows: 2 rows of acrostichal setae, none better developed than others, becoming attenuated posteriorly; 2–3 pair of large

dorsocentral bristles (1 + 1; 1 + 2), if 3 pair, middle pair smaller, 2–3 smaller setae between larger bristles; 2 pair of lateral scutellar bristles, basal pair about one-half length of apical pair, apical pair dorsally projecting, usually cruciate; 1 pair of presutural bristles; supra-alar bristle either lacking or much reduced; 1 pair of postalar bristles; humeral setose but lacking any larger bristles; 2 pair of notopleural bristles, each inserted at same level near anteroventral or posteroventral corner; 1 pair of mesopleural bristles, inserted at posterior margin at upper one-third to one-fourth, mesopleuron setose toward dorsal and posterior margins; 1 pair of sternopleural bristles. Sternopleuron narrowing abruptly along posteroventral margin, somewhat emarginate. Wing micropterous; about equal in length to basitarsus of hind leg; veins greatly reduced, apex generally with 1 larger seta. Femora turgid. Halter reduced, lacking well developed capitellum.

Abdomen: Generally pollinose, similar to vestiture of thorax; generally setose, with those along lateral and posterior margins of each segment slightly larger. Male fifth tergum nearly equal to combined length of third and fourth terga, subtrapezoidal, subtruncate apically. Male terminalia as in diagnosis and species descriptions.

GEOGRAPHIC DISTRIBUTION.—This genus is known to occur along the coasts of continental islands within the Tierra del Fuego region of the South Atlantic. This area is circumscribed by the following coordinates: 58° to 66° W, 51° to 55° S. Land areas within this region include the Falkland Islands, Isla de los Estados, and the eastern tip of Tierra del Fuego.

NATURAL HISTORY.—Dr. O. S. Flint, Jr. and Mr. Gary F. Hevel, Smithsonian Institution, collected both species of *Synhoplos* on the Isla de los Estados (Staten Island), Tierra del Fuego National Territory, Argentina, during May, 1971. The ambient temperature was cool, around 7° C, and on occasion snow fell. Dr. Flint's field notes indicate that collecting of semi-apterous Diptera was productive along rocky beaches, where accumulated debris offered some protection to small arthropods. Under larger objects, such as rocks, logs, and especially kelp holdfasts that had washed ashore, the flies were found in abundance. When a holdfast was shaken over a snow bank, the exposed insects were easily collected. Immature stages were not observed, but it is probable that they also inhabit the same or similar environs, particularly since the adults

are incapable of flight and are not likely to wander far from where they were bred.

Isla de los Estados is situated off the coast of the eastern tip of Tierra del Fuego, across the Estrecho de la Maire. On an east-west axis, the island is approximately 60 km long. Flint (1971) briefly described the topography, vegetation, and collection sites that he and Hevel visited when they surveyed the island for arthropods in 1971.

It is of interest to note that although both species occur on Isla de los Estados and the Falkland Islands, they are not microsympatric and have not been collected together (see "Other Specimens Examined" under each species).

Both species of *Synhoplos* are micropterous according to Hackman's (1964:73) definition: "Micropterous: Wing a small appendage of varying shape, broad or narrow. At most only traces of the radial vein." Hackman (1964) produced a table in which habitat and mode of locomotion were correlated with degree of wing reduction and in which sex, if exclusive to just one, the reduction occurs. Both species of *Synhoplos* could be classed under two of his major headings: "I. Terrestrial habits. a. Secretive habits. b. Cold habitats." and "II. Marine and littoral habitats. a. littoral near water-line." As noted previously, specimens of both species were encountered abundantly along the rocky beaches of the southwestern Atlantic beneath debris that had accumulated on shore; the ambient temperature was cold, sometimes freezing. These habitats occur on continental islands (Falklands, Isla de los Estados, and Tierra del Fuego).

Both species are sympatric in the broad sense, although as noted earlier, they have not been collected together at a specific site. Their rather disjunct distribution across open ocean, especially for flightless insects, does attest to their ability to disperse, and certainly the opportunity to occur sympatrically at the microhabitat level exists if their vagility were the only consideration. If both species can disperse over an area from the Falklands to Tierra del Fuego, then on the same small island (Isla de los Estados) they could disperse to adjacent "bahias." But apparently they have not, which would indicate that other factors are involved, such as ecological ones, and I suspect that at the level of microhabitats, they competitively exclude each other.

From an historical perspective, dispersal between

the Falklands and Tierra del Fuego was less arduous a task in the past when periods of glaciation bound more of the earth's water as ice, thus lowering the sea level. Vuilleumier (1971) produced a map of South America during the Würm period of glaciation. The separating gap between the Falklands and the extended mainland was less than 100 km. Regardless of the distance, however, flightless flies must have been passive voyagers, and in the case of *Synhoplos*, I would speculate that long distance travel occurred via floating debris such as an "uprooted" holdfast.

What vicariance event resulted in the speciation of the two known species is difficult to ascertain. Perhaps it was their isolation during an interglacial period of earth warming, such as during the Pleistocene, when the ocean level was higher, making the Falklands, for example, more remote and inaccessible. Or perhaps the ocean currents changed, making migration between the islands and the mainland nearly impossible for flightless flies. Whatever the event was, however, and speculation knows no end, their broad sympatry now is evidence of subsequent dispersal and at least partial range extension for each species (*Synhoplos neglectus* has not been collected from Tierra del Fuego as yet).

DISCUSSION.—Until this study, *Synhoplos* had been given generic status. But in light of character states of the male terminalia, which ally *Synhoplos* with *Scatella*, and the close relationship between *Synhoplos* and the lineage that gave rise to *Teichomyza*, I am of the opinion that it is better to treat *Synhoplos* as a subgenus within the genus *Scatella*.

Lamb's discussion of the affinities of *Synhoplos* was confused by mixing up generic names. Lamb (1917: 387), for example, credited Becker with the name "*Scatella brevipennis*" [sic] when the actual generic name Becker used was *Scatophila*, and a few sentences later, Lamb continued to use *Scatella* in place of *Scatophila* when he discussed distinguishing characters. Consequently, when Lamb said that his new genus is related to both *Scatella* and *Scatophila*, but that "it will probably be found that the relationships of the new species are to be sought for in *Scatophila*," I am left wondering whether he actually meant *Scatella*. Assuming Lamb consistently confused the names, I agree with his conclusion that the affinities of *Synhoplos* are to be found in *Scatella* (Lamb's *Scatophila*).

Key to Species of the Subgenus *Synhoplos*

- Mesonotum and dorsum of abdomen mostly gray; mesonotal brown vitta not much wider whitish gray humeral callus, notopleuron, and small linear area along dorsocentral tract at 10. *S. sturdeeanus* (Lamb)
- Mesonotum and dorsum of abdomen mostly brown, mesonotum not vittate brown except for than distance between rows of acrostichal setae; smaller species, length 1.83 to 2.46 mm level of wings; larger species, length 2.28 to 3.02 mm 9. *S. neglectus* (Lamb)

9. *Scatella (Synhoplos) neglectus* (Lamb),
new combination

FIGURES 48–50

DIAGNOSIS.—Specimens of this species are similar to those of *S. sturdeeanus* but may be distinguished by the following combination of character states: Specimens larger, appearing more robust and with setae better developed; coloration generally darker, especially mesonotum and abdomen, the latter blackish brown; structures of male terminalia as in Figures 48–49.

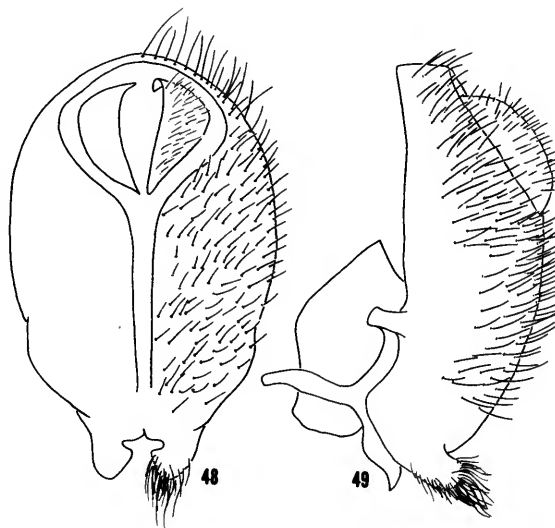
DESCRIPTION.—Moderately small to medium-sized shore flies, length 2.28 to 3.02 mm; generally dark brown, but with some gray to whitish gray areas.

Head: Mesofrons darker than surrounding coloration, blackish; parafrons blackish brown. Antenna yellowish brown, third segment darker than second. Face mostly gray to whitish gray. Gena blackish brown, slightly lighter in coloration than parafrons.

Thorax: Mesonotum mostly brown except for grayish coloration of humeral callus, notopleuron and to a lesser degree along the posterior portion of the dorsocentral tract. Pleural areas more or less unicolorous, brown to blackish brown. Legs darker basally; femora more densely pollinose than remainder, grayish to blackish gray; tibiae and tarsi lighter, mostly yellowish brown. Wing yellowish brown to blackish brown along anterior margin, otherwise mostly blackish.

Abdomen: Mostly dark brown, but with varying amounts of grayish coloration, generally in smaller spots on either side of median toward posterior margin of each segment. Male terminalia (Figures 48, 49) with surstylus densely setose; epandrium shallowly arched in profile.

