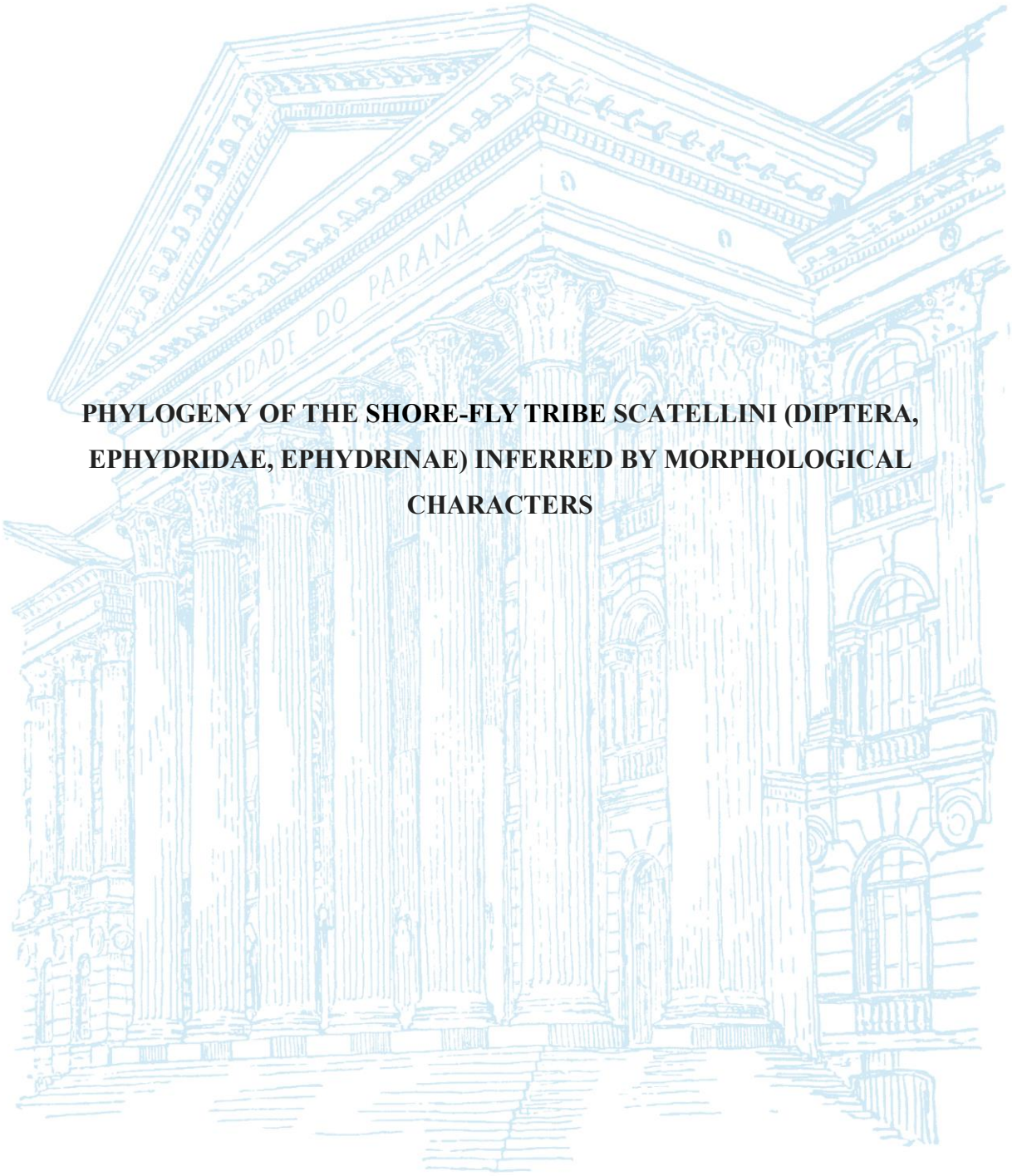
UNIVERSIDADE FEDERAL DO PARANÁ

DANIEL NEGOSEKI ROBALO COSTA



PHYLOGENY OF THE SHORE-FLY TRIBE SCATELLINI (DIPTERA, EPHYDRIDAE, EPHYDRINAE) INFERRED BY MORPHOLOGICAL CHARACTERS

CURITIBA

2017

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Tese apresentada à Coordenação do programa de Pós-Graduação em Ciências Biológicas, Área de Concentração em Entomologia, Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial para obtenção do grau de Doutor em Ciências Biológicas.

Orientadora: Profª Drª Luciane Marinoni
Co-orientador: Dr. Wayne Neilsen Mathis

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Tese aprovada como requisito parcial para obtenção do grau de "Doutor em Ciências", no Programa de Pós-graduação em Ciências Biológicas, Área de Concentração em Entomologia, da Universidade Federal do Paraná, pela Comissão formada pelos professores:

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Curitiba, 04 de setembro de 2017.

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Life seems to be orderly and lawful behavior of matter, not based exclusively on its tendency to go over from order to disorder, but based partly on existing order that is kept up.

Erwin Schrödinger, *What is Life*?

RESUMO

A tribo Scatellini compreende 249 espécies distribuídas em todas as regiões biogeográficas exceto a Antártica. Atualmente a tribo compreende nove gêneros. Um destes gêneros, *Scatella* Robineau-Desvoidy comprende seis subgêneros. Com o intuito de testar a monofilia da tribo e entender o relacionamento entre os gêneros, foi realizada uma análise cladística a partir de pesagens igual e implícita de caracteres, com base na morfologia de machos e fêmeas adultos. Foram incluídas espécies de oito dos nove gêneros de Scatellini, de diversas regiões geográficas, para analisar a maior diversidade morfológica possível. Também foram incluídas espécies das demais tribos de Ephydrinae, com o objetivo de conhecer a posição de Scatellini dentro da subfamília. Os resultados demonstraram que Scatellini, no sentido atual, é um grupo monofilético, assim como, cada um dos demais gêneros incluídos na análise. Na análise de pesagem igual, *Thinoscatella* Mathis é o grupo-irmão dos demais gêneros de Scatellini; *Amalopteryx* Eaton, *Lamproscatella* Hendel, *Scatella* Robineau-Desvoidy e um clado formado por (*Haloscatella* Mathis + (*Philotelma* Becker + (*Limnellia* Malloch + *Scatophila* Becker) aparecem em politomia. Na análise de pesagem implícita, duas grandes linhagens se formaram: 1. O gênero *Scatella* e seus subgêneros; 2. os demais gêneros de Scatellini. Na análise de pesagem implícita um clado inclui (*Lamproscatella* + *Haloscatella*) + *Thinoscatella*) e o clado (*Philotelma* + (*Limnellia* + *Scatophila*) aparece nas análises de pesagem igual e implícita. *Amalopteryx* Eaton compartilha caracteres com os dois últimos grupos, mas não pertence propriamente a nenhum deles. Três subgêneros de *Scatella* foram corroborados como grupos monofiléticos: *Parascatella* Cresson, *Synhoplos* Lamb e *Teichomyza* Macquart. *Apulvillus* Malloch foi corroborado como um grupo monofilético na análise de pesagem implícita. *Neoscatella* Malloch é sinonimizado com *Scatella* (*Scatella*), pois nenhuma sinapomorfia foi encontrada para estes subgêneros. Na análise de pesagem implícita Ephydrini e Scatellini são grupos-irmãos, e a tribo Dagini, como entendida atualmente, não foi corroborada como um grupo monofilético. São apresentadas redescrições de Scatellini e todos os gêneros incluídos, assim como uma chave de identificação para os gêneros.

Palavras-chave: análise cladística, taxonomia, *Scatella*, Ephydrini, Dagini.

ABSTRACT

The Scatellini comprises 249 species distributed in all biogeographical regions except Antarctica. Currently, the tribe comprises nine genera. One genus, *Scatella* Robineau-Desvoidy comprises six subgenera. In order to test the monophyly of the tribe and understand the relationship between the genera, a cladistic analysis was performed with equal and implicit character weighing, based on the morphology of adult males and females. The species of eight of nine genera of Scatellini, from different geographic regions, were included for the introduction of a greater morphological diversity possible. Also included are species of the other tribes of Ephidrinae, in order to know the position of Scatellini within the subfamily. The analysis showed that the tribe Scatellini, as currently characterized is a monophyletic group, as well as the other genera included in the analysis. In the analysis done with equal weighing, *Thinoscatella* Mathis is the sister-group of all other genera of Scatellini; *Amalopteryx* Eaton, *Lamproscatella* Hendel, *Scatella* Robineau-Desvoidy and a clade including (*Haloscatella* Mathis + (*Philotelma* Becker + (*Limnellia* Malloch + *Scatophila* Becker) are in polytomy. Using the analysis of implied weighing, two major lineages emerged: 1. *Scatella* Robineau-Desvoidy and its included subgenera; 2. All other genera of Scatellini. Under implied weighing, one clade includes (*Lamproscatella* + *Haloscatella*) + *Thinoscatella*) and the clade (*Philotelma* + (*Limnellia* + *Scatophila*) appears under equal and implied analysis. *Amalopteryx* shares characters with the last two groups, but does not belong to any group properly. Three subgenera of *Scatella* were corroborated as monophyletic groups: *Parascatella* Cresson, *Synhoplos* Lamb e *Teichomyza* Macquart. *Apulvillus* Malloch was corrobotated only using implied weighting. *Neoscatella* Malloch is synonimized with *Scatella* (*Scatella*), since no synapomorphy was found for this subgenus. Under implied weighing, Ephydrini and Scatellini are sister-groups, and the tribe Dagini, as currently understood, was not recovered as a monophyletic group. Redescriptions of Scatellini and all included genera are presented, as well as an identification key to the genera.

Keywords: cladistic analysis, taxonomy, *Scatella*, Ephydrini, Dagini.

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1. Introduction

What are shore flies?

The Ephydridae, more commonly known as shore or brine flies, are acalyptrate Diptera that usually occur in aquatic and semi-aquatic habitats such as swamps, riverbanks, lagoons, and marine beaches. The family represents great diversity with respect to other families of the superfamily Ephydroidea. Worldwide about 2,000 species are known in this family, and these are arrayed into 128 genera (Mathis and Zatwarnicki 1995, pers. obsv. of Wayne N. Mathis). Their ancestors diverged from other ephydroid flies around 60 Ma (Wiegmann et al., 2011); fossil records from the Eocene, Oligocene and Miocene show five species in four modern genera (Evenhuis, 2017). The family has representatives in all biogeographic regions except Antarctica.

Although most shore flies live in aquatic or semiaquatic habitats, several genera have evolved structural and behavioral modifications that adapt them to inhospitable habitats, including hot springs, highly alkaline or saline lakes, salt marshes, mangrove swamps and, most remarkably, exposed petroleum pools. Feeding habits of shore flies vary considerably. Larvae and adults usually feed on microorganisms such as bacteria and unicellular algae, but some species also feed on decaying animal or vegetal tissue or excrement. Others use nectar or live as leaf-miners and predators of other insects, spiders and even frog eggs. Most species are an important food source for waterfowl and wildlife (Foote, 1995).

The current classification of shore flies was largely influenced by and derived from the papers of Ezra T. Cresson, Jr. during the first half of the 20th century. He proposed four subfamilies (Psilopinae, Notiphilinae, Napaeinae, Ephydrinae) and several tribes, and that classification has been followed by most authors with minor changes and additions (Mathis, 1991).

Today, the Ephydridae, according to the phylogenetic hypothesis presented by Zatwarnicki (1992), are divided into five subfamilies: Discomyzinae (divided into two tribes and comprising about 183 species), Hydrelliinae (five tribes and 506 species), Gymnomyzinae (six tribes and 334 species), Ilytheinae (three tribes and 176 species)

and the subfamily Ephydrinae, currently comprising four tribes (Dagini, Ephydrini, Parydrini e Scatellini), and 445 species.

An overview of Ephydrinae, and its phylogenetic relationships

Ephydrinae are probably the most easily recognized (together with *Ochthera* Latreille) and best-known subfamily of shore flies. They have attracted the attention of students in biology from different backgrounds and interests, due to their peculiar morphology and habitats. Species of this subfamily are associated primarily with freshwater habitats but are also known to occur in the effluent of hot springs and inland saline and alkaline habitats in various regions of the world (Foote, 1995).

The Swedish naturalist, Johan Wilhelm Zetterstedt, proposed the subfamilial name Ephydrinae (1837), based on the genus *Ephydra* Fallén, 1810. The type species of *Ephydra* is *E. riparia* Fallén, 1813 by the subsequent designation of Curtis (1832). Zetterstedt's suprageneric group now includes all species known to date. All subsequent authors have used Ephydridae as the familial name, although sometimes with variant spellings.

Cresson (1930) proposed the basic concept of Ephydrinae that is used today, although it has been revised and updated in several subsequent papers. Wirth and Stone (1956), in a key to North America genera, proposed the tribes Ephydrini and Scatellini, which were characterized by long and straight claws and the absence of pulvilli (Ephydrini) and curved claws and well-developed pulvilli (Scatellini). This concept was followed in subsequent papers. Mathis (1979b) presented the first cladistic analysis of the subfamily (Fig. 1, Table I). His phylogeny presented Ephydrinae as a monophyletic group divided into three principal lineages: (((Ephydrini + (*Paracoenia* + related genera) *Austrocoenia*)) (*Dagus* + related genera) ((*Coenia* + related genera) (*Lamproscatella* + related genera) (*Scatella* + related genera))).

The genera close to Ephydrini, *Paracoenia* Cresson, and related genera, including *Austrocoenia* Wirth, have curved claws and puvilli. Thus, the tribe Scatellini, as initially proposed by Wirth and Stone (1956), is a paraphyletic group that is characterized by plesiomorphies, and the tribe Ephydrini is an ingroup within "Scatellini" (Mathis 1979b).

Mathis (1980) described a new Neotropical genus, *Notiocoenia*, and presented a phylogeny of Ephydrinae similar of that of his previous paper (Mathis 1979b), but excluding *Dagus* Cresson and related genera. These latter genera could not be easily included within existent classifications. Mathis (1982) then proposed a new tribe, Dagini, for this group. Although Scatellini were presented as a paraphyletic group, the tribe continued to be recognized as originally characterized.

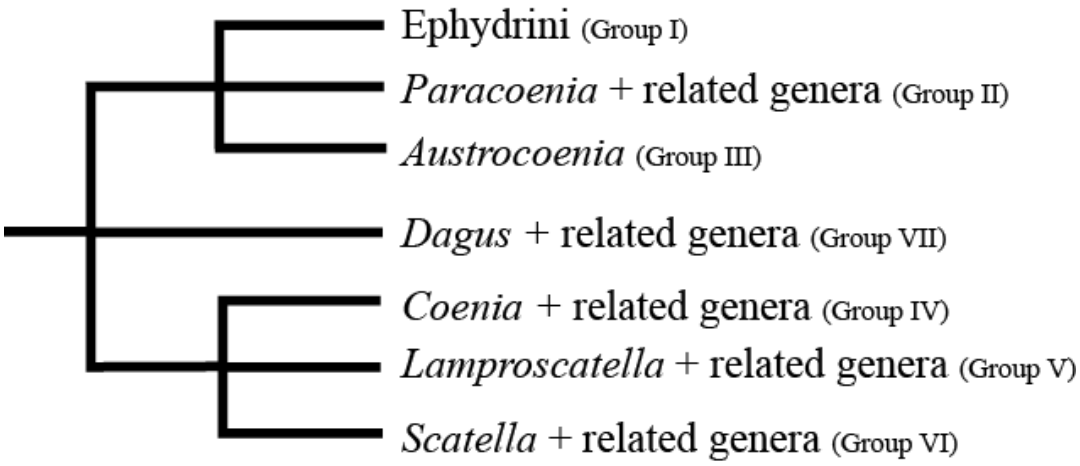


Figure 1. Phylogeny of subfamily Ephydrinae from Mathis (1979b)

Group I	**Group V**
Cirrula Cresson	*Amalopteryx* Eaton
Ephydrella Tonnoir and Malloch	*Philotelma* Becker
Hydropyrus Cresson	*Lamproscatella* Hendel
Halephydra Wirth	**Group VI**
Ephydra Fallén	*Limnellia* Malloch
Two new genera (*Neoephydra* Mathis and *Paraephydra* Mathis)	*Scatophila* Becker
Group II	*Parascatella* Robineau-Desvoidy
Paracoenia Cresson	*Scatella* Robineau-Desvoidy
Calocoenia Mathis	**Group VII**
Group III	*Psilephydra* Hendel
Austrocoenia Wirth	*Dagus* Cresson
Group IV	*Physemops* Cresson
Coenia Robineau-Desvoidy	*Diedrops* Mathis and Wirth
New genus (*Notiocoenia* Mathis)	

Table I. Group of genera of Ephydrinae from Mathis (1979b); subgenera were omitted.

Zatwarnicki (1992) presented a phylogeny for Ephydridae and divided the family into five subfamilies. The subfamily Ephydrinae (Fig. 2) was modified as follows: Parydrini was placed in Ephydrinae; the genus *Brachydeutera* Loew in Dagini, and *Coenia*, *Paracoenia* and *Notiocoenia* were transferred to Ephydrini. The subfamily Halmopotinae, proposed by Canzoneri and Meneghini (1974) and which included only the genus *Halmopota* Haliday, was synonymized with Ephydrini. Zhang, Yang and Mathis (2005) described the Oriental genus *Sinops* Zhang, Yang and Mathis in the tribe Dagini and Mathis (2008) described two new Neotropical genera to Ephydrini: *Paraephydra* and *Neoephydra.* The tribe Scatellini was restricted to 11 genera and was characterized by the proepisternum usually lacking macrosetae (Zatwarnicki, 1992).

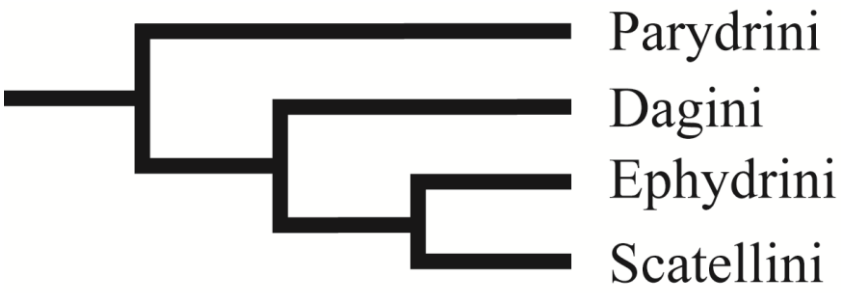


Figure 2. Phylogeny of subfamily Ephydrinae from Zatwarnicki (1992).

The tribe Scatellini and its phylogenetic relationships up to date

The first genera of Scatellini were described in the 19th century: the type-genus, *Scatella* Robineau-Desvoidy, was proposed in 1830, followed by *Teichomyza* Macquart in 1835. Eaton (1875) described *Amalopteryx*, and Becker (1896) proposed *Scatophila* and *Philotelma*. In the 20th Century, Hendel (1917) described *Lamproscatella*, and Lamb (1917) described *Synhoplos*. Malloch (1925, 1933, 1934) described three genera: *Limnellia*, *Neoscatella* and *Apulvillus* respectively. Other genera and subgenera were also proposed but several of them were synonymized, their taxonomic status was changed, or they were transferred to other tribes. The taxonomic changes recognized today are: Stutervant and Wheeler (1954) recognized *Neoscatella* and *Parascatella* as subgenera of *Scatella*; Mathis (1979a) described two new subgenera in *Lamproscatella*: *Haloscatella* and *Thinoscatella,* which were later given

generic status Olafsson (1991); and Mathis (1980) included *Apulvillus*, *Teichomyza* and *Synhoplos* as subgenera of *Scatella* (Table II).

Thus, in the 21th Century the tribe Scatellini comprised 249 species (plus five *nomina dubia*) in nine genera (Mathis and Zatwarnicki, 1995); *Scatella* is divided into six subgenera (Table III), and has the largest number of described species (139 species plus two *nomina dubia*). The tribe has representatives in all biogeographic regions except Antartica.

Wirth and Stone (1956) differentiated Scatellini from Nearctic species with two characters: curved tarsal claws and well-developed pulvilli. Mathis (1979b, 1980) discussed the relationships between the genera of Scatellini.

Mathis (1979b) proposed the group *Scatella* plus related genera (Group VI, Table I) that comprises four genera in the clade sharing white spots on wings: ((*Scatella* + *Parascatella*) + (*Scatophila* + *Limnellia*)); the group *Lamproscatella* plus related genera ((*Amalopteryx* + *Philotelma*) + *Lamproscatella*), characterized by the genal setae reduced or lacking.

In a revision of Neotropical species (Mathis, 1980), *Synhoplos* Lamb and *Teichomyza* Macquart were presented as sister-groups within the genus *Scatella*. Three groups are presented within Ephydrinae: the group *Coenia* plus related genera (group IV; Mathis, 1979b) as the sister-group of *Scatella* and related genera (group VI; Mathis, 1979b), and a group with *Paracoenia* and related genera (group II; Mathis, 1979b), *Austrocoenia,* and Ephydrini.

Olafsson (1991) presented a phylogeny of Ephydrinae based on genera from the western Palearctic Region. In his study, Olafsson proposed a monophyletic group without postpronotal setae and named it as the tribe Scatellini, thus moving *Coenia* to Ephydrini. The other genera, comprising the group, *Paracoenia*, *Austrocoenia* and *Coenia,* 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 group *Philotelma* (*Philotelma, Scatophila and Limnellia),* the group *Lamproscatella* and the group *Scatella.* In the world catalog of shore flies, Mathis and Zarwarnicki (1995) relegated *Parascatella* to subgeneric status within *Scatella*.

The relationships of species within some genera were also investigated: Mathis and Shewell (1978) presented phylogenetic relationships for species within *Parascatella* and the *triseta* group of *Scatella*; a phylogeny of Nearctic species of *Limnellia* was presented in Mathis (1978); Mathis (1979b) presented a phylogeny of *Lamproscatella* based on Nearctic species, proposing the subgenera *Haloscatella* and *Thinoscatella*; a revision of Australian *Neoscatella* includes a phylogeny of the species of that region (Mathis and Wirth, 1981); Zatwarnicki and Mathis (1994) presented a phylogeny for species of *Scatophila* and proposed several species groups; Olafsson (1991) presented a phylogeny for species of *Scatella* (including *Teichomyza*) from the western Palearctic.

In Ephydridae, 33 species have reduced wings to some degree (Costa; Mathis; Marinoni, 2016; Krivosheina and Ozerov, 2016), with a preponderance of reduced wing species being found in the tribe Scatellini (20 species). Two genera are monotypic and 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 altitude, arctic and sub-Antarctic areas of low altitude, coastal and marine habitats; those not in these categories are species with terricolous or hypogeous 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 the reduction of thorax and halters, strong legs, and large abdomens, besides the reduction and/or loss of wings (Wagner and Liebherr, 1992).

Natural history

Most information on the biology and immature forms of Ephydrinae is about species of the tribe Ephydrini. There is a paucity of information on other groups.

Foote (1995), in his synthesis on the biology of Ephydridae, gathered information from various articles about species of Scatellini. The species of this tribe feed on algae, cyanobacteria and particles of various types of decomposing animal and plant organic matter, as well as various microorganisms that proliferate on this substrate. The species of the tribe live in a wide variety of habitats: 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 places with large concentrations of salt. They also occur in muddy and sandy areas along riverbanks and lakes. Some species are found on lawns. *Scatella stagnalis* (Fallén) 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). The larvae of one species, *Scatella* (*Teichomyza*) *fusca* Macquart, occur in an unusual environment: localities and habitats that are soaked in urine, such as outdoor urinals. The larvae and adults feed on human and animal excrements (Vibe-Petersen, 1998). This is also the only known species of the family Ephydridae that is associated with cases of myiasis (James, 1947).

Wirth & Stone, 1956 (North American genera)	**Mathis** (1979a, 1979b, 1980)	**Olafsson, 1991** (Palearctic genera)	**Zatwarnicki, 1992**	**Mathis and Zatwarnicki 1995**
	Amalopteryx Eaton		*Amalopteryx* Eaton	*Amalopteryx* Eaton
	Austrocoenia Wirth			
	Calocoenia Mathis			
Coenia Robineau-Desvoidy	*Coenia* Robineau-Desvoidy			
		Haloscatella Mathis	*Haloscatella* Mathis	*Haloscatella* Mathis
Lamproscatella Hendel	*Lamproscatella* Hendel *L. (Haloscatella)* Mathis *L. (Thinoscatella)* Mathis	*Lamproscatella* Hendel	*Lamproscatella* Hendel	*Lamproscatella* Hendel
Limnellia Malloch	*Limnellia* Malloch	*Limnellia* Malloch	*Limnellia* Malloch	*Limnellia* Malloch
Neoscatella Malloch		*Neoscatella* Malloch		
Paracoenia Cresson	*Paracoenia* Cresson			
Parascatella Cresson	*Parascatella* Cresson			
Philotelma Becker	*Philotelma* Becker	*Philotelma* Becker	*Philotelma* Becker	*Philotelma* Becker
Scatella Robineau-Desvoidy	*Scatella* Robineau-Desvoidy *S. (Apulvillus)* Malloch *S. (Neoscatella)* Malloch *S. (Scatella)* R.-D. *S. (Synhoplos)* Lamb *S. (Teichomyza)* Macquart	*Scatella* Robineau-Desvoidy	*Scatella* Robineau-Desvoidy *S. (Apulvillus)* Malloch *S. (Neoscatella)* Malloch *S. (Parascatella)* Cresson *S. (Scatella)* R.-D.	*Scatella* Robineau-Desvoidy *S. (Apulvillus)* Malloch *S. (Neoscatella)* Malloch *S. (Parascatella)* Cresson *S. (Scatella)* R.-D. *S. (Synhoplos)* Lamb *S. (Teichomyza)* Macquart
Scatophila Becker	*Scatophila* Becker	*Scatophila* Becker	*Scatophila* Becker	*Scatophila* Becker
			Synhoplos Lamb	
			Tauromima Papp	*Tauromima* Papp
		Teichomyza Macquart	*Teichomyza* Macquart	
		Thinoscatella Mathis	*Thinoscatella* Mathis	*Thinoscatella* Mathis

Table II. Taxonomic papers published on tribe Scatellini and the genera included in the tribe.

