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A new classification of *Ephydridae* based on phylogenetic reconstruction
(Diptera: Cyclorrhapha)

TADEUSZ ZATWARNICKI

Department of Zoology, University of Agriculture, Cybulskiego 20, 50-205 Wrocław, Poland

ABSTRACT. A phylogeny of shore flies based on the hypopygial structures is presented. Studies on shore-fly male genitalia indicate two main lineages. The segregation of *Discomyzinae* from *Gymnomyzinae*, and a new arrangement of taxa characterize the proposed classification. The following division of the *Ephydridae* into five subfamilies, and 20 tribes is adopted here: *Discomyzinae* (*Discomyzini*, *Psilopini*); *Hydrelliinae* (*Typopsilopini*, *Atissini*, *Hydrelliini*, *Notiphilini*, *Dryxini*); *Gymnomyzinae* (*Ochtherini*, *Discocerinini*, *Gastropini*, *Gymnomyzini*, *Hecamedini*, *Lipochaetini*); *Ilytheinae* (*Ilytheini*, *Hyadinini*, *Philygriini*), and *Ephydrinae* (*Parydrini*, *Dagini*, *Ephydrini*, *Scatellini*). A new tribe *Dryxini* is described. The subfamily *Halmopotinae* is synonymized with *Ephydrini*. The limits of the tribes *Discomyzini* and *Psilopini* are newly established. New placement for the tribes *Atissini*, *Gastropini*, *Ilytheini* and *Parydrini* is documented. The genus *Brachydeutera* is placed in *Dagini*, *Coenia* and *Notiocoenia* in *Ephydrini*.

Note

T. ZATWARNICKI's "A new classification..." would have probably won any contest for the most reviewed paper, had there been such a contest. Referees - official and unofficial - were seven. The range of opinions expressed was nearly as broad as the number of referees was high. The poor author was advised to: a) publish the paper as it was, b) introduce some minor improvements, c) make major changes, d) change his classification to a point where its authorship should rather be attributed to the referee, and e) not publish it at all. Some of the improvements proposed have been introduced in the ultimate manuscript (so says the author). Some of the referees' comments have been replied in the paper.

We could not resist the temptation of publishing such a controversial paper. The Readers are welcome to send their comments to the Genus.

Editorial Board

1. INTRODUCTION

The shore flies constitute a moderately large cyclorrhaphous family of shiny black or greyish microtomentose flies. About 1640 valid shore-flies species grouped in 118

genera described till the end of 1991 are distributed in all zoogeographic regions and most oceanic islands, except continental Antarctica. Their small or medium sized adults (body mostly 1.5-4.5 mm long, rarely up to 16 mm) are mostly microphagous or, rarely, predacious and can be collected in limnic environments close to developing places of larvae. The larvae live in a wide variety of habitats. The majority of species are aquatic or semi-aquatic algae feeders in fresh or brackish waters. A few inhabit such inhospitable habitats as alkaline and high-salinity waters, hot springs or crude oil pools. They are also leaf-miners of limnic emergent macrophytes, active predators and parasitoids of spiders and frog eggs. A large group of larvae are scavengers developing in decomposing organic matter, e.g. carcasses of small animals, carrion and faeces.

Only about a dozen species of shore flies were described as belonging to other dipterous families. Only two were so described after 1860. One is a species of *Paratissa* twice placed in the family *Drosophilidae*. It was proposed as a *Cacoxenus* and later as a *Drosophila*, because *Paratissa* is externally similar to the hypothetical ancestor of the superfamily *Ephydroidea*. This fact was overlooked by Ezra T. CRESSON Jr., and by subsequent workers, who constructed classifications of the *Ephydriidae*. The system of shore flies currently used begins with CRESSON (1922), and was constructed using simple similarities and differences. This resulted in an artificial classification, which was not based on objective reasons, and has only a historical value. It did not take into account the great biological and morphological variability within the shore flies. Despite the fact that many changes have occurred recently (see discussion in paragraph 4), the phylogenetic system of the shore flies has not been proposed as yet. Up to date only the subfamily *Ephydrinae* (MATHIS, 1979b) was analyzed cladistically. The subfamily is the most specialized in the family, therefore the studies did not influence the general system of the family.

The purpose of this paper is to demonstrate relationships within the family *Ephydriidae* based on synapotypic features that have been intensely analyzed during the last six years. The proposed classification resulted from discoveries of many new characters, especially those of the male terminalia, not directly depending on environmental pressure and complicated enough to avoid simple homoplasies. Characters of hypopygium were compared with those of external structures of adults, immature stages and bionomics. Since a world catalogue of the *Ephydriidae* is being prepared by Dr. Wayne N. MATHIS and myself and in the light of detailed phylogenetic studies on the *Psilopa*-like taxa, I felt this an opportune time to publish this phylogenetic interpretation of the shore-fly classification. Although the arrangement at the subfamilial level seems to be well understood, the confirmation of relationships between some tribes and their taxonomic positions require new, very broad and detailed studies.

2. THE LIMITS OF THE FAMILY

The limits of the family follow CHANDLER (1987), i.e. *Diastata* and *Nannodastinae* are excluded. Although most synapomorphies presented by CHANDLER (1987) that refer to *Ephydriidae* also apply to the family *Risidae*, the group is presently left outside

the shore flies and must await further studies. I disagree with McALPINE's (1989) statement that *Risidae* are closely related to the *Milichidae* and belong to *Carnoidea*. The black coloured *Risidae* with reduced setation are externally similar to *Gymnomyzini*. I have found male terminalia of *Risa* surprisingly similar to those of *Atissini* (s. str.). The dististyli are fused distally, the aedeagal apodeme is fused with the aedeagus, pregonite is lobate, situated closely to the proximal margin of hypandrium (erroneously described by PAPP (1980) as the sixth sternite, see also CHANDLER, 1987). The *Risidae* differ from the *Ephydridae* in having complete subcostal vein and reduced female cerci, but other characters seem to be autapomorphies, thus of no familial importance.

3. MATERIAL, METHODS, AND TERMINOLOGY

The phylogenetic analysis was based mostly on characters of the external and internal male terminalia of about 390 species of 104 genera which were dissected, examined, and illustrated. The structures of the male genitalia of another 8 genera belonging mostly to *Hyadinini*, *Ephydrinae* (including *Parydrini*), and *Beckeriella* (*Gastropini*) were based on literature data. Their examination, although some material was available to the author, was not relevant to this study, as the subfamilies *Ilytheinae* and *Ephydrinae* are very well recognized monophyletic groups with distinct synapotypes. Terminalia of the following monotypic genera, based mostly on single specimens, remain completely unknown: *Subpelignus* (*Atissini*), *Gymnopiella*, *Hoploaegis* (*Gymnomyzini*), *Parahyadina* (*Hyadinini*), and *Tauromima* (*Scatellini*). Two of the above genera were examined by the author, but the genitalia were not removed. In my opinion the lack of data on these five genera should not affect the proposed classification. On the other hand, six groups of *Discocerini* and *Discomyzinae* which should remain at the generic level, and representatives of seven still undescribed genera of four shore-fly subfamilies were included additionally in the analysis.

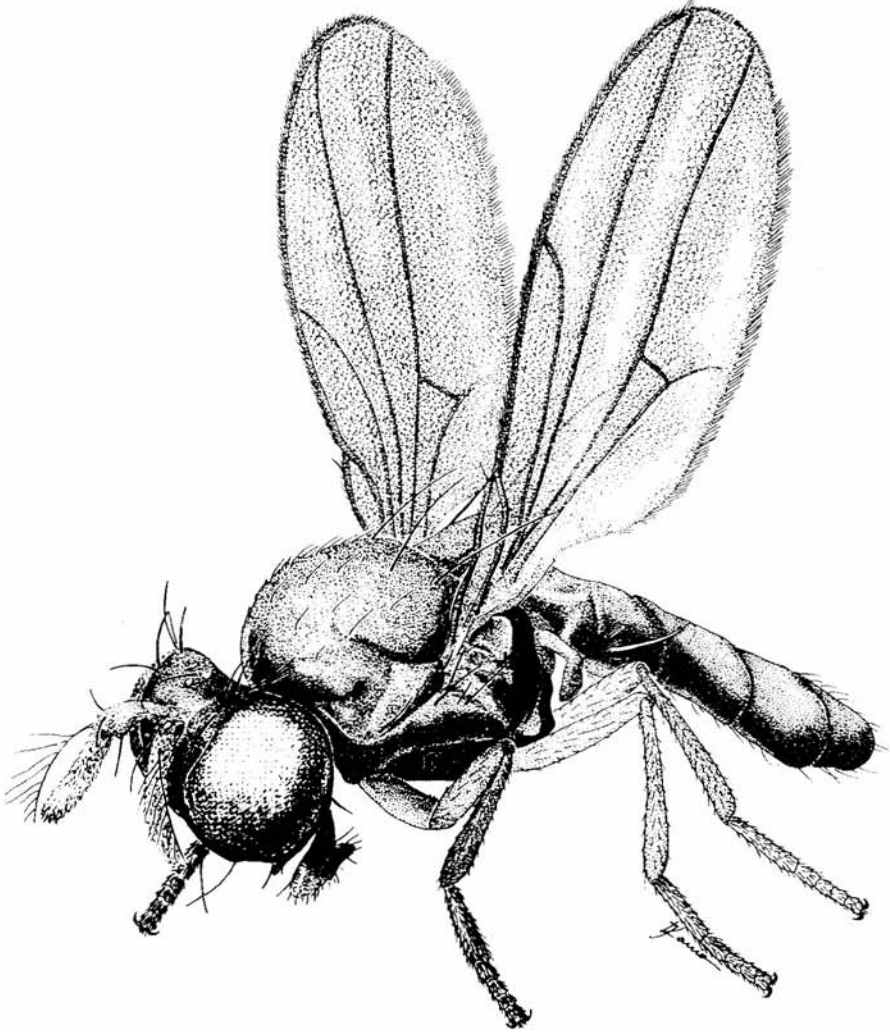
Specimens for this study were loaned from various European and North American museums. Most of the material came from the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, and also from the British Museum of Natural History, London, Great Britain; Zoological Museum in Copenhagen, Denmark; Zoological Institute in Lund, Sweden; and The Academy of Natural Sciences of Philadelphia, USA. The suprageneric nomenclature used in the paper was based on unpublished results of studies on the family-group names in *Diptera* by Dr. Curtis W. SABROSKY (USDA, Washington, USA).