TYPE MATERIAL.—Lectotype male (herein desig-



FIGURES 48–49.—*Scatella (Synhoplos) neglectus*: 48, epandrium and cerci, posterior aspect; 49, male terminalia, lateral aspect.

nated), labeled: “Co-type [round white disk with yellow border]/Falkland Is. R. Vallentin. 1902–193./LECTOTYPE *Synhoplos neglectus* Lamb by W. N. Mathis [handwritten, red].” The lectotype and 12 paralectotypes (4 ♂, 8 ♀; herein designated) are in the British Museum (Natural History).

OTHER SPECIMENS EXAMINED.—ARGENTINA. Tierra del Fuego National Territory: Isla de los Estados: Bahía Colnett, 25 May 1971, O. S. Flint and G. F. Hevel (3 ♂, 3 ♀; USNM); Puerto Vancouver, 7–9 May 1971, O. S. Flint and G. F. Hevel (6 ♂, 1 ♀; USNM).

GEOGRAPHIC DISTRIBUTION. (Figure 50).—*Scatella neglectus* is known only from the Falkland Islands and Isla de los Estados (Staten Island); both are continental islands off the southeastern coast of South America.

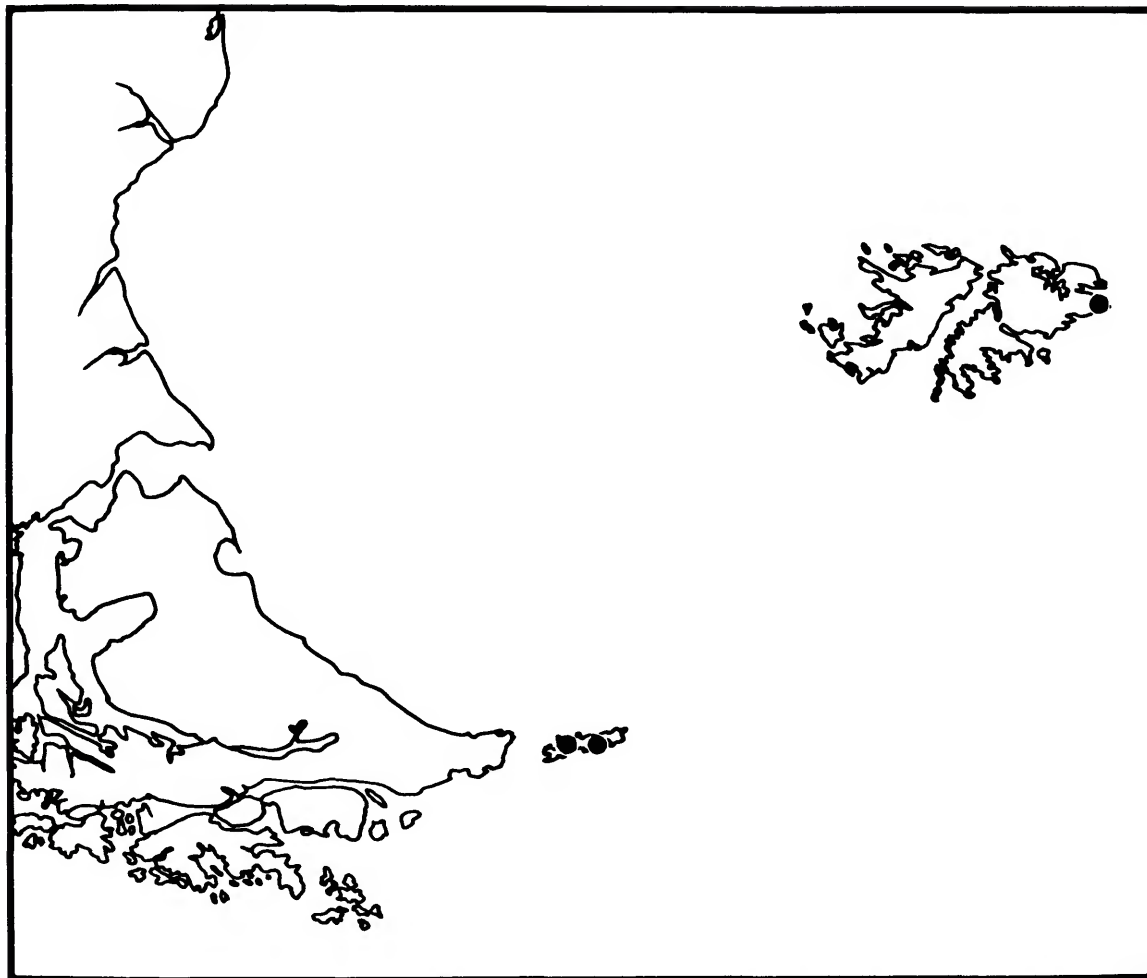


FIGURE 50.—Distribution map of *Scatella (Synhoplos) neglectus*.

10. *Scatella (Synhoplos) sturdeeanus* (Lamb),
new combination

FIGURES 51–59

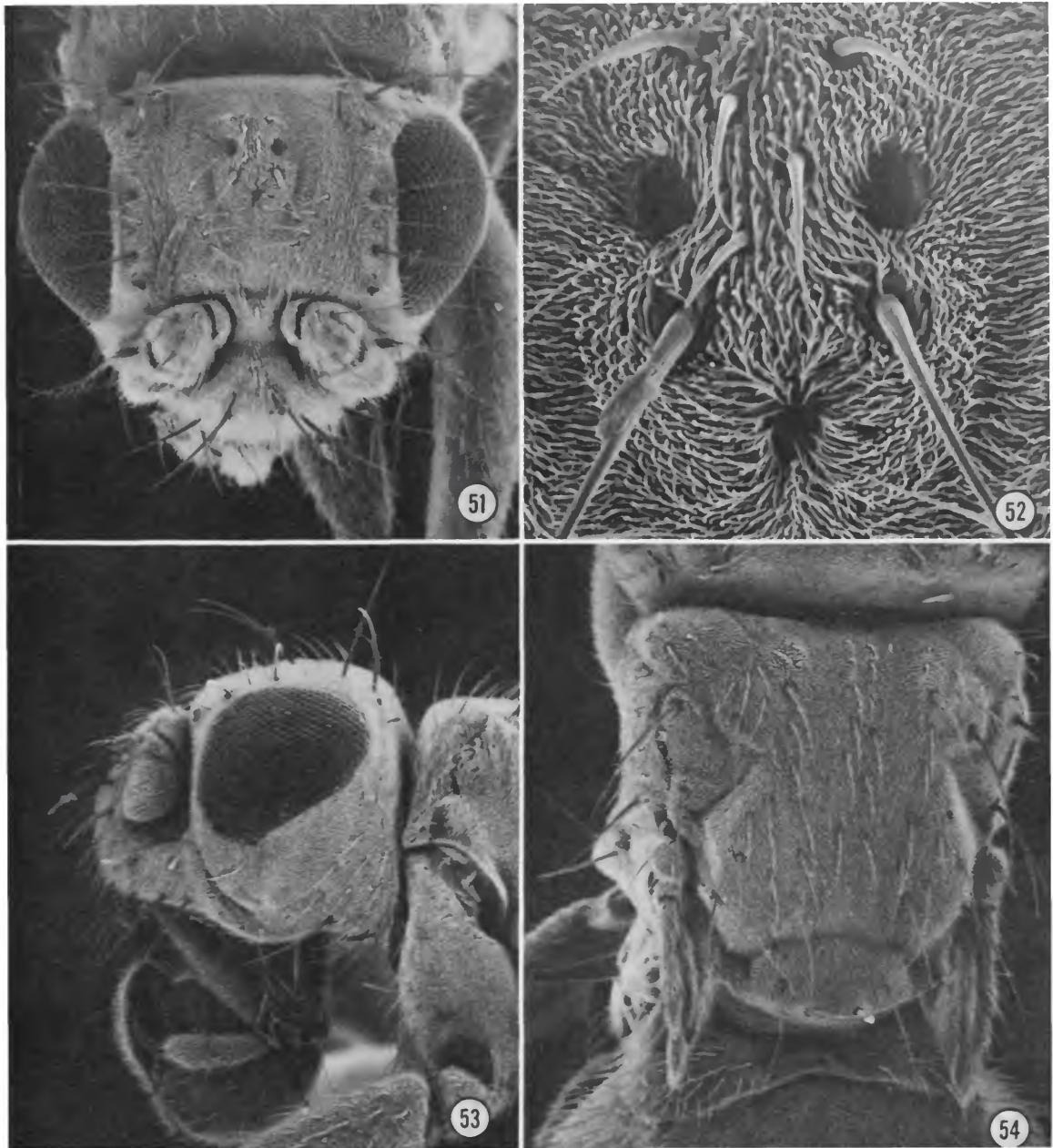
Synhoplos sturdeeanus Lamb, 1917:390.—Wirth, 1968:27
[catalog citation].