Genus	Species number	Geographic distribution
Amalopteryx Eaton	01	ET (Sub-Antarctic)
Haloscatella Mathis	09	AU, CA, NE, PA
Lamproscatella Hendel	14	ET, NE, PA
Limnellia Malloch	24	AU, ET, NE, NT, OR, PA
Philotelma Becker	06	NE, PA
Scatella Robineau-Desvoidy	139	AN, AU, CA, ET, NE, NT, OR, PA
Scatella (*Apulvillus*) Malloch	07	OR
Scatella (*Neoscatella*) Malloch	37	AN, AU, CA, NE, NT, OR, PA
Scatella (*Parascatella*) Cresson	13	AN, NT
Scatella (*Scatella*) Robineau-Desvoidy	79 (+ 2 *nomina dubia*)	AN, AU, CA, ET, NE, NT, OR, PA
Scatella (*Synhoplos*) Lamb	02	AN
Scatella (*Teichomyza*) Macquart	01	AN, PA
Scatophila Becker	52 (+ 3 *nomina dubia*)	AN, AU, ET, NE, NT, OR, PA
Tauromima Papp	01	AU
Thinoscatella Mathis	03	NE, OR, PA
Total	249 (+ 5 *nomina dubia*)	ALL

Table III.Valid genera and subgenera of Scatellini, respective number of species and geographic distribution. AN: Andean; CA: Cape; ET: Ethiopian; NT: Neotropical; NE: Nearctic; OR: Oriental; PA: Palearctic; AU: Australian.

2. Objectives

The taxonomy and phylogeny of the tribe Scatellini have through the years undergone many modifications. These studies were usually based on restricted groups of species or specific geographic areas, never on a general comprehensive basis, making the relationships among these genera poorly understood.

To clarify these relationships, a comprehensive phylogenetic analysis was undertaken to test the monophyly of tribe Scatellini and the tribe's included genera and subgenera, based on the morphology of adult males and females. A hypothesis of relationship between the taxa is presented. Based on this hypothesis, redescriptions of the tribe and its genera are presented, and the relationships between taxa within Scatellini and the other tribes of Ephydrinae are discussed.

3. Material and methods

Specimens examined

Most specimens examined for this study are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Numerous specimens, primary types and photos of the types were also borrowed and studied. The specimens borrowed are from the following museums:

AMNH - American Museum of Natural History, New York, New York (David A. Grimaldi).

ANSP - Academy of Natural Sciences of Philadelphia, Pennsylvania (Jon K. Gelhaus and Jason D. Weintraub).

BMNH - The Natural History Museum (formerly the British Museum (Natural History)), London, England, United Kingdom (Daniel Wittaker).

DEBU - Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada (Stephen A. Marshall).

DZUP - Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (Claudio José Barros de Carvalho).

HNHM - Hungarian Natural History Museum, Budapeste, Hungary (Zoltán Soltész).

MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Carlos José Einicker Lamas).

SMNS - Staatliches Museum für Naturkunde in Stuttgart, Ludwigsburg, Germany (Hans-Peter Tschorsnig).

NZAC - New Zealand Arthropod Collection, Entomology Division, Auckland, New Zealand (Trevor K. Crosby).

UMCE - Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación, Santiago, Chile (Patricia Estrada M.).

Taxonomic sampling

In order to test the monophyly of Scatellini and the relationships among its genera, 67 terminal taxa were chosen, 50 from the ingroup, Scatellini, and 17 as outgroups (Table IV).

Table IV. Terminal taxa included in the cladistic analysis of Scatellini Wirth and Stone, (Diptera, Ephydridae, Ephydrinae) and geographic distribution [*, type-species]. AN: Andean; CA: Cape; ET: Ethiopian; NT: Neotropical; NE: Nearctic; OR: Oriental; PA: Palearctic; AU: Australian.

Outgroup	**Geographic Distribution**
Ilytheinae: Ilytheini	
Ilythea spilota (Curtis, 1832)*	NE, PA
Ilytheinae: Hyadinini	
Hyadina sp.	NT
Ilytheinae: Philygrini	
Philygria longipennis (Hendel, 1930)	NT
Ephydrinae: Parydrini	
Parydra aquila (Fallén, 1813)*	NE, PA
Ephydrinae: Dagini	
Dagus rostratus (Cresson, 1918)*	NT
Brachydeutera neotropica Wirth, 1964	NE, NT
Diedrops steineri Mathis, 1984	NT
Physemops nemorosus (Cresson, 1914)*	NT
Ephydrinae: Ephydrini	
Austrocoenia aczeli Wirth, 1970*	AN
Coenia palustris (Fallén, 1823)*	PA
Ephydra riparia Fallén, 1813*	NE, PA
Ephydrella novaezealandiae (Tonnoir and Malloch, 1926)*	AU
Neoephydra araucaria Mathis, 2008*	AN, NT
Notiocoenia paniculata Mathis, 1980*	AN, NT
Paracoenia bisetosa (Coquillett, 1902)*	NE
Paraephydra freitasi (Oliveira, 1954)*	NT
Setacera pacifica (Cresson, 1925)*	NE
Ingroup	**Geographic Distribution**
Amalopteryx Eaton ,1875	
Amalopteryx maritima Eaton, 1875*	ET
Haloscatella Mathis, 1979	
Haloscatella arichaeta (Mathis, 1979)*	NE
Haloscatella muria (Mathis, 1979)	NE
Haloscatella karekare Mathis, Zatwarnicki and Marris, 2004	AU
Haloscatella salinaria (Sturtevant and Wheeler, 1954)	NE
Lamproscatella Hendel, 1917	
Lamproscatella sibilans (Haliday, 1833)*	NE, PA
Lamproscatella bimaculata Hendel, 1933	NE, PA

Lamproscatella brunipennis (Malloch, 1920)	NE, PA
Lamproscatella mirabilis (Canzoneri & Meneghini, 1969)	ET
Lamproscatella occidentalis Mathis, 1979	NE, PA
Lamproscatella sinica Mathis and Zuyin 1988	PA
Limnellia Malloch, 1925	
Limnellia maculipennis Malloch, 1925*	AU, OR
Limnellia anna Cresson, 1935	NE
Limnellia huachuca Mathis, 1978	NT
Limnellia sejuncta (Loew, 1863)	NE
Limnellia stenhammari (Zetterstedt, 1846)	NE, OR, PA
Philotelma Becker, 1896	
Philotelma nigripennis (Meigen, 1830)*	PA
Philotelma rossi (Canzoneri and Meneghini, 1979)	PA
Scatella Robineau-Desvoidy, 1830	
Apulvillus Malloch, 1934	
Scatella (*Apulvillus*) *bronneci* (Malloch, 1934)*	OR
Scatella (*Apulvillus*) *cheesmanae* (Malloch, 1934)	OR
Scatella (*Apulvillus*) *williamsi* (Wirth, 1948)	OR
Neoscatella Malloch, 1933	
Scatella (*Neoscatella*) *atra* Malloch, 1933*	OR
Scatella (*Neoscatella*) *austrina* Mathis and Wirth, 1981	AU
Scatella (*Neoscatella*) *bicolor* Mathis and Wirth, 1981	AU
Scatella (*Neoscatella*) *immaculata* Malloch, 1925	AU
Parascatella Cresson, 1935	
Scatella (*Parascatella*) *pilifera* Cresson, 1931*	AN
Scatella (*Parascatella*) *spangleri* (Mathis, 1979)	NT
Scatella (*Parascatella*) *penai* (Mathis and Shewell, 1978)	AN
Scatella (*Parascatella*) *semipolita* (Mathis and Shewell, 1978)	AN
Scatella Robineau-Desvoidy, 1830	
Scatella (*Scatella*) *stagnalis* (Fallén, 1813)*	ET, NE, OR, PA
Scatella (*Scatella*) *minima* Wirth, 1955	AN
Scatella (*Scatella*) *paludum* (Meigen, 1830)	CA, ET, NE, OR, PA
Scatella (*Scatella*) *triseta* Coquillett, 1902	NE
Scatella (*Scatella*) *savegre* Mathis and Zumbado, 2005	NT
Scatella (*Scatella*) *tenuicosta* Collin, 1930	NE, OR, PA
Synhoplos Lamb, 1917	
Scatella (*Synhoplos*) *sturdeeana* (Lamb, 1917)*	AN
Scatella (*Synhoplos*) *neglecta* (Lamb, 1917)	AN
Teichomyza Macquart, 1835	
Scatella (*Teichomyza*) *fusc*a Macquart, 1835*	AN, PA
Scatophila Becker, 1896	
Scatophila caviceps (Stenhammar, 1844)*	PA
Scatophila avida Cresson, 1931	NT
Scatophila despecta (Haliday, 1839)	NE, PA
Scatophila exilis Cresson 1935	NE
Scatophila mesogramma (Loew, 1869)	NE, PA
Scatophila noctula (Meigen, 1830)	PA,
Scatophila unicornis Czerny, 1900	NE, PA
Scatophila ordinaria Sturtevant and Wheeler, 1954	NE

Scatophila prainha Mathis, Marinoni and Costa, 2014	NT
Scatophila quadriguttata (Meigen, 1830)	PA
Thinoscatella Mathis, 1979	
Thinoscatella lattini (Mathis, 1979)*	NE
Thinoscatella quadrisetosa (Becker, 1896)	NE, PA

Ingroup

Adult specimens representing 187 of the 249 species of the tribe Scatellini were studied. Of these, 50 species were chosen representing eight of the nine genera currently included in Scatellini (Mathis and Zatwarnicki 1995) and representing the morphological diversity within the tribe. Only *Tauromima* Papp was not included. *Tauromima* is a monotypic genus known only by the holotype male, which was not made available for study or dissection. The choice of representative species for each genus was established considering their morphological diversity and geographical distribution. When these species were previously classified into subgenera or groups of species, taxa were sampled representing the infrageneric groups. Type species of all genera and subgenera were included so that possible taxonomic or nomenclatural changes could be proposed without undue encumbrance.

Outgroup

The choice of outgroup taxa took into account previous phylogenetic hypotheses for Ephydrinae (Mathis 1979a, 1979b, 1980, 1982; Mathis and Simpson, 1981; Olafsson, 1991; Zatwarnicki, 1992). Fourteen species of the tribes Dagini, Ephydrini and Parydrini (Ephydrinae) and three species of the subfamily Ilytheinae, representing the three tribes of this subfamily, were selected as outgroups. Whenever possible, species of each genus and tribe were included. The species chosen from the tribe Ephydrini included genera that were previously part of Scatellini (*Austrocoenia* Wirth, *Coenia* Robineau-Desvoidy, *Paracoenia* Cresson). Four species of the tribe Dagini were selected because this tribe includes genera with controversial taxonomic positions and the recognition of this tribe is in many respects preliminary (Mathis 1982). Three species of the subfamily Ilytheinae, considered the sister-group of Ephydrinae (Zatwarnicki, 1992) were included since *Parydra* and the genera that today

are in Dagini were already reunited in the old subfamily Napaeinae (= Parydrinae), proposed initially by Cresson (1930).

Morphological terminology and identifications

The descriptive terminology follows Cumming and Wood (2010), with the following exceptions: Zatwarnicki (1996) proposed that the pre and postsurstylus correspond to the pre and postgonostylus and that the subepandrial sclerite is the the medandrium. The terminology for structures of the male terminalia is provided directly on Figs. 54, 55, 56, 62, 66, 68. The term basal flagellomere was used for the large antennomere beyond the pedicel. This term was preferred over "first flagellomere" as there may be more than one flagellomere involved, and basal does not imply a number or numbers. We likewise do not use "postpedicel" (Stuckenberg, 1999) for this antennomere because at least the multisegmented arista is beyond the pedicel in addition to the large antennomere, and postpedicel is thus ambiguous and lacking in precision. The terminology for mouthparts follows Clausen and Cook (1971) and description of degrees of wing reduction follows Hackman (1964).

Species were identified with the most appropriate source in each case, either with identification keys (such as Mathis, Zatwarnicki and Kubátová-Hiršová, 2009), with the aid of original descriptions or redescriptions/revisions, and/or checking the type material whenever possible.

Preparation and illustration of the material studied

Because specimens are small, approximately 1.00-5.00 mm in length, study and illustration of the male and female terminalia required use of a compound microscope. Dissections of male and female terminalia were performed following Clausen and Cook (1971) and Grimaldi (1987). Abdomens were removed with microforceps and macerated in a solution of sodium hydroxide. Cleared terminalia were then transferred to glycerin for observation, description, and illustration. The dissected abdomen was placed in a plastic microvial filled with glycerin and attached to the pin supporting the remainder of the insect from which it was removed.

Illustrations of structures of the male terminalia were produced by taking photos using a digital camera (Moticam 2300) attached to a compound microscope (MOTIC BA210) or by drawing pencil illustrations through a camera lucida attached to a compound microscope (Olympus BX51TF). The photos and pencil illustrations were then rendered as a vector file in ©Adobe Illustrator CS5©. The resulting illustration was then compared to the original structure for keeping the accuracy.

The habitus illustrations are digital photographs series taken with a Visionary Digital System, combined with Zerene Stacker™ and enhanced using Photoshop CS5© to adjust the color and make minor corrections (e.g., remove debris). Scanning Electron Microscope (SEM) images were taken with a Hitachi®™ TM3000 desktop unit (Tungsten source). These images were produced at National Musem of Natural History, Smithsonian Institution, Washington, DC.

Character coding

The characters used are related to the external and internal morphology of adult males and females. A survey of characters already used in previous phylogenetic studies (Mathis 1979b, 1980; Olafsson 1991; Zatwarnicki 1992) was performed and these characters were reinterpreted based on the morphological study of the specimens. The potential taxonomic importance and utility of structures that previous Scatellini studies have shown to be useful were also considered.

Character elaboration considered the following criteria: topological correspondence among the observed structures and the independence and hierarchy of characters and states (Hawkins et al. 1997). The characters were treated as hypothesis of grouping (taxic homology *sensu* Patterson, 1982). Most characters are binaries, but in order to preserve morphological diversity in some cases we chose to construct multi-state characters. Contingent coding was used; the characters were coded as present or absent and, if a feature is present, the variation is coded in one or more states. The logical structure of characters follows Sereno (2007). The matrix data were constructed in Winclada ver. 1.00.08 (Nixon 2002). The character states indicated with the symbol [-] mean inapplicable states and those with the symbol [*] are polymorphisms.

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-addtive 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 two character-weighting schemes: equal weights and implied weights (Goloboff, 1993). Heuristic searches using implied weights were carried out using the same parameters cited earlier. A TNT script (setk.run) written by Salvador Arias 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* =10.239258 for our data set, which was then applied.

Branch support was evaluated using "Bremer support" (Bremer, 1994). Absolute Bremer support was utilized for equal weighting analysis using the previous parameters, but maintaining suboptimal trees (ten steps longer than the most-parsimonious trees). For the implied weighting analysis, relative Bremmer support was used (Goloboff *et al.,* 2003). The cladograms recovered with TNT were then manipulated and edited with Winclada version 1.00.08 (Nixon, 2002). Only unambiguous character changes are shown on the trees. In the figures (Figs. 91-94), unique changes are represented by black circles, and homoplasies are represented by white circles in all cladograms.

Taxonomy

Redescriptions of the Scatellini and all included genera are provided, as well as an identification key for these genera. Redescriptions were based on the material examined and the original descriptions. The geographical distribution was based on records from the literature and the material examined. The geographical regions follows Morrone (2015). Comments on the current understanding of each genus are presented.

4. Results and discussion

Cladistic analysis

The matrix of characters and their respective states are represented in Table V. A total of 106 characters were examined and coded for the 67 terminal taxa, including the external morphology, mouthparts and male and female terminalias. 38 new characters are proposed for the first time. Five autapomorphies were excluded from the final analysis. The characters are listed according their position in the body, from anterior to posterior region. Thirty-two characters are from the head, thrity-six from the thorax and thirty-seven from abdomen. Below we present a list of characters and their respective character sates. After some characters, when considered important, we present comments. New characters are indicated with (*).

List of characters and character states

Head:

01. Arista, length:

(0) longer than basal flagellomere (Figs. 18-22, 24-26, 28, 29);

(1) shorter than basal flagellomere (Figs. 23, 27).

02. Arista, rays, length:

(0) long rays, pectinate arista (Fig. 21);

(1) small rays, pubescent arista (Figs. 18-20, 22-29).

03. Pedicel, dorsal seta, length:

(0) smaller than flagellomere (Figs. 18-22, 24-26, 28, 29);

(1) same length of flagellomere (Figs.23, 27).

04. Face, medial facial area and lower facial margin, setulae:

(0) present;

(1) absent.

05. *Face, medial facial area and lower facial margin, setulae, density:

(0) densely setulose (Figs.3, 4);

(1) sparsely setulose (Figs. 5).

Comments. Contingent on character 4, state 0.

06. Face, lateral facial setae, length:

(0) small and undistinguishable from facial setae (Figs.4, 5);

(1) longer and stronger than facial setae (Fig. 3).

Comments. Contingent on character 4, state 0.

07. Face, long lateral facial setae, orientation:

(0) anteroventrally curved (Figs. 4, 5);

(1) lateroventrally curved;

(2) laterodorsally curved (Fig. 3).

Comments. Contingent on character 4, state 0.

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

(0) present;

(1) absent.

09. *Facial projection or hump, height:

(0) less than half of the height of head (Fig. 11);

(1) half the height of head (Fig. 12);

(2) higher than half the height of head (Fig. 13).

Comments: the height is measured from the inferior margin of the face to the top of the hump (Figs 11-13).

10. Frons, width:

(0) wider than long (Fig. 3);

(1) as wide as long.

11. Frontal vitta, shape:

(0) triangular;

(1) subquadrate.

12. Interfrontal seta:

(0) absent;

(1) present.

Comments. This seta is elongated, well developed, and cruciate, and it is present in some genera of Ephydrini.

13. Frontal vitta, anterior margin, setulae:

(0) absent;

(1) present (Fig. 8).

Comments. These setulae are small, but evident and distinct from tomentum.

14. Frontal vitta, tomentose vestiture:

(0) absent;

(1) present.

Comments. When the tomentum is absent, the frontal vitta is bare, shiny; tomentose frontal vitta is dull.

15. Ocelli, arrangement:

(0) equally distant from each other, as an equilateral triangle (Fig. 8);

(1) like an isosceles triangle.

Comments. 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. Ocellar seta, length:

(0) long setae, subequal to fronto-orbital setae;

(1) short setae, half of fronto-orbital seta.

Comments. Contingent on character 16, state 0.

18. Eye, shape:

(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. Fronto-orbital setae, orientation:

(0) proclinate and/or reclinate;

(1) lateroclinate (Figs. 3-5, 18-29).

Comments. Non-Ephydrinae shore flies can present proclinate or reclinate fronto-orbital seta, or both.

20. *Subcranial cavity, opening, size:

(0) large and gapping (Fig. 10);

(1) small (Fig. 9).

21. Fronto-orbital setae, number:

(0) 0;

(1) 1;

(2) 2;

(3) 3;

(4) 4.

Comments. Only long fronto-orbital setae are considered; length subequal to inner and other vertical seta.

22. Posterior fronto-orbital seta, position:

(0) inserted closer to anterior fronto-orbital seta than to inner vertical seta;

(1) inserted closer to inner vertical seta than to anterior fronto-orbital seta (Fig. 24).

23. Gena, genal seta:

(0) present;

(1) absent.

24. Gena, genal seta, length:

(0) long, conspicuous (Figs. 20, 22, 23, 27);

(1) short, indistinguishable from genal setulae (Figs. 18, 19, 21).

Comments. Contingent on character 23, state 0.

25. Gena, height:

(0) low (gena to eye ratio < 0,25);

(1) medium (gena to eye ratio 0,25 to 0,5);

(2) high (gena to eye ratio > 0,5).

26. Face, concavity, shape arching:

(0) vertically arched, shield-like (Figs. 6, 7);

(1) transversely arched (Figs. 3-5).

27. *Palpus, shape:

(0) claviform;

(1) not claviform, slender (Fig. 30).

28. *Lacinia, distal portion, projection, shape, anterior view:

(0) straight-shaped;

(1) T-shaped (Fig. 30).

29. *Cibarium, lateral projections:

(0) present (Fig. 30, 31);

(1) absent.

30. *Cibarium, lateral projections, size:

(0) small, same length as ventral projection (Fig. 31);

(1) large, larger than ventral projection (Fig. 30).

31. *Labellum, sclerite 2, length:

(0) more or less as long as wide of labellum, not overlapping prementum;

(1) longer than wide of labellum, overlapping prementum (Fig. 32).

32. *Mediproboscis, laterals, sclerite:

(0) absent;

(1) present (Fig. 32).

Thorax:

33. Thorax, vestiture, coloration:

(0) unicolorous or with gradual changes in coloration;

(1) distinctly bi- or tricolored, with stripe patterns (Fig. 46).

34. Prosternum, setulae:

(0) present (Fig. 33);

(1) absent (Fig. 34).

35. Presutural dorsocentral setae, number of pairs:

(0) 0 (Fig. 15);

(1) 1 (Fig. 17);

(2) 2.

Comments. Only long presutural dorsocentral setae are considered; length subequal to postalar seta.

36. Postsutural dorsocentral setae, number of pairs:

(0) 0;

(1) 1;

(2) 2 (Fig. 15, 17);

(3) 3.

Comments. Only long postsutural dorsocentral setae are considered; length subequal to postalar seta.

37. Proepisternum, macrosetae:

(0) absent (Fig. 34);

(1) present (Fig. 33).

38. Postpronotum, setation:

(0) 1-3 setae plus scattered setulae (Fig. 33);

(1) with a few setulae.

39. Presutural supra-alar seta:

(0) present (Fig. 14, 15);

(1) absent.

40. Postsutural supra-alar seta:

(0) present (Fig. 14, 15);

(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) at same level as anterior seta;

(1) distinctly elevated above level of anterior seta.

43. Anepisternum, anterodorsal corner, seta:

(0) indistinguishable from surrounding setae;

(1) one strong, distinct seta dorsally curved (Fig. 18).

44. *Acrostichal setae, arrangement:

(0) forming 2 rows (Fig. 15, 17);

(1) scattered setae, not forming a row.

45. *Acrostichal setae, rows, extension:

(0) rows extending to scutellum (Fig. 17);

(1) rows not extending to scutellum (Fig. 15).

Comments. Contingent on character 44, state 0.

46. Sutural acrostichal setae, length:

(0) short, same length as other acrostichal setae (Fig. 17);

(1) longer than other acrostichal setae (Fig. 15).

47. Intrapostalar seta:

(0) present (Fig. 15);

(1) absent.

48. Intrapostalar seta, length:

(0) small seta, much smaller than postalar seta;

(1) long seta, slightly smaller than postalar seta.

Comments. Contingent on character 47, state 0.

49. *Intra-alar seta:

(0) absent;

(1) present (Fig. 15, 17).

50. *Intra-alar seta, arrangement:

(0) scattered setae;

(1) in a row of intra-alar setae (Fig. 15, 17).

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. 17).

52. *Wing, development:

(0) Macropterous ;

(1) Stenopterous (Figs. 35, 37);

(2) Micropterous (Fig. 41);

53. *Wing, infuscation:

(0) hyaline; (Fig. 42)

(1) infuscate, darker on anterior margin and lighter on posterior margin (Fig. 36).

54. Wing, white spots:

(0) absent;

(1) present (Fig. 36, 38, 39).

55. Wing, white spots, density:

(0) wing with many white spots bare of tomentum, even at cell r4 (Fig. 36);

(1) wing with few white spots bare of tomentum, rarely reaching cell r4 (Fig. 38, 39).

Comments. Contingent on character 54, state 1.

56. Costal vein, length:

(0) long, extended to vein M (Figs. 36, 39, 40, 42, 43);

(1) short, extended to vein R_{4+5} (Fig. 38).

57. *Costal vein, subcostal break, overlapping:

(0) Costal vein continuous at subcostal break (Fig. 42);

(1) Costal vein slightly to deeply overlaps itself at subcostal break, sometimes looking like a spur (Figs. 36, 38, 39, 40, 43).

58. *Crossvein r-m, position:

(0) crossvein r-m just posteriorly or slightly distal of subcostal break (Fig. 39, 40);

(1) crossvein r-m distinctly basal to subcostal break (Fig. 42);

(2) crossvein r-m distinctly distal to subcostal break (Fig. 36, 38).

59. Crossvein dm-cu, infuscate spot:

(0) absent;

(1) present (Fig. 43).

60. Costal vein, anterior margin, spines:

(0) present (Fig. 40);

(1) absent.

61. Scutellar seta, number of pairs:

(0) 2;

(1) 3.

Comments. 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. 15, 17).

63. *Anepisternal setae, length:

(0) small setae in addition to a longer, strong seta (Fig. 14);

(1) long setae in addition to a longer, strong seta.

Comments. The anepisternum always presents a long, well developed anepisternal seta.

64. Katepisternal seta, length:

(0) long, well developed (Fig. 14);

(1) short, weak developed.

65. Male midfemur, posteroventral side, setae, shape:

(0) stout (Fig. 45);

(1) slender.

66. Male forefemur, anteroventral side, setae, shape:

(0) stout (Fig. 44); [1]

(1) slender.

Comments. [1] also referred 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.

Abdomen:

69. Abdomen, tomentum:

(0) present;

(1) absent.

Comments. When the tomentum is absent, the abdomen is polished, shiny.

70. Sternite 1:

(0) present;

(1) absent.

71. *Well-developed sternites of male after sternite 4, number:

(0) 2 (Fig. 90);

(1) 1; [2]

(2) 0 (Fig. 89).

Comments. [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. 85).

73. *Female sternites, form:

(0) square to rectangular-shaped, relatively wide (Figs. 87, 88);

(1) distinctly narrow sternites (Fig. 86).

74. *Tergite 5 of male, posterolateral projection:

(0) absent;

(1) present.

75. *Epandrium or epandrium/surstyli, opening:

(0) present (Figs. 54, 63, 65, 67, 81);

(1) absent (Figs. 57, 60, 69, 72, 75, 78).

Comments. Since the epandrium can be indistinguishably fused with surstyli or 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 (Figs. 54, 63, 65, 67, 81);

(1) Wide opening above the cerci (Fig. 79);

(2) Wide opening below the cerci.

77. *Epandrium, ventral projection:

(0) present;

(1) absent.

78. Surstylus, fusion with epandrium:

(0) distinctly separate from epandrium (Figs. 57, 67, 78);

(1) fused to the epandrium but distinguishable as surstyli (Fig. 80);

(2) surstyli indistinguishable from epandrium or absent (Figs. 54, 60, 63, 65, 69).

79. *Surstyli, anterolateral projection:

(0) absent;

(1) present.

80. *Surstylus or surstylus/epandrium, number of pieces:

(0) Surstylus in one piece (Fig. 57);

(1) Surstylus in two pieces (Figs. 67, 78).

81. *Epandrium or epandrium/surstylus, posterior view, shape:

(0) Roughly ellipsoid to subquatrate;

(1) Ovoid (Figs. 63, 65, 67).

82. Epandrium, ventral margin, shape:

(0) Straight or slightly convex (Figs. 60, 75);

(1) Incised medially forming two lateral lobate processes (Figs. 69, 72).

