

RESEARCH ARTICLE

Phylogeny and taxonomy of the shore-fly tribe Scatellini (Diptera: Ephydriidae: Ephydrinae)

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<https://zoobank.org/17D6AEAA-7851-4B4D-9FDB-19E7AB689358>

ABSTRACT. The tribe Scatellini comprises 247 species (plus five nomina dubia) that are distributed in all biogeographical regions except Antarctica. The tribe currently includes nine genera. One genus, *Scatella* Robineau-Desvoidy, 1830, includes six subgenera. To test the monophyly of Scatellini and to understand the phylogenetic relationships among the included genera, a cladistic analysis was performed. The optimization criterion chosen was parsimony using implicit character weighting, and the analysis was based on the morphological characters of adult males and females. The species of eight of nine genera of Scatellini from different geographic regions were studied. Species of the other tribes of Ephydrinae were also included to provide insight on the phylogenetic position of Scatellini within this subfamily. The implied weighting analysis showed that the tribe Scatellini, as currently characterized, is a monophyletic group, as are all the genera included in it. From this analysis, two major lineages emerged: 1. *Scatella* and its included subgenera; 2. All other genera of Scatellini. The latter clade includes (*Thinoscatella* (*Lamproscatella* + *Haloscatella*)) and the clade (*Amalopteryx* (*Philotelma* (*Limnellia* + *Scatophila*))). Five subgenera of *Scatella* were recovered as monophyletic groups: *Parascatella* Cresson, *Synhoplos* Lamb, *Apulvillus* Malloch, *Scatella*, and *Teichomyza* Macquart. *Neoscatella* Malloch is synonymized with *Scatella* sensu stricto. In the implied weighting analysis, Ephydrini and Scatellini are sister-groups. Based on this phylogenetic reconstruction, the taxonomy of Scatellini is presented at the generic level. A key to the included genera and subgenera is also presented.

KEY WORDS. Cladistic analysis, taxonomy, *Scatella*, Ephydrini, Dagini.

INTRODUCTION

Nearly 60 years ago, a noted English dipterist, Harold Oldroyd (1964: 188–189), summarized the shore-fly family Ephydriidae as follows “Clearly, then, Ephydriidae are nothing if not versatile... Evidently we are seeing in the Ephydriidae a family of flies in the full flower of its evolution, and as such they offer attractive material for study.” More recently, Borkent (2018: 108) observed that Diptera are generally “an excellent group for the study of phylogenetic relationships”. We concur with these astute students of Diptera, and as partial fulfillment of their observations and recommenda-

tions, we offer this phylogenetic study of Scatellini Wirth & Stone, 1956 (Ephydrinae Zetterstedt, 1837) with some considerations on other related tribes within the subfamily.

Specimens of Ephydrinae are probably the most easily recognized (together with *Ochthera* Latreille, 1802) within the Ephydriidae and are also among the best-known of shore flies. As such, they have attracted the attention of students in biology from various perspectives due to their peculiar morphology and unusual habitat preferences and tolerances. Ephydrinae is generally recognized by its protuberant face and its laterocline fronto-orbital setae. Species of this subfamily are associated primarily with freshwater habitats,

but they also occur in the effluent of hot springs, or they occur in maritime habitats, as well as in inland saline and alkaline environments in temperate and tropical regions of the world (Foote 1995, Mathis and Zatwarnicki 1995, Mathis and Marinoni 2016).

Cresson (1930) proposed the basic concept of Ephydriinae that is still largely accepted today, although the subfamily has been revised and updated in several subsequent papers. Wirth and Stone (1956), in a key to North America genera, proposed two of the included tribes, Ephydrini and Scatellini, which were characterized by long and straight claws and the absence of pulvilli (Ephydrini) or by curved and generally shorter claws and well-developed pulvilli (Scatellini). In the first cladistic analysis of the subfamily, Mathis (1979b) presented Ephydriinae as a monophyletic group divided into three principal lineages (see details below). In his phylogeny, Mathis (1979b), found that genera close to Ephydrini, such as *Paracoenia* Cresson, 1935 and related genera, including *Austrocoenia* Wirth, 1970, bear curved claws and pulvilli. Thus, the tribe Scatellini, as initially proposed by Wirth and Stone (1956), is a paraphyletic group, being characterized by symplesiomorphies, and having the tribe Ephydrini as an included lineage within “Scatellini” (Mathis 1979b). Although Scatellini, as then characterized, was paraphyletic, the tribe continued to be recognized as originally proposed.

Zatwarnicki (1992) published a phylogeny for Ephydriidae and divided the family into five subfamilies. In this brief but seminal paper, Zatwarnicki modified Ephydriinae as follows: Parydrini was formally placed in Ephydriinae following the suggestion of Mathis and Zatwarnicki (1990); *Brachydeutera* Loew, 1860 was included in Dagini; and *Coenia* Robineau-Desvoidy, 1830, *Paracoenia* and *Notiocoenia* Mathis, 1980 were transferred from Scatellini to Ephydrini. Zatwarnicki (1992) further restricted Scatellini to 11 genera and proposed its monophyly based on the proepisternum usually lacking macrosetae.

Subsequent to Zatwarnicki's (1992) classification, other more recent modifications within Ephydriinae include Zhang et al. (2005; description of the Oriental genus *Sinops* Zhang, Yang & Mathis, 2005 in the tribe Dagini) and Mathis (2008; description of two new Neotropical genera in Ephydrini: *Paraephydra* and *Neoephydra*).

Background history of the tribe Scatellini, including previous phylogenetic research

Scatellini comprises 247 species (plus five nomina dubia) that are classified into nine genera (Mathis and Zatwarnicki 1995). *Scatella* Robineau-Desvoidy, 1830 has been

further subdivided into six subgenera and has the largest number of described species (139 species plus two nomina dubia). The tribe has representatives in all biogeographic regions except Antarctica.

The first genera now included in Scatellini were described in the 19th century as follows: the type genus, *Scatella*, was proposed in 1830, followed by *Teichomyza* Macquart in 1835. Eaton (1875) described *Amalopteryx*, and Becker (1896) then proposed *Scatophila* and *Philotelma*. In the 20th century, Hendl (1917) described *Lamproscatella*, and Lamb (1917) proposed *Synhoplos*. In a series of papers, Malloch (1925, 1933, 1934) described three genera: *Limnellia*, *Neoscatella*, and *Apulvillus*, respectively.

Other genera and subgenera were also proposed, but the taxonomic status of many of these taxa has changed, the names were synonymized or transferred to other tribes. The taxonomic changes recognized today are as follows: Sturtevant and Wheeler (1954) included *Neoscatella* and *Parascatella* as subgenera in *Scatella*; Mathis (1979a) described two new subgenera in *Lamproscatella*, *Haloscatella* Mathis and *Thinoscatella*, and both were later accorded generic status (Olafsson 1991); and Mathis (1980) included *Apulvillus*, *Teichomyza* and *Synhoplos* in *Scatella* as subgenera.

Mathis (1979b) proposed the group “*Scatella* plus related genera” for four genera that have white spots on their wings: ((*Scatella* + *Parascatella*) + (*Scatophila* + *Limnellia*)). In this same paper, the group *Lamproscatella* plus related genera ((*Amalopteryx* + *Philotelma*) + *Lamproscatella*) was characterized by a reduced or absent genal seta. A year later and in a revision of Neotropical species, Mathis (1980) proposed the subgenera *Synhoplos* Lamb and *Teichomyza* Macquart as sister-groups within the genus *Scatella*.

Olafsson (1991) presented a phylogeny of Ephydriinae based on genera from the western Palearctic Region. He proposed a monophyletic group that is characterized by a lack of postpronotal setae and applied the available tribal name Scatellini to this group. The genus *Coenia*, which has a postpronotal seta, was moved to the tribe Ephydrini. The other genera comprising this group, *Paracoenia* and *Austrocoenia*, were later moved to the tribe Ephydrini, leaving 11 genera in Scatellini (Zatwarnicki 1992). Zatwarnicki and Baez (1991) and Zatwarnicki and Mathis (1994) divided Scatellini into three lineages: the first group *Philotelma* (*Philotelma*, *Scatophila*, *Limnellia*, and *Tauromima*), the second group *Lamproscatella* (*Amalopteryx*, *Haloscatella*, *Lamproscatella*, *Thinoscatella*), and the third group *Scatella* (*Scatella*). In the world catalog of shore flies, Mathis and Zatwarnicki (1995) relegated *Parascatella* to subgeneric status within *Scatella*.

The relationships among species within some genera were also investigated. Mathis and Shewell (1978) presented phylogenetic relationships for species within *Parascatella* and for the *trisetata* group of *Scatella*; Mathis (1978) proposed a phylogeny of Nearctic species of *Limnelliinae*; Mathis (1979b) published a phylogeny of *Lamproscatella* based on Nearctic species, proposing the subgenera *Haloscattella* and *Thinoscattella*; Mathis and Wirth (1981) revised the Australian species of *Neoscattella* and included a phylogeny for the species of the Australasian Region; and finally, Zatwarnicki and Mathis (1994) proposed a phylogeny for species of *Scatophila* on a global basis.

As summarized herein, the taxonomy, phylogeny, and classification of Scatellini have undergone many modifications over the years. These studies, however, were usually based on limited groups of species or on taxa from a restricted geographic area—none on global, comprehensive basis except for *Scatophila*. Given these limitations, the relationships among the species and genera included in Scatellini are not as well understood. To clarify these relationships, a comprehensive phylogenetic analysis was undertaken with the following objectives: (i) to test the monophyly of Scatellini and its subordinate groups on a global basis, using morphological characters from adult males and females, and (ii) to propose a hypothesis of cladistic relationships for the taxa included within Scatellini.

MATERIAL AND METHODS

Taxon sampling

The descriptive terminology, with the exceptions noted in Mathis (1986) and Mathis and Zatwarnicki (1990), follows Cumming and Wood (2017).

Our study includes 62 terminal taxa (50 from the ingroup, Scatellini, and 12 outgroups: *Ilythea spilota* (Curtis, 1832), *Philygria debilis* Loew, 1861, *Hyadina furva* Cresson, 1926, *Dagus rostratus* (Cresson, 1918), *Diedrops steineri* Mathis, 1984, *Physemops nemorosus* (Cresson, 1914), *Parydra aquila* (Fallén, 1813), *Brachydeutera neotropica* Wirth, 1964, *Notiocoenia paniculata* Mathis, 1980, *Paracoenia bisetosa* Coquillett, 1902, *Ephydra riparia* Fallén, 1813, *Neoephydra araucaria* Mathis, 2008). The ingroup comprises 50 species with representatives from eight of the nine genera currently included in Scatellini (Mathis and Zatwarnicki 1995) and the morphological diversity within the tribe. Only *Tauromima* Papp, 1979, a monotypic genus from New Guinea and known only by the holotype male, was not made available for our study. The choice of representative

species for each genus was based on morphological diversity and geographical distribution. Type species of all genera and subgenera were included so potential taxonomic or nomenclatural changes would be facilitated without undue encumbrance. The choice of outgroup taxa considered previous phylogenetic hypotheses for Ephydrinae (Mathis 1979a, 1979b, 1980, 1982, Mathis and Simpson 1981, Olafsson 1991, Zatwarnicki 1992). Nine species of the tribes Dagini, Ephydrini and Parydrini (Ephydrinae) and three species of Ilytheinae, representing the three tribes of this subfamily, were selected as outgroups.

The specimens used in this study were borrowed from the following institutions: American Museum of Natural History, New York, USA (AMNH); Academy of Natural Sciences of Philadelphia, USA (ANSP); The Natural History Museum, London, United Kingdom (NHMUK); Insect Collection of the University of Guelph, Guelph, Canada (DEBU); Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil (DZUP); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Staatliches Museum für Naturkunde in Stuttgart, Ludwigsburg, Germany (SMNS); New Zealand Arthropod Collection, Entomology Division, Auckland, New Zealand (NZAC).

Character sampling and coding

We selected characters from the external and internal morphology of adult males and females. We conducted a survey of characters used in previous phylogenetic studies (Mathis 1979b, 1980, Olafsson 1991, Zatwarnicki 1992). These characters were then re-evaluated and sometimes reinterpreted.

Character elaboration considered the following criteria: topological correspondence among the observed structures and the independence of characters and states (Hawkins et al. 1997). The characters were treated as hypotheses for groupings (taxic homology sensu Patterson 1982). Characters are contingent and mostly binary. We chose to construct multi-state characters when necessary to preserve morphological diversity. Character states indicated with the symbol [–] mean inapplicable states. The matrix data was constructed in Winclada ver. 1.00.08 (Nixon 2002). A complete list of the morphological characters is presented in Appendix 1. The character matrix is presented in Supplementary Table S1.

A total of 106 characters were examined and coded for 62 terminal taxa. Thirty-eight characters are proposed for the

first time and are indicated with an asterisk (*). Thirty-two characters are from the head, 36 from the thorax and 38 from the abdomen. After some characters and as appropriate, we present comments (Appendix 1).

Cladistic analysis

The cladistic analyses were carried out using the program TNT version 1.5 no taxon limit (Goloboff and Catalano 2016). The characters were treated as non-additive under Fitch parsimony (Fitch 1971). *Ilythea spilota* (Curtis 1832) was used to root the tree. The analysis was performed with traditional heuristic search (by the command “traditional search”). The parameters utilized in all searches were as follows: “Max.tree”= 100,000; “random seed”=1000; “number of additional sequences”=10,000; “tree to save per replication”=10, utilizing “tree bisection reconnection” (TBR) as the permutation algorithm of the branches.

Searches for the most parsimonious trees were conducted using implied weighting (Goloboff 1993). A TNT script (setk.run) written by Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucuman, Argentina), was used to calculate the appropriate value for the constant K (for details see

Goloboff et al. 2008). The script returned a value of K = 9.6875 for our data set, which was then applied. Relative Bremer support was used in conjunction with the implied weighting analysis (Goloboff et al. 2003). The cladograms recovered with TNT were then edited with Winclada version 1.00.08 (Nixon 2002). Herein, we use the term synapomorphy to refer exclusively to unambiguous synapomorphies identified in our phylogeny by mapping the morphological characters onto the selected tree (Figs 1–2). These synapomorphies are referred to as (i) non-homoplasious, which uniquely identifies a clade, and (ii) homoplasious, which in addition to the clade of interest can identify some other clade. Non-homoplasious and homoplasious synapomorphies are represented by black circles and blank circles, respectively.

RESULTS AND DISCUSSION

From our analysis using implied weighting, five equally parsimonious cladograms were obtained with a length of 343 steps, best score = 15.49, CI = 37 and RI = 77. One most parsimonious cladogram is presented in Fig. 1 and is used as the primary means to convey relationships, and the discus-

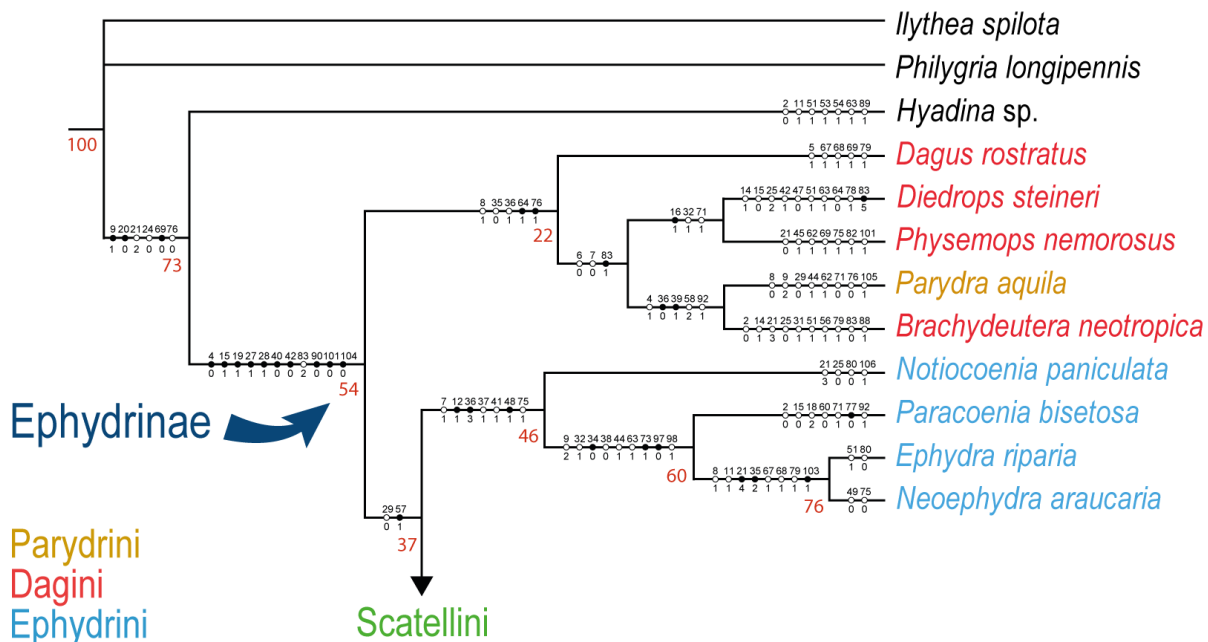


Figure 1. One of the five most parsimonious trees obtained from implied weighting parsimony searches, showing outgroup relationships (Scatellini branch is shown in Fig. 2). Black circles indicate non-homoplasious transformations and blank circles indicate homoplasious transformations. Characters and its states are superimposed on the branches (character number is shown above the circle and the corresponding character state is shown below it). Relative Bremer support values [red] are included below each branch.

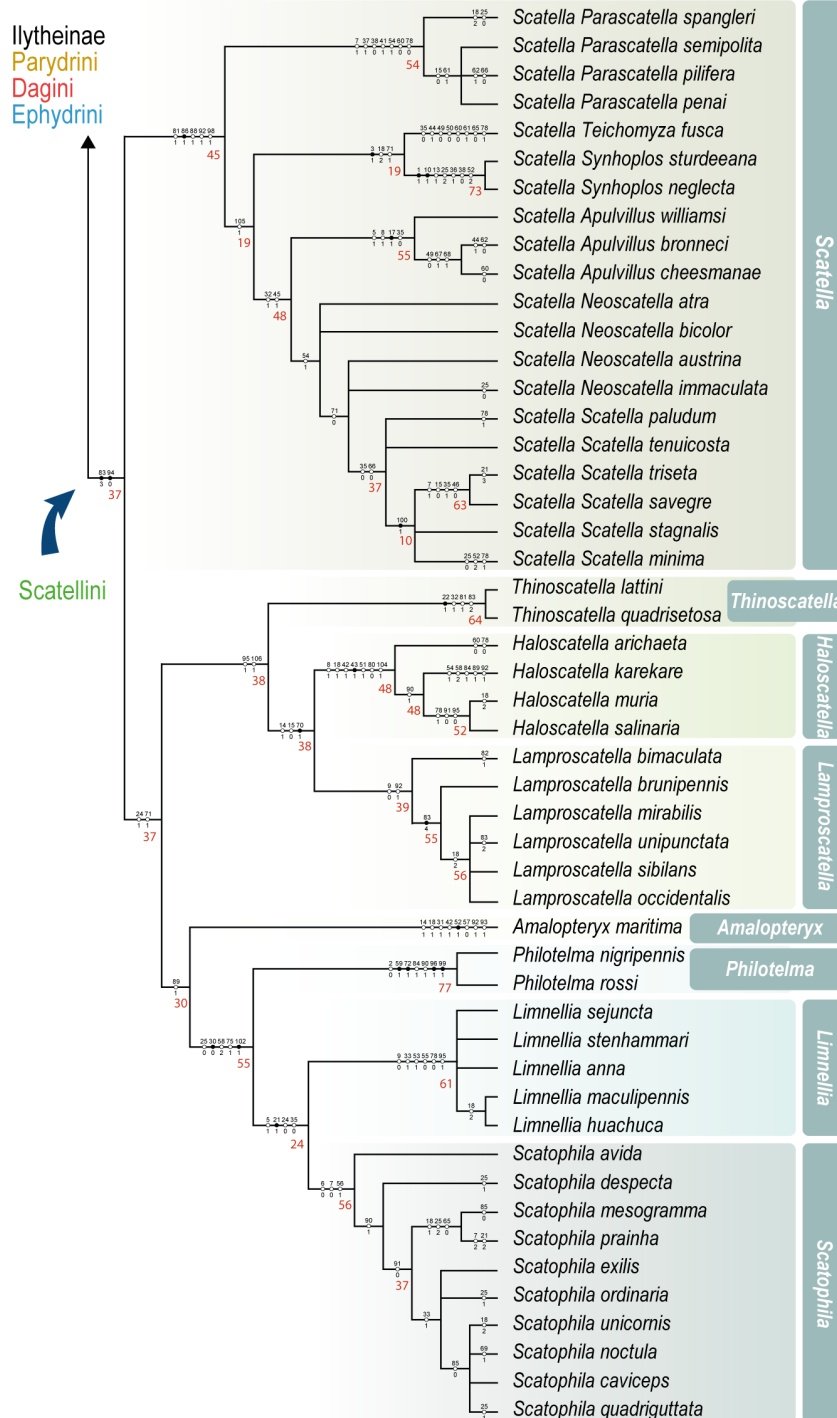


Figure 2. One of the five most parsimonious trees obtained from implied weighting parsimony searches, showing ingroup relationships (outgroup is shown in Fig. 1). Black circles indicate non-homoplasious transformations and blank circles indicate homoplasious transformations. Characters and its states are superimposed on the branches (character number is shown above the circle and the corresponding character state is shown below it). Relative Bremer support values [red] are included below each branch.

sion that follows is simply to augment or highlight specific relationships, especially at the generic level.