The paper as 35 pages manuscript with 16 plates was initially prepared to publish in "Zeitschrift für zoologische Systematik und Evolutionsforschung", and copies were sent in December 1990 to Drs W. N. MATHIS, P. CHANDLER, L. PAPP, R. ZACK and Prof. B. FOOTE. The opinion of anonymous referee was negative, and he(he) and Dr. W. N. MATHIS suggested numerical analysis to support the cladogram. Although many remarks of the referee were to the point and thus considered in the present version of

the paper, I disagree with the necessity of numerical analysis in phylogenetic studies. In my opinion the crucial phase in the reconstruction of phylogeny by any method is the selection and polarization of characters used. The construction of a cladogram is a logical consequence of the previous step. Theoretically 20 taxa can produce 8140 trillions (quintillions in US measures) possible trees, but practically only a few are taken into consideration in analyses. The numerical analysis done by computer software (eg. Hennig 86) counts simple mathematical similarity among the objects having defined characters illustrated in the matrix. The objects of my analysis (the groups of genera) are different enough to construct the phylogeny by manual method. The principles used for the construction of the phylogenetic tree are those of cladistics (HENNIG, 1966): dichotomous cladogenesis in which both sister-groups are characterized by apotypies (or apomorphies, if they have morphological nature). Those characters which could be synapotypic for generic groups (tribe level) and thus support the relationships between taxa were selected and for each group its sister-group was investigated, which made the pair monophyletic. The greatest obstacle in this procedure was the presence of numerous homoplastic characters within most taxa; they could only be recognized by a detailed analysis of the group, its sister group, and the study of higher category taxa. The descriptive terminology of the external structures generally follows McALPINE (1981), but many alterations are proposed with respect to the male genitalia (see paragraph 5).

4. THE ORIGIN OF THE PRESENT CLASSIFICATION OF THE SHORE FLIES

The first suprageneric classification within the family was proposed by ROBINEAU-DESVOIDY (1830), who, based on the biology of the larvae, recognized two "tribus": the *Hydrellideae* and *Putrellideae* (the latter name unavailable). STENHAMMAR (1844) divided the shore flies into two unnamed tribes. One included the bizarre genus *Ochthera*, the other - the rest of the family. MATHIS (1991b) illustrated in detail the history of shore-fly classification at its initial phase. A suprageneric grouping using key characters was constructed by LOEW (1860) who divided the family into 3 "Zünfte": *Hydrellina*, *Notiphilina* and *Ephydrina*, an arrangement followed during the next 70 years. An important modification was postulated by HENDEL (1917) and consisted of the division of the family into two subfamilies: *Hydrelliinae* and *Ephydrinae*, but was not accepted by BECKER (1926), and other authors. In 1922-1930, Ezra T. CRESSON, Jr., an American entomologist, constructed his subfamilial system of the shore flies. CRESSON undoubtedly was acquainted with LOEW's classification. However, when his methods are analyzed, it seems that he ignored the existing systems, describing already named taxa as new, to grant them the new meaning. CRESSON (1922) first recognized the subfamily *Gymnopinae*, then the subfamily *Psilopinae* (CRESSON, 1925). In two subsequent papers CRESSON (1929 and 1930) defined the subfamilies *Notiphilinae*, and *Napaeinae* together with the *Ephydrinae* respectively. In 1942-1949 (last paper posthumous) CRESSON presented a system of tribes within the limits of his subfamilies. The subfamily *Psilopinae* was divided by CRESSON (1942) into four new tribes: *Atissini*, *Discocerinini* (barely mentioned



1. *Ceropsilopa cupreiventris* (VAN DER VULP) (*Psilopini*) from Sabaragamuwa, Sri Lanka. Habitus

earlier), and *Discomyzini*, and also supplied by the subfamily *Gymnopinae* lowered to the tribal rank. The composition of such a stabilized subfamily *Psilopinae* (= *Gymnomyzinae*) was used during the last fifty years. In 1943-1946 CRESSON rearranged the subfamily *Notiphilinae*, first separating the tribe *Ilytheini*, and then describing (or, precisely, defining the scope of) the tribes *Hydrelliini*, *Hydrinini* and *Notiphilini*. In a posthumous paper, CRESSON (1949) divided the subfamily *Napaeinae* into three tribes, *Napaeini*, *Gastropsini* [sic], and *Hyadinini*. The latter taxon was transcribed from CRESSON's notes and provided in square brackets by the editorial board of the "Trans. Am. Entom. Soc.". CRESSON's death prevented the presentation of his arrangement of the subfamily *Ephydrinae*. Apart from some superficial changes in the nomenclature of some taxa, CRESSON's system of four subfamilies has remained essentially intact for the last 40 years for most students. To continue CRESSON's work WIRTH and STONE (1956) divided the *Ephydrinae* into two tribes, the *Ephydrini* and *Scatellini*, and restored the *Lipochaetinae* as a tribe within the *Parydrinae*. MATHIS (1982) proposed the tribe *Dagini* within the *Ephydrinae*. FOOTE (1983) suggested that the *Philygriini* should be better placed in the subfamily *Ilytheinae* (his *Parydrinae*), than in the *Notiphilinae*. The tribe *Philygriini*, originally based on an invalid name (*Hydrina*), was first formally diagnosed by LIZARRALDE DE GROSSO (1989). MATHIS (1984) transferred the tribe *Lipochaetini* from the *Parydrinae* to the *Psilopinae*. The same was done with *Ochtherini* by MATHIS and ZATWARNICKI (1990), who also adopted in the family the name *Gymnomyzinae*, and transferred *Lemnaphila* from the *Philygriini* to the *Hydrelliini*. MATHIS (1991a) proposed the tribe *Hecamedini*, but I have suggested the creation of the tribe during the last phase of preparation of his paper, therefore it was done without an appropriate sister-group analysis.

The existing classification (at the end of 1991) can be summarized as follows (following CRESSON's arrangement; names used by him are given in parentheses):

Gymnomyzinae (= *Psilopinae*): *Gymnomyzini* (= *Gymnopini*), *Ochtherini*, *Atissini*, *Hecamedini*, *Lipochaetini*, *Discocerini*, *Psilopini*, *Discomyzini*.

Hydrelliinae (= *Notiphilinae*): *Typopsilopini*, *Hydrelliini*, *Notiphilini*, *Ilytheini*.

Hyadininae (= *Napaeinae*): *Philygriini* (= *Hydrinini*), *Hyadinini*, *Gastropini*, *Parydrini* (= *Napaeini*).

Ephydrinae: *Dagini*, *Ephydrini*, *Scatellini*.

The arrangement is much as that developed by CRESSON, but most taxa are still based on characters of uncertain value.

The second school of post-CRESSON classification could be characterized by recognizing the subfamilies for some aberrant genera. DAHL (1959) distinguished the *Ochtherinae*, and divided shore flies into six subfamilies (*Ephydrinae*, *Napaeinae*, *Ochtherinae*, *Hydrininae*, *Notiphilinae*, and *Psilopinae*). CANZONERI and MENEGHINI (1974) separated the genus *Halmopota* as a subfamily *Halmopotinae*, and in a faunistic treatment of Italian shore flies (1983), adopting DAHL's classification, they recognized 7 subfamilies of shore flies. Also the classification of MIYAGI (1977) was influenced by DAHL. Other shore-fly workers did not accept any of the proposals.

5. THE STRUCTURE OF THE MALE GENITALIA OF *EPHYDRIDAE*

The proposed classification has been based mostly on genital characters, which should be explained in greater detail. Several existing theories of the origin of the male copulatory apparatus in *Eremoneura* (*Orthogenya* and *Cyclorrhapha*) can be divided into two categories: surstyler-type, assuming that the surstyli are secondary structures, and dististylar-type, assuming a homology of dististyli with the epandrial appendices. Of all the theories HENNIG'S (1936) dististylar theory of the fusion of the epandrium with the gonocoxites is the most parsimonious, thus the term dististyli instead of surstyli is used. The dorsal hypopygial sclerite is called epandrium, in spite of its presumably different origin. The term periandrium (GRIFFITHS, 1972) is restricted to the sclerite which completely replaced the true epandrium. The true surstyli (epandrial appendices) could develop in those lineages in which the dististyli are reduced or primarily fused with the epandrium (*Discocerini*, *Ephydrinae*, some *Hecamedini*). In most cases (except *Limnellia*) there is no articulation between the surstyli and the epandrium (Fig. 95), contrary to its junction with the dististyli.

The shore-fly male terminalia evolved in two distinct ways, and their internal structures could not be homologized satisfactorily. In one cluster (*Discomyzinae* and *Hydrelliinae*) three pairs of internal appendices and internal plate forming an arch (Fig. 1) are documented for the first time in the family. The dististyli are divided, as presented by CHANDLER (1987) in the *Diastatidae*, and named inner and outer clasper. The neutral term "subepandrial plate" (= ventral epandrial plate of McALPINE, 1981), which does not suggest its unclear origin, is used for the internal arch situated between the cerci, dististyli, aedeagus, and gonites (Figs. 5, 8-9, 13-15, 31-32). The structure, which in the *Drosophilidae* is called "decasternum" (GRIMALDI, 1990), and not named by CHANDLER (1987) is very well developed in the *Diastatidae* (Fig. 3), but it is reduced in four specialized tribes of the *Hydrelliinae*. I do not agree with HENNIG (1976) that the subepandrial plate is homologous to the tenth sternite, and, consequently, I do not use the term "decasternum". The internal structures which are connected with hypandrium are pre- and postgonites (GRIMALDI, 1990 used the terms "gonopod" and "paraphysis" for *Drosophilidae*), and in the group they are very much reduced. The pregonite is elongate and situated between the tip of subepandrial plate and hypandrium, sometimes more ventrally (Figs. 10-11, 16, 29, 35). The postgonite is a small, more or less elongate appendix (it is equivalent to "paramere" of WIRTH et al., 1981), or a lobe mostly with 2-3 long setae situated ventrad to the tip of the pregonite (Figs. 14, 30, 39, 46).