83. *Aedeagus, shape:

(0) A quill-like structure (Fig. 51);

(1) A keel-like structure (Fig. 52);

(2) A long and thin tube (Fig. 64);

(3) A shoe-like structure (Figs. 59, 62, 66, 68, 71, 74, 77, 83);

(4) A large and bulky tube (Fig. 56);

(5) "*Diedrops* aedeagus" (Fig. 53). [3]

Comments. [3]The aedeagus in *Diedrops* is unique in shape and structure, so we proposed a separated state to this genus.

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. 61, 62).

85. Aedeagus, ventral process:

(0) present (Fig. 74);

(1) absent.

86. Ejaculatory apodeme:

(0) absent;

(1) present.

87. Ejaculatory apodeme, shape:

(0) L-shaped, flattened dorsoventrally structure (Fig. 66);

(1) crescent shape, laterally flattened (Fig. 68).

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) dorsoventrally flattened, usually with two lateral projections, rod like, lacking a keel (Figs. 61, 62, 71, 72, 73, 74, 82, 83).

Comments. 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.

Comments. The hypandrium is considered fused with gonites within Ephydrinae, and the anterior arms of the gonite/hypandrium is called "gonal arch".

91. Hypandrium, shape:

(0) a straight sclerite hypandrium (Figs. 70, 71, 73, 74);[4]

(1) a bifurcate sclerite hypandrium (Fig. 76, 77);[4]

(2) a U-shaped broad hypandrium.

[4] referred as "neohypandrium" to *Scatophila* (Zatwarnicki and Mathis 1994).

92. *Gonal arch, arms, fusion:

(0) separated;

(1) fused (Figs. 55, 61, 82).

93. *Gonal arch and phallapodeme, fusion:

(0) separated;

(1) fused (Fig. 82).

94. *Posterodorsal arm of gonite:

(0) present;

(1) absent.

95. *Posterodorsal arm and gonal arch, shape:

(0) bulky dorsal arm (Fig. 66, 70, 71,73, 74);

(1) large, more like a flap (Figs. 55, 56, 64).

Comments. Contingent on character 94, state 0.

96. Female sternite 8, setae, length:

(0) same length as other setae:

(1) bearing prominent setae (Fig. 84).

97. Sternite 9/subanal plate, setae, development:

(0) bearing one pair of strong setae (Fig. 86);

(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 (Figs. 16 86);

(2) A long, slender seta inserted posteroventrally (Fig. 84).

99. Female sternite 7:

(0) present;

(1) absent.

100. *Female sternite 7, fusion:

(0) one sclerite (Fig. 86, 88);

(1) two sclerites.

Comments. Contingent on character 99, state 0.

101. *Female sternite 8, number:

(0) two sclerites;

(1) one sclerite. [5]

Comments. [5]The female abdomen of *Brachydeutera* have only seven segments + cerci, instead of usually eight to Ephydrinae, and we are assuming that this state is not applicable to *Brachydeutera.*

102. *Female sternite 8:

(0) two sclerites crescent-shaped (Figs. 86, 87, 88);

(1) two sclerites subquadrate(Fig. 84);

Comments. Contingent on character 101, state 0.

103. *Female tergite 8:

(0) Tergite complete, like an arch;[6]

(1) Tergite incomplete, only two sclerites laterally.

Comments. [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. Ventral receptacle, operculum:

(0) Present (Figs. 47, 48, 50);

(1) Absent (Fig. 49).

105. Ventral receptacle, operculum, shape:

(0) Helmut-like, trapezoidal (Fig. 47);

(1) Tube-like (Fig. 50).

Comments. Contingent on character 104, state 0.

106. Ventral receptacle, operculum, size:

(0) Large and well developed, covering the extended process (Figs. 47, 50);

(1) Small, not covering the extended process (Fig. 48).

Comments. Contingent on character 104, state 0.

Characters not utilized in analysis

Five characters were eliminated from final analysis because they were autapomorphies and, we present them here because they can be useful in a different level of analysis.

01. Face, protrusion:

(0) absent;

(1) present.

Comments. Only three species of the genus *Scatophila* share a protusion at face: *S. noctula*, *S. unicornis* and *S. zlobini.*

02. Paravertical seta, length:

(0) short, only slightly longer than longer postocellar setae;

(1) long, subequal to ocellar seta (*Paracoenia*).

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

03. Inner vertical setae, length:

(0) subequal to the length of outer vertical setae;

(2) very small.

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

04. Cerci of male, height:

(0) cerci low, restricted at the dorsal part of the epandrium;

(1) cerci height, as high as epandrium.

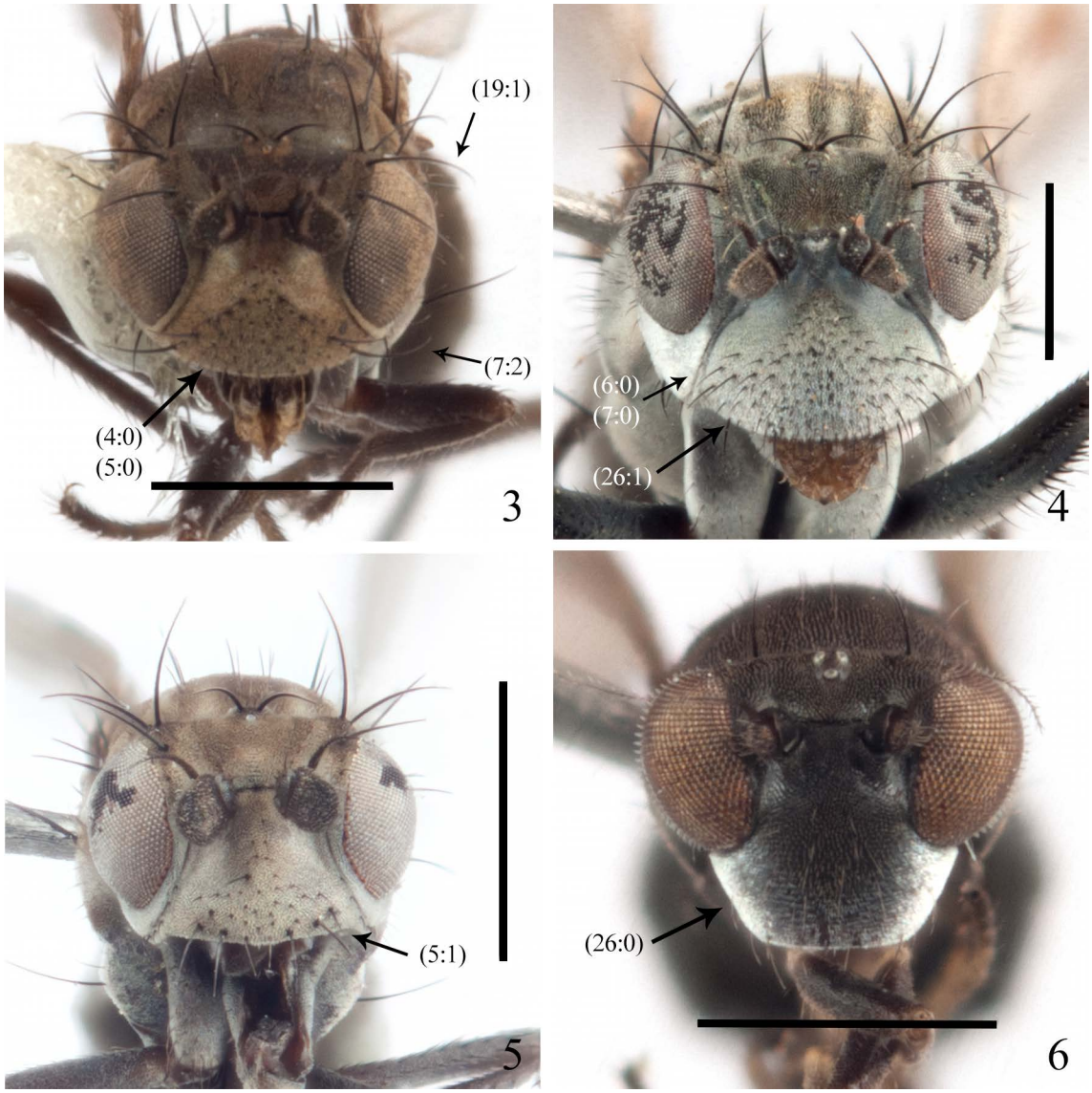
Comments. Only present in *Austrocoenia aczeli.*

05. Epandrium, lateral margins, process:

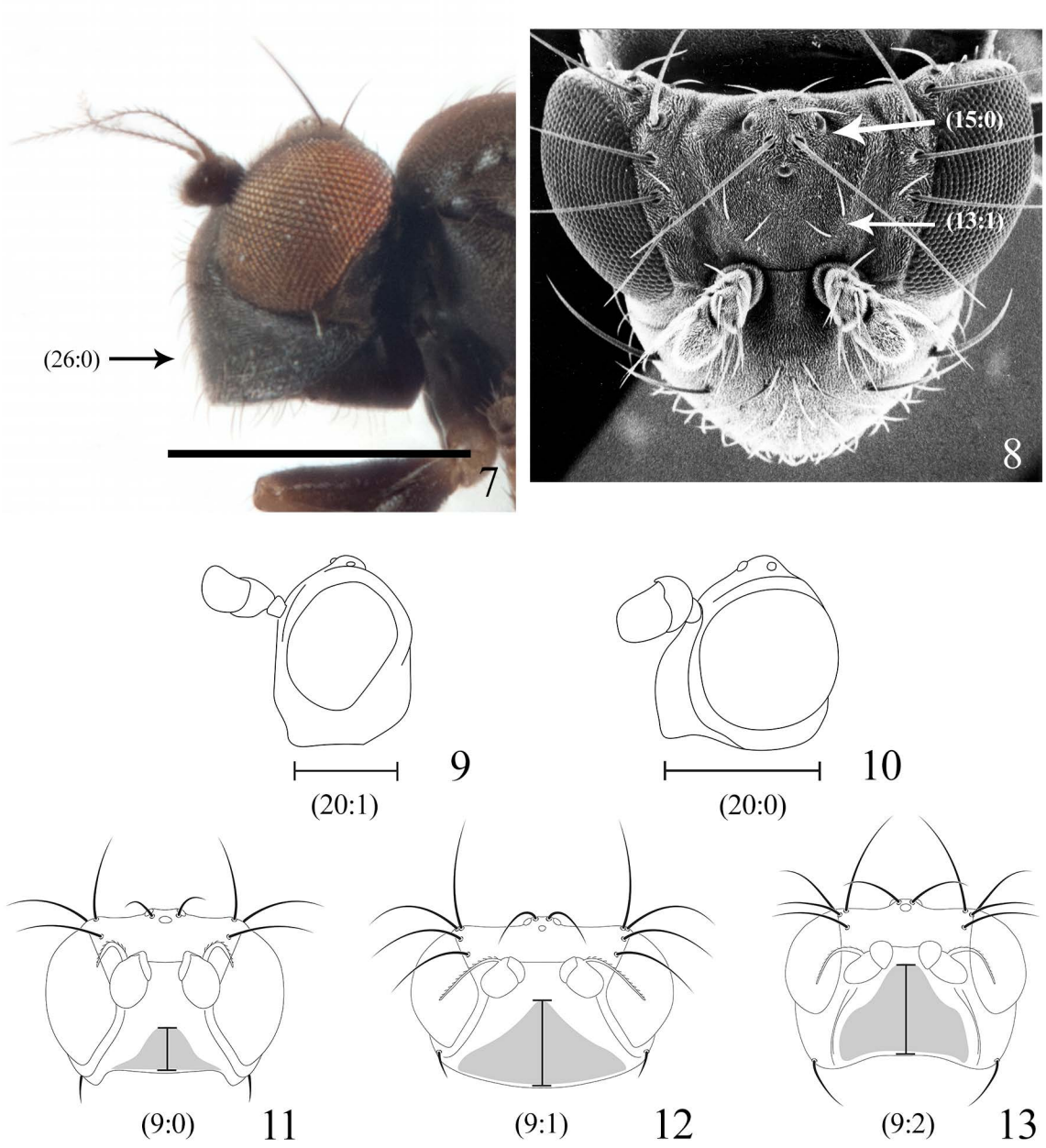
(0) ending at juncture of gonite;

(1) a process continuing from each side which is fused anteromedially.

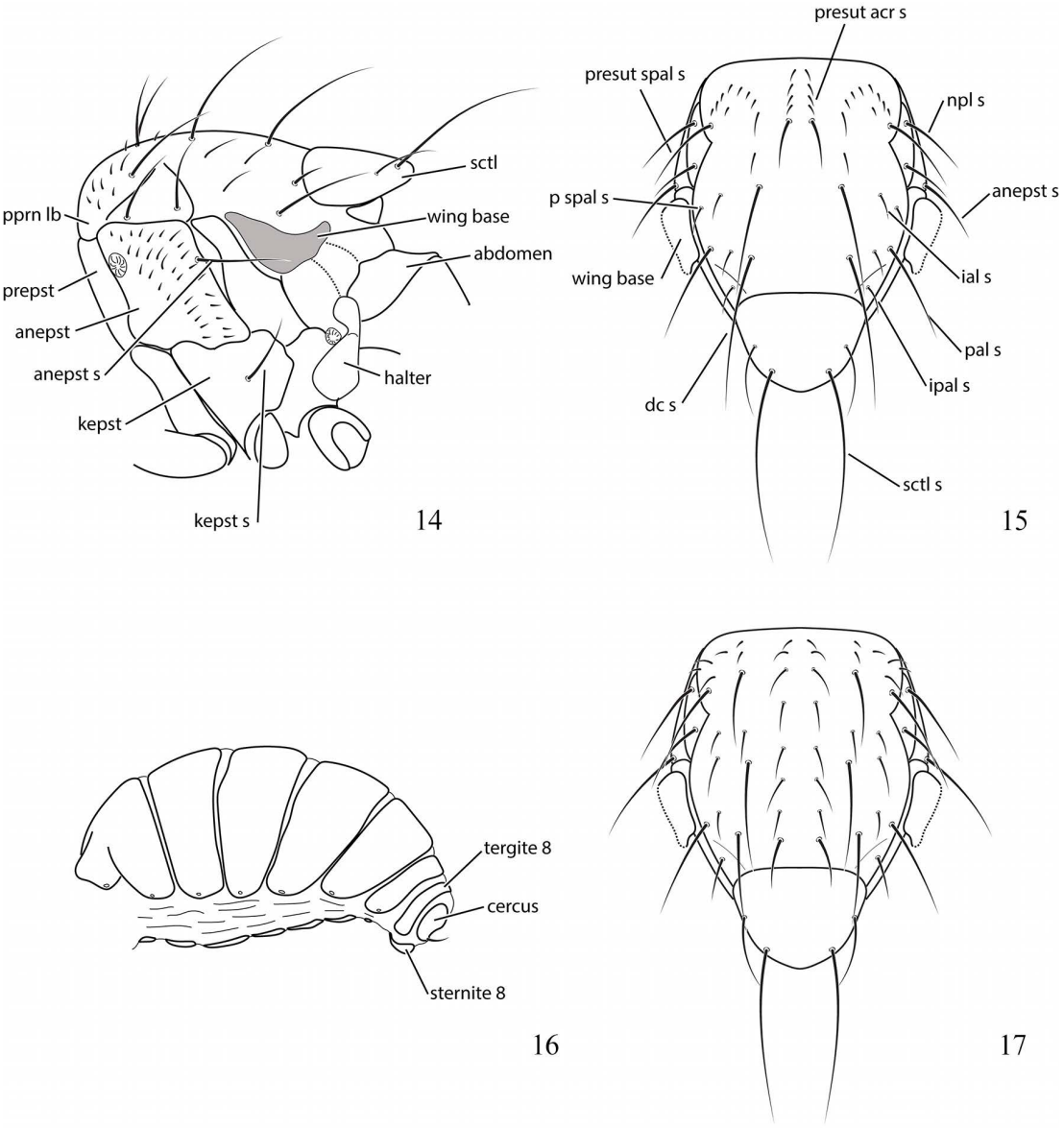
Comments. The process at lateral margins of epandrium is present in three species of *Haloscatella*: *H. arichaeta, H. cephalotes* and *H. nivosa.*



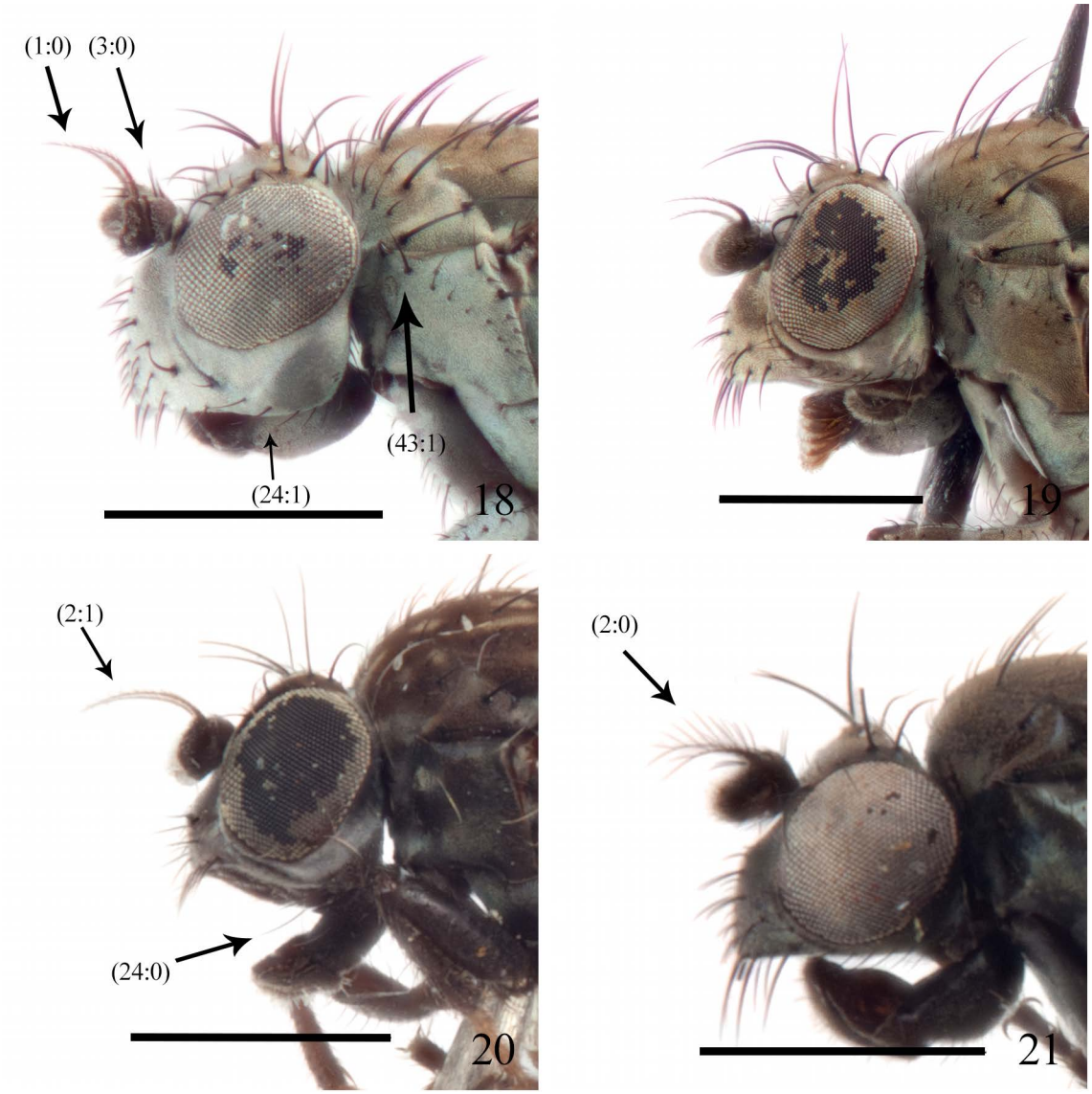
Figures 3-6. 3. *Scatella (Scatella) stagnalis* head, anterior view; **4.** *Scatella (Parascatella) pilifera* same; **5.** *Scatophila caviceps* same; **6.** *Physemops nemorosus* same. Scale bar = 0.5 mm.



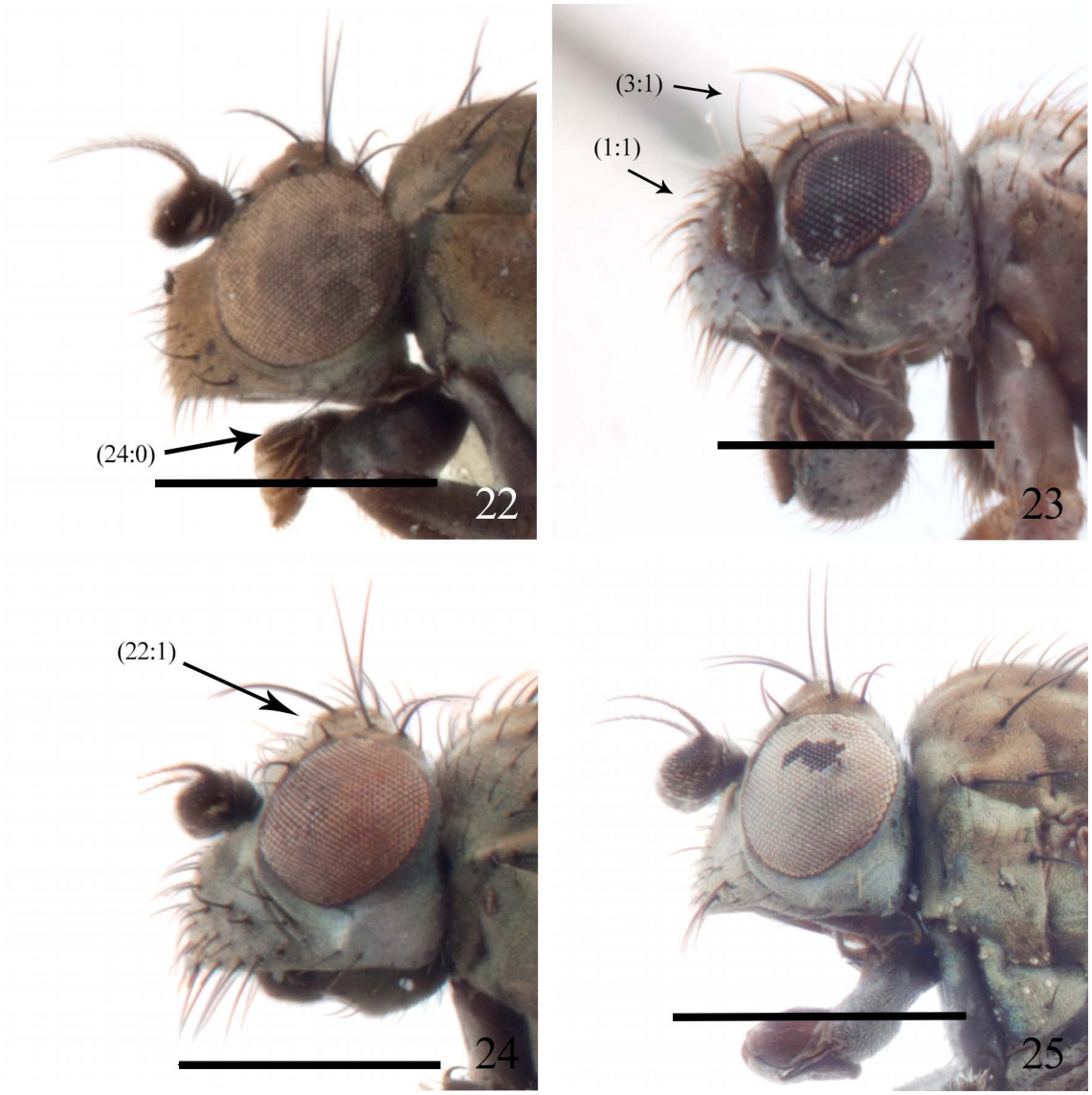
Figures 7-13. 7. *Physemops nemorosus* same, lateral view; **8.** *Lamproscatella cephalotes* same, dorsal view. Scale bar = 0.5 mm. **9.** *Hyadina* sp. head, lateral view; **10.** *Philotelma* sp. same; **11.** *Limnellia* sp head, anterior view; **12.** *Scatella (Scatella)* sp. same; **13.** *Scatella (Parascatella)* sp. same. Scale bar = 0.5 mm.



Figures 14-17. *Scatella stagnalis.* **14.** thorax, lateral view; **15.** same, dorsal view; **16.** female abdomen, lateral view. *Haloscatella arichaeta*. **17.** thorax, dorsal view. Anepst: anepisternum; anepst s: anepisternal seta; dc s: dorsocentral seta; ial s: intra-alar seta; ipal s: intrapostalar seta; kepst: katepisternum; kepst s: katepisternal seta; npl s: notopleural seta; pprn lb: postpronotal lobe; prepst: proepisternum; presut acr s: presutural acrostichal seta; pal s: postalar seta; p spal s: posterior supra-alar seta; presut spal s; presutural supra-alar seta; sctl: scutellum; sctl s: scutellar seta.