The monophyly of Ephydrinae is corroborated by the following synapomorphies: (i) medial facial area and oral margin with setulae (character 4[1]); (ii) ocelli arranged as an isosceles triangle (character 15[1]); (iii) fronto-orbital setae latero-clinate (character 19[1]); (iv) palpus slender, parallel sided, not claviform (character 27[1]); (v) anterior view of the lacinia T-shaped (character 28[1], Fig. 15); (vi) postsutural supra-alar seta present (character 40[1]); (vii) posterior notopleural seta inserted at same level as anterior seta (character 42[1]); (viii) aedeagus keel-like (character 83[1], Fig. 35); (ix) gonites and hypandrium fused (character 90[1]); (x) sternite 8 of female with two sclerites (character 101[1]); (xi) operculum of female ventral receptacle present (character 104[1]).

Ephydrini is the sister-group of Scatellini. The character states that support this relationship are: (i) costal vein slightly to deeply overlaps itself at subcostal break (character 57[1]), a non-homoplasious synapomorphy, and (ii) cibarium with lateral projections (character 29[0].), a homoplasious synapomorphy.

Scatellini, as originally proposed by Wirth and Stone (1956), is a paraphyletic lineage (Mathis 1979b, 1980). In our analysis, however, we recovered a monophyletic clade that included all genera recognized in Scatellini by Zatwarnicki (1992) and Mathis and Zatwarnicki (1995). The arrangement of taxa in this cladogram also corroborated the hypothesis of groupings proposed by Zatwarnicki (1992). The node for Scatellini in the classification of Ephydrinae is supported by two non-homoplasious synapomorphies: (i) the presence of a posterodorsal arm of the gonite (character 94[1]); and (ii) the aedeagus with slipper or shoe-like shape (character 83[3]).

Scatellini is further divided into two primary lineages: 1) *Scatella* Robineau-Desvoidy and its component subgenera; 2) All other genera that are included within Scatellini. The discussion to follow treats these two groupings in this same sequence.

Scatella was recovered as a monophyletic group supported for one non-homoplasious synapomorphy: ejaculatory apodeme present (character 86[1]); and four homoplasious synapomorphies: (i) epandrium ovoid (character 81[1]), (ii) phallapodeme absent (character 88[1]), (iii) gonial arch fused (character 92[1]), and (iv) long, strong setae at female cerci (character 98[1]). The character evidence and its analysis clearly indicate that *Scatella* is a monophyletic genus.

Our analyses also retrieved as a monophyletic lineage, five of the six subgenera known for *Scatella*: *S. (Parascatella)*,

S. (Teichomyza), *S. (Synhoplos)*, *S. (Apulvillus)*, and *S. (Scatella)*. No character was discovered that is a synapomorphy for *Neoscatella* or that consistently distinguishes the species of *Neoscatella* from *Scatella* s. str. Thus, we are formally combining the species of these two groups, making *Neoscatella* a junior synonym of the subgenus *Scatella*. These classificatory and nomenclatural actions follow the precedent proposal by Mathis (1980) who previously suggested that *Neoscatella* was a paraphyletic assembly. The phylogenetic analysis reported herein corroborates this suggestion and hypothesis.

Within *Scatella*, the first division includes *Parascatella* as the sister-group to the other subgenera, and this node is supported by five characters that are homoplasious synapomorphies: (i) facial setae lateroventrally curved (character 7[1]), (ii) proepisternum bearing macrosetae (character 37[1]), (iii) postpronotum with 1–3 setae plus scattered setulae (character 38[0]); (iv) postsutural supra-alar seta as long as postalar seta (character 41[1]), and (v) wing spots evident (character 54[1]). The node giving rise to the other subgenera is established by one homoplasious synapomorphy: female ventral receptacle with tube-like operculum (character 105[1]).

The next division comprises two composite sublineages: (*Teichomyza* + *Synhoplos*) + (*Apulvillus (Scatella, Neoscatella)*). The clustering of the subgenera *Teichomyza* + *Synhoplos* is supported by one unambiguous and two homoplasious synapomorphies, respectively: (i) dorsal seta of pedicel same length as basal flagellomere (character 3[1]), (ii) eye conspicuously higher than wide (character 18[2]), and (iii) male with one well-developed sternite posterior to sternite 4 (character 71[1]). The node giving rise to the subgenera *Apulvillus* and *Scatella* s. str. is supported by two homoplasious synapomorphies: (i) mediproboscis with lateral sclerite present (character 32[1]) and (ii) acrostichal setae not extended to scutellum (character 45[1]). The node leading to the subgenus *Apulvillus* is further supported by one non-homoplasious synapomorphy: ocellar setae short, length is half of fronto-orbital seta (character 17[1]), and two homoplasious synapomorphies: (i) face with medial portion sparsely setulose (character 5[1]), and (ii) face without row of setulae near parafacial (character 8[1]). The presence of white spots in the wing (character 54[1]) is an homoplasious synapomorphy that distinguishes *Scatella* (including *Neoscatella*). Although the subgenus *Apulvillus* is very similar and cladistically close to *Scatella*, we have opted to maintain its current status due to its peculiar morphology and distribution, remotely on island of Hawaii and French Polynesia, a restricted distribution that is somewhat isolated.

Scatella and its subgenera are the sister-group of all other genera within Scatellini. The “all other genera within Scatellini” is a large clade that is further divided into two large sublineages: The first large sublineage is: (*Thinoscattella* (*Haloscattella* + *Lamproscattella*)), which is supported by two homoplasious synapomorphies: (i) large posterodorsal arm and gonial arch like a flap (character 95[1]) and (ii) female ventral receptacle with small operculum, not covering the extended process (character 106[1]). The second large sublineage is: (*Amalopteryx* (*Philotelma* (*Limnellia* + *Scatophila*))), which is supported by a single homoplasious synapomorphy: phallapodeme dorsoventrally flattened, usually with two lateral projections, rod-like, lacking a keel (character 89[1]).

We will now discuss the generic clades within each of these two large sublineages in the same sequence that is presented above.

The first large sublineage comprises the genus *Thinoscattella*, which is the sister-group to the node giving rise to *Haloscattella* and *Lamproscattella*. The monophyly of *Thinoscattella* is supported by one non-homoplasious synapomorphy: posterior fronto-orbital seta inserted closer to the inner vertical seta than to anterior fronto-orbital seta (character 22[1]), and three homoplasious synapomorphies: (i) mediproboscis with a lateral sclerite (character 32[1]); (ii) posterior view of epandrium ovoid (character 81[1]); and (iii) aedeagus long and thin, tubular (character 83[2]). The node giving rise to *Haloscattella* and *Lamproscattella* and the sister-group to *Thinoscattella* is evidenced by one non-homoplasious synapomorphy: sternite 1 absent (character 70[1]), and one homoplasious synapomorphy: frontal vitta invested with microtomentum (character 14[1]). The monophyly of *Haloscattella* is well corroborated by one non-homoplasious synapomorphy: anterodorsal corner of anepisternum with one strong seta curved (character 43[1]), and five homoplasious synapomorphies: (i) parafacial margin lacking row of setulae near parafacial (character 8[1]); (ii) eye conspicuously wider than high, usually obliquely oriented (character 18[1]); (iii) insertion of posterior notopleural setae distinctly elevated above level of anterior seta (character 42[1]); (iv) prescutellar acrostichal seta longer than other acrostichal setae (character 51[1]); and (vi) female ventral receptacle lacking operculum (character 104[1]). We note that the species of *Haloscattella* that share some character states with *Philotelma* and *Scatophila* are from New Zealand, and perhaps the inclusion of these in *Haloscattella* should be examined further. The genus *Lamproscattella* is established by two homoplasious synapomorphies: (i) facial projection less than half height of head (character 9[0]); and (ii) arms of gonial arch fused (character 92[1]).

The monotypic genus *Amalopteryx* appears as the sister-group to the node giving rise to *Philotelma*, *Limnellia*, and *Scatophila*. The node for this composite lineage, however, is supported by a single character: phallapodeme flattened dorsoventrally, usually with two lateral projections (character 89[1]). Whereas the monophyly of *Amalopteryx* is corroborated by one non-homoplasious synapomorphy: stenopterous wing (character 52[1]), and six homoplasious synapomorphies: (i) frontal vitta invested with microtomentum (character 14[1]); (ii) eye conspicuously wider than high, usually obliquely oriented (character 18[1]); (iii) length of sclerite 2 of labellum longer than width of labellum, overlapping prementum (character 31[1]); (iv) posterior notopleural seta inserted distinctly elevated above level of anterior seta (character 42[1]); (v) arms of gonial arch fused (character 92[1]); (vi) gonial arch and phallapodeme fused (character 93[1]). The clade formed by the genera *Philotelma*, *Limnellia*, and *Scatophila* was recovered as a monophyletic lineage. This relationship was proposed previously (Mathis 1979b, Zatwarnicki and Mathis 1994) and is corroborated by two non-homoplasious and two homoplasious synapomorphies, as follows: (i) cibarium with lateral projections short, same length as ventral projection (character 30[1]); (ii) female sternite 8 as two subquadrate sclerites (character 102[1]); (iii) crossvein r-m distinctly distal to subcostal break (character 58[2]); (iv) epandrium lacking epandrial or surstylar separation (character 75[1]). The monophyly of *Philotelma* is well documented by four non-homoplasious synapomorphies: (i) an infusate spot over crossvein dm-m (character 59[1]); (ii) male sternite short and bearing spine-like setae (character 72[1]); (iii) female sternite 8 bearing prominent setulae (character 96[1]); (iv) female sternite 7 lacking (character 99[1]); and two homoplasious synapomorphies: (i) aedeagus with a sclerotized basiphallus and a membranous distiphallus (character 84[1]); (ii) gonite and hypandrium separate (character 90[1]). The sister-group of *Philotelma*, which is the node giving rise to *Limnellia* and *Scatophila*, is corroborated by one non-homoplasious and one homoplasious synapomorphies: (i) a single laterocline fronto-orbital seta (character 21[1]), and (ii) medial area of face sparsely setulose (character 5[1]). Two relatively large genera, *Limnellia* and *Scatophila*, comprise the sister-group of *Philotelma*. *Limnellia* is substantiated by three homoplasious synapomorphies: (i) mesonotum distinctly bi- or tricolored (character 33[1]); (ii) wing infusate, darker toward anterior margin, lighter toward posterior margin (character 53[1]); (iii) a large posterodorsal arm and gonial arch (character 95[1]). The monophyly of *Scatophila* is documented by a single cha-

racter: costal vein short, extended only to vein R_{4+5} (character 56[1]). The taxonomy of the Nearctic species of *Scatophila* is currently being investigated by Zatwarnicki & Mathis.

Phylogenetic conclusions

This cladistic study and analysis are the most comprehensive phylogenetic assessment of Scatellini thus far available. The taxon sampling for this study included representatives of all genera except *Tauromima*. Moreover, these taxa are from several regions of the world and include a rather comprehensive sampling to account for species diversity and morphological variation.

Scatellini, as proposed by Zatwarnicki (1992) and Mathis and Zatwarnicki (1995), was recovered as a monophyletic group, as are all included genera and subgenera. There are two major lineages within Scatellini: first, *Scatella* and its subgenera; and second, all other genera included in Scatellini. The latter clade was separated in the analysis into two groups: the first comprising *Thinoscatella*, *Lamproscatella*, and *Haloscatella* and the second by *Amalopteryx*, *Philotelma*, *Limnellia*, and *Scatophila*. *Tauromima* also seems to be related to this latter group, but only by examining specimens of this genus will we be able to discover its phylogenetic affiliation.

Five subgenera of *Scatella* are corroborated as monophyletic groups: *S. (Apulvillus)*, *S. (Parascatella)*, *S. (Scatella)*, *S. (Synhoplos)* and *S. (Teichomyza)*. We maintain the subgeneric status for *Apulvillus* because of its morphological peculiarities and limited geographical distribution.

The subgenus *Neoscatella*, which was recovered as a paraphyletic group in our analysis, is synonymized with *Scatella (Scatella)*, as no synapomorphy was discovered that supports the species of both subgenera as separate lineages.

TAXONOMY

Below and consistent with the documented monophyletic status of Scatellini, we present a taxonomic treatment for this tribe, including a description of the tribe and all recognized genera and subgenera, plus a key to the genera and subgenera. We also include brief remarks, as appropriate, for each taxon treated.

Scatellini Wirth & Stone, 1956

Scatellini Wirth and Stone 1956: 466. Type genus: *Scatella* Robineau-Desvoidy, 1830. –Olafsson 1991: 55–68 [relationships among Palearctic genera]. –Zatwarnicki 1992: 66–119 [phylogeny and classification]. –Mathis and Zatwarnicki 1995: 254–288 [world catalog]. –Mathis et al. 2014: 561–576 [review of genera and species from Brazil].

Description. Specimens of Scatellini may be distinguished from other Ephydriidae by the following combination of character states: Body length 0.80–5.00 mm; generally dark brown to cinereous (rarely yellow), microtomentose to shiny. Posterodorsal arm of the gonite present and aedeagus with slipper or shoe-like shape.

Head: Mesofrons subquadrate, slightly wider posteriorly, with dull, densely microtomentose to shiny, with metallic luster; lacking interfrontal setae; usually 2 laterocline, fronto-orbital setae (most genera) or 1 (*Limnellia*, *Scatophila*). Antenna relatively short; arista essentially bare, macropubescent (most genera) or bearing long dorsal rays (*Philotelma*); pedicel with a row of setae along anterior margin, setae longer ventrally plus 1 proclinate and 1 vertical seta dorsally. Face protuberant, setulose to moderately densely pilose, marginal setae usually larger; dorsum of interfoveal hump usually similar to rest of face, dark colored in a few species, not shiny; eye bare, usually as long as high, nearly round to obliquely oval, generally oriented obliquely to plane of epistoma; gena short to high, usually bearing a genal seta (most genera) or lacking (*Haloscatella*, *Lamproscatella*, *Philotelma*, *Thinoscatella*); oral opening moderately large, gaping, usually concealing clypeus; oral opening moderately large, gaping, usually concealing clypeus; maxillary palpus long and slender; mediproboscis with small sclerite laterally (*Scatella*, *Thinoscatella*); labellum not overlapping the mentum posteriorly.

Thorax: Dorsocentral setae 2–3 (0+2, 1+2), some setae sometimes weakly developed, the posteriormost seta displaced laterally from alignment of others; postpronotum sometimes with 1 long setae (*Parascatella*); row of small intra-alar setae present; intrapostalar setae small, weakly developed; presutural supra-alar seta present, variable, subequal or larger than anterior notopleural seta; postsutural supra-alar setae small than postalar seta or subequal in length (*Parascatella*); 2 notopleural setae, placement of posterior seta variable, usually at same level as anterior seta; proepisternum lacking setae but often with a few setulae (*Parascatella*); prosternum bare of setae or setulae; anepisternum bearing 1 large seta just dorsad of midheight along posterior margin, several smaller setulae may also be present; anepimeron, meron, and metapleuron bare of setae. Wing hyaline to conspicuously infuscate with or without white spots; costal vein extended to vein M_1 (most genera) or to vein R_{4+5} (*Scatophila*); crossvein r-m just posteriorly to distinctly distal to subcostal break (*Haloscatella* [species from New Zealand], *Philotelma*, *Limnellia*, *Scatophila*) vein R_{2+3} usually long, terminating at approximately same distance from vein R_{4+5} as tip of vein M_1

is from vein R_{4+5} . Hindcoxal strap not setose; pulvilli normally developed; tarsal claws short, curved.

Abdomen: Male with 5 visible abdominal tergites; tergite 5 distinctly trapezoidal or triangular; sternites 5 and 6 well developed, very small or absent; female with 7 visible tergites; tergite 5 subtrapezoidal, not triangular. Male terminalia: surstylus usually fused with ventral margin of epandrium and not evident (most genera) or evident as lobes, perhaps secondarily developed; aedeagus usually a sclerotized structure shoe-shaped (apparently basiphallus) (*Amalopteryx* Eaton, *Haloscatella* [other than New Zealand species], *Lamproscatella*, *Limnellia*, *Scatella*, *Scatophila*, *Thinoscatella*) or with a sclerotized basiphallus and a membranous distiphallus invested with short, sharp scales or scale-like thorns (some *Haloscatella* [species from New Zealand], *Philotelma*); ejaculatory apodeme lacking (*Amalopteryx*, *Haloscatella*, *Lamproscatella*, *Limnellia*, *Philotelma*, *Scatophila*, *Thinoscatella*) or present (as an L-shaped, dorsoventrally flattened structure or a crescent shaped, laterally flattened structure) (*Apulvillus* Malloch, *Parascatella* Cresson, *Scatella*, *Synhoplos* Lamb, *Teichomyza* Macquart); phallapodeme rudimentary, like a laterally flattened bow (*Haloscatella*, *Lamproscatella*, *Haloscatella* [other than New Zealand species]) or rod-like, lacking a keel (*Amalopteryx*, *Haloscatella* [New Zealand species], *Limnellia*, *Philotelma*, *Scatophila*) or greatly reduced or lacking (*Apulvillus*, *Parascatella*, *Scatella*, *Synhoplos*, *Teichomyza*); gonites and hypandrium fused forming a single structure (“gonal arch”) (*Amalopteryx*, *Haloscatella*, *Lamproscatella*, *Thinoscatella*, *Apulvillus*, *Parascatella*, *Scatella*, *Synhoplos*, *Teichomyza*, ground plan of *Limnellia*) or separated into medial sclerite “hypandrium” and lateral structures representing gonites (*Philotelma*, New Zealand *Haloscatella*, most *Scatophila*) or separated medioventrally into 2 lateral structures “gonites” (most *Limnellia*) (2 separate gonites are present also in some *Scatophila* (*avida* group), in which the “hypandrium” is reduced. Female Terminalia: sternite 7 as one rectangular sclerite or 2 lateral, small, circular to partially quadrate sclerites; sternite 8 divided into 2 sclerites; cerci bearing one prominent seta, strong or weak, inserted posteroventrally or without prominent setae; sternite 9/subanal plate without strong setae; operculum present or absent, when present helmet-like or tubular shaped.

Natural history. Foote (1995) compiled and summarized information about the natural history of Scatellini that was extracted from numerous articles that treated various included species. The species of Scatellini generally feed on algae, cyanobacteria and particles of various types of

decomposing animal and plant organic matter, as well as various microorganisms that proliferate on that substrate. Species of Scatellini live in a wide variety of habitats, such as hot springs and alkaline or acid lakes (some species of *Haloscatella*, *Scatella*, *Neoscatella*, *Scatophila*); marshes, mangroves, intertidal areas, dunes and sandy beaches, rocky coasts and other localities with large concentrations of salt. They also occur in muddy and sandy habitats along riverbanks and lakes. Some species are found on urban lawns. *Scatella stagnalis* (Fallén, 1813) is often found in greenhouses and is the vector of a root disease caused by a *Pythium* fungus to crops in hydroponic cultures (Goldberg and Stanghellini 1990). The larvae of one species, *Scatella* (*Teichomyza*) *fusca* Macquart, 1835, occur in an unusual environment: localities and habitats that are soaked in urine, such as outdoor urinals. The larvae and adults of this species feed on human and animal excrement (Vibe-Petersen 1998). This is also the only known species of the family Ephydriidae that has been implicated in cases of myiasis (James 1947).