DIAGNOSIS.—Specimens of this species are similar to those of *S. neglectus* but may be distinguished by the following combination of character states: Specimens smaller, appearing more slender, setae less well developed; coloration generally gray, mesonotum and abdomen with median brown vitta, otherwise gray;

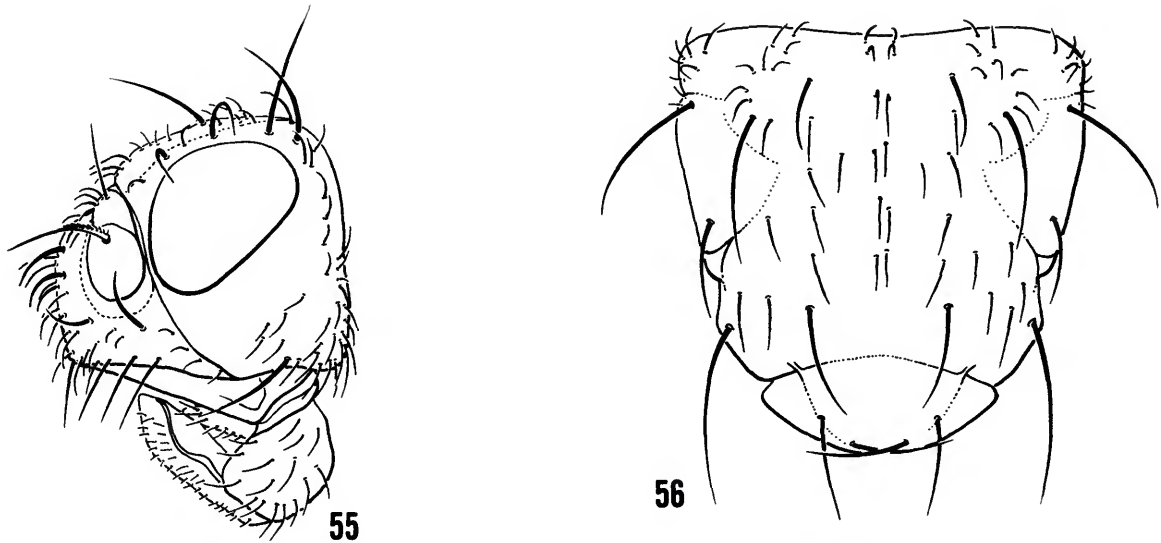
ocelli arranged to form isosceles triangle, distance between posterior ocelli less than distance between posterior ocellus and median ocellus; structures of male terminalia as in Figures 57–58.

DESCRIPTION.—Small to moderately small shore flies, length 1.83 to 2.46 mm; mostly gray, but with some darker brown areas.

Head (Figures 51–53, 55): Frons dark; mesofrons grayish black; parafrons appearing velvety, more charcoal-colored. Antenna yellowish brown to blackish brown, becoming darker toward apex. Face mostly unicolorous, whitish gray. Gena and postoccipt concolorous, mostly black to olivaceous black.



FIGURES 51-54.—*Scatella (Synhoplos) sturdeeanus*: 51, head, dorsal aspect; 52, ocelli, dorsal aspect; 53, head, lateral aspect; 54, thorax, dorsal aspect.



FIGURES 55-56.—*Scatella (Synhoplos) sturdeeanus*: 55, head, lateral aspect; 56, thorax, dorsal aspect.

Thorax (Figures 54, 56): Mesonotum mostly gray to whitish gray except for brown median stripe along acrostichal track and a spot anterolaterad of acrostichal track. Pleural areas gray to brown, becoming darker, more brownish toward venter. Femora nearly concolorous with grayish coloration of pleural areas; tibiae and tarsi yellowish brown. Wing yellowish anteriorly, becoming blackish brown posteriorly.

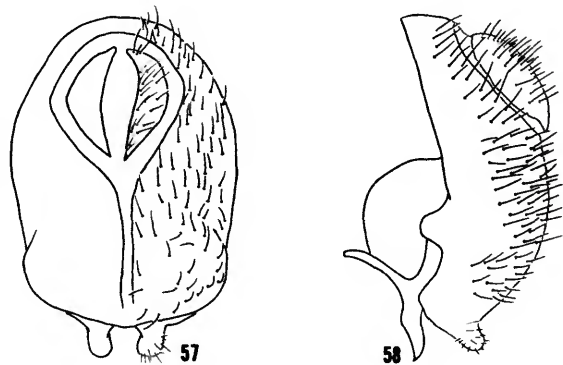
Abdomen: Generally gray except for median area of each tergum and anterolateral margins, which are brownish. Extent of brownish coloration quite variable. Male terminalia (Figures 57, 58) with surstylus nearly bare, with scattered setulae; epandrium conspicuously arched in profile.

TYPE MATERIAL.—Lectotype male (herein designated), labeled: "♂ /Co-type *Synhoplos sturdeeanus* Lamb. [round white disk with yellow border, species name handwritten]/Falkland Is. Port Stanley. On seaweed. 7. XII. 1914. M. Cameron 1915.72 [handwritten]/LECTOTYPE *Synhoplos sturdeeanus* Lamb by W. N. Mathis [handwritten, red]." The lectotype and 3 paralectotypes (2 ♂, 1 ♀; herein designated) are in the British Museum (Natural History).

OTHER SPECIMENS EXAMINED.—ARGENTINA. Tierra del Fuego National Territory: Bahía Buen Suceso, 23-26 Apr 1971, O. S. Flint and G. F. Hevel (11 ♂, 16 ♀; USNM).

Isla de los Estados: Bahía Blossom, 10 May 1971, O. S. Flint and G. F. Hevel (24 ♂, 18 ♀; USNM); Primera Bahía 8 May 1971, O. S. Flint and G. F. Hevel (1 ♂; USNM); Puerto Roca, 22-23 May 1971, O. S. Flint and G. F. Hevel (4 ♂, 13 ♀; USNM).

GEOGRAPHIC DISTRIBUTION. (Figure 59).—*Scatella sturdeeanus* occurs on beaches of continental islands near the southeastern tip of South America.



FIGURES 57-58.—*Scatella (Synhoplos) sturdeeanus*: 57, epandrium and cerci, posterior aspect; 58, male terminalia, lateral aspect.

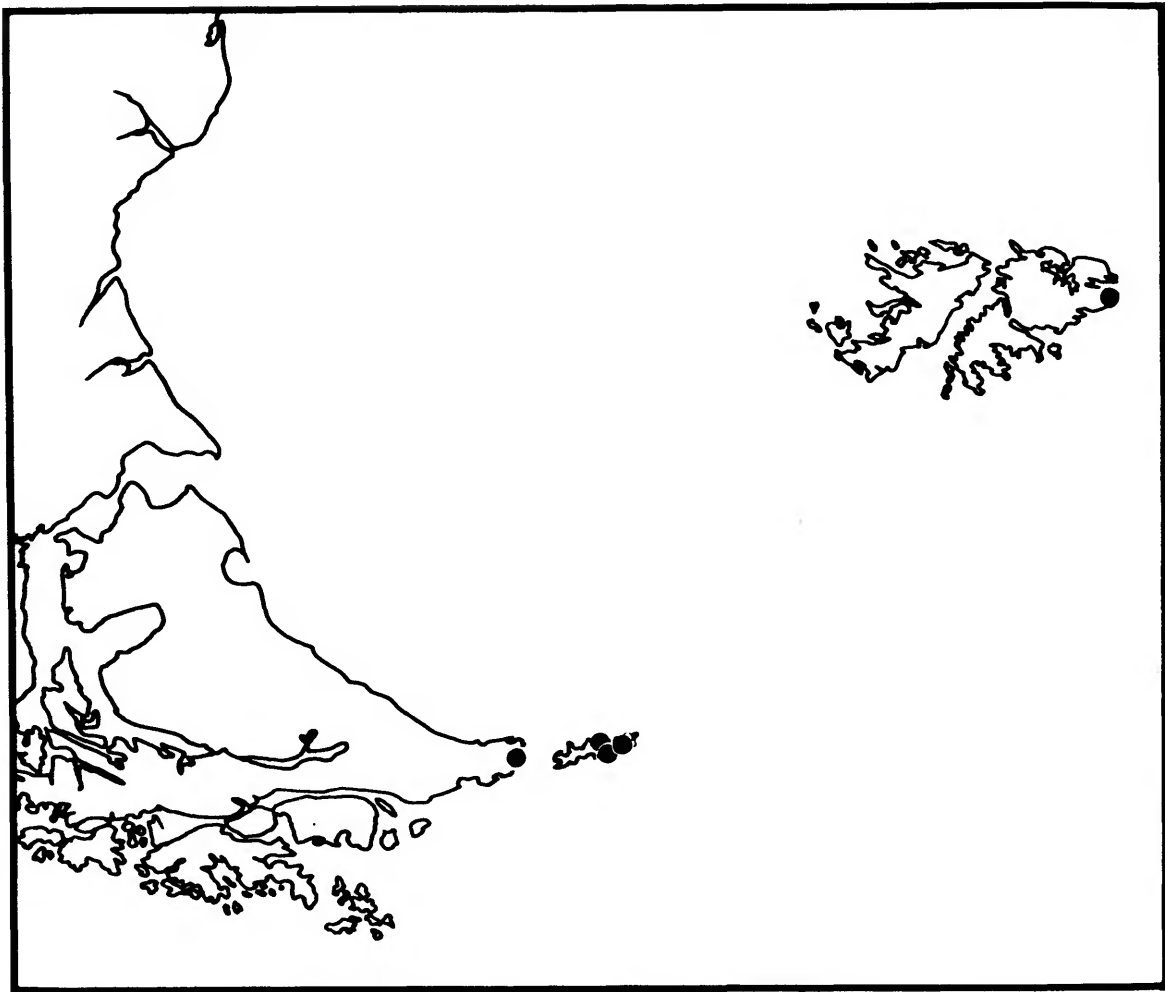


FIGURE 59.—Distribution map of *Scatella* (*Synhoplos*) *sturdeeanus*.

Subgenus *Teichomyza* Macquart, new status

Teichomyza Macquart, 1835:534 [type-species: *Teichomyza fusca* Macquart, by monotypy].—Schiner, 1863:268 [review].—James, 1947:154 [review].—Wirth, 1968:24 [catalog citation].—Papp, 1975:109 [review].