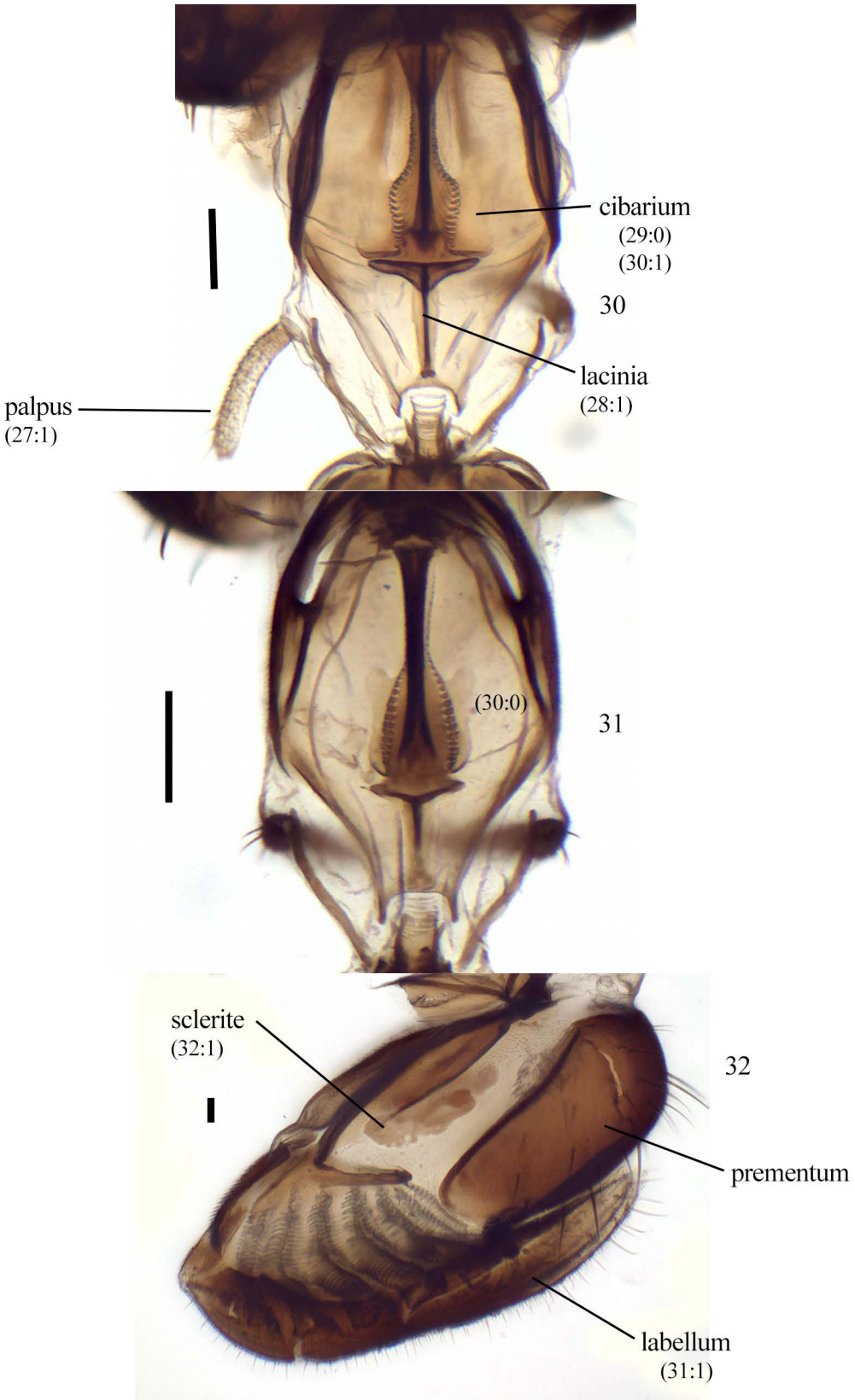


Figures 18-21. Head, lateral view. **18.** *Haloscatella arichaeta*; **19.** *Lamproscatella sibilans*; **20.** *Limnellia maculipennis*; **21.** *Limnellia nigripennis*. Scale bar = 0.5 mm.

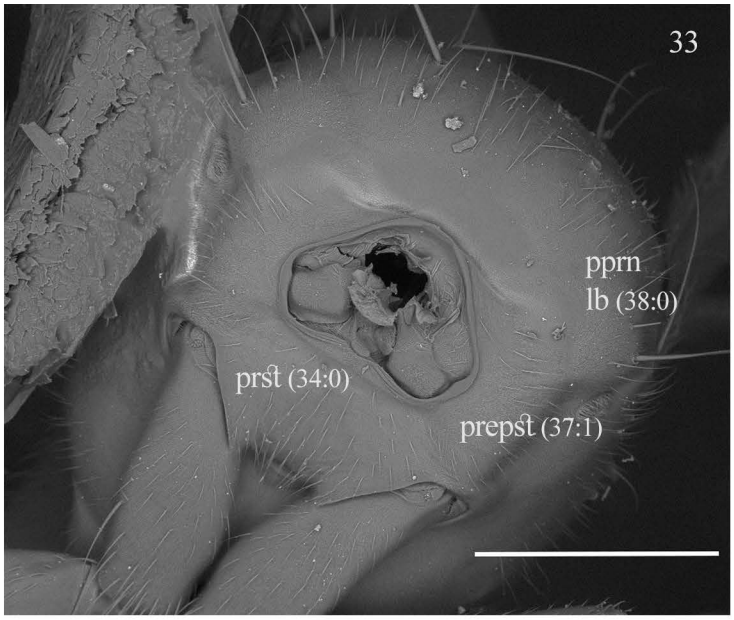


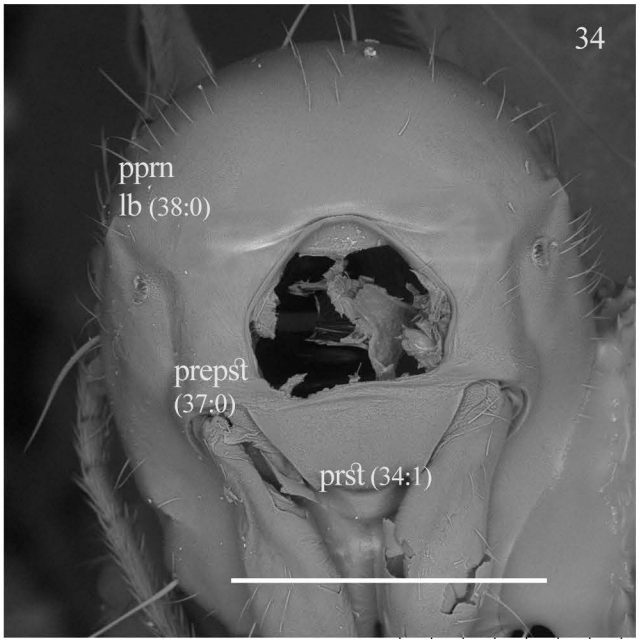
Figures 22-25. Head, lateral view. **22.** *Scatella (Scatella) stagnalis*; **23.** *Scatella (Synhoplos) sturdeeana*; **24.** *Thinoscatella lattini*; **25.** *Scatophila caviceps*. Scale bar = 0.5 mm.

Figures 26-29. Head, lateral view. **26.** *Scatella (Parascatella) pilifera*; **27.** *Scatella (Teichomyza) fusca*; **28.** *Scatella (Apulvillus) bronneci*; **29.** *Amalopteryx maritima*. Scale bar = 0.5 mm.

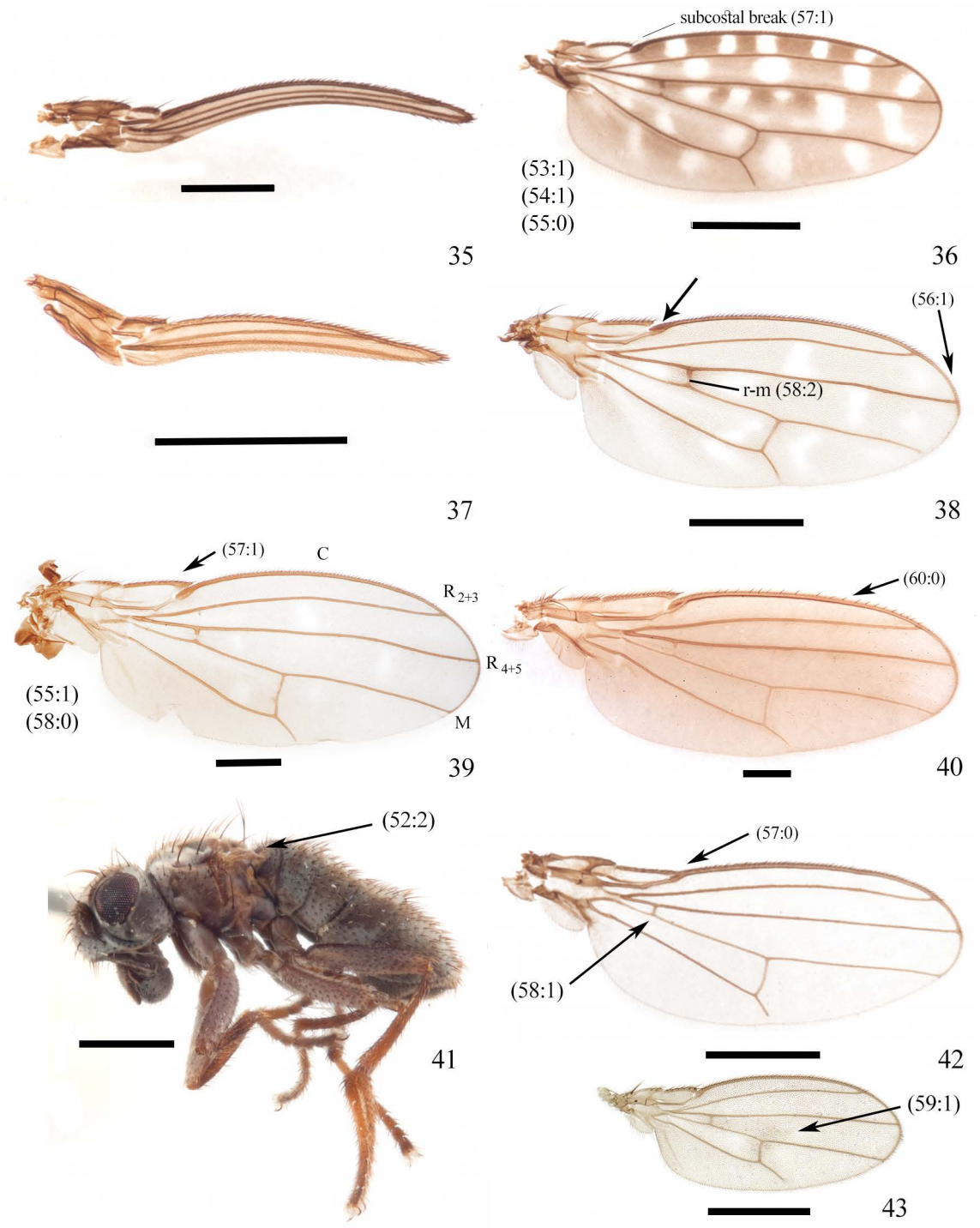


Figures 30-32. Mouth parts. **30.** *Scatella (Scatella) stagnalis*; **31.** *Scatophila caviceps*; **32.** *Ephydra riparia*. Scale bar = 0.1 mm.

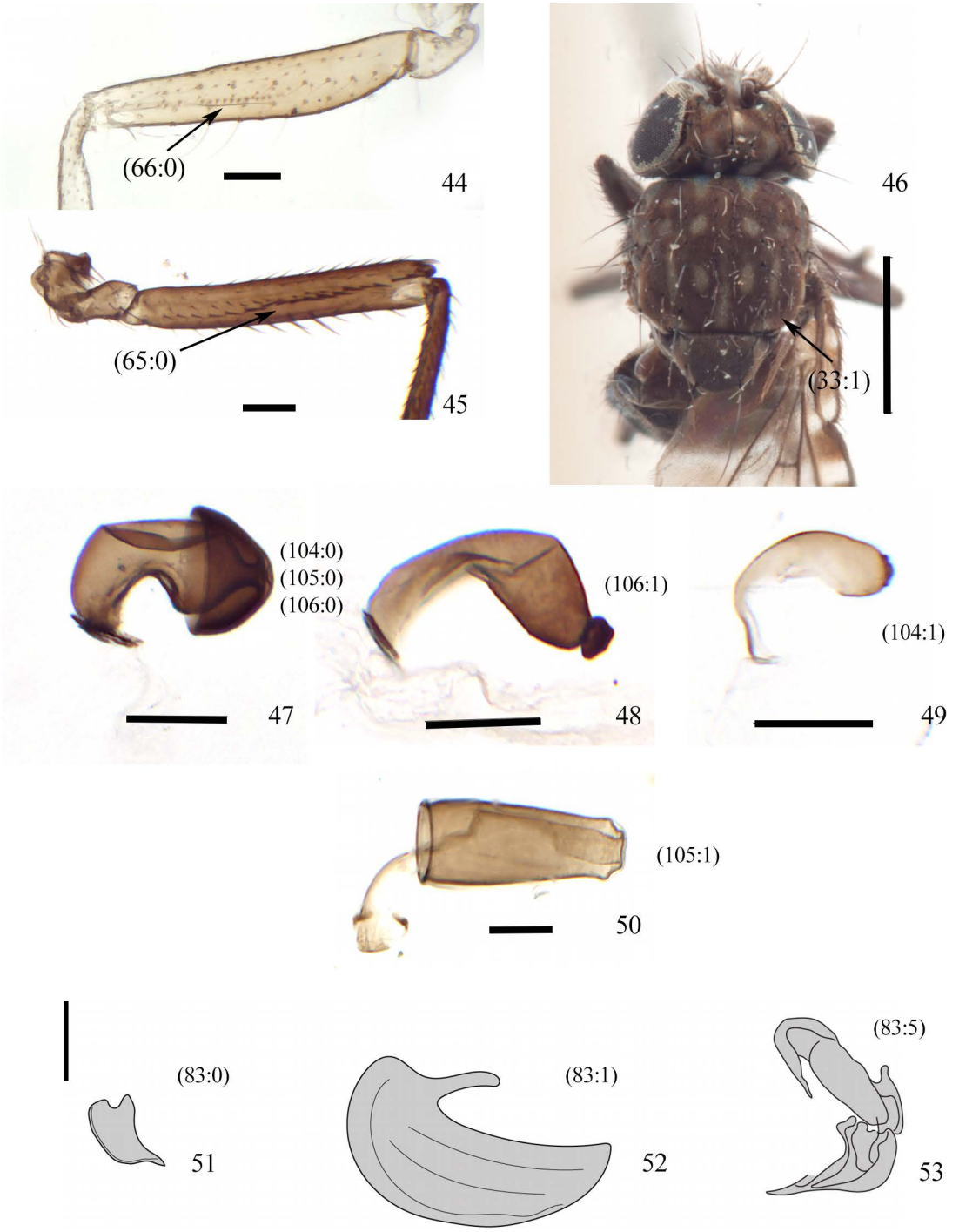




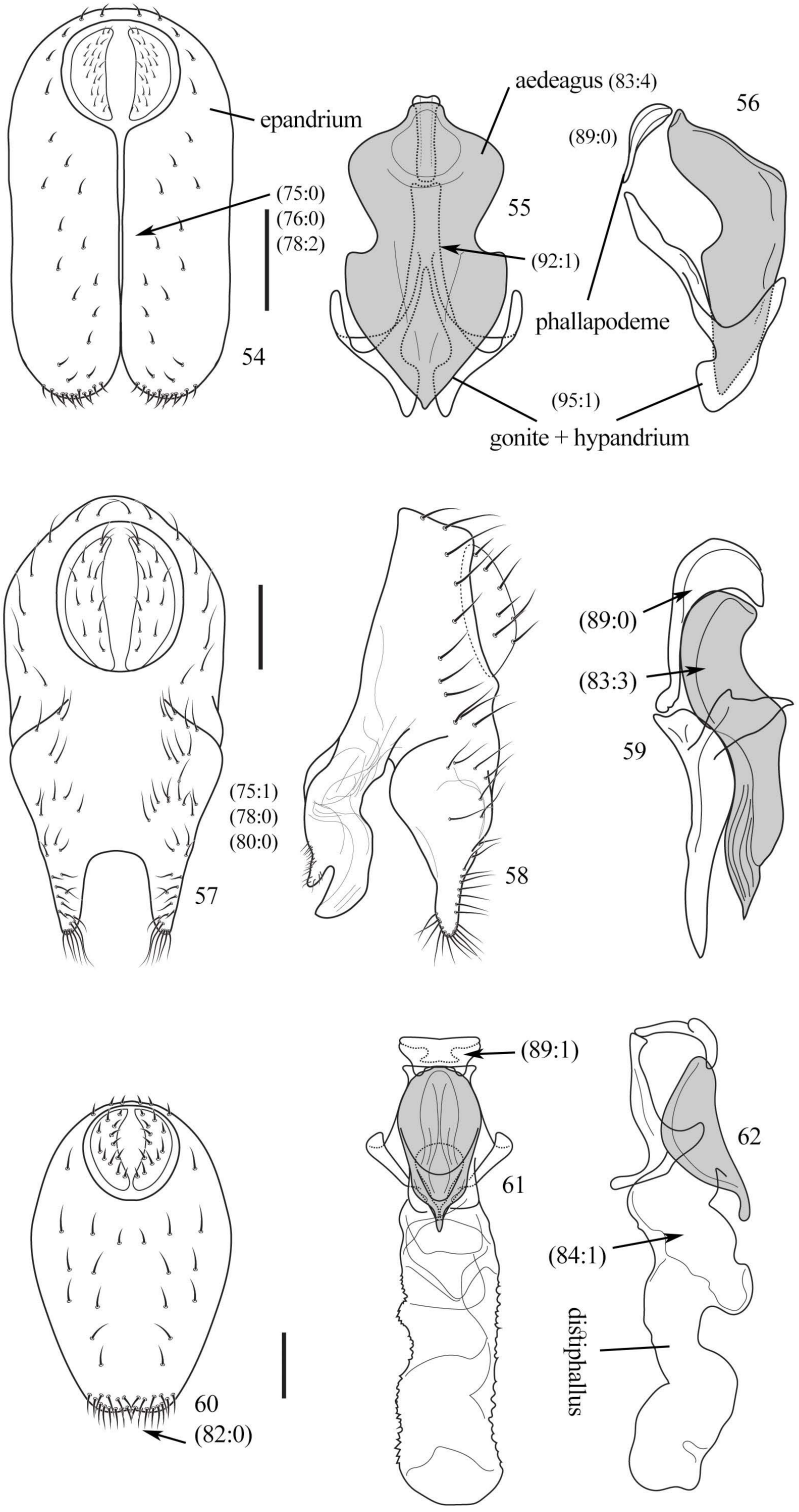
Figures 33-34. Thorax, anterior view. **33.** *Ephydra riparia*; **34.** *Scatella (Scatella) stagnalis.* Scale bar = 0.5 mm. prepst: proepisternum; pprn lb: postpronotal lobe; prst: prosternum.



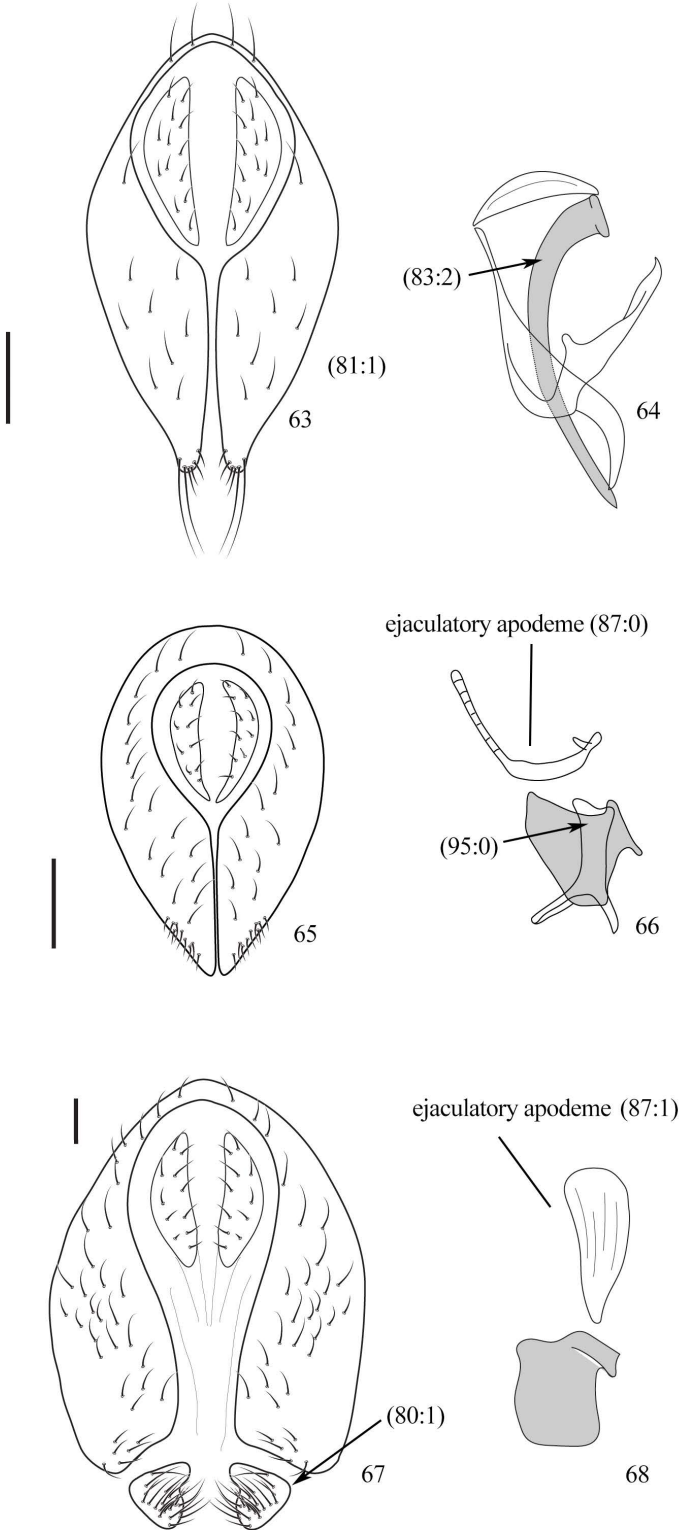
Figures 35-43. Wings. **35.** *Amalopteryx maritima*; **36.** *Limnellia stenhammari*; **37.** *Scatella (Scatella) minima*; **38.** *Scatophila caviceps*; **39.** *Scatella (Scatella) stagnalis*; **40.** *Scatella (Teichomyza) fusca*; **41.** *Scatella (Synhoplos) sturdeeana*; **42.** *Dagus rostratus*; **43.** *Philotelma defectum*. Scale bar = 0.5 mm.



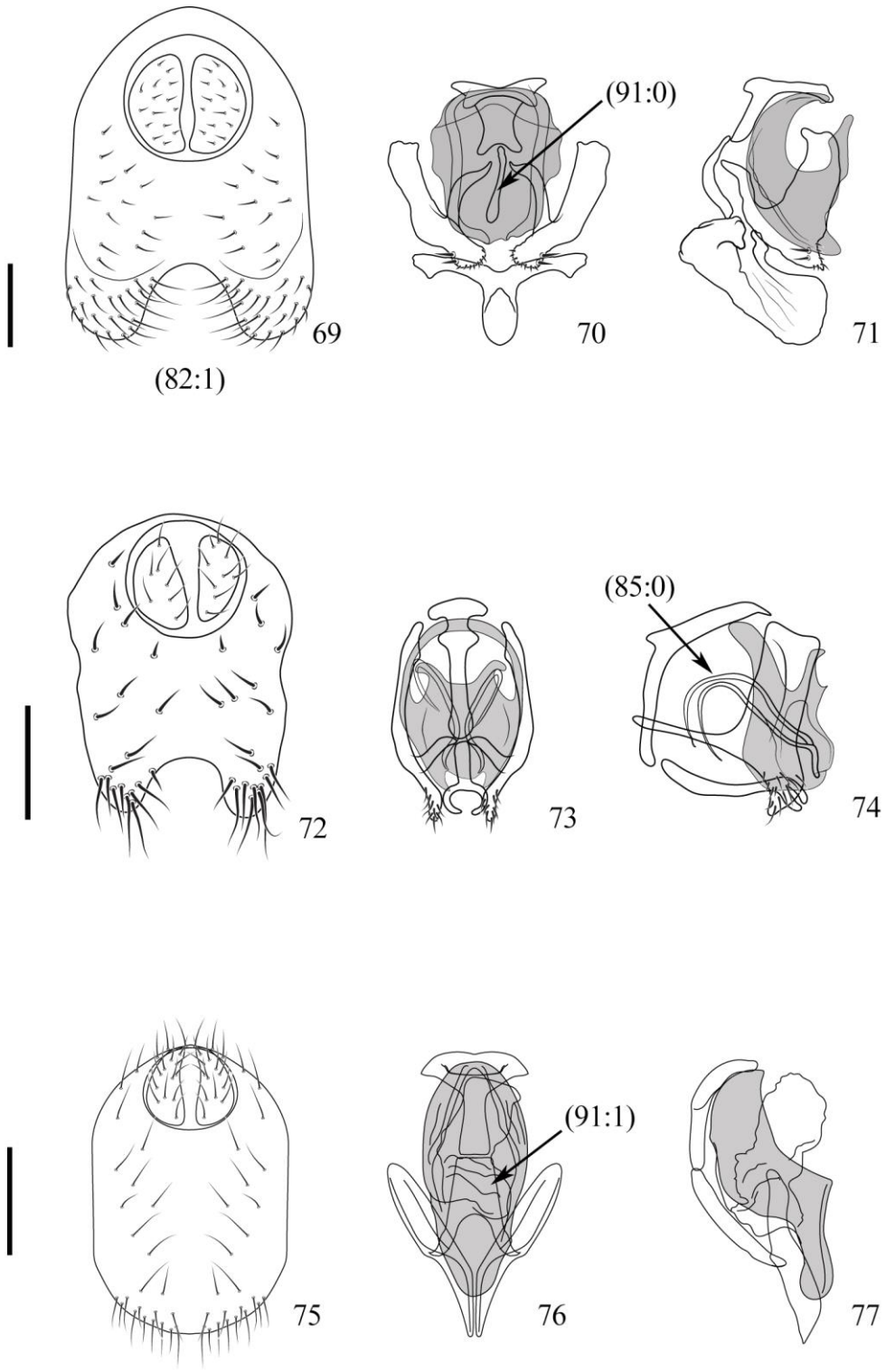
Figures 44-53. 44. *Scatella (Scatella) stagnalis* male forefemur, anteroventral side; **45.** *Scatophila mesogramma* male midfemur, posteroventral surface; **46.** *Limnellia maculipennis* thorax, dorsal view; **47.** *Paracoenia bisetulosa* ventral receptacle, lateral view; **48.** *Notiocoenia paniculata* same, lateral view; **49.** *Philotelma defectum* same, lateral view (Scale bar = 0.5 mm); **50.** *Scatella (Scatella) stagnalis* same, lateral view; **51.** *Hyadina* sp. aedeagus, lateral view; **52.** *Parydra aquila*, same, lateral view; **53.** *Diedrops steineri* same, lateral view. Scale bar = 0.1 mm.