Among all shore flies, Scatellini also includes a disproportionate number of species with reduced wings. We have thus far discovered 34 shore-fly species that have reduced wings to some degree (Costa et al. 2016, Krivosheina and Ozerov 2016, per. obs.), with a preponderance of these, 20 species, occurring in Scatellini. Two monotypic genera in Scatellini are in fact characterized by reduced wings: *Amalopteryx* (*A. maritima* Eaton), and *Tauromima* (*T. mountwilhelmi* Papp). Species of Diptera with reduced wings occur more often in specific environments, such as oceanic islands, mountainous areas of high elevation, arctic and sub-Antarctic areas of low altitude, coastal and marine habitats; those not in these categories are species with terricolous or hypogenous habits, are ectoparasites or they live in social insect nests (Hackman 1964, Roff 1990). These environments and the natural history of these groups promotes the emergence of several features common to these flies by convergent evolution, such as reduction of thoraces and halteres, strong legs, and large abdomens, besides the reduction and/or loss of wings (Wagner and Lieberr 1992).

Distribution. Worldwide there are 247 species in Scatellini (Mathis and Zatwarnicki 1995). This speciose tribe occurs in all biogeographic regions except Antarctica. Many of the nine included genera (*Amalopteryx*, *Haloscatella*, *Lamproscatella*, *Limnellia*, *Philotelma*, *Scatella* [subgenera: *Apulvillus*, *Parascatella*, *Scatella*, *Synhoplos*, *Teichomyza*], *Scatophila*, *Tauromima*, *Thinoscatella*) are found throughout the world in temperate and tropical zones, particularly on shorelines and beaches.

In the Neotropical Region, which has numerous undescribed species, we have discovered considerable species diversity at higher elevations and associated with the Andes Mountains. In Colombia, for example, we collected specimens above 5000 m, (WNM, pers. obs.). There is also considerable diversity worldwide along maritime seashores in temperate and tropical zones. This range in elevation, from sea level to over 5000 m, is matched by few other tribes in Diptera.

Key to genera and subgenera of Scatellini

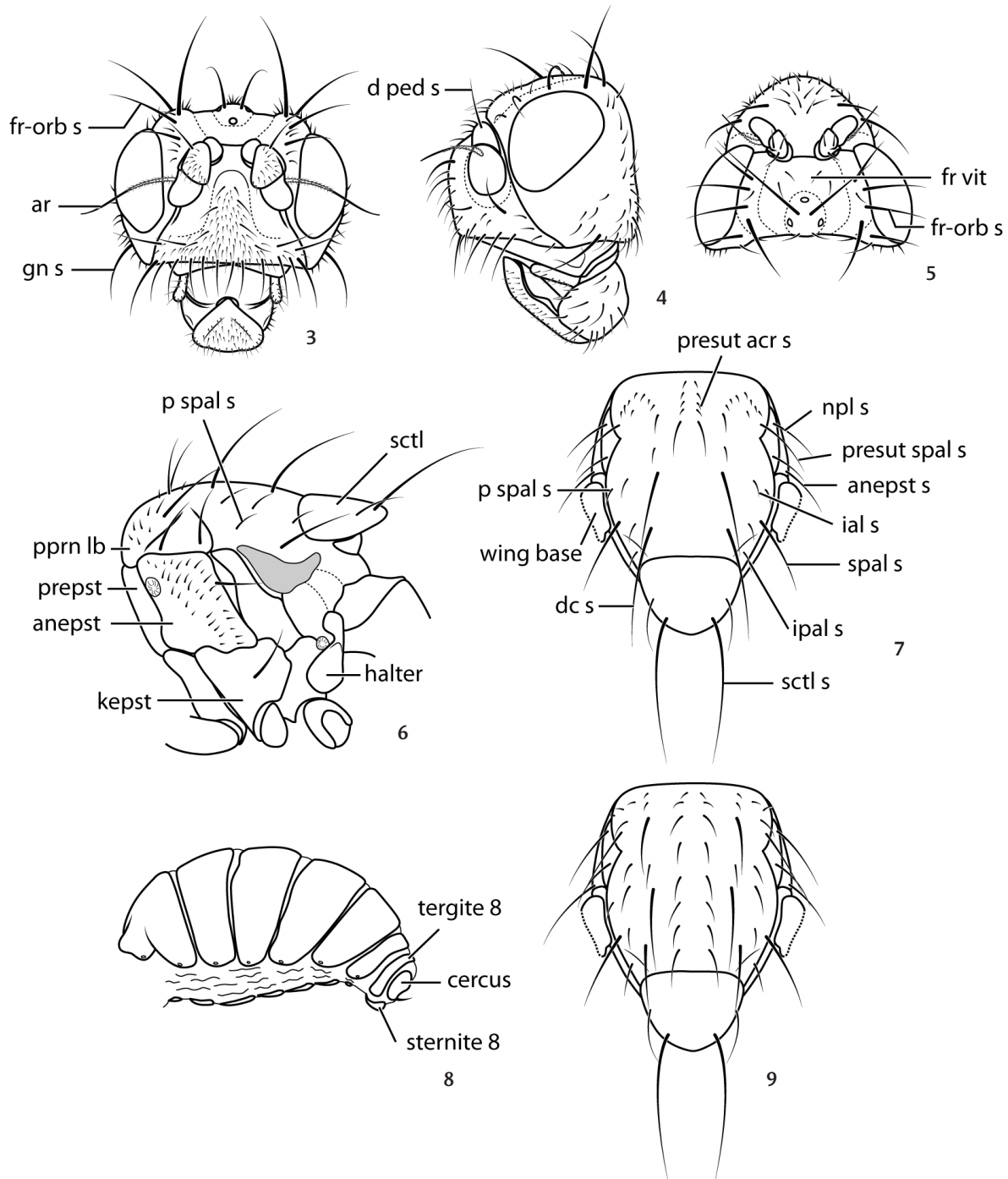
1. Acrostichal setae of mesonotum extended to anterior margin of scutellum, setae subequal in length..... 2
- 1'. Acrostichal setae of mesonotum not extended to anterior margin of scutellum, usually with 1 larger, sutural acrostichal seta (*Scatella*, in part)..... 11
2. Arista shorter than basal flagellomere. Frontal vitta as high as wide 3
- 2'. Arista longer than basal flagellomere. Frontal vitta wider than high 4
3. Pedicel with a long dorsal seta, subequal to length of arista. Apical scutellar seta longer than basal seta (Figs 54, 55, 82, 83)..... *Scatella* (*Synhoplos*) Lamb
- 3'. Pedicel with short dorsal seta, shorter than the length of arista. Apical scutellar seta short, same length of basal seta *Tauromima* Papp
4. Costa short, extended to or slightly beyond apex of vein R_{4+5} (Figs 19, 22) *Scatophila* Becker
- 4'. Costa longer, extended to apex of vein M_1 5
5. Arista pectinate above (Figs 16, 24, 25, 47, 74–81) *Philotelma* Becker
- 5'. Arista bare to macropubescent 6
6. Only one laterocline fronto-orbital seta present. Wing infusate, darker on anterior margin and lighter on posterior margin with distinctive pattern of numerous pale spots (Figs 10, 68–73) .. *Limnellia* Malloch
- 6'. Two or three laterocline fronto-orbital setae present. Wing hyaline to faintly infusate or with pattern of a few pale spots..... 7
7. Gena with a long distinct seta, longer and stronger than genal setulae. Postsutural supra-alar seta subequal to length of postalar seta (Figs 12, 14) *Scatella* (*Parascatella*) Cresson
- 7'. Gena without a long, strong seta, with a series of uniform fine setulae. Postsutural supra-alar seta shorter than half length of postalar seta 8
8. Posterior notopleural seta inserted much farther above ventral notopleural suture than anterior seta 9
- 8'. Anterior and posterior notopleural setae equidistant from ventral notopleural suture 10
9. A strong, conspicuous, dorsally curved seta toward anterodorsal corner of anepisternum; prescutellar acrostichal setae long, conspicuous (Figs 9, 32, 33, 40–43) ... *Haloscatella* Mathis
- 9'. Seta toward anterodorsal corner of anepisternum indistinguishable from surrounding setae; prescutellar acrostichal seta subequal to length of other acrostichal setae *Amalopteryx* Eaton
10. Posterior fronto-orbital seta closer to medial vertical seta than to anterior fronto-orbital seta. Frontal vitta shiny (Fig. 36)..... *Thinoscatella* Mathis
- 10'. Posterior fronto-orbital seta closer to anterior fronto-orbital seta than to medial vertical seta. Frontal vitta microtomentose, appearing dull (Figs 5, 31, 38, 39, 84, 85)..... *Lamproscatella* Hendel
11. Scutellum with three pairs of scutellar setae, these subequal in length; mesonotum covered by scattered setulae, not forming a row of acrostichal and intra-alar setae (Fig. 3) *Scatella* (*Teichomyza*) Macquart
- 11'. Scutellum with two pairs of scutellar seta, basal pair shorter than apical pair; mesonotum with acrostichal and intra-alar setae present, in small rows..... 12
12. Wing slightly infusate with few to several distinct pale spots. Sutural acrostichal seta present, conspicuously longer than other acrostichal setae (if absent, presutural dorsocentral seta present) (Figs 6–8, 15, 27–30, 46, 58–62)..... *Scatella* (*Scatella*) Robineau-Desvoidy
- 12'. Wing hyaline, without pale spots. Sutural acrostichal seta present, weak or indistinguishable than other acrostichal setae *Scatella* (*Apulvillus*) Malloch

Generic descriptions and comments

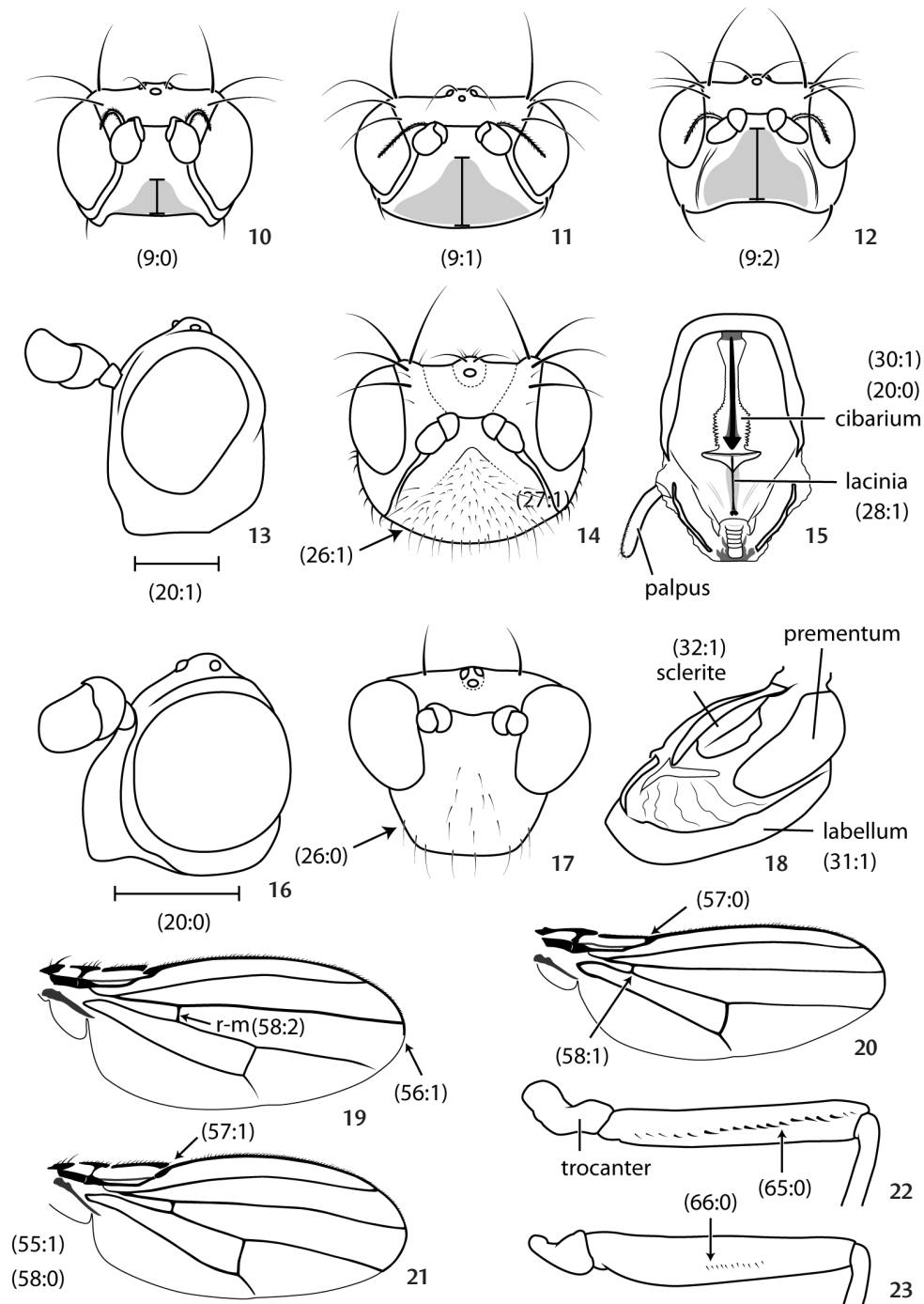
Amalopteryx Eaton, 1875

Amalopteryx Eaton 1875: 58 (feminine). Type species: *Amalopteryx maritima* Eaton 1875, monotypy. –Papp 1979: 360–361 [revision]. –Mathis and Zatwarnicki 1995: 254–255 [world catalog].

Diagnosis. Specimens of *Amalopteryx* are distinguished from other genera of Scatellini by the following combination of characters: Moderately large shore flies, body length: 3.25 mm; dark brown to dark gray species. Stenopterous wing; frontal vitta invested with microtomentum; eye conspicuously wider than high, usually obliquely oriented; length of sclerite 2 of labellum longer than width of labellum, overlapping prementum; posterior notopleural seta inserted distinctly elevated above level of anterior seta; arms of gonial arch fused; and gonial arch and phallopodeme fused.



Figures 3–9. (3) *Scatella (Teichomyza) fusca*, head anterior; (4) *Scatella (Synsoplos) sturdeeanus*, head lateral; (5) *Lamproscatella cephalotes*, head dorsal; (6–8) *Scatella (Scatella) stagnalis*, thorax lateral; (7) thorax dorsal; (8) female, abdomen lateral; (9) *Haloscatella arichaeta*, thorax dorsal. Abbreviations: anepst, anepisternum; ar, arista; d ped s, dorsal pedicel seta; dc s, dorsocentral seta; fr-orb s, fronto-orbital seta; fr vit, frontal vitta; gn s, genal seta; ial s, intra-alar seta; kepst, katepisternum; npl s, notopleural seta; p spal s, posterior supra-alar seta; pprn lb, postpronotal lobe; prepst, proepisternum; presut acr s, presutural acrostichal seta; presut spal s, presutural supra-alar seta; sctl, scutellum; spal s, supra-alar seta; sctl s, scutellar seta.



Figures 10–23. Head, wing and legs characters: (10) *Limnellia* sp., head anterior; (11) *Scatella* (*Scatella*) sp., head anterior; (12) *Scatella* (*Parascatella*) sp., head anterior; (13) *Hyadina* sp., head lateral; (14) *Scatella* (*Parascatella*) *pilifera*, head anterior; (15) *Scatella* (*Scatella*) *stagnalis*, mouth parts; (16) *Philotelma* sp., head lateral; (17) *Physemops* *nemorosus*, head anterior; (18) *Ephydra* *riparia*, mouth parts; (19) *Scatophila* *caviceps*, wing; (20) *Scatella* (*Scatella*) *stagnalis*, wing; (21) *Dagus* *rostratus*, wing; (22) *Scatophila* *mesogramma*, male, mid femur posteroventral; (23) *Scatella* (*Scatella*) *stagnalis*, male, fore femur anteroventral.

Description. Medium-sized shore flies, body length 3.24 mm; dark brown species.

Head: Frontal vitta generally dull, densely microtomentose. Laterocline fronto-orbital setae 2. Antenna short, concolorous with head; basal flagellomere slightly inflated, brown; arista macropubescent. Face conspicuously protruding; interfoveal dorsal hump of face at half the height of head; facial setae conspicuous, 1–2 lateral facial setae curved laterodorsally; long ventrocline setae along oral margin; eye nearly round, slightly wider than high. Genal height medium to high (gena to eye ratio 0.43), a row of setulae at the ventral margin of gena, without a distinct genal seta.

Thorax: Mesonotum dull, densely microtomentose; small setulae towards anterior margin of mesonotum; dorsocentral setae 3 (1+2); a row of small acrostichal setae extending to scutellum, without a longer prescutellar acrostichal setae; intrapostalar setae relatively long, half-length of postalar seta; basal scutellar setae conspicuously smaller than apical setae; posterior notopleural setae distinctly elevated above level of anterior seta; postsutural supra-alar setae small, shorter than postalar seta. Wing length 2.56 mm, width 0.30 mm, stenopterus in only known species, generally infusate. Legs typical, usually without distinct setae, concolorous with thorax; tarsi most brown; tarsal claws conspicuously curved and puvilli present below each claw.

Abdomen: Tergites gray to brown, microtomentose; small and scattered dorsal setae. Male Terminalia: sternite 5 present, sternite 6 absent. Epandrium as a plate roughly ellipsoid, with a narrow opening below the cerci in posterior view; surstyli absent or fused indistinguishably with ventral margin of epandrium; gonites distinctly Y-shaped, dorsal arms sharply terminated, without setae; phallapodeme dorsoventrally flattened, with 2 lateral projections, rod-like, lacking a keel; ejaculatory apodeme lacking. Aedeagus shoe-shaped in lateral view, short and without a distiphallus. Female Terminalia: sternite 8 divided into 2 lateral, lunate sclerites; female cerci with a long, slender setae inserted posteroventrally. Female ventral receptacle apparently absent.

Distribution. Afrotropical (Sub-Antarctic Islands: Crozet Islands, Heard Island, Kerguelen Island, McDonald Island).

Remarks. *Amalopteryx* is a monotypic genus, and the only included species, *A. maritima*, has stenopterus wings. Like *Lamproscatella* and *Haloscatella*, this genus has a row of genal setulae but lacks a distinctive genal seta. Structures of the male terminalia are similar to those of *Scatophila*.

Amalopteryx maritima is a saprophagous and microphagous species. Womersley (1937) described the immature stages of this species.

Haloscatella Mathis, 1979

Figs 9, 32, 33, 40–43

Haloscatella Mathis 1979b: 6 (as a subgenus of *Lamproscatella*; feminine). Type species: *Lamproscatella arichaeta* Mathis 1979a, original designation. –Olafsson 1991: 42 [revised status]. –Mathis and Zatwarnicki 1995: 255–256 [world catalog]. –Mathis et al. 2004: 4–18 [New Zealand fauna].

Diagnosis. *Haloscatella* is distinguished from other genera of Scatellini by the following combination of characters: anterodorsal corner of anepisternum with one strong seta curved; parafacial margin lacking row of setulae near parafacial; eye conspicuously wider than high, usually obliquely oriented; insertion of posterior notopleural setae distinctly elevated above level of anterior seta; prescutellar acrostichal seta longer than other acrostichal setae; and female ventral receptacle lacking operculum.

Some *Haloscatella* similar to *Lamproscatella*, can be differentiated by the following combination of characters: cinereous, densely microtomentose species; frontal vitta with small setulae towards anterior margin; vestiture of frontal vitta usually microtomentose; posterior notopleural seta inserted at distinctly higher level than anterior seta; medial scutellar seta half the length of apical seta.

Description. Small to moderately small shore flies, body length 1.30–2.90 mm; generally cinereous species.

Head: Frontal vitta generally dull, usually densely microtomentose; small setulae towards anterior margin of frontal vitta; long laterocline fronto-orbital setae 2. Antenna short; pedicel with strong seta ventrally and dorsally; basal flagellomere brown; arista macropubescent. Face conspicuously protruding, with an interfoveal, dorsal hump; facial setae conspicuous, 1–3 lateral facial setae curved laterodorsally. Eye usually wider than high, obliquely oriented to general plane of head; gena usually medium to high; a row of setulae at the ventral margin of gena, without a distinct genal seta.

Thorax (Fig. 9): Mesonotum cinereous to brown, microtomentose; dorsocentral setae 3 (1+2); a row of small acrostichal setae extending to scutellum, with a longer prescutellar acrostichal setae; basal scutellar setae conspicuously smaller than apical setae; posterior notopleural seta distinctly elevated above level of anterior seta; a distinct dorsocline seta toward anterodorsal corner of anepisternum; legs typical, usually without distinct setae, color of tarsi brown; stem of halter short, head oval, white; wing mostly hyaline, some species infusate around crossveins and veins; costa relatively long, extended to vein M_1 ; costal vein sometimes bearing spines.