The internal male terminalia of the second group (*Gymnomyzinae*, *Ilytheinae* and *Ephydrinae*) seem to be simple, and easily homologized with those of other cyclorrhaphan flies. The subepandrial plate has been lost, the pre- and postgonites are very well defined (Fig. 6). In most taxa they are fused to each other, and then called gonites (Figs. 64-65, 77-78). The elongate, mostly dorsally setose postgonite is situated slightly dorsoventrally on the lobe-like pregonite. One of the autapomorphic characters of the ephydriids mentioned by WIRTH et al. (1987) was the reduction of the ejaculatory

apodeme, which is not correct. The loose structure connected to the ejaculatory duct was correctly, although accidentally, recognized by WIRTH (1969) in *Mosillus*, though in most genera (with few exceptions of highly specialized taxa), the ejaculatory apodeme is very well visible (Figs. 70, 77-78, 81-82, 90-91). The apodeme is best developed in the genus *Scatella* (Figs. 93-94), as long sinuate band, but erroneously defined as an aedeagal apodeme (see WIRTH, 1947; MATHIS and SHEWELL, 1978).

6. CHARACTER ANALYSIS

Synapotypic characters accompanied by corresponding plesiotypies used in the cladistic analysis of the tribes of *Ephydridae* are explained below. The characters were polarized using *Diastata* (*Diastatidae*) for the out-group comparison. The reduced spermathecae in females and the presence of ventral receptacle define *Diastatidae* with the *Risidae* and *Ephydridae* as monophyletic group, but the *Diastatidae* do not belong to the *Ephydridae* and lack their synapomorphies (see characters no. 1-3 below). The most crucial plesiomorphies resulting from out-group analysis are: two postsutural dorsocentral setae well developed, subepandrial plate present, ejaculatory apodeme present, dististyli separated into two lobes, pre- and postgonites present. The numbers accompanying characters correspond with those used in the cladogram (Fig. 98). In addition to synapotypies I also present the features regarded as convergences (comments marked with an asterisk), whose status may be re-evaluated, if they turn out to result from affinity. Some modifications of characters in highly specialized taxa are also mentioned (marked with **).

1. Postocellar setae absent / Postocellar setae present.
2. Anal vein atrophied, hence anal cell absent / Anal vein and anal cell present.
3. Abdominal spiracles 2-5 included in tergites / Abdominal spiracles 2-5 situated in membrane.
4. Ejaculatory apodeme absent / Ejaculatory apodeme present.
*The presence of the ejaculatory apodeme in the sister group seems to be common, but this needs to be verified. Presumably, the reduction of the ejaculatory apodeme is parallel in the *Ochtherini*, some *Discocerinini*, *Dagini*, *Ephydrini*, and exceptionally in the genus *Scatophila* in the tribe *Scatellini*.
5. Pre- and postgonites poorly developed (Figs. 5, 10, 16, 35, 46) / Pre- and postgonites very well developed.
6. Clasper generally setose over whole surface / Clasper setose on dorsal and apical margin.
7. Face modified, carinate or projecting / Face broadly rounded or nearly flat.
*Face projecting also in some members of the sister-group: *Dryxini* (character no. 33), and some *Atissini*.
8. Subepandrial plate reduced / Subepandrial plate present.
*Subepandrial plate reduced in a sublineage *Notiphilini* + *Dryxini* (character no. 21) and the *Hydrellini* (character no. 28).

9. Clasper reduced, or not developed (Figs. 6, 73-74) / Clasper present.
10. Postsutural dorsocentral setae lacking / Postsutural dorsocentral setae present.
*Convergently postsutural dorsocentral setae reduced also in the *Gymno-myzinae* (character no. 37).
11. Bases of the dististyli joined or dististyli fused to each other (Figs. 33, 44, 48, 55) / Bases of the dististyli widely separate.
12. Presutural dorsocentral setae well developed / Presutural dorsocentral setae absent.
**In most *Atissini* and some highly specialized *Dryxini* the reduction of presutural dorsocentral setae is, in my opinion, secondary.
13. Stem of radial vein with 2-5 setulae dorsally / Stem of radial vein without setulae.
*I interpret the lack of the feature in *Guttipsilopa*, and *Rhysophora* as secondary.
14. Pseudopostocellar setae reduced / Pseudopostocellar setae present.
*Independently pseudopostocellar setae reduced in the *Lipochaetini* (character no. 71).
15. Pregonite elongate (Figs. 34-35) / Pregonite short.
16. Pre- and postgonites fused (Figs. 38-39, 45-46) / Pre- and postgonites widely separate.
17. Dististyli fused to each other / Dististyli widely separate, and not fused to each other.
18. Eye with short dense hairs / Eye bare.
*The eye is also hairy in the *Philygriini* (character no. 91).
19. Gonites lacking (Figs. 57-58, 84-85) / Gonites present.
20. Mid-tibia with three dorsal setae / Mid-tibia without dorsal setae.
21. Subepandrial plate reduced / Subepandrial plate present (see characters no. 8 and no. 28).
22. Aedeagal apodeme combined with aedeagus (Figs. 38-39, 42-43) / Aedeagal apodeme separated from aedeagus.
*The aedeagal apodeme is also fused with aedeagus in *Parydra* (*Chaetoap-naea*) (*Parydrini*), and *Discocerina* (*Discocerina*) (*Discocerinini*).
23. Gonites lobate and joined ventrally to each other (Figs. 38-39, 43) / Gonite elongate widely separated from each other.
24. Fronto-orbital setae in front of the line between ocellar setae / Fronto-orbital setae inserted posterior to the level of ocellar setae.
*The character developed convergently in the *Hecamedini* (character no. 66).
25. Posterior notopleural seta much further from notopleural suture than anterior seta / Posterior notopleural seta as far from the notopleural suture as anterior seta.
*The same position of the posterior notopleural seta is found in a sublineage *Hecamedini* + *Lipochaetini* and *Ilytheinae* (characters no. 60 and no. 77 respectively).
26. Hypandrium with posterolateral flattened appendices / Hypandrium posterolaterally without flattened appendices.

27. Clasper cone-shaped apically (Figs. 45-47) / Clasper broadly rounded.
28. Subepandrial plate reduced / Subepandrial plate present (see characters no. 8 and no. 21).
29. Ocellar setae rarely as strong as pseudopostocellar setae, usually much weaker / Ocellar setae as strong as pseudopostocellar setae.
30. Dististyli absent or fused indistinguishably with epandrium (Fig. 48) / Dististyli present.
 *Dististyli are also absent in the sublineage *Ilytheinae* + *Ephydrinae* (character no. 41), the *Discocerini* (character no. 49), and in some species of *Leptopsilopa* (*Psilopini*).
31. Supra-alar seta strong, longer than the posterior notopleural seta / Supra-alar seta small, weaker than the posterior notopleural seta.
32. Costal vein extended to the third radial vein / Costal vein extended to the first medial vein.
 *The feature is also found in *Axysta* (*Hyadinini*), *Brachydeutera* (*Dagini*), and *Scatophila* (*Scatellini*).
33. Face produced / Face broadly rounded or nearly flat (see character no. 7).
34. Three dorsocentral setae (one presutural) / Two dorsocentral setae.
35. Clasper bifurcate, incised-bent apically (Fig. 54, 57-58) / Clasper simply lobate.
36. Dorsoapical spine on pedicel weak / Dorsoapical spine on pedicel strong.
 *Spine on pedicel reduced also in the *Ochtherini* (character no. 51) and a sublineage *Gymnomyzini* + *Gastropini* (character no. 57).
37. Postsutural dorsocentral setae reduced / Postsutural dorsocentral setae present (see character no. 10).
38. Pregonite developed as a lobate sclerite, seen in the most primitive members of the tribes *Gastropini*, *Gymnomyzini* (e.g. *Athyroglossa*), and *Discocerini* (*Gymnoclasiopa*), or fused indistinguishably with postgonites (Figs. 61-63) / Pregonite crescentic in outline.
39. Gonites fused with hypandrium (Figs. 88-89, 93-94) / Gonites separated from hypandrium.
 **The ventral part of gonite with the lateral portions of hypandrium could be secondarily separated from the central portion of hypandrium, as in some *Parydra* (*Parydrini*), and in the *Philotelma*-group within the *Scatellini* (see ZATWARNICKI and BAÉZ, 1991).
40. Larvae microphagous feeding on algae / Larvae saprophagous, develop in decomposing organic matter.
41. Dististyli absent or fused indistinguishably with epandrium (Figs. 86-87, 92, 95) / Dististyli present (see characters no. 30 and no. 49).
42. Posterior transverse vein displaced anterior to the fusion of the first radial vein with the costa / Posterior transverse vein placed behind the fusion of the first radial vein with the costa.
43. Basal aedeagal opening directed dorsally (Figs. 89, 93-94) / Basal aedeagal opening directed proximally.