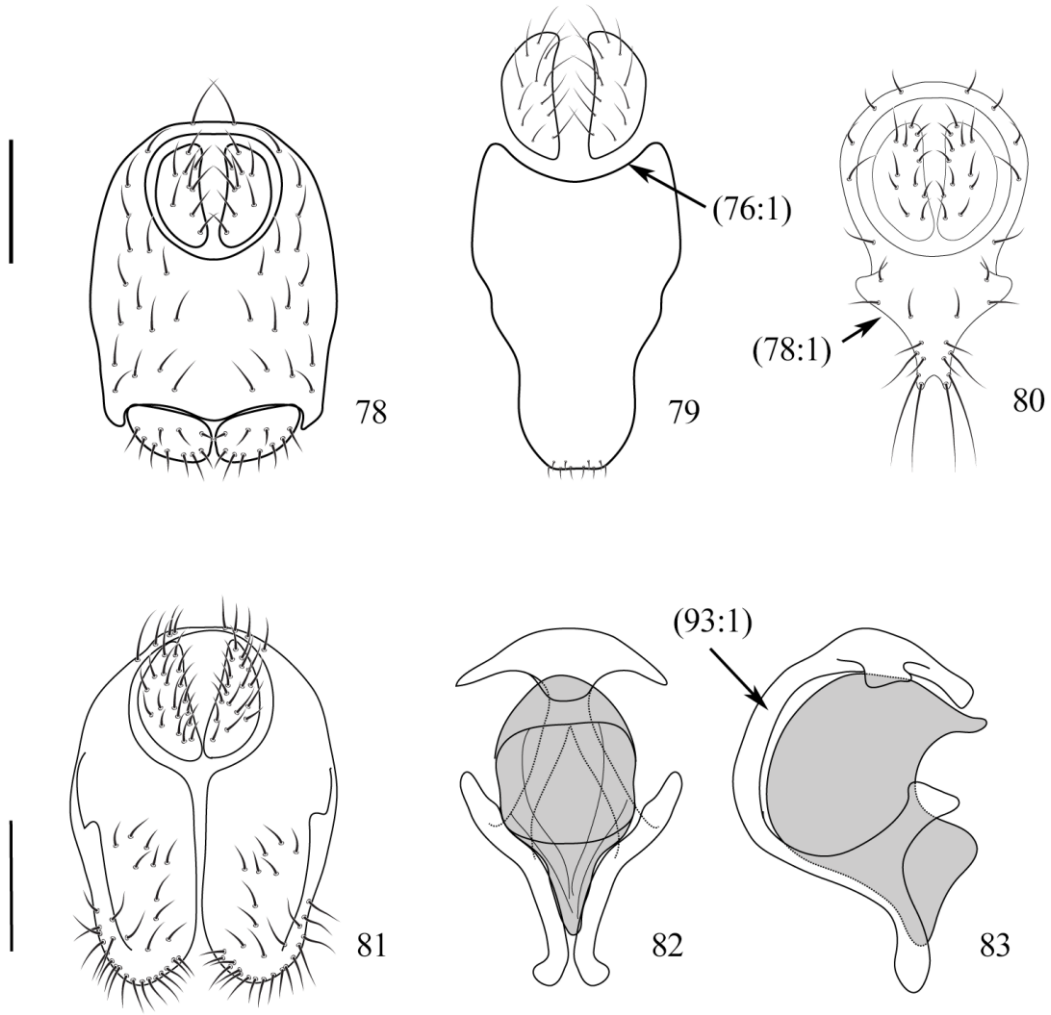
Figures 54-62. 54. *Lamproscatella sibilans* epandrium and cerci, posterior view; **55.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), ventral view; **56.** same, lateral view; **57.** *Haloscatella arichaeta* epandrium and cerci, posterior view; **58.** same, lateral view; **59.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), lateral view; **60.** *Haloscatella karekare* epandrium and cerci, posterior view; **61.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), ventral view; **62.** same, lateral view (Redraw from Mathis et al. 2004). Scale bar = 0.1 mm.



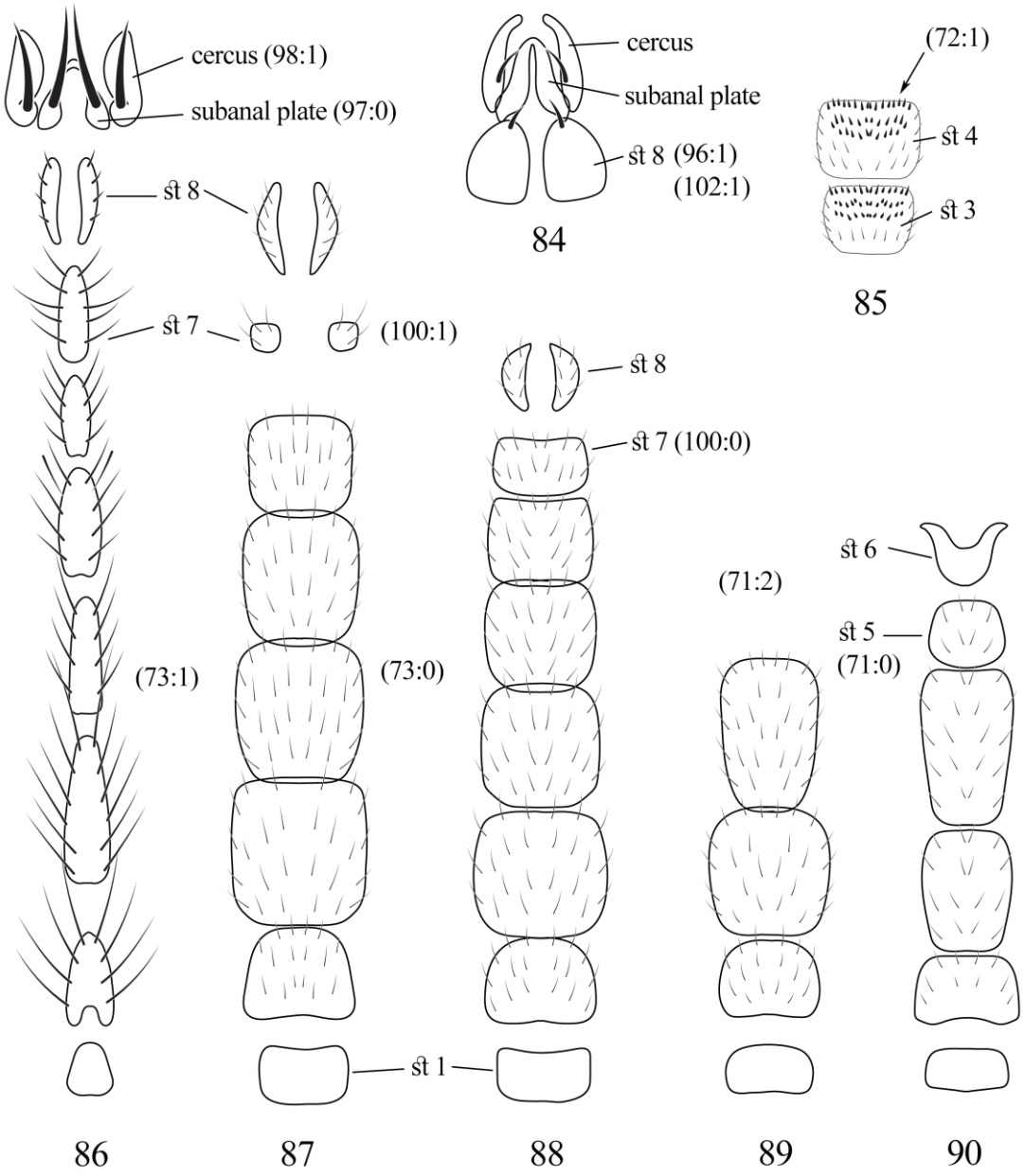
Figures 63-68. 63. *Thinoscatella lattini* epandrium and cerci, posterior view; **64.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), lateral view; **65.** *Scatella (Scatella) stagnalis* epandrium and cerci, posterior view; **66.** internal structures of male terminalia (aedeagus [shaded], ejaculatory apodeme, gonite+hypandrium), lateral view; **67.** *Scatella (Parascatella) pilifera* epandrium and cerci, posterior view; **68.** internal structures of male terminalia (aedeagus [shaded], ejaculatory apodeme), lateral view. Scale bar = 0.1 mm.



Figures 69-77. 69. *Scatophila prainha* epandrium and cerci, posterior view; **70.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite, hypandrium) and sternite 5, ventral view; **71.** same, lateral view; **72.** *Scatophila dianneae* epandrium and cerci, posterior view; **73.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite, hypandrium), ventral view; **74.** same, lateral view; **75.** *Philotelma defectum* epandrium and cerci, posterior view; **76.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite, hypandrium), ventral view; **77.** same, lateral view (Redraw from Mathis et al. 2009). Scale bar = 0.1 mm.



Figures 78-83. 78. *Limnellia maculipennis* epandrium and cerci, posterior view (Redraw from Mathis et al. 2009); **79.** *Brachydeutera neotropica*; **80.** *Haloscatella muria*; **81.** *Amalopteryx maritima* epandrium and cerci, posterior view; **82.** internal structures of male terminalia (aedeagus [shaded], phallapodeme, gonite+hypandrium), ventral view; **83** same, lateral view. Scale bar = 0.1 mm.



Figures 84-90. Abdominal sternites and external terminalia**. 84.** *Philotelma* sp., female; **85.** *Philotelma* sp., male; **86.** *Ephydra riparia* female; **87.** *Scatella (Scatella) stagnalis* female; **88.** *Scatella (Scatella) tenuicosta* female; **89.** *Scatella (Scatella) tenuicosta* male; **90.** *Scatella (Scatella) paludum* male.

Cladistic analysis

From the analysis using equal weights, 486 equally parsimonious cladograms resulted with a length of 386 steps, CI=32 and RI=76. The strict consensus cladogram has a length of 407 steps, with CI=31 and RI=74. The absolute Bremer support is represented on each clade branch and values were calculated from 7,256 suboptimal trees. The topology of the strict consensus is shown in Figs. 91 and 92.

From the analysis using implied weighting ten equally parsimonious cladograms were obtained with a length of 389 steps, 17.14734 adjusted fit, CI=32 and RI=75. The strict consensus cladogram has a length of 391 steps, with the same values to CI and RI. Relative bremer support values were calculated from 3620 suboptimal trees. The topology of the strict consensus is shown in Figs. 93 and 94.

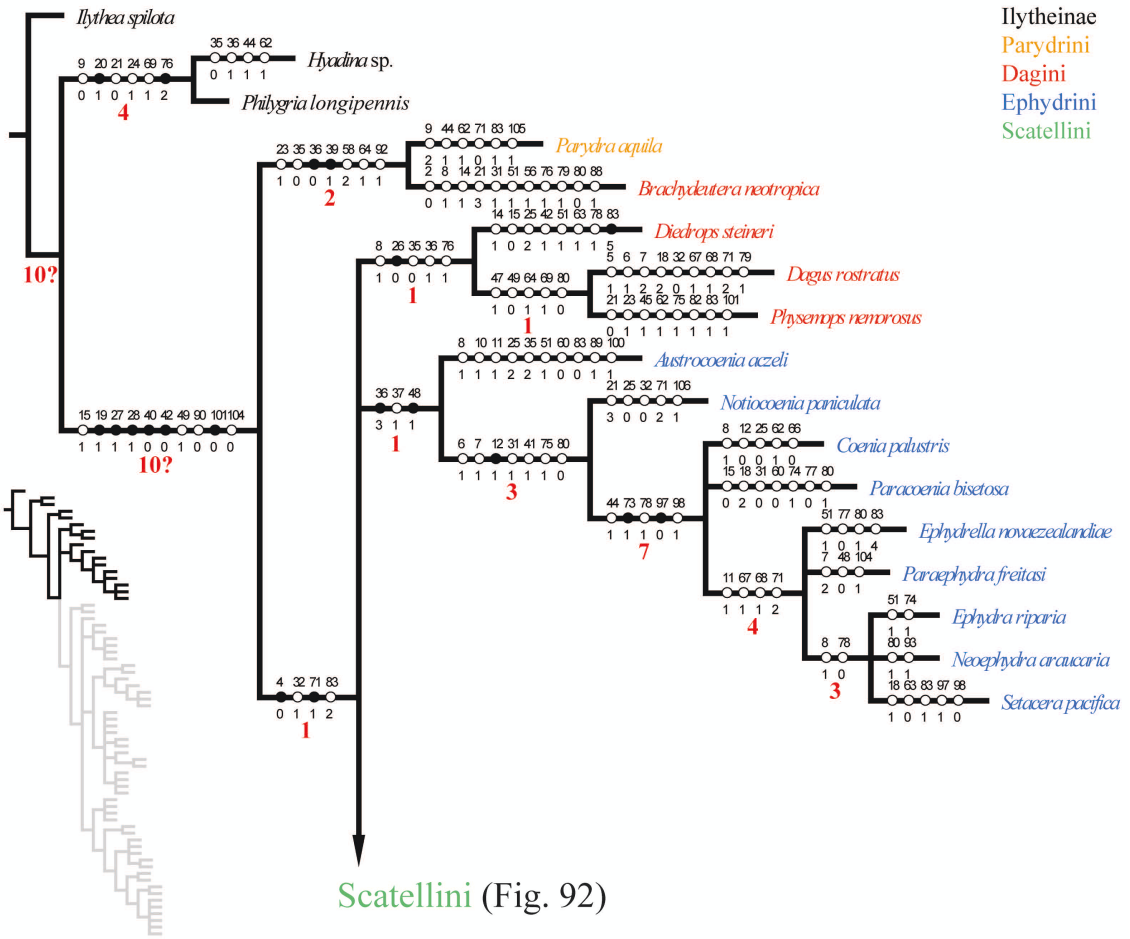


Figure 91. Strict consensus cladogram of outgroup and Ephydrinae obtained from 486 equally parsimonious cladograms under equal weights (407 steps; CI=31 and RI=74). Black circles indicate synapomorphic transformations and white circles indicate homoplastic transformations. The character number is shown above the circle and the corresponding character state is shown below it. Absolute bremer support values [red] are below each branch.

(Fig. 91)

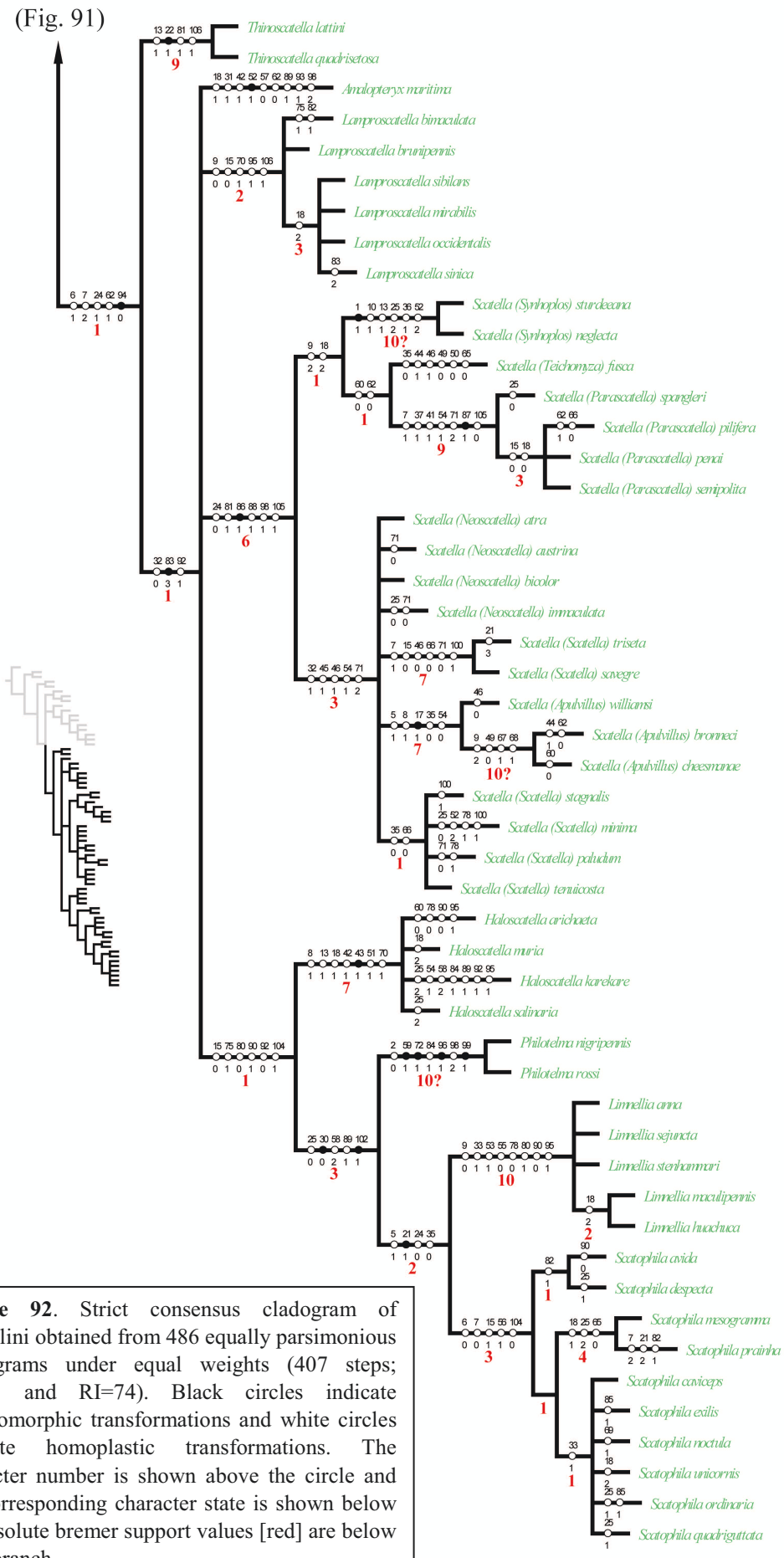


Figure 92. Strict consensus cladogram of Scatellini obtained from 486 equally parsimonious cladograms under equal weights (407 steps; CI=31 and RI=74). Black circles indicate synapomorphic transformations and white circles indicate homoplastic transformations. The character number is shown above the circle and the corresponding character state is shown below it. Absolute bremer support values [red] are below each branch.

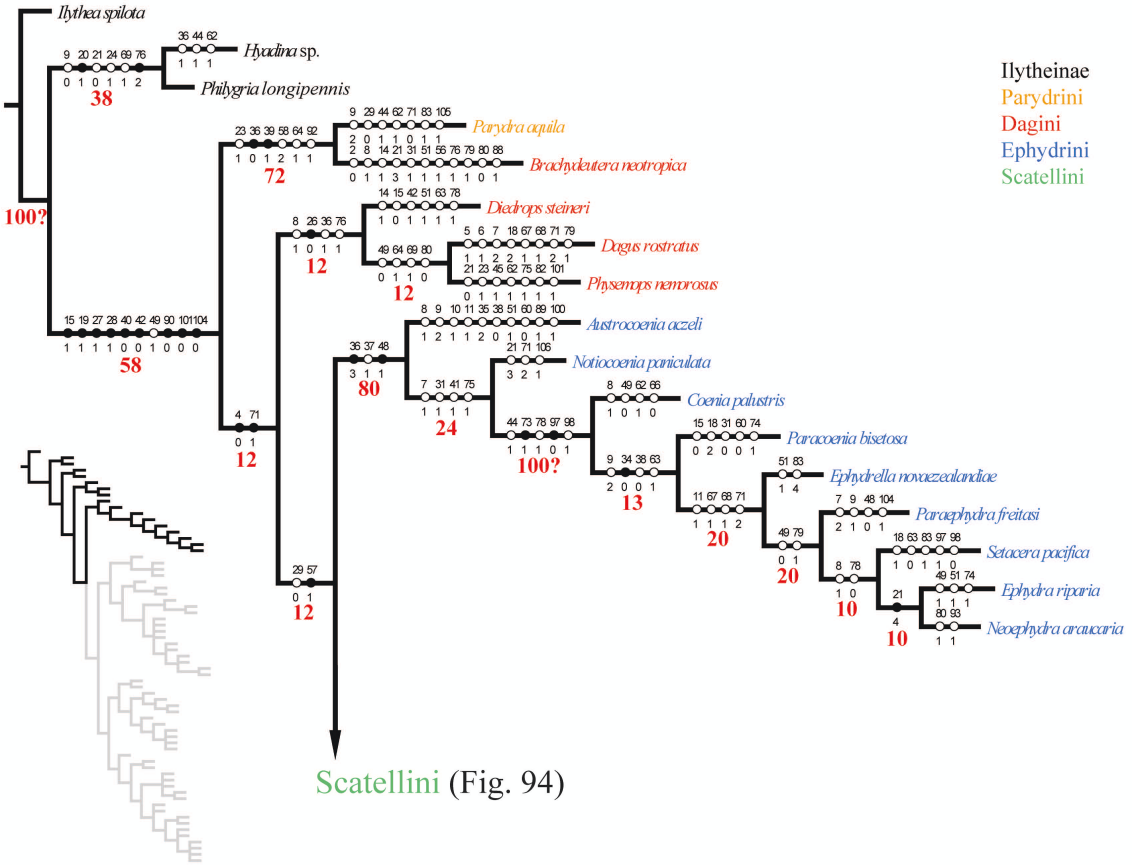


Figure 93. Strict consensus cladogram of outgroup and Ephydrinae obtained from 10 equally parsimonious cladograms under implied weights (391 steps; CI=32 and RI=75). Black circles indicate synapomorphic transformations and white circles indicate homoplastic transformations. The character number is shown above the circle and the corresponding character state is shown below it. Relative bremer support values [red] are below each branch.

(Fig. 93)

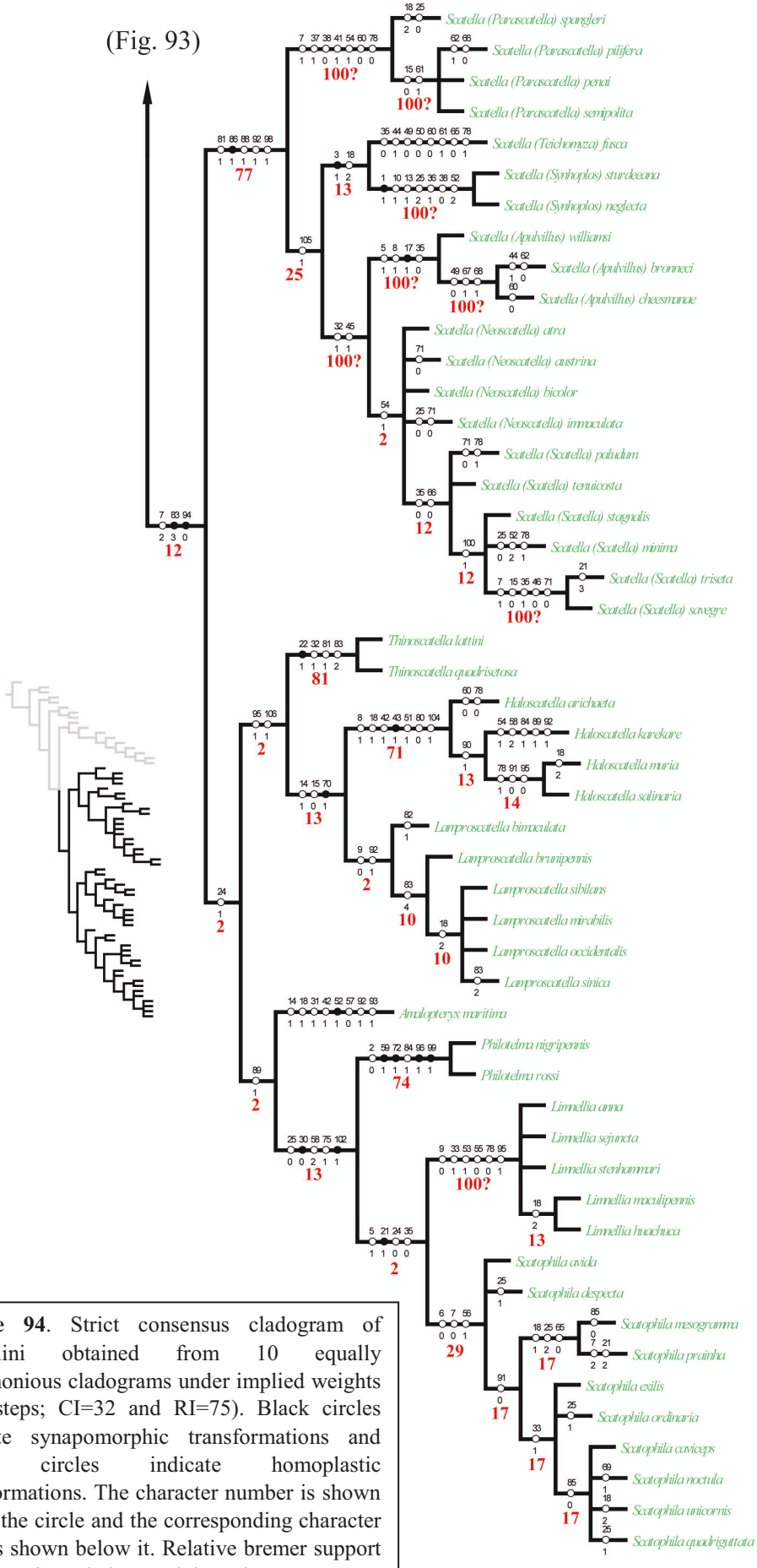


Figure 94. Strict consensus cladogram of Scatellini obtained from 10 equally parsimonious cladograms under implied weights (391 steps; CI=32 and RI=75). Black circles indicate synapomorphic transformations and white circles indicate homoplastic transformations. The character number is shown above the circle and the corresponding character state is shown below it. Relative bremer support values [red] are below each branch.

Ephydrinae

The subfamily Ephydrinae, as expected, is strongly corroborated as a monophyletic clade in all analyses, with six synapomorphies and four homoplasies in the equal weighing consensus tree and nine synapomorphies in the implied weighting consensus tree. New synapomorphies were found for the subfamily: palpus slender [character 27 (1)], T-shaped distal projection of lacinia [character 28 (1)], presence of postsutural supra-alar seta, [character 40 (0)], and female sternite 8 as two sclerites [character 101 (0)]. With the addition of these characters, we strongly corroborate the position of *Parydra* and Dagini as lineages of Ephydrinae, as proposed by Mathis (1979, 1980, 1982) and Zatwarnicki (1992).

In the equal and implied weighing tree, *Parydra aquila* + *Brachydeutera neotropica* appears as a clade supported by two synapomorphies and five homoplasies, which is the sister-group of the other tribes of Ephydrinae, although *Brachydeutera* is currently within the tribe Dagini. The tribe Dagini is sustained by four homoplasies and a single synapomorphy, face vertically arched, shield-like [character 26 (0)], a character already used in Mathis (1982) and Zarwarnicki (1992).

In the equal and implied weighing tree, Dagini (without *Brachydeutera*), Ephydrini and Scatellini form a monophyletic group, but the three tribes appear as a polytomy. This clade, including the three tribes, is supported by the presence of setulae in the medial region of the face (character 4 [0]). In the implied weighing tree, Ephydrini and Scatellini are grouped into a monophyletic group sustained by the overlap of the costal vein at the subcostal break (character 57 [1]).

The tribe Ephydrini also appears as a monophyletic group, corroborating previous hypotheses by Mathis and Simpson (1981), Mathis (1982), and Zatwarnicki (1992). Two synapomorphies were found in both methods of weighing: three pairs of post-sutural dorsocentral seta [character 36 (3)] and a long intrapostalar seta [character 48 (1)]. *Austrocoenia* and *Notiocoenia* seem to belong to the basal lineages of the tribe, the genera with females that have narrow sternites (character 73 [1]) and with strong and long bristles in the subanal plate (character 97 [0]) are a more derived lineage. The genera with tarsal claws near straight 67 [1]) and pulvilli absent (character 68 [1]) are the most derived genera.