Abdomen: Tergites gray to brown, microtomentose; sternite 1 absent or membranous. Male Terminalia (Figs 32, 33, 40–43): epandrium a closed plate around cercal cavity, sometimes with processes laterally; surstyli united but distinguishable of epandrium, or absent; gonites roughly to distinctly Y-shaped, dorsal arms flattened or sharply terminated, generally without setae; phallapodeme laterally flattened, in lateral view curved or dorsoventrally flattened, usually with 2 lateral projections, rod-like, lacking a keel; ejaculatory apodeme lacking. Aedeagus shoe-shaped in lateral view short or elongate; some species with distiphallus; distiphallus, if present, with membranous ventral elongate process that originates from distal aedeagal margin, covered by short, sharp scales or scale-like thorns. Female Terminalia: sternite 8 divided, as 2 lateral, subquadrate sclerites; female cerci without prominent setae. Female ventral receptacle without operculum only extended process present.

Distribution. Afrotropical (Cape), Australasian, Nearctic (including northern Mexico), Palearctic Regions.

Remarks. Species of this genus often proliferate best where saline or alkaline conditions are near saturation (Mathis 1979b, Mathis et al. 2004). Immature stages are unknown. The nine species of *Haloscatella* are quite homogeneous in overall appearance, but structures of the male terminalia are also similar to males of other tribes of Ephydrinae, especially Ephydrini, as well as to the genera *Philotelma* and *Scatophila* within Scatellini. The species of *Haloscatella* that share the same states of characters with *Philotelma* and *Scatophila* are all from New Zealand. This peculiarity makes *Haloscatella* an important and pivotal genus in our understanding of the evolution of Scatellini.

Lamproscatella Hendel, 1917

Figs 5, 31, 38, 39, 84, 85

Lamproscatella Hendel 1917: 42 (feminine). Type species: *Ephydra sibilans* Haliday 1833, original designation. –Mathis 1979a: 1–41 [phylogeny, biogeography]. –Mathis and Zuyin 1988: 540–548 [review, Asian species]. –Olafsson 1991: 38–41 [revision of northern European species]. –Mathis and Zatwarnicki 1995: 256–258 [world catalog]. –Krivoshchina 2004: 321–329 [Russian fauna].

Diagnosis. Specimens of *Lamproscatella* are diagnosed by the following combination of characters: facial projection less than half height of head; and arms of gonial arch fused. Other characters that may help determine *Lamproscatella* from *Thinoscatella*, include the following: frontal vitta mostly microtomentose, appearing dull; setulae towards anterior margin of frontal vitta absent; posterior notopleural seta at same level as anterior seta.

Description. Small to moderately small shore flies, body length 1.25–2.90 mm; dark brown to cinereous species.

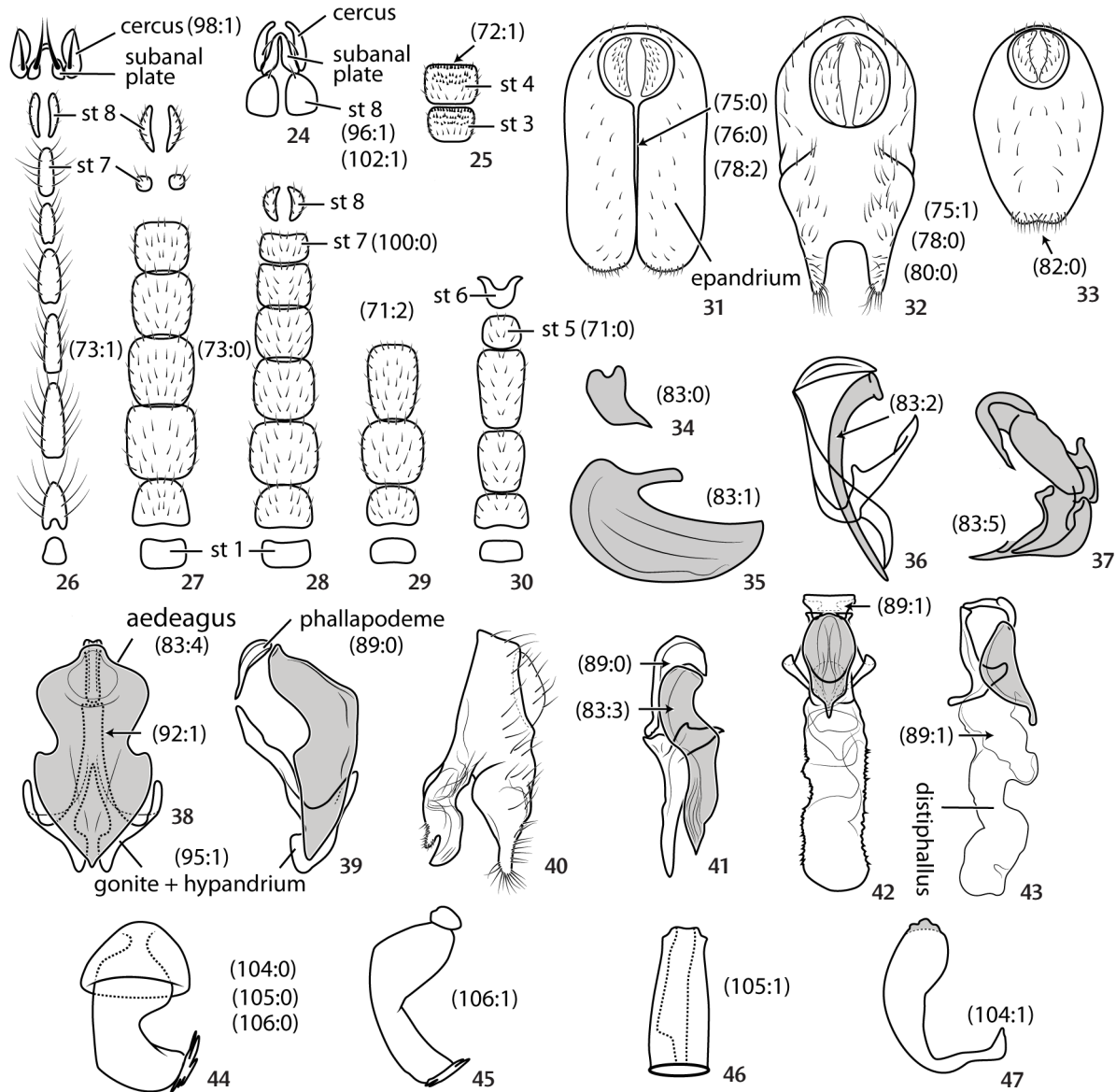
Head (Fig. 5): Frontal vitta mostly microtomentose, appearing dull. Face prominent, interfoveal dorsal hump of face low, at middle of the face; arched, laterocline fronto-orbital seta 2; ocelli arranged in isosceles triangle. Antenna dark colored; arista pubescent; facial setae conspicuous, with 1–3 pair of dorsally curved, larger setae toward lateral margins. Eye usually higher than wide, sometimes wider than high; gena short to medium (gena to eye ratio 0.12–0.25); a row of setulae at the ventral margin of gena, without a distinct genal seta.

Thorax: Mesonotum mostly microtomentose, dull colored to subshiny, generally unicolorous or with faintly longitudinal stripes; pleural areas generally concolorous with mesonotum: 3 pair of dorsocentral bristles (1+2); acrostichal setae in 2 rows extending to scutellum, setae generally subequal to each other, small, prescutellar acrostichal absent; 2 pair of lateral scutellar setae, basal pair shorter than apical pair. Legs mostly concolorous with pleural areas, without distinct setae, color of tarsi pale brown. Wing immaculate, hyaline to slightly infusate; costa relatively long, extended to vein M_1 ; stem of halter short, head oval, white; costal vein sometimes with spine-like setae along costal margin in some species.

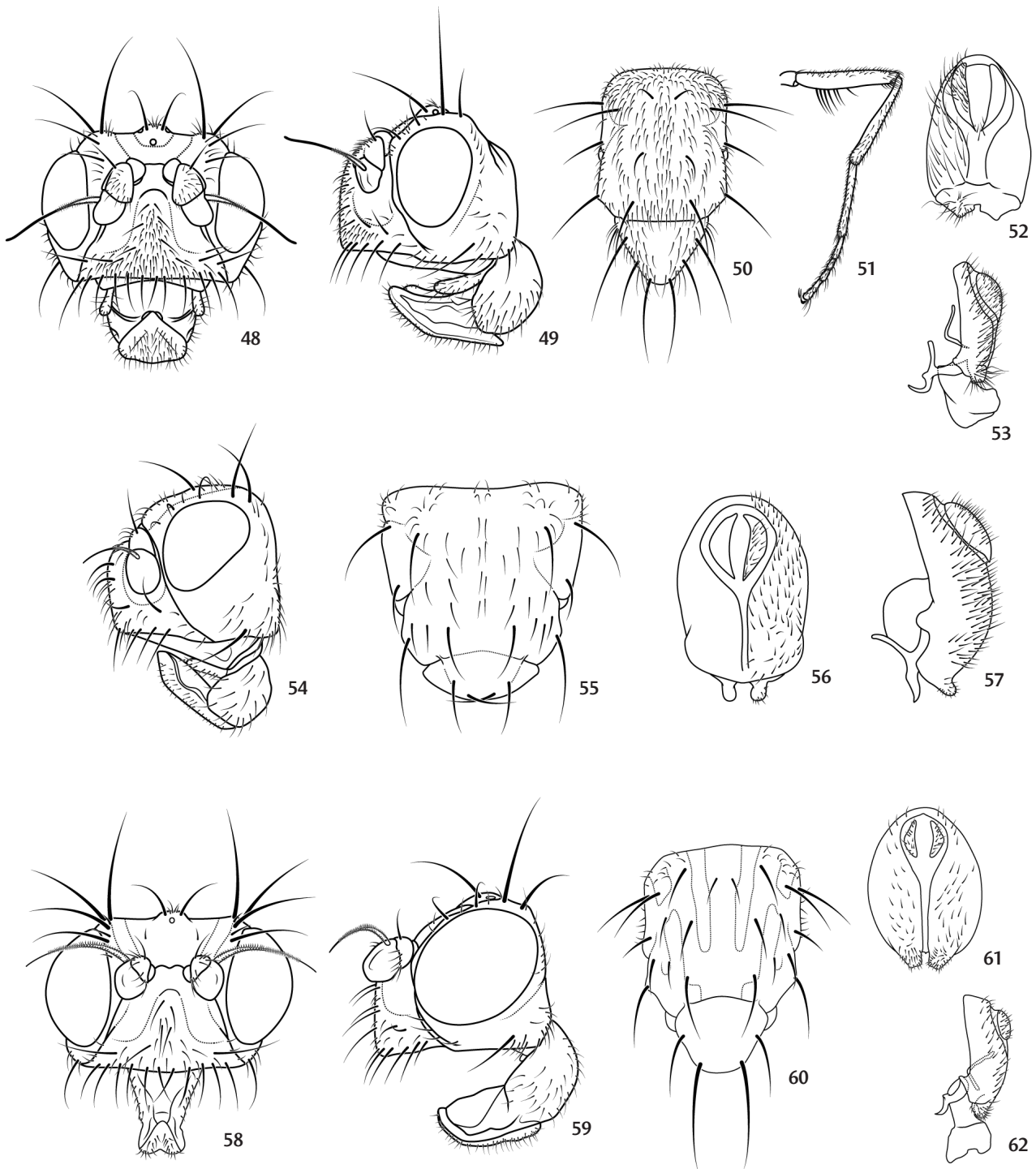
Abdomen: Tergites gray to brown, microtomentose, sometimes slightly darker toward margins; dorsal setae small and scattered. Male Terminalia (Figs 31, 38, 39, 84, 85): sternite 1 membranous or absent; sternite 5 present, sternite 6 absent; Epandrium as an elongated plate subquadrate but strongly rounded at corners, or roughly ellipsoid, with a narrow opening below the cerci; surstyli fused indistinguishably to ventral margin of epandrium; phallapodeme laterally flattened, curved, C- to J-shaped; gonites roughly to distinctly Y-shaped, dorsal arms flattened, without setae. Aedeagus variable, a bulky or thin tube, when thin sometimes strongly tapered at apex. Female Terminalia: sternite 8 divided, as 2 lateral, lunate sclerites; female cerci without prominent setae. Female ventral receptacle with a helmet-like operculum, small, not covering extended process.

Distribution. Afrotropical (Saharo-Arabian-Palearctic transition), Nearctic (including northern Mexico), Oriental (Chinese-Palearctic–Oriental transition), Palearctic Regions.

Remarks. This genus, comprising 15 species, has not been discovered in the Neotropical or Australasian Regions. Very little is known about the habitat preferences of this genus. North American species generally occur in freshwater environments, but specimens are occasionally collected in



Figures 24–47. Abdominal sternites and terminalia: (24) *Philotelma* sp., female; (25) *Philotelma* sp., male; (26) *Ephydra* (*Ephydra*) *riparia*, female; (27) *Scatella* (*Scatella*) *stagnalis*, female; (28) *Scatella* (*Scatella*) *tenuicosta*, female; (29) *Scatella* (*Scatella*) *tenuicosta*, male; (30) *Scatella* (*Scatella*) *paludum*, male; (31) *Lamproscatella sibilans*, epandrium and cerci, posterior; (32) *Haloscatella arichaeta*, epandrium and cerci, posterior; (33) *Haloscatella karekare*, epandrium and cerci, posterior; (34) *Hyadina* sp., aedeagus lateral; (35) *Parydra aquila*, aedeagus lateral; (36) *Thinoscatella lattini*, internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), lateral; (37) *Diedrops steineri*, aedeagus, lateral; (38) *Lamproscatella sibilans*, internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), ventral; (39) *Lamproscatella sibilans*, internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), lateral; (40) *Haloscatella arichaeta* epandrium and cerci, lateral; (41) *Haloscatella arichaeta*, internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), lateral; (42) *Haloscatella karekare*, internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), ventral; (43) *Haloscatella karekare*, internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), lateral; (44) *Paracoenia bisetulosa*, ventral receptacle lateral; (45) *Notiocoenia paniculate*, ventral receptacle lateral; (46) *Scatella* (*Scatella*) *stagnalis*, ventral receptacle lateral; (47) *Philotelma defectum*, ventral receptacle lateral.



Figures 48–62. *Scatella fusca*: (48) head, anterior; (49) head, lateral; (50) thorax, dorsal; (51) male mid leg, posterior; (52) epandrium and cerci posterior; (53) male internal terminalia, lateral. *Scatella (Synhoplos) sturdeeanus*: (54) head, lateral; (55) thorax, dorsal; (56) epandrium and cerci, posterior; (57) male terminalia, lateral. *Scatella (Scatella) curtipennis*: (58) head, anterior; (59) head, lateral; (60) thorax, dorsal; (61) epandrium and cerci, posterior; (62) male terminalia, lateral.

association with saline or alkaline water systems (Mathis 1980). The immature stages are unknown.

The species included in the phylogenetic analysis cluster together as the sister group to *Haloscatella*.

Limnellia Malloch, 1925

Figs 10, 68–77

Limnellia Malloch 1925: 331 (feminine). Type species: *Limnellia maculipennis* Malloch 1925, original designation. –Andersson 1971: 53–59 [review, European species]. –Mathis 1978: 250–293 [revision of Nearctic species]. –Mathis and Zatwarnicki 1995: 258–261 [world catalog]. –Zhang and Yang 2009: 558–64 [review, Chinese fauna]. –Krivoshchina 2012: 1–7 [review, Russian species]. –Mathis et al. 2014: 563–564 [review, Brazilian species].

Eustigoptera Cresson 1930: 126 (feminine). Type species: *Notiphila quadrata* Fallén 1813, original designation. –Cresson 1935: 362 [objective synonymy and as stated].

Stictoscatella Collin 1930: 133 (feminine). Type species: *Notiphila quadrata* Fallén 1813, original designation. –Cresson 1935: 362 [objective synonymy and as stated].

Stranditella Duda 1942: 30 (as a subgenus of *Lamproscatella*; feminine). Type species: *Notiphila quadrata* Fallén 1813, original designation. –Dahl 1959: 126 [objective synonymy and as stated].

Diagnosis. *Limnellia* is distinguished from other genera of the tribe Scatellini by the following combination of characters: mesonotum distinctly bi- or tricolored; wing infuscate, darker toward anterior margin, lighter toward posterior margin; and a large posterodorsal arm and gonial arch. Other characters useful to diagnose *Limnellia* species, include: 1 pair of well-developed, laterocline fronto-orbital seta; gena small (gena to eye ratio < 0.21); mesonotum usually conspicuously multicolored with pattern of bands and/or spots.

Description: Minute to moderately small shore flies, body length 1.00–2.50 mm; mostly dark brown to black, microtomentose to bare, shiny, frequently with cinereous guttate and vittate maculae; species macropterous or brachypterous.

Head (Fig. 10): Frontal vitta distinct from duller parafrens, subshiny; laterocline fronto-orbital seta 1 (rarely 2); medial and lateral vertical setae both well developed; ocelli arranged in isosceles triangle or absent. Antenna dark, arista at most macropubescent. Interfoveal dorsal hump of face low, face with shallow antennal grooves; facial setae mostly small, 1–2 lateral facial setae curved laterodorsally. Eye nearly round. Gena relatively short (gena to eye ratio < 0.21), bearing 1 well-developed seta.

Thorax: Mesonotum usually conspicuously multicolored with pattern of bands and/or spots. Pleural areas

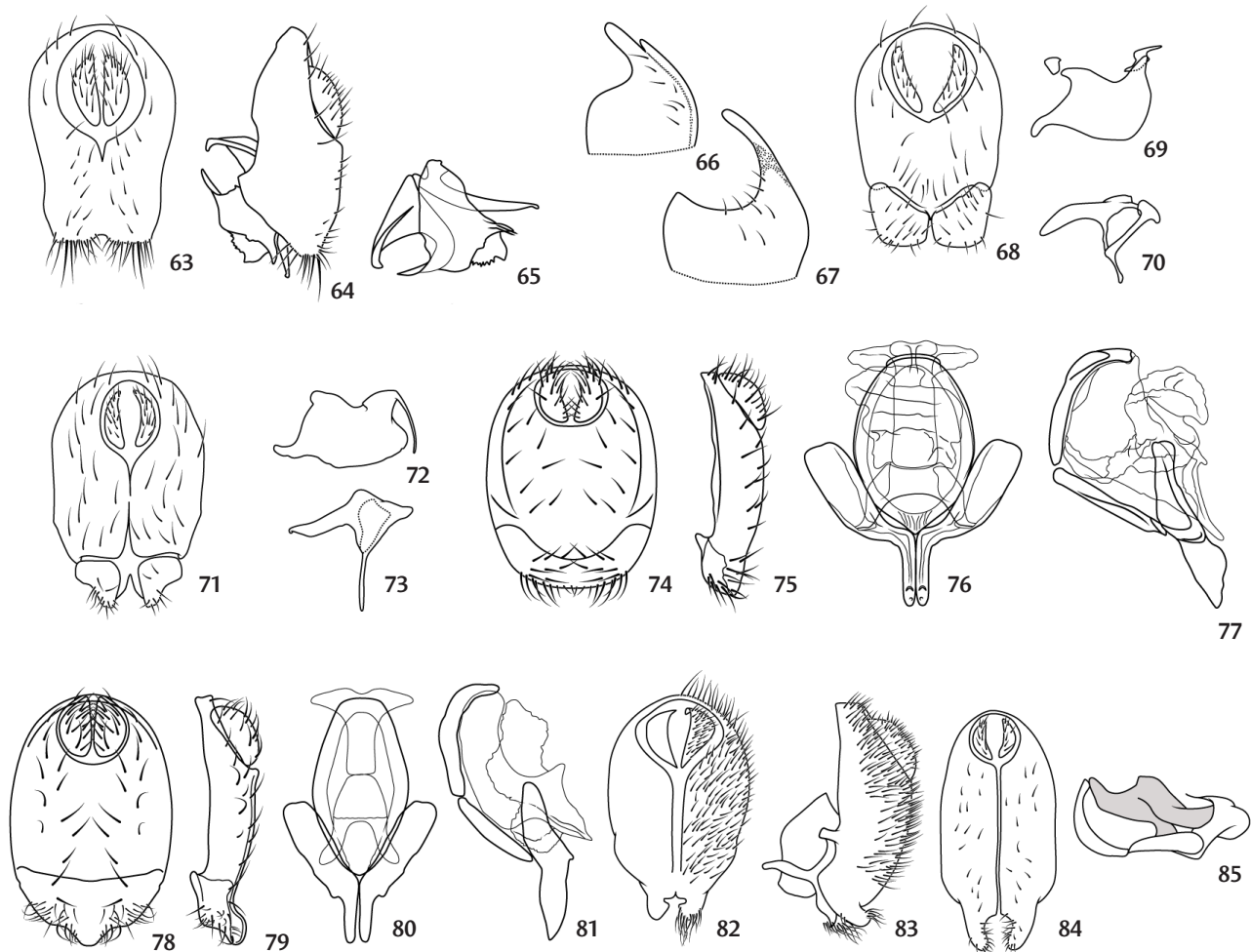
usually dark brown with cinereous areas. Acrostichal setae uniform in size, small, arranged in 2 rows that extend to base of scutellum; dorso-central setae 2 (0+2); supra-alar seta either reduced or lacking; disc of scutellum bare; lateral scutellar setae 2, basal pair one-third length of posterior pair. Legs typical, without distinct setae; color of tarsi variable but usually paler than tibiae; tarsal claws conspicuously curved and puvilli present below each claw. Wing strongly infuscate, darker on anterior margin and lighter on posterior margin, with several white spots in all cells; costa relatively long, extended to vein M₁; crossvein r-m distinctly distal to subcostal break; maculation pattern variable but generally recognizable for each species. Wing brachypterous to micropterous in a few species.