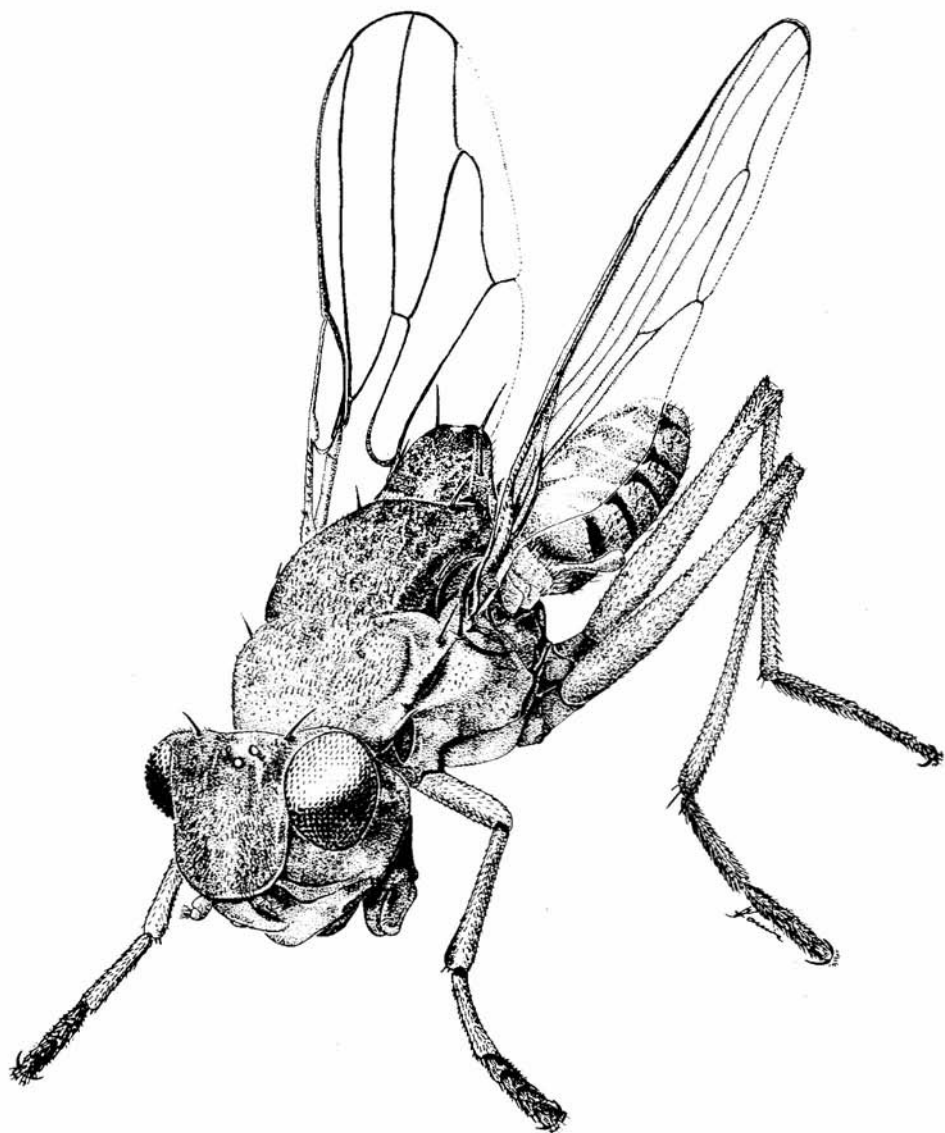
44. Posteroventral margin of dististyli extended under the anterior margin of epandrium (Figs. 71, 75, 79-80) / Posteroventral margin of dististyli situated anterior to, or level with the anterior margin of epandrium.
45. Clypeus protruding before the oral margin / Clypeus not exceeding the oral margin.
46. Prescutellar acrostichal setae small, inserted close together / Prescutellar acrostichal setae distinct, inserted far from each other.
47. Ocellar setae inserted anterior to the level of anterior ocellus / Ocellar setae inserted posterior to the level of anterior ocellus.
*The ocellar setae are similarly situated in the *Hecamedini* (character no. 67).
48. Pseudopostocellar setae proclinate, parallel or slightly divergent, moderately strong / Pseudopostocellar setae lateroclinated and strongly divergent.
49. Dististyli reduced or fused indistinguishably with epandrium (Fig. 67) / Dististyli present (see characters no. 30 and no. 41).
50. Dististyli well developed, elongate and undulating ventrally / Dististyli short, lobate and distally rounded.
51. Dorsoapical spine on pedicel weak / Dorsoapical spine on pedicel strong (see characters no. 36 and no. 57).
52. Forefemur greatly enlarged / Forefemur of typical shape.
53. Foretibia ending in a spur / Foretibia without spur.
54. Palpus apically broadened, spoon-like / Palpus elongated.
55. Anterior supra-alar, presutural alar, and post-pronotal setae lacking / Anterior supra-alar, presutural alar, and post-pronotal setae present.
56. Prescutellar acrostichal seta lacking / Prescutellar acrostichal seta present.
*Prescutellar acrostichal seta is also lacking in the sublineage *Hyadinini* + *Philygriini* (character no. 80).
57. Seta on the pedicel reduced / Seta on the pedicel present (see characters no. 36 and no. 51).
58. Upper half of face conspicuously swollen / Face slightly convex.
59. Pre- and postgonites fused, or reduced (Figs. 77-78, 81-82) / Pre- and postgonites separate.
60. Posterior notopleural seta much farther from notopleural suture than anterior seta / Posterior notopleural seta level with the anterior seta (see characters no. 25 and no. 77).
61. Posterior margin of gena acutely angulate and marginate / Posterior margin of gena rounded.
62. Postgena with fine pale setulae / Postgena without fine pale setulae.
63. Head in anterior view subtriangular / Head in front view oval.
64. Mesonotum and abdominal tergites covered by long hairs / Mesonotum and abdominal tergites bare, or covered by short hairs.
65. Larvae living in frog eggs / Larvae living in decomposing organic matter.
66. Fronto-orbital setae approximately aligned transversely with ocellar setae / Fronto-orbital setae inserted posterior to ocellar setae (see character no. 24).

67. Ocellar setae inserted anterior to the level of anterior ocellus / Ocellar setae inserted posterior to the level of anterior ocellus (see character no. 47).
68. Arista with 3-5 branching rays inserted toward arista base / Arista with 8-12 branching rays inserted along its dorsum.
69. Gonite reduced (Figs. 77-78, 81-82) / Gonite present.
70. Aedeagus with appendix folded back dorsally (Figs. 77-78, 81-82) / Aedeagus as a simple tube, and without appendix folded back dorsally.
71. Pseudopostocellar seta absent / Pseudopostocellar seta distinct (see character no. 14).
72. Ocellar seta absent or weak / Ocellar seta distinct.
73. Frontal vitta with many short hairs / Frontal vitta without hairs.
74. Arista microsetose, but without dorsal rays / Arista with 8-12 long branching rays.
75. Anterior spiracle in larva with two elongate branches / Anterior spiracle in larva cauliflower-shaped, with blunt, round-ending branches.
76. Extending process of ventral receptacle sinuate and lacking operculum / Extending process of ventral receptacle L-shaped with distinct operculum.
77. Posterior notopleural seta much farther from notopleural suture than the anterior seta / Posterior notopleural seta level with the anterior seta (see characters no. 25 and no. 60).
78. Face broadly projected anteriorly / Face slightly convex or flat.
79. Fronto-orbital setae latero-clinate / Fronto-orbital setae pro- and/or reclinate.
80. Anterior spiracle in larva with long finger-like branches or clavate / Anterior spiracle in larva without long finger-like branches and not clavate.
81. Proximal margin of gonite nearly flat or slightly rounded / Proximal margin of gonite concave forming posterodorsal appendix.
82. Prescutellar acrostichal setae lacking / Prescutellar acrostichal setae present (see character no. 56).
83. Gonite reduced, or fused indistinguishably with hypandrium / Gonite present.
84. Aedeagal apodeme in lateral view triangular with deep anterior incision (Figs. 84-85) / Aedeagal apodeme in lateral view hemispherical.
85. Four long, hair-like acrostichal setae present / Acrostichal setae short, serrate or not recognized among mesonotal setation.
86. Wing uniformly maculated with white and black spots / Wing transparent.
*A similar wing maculation occurs in some *Scatellini*.
87. Anterior notopleural seta absent / Anterior notopleural seta present.
88. Epandrium distally tapered / Epandrium distally round.
89. Gonite with reduced setulae (Figs. 90-91) / Gonite setose.
90. Long seta inserted at connection of gonite with hypandrium (Figs. 88-89) / Gonital arch without long setae.
91. Eye with short dense hairs / Eye bare (see character no. 18).
92. Subcranial cavity large and gaping / Subcranial cavity small.
93. Median facial area and lower facial margin setose / Median facial area and lower facial margin without setae.

94. Central part of gonital arch narrow, band-like / Central part of gonital arch forming broad sclerite homologous to hypandrium.
95. Face vertically arched, and extending ventrally, giving an appearance of a shield / Face transversely arched, oral opening large, sometimes gaping.
96. Katepisternal seta weak / Katepisternal seta well developed.
97. Anterior spiracle in larva clavate / Anterior spiracle in form of a few elongated branches.
98. Basal aedeagal opening modified: anterior margin thickened with a collar, or dorsally overlapping the opening, and forming an incision in the opening in lateral view (Figs. 93-94) / Basal aedeagal opening simple, situated in proximal end of aedeagus.
99. Gonite combined with aedeagal apodeme (Fig. 96) / Gonite separated from aedeagal apodeme.
100. Five dorsocentral setae / Three dorsocentral setae.
101. Proepisternum usually without macrosetae / Proepisternum with one or two macrosetae.

**This character is also present in the *Coenia*-group of the *Ephyrini* (*Coenia* and *Noticoenia*).

Discussion. Of 101 characters used in the analysis 3 support the monophyly of the family, 58 - the monophyly of 20 tribes, and the remaining 40 - the relationships among taxa. Twelve of the latter characters are a result of homoplasy. Another 14 homoplasies are used in the characteristics of tribes. The percentage of homoplasies in the total amount of derived characters is relatively high (about 26 percent), but only the *Psilopini* are based on a single homoplasy. In all the remaining cases there are also other apotypies, which support the monophyly of each taxon, and sister group relationships. The presence of ejaculatory apodeme in the family (character no. 4) needs further studies, but the distribution of other homoplasies, which constitute 11 kinds of homoplastic characters is clear (Fig. 99). Seven of them involve the position or reduction of appropriate setae. In many cases appearance of the same setation could be found in various lineages lacking other synapotypies. For example upturned posterior seta developed independently at least in three taxa (characters nos. 25, 60 and 77), because no other evidence corroborates their affinity. The *Discomyzinae* and *Gymnomyzinae* differ in nine characters, hence the absence of prescutellar seta (character no. 10) is considered to be a homoplasy. Another two homoplasies are also external. These are: the shape of face and vestiture of eyes. The protruding face could be a doubtful character since it developed not only in the *Gymnomyzinae* subfamily group (character no. 7) but also in taxa with clasper: *Dryxini* (character no. 33), some *Atissini*, and exceptionally slightly expressed in *Psilopini*. Hairy eyes seemingly link the *Philygrini* and a sublineage *Atissini*+*Hydrellini*. Only two homoplasies are connected with male terminalia. The representatives of three *Hydrelliinae* tribes lacking subepandrial plate, like in the *Gymnomyzinae* subfamily group (characters nos. 8, 21 and 28), but contrary to the latter lineage these tribes have other genital structures



2. *Dryxoisipoidea* ROB.-DESV. (*Dryxini*) from Kadaimparu, Sri Lanka. Habitus

(clasper or dististyli) typical for other taxa from the *Hydrelliinae* subfamily group. The reduction of dististyli in the *Discocerini* (character no. 49) is not of phylogenetic importance, since the tribe has two synapotypies which link it with the *Gymnomyzini*, but does not possess the five apotypies of the *Ilytheinae-Ephydrinae* lineage.