Scatellini

The tribe Scatellini, as originally proposed by Wirth and Stone (1956), is a paraphyletic group, as noted previously by Mathis (1979b, 1980). In this paper, using the analyses with equal and implied weighing we recovered a monophyletic group, including all genera recognized for the Scatellini in Zatwarnicki (1992) and Mathis and Zatwarnicki (1995), and corroborating the hypothesis of grouping proposed by Zarwarnicki (1992). This clade is supported by four homoplasies and one synapomorphy, posterodorsal arm of gonite present (character 94 [0]) and in the implicit weighing tree, besides character 94, the aedeagus has a shoe-like structure (character 86 [3]).

The clade that includes all the genera of Scatellini is supported by two homoplasies and one synapomorphy, the aedeagus has a shoe-like form (character 86 [3]). In the consensus tree with equal weighing, the genus *Thinoscatella* Mathis appears as the sister-group of the other genera of this tribe.

In this clade, *Amalopteryx* Eaton, *Lamproscatella* Hendel, *Scatella* Robineau-Desvoidy, and clade of all the other genera appear in a polytomy: (*Haloscatella* Mathis + (*Philotelma* Becker +)); supported exclusively by homoplasies. The group (*Philotelma* + (*Limellia* Malloch, + *Scatophila* Becker)) is supported by three homoplasies and two synapomorphies: lateral projections of cibarium small (character 30 [0]) and female sternite 8 as two subquatrate sclerites (character 102 [1]). The latter clade had already been proposed in Zatwarnicki and Mathis (1994).

In the consensus tree with implied weighing *Scatella* Robineau-Desvoidy is the sister-group of all the other genera of Scatellini. This large clade is divided into two groups: *Thinoscatella* + (*Haloscatella* + *Lamproscatella*), supported only by homoplasies (*Haloscatella* + *Lamproscatella*) is supported by two homoplasies and one synapomorphy, the absence of sternite 1 (charater 70 [1]). The second group, formed by *Amalopteryx* + (*Philotelma* + (*Limellia* + *Scatophila*)) is similar to that recovered by equal weighing of characters, with the addition of *Amalopteryx*. Only one homoplasy supports *Amalopteryx* as sister-group of the other genera, the phallapodeme dorsoventrally flattened. (Character 89 [0]).

Scatella Robineau-Desvoidy and four of its six subgenera were recovered as a monophyletic group in all analyses, but the relationship among them diverge between trees with equal and implied weighing. In the consensus tree with equal weighing, two clades were found: (*Synhoplos* + (*Teichomyza* + *Parascatella*)). This relationship is supported only by homoplasies. All species of these subgenera are from Neotropical Region, with the exception of *Scatella* (*Teichomyza*), which also occurs in the Palearctic. The second clade includes the species of *Scatella* (*Scatella*) and *Neoscatella* in politomy with a clade that includes the species of the subgenus *Apulvillus*, supported by four homoplasies with emphasis on wings without white spots (character 54 [0]), a diagnosis for the group and a synapomorphy, the ocellar bristle small (character 17 [1]). Species of this subgenus are from the islands of Hawaii and French Polynesia.

In the consensus tree with implicit weighing, five subgenera were found, with the exception of *Neoscatella*. Two clades have also been formed: *Parascatella* is the sister-group of the other subgenera: (*Teichomyza* + *Synhoplos*) + (*Apulvillus* + (*Scatella*, *Neoscatella*)). (*Teichomyza* + *Synhoplos)* is supported by two homoplasies and one synapomorphy, dorsal seta of pedicel same length as the flagellomere (character 3 [1]).

Although *Scatella* (*Scatella*) forms a clade supported by two homoplasies, a pair of presutural dorsocentral seta (character 35 [0]) and stout setae at the anteroventral margin of forefemur (character 66 [0]), it is in a polytomy including all species of *Neoscatella*.

Relationships among the tribes of Ephydrinae.

Two tribes in current sense, Ephydrini and Scatellini, were recovered as monophyletic groups in our analysis. These tribes also form a monophyletic group in the consensus tree derived by implied weighing. The presence of lateral projections of cibarium (character 29 [1]) and the overlapping of costal vein (character 57 [1]) support this relationship.

Parydrini and Dagini do not appear as monophyletic groups in any analyses. Originally, the tribe Dagini was proposed based on two synapomorphies (Mathis 1982) which, in this work, are the face vertically arched (character 26 [0]), and the short katepisternal seta (character 64 [1]). Only character 26 [0] appears as a synapomorphy of the Dagini species in the cladogram with equal weights, excluding *Brachydeutera* (character 26 [1]). *Brachydeutera* appears as the sister-group of *Parydra* in all analyses. *Brachydeutera* has been included in several different tribes, including Parydrini (Mathis and Winkler 2003) and its phylogenetic position remains controversial.

The tribe Ephydrini was already widely recognized as a monophyletic group (Mathis 1979b) and our analysis sheds some light on relationships within the tribe. *Austrocoenia* and *Notiocoenia* are the basal lineages. The genera with females that presents narrow sternites (character 73 [1]) and with strong and long bristles in the subanal plate (character 97 [0]) are a more derived lineage, and finally, the genera with tarsal claws near straight 67 [1]) and pulvilli absent (character 68 [1]) are the most derived genera. This latter group comprises Ephydrini *sensu* Wirth and Stone (1956).

Relationships within Scatellini

Three large groups can be distinguished in Scatellini: the group corresponding to the genus *Scatella* (obtained in all analyses), a group formed by the genera *Thinoscatella*, *Lamproscatella* and *Haloscatella* (obtained as monophyletic group only in the analyses with implied weighing) and a group formed by the genera *Scatophila*, *Limnellia* and *Philotelma*.

Thinoscatella, in the equal weighing cladogram, is the sister-group of the other species of Scatellini. Together with *Lamproscatella* and *Haloscatella*, they form a heterogenous group, and share characters present in the other tribes of Ephydrinae, as the phallapodeme laterally flattened (character 89 [0]). The groundplan of internal structures of male genitalia are more similar to Ephydrini also (Figs. 54-59) *Haloscatella* is a particularly interesting genus because it presents characters referring to the genitalia of the male of other tribes of Ephydrinae, as characters of the genera *Philotelma* and *Scatophila*. These characters are the crossvein r-m distinctly distal to subcostal break (character 58 [2]), degree of fusion between the epandrium and the surstylus (character 78 [0-2]), components of aedeagus (characters 84 [0-1]) and shape of phallapodeme (character 89 [0-1]). The species of *Haloscatella* that share the same states of characters that *Philotelma* and *Scatophila* are all from New Zealand. In equal weight analysis, *Haloscatella* appears as the sister-group of *Philotelma*, *Scatophila* and *Limnellia*.

The group formed by the genera *Philotelma*, *Scatophila* and *Limnellia* was recovered in all the analyses. This relationship has already been proposed by other authors (Mathis, 1979b; Zatwarnicki and Mathis, 1994) and we have discovered two new synaphomorfies that support this clade: small side projections of cibarium (character 30 [1]) and female sternite 8 as two subquadrate sclerites (characters 102 [1]).

Between these two groups, is the monotypic genus *Amalopteryx*. In the analysis based on implied weighing, it appears as the sister-group of *Philotelma*, *Scatophila* and *Limnellia* but this relationship is sustained by only one homoplasy, the phallapodeme dorsoventrally flattened (character 89 [1]). However, considering the groudplan of the *Amalopteryx* genitalia (Figs. 81-83) and considering the implied weighing phylogeny, in which two important homoplasies bring together in a monophyletic group the clades (*Thinoscatella*, *Lamproscatella* and *Haloscatella*) and (*Scatophila*, *Limnellia* and *Philotelma*): a genal seta small (character 24 [1]) and the presence of sternite 5 in males (character 71 [1]). Therefore, we believe that the relationship with *Amalopteryx* in the implicit weighing tree is more correct.

We advocate the same for the monotypic genus not included in the analysis, *Tauromima* Papp. A small genal seta (character 24 [1]) is present in the genus. Zatwarnicki and Mathis (1994) proposed that *Tauromima* is the sister-group of

Scatophila and *Limnelia*, based on a cladistic analysis that included only *Philotelma*, *Tauromima*, *Scatophila* and *Limnellia*.

Scatella is a large genus, with 139 species described to date. It is divided into six subgenera (Mathis and Zatwarnicki 1995). Four of the six subgenera were corroborated in all analyses: *Apulvillus*, *Parascatella*, *Synhoplos* and *Teichomyza*. In the equal weighing analysis, a clade was obtained with the species of *Scatella* (*Scatella*), *Neoscatella* and *Apulvillus*. *Apulvillus* appears as a monophyletic group, but in polytomy with several species of *Neoscatella* and *Scatella* (*Scatella*).

Parascatella, *Teichomyza* and *Synhoplos* were already considered genera, but all share the same synapomorphy, ejaculatory apodeme present (character 86 [1]), shared by all species of the genus. The phallapodeme absent (character 88 [1]) and the long, strong setae at female cerci (character 98 [1]) are homoplasies shared only by *Scatella* species in the Scatellini.

In both analyses, two important homoplasies bring together the subgenus *Scatella* (*Scatella*), *Neoscatella* and *Apulvillus*: the lateral sclerites at mediproboscis (character 32 [1]) and rows of acrostichal setae not extending to the scutellum (character 45 [1]). In the implied weighing tree, the presence of white spots in the wings (character 54 [1]) separates *Neoscatell*a and *Scatella* (*Scatella*) from *Apulvillus*. No character was found separating *Neoscatella* and *Scatella* (*Scatella*) in any of the analyses. Mathis (1980) already argued that *Neoscatella* could be paraphyletic, and our results corroborate this hypothesis. *Neoscatella* can be easily distinguished from *Scatella* (*Scatella*) by the presence of a presutural dorsocentral seta (character 35 [1]). But neither this nor any character found for the subgenera established the monophyly of these subgenera.

Therefore, we suggest to synonymize *Neoscatella* with *Scatella* (*Scatella*), including species with white wing spots (character 54 [1]). Although the subgenus *Apulvillus* is very close to these two subgenera, we decided to maintain its current status due to its morphological peculiarities, as some species with tarsal claws near straight (character 67 [1]), pulvilli absent, (character 68 [1]), ocellar seta small (character 17 [1]) and wings without white spots (character 54 []) in all species. All species of *Apulvillus* are also from Hawaii islands and French Polynesia.

5. Taxonomy

Tribe Scatellini Wirth and Stone, 1956

Scatellini Wirth and Stone 1956: 466. Type genus: *Scatella* Robineau-Desvoidy 1830.─Mathis and Zatwarnicki 1995: 254-288 [world catalog].─Mathis *et al.* 2014: 561–576 [review of genera and species from Brazil].

Diagnosis. Specimens of Scatellini may be distinguished from other Ephydrinae by the following combination of character states: 1-3 lateral facial setae curved laterodorsally or ventrally curved, indistinctly from medial facial setae; mesonotum triangular; postsutural dorsocentral setae 2; intrapostalar seta small, weakly developed; prosternum bare of setae or setulae; Costal vein slightly to deeply overlaps itself at subcostal break, sometimes looking like a spur.

Redescription. Very small to moderately large species, body length 0.80-5.00 mm; generally dark brown to cinereous (rarely yellow), tomentose to shiny. *Head:* frontal vitta triangular, appearing dull, densely tomentose or shiny with metallic luster; frontal vitta sometimes with small setae towards anterior margin of frontal vitta; lacking interfrontal setae; usually 2 (rarely 3) lateroclinate, fronto-orbital setae (most genera) or 1 (*Limnellia* Malloch, most *Scatophila* Becker). Antenna relatively short; arista essentially bare, macropubescent (most genera) or bearing long dorsal rays (*Philotelma* Becker). Pedicel with a row of setae along anterior margin, setae longer ventrally plus one proclinate and one vertical seta dorsally. Face conspicuously to moderately protruding, setulose to moderately densely pilose, 1-3 lateral facial setae curved laterodorsally or ventrally curved, indistinctly from medial facial setae; interfoveal hump high to low, usually just below of antennae; dorsum of interfoveal hump usually similar to rest of face, dark colored in a few species, not shiny; eye bare, usually as wide 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 with a row of setulae at the ventral margin of gena (*Amalopteryx* Eaton, *Haloscatella* Mathis, *Lamproscatella* Hendel, *Philotelma*, *Tauromima* Papp, *Thinoscatella* Mathis); 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 seta small, weakly developed; presutural supra-alar seta present, variable, subequal or larger than anterior notopleural seta; postsutural supra-alar seta 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 (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 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* Robineau-Desvoidy, *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 helmut-like or tubular shaped.

Discussion. 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. Although largely undescribed, there is considerable species diversity at higher elevations associated with the Andes in South America, where specimens were collected at localities in Colombia above 5000 m (pers. obsv. of WNM).

Worldwide there are over 250 species in Scatellini (Mathis and Zatwarnicki 1995 and pers. obsv. of WNM), and in the Neotropical Region there are records of four genera and nearly 70 species with a majority being classified in the genus *Scatella* and its included subgenera.

Key to Genera and Subgenera of Scatellini Wirth and Stone

1. Mesonotum bearing 2 rows of acrostichal setae extended to anterior margin of scutellum and setae subequal in length..... 2

- Mesonotum bearing 2 rows of acrostichal setae not extended to anterior margin of scutellum, usually with 1 larger, sutural acrostichal seta (*Scatella* Robineau-Desvoidy, in part) 11

2. Arista shorter than basal flagellomere. Frontal vitta as long as wide..... 3

- Arista longer than basal flagellomere. Frontal vitta wider than long 4

3. Pedicel with a long dorsal seta, subequal to length of arista. Apical scutellar seta longer than basal seta..... *Scatella* (*Synhoplos*) Lamb

- Pedicel with short dorsal seta, shorter than the length of arista. Apical scutellar seta same length of basal seta, small .....*Tauromima* Papp

4. Costa short, extended to or slightly beyond apex of vein R_{4+5}..... *Scatophila* Becker

- Costa longer, extended to apex of vein M 5

5. Arista pectinate above .....*Philotelma* Becker

- Arista bare to macropubescent 6

6. Only 1 lateroclinate fronto-orbital seta present. Wing infuscate, darker on anterior margin and lighter on posterior margin with distinctive pattern of numerous pale spots.....*Limnellia* Malloch

- Two or 3 lateroclinate fronto-orbital setae present. Wing hyaline to faintly infuscate or with pattern of a few pale spots 7

7. Gena usually bearing a long distinct seta, longer and stronger than other genal setae or setulae. Postsutural supra-alar seta subequal to length as postalar seta .....

..... *Scatella* (*Parascatella*) Cresson

- Gena without long, strong seta, with a series of uniform fine hairs. Postsutural supra-alar seta shorter than half length of postalar seta..... 8

8. Posterior notopleural seta much farther dorsad from ventral notopleural suture than anterior seta..... 9

- 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.....

.....*Haloscatella* Mathis

- 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 .....*Thinoscatella* Mathis

- Posterior fronto-orbital seta closer to anterior fronto-orbital seta than to medial vertical seta. Frontal vitta tomentose, appearing dull .....*Lamproscatella* Hendel

11. Scutellum with 3 pairs of scutellar seta, these subequal in length; mesonotum covered by scattered setulae, not forming a row of acrostichal and intra-alar setae ..

..... *Scatella* (*Teichomyza*) Macquart

- Scutellum with 2 pairs of scutellar seta, basal pair shorter than apical pair; acrostichal and intra-alar setae present, in small rows 12

12. Wing slightly infuscate with few to several distinct pale spots. Sutural acrostichal seta present, conspicuously longer than other acrostichal setae (if absent, presutural dorsocentral seta present) ..... *Scatella* (*Scatella*) Robineau-Desvoidy

- Wing hyaline, without pale spots. Sutural acrostichal seta present, weak or indistinguishable than other acrostichal setae ..... *Scatella* (*Apulvillus*) Malloch

Genus ***Amalopteryx*** Eaton, 1875

Amalopteryx Eaton 1875: 58 (feminine). Type species: *Amalopteryx maritima* Eaton 1875, monotypy.

Diagnosis. *Amalopteryx* is distinguished from other genera of Scatellini by the following combination of characters: Eye slightly wider than high (Eye ratio < 1.1); posterior notopleural seta distinctly elevated above level of anterior seta; intrapostalar relatively long, half of the length of postalar seta.

Redescription. Moderately large shore flies, body length: 3.24 mm; dark brown to dark gray species. Stenopterous species.

Head: frontal vitta generally dull, densely tomentose. Lateroclinate 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 ventroclinate setae along oral margin; eye nearly round, slightly wider than high. Gena 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 tomentose; 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 seta relatively long, half of the length of postalar seta; basal scutellar setae conspicuously smaller than apical setae; posterior notopleural seta distinctly elevated above level of anterior seta; postsutural supra-alar seta small, shorter than postalar seta; legs typical, usually without

distinct setae, concolorous with thorax; tarsi most brown; tarsal claws conspicuously curved and puvilli present below each claw; Wing infuscate, stenopterous in only known species.

Abdomen: tergites gray to brown, tomentose; 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 two 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, as 2 lateral, lunate sclerites; female cerci with a long, slender setae inserted posteroventrally. Ventral receptacle absent.

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

Remarks. A monotypic genus with stenopterous wings. *Amalopteryx* share a row of genal setulae with *Lamproscatella* and *Haloscatella*, and the groundplan of male terminalia with *Scatophila*. This is reflected in the position of the genus obtained in the cladisc analysis presented herein. *Amalopteryx maritima* is a saprophagous and microphagous species and its immature stages were described by Womersley (1937).

Genus ***Haloscatella*** Mathis, 1979

Haloscatella Mathis 1979b: 6 (as a subgenus of *Lamproscatella;* feminine). Type species: *Lamproscatella arichaeta* Mathis 1979, original designation.─Olafsson 1991: 42 [revised status].─Mathis, Zatwarnicki and Marris 2004: 4-18 [New Zealand fauna].

Diagnosis. *Haloscatella* is distinguished from other genera of Scatellini, especially those related to *Lamproscatella,* by the following combination of characters: cinereous, densely tomentose species; small setulae towards anterior margin of frontal vitta;

vestiture of frontal vitta usually tomentose, appearing dull; posterior notopleural seta inserted at distinctly higher level than anterior seta; a short, strong seta dorsally curved toward anterodorsal corner of anepisternum; prescutellar acrostichal seta present, conspicuous; medial scutellar seta 1/2 length of apical seta.

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

Head: frontal vitta generally dull, usually densely tomentose; small setulae towards anterior margin of frontal vitta; long lateroclinate 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, ob1iquely 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: mesonotum cinereous to brown, tomentose; 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 dorsoclinate 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 infumate around crossveins and veins; costa relatively long, extended to vein M; costal vein sometimes bearing spines.

Abdomen: tergites gray to brown, tomentose; sternite 1 absent or membranous. Male Terminalia : 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. Ventral receptacle without operculum only extended process present.

Distribution. Cape, Australian, Nearctic (including northern Mexico), Palearctic.

Remarks. Species of this genus proliferate best where saline or alkaline conditions are near saturation (Mathis 1979b, Mathis at al. 2004). Immature stages are unknown. Members of *Haloscatella* are quite homogeneous in overall appearance, but the characters of the male terminalia are 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 that *Philotelma* and *Scatophila* are all from New Zealand. This particularity makes *Haloscatella* an important genus to understand the evolution of Scatellini.

Genus ***Lamproscatella*** Hendel, 1917

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].─Krivosheina 2004: 321-329 [Russian fauna].

Diagnosis. Specimens of *Lamproscatella* are similar to *Thinoscatella* but may be distinguished by the following combination of characters: Interfoveal dorsal hump of face low, less than half of the height of head; Frontal vitta mostly tomentose, appearing dull; setulae towards anterior margin of frontal vitta absent; posterior notopleural seta at same level as anterior seta.

Redescription. Small to moderately small shore flies, length 1.25-2.90 mm; dark brown to cinereous species.

Head: frontal vitta mostly tomentose, appearing dull. Face prominent, interfoveal dorsal hump of face low, at middle of the face; arched, lateroclinate 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 tomentose, 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 infumate; costa relatively long, extended to vein M; 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, tomentose, sometimes slightly darker toward margins; dorsal setae small and scattered. Male Terminalia: sternite 1 membranous or absent; sternite 5 present, sternite 6 absent; Epandrium as a 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. Ventral receptacle with a helmut-like operculum, small, not covering extended process.

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

Remarks. This genus is not found in the Neotropical and Australian Regions. Very little is known concerning the habitat preferences of members of this subgenus. North American species generally occur in freshwater environments, but specimens are

occasionally collected near saline or alkaline water systems (Mathis, 1980). Immature stages are unknown.

Genus ***Limnellia*** Malloch, 1925

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].─Zhang and Yang 2009: 558-64 [review, Chinese fauna].─Krivosheina 2012: 1-7 [review, Russian species].─Mathis *et al.* 2014: 563-564 [review, Brazilian species].

Eustigoptera Cresson 1930a: 126 (feminine). Type species: *Notiphila quadrata* Fallén 1813, original designation.─Cresson 1935: 362 [synonymy].

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

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

Diagnosis. *Limnellia* is distinguished from other genera of the tribe Scatellini by the following combination of characters: 1 pair of well-developed, lateroclinate fronto-orbital seta; gena small (gena to eye ratio < 0.21); mesonotum usually conspicuously multicolored with pattern of bands and/or spots; wing strongly infuscate, darker on anterior margin and lighter on posterior margin, with several white spots in all cells.

Redescription: Small to moderately small shore flies, body length 1.00-2.50 mm; mostly dark brown to black, tomentose to bare, shiny, frequently with cinereous guttate and vittate maculae; species macropterous or brachypterous.

Head: frontal vitta distinct from duller parafrons, subshiny; lateroclinate fronto-orbital seta 1; 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 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; dorsocentral 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 M; 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: sternite 5 present, sternite 6 absent. Epandrium a closed plate around cercal cavity, bearing articulated surstyli on anterior margin; surstylus as two plates or fused; gonites broadly Y-shaped, with broad base, bearing setae on ventral portion; aedeagus in lateral view shoe-shaped, without distiphallus; phallapodeme dorsoventrally flattened, usually with two 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. Ventral receptacle without operculum, only extended process present.

Distribution., Australian, Chinese (Palearctic–Oriental transition), Ethiopian, Nearctic, Neotropical, Oriental, Palearctic.

Remarks. *Limnellia* Malloch is an easily reconized genus within Scatellini, due to the conspicuously multicolored mesonotum with patterns of bands and/or spots and the infuscate wing with several white spots. Twent-four species are known in the genus, mostly from Nearctic Region (10 species). Nothing is known about immature stages, behavior, and the habitat of this genus. Mathis (1978) presented a phylogeny of Nearctic species. Four species from Neotropical, Palearctic and Australasian Regions have different degrees of reduced wings (Hollmann-Schirrmacher and Zatwarnicki 1995;

Mathis et al. 2004; Costa et al. 2016) suggesting this feature evolved independently in *Limnellia.* This work and previous papers (Mathis 1978, Mathis and Zatwarnicki 1994) document that the *Limnellia* is the sister-group of *Scatophila.*

Genus ***Philotelma*** Becker, 1896

Philotelma Becker 1896: 163 (neuter). Type species: *Philotelma anomalum* Becker 1896 (= *Notiphila nigripennis* Meigen 1830), monotypy.─Zatwarnicki and Baéz 1991: 209-210 [review].─Mathis, Zatwarnicki and Kubátová-Hiršová 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 others genera of Scatellini by the following combination of characters: 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-cu covered with dark spot.

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

Head: frontal vitta shiny, sparsely tomentose, 2 lateroclinate 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 ventroclinate 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. legs typical, without distinct setae; tarsi light brown; tarsal claws conspicuously

curved and puvilli present below each claw. Wing faintly to moderately infuscate, with pale white spots; costal vein relatively long, extended to vein M; crossvein r-m distinctly distal to subcostal break; crossvein dm-cu covered with infuscate spot that usually extends into cell R_5.

Abdomen: tergites shiny black, sparsely tomentose. Male terminalia: sternite 5 present, sternite 6 absent; Epandrium in posterior view broadly oval, ventral margin usually slightly to obviously flatter than dorsal margin, sometimes with medial projection, without an opening; surstyli absent or probably fused indistinguishably with ventral margin of epandrium; gonites straight, paired, one on each side, and hypandrium as an inverted V-shaped structure, bounded with the gonites; aedeagus in lateral view shoe-shaped, elongate, with a membranous distiphallus that is invested with short, sharp scales or scale-like thorns; phallapodeme 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, bearing a long seta on posterior margin; female cerci without prominent setae. Ventral receptacle without operculum, only extended process present.

Distribution. Nearctic, Palearctic.

Remarks. *Philotelma* is a small genus, comprising five species and is only known from Nearctic and Palearctic Regions. Adults usually occur in habitats slightly to notably alkaline or saline (Dahl 1959, Kubatova-Hiršova 2005). Mathis et al. (2009) published a revision of all known species.

Genus ***Scatella*** Robineau-Desvoidy, 1830

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 infuscate 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.

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

Head: frons dull usually with distinct, subshiny to shiny frontal vitta; lateroclinate 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, hair-like 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: mesonotum generally dark colored, tomentose, 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 palely to conspicuously infuscate with white spots, especially in cells R_{2+3}, R_{4+5}, and dm but exceptionally in cell R_1 and CuA_1; costa relatively long, extended to vein M, sometimes bearing spines; wing brachypterous in a few species.

Abdomen: tergites gray to brown, tomentose, sometimes with lighter posterior margins, or mostly shiny, blackish brown. Male terminalia: 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: 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. Ventral receptacle tubular shaped, one to five times longer than wide.

Distribution. Andean, Australian, Cape, Ethiopian, Nearctic, Neotropical, Oriental, Palearctic.

Remarks. *Scatella* is a large genus, with 139 species and occurs in all biogeographic regions. 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 includes species previously included in *Neoscatella* Malloch.

Subgenus *Apulvillus* Malloch 1934

Apulvillus Malloch 1934: 197 (as a genus; masculine). Type species: *Apulvillus bronneci* Malloch 1934, original designation.─Mathis 1980: 26 [revised status].

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

Diagnosis. Specimens of *Apulvillus* are similar to those of *Scatella* but may be distinguished by the following combination of characters: face with very small,

dispersed setulae; presutural dorsocentral seta inconspicuous or absent; row of acrostichal setae not extending to scutellum; thorax setae generally small; wing hyaline, without white spots.

Redescription. 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; lateroclinate fronto-orbital seta 2; inner 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, tomentose, 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 palely to slightly infuscate, without white spots.

Abdomen: Tergites dark brown, tomentose. Male terminalia: sternites 5 and 6 absent. Epandrium and internal genitalia 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; Ventral receptacle tubular shaped, one to five times longer than wide.

Distribution. Oriental (Hawaii islands, French Polynesia).

Remarks. *Apulvillus* comprises seven species from the Hawaii islands and French Polynesia. They are closely related with *Scatella* (*Scatella*), and are distinguished in

particular by the wing being hyaline, without white spots. It is a heterogeneous subgenera, with some species lacking pulvilli, and with different setae from head and mesonotum being reduced. Tenorio (1980) reported that the adults are generally found in freshwater streams and described the puparium of *Apulvillus mauiensis* (Wirth).