Abdomen: Tergites black, becoming shiny and polished posteriorly. Male terminalia (Figs 68–77): sternite 5 present, sternite 6 absent. Epandrium a closed plate around cercal cavity, bearing articulated surstyli on anterior margin; surstylus as 2 plates or fused; gonites broadly Y-shaped, with broad base, bearing setae on ventral portion; aedeagus in lateral view shoe-shaped, without distiphallus; phallopodeme dorsoventrally flattened, usually with 2 lateral projections, rod-like, lacking a keel; ejaculatory apodeme lacking. Female terminalia: sternite 8 divided, as 2 lateral, subquadrate sclerites; female cerci without prominent setae. Female ventral receptacle without operculum, only extended process present.

Distribution. Widespread: Afrotropical, Australasian, Nearctic, Neotropical, Oriental (Chinese-Palearctic-Oriental transition), Palearctic Regions.

Remarks. *Limnellia* Malloch is an easily recognized genus within Scatellini because of the conspicuously multicolored mesonotum with patterns of bands and/or spots and the infuscate wing with several to numerous white spots. There is also a single laterocline fronto-orbital seta. Twenty-four species are known in the genus, mostly from the Nearctic Region (10 species). Nothing is known about the immature stages, behavior, or habitat preferences of this genus. Mathis (1978) presented a phylogeny of Nearctic species. Herein and following the precedent of previous papers (Mathis 1978, Mathis and Zatwarnicki 1995), *Limnellia* was recovered as the sister-group of *Scatophila*.

Four species of *Limnellia* from Neotropical, Palearctic and Australasian Regions demonstrate varying levels of brachyptery (Hollmann-Schirmacher and Zatwarnicki 1995, Mathis et al. 2004, Costa et al. 2016). *Limnellia helmuti* Hollmann-Schirmacher and Zatwarnicki has a short and broad wing, and *L. abbreviata*, has a narrow wing. Neither species is capable of flight.



Figures 63-85. Male terminalia: (63–65) *Notiocoenia acutella*; (66–67) *Halmopota mediterranea*; (68–70) *Limnellia huachuca*; (71–73) *Limnellia itatiaia*; (74–77) *Philotelma nigripenne*; (78–81) *Philotelma rossii*; (82–83) *Scatella (Synhoplos) neglectus*; (84–85) *Lamproscatella occidentalis*.

More recently, Costa et al. (2016) described two brachypterous species (*L. flavifrontis* and *L. vounitis*) from the Paramo of Venezuela and suggested that the brachyptery of these two species evolved independent of other congeners within *Limnellia*. These two species also have several modifications that are apparently related to their brachyptery, such as a compact thorax and reduced size of the halteres. There is also the complete loss of ocelli and ocellar setae as well as the first abdominal tergite. These features are synapomorphies that are unique to these two species. According to the collector of the two Venezuelan species, specimens were found in rotting wood or in leaf litter at high elevations, which are typical niches for brachypterous species (Hackman 1964).

Philotelma Becker, 1896

Figs 16, 24, 25, 47, 74–81

Philotelma Becker 1896: 163 (neuter). Type species: *Philotelma anomalum* Becker 1896 (= *Notiphila nigripennis* Meigen 1830), monotypy. –Zatwarnicki and Baéz 1991: 209–210 [review]. –Mathis and Zatwarnicki 1995: 261–262 [world catalog]. –Mathiset al. 2009: 121–158 [revision].

Pseudoscatella Becker 1902: 298 (feminine). Type species: *Notiphila nigripennis* Meigen 1830, monotypy. –Becker 1903: 46 [synonymy].

Diagnosis. *Philotelma* can be distinguished from other genera of Scatellini by the following combination of characters: infuscate spot over crossvein dm-m; male sternite short and bearing spine-like setae; female sternite 8 bearing prominent setulae; aedeagus with a sclerotized basiphallus

and a membranous distiphallus; gonite and hypandrium separate. Other characters important to differentiate *Philotelma*, include the following: arista pectinate; gena small (gena to eye ratio <0.2); posterior notopleural seta inserted at the same level of anterior seta; wing with faint white spots; crossvein dm-m covered with dark spot.

Description. Small to moderately small shore flies, body length 1.20–2.10 mm; generally dark colored, grayish brown to blackish brown.

Head (Fig. 16): Frontal vitta shiny, sparsely microtomentose, 2 latero-clinate fronto-orbital setae, 2 much smaller fronto-orbital setae alternating with larger setae. Antenna short, dark; basal flagellomere round; arista pectinate, bearing 5–6 dorsal, hair-like rays. Face conspicuously protruding, with an interfoveal, dorsal hump; facial setae conspicuous, 1–2 lateral facial setae curved laterodorsally; long ventro-clinate setae along oral margin. Eye nearly round. Gena small (gena to eye ratio <0.2); a row of setulae at the ventral margin of gena, without a distinct genal seta.

Thorax: Mesonotum generally dark colored; acrostichal setulae short, in 2 distinct rows, lacking larger, prescutellar setae; dorsocentral setae 3 (1+2); posterior notopleural seta inserted at the same level of anterior seta; basal scutellar seta much shorter than apical seta. Wing faintly to moderately infusate, with pale white spots; costal vein relatively long, extended to vein M_1 ; crossvein r-m distinctly distal to subcostal break; crossvein dm-m covered with infusate spot that usually extends into cell r5. Legs typical, without distinct setae; tarsi light brown; tarsal claws conspicuously curved and puvilli present below each claw.

Abdomen: Tergites shiny black, sparsely microtomentose; sternite 5 of male present, sternite 6 absent. Male terminalia (Figs 74–81): Epandrium in posterior view broadly oval, ventral margin usually slightly to obviously flatter than dorsal margin, sometimes with medial projection, in lateral view elongate, height 3–4x width, bar-like, ventral margin usually pointed or somewhat projected; cerci semihemispherical to broadly lunate; cercal cavity in dorsal 1/4–1/3 of epandrium, broadly oval, as wide as high; surstyli not evident, probably fused indistinguishably with ventral margin of epandrium; gonites paired, one on each side, in ventral view both gonites together forming a V-shaped structure, with vertex (apicomedial convergence of gonite from each side) apically, usually lacking a ventral process; aedeagus in lateral view with basal portion conspicuously excavate dorsally, apical portion variously shaped, in ventral view usually broadly to narrowly oval, sometimes lateral margins angulate, with a membranous distiphallus (sometimes not extended

or inflated or even protruding through basal opening of aedeagus); phallapodeme in lateral view narrow, elongate, shallowly curved, with more curvature toward attachment with base of aedeagus, in ventral view T-shaped, with bar of T at basal attachment with aedeagus; hypandrium in ventral view usually broadly Y-, U-, or V-shaped, with extended arms touching basal portion of gonite. Female Terminalia (Figs 24, 25, 47): sternite 7 lacking (character 99[1]); sternite 8 divided, as 2 lateral, subquadrate sclerites, bearing a long seta on posterior margin; female cerci without prominent setae. Ventral receptacle without operculum, only extended process present.

Distribution. Holarctic.

Remarks. *Philotelma* is a small genus of six species, and thus far, it is only known from the Nearctic and Palearctic Regions. Adults usually occur in habitats that are slightly to notably alkaline or saline (Dahl 1959). Mathis et al. (2009) published a revision of all known species.

In the phylogenetic analysis, the two species of *Philotelma* cluster together and their common node is the sister group to the node giving rise to *Limnellia* and *Scatophila*.

Scatella Robineau-Desvoidy, 1830

Figs 3, 4, 6–8, 11, 12, 14, 15, 20, 23, 27–30, 46, 48–62, 82, 83

Scatella Robineau-Desvoidy 1830: 801. Type species: *Scatella buccata* Robineau-Desvoidy 1830 (= *Ephydra stagnalis* Fallén 1813), subsequent designation of Coquillett 1910: 603. –Harrison 1959: 236–244 [fauna of New Zealand]. –Mathis 1989: 648–649 [Australasian/Oceanian catalog]. –Mathis and Zatwarnicki 1995: 262–281 [world catalog].

Diagnosis. *Scatella* is distinguished from other genera of the tribe Scatellini by the following combination of characters: genal seta distinct, long; wings lightly to darkly infusate with few to several white spots; epandrium generally ovoid in posterior view; phallapodeme absent; ejaculatory apodeme present; female cerci bearing one strong, prominent seta, inserted posteroventrally.

Description. Minute to large shore flies, body length 1.00–5.00 mm; blackish brown to cinereous species, rarely yellow; species macropterous or brachypterous.

Head (Figs 3, 4, 11, 12, 14, 15, 48, 49, 54, 58, 59): Frons dull usually with distinct, subshiny to shiny frontal vitta; latero-clinate fronto-orbital seta 2, rarely 3. Antenna short, dark; pedicel with strong seta ventrally; basal flagellomere round; arista macropubescent to at most bearing short, dorsal, hairlike branches. Face conspicuously protruding, with an interfoveal, dorsal hump, uniformly sclerotized, no processes; facial setae conspicuous, 1–3 lateral facial setae

curved laterodorsally or ventrally curved, indistinctly from medial facial setae; small to long ventroclinate setae along oral margin. Eye usually nearly round. Gena short to moderately high, usually bearing a large seta; palpus elongate, mostly dark, exceptionally yellow.

Thorax (Figs 6, 7, 20, 23, 50, 51, 55, 60): Mesonotum generally dark colored, microtomentose, density of tomentum varying, generally unicolorous or with longitudinal stripes, not conspicuously multicolored with pattern of bands and/or spots; dorsocentral setae usually 2 (0+2), sometimes 3 (1+2); scutellum flat, disc bare, bearing 2 pairs of marginal setae, sometimes 3; basal scutellar setae smaller than apical setae or equal; pleural region generally gray, lighter than mesonotum; postsutural supra-alar seta long, subequal in length to postalar seta or much smaller; legs typical, usually without distinct setae (forefemur with a row of short, stout setae anteroventrally in some species); color of tarsi variable; tarsal claws conspicuously curved and puvilli present below each claw (claws near straight and pulvilli absent in some *Apulvillus* species); stem of halter short, head oval, white. Wing generally pale to conspicuously infusate with white spots, especially in cells r_{2+3} , r_{4+5} , and dm but exceptionally in cell r_1 and m_4 ; costa relatively long, extended to vein M_1 , sometimes bearing spines; wing brachypterous in a few species.

Abdomen: Tergites gray to brown, microtomentose, sometimes with lighter posterior margins, or mostly shiny, blackish brown. Male terminalia (Figs 56, 57, 61, 62, 82, 83): sternites 5 and 6 well developed, very small or absent; epandrium as a plate generally ovoid in posterior view, with a narrow opening below the cerci; ventral projections of epandrium separated or indistinguishable; cercal cavity completely round; phallapodeme absent; ejaculatory apodeme present, L shaped, dorsoventrally flattened or crescent shaped, laterally flattened; gonite distinctly Y-shaped, elongate, sharply terminated, sometimes bearing setae on dorsal margin of anterior portion; aedeagus shoe-shaped in lateral view. Female terminalia (Figs 8, 27–30, 46): sternite 7 as one rectangular sclerite or 2 lateral, small, circular to partially quadrate sclerites; tergite 8 a complete arch; sternite 8 divided as 2 lateral, lunate sclerites; female cerci bearing one strong, prominent seta, inserted posteroventrally. Female ventral receptacle tubular shaped, one to five times longer than wide.

Distribution. Widespread: Afrotropical, Australasian/Oceanian, Nearctic, Neotropical (especially Andean), Oriental, Palearctic.

Remarks. *Scatella* is a large genus with 139 species and occurs in all biogeographic regions except Antarctica. The

principal characters for recognizing *Scatella* are structures of male terminalia and the strong and long setae of female cerci. Our analysis recognizes five subgenera: *Parascatella* Cresson, *Teichomyza* Macquart, *Synhoplos* Lamb, *Apulvillus* Malloch and *Scatella* (*Scatella*). The latter subgenus includes species previously included in *Neoscatella* Malloch (see below).

Scatella (*Apulvillus*) Malloch 1934

Apulvillus Malloch 1934: 197 (as a genus; masculine). Type species: *Apulvillus bronnecki* Malloch 1934, original designation. –Mathis 1980: 26 [revised status]. –Mathis and Zatwarnicki 1995: 262–263 [world catalog].

Chaetoscatella Malloch 1934: 199 (as a genus; feminine). Type species: *Chaetoscatella cheesmanae* Malloch 1934, monotypy. –Wirth 1948: 296 [synonymy].

Diagnosis. Specimens of *Scatella* (*Apulvillus*) can be diagnosed by the following characters: ocellar seta short, length is half of fronto-orbital seta; face with medial portion sparsely setulose; face without row of setulae near parafacial. Species of *Apulvillus* are similar to those of *Scatella* but may be distinguished by the following characters: presutural dorsocentral seta inconspicuous or absent; row of acrostichal setae not extending to scutellum; thorax setae generally small; wing hyaline, without white spots.

Description. Moderately small to moderately large shore flies, body length 2.90–4.50 mm; blackish brown to brown species.

Head: Frons dull usually with distinct, subshiny to shiny frontal vitta; ocellar seta long or short; laterocline fronto-orbital seta 2; medial vertical seta long or short. Antenna short, concolorous; setae of pedicel typical; basal flagellomere round; arista macropubescent. Face conspicuously protruding, with an interfoveal, dorsal hump, medium to high; facial setae small, hair-like; 1–2 lateral facial setae curved laterodorsally; small ventroclinate setae along oral margin. Eye nearly round. Gena medium to moderately high, bearing a genal seta.

Thorax: Mesonotum generally dark brown colored, microtomentose, setae generally small; dorsocentral setae usually 2 (0+2); sutural acrostichal seta long, well developed or small, same length than other acrostichal setae; scutellum flat, disc bare, bearing 2 pairs of marginal setae; basal scutellar setae smaller than apical setae; postsutural supra-alar seta much smaller than postalar seta; legs typical, usually without distinct setae; color of tarsi variable; tarsal claws conspicuously curved and puvilli present below each claw or claws near straight and pulvilli absent; stem of halter short, head oval, white or dark. Wing generally pale to slightly infusate, without white spots.

Abdomen: Tergites dark brown, microtomentose. Male terminalia: sternites 5 and 6 absent. Epandrium and internal structures typical of *Scatella*; ventral projections of epandrium not separated; phallapodeme absent; ejaculatory apodeme present, L shaped, dorsoventrally flattened. Female terminalia: typical of *Scatella*; sternite 7 as a rectangular sclerite. Female ventral receptacle tubular shaped, one to five times longer than wide.

Distribution. Oceanian (Hawaii islands, French Polynesia).

Remarks. *Scatella* (*Apulvillus*) comprises seven species that are closely related to *Scatella* (*Scatella*) and are distinguished by the wing being mostly hyaline without obvious white spots. It is a heterogeneous subgenus with some species lacking pulvilli, and with some setae from the head and mesonotum being reduced. Tenorio (1980) reported that adults are generally found in freshwater streams and described the puparium of *Apulvillus mauiensis* (Wirth, 1948).

Scatella (*Parascatella*) Cresson, 1935

Figs 12, 14

Parascatella Cresson 1935: 357 (as a genus; feminine). Type species: *Scatella pilifera* Cresson 1931, original designation. –Sturtevant and Wheeler 1954: 178 [revised status]. –Mathis and Zatwarnicki 1995: 268–270 [world catalog].

Diagnosis. Specimens of *Scatella* (*Parascatella*) are similar to those of *Scatella* but may be distinguished by the following combination of characters: facial setae lateroventrally curved; proepisternum bearing macrosetae; postpronotum with 1–3 setae plus scattered setulae; postsutural supra-alar seta as long as postalar seta; wing spots evident.

Description. Moderately small to moderately large shore flies, body length 2.50–4.90 mm; blackish brown to cinereous species.

Head (Figs 12, 14): Frons dull usually with distinct, subshiny to shiny frontal vitta; laterocline fronto-orbital seta 2, rarely 3. Antenna short, dark; pedicel with strong seta ventrally; basal flagellomere brown; arista macropubescent to at most bearing short, dorsal, hairlike branches. Face conspicuously protruding, facial setae conspicuous, lateral facial setae ventrally curved, indistinctly from medial facial setae; small to long ventroclinate setae along oral margin. Eye usually nearly round. Gena short to moderately high, usually bearing a large seta.

Thorax: Mesonotum microtomentose, density of tomentum varying, generally unicolorous or with longitudinal stripes; dorsocentral setae 3 (1+2, usually with several smaller setae between larger bristles); acrostichal setae in

2 rows extending to scutellum, equal in length; prescutellar acrostichal absent; postsutural supra-alar seta long, subequal in length to postalar seta; postpronotum with 1 long setae; scutellum with 2–3 setae, basal scutellar setae long or short; legs typical, usually without distinct setae (forefemur with a row of stout setae anteroventrally and posteroventrally in some species); color of tarsi variable; halter pale yellowish; Wing with faint white spots; costal vein bearing spinelike setae along costal margin.

Abdomen: Tergites gray to brown, microtomentose, sometimes with lighter posterior margins, or mostly shiny, generally lacking prominent macrosetae. Male terminalia: sternites 5 and 6 absent. Epandrium and internal structures typical of *Scatella*; ventral projections of epandrium separated; ejaculatory apodeme present, crescent shaped, laterally flattened. Female terminalia: typical of *Scatella*; sternite 7 as a rectangular sclerite; female ventral receptacle tubular shaped, as long as wide.

Distribution. Neotropical (especially Andean transition).

Remarks. *Parascatella* was originally described as a genus and comprises 13 species from western South America. Nothing is known about the natural history of this subgenus except that adults are associated with aquatic or semi-aquatic habitats. Some species exhibit sexual dimorphism in the maculation pattern of wings, and/or in the shape of tarsomeres. Mathis and Shewell (1978) presented a revision and a cladistics analysis of the subgenus.

Scatella (*Scatella*) Robineau-Desvoidy, 1830

Figs 6–8, 15, 27–30, 46, 58–62

Scatella Robineau-Desvoidy 1830: 801 (as a genus; feminine). Type species: *Scatella buccata* Robineau-Desvoidy 1830 (= *Ephydra stagnalis* Fallén 1813), designated by Coquillett 1910: 603. –Mathis and Zatwarnicki 1995: 270–279 [world catalog]. –Zhang and Yang 2005: 1–11 [review, Chinese fauna].

Neoscatella Malloch 1933: 9 (as a genus; feminine). Type species: *Neoscatella atra* Malloch 1933, original designation. –Sturtevant and Wheeler 1954: 178 [as a subgenus]. –Beardsley 1991: 142–145 [parasite of a Hawaiian species (Eucoilidae)]. syn. nov. *Strandella* Duda 1942: 30 (as a subgenus of *Scatella*; feminine). Type species: *Scatella silacea* Loew 1860, original designation. –Dahl 1959: 119 [synonymy].

Trixostomus Rondani 1856: 130 (as a genus; masculine). Type species: *Ephydra stagnalis* Fallén 1813, original designation. –Becker 1905: 210 [synonymy].