The proposed tree (Fig. 98) includes as few convergences as possible, and in my opinion is the most parsimonious. Both dr. Wayne N. MATHIS and the anonymous referee objected to the statement. It is simple to show that any change in the position of any taxon results in more homoplasies, and no computer is necessary to prove it. The placement of only four tribes is supported by 5 or less synapotypies accumulated from all levels of the tree (*Discomyzini* 4, *Psilopini* 4, *Discocerini* 5 and *Typopsilopini* 5), but the position of other tribes is supported by 7-14 such synapotypies. For example, if the tribe *Hyadinini* were placed in any position in the subfamily *Hydrelliinae*, the amount of homoplasies would increase to 12, and there would be 10 more homoplasies if the tribe were placed close to the *Gymnomyzini*. Two homoplasies (character no. 7 supplied with no. 24) suggest that the *Atissini* could belong to the *Gymnomyzinae*, but there are 8 other characters, which support their placement close to the *Hydrelliini*. If CRESSON's system is used (*Atissini* near the *Hecamedini*) there will be a disagreement of at least 14 synapotypies.

It is difficult for me to understand the extremes of scientist's opinions. MATHIS (1991b) mentioned that "Most tribes are monophyletic in a rigorous, cladistic sense ...", but the anonymous referee proposed that "... some postulated homoplasies suggest that all of the tribes studied may not be monophyletic in the sense of HENNIG". Both statements were postulated almost at same time and pertain to the same tribes, but the former is an opinion on previous, non-phylogenetic system, the latter is an evaluation of the presented classification. Because my comments on the matter could be subjective I leave conclusions to the Readers.

7. PHYLOGENY OF THE EPHYDRIDAE

Two distinct sister groups are indicated in the cladogram, but the more specialized lineage (the *Gymnomyzinae* subfamily group) could have originated from ancestors of the most generalized discomyzids, e.g. *Paratissa*-related genera. Both main assemblages are defined below:

The hydrelliine group of subfamilies: face flat, sometimes protruding antero-ventrally; postocellar seta present; dististyli divided in two parts; subepandrial plate present, well developed in form of a dorsal arch, or sometimes separated dorsally, presumably forming lateral plates; pre- and postgonite poorly developed, inconspicuous (Fig. 5); prescutellar seta well developed far from the scutellar margin; ejaculatory apodeme absent.

The gymnomyzine group of subfamilies: face with medial carina, or projecting, convex below antennae; postocellar seta absent; prescutellar setae small, or absent, and close to the margin of scutellum; dististylus, if present, not subdivided; subepandrial plate wholly reduced; pregonites occurring as small lateral lobes or fused with

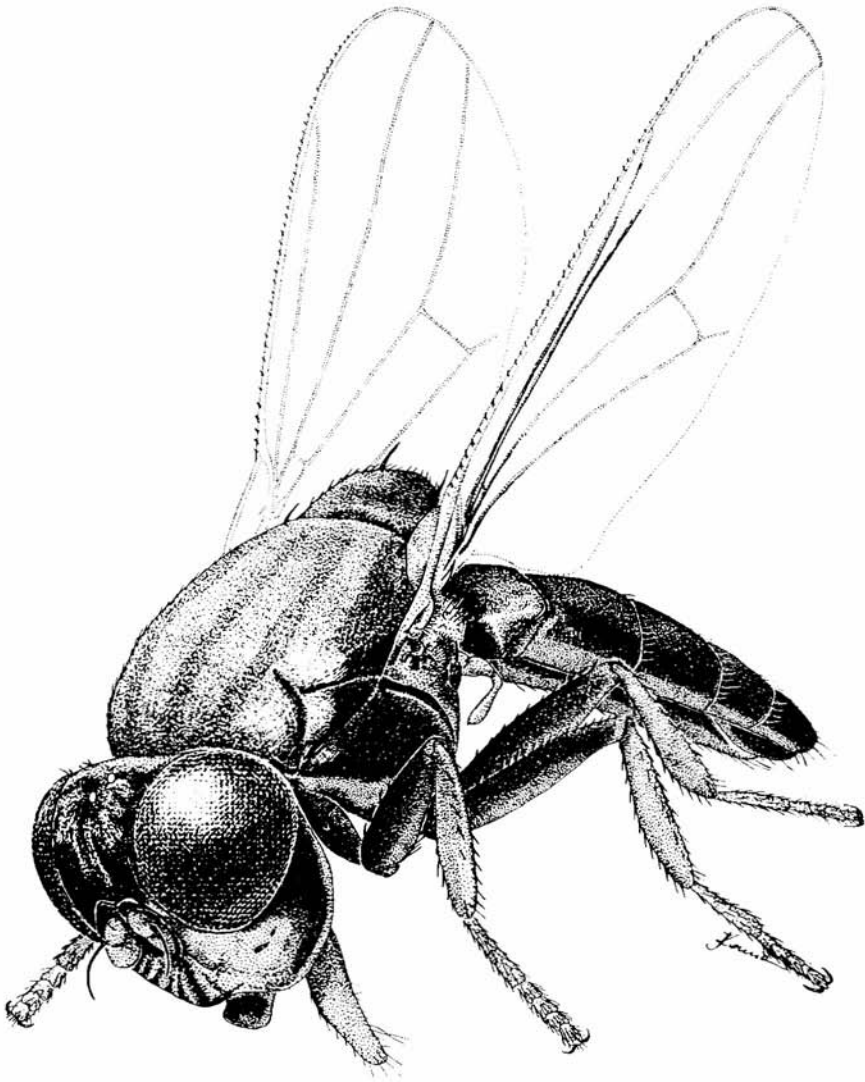
postgonite; postgonite elongate and weakly setulose, ejaculatory apodeme often present (Fig. 6).

The *Discomyzinae* having complicated genital structure (Figs. 10, 14, 35) with separate appendices (especially pre- and postgonites) are the most primitive in the first group. Their larvae are cylindrical in shape with short anterior spiracles and are saprophagous, developing in decaying organic matter. The *Hydrelliinae*, which constitute their more advanced sister group have retained dorsocentral setae, and genitalia in which the dististyli are fused. A prominent face, the presence of 3 dorsocentral setae, elongation of legs, and fusion of the dististyli with the epandrium and reduction of gonites in the male genitalia characterize their more derived lineages. The trend in biology goes from feeding on decaying plant tissue through miners within macrophyte tissue. The most specialized larvae have reduced anterior spiracles and spinose or elongated distal parts of body.

In the second group the tendencies toward projection of the face, simplification of the male terminalia, and multiplication of dorsocentral setae are similar, but developed in different ways. In the *Gymnomyzinae* the face is carinate, and the larvae are saprophagous with an inclination toward predation. The most primitive sublineage has developed dististyli that are situated in front of the epandrium, and separated pre- and postgonites (Figs. 61-63, 68-69). In the most advanced lines the base of the dististyli is displaced under the anterior margin of the epandrium, and elongate or indistinguishably fused with the epandrium (Figs. 86-87, 92). In the *Ilytheini* the gonites and claspers were lost (Figs. 84-85). The fusion of the gonites with the hypandrium (Figs. 88-91, 93-94, 96-97) and other synapomorphies (no. 58-61) make the *Ilytheinae* (= *Hyadininae*) with the *Ephydrinae* the most distinct monophyletic group within the shore flies. The microphagous larvae have elongated anterior spiracles and often a breathing tube. The face is generally carinate in the *Ilytheinae* and produced in the *Ephydrinae*. In the latter lineage the maculation of wing, and 3-5 dorsocentral setae are significant. In some *Ephydrini* the aedeagal apodeme is associated with the gonial arch, but the genital structure of *Scatella* is extremely simple, with the simple U-shaped epandrium tapered anteriorly, and the aedeagal apodeme is reduced.

8. PROPOSED CHANGES IN THE CLASSIFICATION

To follow the phylogeny, the shore flies are grouped into five subfamilies and 20 tribes (1 of them being new). The new classification differs from CRESSON's system, in which taxa were linearly ordered with the *Gymnomyzinae* at the beginning, by being branched and starting with the most generalized taxon (tribe *Discomyzini*). The first branch comprises the *Discomyzinae* with the sister group *Hydrelliinae*, and the second - more modified *Gymnomyzinae* with the specialized *Ilytheinae* + *Ephydrinae*. The *Discocerini* form an excellent intermediate group between both those taxa. The composition of the *Ephydrinae* is most similar to CRESSON's system, with only the *Parydrini* being added. The most different are the *Discomyzinae* (*Psilopinae* of



3. *Mosillus bidentatus* (CRESSON) (*Gymnomyzini*) from Soap Lake, Washington, USA. Habitus

CRESSON, 1925) from which *Discocerinini*, *Atissini*, *Hecamedini*, and some genera at present placed in the *Lipochaetini* are removed.

CRESSON's *Gymnomyzinae* were recognizable using external features that are mostly plesiomorphies. Only a few authors dealt with the relationships among the gymnomyzine genera. DAHL (1959), based on an analysis of the male terminalia of Scandinavian species, discovered that the genera of *Psilopinae* constituted a very heterogeneous assemblage. He suggested that the three tribes erected by E. T. CRESSON might be ranked as subfamilies, but made no formal changes. Another argument in support of the division is the fact that one sublineage within the *Gymnomyzinae* (in broad sense), namely *Psilopini* with *Discomyzini*, is more closely related to the subfamily *Hydrelliinae* than to the other tribes within the *Gymnomyzinae*. The tribe *Typopsilopini* is an intermediate group between the *Discomyzinae* and *Hydrelliinae*. It differs from the *Discomyzinae* only in possessing presutural dorsocentral setae, but on the other hand the border between the *Discomyzinae* and *Gymnomyzinae* is very sharp, without intermediate stages. Basing on those facts I recommend the division of the *Gymnomyzinae* LATREILLE, 1829, in their previous sense (= *Psilopinae* sensu CRESSON, 1942), into two subfamilies: *Gymnomyzinae* (s. str.), and *Discomyzinae*.

In my classification the tribes *Discomyzini* and *Psilopini* are sister-groups, both constitute the subfamily *Discomyzinae*. In CRESSON's system the tribe *Discomyzini* with two genera: *Clanoneurum* and *Discomyza* was morphologically highly specialized, distinguished by the reduced setation, and structure of face, but compared with the *Psilopini* they turn out to be paraphyletic. Many biological and morphological characters (e. g. larval feeding, shape of clasper and dististyli) support the opinion that other genera of the *Psilopini* are much closer related to *Discomyza* than is *Clanoneurum*. The characters purportedly shared by the two taxa are autapomorphies, and could have developed independently in both genera. The new synapomorphy I selected for the *Discomyzini* (stem of radial vein with 2-5 setulae dorsally) makes its meaning broader, therefore ten genera previously placed in the *Psilopini* were included. In the subfamily at least three genera were found to be polyphyletic, and the new generic synapomorphies have to be corroborated first, the present solution being only tentative.