Subgenus *Parascatella* Cresson, 1935

Parascatella Cresson 1935: 357 (as a genus; feminine). Type species: *Scatella pilifera* Cresson 1931, original designation.─Sturtevant and Wheeler 1954: 178 [revised status].

Diagnosis. Specimens of *Parascatella* are similar to those of *Scatella* but may be distinguished by the following combination of characters: Face setulose, undistinguished from facial setae; postpronotum with 1 long seta; postsutural supra-alar seta long, same length as postalar seta; wing hyaline, with faint white spots; costal vein with spines.

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

Head: frons dull usually with distinct, subshiny to shiny frontal vitta; lateroclinate 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, hair-like 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 tomentose, 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 spine-like setae along costal margin.

Abdomen: tergites gray to brown, tomentose, sometimes with lighter posterior margins, or mostly shiny, generally lacking prominent macrosetae. Male terminalia: sternites 5 and 6 absent. Epandrium and internal genitalia 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; ventral receptacle tubular shaped, as long as wide.

Distribution. Neotropical, South American (Neotropical–Andean transition), Andean.

Remarks. *Parascatella* was originally described as a genus and now comprises 13 species from western South America. Nothing is known about natural history; the adults are associated with aquatic or semiaquatic 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.

Subgenus *Scatella* Robineau-Desvoidy, 1830

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.─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. n.**

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* by the following combination of characters: 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).

Redescription. Minute to moderately large shore flies, body length 1.00-3.00 mm; blackish brown to cinereous species, rarely yellow; species macropterous or with wings reduced.

Head: frons dull usually with distinct, subshiny to shiny frontal vitta; lateroclinate 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 ventroclinate setae along oral margin. Eye usually nearly round. Gena short to moderately high, usually bearing a large seta.

Thorax: mesonotum generally dark colored, tomentose, 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 palely to conspicuously infuscate with white spots, especially in cells R_{2+3}, R_{4+5}, and dm but

exceptionally in cell R_1 and CuA_1; costa long, extended to vein M, sometimes bearing spines; wing reduced, usually stenopterous in a few species.

Abdomen: tergites gray to brown, tomentose, sometimes with lighter posterior margins, or mostly shiny, blackish brown. Male terminalia: sternites 5 and 6 well developed, very small or absent. Epandrium and internal genitalia typical of *Scatella*; ventral projections of epandrium separated or indistinguishable; phallapodeme absent; ejaculatory apodeme present, L shaped, dorsoventrally. Female terminalia: 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. Ventral receptacle tubular shaped, one to five times longer than wide.

Species moved from *Neoscatella* Malloch: *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 and Wirth, 1981; *S. (S.) bicolor* Mathis and 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 and Malloch, 1926; *S. (S.) norrisi* Mathis and Wirth, 1981; *S. (S.) oahuense* Williams 1938; *S. (S.) obscuriceps* Cresson 1915; *S. (S.) praia* Mathis, Marinoni and 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 and Wirth, 1981; *S. (S.) terryi* Cresson 1926; *S. (S.) victoria* (Cresson, 1935); *S. (S.) vittithorax* Malloch 1925; *S. (S.) warreni* Cresson 1926.

Distribution. Cape, Andean**,** Australian, Ethiopian, Nearctic, Neotropical, Oriental, Palearctic.

Remarks. This subgenus comprises 116 species from all biogeographic regions. Most species occur in the Australasian/Oceanic and Neotropic Regions (Mathis and Zatwarnicki 1995 and pers. obsv. of Wayne N. Mathis). 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 1979). Sixteen species have some immature state described (pers. obsv. of the author; see Willians (1938), Tenorio (1980) for the main examples). *Scatella stagnalis* (Fallén) 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).

Subgenus *Synhoplos* Lamb, 1917

Synhoplos Lamb 1917: 390 (as a genus; masculine). Type species: *Synhoplos sturdeeanus* Lamb 1917, designated by Wirth 1968: 27.─Mathis 1980: 29 [revised status].

Diagnosis. Specimens of *Synhoplos* are most similar to *Teichomyza* and some brachypterous *Scatophila* and *Scatella* (*Scatella*), but may be distinguished following combination of character: Frons as long as wide; arista shorter than basal flagellomere; 1 long dorsal seta on pedicel, subequal to length of arista; gena high (gena to eye ratio > 0.6); one long presutural and 1 postsutural dorsocentral seta.

Redescription. Small to moderately small shore flies, body length 1.80-3.10 mm; brown to cinereous species; only micropterous species known.

Head: frons as long as wide, usually dull with distinct, subshiny frontal vitta; lateroclinate fronto-orbital seta 2. Antenna short, concolorous with head; pedicel with one long setae 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-quadrate, ob1iquely oriented to general plane of head; gena high (gena to eye ratio > 0.6), one strong genal seta.

Thorax: 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 seta small, much smaller than postalar. Legs typical, without distinct setae; femur stronger than tibiae and tarsi; tibia and tarsi light brown; halters reduced; wing micropterous.

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

Distribution. Andean.

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

Subgenus *Teichomyza* Macquart, 1835

Teichomyza Macquart 1835: 534 (as a genus; feminine). Type species: *Teichomyza fusca* Macquart 1835, monotypy.─Mathis 1980: 36 [revised status].

Tichomyza, error for *Teichomyza.*

Diagnosis. Specimens of *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: interfoveal dorsal hump of face high, between antennae; thorax covered by small and scattered setulae, acrostichal row and intra-alar setae indistinguishable; 3 pairs of long scutellar setae. Wing without white spots.

Redescription. Moderately small to large shore flies, about 3.5-5.0 mm: dark brown to dark gray species.

Head: frontal vitta tomentose, appearing dull; ocelli arranged as an isosceles triangle; Lateroclinate 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 ventroclinate setae along oral margin. Eye higher than wide; Gena moderately high, bearing a large seta.

Thorax: mesonotum tomentose, 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, unseriated; 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 infuscate, without white spots.

Abdomen: Tergites gray to brown, tomentose, dorsal setae long and scattered: Male terminalia: sternites 5 and 6 absent; Epandrium and internal genitalia 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; ventral receptacle tubular shaped, longer than wide.

Distribution. Andean, Palearctic.

Remarks. This subgenus includes a single species, *Scatella (Teichomyza) fusca*, and has a disjunct distribution, occurring in both South America and in Europe. Mathis (1980) suggests that this species was introduced in Europe through ships from South America, and due to the relationship of this species with Neotropical taxa such as *Synhoplos* and *Parascatella*, this should be the most probable hypothesis.

Scatella (Teichomyza) fusca is better known by the name "urine fly". The larvae and adults occur in localities and habitats that are soaked in urine, such as outdoor urinals. Ephydridae is associated with cases of myiasis (James, 1947). Laboulbène (1867) provided a deitailed study of the natural history of this species.

Genus ***Scatophila*** Becker, 1896

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].

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 the tribe Scatellini by the following combination of characters: 1 fronto-orbital seta (some Neotropical species with 2); costa relatively short, extended to vein R_{4+5}; crossvein r-m distinctly distal to subcostal break.

Redescription. Small 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.

Thorax: mesonotum tomentose, appearing with a multicolorus 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 infuscate with white spots distributed over most of

wing, but exceptionally within cell R_1; costa short, extended to vein R_{4+5}; crossvein r-m distinctly distal to subcostal break; wings reduced in a few species.

Abdomen: Tergites gray tomentose, sometimes with lighter posterior margins, or entirely shining black. Male terminalia: sternite 5 present, sternite 6 absent.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 ventral receptacle helmut-like, somewhat round, covering extended process.

Distribution. Andean, Australian, Ethiopian, Nearctic, Neotropical, Oriental, Saharo-Arabian (Palearctic–Ethiopian transition), Palearctic.

Remarks. *Scatophila* comprises 52 species, mostly from Neactic and Paleactic Regions (Mathis and Zatwarnicki 1995 and pers. obsv. of WNM). The habitat is the typical for the tribe, and they feed on algae and bacteria (Deonier 1974) and the immature stages are known only 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).

Genus ***Tauromima*** Papp, 1979

Tauromima Papp 1979: 359 (feminine). Type species: *Tauromima mountwilhelmi* Papp 1979, original designation.

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.

Redescription. 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 tomentose; lateroclinate fronto-orbital seta 2. 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 ventroclinate setae along oral margin. Eye wider than high, ob1iquely 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; 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 lenght 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. 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; apterous, halters absent.

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

Distribution. Australian.

Remarks. This genus includes only one species, *Tauromima mountwilhelmi*, the only completely apterous shore fly known. This species was collected at Mount Wilhelm (3400 m) high, Papua New Guinea. Nothing is known about the natural history of this species. *Tauromima* seems to be related to genera of Scatellini with only 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 *Limnellia* and *Scatophila*.

Genus ***Thinoscatella*** Mathis, 1979

Thinoscatella Mathis 1979a: 20 (as a subgenus of *Lamproscatella;* feminine). Type species: *Lamproscatella lattini* Mathis 1979, original designation.─Olafsson 1991: 41 [revised status].

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 inner vertical seta than to anterior fronto-orbital seta; wings hyaline, immaculate.

Redescription. Small to moderately small shore flies, body length 1.86-2.80 mm; brown to cinereous species.

Head: frons dull usually with distinct, subshiny to shiny frontal vitta; small, compiscuous setae towards anterior margin of frontal vitta; ocelli arranged as an isosceles triangle; lateroclinate fronto-orbital seta 2; posterior fronto-orbital seta inserted closer to inner 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 ventroclinate 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 tomentose, 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, hyaline; costa relatively long, extended to vein M; stem of halter short, head oval, pale yellow.

Abdomen: tergites gray to brown, tomentose, sometimes slightly darker toward margins; dorsal setae small and scattered. Male Terminalia: 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 flattened, straight to slightly curved; Female Terminalia: sternite 8 divided, as 2 lateral, lunate sclerites; female cerci without prominent setae. Ventral receptacle with a helmut-like operculum, small, not covering extended process.

Distribution. Chinese (Palearctic–Oriental transition), Nearctic, Oriental, Palearctic.

Remarks. This genus comprises three species. Adults prefer the 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.

6. Final Considerations

This study is, so far, the most complete phylogenetic analysis of Scatellini. It was possible to sample all genera (except *Tauromima* Papp) from several regions of the world, including a considerable sample of their morphological variation. This work also presents considerable information on the relationships among the genera of the tribe Ephydrini, showing the basic topology of the tribe. Dagini, on the other hand, is a challenging tribe, and no proposed character has been able to recover the monophyly of the tribe as it is understood today.

Scatellini, as proposed by Zatwarnicki (1992) and Mathis and Zatwarnicki (1995) formed a monophyletic group with all genera included. There are two major lineages within Scatellini: 1. the genus *Scatella* and its subgenera; 2. the other genera, separated in the analysis of implicit weighing into two groups: the first comprising *Thinoscatella*, *Lamproscatella* and *Haloscatella* and the second by *Philotelma*, *Limnellia* and *Scatophila*. *Amalopteryx* shares characters with both groups, but can't be placed into any group properly. *Tauromima* also seems seems to be related with this group, but only by examining more specimens of this genus we can discover its real relationship.

Three subgenera of *Scatella* are corroborated as monophyletic groups: *Parascatella*, *Teichomyza* and *Synhoplos*. *Apulvillus* appeared as a monophyletic group only in the implicit weighing analysis. We decided to maintain the subgenus status for *Apulvillus*, because of its morphological peculiarities and geographical distribution.

The subgenus *Neoscatella* was synonimized with *Scatella* (*Scatella*), because no synapomorphy was found to support both subgenus.

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Appendix

Taxon	Head																																Thorax		
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Hyadina sp.	0	0	0	1	-	-	-	0	1	0	1	0	0	0	0	0	0	2	0	0	2	0	0	0	0	1	0	0	1	-	0	0	0	1	1
Ilythea spilota	0	1	0	1	-	-	-	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1	1	1	0	0	1	-	0	0	0	1	0
Philygria longipennis	0	1	0	1	-	-	-	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0	1	0	0	1	-	0	0	0	1	1
Parydra aquila	0	1	0	1	-	-	-	0	2	0	0	0	0	0	1	0	0	0	1	0	2	0	1	-	1	1	1	1	0	1	0	0	0	1	0
Dagus rostratus	0	1	0	0	1	1	2	1	1	0	0	0	0	0	1	0	0	2	1	0	2	0	0	0	1	0	1	1	1	-	0	0	0	1	0
Brachydeutera neotropica	0	0	0	1	-	0	0	1	1	0	0	0	0	1	1	0	0	2	1	0	3	0	1	-	0	1	1	1	1	-	1	0	0	1	0
Diedrops steineri	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	-	0	1	0	2	0	0	0	2	0	1	1	1	-	0	1	0	1	0
Physemops nemorosus	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	-	0	1	0	0	0	1	-	1	0	1	1	1	-	0	1	0	1	0
Austrocoenia aczeli	0	1	0	0	0	0	0	1	2	1	1	0	0	0	1	0	0	0	1	0	2	0	0	0	2	1	1	1	0	1	0	1	0	1	2
Coenia palustris	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	1	1	1	0	1	1	1	0	1	1
Ephydra riparia	0	1	0	0	0	1	1	1	2	0	1	1	0	0	1	0	0	0	1	0	4	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Ephydrella novaezealandiae	0	1	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Neoephydra araucaria	0	1	0	0	0	1	1	1	2	0	1	1	0	0	1	0	0	0	1	0	4	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Notiocoenia paniculata	0	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	0	1	0	3	0	0	0	0	1	1	1	0	1	1	0	0	1	1
Paracoenia bisetosa	0	0	0	0	0	1	1	0	2	0	0	1	0	0	0	0	0	2	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	0	1
Paraephydra freitasi	0	1	0	0	0	1	2	0	1	0	1	1	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	1	1	0	0	1
Setacera pacifica	0	1	0	0	0	1	1	1	2	0	1	1	0	0	1	0	0	1	1	0	2	0	0	0	1	1	1	1	0	1	1	1	0	0	2
Amalopteryx maritima	0	1	0	0	0	1	2	0	1	0	0	0	0	1	1	0	0	1	1	0	2	0	0	1	1	1	1	1	0	1	1	0	0	1	1
Haloscatella arichaeta	0	1	0	0	0	1	2	1	1	0	0	0	1	1	0	0	0	1	1	0	2	0	0	1	1	1	1	1	0	1	0	0	0	1	1
Haloscatella muria	0	1	0	0	0	1	2	1	1	0	0	0	1	1	0	0	0	2	1	0	2	0	0	1	1	1	1	1	0	1	0	0	0	1	1
Haloscatella karekare	0	1	0	0	0	1	2	1	1	0	0	0	1	1	0	0	0	1	1	0	2	0	0	1	2	1	1	1	0	1	0	0	0	1	1
Haloscatella salinaria	0	1	0	0	0	1	2	1	1	0	0	0	1	1	0	0	0	1	1	0	2	0	0	1	2	1	1	1	0	1	0	0	0	1	1
Lamproscatella sibilans	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	2	1	0	2	0	0	1	0	1	1	1	0	1	0	0	0	1	1
Lamproscatella bimaculata	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	0	1	0	1	1	1	0	1	0	0	0	1	1
Lamproscatella brunipennis	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	0	1	1	1	1	1	0	1	0	0	0	1	1
Lamproscatella mirabilis	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	2	1	0	2	0	0	1	0	1	1	1	0	1	0	0	0	1	1
Lamproscatella occidentalis	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	2	1	0	2	0	0	1	0	1	1	1	0	1	0	0	0	1	1
Lamproscatella unipunctata	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	2	1	0	2	0	0	1	0	1	1	1	0	1	0	0	0	1	1
Limnellia maculipennis	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Limnellia anna	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Limnellia huachuca	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0

Table V. Matrix of character states used in the cladistic analysis. [-] characters not applied.

Taxon	Thorax																																	Abm	
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7
	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
***Hyadina* sp.**	2	0	1	0	1	-	1	0	0	0	0	0	0	0	-	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	1	0	0	0	0
Ilythea spilota	1	0	1	0	1	-	1	0	1	-	0	1	-	0	-	0	0	0	0	-	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0
Philygria longipennis	2	0	1	0	1	-	1	0	0	0	0	1	-	0	-	0	0	0	0	-	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0
Parydra aquila	0	0	1	1	0	0	0	0	1	-	0	1	-	1	0	0	0	0	0	-	0	0	2	0	1	0	1	0	1	1	1	0	0	0	0
Dagus rostratus	1	0	1	0	0	0	0	0	0	0	0	1	-	0	-	0	0	0	0	-	0	0	1	0	1	0	0	0	1	1	1	1	1	1	0
Brachydeutera neotropica	0	0	1	1	0	0	0	0	0	0	0	1	-	1	0	1	0	0	0	-	1	0	2	0	1	0	0	0	1	1	1	0	0	0	0
Diedrops steineri	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	-	0	0	1	0	1	0	0	1	0	1	1	0	0	0	0
Physemops nemorosus	1	0	1	0	0	0	0	0	0	1	0	1	-	0	-	0	0	0	0	-	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0
Austrocoenia aczeli	3	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	-	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Coenia palustris	3	1	1	0	0	1	0	0	1	-	0	0	1	0	-	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Ephydra riparia	3	1	0	0	0	1	0	0	1	-	0	0	1	1	0	1	0	0	0	-	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Ephydrella novaezealandiae	3	1	0	0	0	1	0	0	1	-	0	0	1	1	0	1	0	0	0	-	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Neoephydra araucaria	3	1	0	0	0	1	0	0	1	-	0	0	1	0	-	0	0	0	0	-	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Notiocoenia paniculata	3	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	-	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0
Paracoenia bisetosa	3	1	0	0	0	1	0	0	1	-	0	0	1	1	0	0	0	0	0	-	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0
Paraephydra freitasi	3	1	0	0	0	1	0	0	1	-	0	0	0	0	-	*	0	0	0	-	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Setacera pacifica	3	1	0	0	0	1	0	0	1	-	0	0	1	0	-	0	0	0	0	-	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0
Amalopteryx maritima	2	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	-	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Haloscatella arichaeta	2	0	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	-	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1
Haloscatella muria	2	0	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Haloscatella karekare	2	0	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	1	1	0	1	2	0	1	0	1	0	0	1	1	0	0	0	1
Haloscatella salinaria	2	0	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Lamproscatella sibilans	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Lamproscatella bimaculata	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Lamproscatella brunipennis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Lamproscatella mirabilis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Lamproscatella occidentalis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Lamproscatella unipunctata	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1
Limnellia maculipennis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	1	0
Limnellia anna	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	1	0
Limnellia huachuca	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	1	0

Table V. Continuation. [-] characters not applied; [*] polymorphisms.

Taxon	Abdomen																																				
	07	07	07	07	07	07	07	07	07	08	08	08	08	08	08	08	08	08	08	09	09	09	09	09	09	09	09	09	09	10	10	10	10	10	10	10
	01	02	03	04	05	06	07	08	09	00	01	02	03	04	05	06	07	08	09	00	01	02	03	04	05	06	07	08	09	00	01	02	03	04	05	06
***Hyadina* sp.**	2	0	0	0	0	0	1	2	0	1	0	0	0	0	1	0	-	0	1	1	2	0	0	1	-	0	1	0	0	0	1	-	0	1	-	-
Ilythea spilota	2	0	0	0	0	2	1	2	0	1	0	0	0	0	1	0	-	0	0	1	2	0	0	1	-	0	1	0	0	0	1	-	0	1	-	-
Philygria longipennis	2	0	0	0	0	2	1	2	0	1	0	0	0	0	1	0	-	0	0	1	2	0	0	1	-	0	1	0	0	0	1	-	0	1	-	-
Parydra aquila	0	0	0	0	0	0	1	2	0	1	0	0	1	0	1	0	-	0	0	0	-	1	0	1	-	0	1	0	0	0	0	0	0	0	1	0
Dagus rostratus	2	0	0	0	0	1	1	2	1	0	0	0	2	0	1	0	-	0	0	0	-	0	0	1	-	0	1	0	0	0	0	0	0	0	0	0
Brachydeutera neotropica	2	0	0	0	0	1	1	2	1	0	0	0	0	0	1	0	-	1	-	0	-	1	0	1	-	0	1	0	0	0	-	-	-	0	0	0
Diedrops steineri	1	0	0	0	0	1	1	1	0	1	0	0	5	0	1	0	-	0	0	0	-	0	0	1	-	0	1	0	0	0	0	0	0	0	0	0
Physemops nemorosus	1	0	0	0	1	-	1	2	0	0	0	1	1	0	1	0	-	0	0	0	-	0	0	1	-	0	1	0	0	0	1	-	0	0	0	0
Austrocoenia aczeli	1	0	0	0	0	0	1	2	0	1	0	0	0	0	1	0	-	0	1	0	-	0	0	1	-	0	1	0	0	1	0	0	0	0	0	0
Coenia palustris	1	0	1	0	1	-	1	1	0	0	0	0	2	0	1	0	-	0	0	0	-	1	1	1	-	0	0	1	0	0	0	0	1	0	0	0
Ephydra riparia	2	0	1	1	1	-	1	0	1	0	0	0	2	0	1	0	-	0	0	0	-	0	0	1	-	0	0	1	0	0	0	0	1	0	0	0
Ephydrella novaezealandiae	2	0	1	0	0	0	0	1	0	1	0	0	4	0	1	0	-	0	0	0	-	0	0	1	-	0	0	1	0	0	0	0	1	0	0	0
Neoephydra araucaria	2	0	1	0	0	0	1	0	1	1	0	0	2	0	1	0	-	0	0	0	-	0	1	1	-	0	0	1	0	0	0	0	1	0	0	0
Notiocoenia paniculata	2	0	0	0	1	-	1	2	0	0	0	0	2	0	1	0	-	0	0	0	-	0	0	1	-	0	1	0	0	0	0	0	0	0	0	1
Paracoenia bisetosa	1	0	1	1	1	-	0	1	0	1	0	0	2	0	1	0	-	0	0	0	-	1	1	1	-	0	0	1	0	0	0	0	0	0	0	0
Paraephydra freitasi	2	0	1	0	1	-	1	1	1	0	0	0	2	0	1	0	-	0	0	0	-	0	0	1	-	0	0	1	0	0	0	0	1	1	-	-
Setacera pacifica	2	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	-	0	0	0	-	0	0	1	-	0	1	0	0	0	0	0	1	0	0	0
Amalopteryx maritima	1	0	0	0	0	0	1	2	0	1	0	0	3	0	1	0	-	0	1	0	-	1	1	0	0	0	1	2	0	0	0	0	0	-	-	-
Haloscatella arichaeta	1	0	0	0	1	-	1	0	0	0	0	0	3	0	1	0	-	0	0	0	-	0	0	0	1	0	1	0	0	0	0	0	0	1	-	-
Haloscatella muria	1	0	0	0	1	-	1	1	0	0	0	0	3	0	1	0	-	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	-	-
Haloscatella karekare	1	0	0	0	1	-	1	2	0	0	0	0	3	1	1	0	-	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	-	-
Haloscatella salinaria	1	0	0	0	1	-	1	1	0	0	0	0	3	0	1	0	-	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	-	-
Lamproscatella sibilans	1	0	0	0	0	0	1	2	0	1	0	0	4	0	1	0	-	0	0	0	-	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Lamproscatella bimaculata	1	0	0	0	1	0	1	2	0	1	0	1	3	0	1	0	-	0	0	0	-	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Lamproscatella brunipennis	1	0	0	0	0	0	1	2	0	1	0	0	4	0	1	0	-	0	0	0	-	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Lamproscatella mirabilis	1	0	0	0	0	0	1	2	0	1	0	0	4	0	1	0	-	0	0	0	-	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Lamproscatella occidentalis	1	0	0	0	0	0	1	2	0	1	0	0	4	0	1	0	-	0	0	0	-	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Lamproscatella unipunctata	1	0	0	0	0	0	1	2	0	1	0	0	2	0	1	0	-	0	0	0	-	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Limnellia maculipennis	1	0	0	0	1	-	1	0	0	1	0	0	3	0	1	0	-	0	1	0	-	0	0	0	1	0	1	0	0	0	0	1	0	1	-	-
Limnellia anna	1	0	0	0	1	-	1	0	0	1	0	0	3	0	1	0	-	0	1	0	-	0	0	0	1	0	1	0	0	0	0	1	0	1	-	-
Limnellia huachuca	1	0	0	0	1	-	1	0	0	1	0	0	3	0	1	0	-	0	1	0	-	0	0	0	1	0	1	0	0	0	0	1	0	1	-	-

Table V. Continuation. [-] characters not applied.

Taxon	Head																																Thorax		
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Limnellia sejuncta	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Limnellia stenhammari	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Philotelma nigripennis	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	1	1	1	0	0	0	0	0	1	1
Philotelma rossi	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	1	1	1	0	0	0	0	0	1	1
Scatella (Apulvillus) bronneci	0	1	0	0	1	1	2	1	2	0	0	0	0	0	1	0	1	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	0
Scatella (Apulvillus) cheesmanae	0	1	0	0	1	1	2	1	2	0	0	0	0	0	1	0	1	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	0
Scatella (Apulvillus) williamsi	0	1	0	0	1	1	2	1	1	0	0	0	0	0	1	0	1	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	0
Scatella (Neoscatella) atra	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	1
Scatella (Neoscatella) austrina	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	1
Scatella (Neoscatella) bicolor	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	1
Scatella (Neoscatella) immaculata	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	1	1	1	0	1	0	1	0	1	1
Scatella (Parascatella) pilifera	0	1	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	0	0	1	1
Scatella (Parascatella) spangleri	0	1	0	0	0	1	1	0	2	0	0	0	0	0	1	0	0	2	1	0	2	0	0	0	0	1	1	1	0	1	0	0	0	1	1
Scatella (Parascatella) penai	0	1	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	0	0	1	1
Scatella (Parascatella) semipolita	0	1	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	0	0	1	1
Scatella (Scatella) stagnalis	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	0
Scatella (Scatella) minima	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	1	1	1	0	1	0	1	0	1	0
Scatella (Scatella) paludum	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	0
Scatella (Scatella) triseta	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	1	1	1	1	0	1	0	1	0	1	1
Scatella (Scatella) savegre	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	1
Scatella (Scatella) tenuicosta	0	1	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0	1	0	1	0	1	0
Scatella (Synhoplos) sturdeeana	1	1	1	0	0	1	2	0	2	1	0	0	1	0	1	0	0	2	1	0	2	0	0	0	2	1	1	1	0	1	0	0	0	1	1
Scatella (Synhoplos) neglecta	1	1	1	0	0	1	2	0	2	1	0	0	1	0	1	0	0	2	1	0	2	0	0	0	2	1	1	1	0	1	0	0	0	1	1
Scatella (Teichomyza) fusca	0	1	1	0	0	1	2	0	2	0	0	0	0	0	1	0	0	2	1	0	2	0	0	0	1	1	1	1	0	1	0	0	0	1	0
Scatophila caviceps	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Scatophila avida	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0
Scatophila despecta	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	1	0
Scatophila exilis	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Scatophila mesogramma	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	2	1	1	1	0	0	0	0	0	1	0
Scatophila noctula	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0
Scatophila unicornis	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	2	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0

Table V. Continuation. [-] characters not applied.