Diagnosis. *Scatella* (*Scatella*) is distinguished from other subgenera of the genus *Scatella* mainly by the presence of white spots in the wing. Other characters useful to differentiate species of *Scatella* include the following: facial setae conspicuous, 1–2 lateral facial setae curved

laterodorsally; wings lightly to darkly infuscate with few to several white spots; row of acrostichal setae not extending to scutellum; sutural acrostichal setae usually longer than other acrostichal setae (if absent, presutural dorsocentral seta present).

Description. Minute to medium-sized shore flies, body length 1.00–3.00 mm; blackish brown to cinereous species, rarely yellow; species macropterous or with wings reduced.

Head (Figs 15, 58, 59): Frons dull usually with distinct, subshiny to shiny frontal vitta; laterocline fronto-orbital seta 2 rarely 3. Antenna short, dark; pedicel setae typical; basal flagellomere round; arista macropubescent to at most bearing short, dorsal, hair-like branches. Face conspicuously protruding, with an interfoveal, dorsal hump, uniformly sclerotized, no processes; facial setae conspicuous, 2–3 lateral facial setae curved laterodorsally or ventrally curved, indistinctly from medial facial setae; small to long ventrocline setae along oral margin. Eye usually nearly round. Gena short to moderately high, usually bearing a large seta.

Thorax (Figs 6, 7, 60): Mesonotum generally dark colored, microtomentose, density of tomentum varying, generally unicolorous or with longitudinal stripes, not conspicuously multicolored with pattern of bands and/or spots; dorsocentral setae 2 (0+2), or 3 (1+2); scutellum flat, disc bare, bearing 2 pairs of marginal setae; basal scutellar setae smaller than apical setae; pleural region generally gray, lighter than mesonotum; legs typical, usually without distinct setae (forefemur sometimes with a row of short, stout setae anteroventrally in some species); color of tarsi variable; tarsal claws conspicuously curved and puvilli present below each claw; stem of halter short, head oval, white. Wing generally pale to conspicuously infuscate with white spots, especially in cells r_{2+3} , r_{4+5} , and dm but exceptionally in cell r_1 and m_4 ; costa long, extended to vein M_1 , sometimes bearing spines; wing reduced, usually stenopterous in a few species.

Abdomen: Tergites gray to brown, microtomentose, sometimes with lighter posterior margins, or mostly shiny, blackish brown. Male terminalia (Figs 61, 62): sternites 5 and 6 well developed, very small or absent. Epandrium and internal structures typical of *Scatella*; ventral projections of epandrium separated or indistinguishable; phallopodeme absent; ejaculatory apodeme present, L shaped, dorsoventrally. Female terminalia (Figs 8, 27–30, 46): sternite 7 as one rectangular sclerite or 2 lateral, small, circular to partially quadrate sclerites; sternite 8 divided, as 2 lateral, lunate sclerites; female cerci bearing one strong, prominent seta, inserted posteroventrally. Female ventral receptacle

tubular shaped, one to five times longer than wide. Species moved from *Neoscatella* Malloch as new combinations: *S. (S.) albilutea* Mathis and Wirth, 1981; *S. (S.) amnica* (Tenorio, 1980), *S. (S.) atra* (Malloch, 1933); *S. (S.) aurulenta* Giordani Soika, 1956; *S. (S.) austrina* Mathis & Wirth, 1981; *S. (S.) bicolor* Mathis & Wirth, 1981; *S. (S.) bryani* Cresson, 1926; *S. (S.) cilipes* (Wirth, 1948); *S. (S.) clavipes* (Wirth, 1948); *S. (S.) crassicosta* Becker, 1896; *S. (S.) curtipennis* (Becker, 1905); *S. (S.) fluvialis* (Tenorio, 1980); *S. (S.) furens* Cresson, 1931; *S. (S.) gestiens* Cresson, 1931; *S. (S.) gregaria* Cresson, 1931; *S. (S.) hawaiiensis* Grimshaw, 1901; *S. (S.) ignara* Cresson, 1931; *S. (S.) immaculata* Malloch, 1925; *S. (S.) insularis* Mathis and Wirth, 1981; *S. (S.) karakensis* Stuke, 2012; *S. (S.) kauaiensis* (Wirth, 1948); *S. (S.) megastoma* (Zetterstedt, 1855); *S. (S.) nelsoni* Tonnoir & Malloch, 1926; *S. (S.) norrisi* Mathis & Wirth, 1981; *S. (S.) oahuense* Williams, 1938; *S. (S.) obscuriceps* Cresson, 1915; *S. (S.) praia* Mathis, Marinoni & Costa, 2014; *S. (S.) setosa* Coquillett, 1900; *S. (S.) sexnotata* Cresson, 1926; *S. (S.) silacea* Loew, 1860; *S. (S.) stuckenbergi* (Wirth, 1956); *S. (S.) subguttata* (Meigen, 1830); *S. (S.) tasmaniae* Mathis & Wirth, 1981; *S. (S.) terryi* Cresson, 1926; *S. (S.) victoria* (Cresson, 1935); *S. (S.) vittithorax* Malloch, 1925; *S. (S.) warreni* Cresson, 1926.

Distribution. Widespread: Afrotropical (Ethiopia to Cape), Australasian/Oceanian, Nearctic, Neotropical (especially Andean), Oriental, Palearctic Regions.

Remarks. This subgenus comprises 116 species from all tropical and temperate biogeographic regions and is the most speciose taxon in the tribe and subfamily. Most species occur in the Australasian/Oceanic and Neotropical Regions (Mathis and Zatwarnicki 1995). The species occur in typical habitats to the tribe, such as marshes, mangroves, intertidal areas, dunes and sandy beaches, rocky coasts, muddy and sandy areas along riverbanks and lakes, with emphasis on the species that occur in alkaline or acid hot springs (Wirth and Mathis 1979). Sixteen species have some immature stage described (see Williams 1938, Tenorio 1980 for the main examples). *Scatella stagnalis* is found in greenhouses and is the vector of a root disease caused by a *Pythium* fungus to crops in hydroponic cultures (Goldberg and Stanghellini 1990). Nine species with reduced wings are known, three from New Zealand and six from Neotropical Region (Mathis 1980, Harrison 1964, 1976, Wirth 1955).

The species that were formally classified in *Neoscatella* are interspersed with those of this subgenus, and lacking evidence of monophyly, we have elected to recognize a single subgenus; thus, the synonymy of *Neoscatella* with *Scatella*.

Scatella (Synhoplos) Lamb, 1917

Figs 54, 55, 82, 83

Synhoplos Lamb 1917: 390 (as a genus; masculine). Type species: *Synhoplos sturdeeana* Lamb 1917, designated by Wirth 1968: 27. –Mathis 1980: 29 [revised status]. –Mathis and Zatwarnicki 1995: 279–280 [world catalog].

Diagnosis. Specimens of *Scatella (Synhoplos)* are most similar to *Teichomyza* and some brachypterous *Scatophila* and *Scatella (Scatella)*, but may be distinguished following combination of characters: arista shorter than basal flagellomere; frons as wide as long; setulae along anterior margin of frontal vitta present; genal to eye ratio > 0.50; one pair of postsutural dorsocentral setae; macropterous wing.

Description. Small to medium-sized shore flies, body length 1.80–3.10 mm; brown to cinereous species; only micropterous species known.

Head (Fig. 54): Frons as long as wide, usually dull with distinct, subshiny frontal vitta; laterocline fronto-orbital seta 2. Antenna short, concolorous with head; pedicel with one long seta dorsally, subequal to length of arista; arista shorter than basal flagellomere, macropubescent. Face conspicuously protruding, interfoveal dorsal hump of face high, between antennae; facial setae conspicuous, 2 lateral facial setae curved laterodorsally. Eye subglobose-quadrangle, obliquely oriented to general plane of head; gena high (gena to eye ratio > 0.6), one strong genal seta.

Thorax (Fig. 55): Generally reduced; mesonotum flat; two rows of acrostichal setae, extending to scutellum, size of setae uniform; a row of small dorsocentral setulae plus 1 pair of presutural and 1 postsutural dorsocentral setae; scutellum short; basal scutellar setae smaller than apical setae; postsutural supra-alar setae small, much smaller than postalar. Legs typical, without distinct setae; femur stronger than tibiae and tarsi; tibia and tarsi light brown; halteres reduced; wing micropterous.

Abdomen: Tergites gray to brown, microtomentose, densely setose; Male Terminalia (Figs 82, 83): sternite 5 present, formed by two sclerites; sternite 6 absent; Epandrium and internal structures typical of *Scatella*; ventral projections of epandrium well-developed. Female terminalia typical of *Scatella*; sternite 7 as a rectangular sclerite. Female ventral receptacle tubular shaped, as long as wide.

Distribution. Neotropical (Tierra del Fuego region).

Remarks. Both species of *Synhoplos* are micropterous and occur along the coasts of continental islands within the Tierra del Fuego region of South America. Immature stages are unknown.

Scatella (Teichomyza) Macquart, 1835 (1 species)

Fig. 3

Teichomyza Macquart 1835: 534 (as a genus; feminine). Type species: *Teichomyza fusca* Macquart 1835, monotypy. –Mathis 1980: 36 [revised status]. –Mathis and Zatwarnicki 1995: 280 [world catalog].

Tichomyza, error for *Teichomyza*.

Diagnosis. Specimens of *Scatella (Teichomyza)* are similar to those of *Parascatella* and *Synhoplos* but may be distinguished from the other subgenera of *Scatella* by the following combination of characters: acrostichal setae scattered, not forming a row; three pairs of scutellar setae; and surstylus fused to epandrium but distinguishable as surstyli. Also, useful to diagnose *Teichomyza* species, are: interfoveal dorsal hump of face high, between antennae; thorax covered by small and scattered setulae; wing mostly hyaline without obvious white spots.

Description. Medium-sized to large shore flies, about 3.50–5.00 mm: dark brown to dark gray species.

Head (Fig. 3): Frontal vitta microtomentose, appearing dull; ocelli arranged as an isosceles triangle; Laterocline fronto-orbital setae 2. Antenna short, concolorous with head; arista micropubescent. Face conspicuously protruding, interfoveal dorsal hump of face high, between antennae; facial setae conspicuous, 2–3 lateral facial setae curved laterodorsally, stout; long ventrocline setae along oral margin. Eye higher than wide; Gena moderately high, bearing a large seta.

Thorax: Mesonotum microtomentose, covered by small and scattered setulae; dorsocentral setae 2 (0+2); 1 pair of long acrostichal setae at transversal suture; acrostichal of setae hair-like, uniseriate; postsutural supra-alar seta hair-like or lacking; scutellum with 3 pair of long setae; legs typical (forefemur with a row of long, stout setae anteroventrally in some species), color of tarsi pale brown; tarsal claws conspicuously curved and puvilli present below each claw. Wing lightly infusate, without white spots.

Abdomen: Tergites gray to brown, microtomentose, dorsal setae long and scattered: Male terminalia: sternites 5 and 6 absent; Epandrium and internal structures typical of *Scatella*; ventral projections of epandrium separated; ejaculatory present, L shaped, dorsoventrally flattened. Female terminalia typical of *Scatella*; sternite 7 as a rectangular sclerite. Female ventral receptacle tubular shaped, longer than wide.

Distribution. Neotropical (south Andean), Palearctic (especially Mediterranean).

Remarks. This monotypic subgenus includes only *Scatella (Teichomyza) fusca*, which has a disjunct distribution, oc-

curring in both southern South America and Europe. Mathis (1980) suggested that this species was introduced to Europe through shipping commerce to and from South America. However, just the opposite would now seem more likely, especially as adults were found in urine-soaked fabric that was recovered from Roman times (Brian H. Cogan per. obs.) and well before the Columbus discovery of the New World and any commerce. *Scatella* (*Teichomyza*) *fusca* is better known by the name “urine fly.” Larvae and adults occur in localities and habitats that are soaked in urine, such as outdoor urinals. This species is the only Ephydriidae that is associated with cases of myiasis (James 1947). Laboulbène (1867) provided a detailed study on the natural history of this species.

Scatophila Becker, 1896

Figs 19, 22

Scatophila Becker 1896: 237 (feminine). Type species: *Ephydra caviceps* Stenhammar 1844, original designation. –Zatwarnicki 1987: 277–298 [checklist]. –Zatwarnicki and Mathis 1994: 351–370 [classification, phylogeny]. –Mathis and Zatwarnicki 1995: 281–287 [world catalog].

Centromeromyia Frey 1954: 40 (feminine). Type species: *Centromeromyia eremita* Frey 1954, original designation. –Zatwarnicki 1991: 329 [synonymy].

Diagnosis. *Scatophila* is distinguished from other genera of Scatellini mainly by the costal vein short, extended only to vein R_{4+5} . Other diagnostic characters, include: 1 fronto-orbital seta (some Neotropical species with 2); and crossvein r-m distinctly distal to subcostal break.

Description. Minute to moderately small shore flies, body length 0.80–2.00 mm.

Head: Frons dull usually with distinct, subshiny to shiny frontal vitta; generally, 1 fronto-orbital seta (some Neotropical species with 2). Antenna short, dark colored; pedicel setae typical; basal flagellomere round; arista almost bare, without long dorsal branches. Face projected, sometimes central portion membranous and distinctly incised or oral margin with a protruding, narrow, sometimes spine-like projection (sexual dimorphism is frequently evident in the conformation of the face); facial setae conspicuous, lateral facial setae ventrally curved, usually indistinctly from medial facial setae, inserted mostly in the middle and ventral portions of face, 4–8 setae on the oral margin. Eye nearly round. Genal seta generally present; genal height small to high. Maxillary palpus elongate, mostly dark, as an exception yellow.

Thorax (Figs 19, 22): Mesonotum microtomentose, appearing with a multicolored pattern of bands and/or spots in many species; postsutural dorsocentral setae 2;

acrostichal setae in 2 rows extending to scutellum, equal in length; scutellum flat, disc bare, bearing 2 posterior setae laterally, basal scutellar setae smaller than apical setae; pleurae generally gray, lighter than mesonotum; stem of halter short, head oval, white. Legs typical, usually without distinct setae (ventral row of spinulae on mid tibiae of males of some species); color of tarsi variable; tarsal claws conspicuously curved and puvilli present below each claw. Wing faintly to conspicuously infusate with white spots distributed over most of wing, but exceptionally within cell r1; costa short, extended to vein R_{4+5} ; crossvein r-m distinctly distal to subcostal break; wings reduced in a few species. Legs typical, usually without distinct setae (ventral row of spinulae on mid tibiae of males of some species); color of tarsi variable; tarsal claws conspicuously curved and puvilli present below each claw.

Abdomen: Tergites gray microtomentose, sometimes with lighter posterior margins, or entirely shining black; male sternite 5 present, sternite 6 absent. Male terminalia: epandrium a closed plate; cerci completely round, rarely separated anteriorly; ventral margin of epandrium straight or slightly convex to incised medially forming two lateral lobate process; gonites Y-shaped, sharply terminated, sometimes bearing setae on dorsal margin of anterior portion; hypandrium, when present, as an inverted V-shaped structure bounded with the gonites or as a more or less sinuous band; phallapodeme dorsoventrally flattened, broad on margin connected to dorsal aedeagal opening, usually with two lateral projections, rod-like, lacking a keel; aedeagus shoe-shaped in lateral view, in most species bearing narrow, un- or paired sinuous ventral process that originates from ventral side of distal aedeagal margin; ejaculatory apodeme lacking. Female Terminalia: sternite 8 divided, as 2 lateral, subquadrate sclerites, bearing a long seta on posterior margin; female cerci without prominent setae. Operculum of female ventral receptacle helmet-like, somewhat round, covering extended process.

Distribution. Widespread: Afrotropical (Saharo-Arabian), Australiasian/Oceanian, Nearctic, Neotropical (especially Andean), Oriental, Palearctic Regions.

Remarks. *Scatophila* comprises 50 species and is the second most speciose taxon in the tribe. The genus mostly occurs in the Nearctic and Palearctic Regions (Mathis and Zatwarnicki 1995). Like many other taxa in the tribe, congeners of *Scatophila* feed on algae and bacteria (Deonier 1974). The immature stages are known for two species: *Scatophila unicornis* and *Scatophila iowana* (Bolwig 1940, Deonier 1974). Zatwarnicki and Mathis (1994) presented a phylogeny of

the genus and proposed nine species groups. Two species have reduced wings: *Scatophila gorodkovi* (Krivosheina and Ozerov 2016) and *Scatophila stenoptera* (Papp 1979). In all of the phylogenetic analyses, the species of *Scatophila* were recovered as a cluster, and the node giving rise to this cluster is the sister group of *Limmellia*. These two clades in turn are related to *Philotelma*.

Tauromima Papp, 1979

Tauromima Papp 1979: 359 (feminine). Type species: *Tauromima mountwilhelmi* Papp 1979, original designation. –Mathis and Zatwarnicki 1995: 288 [world catalog].

Diagnosis. *Tauromima* is distinguished from other genera of Scatellini by the following combination of characters: frons as long as wide; genal setae absent, only a row of setulae at ventral margin of gena: posterior notopleural setae at the same level of anterior setae; two rows of acrostichal setae, extending to scutellum, size of setae uniform.

Description. Small shore flies, body length 1.73 mm; dark brown species. Only apterous species known.

Head: Frons as long as wide, frontal vitta subshiny, not densely microtomentose; 2 laterocline fronto-orbital setae. Antenna short, concolorous with head; setae of pedicel typical; arista shorter than antenna, pubescent. Face conspicuously protruding, with an interfoveal, dorsal hump; facial setae conspicuous, 1–2 lateral facial setae curved laterodorsally; long ventrocline setae along oral margin. Eye wider than high, obliquely oriented to general plane of head; gena small (gena to eye ratio < 0.2); a row of setulae at the ventral margin of gena, without a distinct genal seta.

Thorax: Generally reduced, length shorter than length of head; mesonotum flat; two rows of acrostichal setae, extending to scutellum, size of setae uniform; a row of small dorsocentral setulae plus 1 pair of postsutural dorsocentral setae; scutellum short; basal scutellar setae same length as apical setae; pre and postsutural supra-alar seta indistinguishable or absent; one pair of setae on the side of scutellum, same length of scutellar setae; posterior notopleural seta same level of anterior seta. Wing almost apterous, only a slight bump evident; halteres absent. Legs typical, without distinct setae; femur stronger than tibiae and tarsi; tarsi concolorous with legs; tarsal claws conspicuously curved and puvilli present below each claw.

Abdomen: Tergites concolorous with the thorax, microtomentose but somewhat subshiny, densely setulose. Male terminalia: unknown; female terminalia: unknown.

Distribution. Australasian/Oceanian: Papua New Guinea (New Guinea).

Remarks. This genus includes a single species, *T. mountwilhelmi*, the only essentially apterous shore fly known. This species was collected at Mount Wilhelm (3400 m), Papua New Guinea. Nothing is known about the natural history of this species. *Tauromima* seems to be related to genera of Scatellini that have a single row of setulae along the ventral margin of the gena, similar to *Haloscatella*, *Amalopteryx* and *Philotelma*. Zatwarnicki and Mathis (1994) proposed *Tauromima* as the sister-group of *Limmellia* and *Scatophila*. We did not include this species in our taxon sampling; thus, we advocate the precedent of Zatwarnicki and Mathis (1994) and place this genus near *Limmellia* and *Scatophila*.

Thinoscatella Mathis, 1979

Fig. 36

Thinoscatella Mathis 1979a: 20 (as a subgenus of *Lamproscatella*; feminine). Type species: *Lamproscatella lattini* Mathis 1979a, original designation. –Olafsson 1991: 41 [revised status]. –Mathis and Zatwarnicki 1995: 288 [world catalog].

Diagnosis. This genus is similar to *Lamproscatella* Hendel but may be distinguished by the following combination of characters: small but conspicuous setae towards anterior margin of frontal vitta; posterior fronto-orbital seta inserted closer to medial vertical seta than to anterior fronto-orbital seta; wings hyaline, immaculate.

Description. Small to moderately small shore flies, body length 1.85–2.80 mm; brown to cinereous species.

Head: frons dull usually with distinct, subshiny to shiny frontal vitta; small, conspicuous setae towards anterior margin of frontal vitta; ocelli arranged as an isosceles triangle; laterocline fronto-orbital seta 2; posterior fronto-orbital seta inserted closer to medial vertical seta than to anterior fronto-orbital seta. Antenna short, dark; pedicel setae typical; basal flagellomere round, brown; arista macropubescent. Face conspicuously protruding, with an interfoveal, dorsal hump; facial setae conspicuous, 2–3 lateral facial setae curved laterodorsally; long ventrocline setae along oral margin; Eye nearly round; gena medium (gena to eye ratio 0.38); a row of setulae at the ventral margin of gena, without a distinct genal seta.