Tichomyza.—Loew, 1860:45 [unjustified emendation, review].—Becker, 1896:206 [review]; 1905a:214 [catalog citation]; 1926:91 [review].—Nartschuk, 1970:386 [key].
Tychomyza.—Becker, 1926:91 [unjustified emendation].

DIAGNOSIS.—Specimens of *Teichomyza* are similar to those of some *Scatella* (*Neoscatella*), particularly *S. furens* Cresson, but may be distinguished from the latter and other subgenera of *Scatella* by the following

combination of character states: Generally dark colored; mesofrons recessed from level of fronto-orbits and ocellar triangle, bare of setae, pollinose, appearing dull; ocelli arranged to form isosceles triangle, distance between posterior pair greater than distance between either posterior ocellus and median one; second antennal segment subequal to length of third, with 1 long slender dorsal seta equal to length of segment; arista bare, equal to or longer than length of inner vertical bristle, basal one-fourth to one-third thickened, otherwise slender, hairlike; marginal facial setae generally stout, larger, particularly those along oral margin and descending posteroventrally from

interfoveal carina; interfoveal carina with distinct dorsal crease; eye subovate, higher than wide, slightly wider dorsally; gena moderately high, about one-third eye height; mesonotum arched; acrostichal setae, except for 1 pair of larger antesutural bristles mostly small, hairlike, uniseriated, 3-4 irregular rows; 2 pair of dorsocentral bristles (0 + 2); humeral cellus uniformly setose generally but lacking bristles; supra-alar bristle either lacking or hairlike; scutellum as long as wide with 3 pair of lateral bristles, middle pair smaller; lateral margins of scutellar disc setose; wing normally developed, infumated, lightly brownish, lacking lighter-colored spots; legs normally developed, not turgid.

DESCRIPTION.—Moderately small to large shore flies, about 3.5 to 5 mm; mostly dull colored; pollinose.

Head: Head wider than high from anterior. Frons dull, mostly pollinose; mesofrons recessed, mostly flat; parafrons, fronto-orbits, and ocellar triangle raised in relief from mesofrons; ocelli arranged to form isosceles triangle, distance between posterior pair greater than distance between either posterior ocellus and median ocellus; 1 pair of divergent ocellar bristles, 2-3 pair of smaller hairlike setae posterior of larger bristles; 2 pair of laterocliniate fronto-orbital bristles and a few scattered smaller setae in between larger bristles; inner and outer vertical bristles both well developed; paraverticlar bristle either lacking or much reduced; mesofrons generally bare except for a few small, inconspicuous setae near anterolateral margin. Third antennal segment shorter than combined length of first and second segments; second segment with numerous short setae along median and ventral surfaces, with 1 larger, slender, dorsal seta with anterodorsal orientation; third segment evenly rounded apically; arista bare, becoming gradually thicker along basal one-fourth to one-third, subequal to combined length of segments 1-3. Face distinctly protruding, interfoveal carina distinct with well-marked dorsal crease; antennal fovea well-recessed; facial setae along margins very stout and well developed, particularly along oral margin, remaining facial setae much less developed but of uniform size, vestiture pollinose, appearing dull. Eye higher than wide, subovate, slightly wider dorsally, bare. Gena generally bare anteriorly, posterior portion sparsely setose, with 1 large genal bristle; genal height about one-third eye

height. Clypeus concealed within oral cavity; prementum large, bulbous, uniformly setose.

Thorax: Uniformly pollinose, appearing dull. Chaetotaxy of thorax as follows: 1 pair of larger acrostichal bristles, inserted anterior of transverse suture, other acrostichal setae uniseriated and much smaller, hairlike, in 3-4 irregular rows; 2 pair of dorsocentral bristles (0 + 2), numerous smaller setae along same tract; 1 pair of presutural bristles; supra-alar bristles either lacking or much reduced, hairlike; 1 pair of postalar bristles; 3 large pair of lateral scutellar bristles, middle pair much smaller, 2-3 pair of moderately larger setae and several smaller setae laterally and along lateral margins of scutellar disc; no well-developed humeral bristles, but uniformly setose; 2 pair of notopleural bristles; 1 pair of mesopleural bristles inserted at posterior margin near upper one-third, generally setulose toward dorsal and posterior margins; 1 pair of sternopleural bristles, a few smaller setae just anterior of larger bristle. Wing normally developed; generally infuscated, lightly brownish to gray in coloration, lacking pattern of white spots.

Abdomen: More or less uniformly pollinose, dull. Setae slender, larger along lateral and posterior margins; setae of terminal terga of female larger. Male fifth tergum longer than combined length of third and fourth terga. Male terminalia as in species Figures 64, 65.

GEOGRAPHIC DISTRIBUTION.—This genus occurs in two widely disjunct regions of the world. In Europe, it occurs from Ireland to European Russia and south to Bulgaria and Italy. In western South America, it is known to occur in Chile and along the coast of Peru.

DISCUSSION.—The relationship of *Teichomyza* with other ephydrid taxa has been confusing. Macquart (1835) compared it with *Ephydra* and Haliday (1837) thought that it should be no more than a "section" of *Ephydra*. Meigen (1838), in fact, named the first junior synonym as a species in the genus *Ephydra*, *E. longipennis*. Robineau-Desvoidy (1848) stated that he had intended to make his *Scatella urinaria* the type of *Scatella* when he erected the latter in 1830. According to Robineau-Desvoidy, a printer's lapsus precluded his intention.

Subsequent authors treated *Teichomyza* as a distinct genus in the subfamily *Ephydrinae*, and when tribes were erected within that subfamily (Wirth and Stone, 1956), it was listed under the tribe Ephydrini (Wirth, 1968:24). This alliance is not tenable, however, as specimens of Ephydrini are characterized by

their long, shallowly curved tarsal claws and the absence of well-developed pulvilli. Specimens of *Teichomyza* have well-developed pulvilli, and the tarsal claws are of normal size and are distinctly curved, which would place them in the tribe Scatellini.

Within Scatellini, I have relegated *Teichomyza* to subgeneric status in the genus *Scatella*. Characters of the male terminalia provide the primary evidence to support this relationship. Like males of *Scatella*, those of *Teichomyza* have a dorsoventrally flattened, slightly angulate aedeagal apodeme that is attached to, or articulated with, the base of the aedeagus only. There is no point of articulation or attachment with the hypandrium. Similarly, the gonite in both *Scatella* and *Teichomyza* bears a ventrally projecting, pointed process and an anterior projection that is fused with a similar process from the opposite side to form a loop through which the aedeagus can be extended or retracted. Finally, the supra-alar bristle is either lacking or reduced, not subequal to the postalar bristle.

11. *Scatella (Teichomyza) fusca* Macquart, new combination

FIGURES 60–65, 72

Teichomyza fusca Macquart, 1835:535.—Haliday, 1837:148 [review].—Schiner, 1863:268 [review].—Bezzi, 1892:41 [review].—James, 1947:154 [review].—Wirth, 1968:24 [catalog citation].—Papp, 1975:110 [review].

Ephydra longipennis Meigen, 1838:382 [synonymy by Schiner, 1863:268].

Teichomyza muraria Robineau-Desvoidy, 1848:xciv [nomen nudum; attributed to Macquart in discussion of *Scatella urinaria*].

Scatella urinaria Robineau-Desvoidy, 1848:xciv [nomen nudum; proposed as a replacement name for "*muraria* Macquart" (q.v.); synonymy by Schiner, 1863:268].

Tichomyza fusca.—Loew, 1860:45.—Becker, [unjustified emendation; review].—Becker, 1896:206 [review]; 1905a:214 [catalog citation]; 1926:91 [review].—Nartschuk, 1970:386 [key].

DIAGNOSIS.—Mostly dark brown; middle coxa with patch of about 10 larger setae inserted anteroventrally; male middle femur with short row of 7–10 bristles along middle of posteroventral surface; male terminalia as in Figures 64–65.

DESCRIPTION.—Medium-sized to large shore flies, length 3.70 to 5.07 mm; generally appearing dull, mostly brown with some gray areas.

Head: (Figures 60, 61): Mesofrons and ocellar

triangle rusty brown to blackish rust colored; fronto-orbits blackish; antenna, dorsum of interfoveal carina, and antennal fovea rusty brown, remainder of face becoming grayer; gena mostly blackish but usually with small, rusty colored area just below eye. Eye height-to-width ratio averaging 1:0.84; eye-to-cheek ratio averaging 1:0.33.

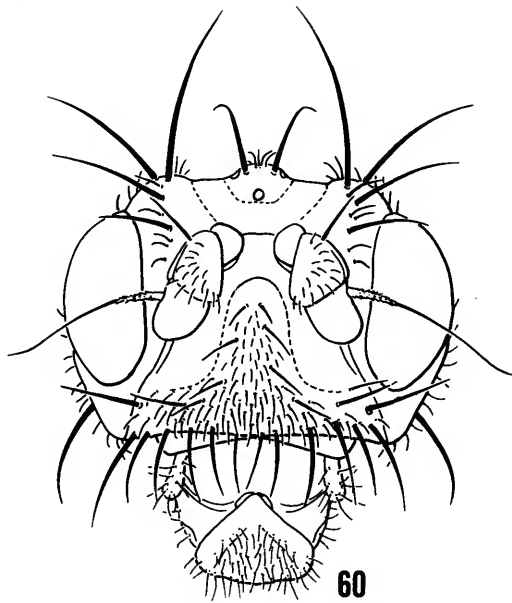
Thorax (Figure 62): Mesonotum blackish brown to grayish brown, becoming lighter colored posteriorly, with 2 bluish gray vittae along acrostichal tracks anteriorly, both fading and merging with surrounding color posteriorly; disc of scutellum gray to bluish gray, becoming brownish laterally; pleural areas, including notopleuron, mostly uniform in coloration, blackish gray with rusty background coloration becoming evident in less pollinose areas. Wing (Figure 72) length-to-width ratio averaging 1:0.44; costal vein index averaging 1:0.20; M_{1+2} vein ratio averaging 1:0.71. Middle, and to a lesser degree, male front femur with row of larger setae near middle along posteroventral margin, these particularly strong on middle femur; middle coxa with much stronger setae along anterior surface.