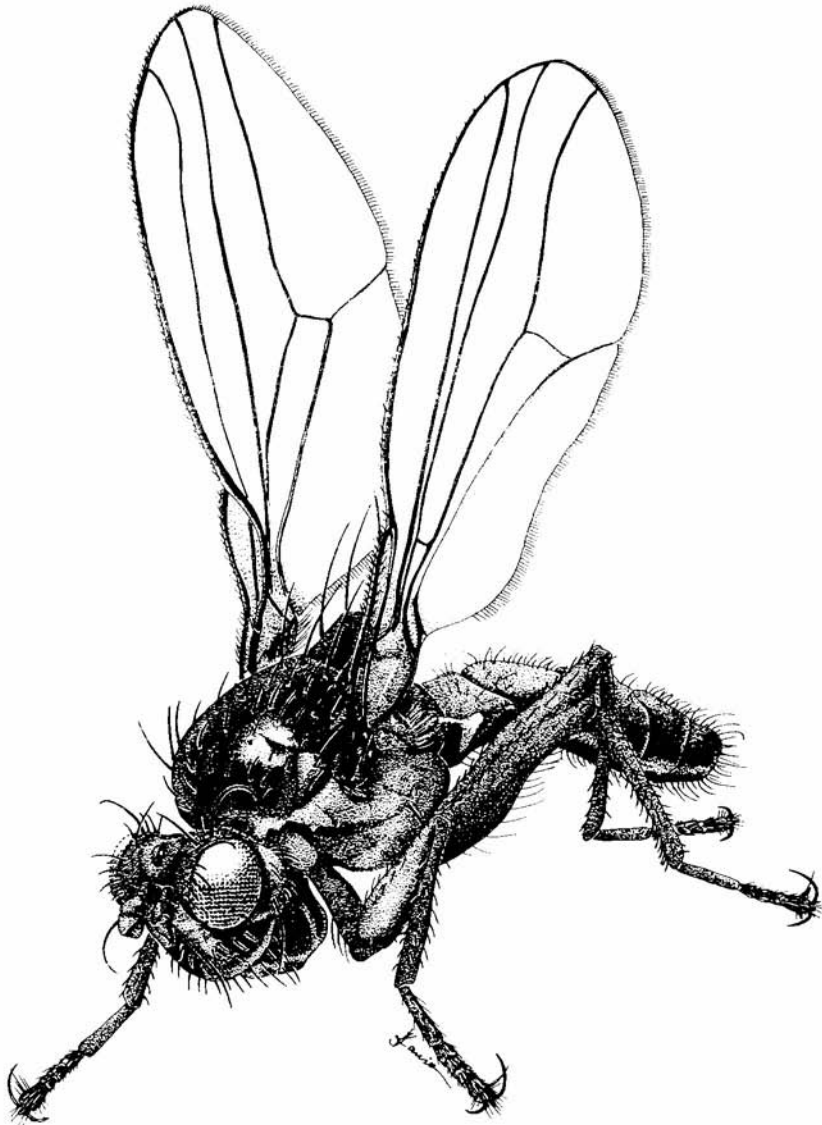
The tribe *Gastropini*, with its two genera *Beckeriella* and *Gastrops*, was commonly placed in the "*Parydrinae*" (at present *Ilytheinae*). However, the distinctive characteristics of the tribe: parasitoid larvae, presence of evident dististyli, separation of hypandrium and gonites, and junction of pre- and postgonites (see LIZARRALDE DE GROSSO, 1986, and ZATWARNICKI, 1991), are very unusual for the *Hyadinini*, and suggest that the lineage more resembles members of the *Gymnomyzinae*, especially the *Gymnomyzini* (Figs. 61-63) and *Ochtherini*. The shape of the male genitalia resembles that of *Athyroglossa*, but the feeding habits of larvae are similar to those of *Ochthera*.

The tribe *Ilytheini* was originally placed by CRESSON (1943) in the subfamily *Notiphilinae* (= *Hydrelliinae*), and then commonly situated close to the tribe *Notiphilini*, probably because of the general external resemblance of both tribes. The

male genitalia of the genera constituting the tribe *Ilytheini* (*Ilythea*, *Donaceus* and *Zeros*) differ greatly from those of other hydrelline tribes. Internal structure of the hypopygium is much simplified, with only hypandrium, aedeagus and aedeagal apodeme developed, but clasper, dististyli and gonites are reduced, and proximal aedeagal opening is situated more or less dorsally. According to FOOTE (1979) pinnate diatoms constituted well over 90 percent of the larval gut contents, and a diet of *Navicula pelliculosa*, a diatom, resulted in successful rearing of *Ilythea* and *Zeros*. The floor of the pharyngeal sclerite in *Ilytheini* larvae bears Y-shaped ridges. The same ridges were illustrated for *Pelina* and *Setacera* larvae (FOOTE, 1981 and 1982 respectively). The presence of the structures within the *Discomyzinae* and *Hydrelliinae* is not adequately known. The female ventral receptacle of the *Ilytheini* and a sublineage *Hyadinini* + *Philygrini* is roundly sinuate and has reduced operculum. Most of the internal characters of adults, shape and feeding of larvae, shared by the *Hyadinini*, *Philygrini* and *Ephydrinae* were found also in the *Ilytheini*. This supports the position of the tribe within the *Gymnomyzinae* subfamily group close to the *Philygrini* + *Hyadinini* sublineage. Unfortunately the transfer of the tribe causes a nomenclatural change, since the name *Ilytheini* is older than *Hyadininae*, and it has to replace the latter.

MATHIS and ZATWARNICKI (1990) suggested a close relationship between the *Parydrini* and *Ephydrinae* and provided five synapomorphic conditions for both lineages, but made no formal change. Since the only derived character (katepisternal seta reduced) shared by the *Parydrini* and two tribes of the *Ilytheinae* may be a convergence, I propose to transfer the tribe *Parydrini* to the subfamily *Ephydrinae*, and to leave the subfamily *Ilytheinae* with three tribes, the *Ilytheini*, *Philygrini* and *Hyadinini*. The *Ilytheinae* without the *Parydrini* are very well defined by the shape of ventral receptacle and the bifurcated anterior spiracles of the larva. The border between the *Ilytheinae* and the *Ephydrinae* can be, based on our present knowledge, conventional. The group formed by the latter two is the best documented monophyletic lineage; nevertheless a division of the group depends on criteria which I accept as distinct synapomorphies, namely the shape of the anterior larval spiracles, and the orientation of the orbital setae. Members of the tribe *Parydrini* have laterocline fronto-orbital setae, the only universal character that is common to all the *Ephydrinae*. Hence the change.

The action of distinguishing a tribe *Hecamedini* done by MATHIS (1991a) did not result in a natural system. Both tribes, *Hecamedini* and *Atissini* are not sister-groups and should be placed in different lineages. The *Hecamedini* are typical members of the *Gymnomyzinae* and are closely related to the *Lipochaetini*. The *Atissini* (sensu stricto) with their well developed subepandrial plate, fusion of the aedeagal apodeme with aedeagus (Figs. 38-39, 42-43), dististyli generally fused with each other forming the so called "genital plate" (Fig. 36), gonite occurring as lobe-like structure; and clasper present, elongate, and broadly rounded apically with only a few short setae (Figs. 38-39, 42-43), should be placed in the *Hydrelliinae* close to the *Typopsilopini*. Both the *Hecamedini* and the *Atissini* (s. str.) were classified together based on the position of the second notopleural and ocellar setae, a typical convergence among the shore flies.



4. *Diedrops steineri* MATHIS (*Dagini*) from Chiriqui, Bambito, Panama. Habitus

The male terminalia in the *Hecamedini* lack a subepandrial plate and clasper; dististyli, if present, are widely separate (Figs. 71-72); the gonite is generally elongate, tapered, mostly with 2 conspicuous setae (rarely with 6) (Figs. 72-74).

To make the subfamily *Ilytheinae* more uniform I recommend the placement of the genus *Brachydeutera* in the tribe *Dagini* (subfamily *Ephydrinae*). Only the reduction of the dorsocentral setae (a character, which I believe to be secondary) justified its placement in the tribe *Hyadinini*. However, many other features, such as laterocline orbital setae, presence of cruciate and procline interfrontal setae, prominent vertical facial carina between the antennae, epandrium fused apically, dististyli reduced or fused indistinguishably with the epandrium forming a single ventral projection, and the elongate anterior spiracles of the larvae justify this change.

MATHIS (1979b) reconstructed the phylogeny of the *Ephydrinae*, but the classification resulting from his studies has not been completed as yet. The creation of the tribe *Dagini* (MATHIS, 1982) suggested that the remaining main lineages should obtain tribal rank, and consequently *Coenia*-group (including genera *Coenia* and *Noticoenia*) should be placed in the *Scatellini*. Since the genera have five dorsocentral setae I interpret the presence of postpronotal macrosetae as a homoplasy. Because the aedeagal apodeme is associated with the gonite, a typical synapomorphy for many of the *Ephydrini*, not observed in the *Scatellini*, I propose to transfer the group to the tribe *Ephydrini* close to *Paracoenia*-group.

CANZONERI and MENEGHINI (1974) created the subfamily *Halmopotinae*, which included only the nominate genus. Parallely to *Austrocoenia* the face of *Halmopota* is not setose, which character, being unique in the *Ephydrini*, is interpreted here as an autapomorphy. *Halmopota* has postpronotal macrosetae and five dorsocentral setae, the characters being synapomorphic for both *Ephydrini* and *Scatellini* (MATHIS, 1979b). Like in *Coenia*-group the first character could be questioned, but the latter character is strong enough to place the genus in the tribe *Ephydrini*. As a consequence the *Halmopotinae* are synonymized with the *Ephydrini*.

To make the taxa within the cluster *Discomyzinae-Hydrelliinae* monophyletic and equivalent to each other, one generic group is given tribal rank. This is diagnosed below:

Dryxini, new tribe

Type genus: *Dryxo* ROBINEAU-DESVOIDY¹.