Thorax: mesonotum mostly microtomentose, dull colored, unicolorous; pleural areas generally concolorous with mesonotum: 3 pair of dorsocentral bristles (1+2); acrostichal setae in 2 rows extending to scutellum, setae generally subequal to each other, small, prescutellar acrostichal absent; 2 pair of lateral scutellar setae, basal pair shorter than apical pair; Legs mostly concolorous with pleural areas, without distinct setae, color of tarsi brown. Wing immaculate, hya-

line; costa relatively long, extended to vein M_1 ; stem of halter short, head oval, pale yellow.

Abdomen: tergites gray to brown, microtomentose, sometimes slightly darker toward margins; dorsal setae small and scattered. Male Terminalia (Fig. 36): sternite 1 present; sternite 5 present, sternite 6 absent. Epandrium as a plate generally ovoid in posterior view or elongated ellipsoid, with a narrow opening below the cerci; surstyli either lacking or fused indistinguishably with ventral margin of epandrium; ejaculatory apodeme lacking; aedeagus tube-like, slender, sometimes strongly tapered at apex; gonites roughly to distinctly Y-shaped, dorsal arms flattened, without setae; phallapodeme laterally compressed, straight to slightly curved; Female Terminalia: sternite 8 divided, as 2 lateral, lunate sclerites; female cerci without prominent setae. Female ventral receptacle with a helmet-like operculum, small, not covering extended process.

Distribution. Holarctic and Oriental (Tibet) Regions.

Remarks. This genus comprises three species, and we included two, *T. lattini* (Mathis) and *T. quadrisetosa* (Becker), in our taxon sampling. Adults prefer mud-sand beaches (Mathis 1979a) and are found in considerable numbers on flat, sand-covered beaches with growths of blue-green algae (Olafsson 1991). Immature stages are unknown.

In our phylogenetic analyses, the node giving rise to the species of *Thinoscatella* was the sister group to the nodes giving rise to *Haloscatella* and *Lamproscatella*.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance and cooperation of many organizations and individuals who contributed to the field work and production of this paper. For reviewing a draft of this paper, we thank Stephen Gaimari, Anthony “Tony” G. Irwin and Jens-Hermann Stuke. For general assistance, we thank Erin Kolski (USNM). We thank the curators and collections managers who loaned collections or facilitated work in their museums: David A. Grimaldi (AMNH); Jon K. Gelhaus and Jason D. Weintraub (ANSP); Ashley-Kirk Spriggs (BMNH); Stephen A. Marshall (DEBU); Luciane Marinoni (DZUP); Laszlo Papp (HNHM); Carlos José Einicker Lamas (MZUSP); Hans-Peter Tschorsnig (SMNS); Trevor K. Crosby (NZAC). This study was supported by grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq process 234167/2014-9 and PQ grant process 311744/2021-4) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, including a recent field work in Brazil (December 2009-June 2010) that resulted in the vast

majority of specimens from Brazil that were studied in this paper (CNPq Visiting Researcher process 401609/2009-0), which we gratefully acknowledge. We thank Dianne Mathis for helping with all aspects of the production of this paper, especially the field work in Brazil. We also thank A. Bernardo Carvalho and his lab (Elisa Carvalho, Monica Carvalho, Susana Vaz) for hosting us while conducting field work along the coast of São Paulo, and José Albertino Rafael and Rosaly Ale-Rocha (INPA) for hosting us while working at INPA and conducting field work in the general environs of Manaus.

LITERATURE CITED

- Andersson H (1971) The European species of *Limnellia* (Dipt., Ephydriidae). *Entomologica Scandinavica* 2(1): 53–59.
- Beardsley JW (1991) The genus *Kleidotoma* Westwood in Hawaii, with descriptions of three new species (Hymenoptera: Cynipoidea: Eucoilidae). *Proceedings of the Hawaiian Entomological Society* 30: 131–146.
- Becker Th (1896) *Dipterologische Studien IV. Ephydriidae*. *Berliner Entomologische Zeitschrift* 41(2): 91–276.
- Becker Th (1902) Die Meigen'schen Typen der sogen. Muscidae acalypterae (*Muscaria holometopa*) in Paris und Wien. *Zeitschrift für systematische Hymenopterologie und Dipterologie* 2(5): 209–256, 289–349.
- Becker Th (1903) Berichtigung zu Jahrg. II. Heft 5, p. 298. *Zeitschrift für systematische Hymenopterologie und Dipterologie* 3: 45–46.
- Becker Th (1905) Ephydriidae. In: Becker Th, Bezzi M, Kerécs K, Stein P (Eds) *Katalog der paläarktischen Dipteren*. G. Wesselényi in Hódmezővásárhely, Budapest, vol. 4, 185–215.
- Bolwig N (1940) The description of *Scatophila unicornis* Czerny 1900 (Ephydriidae, Diptera). *The Proceedings of the Royal Entomological Society of London, Series B*, 9: 129–137.
- Borkent A (2018) The State of Phylogenetic Analysis: Narrow Visions and Simple Answers – Examples from the Diptera (flies). *Zootaxa* 4374(1): 107–143. <https://doi.org/10.11646/zootaxa.4374.1.7>
- Collin JE (1930) Some new species of the dipterous genus *Scatella* Dsv. and the differentiation of *Stictoscatella* gen. nov. (Ephydriidae). *The Entomologist's Monthly Magazine* 66: 133–39.
- Coquillett DW (1910) The type-species of the North American genera of Diptera. *Proceedings of the United States National Museum* 37: 499–647.
- Costa DNR, Savaris M, Marinoni L, Mathis WN (2016) Two new, brachypterous *Limnellia* species from the Vene-

- zuelan Andes (Diptera: Ephydriidae). *Zootaxa* 4144(3): 301–315. <https://doi.org/10.11646/zootaxa.4144.3.1>
- Cresson ET Jr (1930) Studies in the dipterous family Ephydriidae. Paper III. Transactions of the American Entomological Society 56: 93–131.
- Cresson ET Jr (1931) Descriptions of new genera and species of the dipterous family Ephydriidae. Paper IX. Entomological News 42(4): 104–108.
- Cresson ET Jr (1935) Descriptions of genera and species of the dipterous family Ephydriidae. Transactions of the American Entomological Society 61: 345–372.
- Cumming JM, Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. SANBI Graphics and Editing, Pretoria, vol. 1, 89–133.
- Curtis J (1832) British Entomology; Being illustrations and descriptions of the genera of insects found in Great Britain and Ireland: containing coloured figs. from nature of the most rare and beautiful species, and in many instances of the plants upon which they are found. E. Ellis and Company, Simpkin and Marshall, J.B. Bailliere, London, vol. 9.
- Dahl RG (1959) Studies on Scandinavian Ephydriidae (Diptera Brachycera). *Opuscula Entomologica Supplementum* 15: 1–224.
- Deonier DL (1974) Biology and descriptions of immature stages of the shore fly *Scatophila iowana* (Diptera: Ephydriidae). *Iowa State Journal of Research* 49(1): 17–22.
- Duda O (1942) Neue oder ungenügend bekannte Zweiflügler der paläarktischen Region aus meiner Sammlung. 2. Fortsetzung. *Deutsche Entomologische Zeitschrift* 1942(1–4): 1–39.
- Eaton AE (1875) Breves Dipterarum uniusque Lepidopterarum Insulae Kerguelensi indigenarum diagnoses. *The Entomologist's Monthly Magazine* 12: 58–61.
- Fallén CF (1813) Beskrifning öfver några i Sverige funna Vattenflugor (Hydromyzides). *Kongliga Vetenskaps-Academiens Handlingar, Series 3, 1813*: 240–257.
- Fitch WM (1971) Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Biology* 20(4): 406–416.
- Footo BA (1995) Biology of shore flies. In: Mittler TE, et al. (Eds) *Annual Review of Entomology*. Palo Alto, California, vol. 40, 417–442.
- Frey R (1954) Diptera Brachycera und Sciaridae von Tristan da Cunha (with a Contribution by J. Becquaert, Cambridge, USA). *Results of the Norwegian Scientific Expedition to Tristan da Cunha* 4(26): 1–55.
- Goldberg NP, Stanghellini ME (1990) Ingestion-egestion and aerial transmission of *Pythium aphanidermatum* by shore flies (Ephydriinae: *Scatella stagnalis*). *Phytopathology* 80(11): 1244–1246.
- Goloboff PA (1993) Estimating character weights during tree search. *Cladistics* 9(1): 83–91. <https://doi.org/10.1111/j.1096-0031.1993.tb00209.x>
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32(3): 221–238. <https://doi.org/10.1111/cla.12160>
- Goloboff PA, Carpenter JM, Arias JS, Esquivel DRM (2008) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 24(5): 758–773. <https://doi.org/10.1111/j.1096-0031.2008.00209.x>
- Goloboff PA, Farris JS, Källersjö M, Oxelmann B, Ramírez MJ, Szumik CA (2003) Improvements to resampling measures of group support. *Cladistics* 19(4): 324–332. <https://doi.org/10.1111/j.1096-0031.2003.tb00376.x>
- Hackman W (1964) On reduction and loss of wings in Diptera. *Notulae Entomologicae* 44 (3): 73–93.
- Haliday AH (1833) Catalogue of Diptera occurring about Holywood in Downshire. *Entomological Magazine* 1: 147–180.
- Hawkins JA, Hughes CE, Scotland RW (1997) Primary homology assessment, characters and character states. *Cladistics* 13(3): 275–283. <https://doi.org/10.1111/j.1096-0031.1997.tb00320.x>
- Harrison RA (1959) Acalypterate Diptera of New Zealand. *Bulletin of the New Zealand Department of Scientific and Industrial Research* 128: 1–382.
- Harrison RA (1964) Insects of Campbell Island. *Diptera. Pacific Insects Monograph* 7: 304–324.
- Harrison RA (1976) The Arthropoda of the southern islands of New Zealand (9) Diptera. *Journal of the Royal Society of New Zealand* 6(2): 107–152.
- Hendel F (1917) Beiträge zur Kenntnis der acalyptraten Musciden. *Deutsche Entomologische Zeitschrift* 1917(6): 33–47.
- Hollmann-Schirrmacher V, Zatwarnicki T (1995) A new species of *Limnellia* from the Azores Islands (Diptera: Ephydriidae). *Aquatic Insects* 17(2): 77–82.
- James MT (1947) The Flies that cause Myiasis in Man. *Miscellaneous Publications (United States Department of Agriculture)* 631: 1–175.
- Krivoshaina MG (2004) A review of shore-flies of the genus *Lamproscatella* (Diptera, Ephydriidae) from Russia and adjacent territories. *Zoological Journal* 83(3): 321–329.

- Krivosheina MG (2012) Review of the shore-fly genus *Limnelli* Malloch, 1925 (Diptera, Ephydriidae) of Russia. *Far Eastern Entomologist* 246: 1–7.
- Krivosheina MG, Ozerov AL (2016) A new species of the shore-fly genus *Scatophila* Becker, 1896 (Diptera, Ephydriidae) with reduced wings from Wrangel Island, Russia. *Far Eastern Entomologist* 311: 1–6.
- Laboulbène A (1867) Histoire des métamorphoses de la *Teichomyza fusca*. *Annales de la Société Entomologique de France, Series 4, 7*: 33–42.
- Lamb CG (1917) Falkland Islands Diptera. *The Transactions of the Entomological Society of London* 1916: 387–395.
- Loew H (1860) Neue Beiträge zur Kenntniss der Dipteren. Siebenter Beitrag. Die Europaeischen Ephydrinidae und die bisher in Schlesien beobachteten Arten derselben. Programm der Königlichen Realschule zu Meseritz 1860, 46 pp.
- Macquart MJ (1835) Diptères. In: *Histoire Naturelle des Insectes*. In: Roret NE (Ed.) *Collection des suites à Buffon, Formant avec les oeuvres de cet auteur un cours complet d'histoire naturelle*. Tome deuxième. Pourrat Frères, Paris, vol. 2, 703 pp.
- Malloch JR (1925) Notes on Australian Diptera. No. vii. *Proceedings of the Linnean Society of New South Wales* 50(4): 311–340.
- Malloch JR (1933) Some Acalyptrate Diptera from the Marquesas Islands. *Bulletin of the Bernice P. Bishop Museum* 114: 3–31.
- Malloch JR (1934) Additional new species and other records of Acalyptrate Diptera (Sapromyzidae, Asteiidae, Drosophilidae, Ephydriidae and Trypetidae) from the Marquesas Island. *Bulletin of the Bernice P. Bishop Museum* 114: 179–200.
- Mathis WN (1978) A revision of the Nearctic species of *Limnelli* Malloch (Diptera: Ephydriidae). *Proceedings of the Biological Society of Washington* 91(1): 250–293.
- Mathis WN (1979a) Studies of Ephydrinae (Diptera: Ephydriidae), II: Phylogeny, classification, and zoogeography of Nearctic *Lamproscatella* Hendel. *Smithsonian Contributions to Zoology* 295: 1–41.
- Mathis WN (1979b) Ephydrinae (Diptera: Ephydriidae) – A new perspective. In: Deonier DL (Ed.) *First Symposium on the Systematics and Ecology of Ephydriidae (Diptera)*. North American Benthological Society, Oxford, 47–60.
- Mathis WN (1980) Studies of Ephydrinae (Diptera: Ephydriidae), III: Revision of some Neotropical genera and species. *Smithsonian Contributions to Zoology* 303: 1–50.
- Mathis WN (1982) Studies of Ephydrinae (Diptera: Ephydriidae), VI: Review of the tribe Dagini. *Smithsonian Contributions to Zoology* 345: 1–30.
- Mathis WN (1986) Studies of Psilopinae (Diptera: Ephydriidae), I: A revision of the shore fly genus *Placopsidella* Kertész. *Smithsonian Contributions to Zoology* 430: 1–30.
- Mathis WN (1989) Family Ephydriidae. In: Evenhuis NL (Ed.) *Catalog of the Diptera of the Australasian and Oceanian Regions*. E.J. Brill, Leiden, B.P. Bishop Museum special publication 86, 639–649.
- Mathis WN (2008) Two new neotropical genera of the shore-fly tribe Ephydrini Zetterstedt (Diptera: Ephydriidae). *Zootaxa* 1874: 1–15.
- Mathis WN, Marinoni L (2016) Revision of Ephydrini Zetterstedt (Diptera: Ephydriidae) from the Americas south of the United States. *Zootaxa* 4116(1): 1–110.
- Mathis WN, Shewell GE (1978) Studies of Ephydrinae (Diptera: Ephydriidae), I: Revisions of *Parascatella* Cresson and the *triseta* Group of *Scatella* Robineau-Desvoidy. *Smithsonian Contributions to Zoology* 285: 1–44.
- Mathis WN, Simpson KW (1981) Studies of Ephydrinae (Diptera: Ephydriidae), V: The genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America. *Smithsonian Contributions to Zoology* 329: 1–51.
- Mathis WN, Wirth WW (1981) Studies of Ephydrinae (Diptera: Ephydriidae), IV: Revision of the Australian species of subgenus *Neoscatella* Malloch. *Smithsonian Contributions to Zoology* 325: 1–27.
- Mathis WN, Zatwarnicki T (1990) Taxonomic notes on Ephydriidae (Diptera). *Proceedings of the Biological Society of Washington* 103(4): 891–906.
- Mathis WN, Zatwarnicki T (1995) A world catalog of the shore flies (Diptera: Ephydriidae). *Memoirs on Entomology, International* 4: 1–423.
- Mathis WN, Marinoni L, Costa DNR (2014) A review of Scatellini Wirth and Stone (Diptera: Ephydriidae) from Brazil. *Zoologia* 31(6): 561–576. <https://doi.org/10.1590/S1984-46702014000600005>
- Mathis WN, Zatwarnicki T, Kubátová-Hiršová H (2009) A revision of the shore-fly genus *Philotelma* Becker (Diptera: Ephydriidae). *Insect Systematics and Evolution* 40: 121–158.
- Mathis WN, Zatwarnicki T, Marris JWM (2004) Review of unreported shore-fly genera of the tribe Scatellini from the New Zealand subregion (Diptera: Ephydriidae) with description of three new species. *Zootaxa* 622: 1–27.
- Mathis WN, Zuyin J (1988) A review of the Asian species of the genus *Lamproscatella* Hendel (Diptera: Ephydriidae).

- Proceedings of the Biological Society of Washington 101(3): 540–548.
- Meigen JW (1830) Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. Schulz-Wundermann, Hamm, vol. 6, 401 pp.
- Nixon KC (2002) Winclada. Published by the Author, Ithaca, ver. 1.00.08.
- Olafsson E (1991) Taxonomic revision of western Palaearctic species of the genera *Scatella* R.-D. and *Lamproscatella* Hendel, and studies on their phylogenetic positions within the subfamily Ephydrinae (Diptera, Ephydriidae). *Entomologica Scandinavica* 37(Suppl.): 1–100.
- Oldroyd H (1964) The Natural History of Flies. W.W. Norton and Company, New York, 324 pp.
- Papp L (1979) On apterous and reducedwinged forms of the families Drosophilidae, Ephydriidae, and Sphaeroceoridae (Diptera). *Acta Zoologica Academiae Scientiarum Hungaricae* 25(3–4): 357–374.
- Patterson C (1982) Morphological characters and homology. In: Joysey KA, Friday AE (Eds) Problems in phylogenetic reconstruction. Academic Press, London, 21–74.
- Robineau-Desvoidy JB (1830) Essai sur les Myodaires. Mémoires Présentés par divers Savans a l'Académie Royale des Sciences de l'Institut de France, et Imprimés par son Ordre Sciences Mathématiques et Physiques 2(2): 1–813.
- Roff DA (1990) The evolution of flightlessness in insects. *Ecological Monographs* 60(4): 389–421.
- Rondani C (1856) Dipterologiae italicae prodromus. Genera Italica ordinis dipterorum ordinatim disposita et distincta et in familias et stirpes aggregata. A. Stoschi, Parmae, vol. 1, 228 pp.
- Stenhammar C (1844) Försök till Gruppering och Revision af de Svenska Ephydrinae. Kongliga Vetenskaps-Akademiens Handlingar, Series 3, 1843: 75–272.
- Sturtevant AH, Wheeler MR (1954) Synopses of Nearctic Ephydriidae (Diptera). *Transactions of the American Entomological Society* 79: 151–257.
- Tenorio JA (1980) Family Ephydriidae. In: Hardy DE, Delfinado MD (Eds) Insects of Hawaii. The University Press of Hawaii, Honolulu, vol. 13, 251–351.
- Vibe-Petersen S (1998) Laboratory rearing of the urine fly, *Scatella* (*Teichomyza*) *fusca* and observations on feeding and oviposition on pig farms. *Entomologica Experimentalis et Applicata* 87: 157–169.
- Wagner DL, Liebherr JK (1992) Flightlessness in Insects. *Trends in Ecology and Evolution* 7(7): 216–220.
- Williams FX (1938) Biological studies in Hawaiian water-loving insects. Part III. Diptera or flies. A, Ephydriidae and Anthomyiidae. *Proceedings of the Hawaiian Entomological Society* 10(1): 85–119.
- Wirth WW (1948) A taxonomic study of Hawaiian Ephydriidae (Diptera) related to *Scatella* Robineau-Desvoidy. *Proceedings of the Hawaiian Entomological Society* 13(2): 277–304.
- Wirth WW (1955) Los Insectos de las Islas Juan Fernandez. 20. Ephydriidae (Diptera). *Revista Chilena de Entomologia* 4: 51–72.
- Wirth WW (1964) A revision of the shore flies of the genus *Brachydeutera* Loew (Diptera: Ephydriidae). *Annals of the Entomological Society of America* 57(1): 3–12.
- Wirth WW (1968) Family Ephydriidae. In: Papavero N (Ed.) A Catalogue of the Diptera of the Americas South of the United States. Departamento de Zoologia, Secretaria da Agricultura, São Paulo, 1–43.
- Wirth WW (1970) A new genus and species of shore fly (Diptera, Ephydriidae) from southern Patagonia. *Acta Zoologica Lilloana* 26(1): 1–8.
- Wirth WW, Mathis WN (1979) A review of the Ephydriidae (Diptera) living in thermal springs. In: Deonier DL (Ed.) First symposium on the systematics and ecology of Ephydriidae (Diptera). North American Benthological Society, Oxford, 21–45.
- Wirth WW, Stone A (1956) Aquatic Diptera. In: Usinger RL (Ed.) Aquatic Insects of California. University of California Press, Berkeley, 372–482.
- Womersley H (1937) Diptera. In: Johnson TH (Ed.) B.A.N.Z. Antarctic Research Expedition 1929–1931. Adelaide, Australia, Reports Series B IV(3), 59–79.
- Zatwarnicki T (1987) New synonyms and records of Palearctic *Scatophila* (Diptera, Ephydriidae). *Polskie Pismo Entomologiczne* 57(2): 277–298.
- Zatwarnicki T (1991) Changes in nomenclature and synonymies of some genera and species of Ephydriidae (Diptera). *Deutsche Entomologische Zeitschrift* 38(4–5): 295–333.
- Zatwarnicki T (1992) A new classification of Ephydriidae based on phylogenetic reconstruction (Diptera: Cyclorhapha). *Genus* 3(2): 65–119.
- Zatwarnicki T, Báez M (1991) Notes on *Philotelma* (Diptera, Ephydriidae) with description of a new species from the Canary Islands. *Aquatic Insects* 13(4): 209–216.
- Zatwarnicki T, Mathis WN (1994) Phylogeny and classification of the genus *Scatophila* Becker (Diptera: Ephydriidae). *Annales de la Société Entomologique de France* 29[1993](4): 351–370.