Abdomen: Mostly concolorous with mesonotum, but more thinly pollinose and more rusty brown in coloration. Male terminalia as in Figures 64, 65.

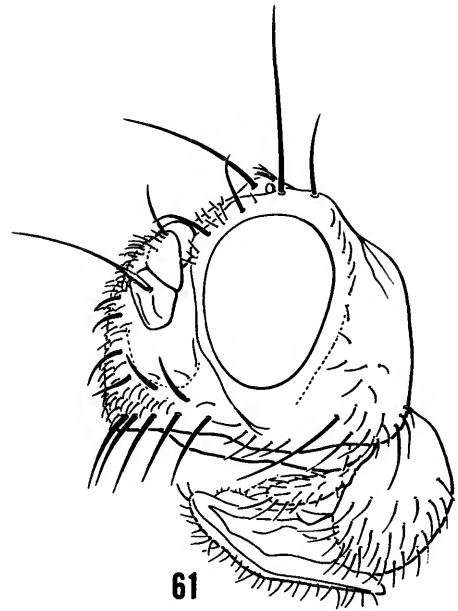
TYPE MATERIAL.—I have not studied the type or type series of the senior or junior synonyms. Macquart (1835) indicated that the type series of *Teichomyza fusca* included male and female specimens, and he stated that the species was "Commune en France." According to Meigen (1838), the type series of *Ephydra longipennis* was collected by "Robert zu Ghenée" from near the city of Lütticher (Liege), Belgium. I have no data concerning the type series of *Scatella urinaria* Robineau-Desvoidy. The specimens of all three type series are probably in Paris or Lille, France.

SPECIMENS EXAMINED.—CHILE: Antofagasta Province: Antofagasta, Aug, at light, T. Cockerell (1♀; USNM). PERU: Moquegua Province: Ilo, at light, 9 Aug, T. Cockerell (2♂, 1♀; USNM). Ica Province: Pisco, on board Santa Inez, 16 July 1930 (2♀; USNM).

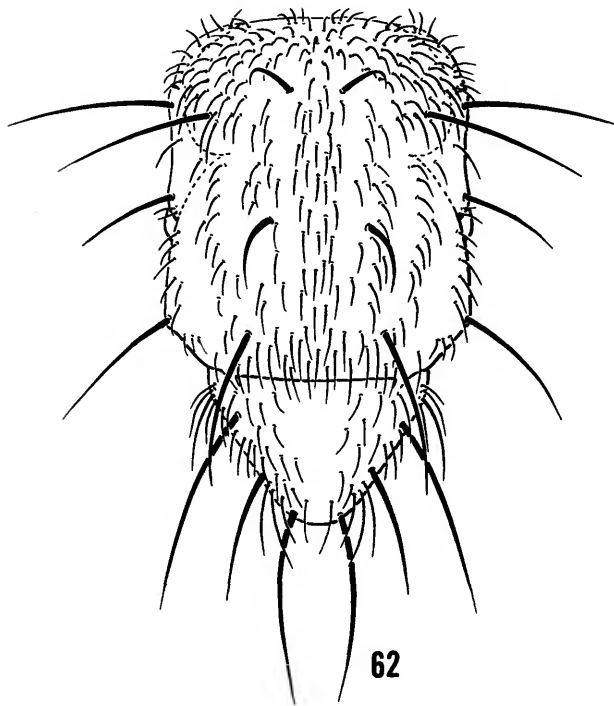
GEOGRAPHIC DISTRIBUTION.—This species has been collected from only three localities in western South America as listed previously, but I suspect that it will be found to be more widespread in the Neotropics when the specific habitat is more thoroughly collected. Wirth (1968:24) suggested that this species was introduced into South America by ship from Europe,



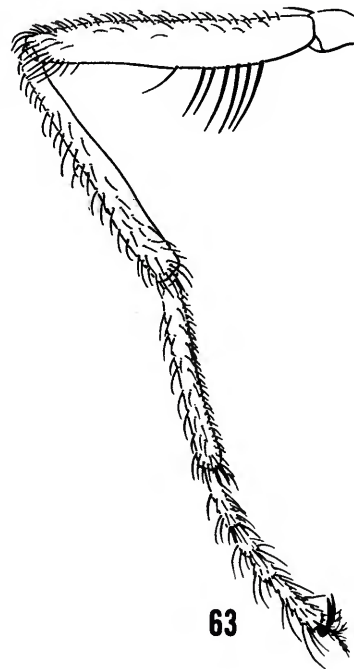
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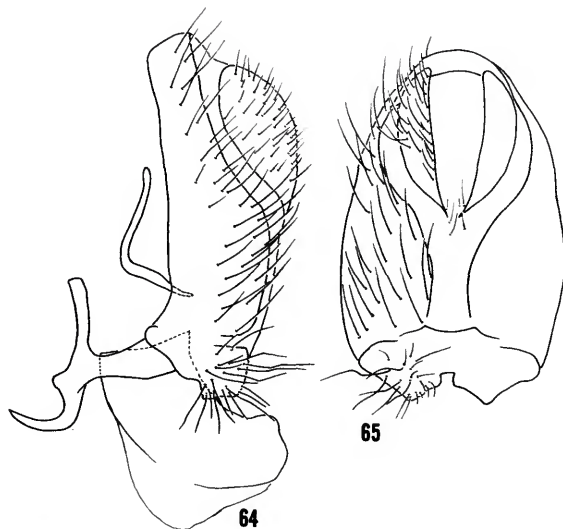


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63

FIGURES 60-63.—*Scatella (Teichomyza) fusca*: 60, head, anterior aspect; 61, head, lateral aspect; 62, thorax, dorsal aspect; 63, middle leg of male, posterior aspect.



FIGURES 64-65.—*Scatella (Teichomyza) fusca*: 64, male terminalia, lateral aspect; 65, cerci and epandrium, posterior aspect.

but in view of the discovery that its probable sister group is from temperate South America, I suggest that the introduction was to Europe from South America, rather than the reverse.

NATURAL HISTORY.—*Teichomyza fusca* has frequently been referred to by the vernacular name “urine fly,” and the larvae and adults are generally encountered around outdoor urinals and excrement (James, 1947). Robineau-Desvoidy (1848) was apparently the first to observe this and belatedly reported it in responding to earlier inaccuracies of Macquart (1835), who mentioned that the fly is found on damp walls of old buildings and that the larvae feed among the decayed mortar. In this conjunction, Robineau-Desvoidy also stated that he had intended to describe this species under the *Scatella urinaria* because of their habit, and to make it the type of *Scatella*, but because of a printer’s lapsis, his species did not appear in print.

Because of its propensity, this species has received greater attention than most shore flies from the standpoint of natural history. Laboulbène (1867) provided what is still the most detailed study of *T. fusca*, including descriptions and figures, albeit old, of the immature and adult stages plus observations concerning the life history. Subsequent studies by Vogler

(1900), Johannsen (1935), and James (1947) are essentially recapitulations. Hennig (1952) included *Teichomyza* in his generic key to the larvae of Ephydriidae.