Diagnosis: Small to large shore flies, length 3.0 to 12.0 mm. Face with prominent interfoveal protuberance. Three dorsocentral setae (one presutural) in *Paralimna* and *Oedenops*, but they are reduced in other taxa. Mid-tibia with three dorsal setae, but reduced in *Oedenops*. Costal vein extending to the first medial vein. Male genitalia: epandrium U-shaped; lobate or L-shaped dististyli articulated with epandrium; the dististyli are separate, or their bases connect to each other internally (Fig. 55-56); both

¹The genus *Paralimna* with dozens of species is the better example for the generic group, but the tribe *Paralimnini* DISTANT, 1908 already exists in *Cicadellidae* (Homoptera) based on *Paralimnus*.

pre- and postgonites reduced; clasper setose, with incised-bent tip; aedeagus with a basal fold, or with lateral appendices; aedeagal apodeme broadened basally (Figs. 57-58).

Discussion: Externally this is a very heterogeneous group, but obviously monophyletic, with distinct apomorphic characters in the male genitalia. Previously COGAN (1968) suggested that the highly specialized *Dryxo* might possibly require creation of a separate tribe. The male genitalia of *Dryxo* are structurally similar to those of other members of the tribe (except for *Notiphila* and *Dichaeta*), and have some specific synapomorphic characters not observed in the genera just named, hence the elevation of the group to the tribal status. The differences both in external morphology and male terminalia between *Notiphila* generic group and genera related to *Dryxo* are strong enough to justify maintaining separate tribes for both generic groups. The biology and morphology of immature stages of the only species of *Dryxini* studied in this respect are insufficiently known. Larvae and puparia of *Paralimna aequalis* CRESSON, described briefly by BOHART and GRESSITT (1951), differ greatly from those of other *Notiphilini* and *Hydrelliini* having the anterior spiracles with two finger-like processes, and developing in pig droppings and human carcasses.

9. CLASSIFICATION SYSTEM OF THE FAMILY

The classification resulting from the reconstructed phylogeny is as follows:

Family Ephydriidae ZETTERSTEDT, 1837

The priority of the name *Hydrelliidae* ROBINEAU-DESVOIDY, 1830 was suppressed by ICZN, 1985 (Opinion No 1321) upon request of MATHIS (1981). The suppression of the priority of the name *Gymnomyzidae* LATREILLE, 1829 has been proposed by MATHIS and ZATWARNICKI (1992). Five taxa (*Dichaeta*, *Thiomyia*, *Synhoplos*, *Teichomyza*, and *Pseudohecamele*) treated by MATHIS (1979a, 1980 and 1991a) as subgenera are ranked here as full genera.

1. Subfamily Discomyzinae ACLOQUE, 1897: 486 (22 genera, 183 species).

Diagnosis: Face flat or broadly rounded. Spine on pedicel long and conspicuous. Orbital setae pro- and anaclinate. Postsutural dorsocentral setae reduced. Dististyli well developed. Clasper lobate, generally setose over whole surface. Subepandrial plate present. Pre- and postgonites poorly developed, separate. Hypandrium round, more or less incised. Aedeagus simple, tubular. Aedeagal apodeme generally hemispherical in outline. Ejaculatory apodeme absent. Ventral receptacle of typical shape. Anterior spiracle in larvae cauliflower-shaped.

A. Tribe *Discomyzini* ACLOQUE, 1897: 486 (= *Heringiinae* ENDERLEIN, 1934: 191; = *Clanoneurinae* ENDERLEIN, 1936: 168) (12 genera).

Genera: *Actocetor* BECKER, 1903 (subgenera: *Actocetor* s. str. and *Poecilostenia* BEZZI, 1908); *Clanoneurum* BECKER, 1903; *Clasiopella* HENDEL, 1914; *Discomyza* MEIGEN, 1830; *Eremomusca* MATHIS, 1985; *Guttiopsilopa* WIRTH, 1956 (subgenera: *Guttiopsilopa* s. str. and *Nesopsilopa* MATHIS and WIRTH, 1977); *Helaeomyia* CRESSON, 1941; *Hostis* CRESSON, 1944; *Mimapsilopa* CRESSON, 1941; *Paratissa* COQUILLET, 1900; *Rhysophora* CRESSON, 1924; *Trypetomima* DE MEIJERE, 1916.

B. Tribe *Psilopini* CRESSON, 1925: 241 (10 genera).

Genera: *Ceropasilopa* CRESSON, 1917; *Cnestrum* BECKER, 1896; *Cressonomya* ARNAUD, 1958; *Leptopsilopa* CRESSON, 1922; *Peltopsilopa* HENDEL, 1914; *Psilopa* FALLÉN, 1823; *Rhynchopsilopa* HENDEL, 1913; *Scoliocephalus* BECKER, 1903; *Trimerina* MACQUART, 1835; *Trimerinoides* CRESSON, 1925.

2. Subfamily *Hydrelliinae* ROBINEAU-DESVOIDY, 1830: 783 (18 genera, 506 species).

Diagnosis: Face generally flat or broadly rounded, but projected in the *Dryxini* and some *Atissini*. Spine on pedicel generally conspicuous, but in the *Dryxini* reduced. Orbital setae pro- and anaclinate. Pre- and postsutural dorsocentral setae present. Dististyli present, exceptionally fused with epandrium in the *Notiphilini*. Clasper generally present, but reduced in most *Notiphilini* (except the subgenus *Agrolimna*). Subepandrial plate present in the *Typopsilopini* and some *Atissini*, reduced in the remaining taxa. Pre- and postgonites separate in the *Typopsilopini*, in other taxa fused with each other, in the *Dryxini* and some *Notiphilini* reduced. Hypandrium sometimes with posterolateral appendices. Aedeagus often with lateral appendices. Aedeagal apodeme elongate. Ejaculatory apodeme reduced. Ventral receptacle of typical shape. Anterior spiracule of larvae generally reduced, but cauliflower-shaped if present.

A. Tribe *Typopsilopini* CRESSON, 1946: 239 (3 genera).

Genera: *Eleleides* CRESSON, 1948; *Psilopoidea* CRESSON, 1939; *Typopsilopa* CRESSON, 1916.

B. Tribe *Atissini* CRESSON, 1942: 103 (7 genera).

Genera: *Asmeringa* BECKER, 1903; *Atissa* HALIDAY, 1837; *Cerobothrium* FREY, 1958; *Isgamera* GIORDANI SOIKA, 1956; *Ptilomyia* COQUILLET, 1900; *Schema* BECKER, 1907; *Subpelignus* PAPP, 1983.

C. Tribe *Hydrelliini* ROBINEAU-DESVOIDY, 1830: 783 (= *Hydropotini* COE in KLOET and HINCKS, 1945: 396) (2 genera).

Genera: *Hydrellia* ROBINEAU-DESVOIDY, 1830; *Lemnaphila* CRESSON, 1933.

D. Tribe *Notiphilini* BIGOT, 1853: 312 (2 genera).

Genera: *Dichaeta* MEIGEN, 1830; *Notiphila* FALLÉN, 1810 (subgenera: *Notiphila* s. str. and *Agrolimna* CRESSON, 1917).

E. Tribe *Dryxini*, new tribe (4 genera).

Genera: *Dryxo* ROBINEAU-DESVOIDY, 1830 (subgenera: *Dryxo* s. str. and *Cyphops* JAENNICKE, 1867); *Karema* CRESSON, 1929; *Oedenops* BECKER, 1903; *Paralimna* LOEW, 1862 (subgenera: *Paralimna* s. str., *Afrolimna* COGAN, 1968, *Oedenopiforma* COGAN, 1968, *Phaiosterna* CRESSON, 1916, and *Poecilothorax* BECKER, 1922).

3. Subfamily *Gymnomyzinae* LATREILLE, 1829: 536 (32 genera, 334 species).

Diagnosis: Face protruding, generally carinate. Spine on pedicel generally reduced, or inconspicuous. Orbital setae pro- and anaclinate. Postsutural dorsocentral seta reduced. Dististyli elongate, their posteroventral margin extended under the anterior margin of epandrium, in the *Discocerinini* reduced. Clasper and subepandrial plate reduced. Pre- and postgonites separate in primitive taxa of the *Gymnomyzini*, *Gastropini* and *Discocerinini*, but generally fused with each other. Hypandrium variable. Aedeagus typical, rarely with anteroventral or anterodorsal appendix. Aedeagal apodeme generally triangular in outline, medially with ventral projection. Ejaculatory apodeme in form of plate with a few colourless "windows". Ventral receptacle rarely with small operculum. Anterior spiracle in larvae with several short branches.

A. Tribe *Gastropini* CRESSON, 1949: 250 (as *Gastropsini*) (2 genera).

Genera: *Beckeriella* WILLISTON, 1897; *Gastrops* WILLISTON, 1897.

B. Tribe *Gymnomyzini* LATREILLE, 1829: 536 (= *Gymnopinae* CRESSON, 1922: 326) (11 genera).

Genera: *Athyroglossa* LOEW, 1860 (subgenera: *Athyroglossa* s. str. and *Parathyroglossa* HENDEL, 1931); *Cerometopum* CRESSON, 1914; *Chaetomosillus* HENDEL, 1934; *Chlorichaeta* BECKER, 1922; *Gymnopiella* CRESSON, 1945; *Hoploaegis* CRESSON, 1944; *Mosillus* LATREILLE, 1804; *Placopsidella* KERTESZ, 1901; *Platygymnopa* WIRTH, 1971; *Stratiothyrea* DE MEIJERE, 1913; *Trimerogastra* HENDEL, 1914.

C. Tribe *Hecamedini* MATHIS, 1991a: 2 (6 genera).

Genera: *Allotrichoma* BECKER, 1896; *Diphuia* CRESSON, 1944; *Elephantinosoma* BECKER, 1903; *Eremotrichoma* GIORDANI SOIKA, 1956; *Hecamede* HALIDAY, 1837

(subgenera: *Hecamede* s. str. and *Soikia* CANZONERI and MENEGHINI, 1969); *Pseudohecamede* HENDEL, 1936.

D. Tribe *Lipochaetini* BECKER, 1896: 275 (4 genera).

Genera: *Glenanthe* HALIDAY, 1839; *Homalometopus* BECKER, 1903; *Lipochaeta* COQUILLET, 1896; *Paraglenanthe* WIRTH, 1956.