Taxon	Thorax																																	Abm	
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7
	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Limnellia sejuncta	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	1	0
Limnellia stenhammari	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	1	0
Philotelma nigripennis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	2	1	1	0	1	0	0	1	1	0	0	1	0
Philotelma rossi	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	2	1	1	0	1	0	0	1	1	0	0	1	0
Scatella (Apulvillus) bronneci	2	0	1	0	0	0	0	0	1	-	1	0	0	0	-	0	0	0	0	-	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0
Scatella (Apulvillus) cheesmanae	2	0	1	0	0	0	0	0	0	1	1	0	0	0	-	0	0	0	0	-	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0
Scatella (Apulvillus) williamsi	2	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Neoscatella) atra	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Neoscatella) austrina	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Neoscatella) bicolor	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Neoscatella) immaculata	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Parascatella) pilifera	2	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Scatella (Parascatella) spangleri	2	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Scatella (Parascatella) penai	2	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0
Scatella (Parascatella) semipolita	2	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0
Scatella (Scatella) stagnalis	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Scatella (Scatella) minima	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	2	0	1	-	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Scatella (Scatella) paludum	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Scatella (Scatella) triseta	2	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Scatella (Scatella) savegre	2	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Scatella (Scatella) tenuicosta	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Scatella (Synhoplos) sturdeeana	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Synhoplos) neglecta	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Scatella (Teichomyza) fusca	2	0	1	0	0	0	0	0	1	-	1	0	0	0	0	0	0	0	0	-	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila caviceps	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0
Scatophila avida	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0
Scatophila despecta	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0
Scatophila exilis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0
Scatophila mesogramma	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	0	1	0	0	0	0
Scatophila noctula	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	1	0
Scatophila unicornis	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0

Table V. Continuation. [-] characters not applied.

Taxon	Abdomen																																				
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Limnellia sejuncta	1	0	0	0	1	-	1	0	0	1	0	0	3	0	1	0	-	0	1	0	-	0	0	0	1	0	1	0	0	0	0	1	0	1	-	-
Limnellia stenhammari	1	0	0	0	1	-	1	0	0	1	0	0	3	0	1	0	-	0	1	0	-	0	0	0	1	0	1	0	0	0	0	1	0	1	-	-
Philotelma nigripennis	1	1	0	0	1	-	1	2	0	0	0	0	3	1	1	0	-	0	1	1	1	0	0	0	0	1	1	2	1	-	0	1	0	1	-	-
Philotelma rossi	1	1	0	0	1	-	1	2	0	0	0	0	3	1	1	0	-	0	1	1	1	0	0	0	0	1	1	2	1	-	0	1	0	1	-	-
Scatella (Apulvillus) bronneci	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Apulvillus) cheesmanae	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Apulvillus) williamsi	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Neoscatella) atra	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Neoscatella) austrina	0	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Neoscatella) bicolor	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Neoscatella) immaculata	0	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Parascatella) pilifera	2	0	0	0	0	0	1	0	0	1	1	0	3	0	1	1	1	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Scatella (Parascatella) spangleri	2	0	0	0	0	0	1	0	0	1	1	0	3	0	1	1	1	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Scatella (Parascatella) penai	2	0	0	0	0	0	1	0	0	1	1	0	3	0	1	1	1	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Scatella (Parascatella) semipolita	2	0	0	0	0	0	1	0	0	1	1	0	3	0	1	1	1	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Scatella (Scatella) stagnalis	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0
Scatella (Scatella) minima	2	0	0	0	0	0	1	1	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0
Scatella (Scatella) paludum	0	0	0	0	0	0	1	1	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Scatella) triseta	0	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0
Scatella (Scatella) savegre	0	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0
Scatella (Scatella) tenuicosta	2	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Synhoplos) sturdeeana	1	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Synhoplos) neglecta	1	0	0	0	0	0	1	2	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatella (Teichomyza) fusca	1	0	0	0	0	0	1	1	0	1	1	0	3	0	1	1	0	1	-	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Scatophila caviceps	1	0	0	0	1	-	1	2	0	0	0	0	3	0	0	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila avida	1	0	0	0	1	-	1	2	0	0	0	1	3	0	1	0	-	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila despecta	1	0	0	0	1	-	1	2	0	0	0	1	3	0	1	0	-	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila exilis	1	0	0	0	1	-	1	2	0	0	0	0	3	0	1	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila mesogramma	1	0	0	0	1	-	1	2	0	0	0	0	3	0	0	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila noctula	1	0	0	0	1	-	1	2	0	0	0	0	3	0	0	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Scatophila unicornis	1	0	0	0	1	-	1	2	0	0	0	0	3	0	0	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0

Table V. Continuation. [-] characters not applied.

Taxon	Head																															Thorax		
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Scatophila ordinaria	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	0	0	1	1	0
Scatophila prainha	0	1	0	0	1	0	2	0	1	0	0	0	0	0	1	0	0	1	1	0	2	0	0	0	2	1	1	1	0	0	0	0	0	1	0
Scatophila quadriguttata	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	0	0	1	1	0
Thinoscatella lattini	0	1	0	0	0	1	2	0	1	0	0	0	1	0	1	0	0	0	1	0	2	1	0	1	1	1	1	1	0	1	0	1	0	1	1
Thinoscatella quadrisetosa	0	1	0	0	0	1	2	0	1	0	0	0	1	0	1	0	0	0	1	0	2	1	0	1	1	1	1	1	0	1	0	1	0	1	1

Taxon	Thorax																																Abm	
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	7
	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Scatophila ordinaria	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0
Scatophila prainha	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	0	1	0	0	0	0
Scatophila quadriguttata	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	2	0	1	0	1	0	0	1	1	0	0	0	0
Thinoscatella lattini	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0
Thinoscatella quadrisetosa	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0

Taxon	Abdomen																																				
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	
Scatophila ordinaria	1	0	0	0	1	-	1	2	0	0	0	0	3	0	1	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	
Scatophila prainha	1	0	0	0	1	-	1	2	0	0	0	1	3	0	1	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	
Scatophila quadriguttata	1	0	0	0	1	-	1	2	0	0	0	0	3	0	0	0	-	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	
Thinoscatella lattini	1	0	0	0	0	0	1	2	0	1	1	0	2	0	1	0	-	0	0	0	-	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	
Thinoscatella quadrisetosa	1	0	0	0	0	0	1	2	0	1	1	0	2	0	1	0	-	0	0	0	-	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	

Table V. Continuation. [-] characters not applied.

Specimens Examined

Ilythea spilota

UNITED STATES. West Virginia: Hardy Co. Lost River St. Park, 20 Jun 2007, D. & Wayne N. Mathis (2♂, 2♀; USNM).

Hyadina sp.

BRAZIL. Parana: Curitiba. Universidade Federal do Paraná, Reserva Biológica (25°26.9'S, 49°14'W; 915 m), 9 Dec-5 Nov 2009, 2010, D. and W. N. Mathis (2♂, 2♀; DZUPM).

Philygria longipennis

BRAZIL. Parana: Castro (8 km N; 24°45.3'S, 49°58.9'W; 1010 m), 25 Dec-1 Jan-4 Apr 2010, D. and W. N. Mathis (2♂, 2♀; DZUP).

Parydra aquila

UNITED STATES. Ohio: Ashtabula Co. Pymatuning Lake S. P. (41º34.8'N, 81º31.9'W), 13 Sept 1976, B. A. Stanley (2♂, 2♀; USNM).

Dagus rostratus

ST. VINCENT. Charlotte: South Rivers (13º14.6'N, 61º09.3'W), 8 Sept 1997, Wayne N. Mathis (1♂, 2♀; USNM). DOMINICA. Clarke Hall, Cocoa Trail, 16 Jan 1965, W. W. Wirth (2♂; USNM).

Brachydeutera neotropica

BRAZIL. Parana: Curitiba. Universidade Federal do Paraná, Reserva Biológica (25°26.9'S, 49°14'W; 915 m), 9 Dec-5 Nov 2009, 2010, D. and W. N. Mathis (2♂, 2♀; DZUP).

Diedrops steineri

COSTA RICA. Cartago Prov: Pejibaye, 24 March 1987, W. E. Steiner, J. M. Mill, S. E. Frye (2♂, 2♀; USNM).

Physemops nemorosus

PERU. Madre de Dios: Manu, Erika (near Salvacion), 550 m, 5-6 Sept 1988, W. N. Mathis (3♂, 3♀; USNM).

Austrocoenia aczeli

Paratype: ARGENTINA. Santa Cruz: Cabo Buen Tiempo Gallegos (51°34'S, 69°05'W), 29 Feb 1953, Biraben (2♂, 2♀; USNM).

Coenia palustris

FINLAND. Helsinki, 16 May 1956, R. Dahl (2♂, 1♀; USNM).

Ephydra riparia

UNITED STATES. Ohio: Wayne Country, Rittman Salt Works (40º58.1'N, 81º46.4'W), 17 Jul 1976, 30 Jun 1977, B. A. Steinly (4♂, 4♀; USNM).

Ephydrella novaezealandiae

NEW ZEALAND. N. Isl. ND: Whananaki South (35°31.1'S, 174°27.2'E), 6-8 Oct 2002, D. and W.N. Mathis (3♂, 2♀; USNM).

Neoephydra araucaria

Paratype: CHILE. Orsono: Anticura (4 km W; 37°40'S, 72°01'W; 400 m), 3 Feb 1978, W. N. Mathis (2♂, 3♀; USNM).

Notiocoenia paniculata

Paratype: CHILE. Osorno Prov: Termas de Aguas Calientes (1 km SE; 40°41'S, 72°21'W; 530 m), 7–8 Feb. 1978, W.N.Mathis (2♂, 3♀; USNM).

Paraephydra freitasi

PERU. Lima: Lima, Lagunas de Villa (12°03.3'S, 77°03'W), 14 Feb 1984, W. N. Mathis (2♂, 2♀; USNM).

Paracoenia bisetosa

UNITED STATES. Oregon: Lake Co. Summer Lake, 25 Sept 1971, Wayne N. Mathis (3♂, 12♀; USNM).

Setacera pacifica

UNITED STARES. Utah: Utah County, Goshen Pond, 1 Feb-27 Apr, 1968-1969, W. N. Mathis (3♂, 2♀; USNM).

Amalopteryx maritima

FRANCE. French Southern and Antarctic Lands: Kerguelen Island (49°15′ S, 69°10′ E), May 1952, Aubrey La Rue (12♂, 8♀; USNM).

Haloscatella arichaeta

Holotype male: UNITED STATES. Washington: Grant Country, Soap Lake, 5 Aug 1973, Wayne Mathis (USNM). Paratypes: (2♂, 2♀; USNM) from the same locality data as the holotype.

Haloscatella karekare

Paratype: NEW ZEALAND. N. Isl. AK: Karekare (37°00.2'S, 174°28.8'E), 10 October 2002, D. and W.N. Mathis. (17♂', 14♀; USNM).

Haloscatella muria

Paratype: UNITED STATES. Colorado: Archuleta Co., Pagosa Springs, 27 May 1969, W. W. Wirth (1♂; USNM); Nebraska: Cherry Co., Big Alkali Lake, 2 Jun 1969, W. W. Wirth (1♀; USNM); Snake River, 2 June 1969, W. W. Wirth (1♂, USNM); Twin Lake, 2 Jun 1969, W. W.Wirth (5♂, 4♀; USNM).

Haloscatella salinaria

Paratype: UNITED STATES. California: San Berna. Co., Salt Wells, 30 Mar 1951, P. D. Hurd (4♂, 5♀). Trona, 31 Mar 1951, 31 Mar 1953, P. D. Hurd, J. C. MacSwain, A.H. Sturtevant (8♂, 7♀; USNM).

Lamproscatella bimaculata

UNITED STATES. Washington: Pierce Co. Mt. Rainier, Berkeley Park, 23 Aug 1934 (1♂; USNM); Mt. Rainier, Paradise Park, Aug 1917, A. L. Melander (1♂*;* USNM). Mt. Rainier, Yakima Park, 14-19 Aug, 1934-1940, A. L. Melander (2♂*;* USNM). Oregon: Harney Co., 29 Jun 1953, A. B. Gurney (5♂, 3♀ ; USNM).

Lamproscatella brunnipennis

CANADA. Manitoba: Churchill, 2-9 Aug, 1937, D. G. Denning, (2♂, 2♀; USNM). Yukon Territory: Herschell I., 20 July 1930, O. Bryant, (2♂, 7♀; USNM). Shingle Point, Mackenzie River, 29 Aug 1929, O. Bryant (1♀; USNM).

Lamproscatella mirabilis

UGANDA. Kigezi Province: Mt. Muhavura (ex. Senecio alticola; 3960 m), Nov 1934, J. Ford (1♂, 2♀ USNM). Mt. Muhavura (4115 m), Nov 1934, J. Ford (5♂ 8♀; USNM). Mt. Sabinio (3350-3505 m), Nov 1934, J. Ford (2♂; USNM). Lake Mutanda (1825 m), 20 Nov 1934, J. Ford (4♀ USNM).

Lamproscatella occidentalis

Paratype: UNITED STATES. New Mexico: Rabbit Mtn. Sandoval Co., 25 May 1969, W. W. Wirth (2♂, 7♀; USNM).

Lamproscatella sibilans

NORWAY. Finnm., Lakselv, 5 Aug 1975, Erling Olafsson (1♂, 2♀; USNM). Alacsony Tátra, Mala Vapenica, 21 Jul 1964, Hovartovich (1♂, 1♀; USNM). Thorsø, 20 mai 1922 (1♀; USMN) A. H. Sturtevant Collection.

SCOTLAND. Dunoon, July 1912, J.R. Malloch (2♂, 2♀, USNM). ENGLAND. Oxford, 18 Jun 1922 (1♀; USNM) A. H. Sturtevant Collection.

HOLLAND. Driebergen, 11 Jun 1922, A. H. Sturtevant Collection (3♂; USNM). Lunteren, 11 Jun 1922, A. H. Sturtevant Collection (3♀; USNM).

Lamproscatella sinica

Holotype and Paratype: CHINA. Szechuan Prov., Beh Luh Din, 30 mi N Chengtu 1-15 Apr 1935 (2♂, 5♀).

Limnellia anna

UNITED STATES. Maryland: Montgomery Co., Colesville, malaise trap, 15 Aug 1975, 26 Jun 1977, 3 Aug 1979, W. W. Wirth (1♂**, 2**♀ **;** USNM). Montgomery Co., 4 mi SW of Ashton, 18 July 1983, 12 Jun 2002, G. F. Hevel (2♂; USNM). Saint Louis Co., St. Louis, 2 mi W (1♀, USNM).

Limnellia huachuca

Paratype: UNITED STATES. Arizona: Cochise Co., Ramsey Cyn. 6000' 15 mi. S. Sierra Vista Huachuca Mts., 13 Apr-13 Aug 1967, Sternitsky (9♂, 9♀; USNM). Chiricahua Mts., 15 June 1951, 4000 ft. (1♂, 2♀, USNM).

Limnellia maculipennis

NEW ZEALAND. North Island. AK: Huia, George's Stream (bush), Waitakere, 2 Dec 1967, H. A. Oliver (1♀; USNM). WO: Hamilton, McKenzies Bush, Dinsdale (Malaise trap), 31 Oct 1970, H. A. Oliver (1♀; USNM).

Limnellia sejuncta

UNITED STATES. California: Berkeley, Aug 1915, Jun 1921, A. L. Melander (7♂, 7 ♀; USNM), Humboldt Co., Dyerville, 20 June 1935, A. L. Melander (1♀; USNM).

Limnellia stenhammari

CANADA. Northwest Territories: Aklavik, 4 Aug 1930, 16 Jun 1953, Bryant, JS Waterhouse (2♂, 2♀; USNM). Manitoba: Treesbank, 14 Oct 1915, ??? (1♂, 4♀; USNM).

UNITED STATES. Maryland: Plummer Island, 28 Oct 1914, 5 Apr 1914, R C Shannon (2♂, USNM). Alaska: Matanuska, 10-31 Mai 1944, JC Chamberlin (4♂, 8♀; USNM). Washington: Spokane Co., Deer Park (1♂, 1♀, USNM). Whitman Co., Pullman, 16 June 1912, 17 Oct 1915, ???, AL Melander Collection (2♀,USNM).

Philotelma defectum

UNITED STATES. North Dakota: Burleigh, Long Lake (46°41.5'N, 100°17'W), 4 Jun 1969, W. W. Wirth (1♂, 1♀; USNM). McHenry: Upham (6.5 km N; 48°34.9'N, 100°43.7'W), 5 Jun 1969, W. W. Wirth (1♀; USNM).

Philotelma nigripenne

POLAND. Lower Silesia: Wroclaw-Wojnów (51°06.1'N, 17°08.4'E; pond), 30 Jul 2004, D. & W. N. Mathis (1♀; USNM).

Philotelma parvum

POLAND. Upper Silesia: Wroclaw-Wojnów (51°06.2'N, 17º07.5'E*;* Oder River), 30 Ju1 2004, D. & W N. Mathis (2♀; USNM).

Philotelma rossii

ISRAEL. Hof Mineral (31°33'N, 35º24.8'E), 3 Feb 1998, A. Freidberg (1♂; USNM). 'Enot Zukim (31°42.7'N, 35º27.6'E), 22 Mar 1993, A. Freidberg (1♀;USNM).

Scatella (Apulvillus) bronneci

Paratype: FRANCE. French Polynesia. Uapou, Marquesas Is., Vaikokoo, Paaumea Valley, 26 Nov 1931, 2200 ft., LeBronnec (1♂; USNM).

Scatella (Apulvillus) cheesmanae

FRANCE. French Polynesia. Society Islands: Tahiti, Fautaua Valley, 3 March 1934, 300-700 meters; E. C. Zimmerman (1♂, 1♀. USNM).

Scatella (Apulvillus) williamsi

UNITED STATES. Hawaii: Hilo, Akaka Falls, March 1946, W. W. Wirth (2♀; USNM); NW of Hilo, 5 March 1946, W. W. Wirth (2♀; USNM).

Scatella (Neoscatella) atra

Paratype: FRANCE. French Polynesia: Marquesas islands, Atuona Valley, Hivaoa, 330 ft., 28 March 1929, Munford Adamson (3♂, 1♀; USNM). Fatu Hiva, Teaotu, Hanavave Valley 800 ft, 9 Sept 1930, LeBronnec (2♂, 2♀; USNM).

Scatella (Neoscatella) austrina

Paratype: AUSTRALIA. Potato Point: NSW 9.5 km E. of Bodalla, 20 July 1973, Z. Liepa (4♂, 2♀ USNM). Lake Curalo, Eden (nr. sandbar), 3 Aug 1973, Z. Liepa (1♂, USNM). Victoria: Lake Tyers (inlet, nr. sandbar), 5 Aug 1973, Z. Liepa (1♂, 1♀; USNM).

Scatella (Neoscatella) bicolor

Paratype: AUSTRALIA. New South Wales: Narrabeen. NSW Narrabeen Lagoon, 12 Oct 1956, W. W. Wirth (4♂, 3♀; USNM).

Scatella (Neoscatella) immaculata

AUSTRALIA. Northern Territory: 41 km S by E of Alice Springs, 4 Oct 1978, D. H. Colless (1♂, 3♀; USNM). Todd Riv., 9 km N by E Alice Springs, 10 Oct 1978, D. H. Colles (1♂, USNM). South Australia: 4.8 km NE. of Marree, 15 Sep 1972, Z. Liepa (1♂, 2♀; USNM). Queensland: Longreach, F. H. Taylor (2♀, USNM).

Scatella (Parascatella) pilífera

CHILE. Coquimbo: Hda Illapel, 800 m, 28 Oct 54, L. E. Peña (5 ♂, 3♀; USNM).

Scatella (Parascatella) semipolita

ARGENTINA. Jujuy: Suripujio, Oct 1968, L. E. Peña (1♂; MZUSP).

Scatella (Parascatella) penai

ARGENTINA. Jujuy: Suripujio, Oct 1968, L. E. Peña (1♂.1♀; MZUSP).

Scatella (Parascatella) spangleri

ECUADOR. Pinchincha: Santo Domingo (79.6 km. E.) 2545 m., 7 Jan 1978, W. N. Mathis (5 ♂, 3♀; USNM).

Scatella (Scatella) minima

CHILE. Juan Fernandez Island. Robson Cruzoe island, 28 jan 1992, 67 jan 1993, S. A. Marshall (2 ♂, 3♀; USNM).

Scatella (Scatella) paludum

UNITED STATES. California: Trinidad, 18 Sept 1934, A. L. Melander. Yosemite, 11 June 1935, AL Melander (1 ♂, 13♀; USNM).

Scatella (Scatella) savegre

COSTA RICA. San Jose: Río Savegre. San Gerardo de Dota (9°39.5'N, 83°51'W; 2.180 m). 29- 30 Jun 2001. W. N. Mathis (9♂, 8♀; USNM).

Scatella (Scatella) stagnalis

UNITED STATES. Ohio, Clark co. medway (39º52.4'N, 83º57'W) 5 Nov 1975; Washington Pierce co. Port of Tacoma, 3 Apr 1971, Wayne N. Mathis.
SWEEDLAND, Ostersund, 21, 22 Jul 1929 (Aldrich) (3♂, 2♀; USNM).

Scatella (Scatella) tenuicosta

UNITED STATES. Sussex: Indian rivinlet (38º36.9'N, 75º04.3'W), 17 may 2008, D. & W. Mathis (1♂; USNM). Va. Stafford: White oak (38º19.3'N, 77º24.1'W) 28 apr 2006), D. & W. Mathis (1♂, 2♀; USNM). Alaska, Mat-.Su Lucile lake (61º 34.2' N 149º 28.6'W), 15 aug 2012, D. & W. Mathis (1♂, 2♀; USNM).

Scatella (Scatella) triseta

UNITED STATES. Utah. Thompson springs (9km 39º2.3'N 109º43.4'W 1740m, 16 aug 2008, D. & W. Mathis (1♂, 2♀; USNM).

Scatella (Teichomyza) fusca

GEMANY. Saxony: Dresden, 12 Jan 1902, ??? (1♀; USNM).
PERU: Moquegua Province: Ilo, at light, 9 Aug, T. Cockerell (1♂; USNM).

Scatella (Synhoplos) neglecta

ARGENTINA. Tierra del Fuego: Isla de los estados, puerto Vancouver, 7-9 May 1971, OS Flint & GF Hevel (1♂; USNM). Bahia Blosson, 10 May 1971, OS Flint & GF Hevel (1♂; USNM). Bahia Colnett, 25 May 1971, OS Flint & GF Hevel (1♀; USNM).

Scatella (Synhoplos) sturdeeana

ARGENTINA. Tierra del Fuego: Bahia Blosson, 10 May 1971, OS Flint & GF Hevel (2♂, 1♀; USNM).

Scatophila avida

Paratype: ARGENTINA. Buenos Aires, 21 Dec 1926, (1♀; ANSP).

Scatophila caviceps

POLAND. Wroclaw, Wojnòw (51º06.2'N, 17º07.5'E), 30 Jun 2004 D. & W. Mathis (2♂, 2♀; USNM).

Scatophila despecta

UNITED STATES. Arizona: Chiricahua. Mts. Rustlers Pk., 7 Jun 1969, 8200 ft, Stephen L. Wood (2♂, 2♀; USNM). Oregon: Josephine Co, 2 mi W. Merlin, 13 May 1972, Wayne Mathis (1♂; USNM).

Scatophila dianneae

Holotype male: BRAZIL**.** Paraná: Curitiba, UFPR [Universidade Federal do Paraná, Reserva Biológica Mata Viva] (25°26.9'S, 49°14'W; 915 m), 28-31 Dec 2009, D. & W. N. Mathis.

Paratypes: BRAZIL. Santa Catarina: Nova Teutônia (27°11'S, 52°23'W; 3-500 m), Jun-Jul 1970, 1971, F. Plaumann *leg.* (1♂ ; MZUSP, USNM); São Bento do Sul 26°15.2'S, 49°22.8'W), 16-19 Oct 2001 (1♂; MZUSP).

Scatophila exilis

Paratype: UNITED STATES. Colorado: Boulder. W. E. Watkins (1♂; USNM).

Other specimens examinated: UNITED STATES. California: Pasadena, 7 March 1950, ??? (1♂; USNM).

MEXICO. Baja Califórnia: Santo Tomáz, 6 May 1950, Lindsley (1♂; USNM).

Scatophila mesogramma

UNITED STATES. Delaware. Rehoboth, 25 Jun 1939, A. L. Melander (1♂; USNM). Virginia. Accomack: Assentague Is. Toms Cove (37º53.1'N, 75º20.7'W) 16 Jun 2007, D. & W. Mathis (1♂, 1♀; USNM).

Scatophila noctula

SWITZERLAND. Valais: Leuk-Rotafen (46º18,4'N, 07º40.2'E, 650 m) 22 Jun 2004 D. & W. Mathis (1♂, 1♀; USNM).

Scatophila prainha

BRAZIL, Rio Grande do Sul: Torres (29°21'S, 49°44'W), Jun 1965, N. Papavero leg. (1♂; MZUSP). Tramandaí (Praia do Tramandaí; 29°56.5'S, 50°07.8'W), 20 May-1 Jul 2013, R.M. Carvalho, C. Ozorio leg. (1♂, 6♀; DZUP).

Scatophila quadriguttata

GERMANY. Steinfurt: Wersen, sandpit, 17 August 1996, W. Mathis (1♂, 1♀; USNM).

Scatophila unicornis

UNITED STATES. Califórnia. Pasadena, 21 -28 Mar 1950, (1♂, 1♀; USNM).

Scatophila ordinaria

Paratypes: UNITED STATES. Texas. Lake Austin, Travis Co. 31 Mar. 1953 (4♂, 5♀; AMNH).

Tauromima mountwilhelmi

Holotype: NEW GUINEA: Mt. Wilhelm, 6 Aug 1969, J. Balogh (1♂; HNHM – Photos from the holotype).

Thinoscatella lattini

UNITED STATES. California. Santa Cruz Co., Big Basin, 18 Jul 1954, A. L. Melander (4♂, 5♀; USNM).

Thinoscatella quadrisetosa

CANADA. Northwest Territories: Eskimo Point, 28 Jun-29 Jul, 1948-1950, J. R. Vockeroth, G. R. Roberts (4♂, 5♀; USNM).