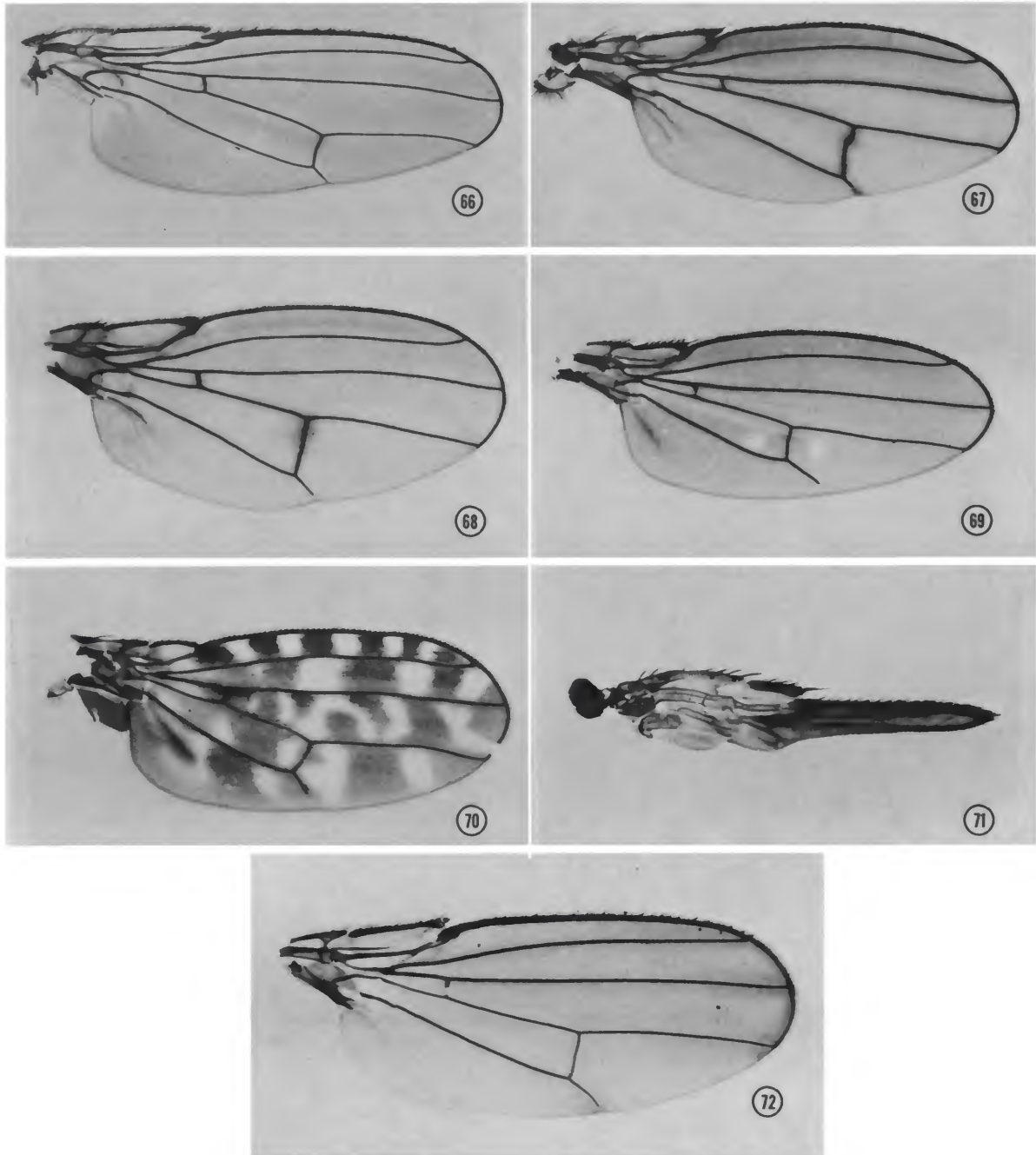
This is the only species of Ephydriidae that has been implicated to cause myiasis (James, 1947). Although numerous cases of urinary myiasis involving this species have been recorded, few, if any, have been confirmed. Chevrel (1909) discussed three cases of urinary myiasis in detail, but, as pointed out by James (1947), their authenticity was not clearly established. Evidence does implicate them, however, as causing facultative urinary or possible intestinal myiasis.

Three additional observations are of interest. Adults are apparently attracted to lights at night. The specimens Cockerell collected off the coast of western South America were taken “at lights.” Haliday (1837) and Bezzi (1892) both observed that adults were collected only during the winter (in Europe). Finally, during the middle nineteenth century, this species was reported to be extremely common in Paris (Laboulbène, 1867), but with the disappearance of outdoor urinals and other sites where highly organic water can accumulate, the fly has become less abundant.

Phylogeny

Ephydrinae is presently divided into two tribes, Ephydrini and Scatellini. The current concept of each tribe was delimited initially by Wirth and Stone (1956) and was adhered to in recent catalogs with minor exceptions (Wirth, 1965, 1968; Cogan and Wirth, 1977) and in subsequent revisions (Mathis and Shewell, 1978).

As noted in an earlier paper (Mathis and Shewell, 1978), Scatellini is paraphyletic, and as characterized, it is an assemblage of convenience. Wirth and Stone (1956) erected Scatellini largely to accommodate genera not included within their concept of Ephydrini. But unlike Ephydrini, Scatellini was characterized by symplesiotypies, and it is now apparent that Ephydrini, for example, is but one of five equivalent monophyletic sublineages of “Scatellini” (Figure 73). Despite these inconsistencies, I have continued to recognize Scatellini as originally characterized. I have, however, indicated the sublineages of Ephydrinae and their relationships according to my current understanding. The relationships I have outlined should be considered tentative, as their basis was derived from the Neo-



FIGURES 66-72.—Wings: 66, *Austrocoenia aczeli*; 67, *Paracoenia wirthi*; 68, *Notiocoenia paniculata*; 69, *Notiocoenia pollinosa*; 70, *Limnellia huachuca*; 71, *Scatella* (*Neoscatella*) *curtipennis*; 72, *Scatella* (*Teichomyza*) *fusca*.

tropical fauna only. A more comprehensive study of the higher classification of Ephydrinae is in preparation and will include formalized tribal rankings.

The discussion to follow is primarily to supplement the cladograms (Figures 73–77) and to introduce supporting character evidence. Numbered character states in the text correspond with those on the cladograms. I have incorporated character evidence in the text rather than in a table to more satisfactorily explain the character states.

I have divided Scatellini into two principal sublineages as follows (Figure 73): Ephydrini plus related genera; and *Scatella-Coenia* plus related genera. The lineage giving rise to Ephydrini and related genera is characterized by:

1. *Number of Dorsocentral Bristles*: The generalized condition in Ephydrinae is three pair of dorsocentral bristles (1 + 2). In this lineage there are five pair, an autapotypic condition.

Scatella-Coenia plus related genera are characterized by:

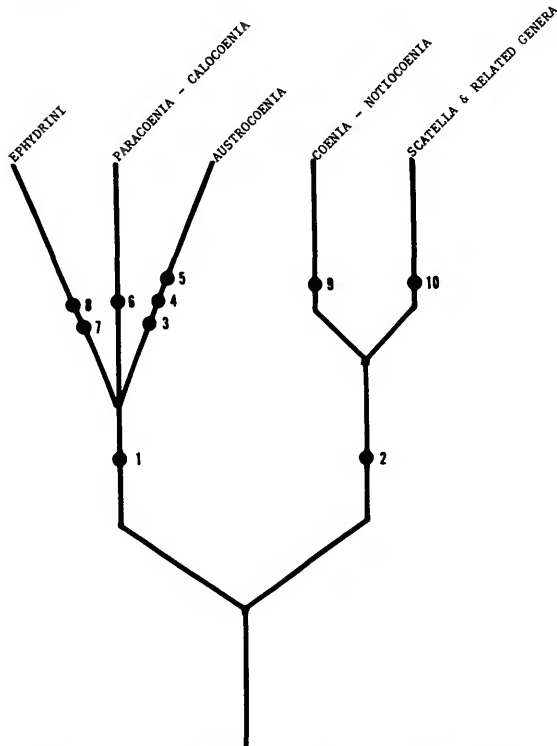


FIGURE 73.—Hypothetical phylogeny of subfamily Ephydrinae.

2. *Vestiture of Humeral Callus*: I interpret the generalized state in Ephydrinae to be one or two macrosetae plus scattered setulae. Consequently, the absence of macrosetae, as in *Scatella* and related genera, is a synapotypic character state.

The lineage of Ephydrini plus related genera is subdivided into three groups (Figure 73): Ephydrini, *Paracoenia-Calocoenia*, and *Austrocoenia*. The genus *Austrocoenia* is tentatively placed here, with equivalent ranking, because I have not found evidence that would ally it with another generic level taxon. The monophyly of *Austrocoenia* is established as follows:

3. *Length of Arista*: Generally the arista is as long or longer than the combined length of the antennal segments. In specimens of *Austrocoenia*, the arista is about as long as the third segment alone.

4. *Vestiture of Mesofrons*: The plesiotypic state in Ephydrinae is one or two strong cruciate pair of macrosetae, and/or bare or setulose. The mesofrons in specimens of *Austrocoenia* is distinctly setose, an apotypic character state.

5. *Strength of Dorsocentral Bristles*: Normally, all pairs of dorsocentral bristles are equivalent in size, but in specimens of *Austrocoenia*, the anterior three to four pair are weakly developed, not conspicuously larger than the surrounding setae.

The second assemblage of this sublineage, *Paracoenia-Calocoenia*, is characterized by:

6. *Length of Paravertical Bristle*: The paravertical bristles are generally small in Ephydrinae, not much larger than the larger postocular setae. In specimens of *Paracoenia-Calocoenia*, the paravertical bristles are subequal in length to the ocellar bristles.

The third assemblage of this sublineage is Ephydrini and is characterized by two synapotypies:

7. *Length of Tarsal Claws*: The generalized condition in Ephydridae is for the tarsal claws to be distinctly arched and generally short. In specimens of Ephydrini, the claws are very shallowly curved, nearly straight, and frequently they are long.

8. *Pulvilli*: Throughout most of Ephydridae, the pulvilli are conspicuous beneath the tarsal claws, but in Ephydrini, the pads are either greatly reduced or absent.

The second sublineage of Scatellini, *Scatella-Coenia* plus related genera, is subdivided into two assemblages of genera (Figure 73): *Coenia-Notio-coenia* and *Scatella* plus related genera.

The *Coenia-Notio-coenia* assemblage is characterized by:

9. *Number of Dorsocentral Bristles* (see character state number 1): As noted previously, the generalized condition is for three pair of dorsocentral bristles. Specimens of this assemblage have four, rarely five, pair of bristles.

The second assemblage of genera of this sublineage, *Scatella* and related genera are characterized and their monophyly established by:

10. *Maculation of Wing*: The plesiotypic state is a hyaline wing, characteristic of most members of Ephydrinae. This assemblage, however, is characterized by a generally infuscated, usually brownish, wing with a pattern of white areas arranged as follows: Cell R_1 with one white spot, sometimes subquadrate, more or less aligned or slightly apical 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 of cell.