Zhang J, Yang D (2005) Review of the subgenus *Scatella* Robineau-Desvoidy, 1830 from China (Diptera: Ephydriidae). *Zootaxa* 931: 1–11.

Zhang J, Yang D (2009) Species of the genus *Limmellia* from China (Diptera: Ephydriidae). *Zootaxa* 2308: 58–64.

Zhang J, Yang D, Mathis WN (2005) A new genus and species of Ephydriidae (Diptera) from the Oriental Region. *Zootaxa* 1040: 31–43.

Submitted: December 8, 2023

Accepted: March 8, 2024

Editorial responsibility: Alessandra Rung

Author Contributions

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Competing Interests

The authors have declared that no competing interests exist.

How to cite this article

Costa DNR, Mathis WN, Marinoni L, Sepúlveda TA (2024) Phylogeny and taxonomy of the shore-fly tribe Scatellini (Diptera: Ephydriidae: Ephydriinae). *Zoologia* 41: e23100. <https://doi.org/10.1590/S1984-4689.v41.e23100>

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Supplementary material 1

Table S1. Matrix of Characters with complete list of terminal taxa included in the cladistic analyses and their geographic distribution.

Authors: D.N.R. Costa, W.N. Mathis, L. Marinoni, T.A. Sepúlveda

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Link: <https://doi.org/10.3897/zoologia.41.e23100>

Appendix 1. Annotated list of characters and character states.

Head

1. Aristal length:

- (0) longer than basal flagellomere;
- (1) shorter than basal flagellomere.

2. Length of aristal rays:

- (0) long, pectinate arista;
 - (1) short, pubescent arista.
- ##### 3. Pedicel, length of dorsal seta:
- (0) shorter than basal flagellomere;
 - (1) same length as basal flagellomere.

4. Face, setulae on medial area and lower facial margin (oral margin):

- (0) present;
- (1) absent.

5. *Face, density of setulae on medial area and lower margin:

- (0) densely setulose;
- (1) sparsely setulose.

Comments. Contingent on character 4, state 0.

6. Face, length of lateral setae:

- (0) short and undistinguishable from other facial setae;
- (1) longer and stronger than other facial setae.

Comments. Contingent on character 4, state 0.

7. Face, orientation of long lateral setae:

- (0) curved anteroventrally (Fig. 3);
- (1) curved lateroventrally;
- (2) curved laterodorsally (Fig. 4).

Comment. This character is contingent on character 6, state 0.

8. *Face, row of setulae near parafacial margin:

- (0) present;
- (1) absent.

9. *Relative height of facial projection or hump:

- (0) less than half height of head (Fig. 10);
- (1) half height of head (Fig. 11);
- (2) higher than half height of head (Fig. 12).

Comment: The height is measured from the inferior margin of the face to dorsum of hump.

10. Width of frons:
(0) wider than long;
(1) as wide as long.
11. Shape of frontal vitta:
(0) triangular;
(1) subquadrate.
12. Interfrontal seta:
(0) absent;
(1) present.
Comment. This seta is elongated, well developed, and cruciate, and is present in some genera of Ephydrini.
13. Setulae along anterior margin of frontal vitta (mesofrons):
(0) absent (Fig. 3);
(1) present (Fig. 5).
Comment. These setulae are small but evident and distinct from microtomentum.
14. Microtomentose vestiture of frontal vitta:
(0) absent;
(1) present.
Comments. When the microtomentum is absent, the frontal vitta is bare, shiny; microtomentose frontal vitta is dull.
15. Arrangement of ocelli:
(0) equally distant from each other, as an equilateral triangle (Fig. 5);
(1) as an isosceles triangle.
Comment. When the ocelli are arranged in an isosceles triangle, the anterior ocellus is farther away from the posterior ocelli.
16. Ocellar seta:
(0) present;
(1) absent.
17. Length of ocellar seta:
(0) seta long, subequal to fronto-orbital setae;
(1) seta short, half of fronto-orbital seta.
Comment. This character is contingent on character 16, state 0.
18. Shape of eye:
(0) round or nearly so (Eye ratio 0.9 to 1.1);
(1) conspicuously wider than high, usually obliquely oriented (Eye ratio > 1.1);
(2) conspicuously higher than wide than high (Eye ratio < 0.9).
19. Orientation of fronto-orbital setae:
(0) proclinate and/or reclinate;
(1) latero-clinate (Figs. 3, 4).
Comment. Non-Ephydrinae shore flies usually have proclinate or reclinate fronto-orbital seta.
20. *Size of subcranial cavity:
(0) large and gaping (Fig. 14);
(1) small (Fig. 13).
21. Number of fronto-orbital setae:
(0) 0;
(1) 1;
(2) 2;
(3) 3;
(4) 4.
Comments. Only well-developed fronto-orbital setae are counted; i.e., length subequal to that of medial and lateral vertical setae.
22. Posterior fronto-orbital seta, position:
(0) inserted closer to anterior fronto-orbital seta than to medial vertical seta;
(1) inserted closer to medial vertical seta than to anterior fronto-orbital seta.
23. Genal seta:
(0) present (Fig. 3);
(1) absent.
24. Genal seta, length:
(0) long, conspicuous;
(1) short, indistinguishable from genal setulae.
Comment. This character is contingent on character 23, state 0.
25. Genal height:
(0) low (gena to eye ratio < 0.25);
(1) moderately high (gena to eye ratio 0.25 to 0.50);
(2) high (gena to eye ratio > 0.50).
26. Facial concavity, shape of arching:
(0) vertically arched, shield-like (Fig. 16);
(1) transversely arched (Fig. 15).
27. *Palpus, shape:
(0) claviform;
(1) slender, parallel sided, not claviform (Fig. 15).
28. *Lacinia, distal portion, projection, shape, anterior view:
(0) straight;
(1) T-shaped (Fig. 15).
29. *Cibarium, lateral projections:
(0) present (Fig. 15);
(1) absent.
30. *Cibarium, lateral projections, size:
(0) long, longer than ventral projection (Fig. 15);
(1) short, same length as ventral projection.

31. *Labellum, sclerite 2, length:
(0) more or less as long as wide of labellum, not overlapping prementum;
(1) longer than width of labellum, overlapping prementum (Fig. 18).
32. *Mediproboscis, lateral sclerite:
(0) absent;
(1) present.
- Thorax**
33. Thorax, vestiture, coloration:
(0) unicolorous or with gradual changes in coloration;
(1) distinctly bi- or tricolored, with stripe patterns.
34. Prosternum, setulae:
(0) present;
(1) absent.
35. Presutural dorsocentral setae, number of pairs:
(0) 0 (Fig. 7);
(1) 1 (Fig. 8);
(2) 2.
Comment. Only long presutural dorsocentral setae are counted; length of these is subequal to postalar seta.
36. Postsutural dorsocentral setae, number of pairs:
(0) 0;
(1) 1;
(2) 2 (Figs 7, 8);
(3) 3.
Comment. Only long postsutural dorsocentral setae are considered; length subequal to postalar seta.
37. Proepisternal macrosetae:
(0) absent;
(1) present.
38. Postpronotal setation:
(0) 1-3 setae plus scattered setulae;
(1) with a few setulae.
39. Presutural supra-alar seta:
(0) present (Figs 6, 7);
(1) absent.
40. Postsutural supra-alar seta:
(0) present (Figs 6, 7);
(1) absent.
41. Postsutural supra-alar seta, length:
(0) smaller than postalar seta;
(1) as long as postalar seta.
42. Posterior notopleural seta, position:
(0) inserted at same level as anterior seta;
(1) insertion distinctly elevated above level of anterior seta.
43. Anepisternum, anterodorsal corner, seta:
(0) indistinguishable from surrounding setae;
(1) one strong, distinct seta dorsally curved.
44. *Acrostichal setae, arrangement:
(0) forming 2 rows (Figs 7, 8);
(1) scattered, random setae, not forming a row.
45. *Acrostichal setae, extension of rows:
(0) rows extended to scutellum (Fig. 8);
(1) rows not extended to scutellum (Fig. 7).
Comment. This character is contingent on character 44, state 0.
46. Sutural acrostichal setae, length:
(0) short, same length as other acrostichal setae (Fig. 8);
(1) longer than other acrostichal setae (Fig. 7).
47. Intrapostalar seta:
(0) present (Fig. 7);
(1) absent.
48. Intrapostalar seta, length:
(0) small seta, much smaller than postalar seta;
(1) long seta, slightly smaller than postalar seta.
Comment. This character is contingent on character 47, state 0.
49. *Intra-alar seta:
(0) absent;
(1) present (Fig. 7, 8).
50. *Intra-alar seta, arrangement:
(0) scattered setae;
(1) aligned with row of intra-alar setae (Fig. 7, 8).
Comments. Contingent on character 49, state 1.
51. Prescutellar acrostichal seta, length:
(0) short, same length as other acrostichal setae;
(1) long, longer than other acrostichal setae (Fig. 8).
52. *Wing development:
(0) macropterous;
(1) stenopterous;
(2) micropterous;
53. *Wing infuscation:
(0) essentially hyaline;
(1) infuscate, often darker on anterior margin and lighter on posterior margin.
54. Wing, white spots:
(0) absent;
(1) present, pale to conspicuous (Fig. 19, 20).
55. Wing, white spots, density:
(0) wing with many white spots bare of microtrichia, even at cell r4;
(1) wing with few white spots bare of microtrichia, rarely reaching cell r4 (Figs 19, 20).

- Comment. This character is contingent on character 54, state 1.
56. Costal vein, length:
(0) long, extended to vein M₁ (Figs 20, 21);
(1) short, extended to vein R₄₊₅ (Fig. 19).
57. *Costal vein, subcostal break, overlapping:
(0) Costal vein continuous at subcostal break (Fig. 21);
(1) Costal vein slightly to deeply overlaps itself at subcostal break, sometimes looking like a spur (Figs 19, 20).
58. *Crossvein r-m, position:
(0) crossvein r-m just posteriorly or slightly distal of subcostal break (Fig. 20);
(1) crossvein r-m distinctly basal to subcostal break (Fig. 21);
(2) crossvein r-m distinctly distal to subcostal break (Fig. 19).
59. Crossvein dm-m with infusate spot:
(0) absent;
(1) present.
60. Costal vein spines along anterior margin:
(0) present;
(1) absent.
61. Scutellar seta, number of pairs:
(0) 2;
(1) 3.
Comment. When the number of pairs of scutellar seta is three, the extra pair is always located at the base of the scutellum.
62. Medial scutellar seta, length:
(0) long, at least 2/3 of apical seta;
(1) short, at most 1/2 of apical seta (Figs 7, 8).
63. *Anepisternal setae, length:
(0) small setae in addition to a longer, strong seta (Fig. 6);
(1) long setae in addition to a longer, strong seta.
Comment. The anepisternum always bears a long, well-developed anepisternal seta.
64. Katepisternal seta, length:
(0) long, well developed (Fig. 6);
(1) short, weak developed.
65. Male midfemur, posteroventral side, setae, shape:
(0) stout (Fig. 22);
(1) slender.
66. Male forefemur, anteroventral side, setae, shape:
(0) stout (Fig. 23);^[1]
(1) slender.
Comment. ^[1] Also referred to as “wart-like structures” (Olafsson 1991).
67. Tarsal claws, shape:
(0) conspicuously curved;
(1) near straight.
68. Pulvilli:
(0) conspicuous below each claw;
(1) absent or greatly reduced.
- Abdomen**
69. Abdomen, microtomentum:
(0) present;
(1) absent.
Comments. When the microtomentum is absent, the abdomen appears polished, shiny.
70. Sternite 1:
(0) present;
(1) absent.
71. *Number of well-developed sternites of male after sternite 4:
(0) 2 (Fig. 30);
(1) 1;^[2]
(2) 0 (Fig. 29).
Comment. ^[2] Previous authors proposed that the sternite 5 is absent and only sternite 6 is present (Olafsson 1991).
72. Male sternites 3 and 4, setae, shape:
(0) slender;
(1) short, spine-like setae (Fig. 25).
73. *Female sternites, form:
(0) square to rectangular-shaped, relatively wide (Figs 27, 28);
(1) distinctly narrow sternites (Fig. 26).
74. *Tergite 5 of male, posterolateral projection:
(0) absent;
(1) present.
75. *Epandrium or epandrium/surstyli, opening:
(0) present (Fig. 31);
(1) absent (Fig. 32).
Comment. Since the epandrium may be fused indistinguishably with surstyli or the surstyli are absent, we refer to them as “epandrium or epandrium/surstyli” (see character 78).
76. *Epandrium or epandrium/surstyli, opening, size:
(0) narrow opening below the cerci (Fig. 31);
(1) wide opening above the cerci;
(2) wide opening below the cerci.
77. *Epandrium, ventral projection:
(0) present;
(1) absent.

78. Surstylus, fusion with epandrium:
(0) distinctly separate from epandrium (Fig. 32);
(1) fused to the epandrium but distinguishable as surstyli;
(2) surstyli indistinguishable from epandrium or absent (Fig. 31).
79. *Surstyli, anterolateral projection:
(0) absent;
(1) present.
80. *Surstylus or surstylus/epandrium, number of pieces:
(0) surstylus IN a single piece (Fig. 32);
(1) surstylus in two pieces.
81. *Epandrium or epandrium/surstylus, posterior view, shape:
(0) roughly ellipsoid to subquadrate;
(1) ovoid.
82. Epandrium, ventral margin, shape:
(0) straight or slightly convex (Fig. 33);
(1) incised medially forming 2 lateral, lobate processes.
83. *Aedeagal shape:
(0) quill-like (Fig. 38);
(1) keel-like (Fig. 39);
(2) long and thin, tubular (Fig. 40);
(3) shoe-like (Fig. 37);
(4) large and bulky tube (Fig. 35);
(5) “*Diedrops* aedeagus” (Fig. 41).^[3]
Comment. ^[3] The aedeagus in *Diedrops* is uniquely shaped, and we propose a separated state for this condition.
84. Aedeagus, constitution:
(0) sclerotized structure (apparently the basiphallus) only, lacking a membranous distiphallus;
(1) with a sclerotized basiphallus and a membranous distiphallus that is invested with short, sharp scales or scale-like thorns (Figs 42, 43).
85. Aedeagus, ventral process:
(0) present;
(1) absent.
86. Ejaculatory apodeme:
(0) absent;
(1) present.
87. Ejaculatory apodeme, shape:
(0) L-shaped, flattened dorsoventrally structure;
(1) crescent shaped, laterally flattened.
Comments. Contingent on character 86, state 1.
88. Phallapodeme:
(0) present;
(1) absent.
89. *Phallapodeme, shape:
(0) a laterally flattened bow, often with an extended keel (Fig. 56, 59, 64);
(1) flattened dorsoventrally, usually with 2 lateral projections, rod-like, lacking a keel (Figs 42, 43).
Comment. This character is contingent on character 88, state 0.
90. Gonites and hypandrium, fusion:
(0) complete as single structure, i.e., gonites and hypandrium fused;
(1) separated into a sclerite hypandrium and lateral structures representing gonites.
Comment. The hypandrium is considered fused with gonites within Ephydrinae, and the anterior arms of the gonite/hypandrium is called “gonal arch”.
91. Hypandrial shape:
(0) a straight sclerite hypandrium;^[4]
(1) a bifurcate sclerite hypandrium;^[4]
(2) a U-shaped broad hypandrium.
^[4] referred as “neohypandrium” to *Scatophila* (Zatwarnicki and Mathis 1994).
92. *Gonal arch, arms, fusion:
(0) arms separated;
(1) arms fused (Figs 34, 42).
93. *Gonal arch and phallapodeme, fusion:
(0) separated, not fused;
(1) fused (Fig. 82).
94. *Posterodorsal arm of gonite:
(0) absent;
(1) present.
95. *Posterodorsal arm and gonal arch, shape:
(0) bulky dorsal arm;
(1) large, more like a flap (Figs 35, 35, 40).
Comments. Contingent on character 94, state 0.
96. Female sternite 8, setae, length:
(0) same length as other setae;
(1) bearing prominent setae (Fig. 24).
97. Sternite 9/subanal plate, setae, development:
(0) bearing one pair of strong setae (Fig. 26);
(1) slender, indistinguishable from surrounding setae.
98. Female cerci, setae, development:
(0) slender, indistinguishable from surrounding setae;
(1) bearing one long, strong, prominent seta, inserted posteroventrally (Fig. 26);
(2) a long, slender seta inserted posteroventrally (Fig. 24).
99. Female sternite 7:
(0) present;
(1) absent.

100. *Female sternite 7, fusion:

- (0) 1 sclerite (Figs 26, 28);
- (1) 2 sclerites.

Comment. This character is contingent on character 99, state 0.

101. *Female sternite 8, number:

- (0) 2 sclerites;
- (1) 1 sclerite.^[5]

Comment.^[5] The female abdomen of *Brachydeutera* has only seven segments + cerci, instead of usually eight to Ephydrinae. We are assuming that this state is not applicable to *Brachydeutera*.

102. *Female sternite 8, shape:

- (0) 2 sclerites, crescent-shaped (Figs 26, 27, 28);
- (1) 2 sclerites, subquadrate (Fig. 24);

Comment. This character is contingent on character 101, state 0.

103. *Female tergite 8:

- (0) tergite complete, like an arch;^[6]
- (1) tergite incomplete, only 2 sclerites laterally

Comment.^[6] The female abdomen of *Brachydeutera* only has seven segments + cerci, instead of the usual eight in Ephydrinae, and we are assuming that this state is not applicable to *Brachydeutera*.

104. Female ventral receptacle, operculum:

- (0) Present (Fig. 44);
- (1) Absent (Fig. 47).

105. Female ventral receptacle, operculum, shape:

- (0) helmet-like, trapezoidal (Fig. 44);
- (1) tube-like (Fig. 46).

Comment. This character is contingent on character 104 state 0.

106. Female ventral receptacle, operculum, size:

- (0) large and well developed, covering the extended process (Fig. 44);
- (1) small, not covering the extended process (Fig. 45).

Comment. This character is contingent on character 104 state 0.

Characters not utilized in the analysis

Five characters were eliminated from the final analysis because they are autapomorphies. We present them here because they can be useful in a different level of analysis.

1. Face, protrusion:

- (0) absent;
- (1) present.

Comments. Only a few species of the genus *Scatophila* share a protrusion at face.

2. Paraverticlar seta, length:

- (0) short, only slightly longer than longer postocellar setae;
- (1) long, subequal to ocellar seta (*Paracoenia*).

Comment. Species of the genera *Paracoenia*, *Calocoenia* and *Cirrula* (Ephydrini) share a long paraverticlar seta.

3. Medial vertical setae, length:

- (0) subequal to the length of lateral vertical setae;
- (2) very small.

Comment. Two species of the subgenus *Scatella* (*Apulvillus*) share a very small medial vertical seta: *S. (A.) mauiensis* and *S. (A.) williamsi*.

4. Cerci of male, height:

- (0) cerci low, restricted at the dorsal part of the epandrium;
- (1) cerci height, as high as epandrium.

Comment. Only present in *Austrocoenia aczeli*.

5. Epandrium, lateral margins, process:

- (0) ending at juncture of gonite;
- (1) a process continues from each side that is fused anteromedially.

Comment. The process at lateral margins of epandrium is present in three species of *Haloscatella*: *H. arichaeata*, *H. cephalotes* and *H. nivosa*.