The assemblage of *Scatella* and related genera appears to be monophyletic, as indicated by character state number 10. Within this assemblage, I recognize four genera in two groups (Figure 74). The first group comprises two genera, *Scatophila* and *Limnelli*. Character state evidence to establish this sister group relationship and to indicate their monophyly is:

11. *Number of Fronto-orbital Bristles*: The common number throughout the subfamily is two pair of laterocline fronto-orbital bristles. Specimens of *Limnelli* and *Scatophila* have only one pair.

12. *Thoracic Coloration and Vestiture*: The plesiotypic condition is for a more or less unicolorous thorax or one with gradually blending color changes. The thorax in specimens of *Scatophila* and *Limnelli* is bi- to tricolored, with each color being sharply demarcated from the other(s). Frequently the contrasting marks are cinereous, either as guttate or vittate maculae, and are particularly evident on the dorsum.

13. *Aedeagal Apodeme*: The shape of this structure appears to form a multidirectional morphocline. In males of *Scatophila* and *Limnelli*, this structure is rudimentary as a connecting, rodlike structure between the base of the aedeagus and the hypandrium or fused apices of the ventral gonapophyseal process. Basally, the apodeme is frequently bifurcate, as in *Limnelli* males, forming a Y-shaped structure.

Apotypic character states distinguishing *Scatophila* and establishing its monophyly are:

14. *Extension of Costal Vein*: The costa extends to vein R_{4+5} (third vein) in *Scatophila* wings. Throughout the remainder of the subfamily, the costa reaches vein M_{1+2} (fourth vein).

15. *Surstyli*: Paired surstyli are lacking or have been fused indistinguishably with the ventral margin of the epan-

drium in males of *Scatophila*. In males of *Limnelli*, as well as the subfamily in general, the surstyli are conspicuous, usually as setose processes. The surstyli are frequently of diagnostic importance for distinguishing taxa at various levels in the subfamily.

Apotypic character states distinguishing *Limnelli* and establishing its monophyly are:

16. *Wing Maculation* (see character state number 10): The wing maculation appears to be a simple morphocline in which the plesiotypic state is a hyaline wing. The next level is as described under character state number 10. In wings of *Limnelli*, the addition of several more white spots becomes consistent and the wing membrane around the spots becomes darker, brownish black.

17. *Aedeagus*: the aedeagus of *Limnelli* males has an anteroventral, median, slightly-curved prong that to my knowledge is unique within this subfamily.

The second group within the *Scatella* and related genera assemblage comprises two genera, *Scatella* and *Parascatella* (Figure 74). The sister group relationship between these two genera is established as follows:

18. *Aedeagal Apodeme* (see character state number 13): The shape and attachment of this structure appear to form a multidirectional 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 *Paracoenia* (Mathis, 1975) as well as to the base of the aedeagus. In males of these two genera, the apodeme has lost its attachment (articulation) with the hypandrium and is only loosely attached to the base of the aedeagus.

19. *Shape of Gonite*: Typically the gonites are paired structures extending from the sides of the aedeagus, connecting the latter with the hypandrium. In *Scatella* and *Parascatella*, 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. There is also a secondary ventral process. The apices of each ventral gonapophyseal process fuse to form a loop through which the aedeagus projects.

The monophyly of *Parascatella* is indicated by two character states:

20. *Aedeagal Apodeme* (see character state number 18): The shape of this structure in males of *Parascatella* is unique, being tear-drop shaped and flattened laterally.

21. *Supra-alar Bristle*: Within this entire sublineage, the generalized condition is for the supra-alar bristle to be weakly developed (less than length of postalar bristle) or absent. In specimens of *Parascatella*, this bristle is well developed, subequal to the postalar bristle.

The monophyly of *Scatella* is established as follows:

22. *Aedeagal Apodeme* (see character state number 20): Males of *Scatella* have an aedeagal apodeme that is dorso-ventrally flattened, and in profile it is usually angulate,

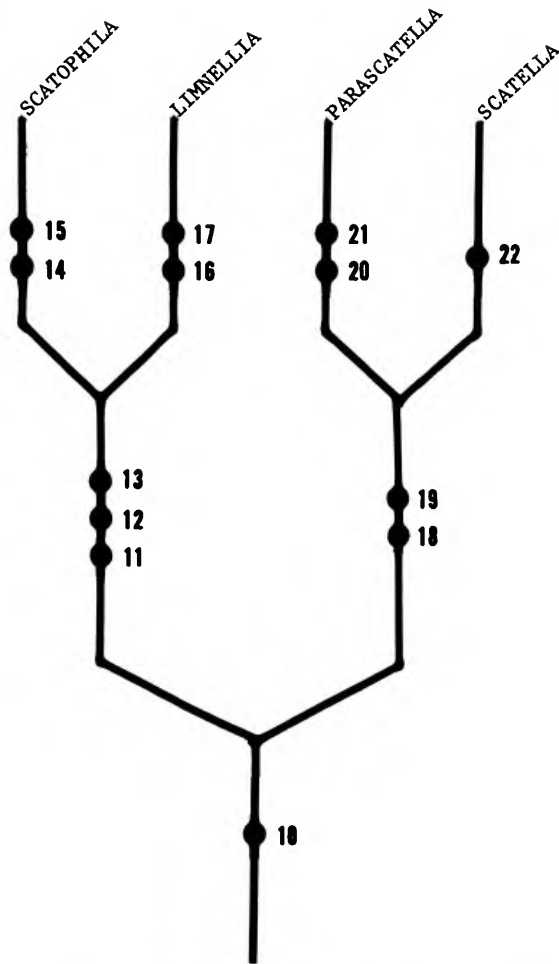


FIGURE 74.—Hypothetical phylogeny of *Scatella* and related genera.

sometimes L-shaped. This conformation is unique to males of this genus.

My study of the subgenera of *Scatella* is incomplete, as I have not examined specimens of all described subgenera in detail. Some of the subgenera, however, do appear to form a recognizable monophyletic lineage as I have indicated in Figure 75. Subgenera included are *Synhoplos* and *Teichomyza*, and the character state evidence to support this cladogram is as follows:

23. *Vestiture and Coloration of Frons*: Generally the mesofrons is differentiated from the remainder of the frons by its vestiture. In most cases, it is less pollinose, appearing

subshiny to shiny. The two subgenera have the frons uniformly pollinose, appearing consistently dull.

24. *Strength of Larger Facial Setae*: Marginal facial setae are generally larger in this subfamily, but in specimens of these two subgenera they are even more stoutly developed. This is especially evident in the setae along the oral margin.

The genus *Synhoplos* is obviously monophyletic, and I am of the opinion that it is the sister group of the lineage that gave rise to *Teichomyza* (Figure 75). The monophyly of *Synhoplos* is established as follows:

25. *Wing Development*: The typical condition in all of Ephyrinae as well as the entire family and order is for normally developed wings that enable flight. In specimens of *Synhoplos*, the wings are micropterous, not longer than the basitarsus of the hind leg.

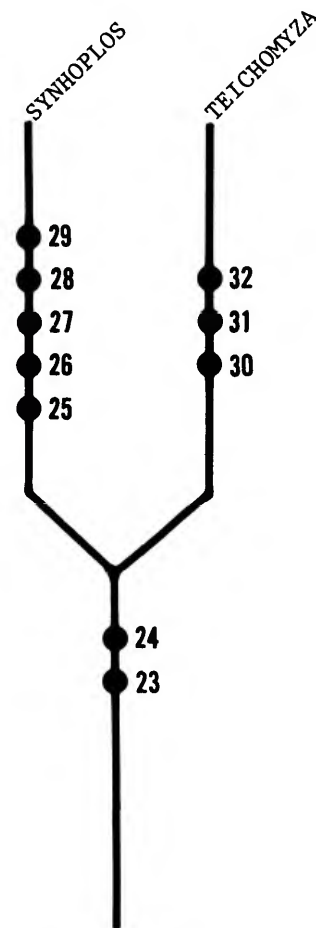


FIGURE 75.—Hypothetical phylogeny of *Scatella* (*Synhoplos*) and *Scatella* (*Teichomyza*).

26. *Length of Seta of Second Antennal Segment*: The second antennal segment generally has one larger seta, frequently spinelike. In *Synhoplos*, the second antennal segment bears a dorsally oriented seta that is subequal in length.

27. *Orientaion of Apical Pair of Scutellar Bristles*: Throughout most of the family, the apical pair of scutellar bristles project along the same plane as the body. In specimens of *Synhoplos*, these bristles are abruptly dorsally oriented, and frequently they are cruciate.

28. *Conformation of Scutellum*: The typical shape of the scutellum is triangular or roughly so, and usually its width is not more than its length. The scutellum in specimens of *Synhoplos* is very short, its length is about one-half its width.

29. *Turgidity of Femora*: This character corresponds with the micropterous wing development. With the shortened wing, making flight impossible, the legs of specimens of *Synhoplos* are better developed, particularly the femora, which are conspicuously swollen.

The monophyly of *Teichomyza* is indicated by three character states:

30. *Maculation of Wing* (see character state number 10): The condition of the wing of *Teichomyza*, being lightly infuscated but lacking a pattern of white spots, is apparently a reversal of the character state used to establish the monophyly of the lineage (*Scatella* and related genera) from which this subgenus arose.

31. *Vestiture of Scutellum*: In most other genera of *Scatellini*, the scutellum is bare, but in *Teichomyza*, the lateral margins of the scutellar disc are conspicuously setose.

32. *Strength of Setae of Middle Femur of Males*: Generally there is a row of short setae along the posteroventral margin of the middle femur in males of Ephydrinae. In males of *Teichomyza*, however, there is a short row, near the middle of the femur, of seven to ten long setae. Each of these longer setae is as long as the femoral width.

The monophyly and sister group relationship of the *Coenia-Notiocoenia* lineage (Figure 76) is indicated by character state number nine as noted earlier. The monophyly of *Coenia* is established by:

33. *Vestiture of Vein R₁*: The wing veins are generally bare in Ephydridae, a condition I interpret to be plesiotypic. Vein R₁ in specimens of *Coenia* has one to three dorsal setae near its base, which is a condition unique to specimens of *Coenia*.

Notiocoenia is the sister group of *Coenia* (Figure 76), and its monophyly is confirmed by:

34. *Vestiture and Coloration of Frons* (see character state number 23): The common, plesiotypic condition, as noted previously, is for the mesofrons to be differentiated by its color or vestiture. The entire frons, in specimens of *Notiocoenia*, is uniformly pollinose, dull appearing.

35. *Inter Alar Bristles*: Inter alar bristles are uncommon in Ephydridae and I interpret their presence, as in specimens of *Notiocoenia*, to be apotypic.

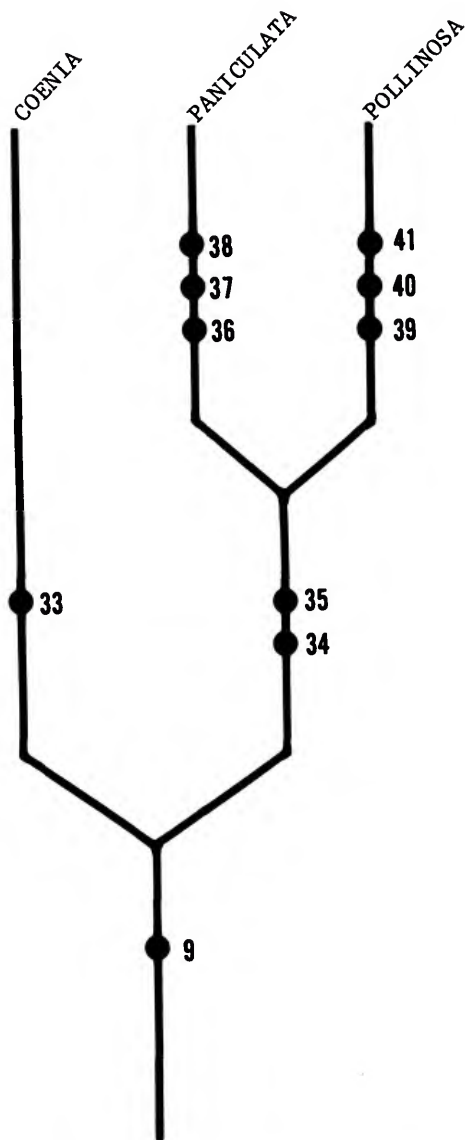


FIGURE 76.—Hypothetical phylogeny of *Coenia* and *Notiocoenia*.

Within the genus *Notiocoenia*, I have distinguished two species groups, the *pollinosa* and *paniculata* groups (Figure 76). The monophyly of the *paniculata* group is clearly indicated by the following synapotypic character states:

36. *Outer Vertical Bristles*: Two vertical bristles are generally present in Ephydridae, an anterior convergent pair

and a divergent posterior pair. In specimens of the *paniculata* group the outer pair is lacking.

37. *Vestiture of Humeral Callus* (see character state number 2): Generally there are macrosetae or at least some arising from the humeral callus. Their absence, as in specimens of the *paniculata* group, is autapotypic.

38. *Length of Fifth Tergum of Male*: In the majority of Ephydrinae, the fifth tergum of males is as long or longer than the fourth, but in males of the *paniculata* group, the fourth is much longer than the fifth, an apotypic condition.

The *pollinosa* group is distinguished by three apotypic character states:

39. *Supra-alar Bristle* (see character state number 21): I have noted earlier that the generalized condition is for a well-developed supra-alar bristle. In specimens of the *pollinosa* group, like specimens of *Scatella*, the supra-alar is reduced.

40. *Vestiture of Arista*: The *Coenia-Notiocoenia* lineage is generally characterized by the nearly plumose arista; there are usually numerous dorsally branching rays. In specimens of the *pollinosa* group, the arista is at most macropubescent.

41. *Maculation of Wing* (see character state number 10): Again, as indicated previously, the plesiotypic condition is a hyaline to lightly infuscated wing without a pattern of white spots. As in *Scatella* and related genera, the wing of specimens of the *pollinosa* group is infuscated and has white spots (see species group description for details).

The last lineage that I will discuss in detail is that which gave rise to the genera *Paracoenia* and *Calocoenia* (Figure 77). I have already established the monophyly of this group earlier (see character state number 6) and here wish to characterize the included genera.

Paracoenia is characterized by three apotypic character states:

42. *Conformation of Female Ventral Receptacle*: In Ephydrinae, the operculum of the female ventral receptacle is generally much wider than high, but in females of *Paracoenia*, it is as high as wide.

43. *Radial Stem Vein*: Generally the radial stem vein is bare, the plesiotypic condition. The wings of *Paracoenia* have the radial stem vein with one or two dorsal setae.

44. *Conformation of Male Terminalia*: I have lumped three characters here for convenience. The conditions as found in *Paracoenia*, are unique with respect to the shape of the surstylus, gonite and aedeagus, and a median triangular process between the base of the surstylus.

I am recognizing two subgenera of *Paracoenia*, *Paracoenia sensu stricto*, and *Thiomyia* (Figure 77). The monophyly of *Thiomyia* is established by:

45. *Puvilli* (see character state number 8): Like Ephydrini, specimens of *Thiomyia* lack puvilli, an apotypic character state in both taxa.

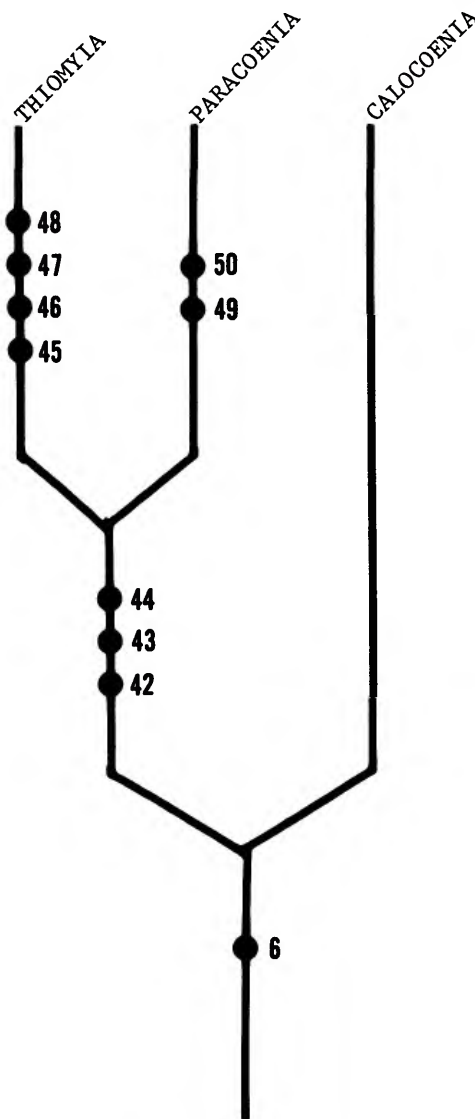


FIGURE 77.—Hypothetical phylogeny of *Paracoenia* (*Thiomyia*), *Paracoenia* (*Paracoenia*), and *Calocoenia*.

46. *Conformation of Tarsomeres*: The tarsomeres, particularly the apical four, are generally cylindrical, but in specimens of *Thiomyia*, there is a tendency for these to be explanate, an unique character state.

47. *Supra-alar Bristle* (see character state number 21): Within the Ephydrini plus related genera assemblage, a well-developed supra-alar bristle is present. In specimens of *Thiomyia*, it is lacking.

48. *Sternopleural Bristle*: Like the supra-alar bristle, the

sternopleural bristle in specimens of *Thiomyia* is lacking, a condition unique to this subgenus.

Paracoenia sensu stricto is distinguished from and its monophyly established by the following:

49. *Seriation of Acrostichal Setae*: The generalized condition throughout Ephydrinae is for two rows of acrostichal setae. In specimens of the subgenus *Paracoenia* the acrostichal setae are in four to six unserialated, irregular rows.

50. *Vestiture of Middle Femur of Male*: I have previously noted that the middle femur of the male has a row of short setae along the posteroventral surface (character state number 32). Males of the subgenus *Paracoenia* are unique in having a dense, comblike row of longer setae.

In the preceding, I have enumerated my concept

of the phylogeny of Scatellini, that is, the sequence of cladistic events from which our present-day fauna resulted. With few exceptions, each taxon is characterized by one or more synapotypies to establish its monophyly and the sister group status of included taxa. While doing this, it became apparent that some genera were paraphyletic, i.e., did not include all descendent species of a common ancestor, and to be monophyletic should include another genus or genera. These taxa are consigned to subgeneric status to make all genera monophyletic. Thus, according to my classification, *Thiomyia* is a subgenus of *Paracoenia*, and *Apulvillus*, *Neoscatella*, *Synhoplos*, and *Teichomyza* are subgenera of *Scatella*.

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