E. Tribe *Discocerini* CRESSON, 1925: 228 (as *Discocerini*) (8 genera).

Genera: *Diclasiopa* HENDEL, 1917; *Discocerina* MACQUART, 1835 (subgenera: *Discocerina* s. str., *Basila* CRESSON, 1942, and *Lamproclasiopa* HENDEL, 1933); *Ditrichophora* CRESSON, 1924; *Gymnoclasiopa* HENDEL, 1917; *Hecamedoides* HENDEL, 1917; *Hydrochasma* HENDEL, 1936; *Pectinifer* CRESSON, 1944; *Polytrichophora* CRESSON, 1924.

F. Tribe *Ochtherini* DAHL, 1959: 105 (1 genus).

Genus: *Ochthera* LATREILLE, 1802.

4. Subfamily *Ilytheinae* CRESSON, 1943: 1 (14 genera, 176 species).

Diagnosis: Face protruding. Spine on pedicel inconspicuous. Orbital setae pro- and anaclinate. Presutural dorsocentral setae present, but reduced in the *Hyadinini* and some *Philygrini*. Dististyli, clasper and subepandrial plate absent. Pre- and postgonites fused to each other and joined with hypandrium forming gonital arch, in the *Ilytheini* gonites reduced. Basal opening of aedeagus directed dorsally. Aedeagal apodeme triangular in outline. Ejaculatory apodeme generally present. Ventral receptacle with reduced operculum. Anterior spiracle in larvae with two elongate branches.

A. Tribe *Ilytheini* CRESSON, 1943: 1 (3 genera).

Genera: *Donaceus* CRESSON, 1943; *Ilythea* HALIDAY, 1837; *Zeros* CRESSON, 1943.

B. Tribe *Hyadinini* PHILLIP et al. in CRESSON, 1949: 251 (9 genera).

Genera: *Axysta* HALIDAY, 1839; *Hyadina* HALIDAY, 1837; *Lytogaster* BECKER, 1896; *Microlytogaster* CLAUSEN, 1983; *Parydroptera* COLLIN, 1913; *Parahyadina* TONNOIR and MALLOCH, 1926; *Pelina* HALIDAY, 1837; *Pelinoidea* CRESSON, 1931; *Pseudohyadina* CLAUSEN, 1983.

- C. Tribe *Philygrini* LIZARRALDE DE GROSSO, 1989: 51-52 (= *Hydrinini* CRESSON, 1944: 175, unavailable, based on junior homonym) (2 genera).

Genera: *Nostima* COQUILLET, 1900; *Philygria* STENHAMMAR, 1844.

5. Subfamily *Ephydrinae* ZETTERSTEDT, 1837: 48 (30 genera, 445 species).

Diagnosis: Upper portion of face projected anteriorly, in the *Scatellini* and *Ephydrini* setose in the central part. Spine on pedicel generally present. Orbital setae laterocline. Pre- and postsutural dorsocentral setae generally present. Dististyli, clasper and subepandrial plate absent. Pre- and postgonites fused with each other and joined with hypandrium. Basal opening of aedeagus directed dorsally, its anterior margin often thickened. Aedeagal apodeme elongate, rarely reduced. Ejaculatory apodeme variable, frequently almost reduced, sometimes like a long band. Ventral receptacle simple and generally elongate. Anterior spiracle in larvae clavate or with long finger-like branches.

- A. Tribe *Parydrini* WIRTH and STONE, 1956: 469 (= *Napaeini* CRESSON, 1930: 100, unavailable, based on junior homonym) (4 genera).

Genera: *Callinapaea* STURTEVANT and WHEELER, 1954; *Eutaenionotum* OLDENBERG, 1923; *Parydra* STENHAMMAR, 1844 (subgenera: *Parydra* s. str., *Chaetoapnaea* HENDEL, 1930, and *Paranapaea* HENDEL, 1930); *Rhinonapaea* WIRTH, 1965.

- B. Tribe *Dagini* MATHIS, 1982: 3 (5 genera).

Genera: *Brachydeutera* LOEW, 1862; *Dagus* CRESSON, 1935; *Diedrops* MATHIS and WIRTH, 1976; *Physemops* CRESSON, 1934; *Psilephydra* HENDEL, 1914.

- C. Tribe *Ephydrini* ZETTERSTEDT, 1837: 48 (= *Halmopotinae* CANZONERI and MENEGHINI, 1972: 147) (12 genera).

Genera: *Austrocoenia* WIRTH, 1970; *Calocoenia* MATHIS, 1970 (subgenera: *Calocoenia* s. str. and *Leptocoenia* MATHIS, 1975); *Cirruia* CRESSON, 1915; *Coenia* ROBINEAU-DESVOIDY, 1830; *Dimecoenia* CRESSON, 1916; *Ephydra* FALLÉN, 1810 (subgenera: *Ephydra* s. str., *Halephydra* WIRTH, 1971, and *Hydropyrus* CRESSON, 1934); *Ephydrella* TONNOIR and MALLOCH, 1926; *Halmopota* HALIDAY, 1856; *Notiocoenia* MATHIS, 1980; *Paracoenia* CRESSON, 1935; *Setacera* CRESSON, 1930; *Thiomyia* WIRTH, 1954.

- D. Tribe *Scatellini* WIRTH and STONE, 1956: 473 (11 genera).

Genera: *Amalopteryx* EATON, 1875; *Lamproscatella* HENDEL, 1917; *Haloscatella*

MATHIS, 1979; *Thinoscatella* MATHIS, 1979; *Limmellia* MALLOCH, 1925; *Philotelma* BECKER, 1896; *Scatella* ROBINEAU-DESVOIDY, 1835 (subgenera: *Scatella* s. str., *Apulvillus* MALLOCH, 1934, *Neoscatella* MALLOCH, 1933, and *Parascatella* CRESSON, 1935); *Scatophila* BECKER, 1896; *Synhoplos* LAMB, 1917; *Tauromima* PAPP, 1979; *Teichomyza* MACQUART, 1835.

10. CONCLUDING REMARKS

The greatest problem in the reconstruction of the phylogeny is the abundance of convergences. Some of them are easily recognized, but others need to be evaluated by reference to other criteria, especially immature stage characters. Characters well known to be convergences in shore flies are: shortening of the costal vein to medial vein; reduction of dorsocentral setae; upturning of the second notopleural seta, and maculation of wing. Since convergences in male and female reproductive apparatus are still inadequately known, I have not introduced changes in the tribal status. However, I would suggest the direction of further studies on the problem. The tribes *Lipochaetini* and *Ilytheini* which are placed in different subfamilies share many important characteristics such as reduced gonites (and clasper), and a modified ventral receptacle without operculum, but other characters do not corroborate their affinity. The placement of the *Discocerinini* within the *Gymnomyzinae* is also tentative. Members of this tribe lack developed dististyli, and their larvae are microphagous and in some respects resemble the *Ilytheinae* rather than the other tribes within the *Gymnomyzinae*. However, these features could have developed parallelly, and the position of the *Discocerinini* is not changed at present. Some sister-groups are very close to each other, and only slight differences occur between the *Gastropini* and *Gymnomyzini*, *Philygrini* and *Hyadinini*, and also between the *Hydrelliini* and *Notiphilini* s. str. The relationships between these sister-groups merit a further study. In my personal view, without a further study, it is better to maintain a great number of true monophyletic tribal groups than to create few paraphyletic assemblages. It is much easier to create and/or correct a system in which the components are homogeneous than to change one containing taxa of doubtful monophyly.

11. ACKNOWLEDGMENTS

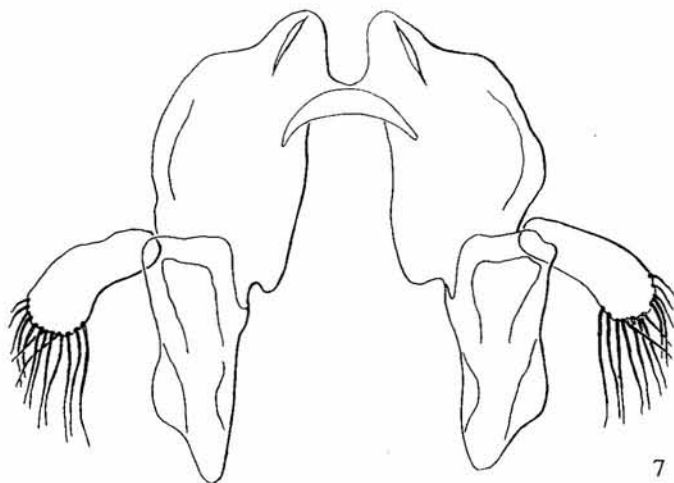
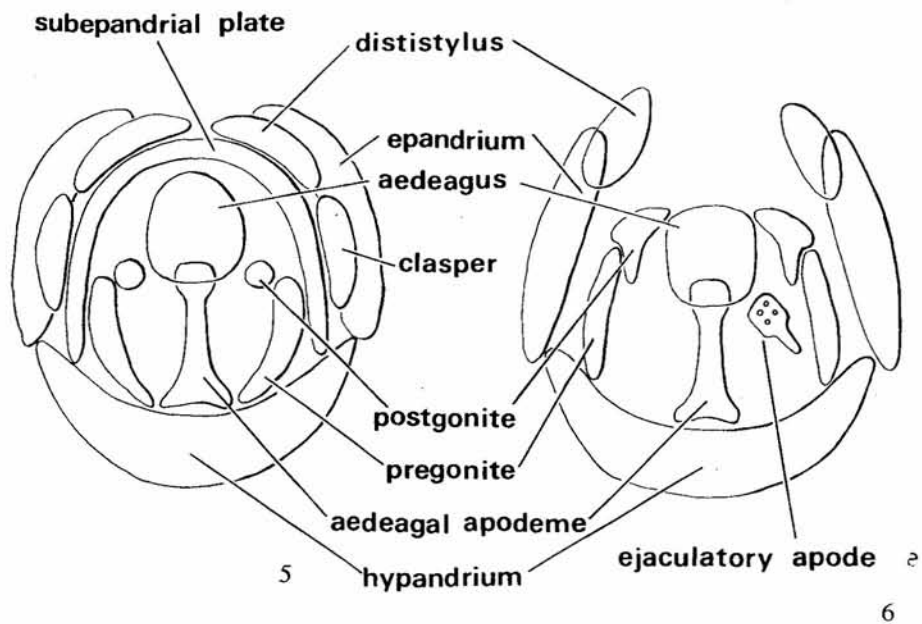
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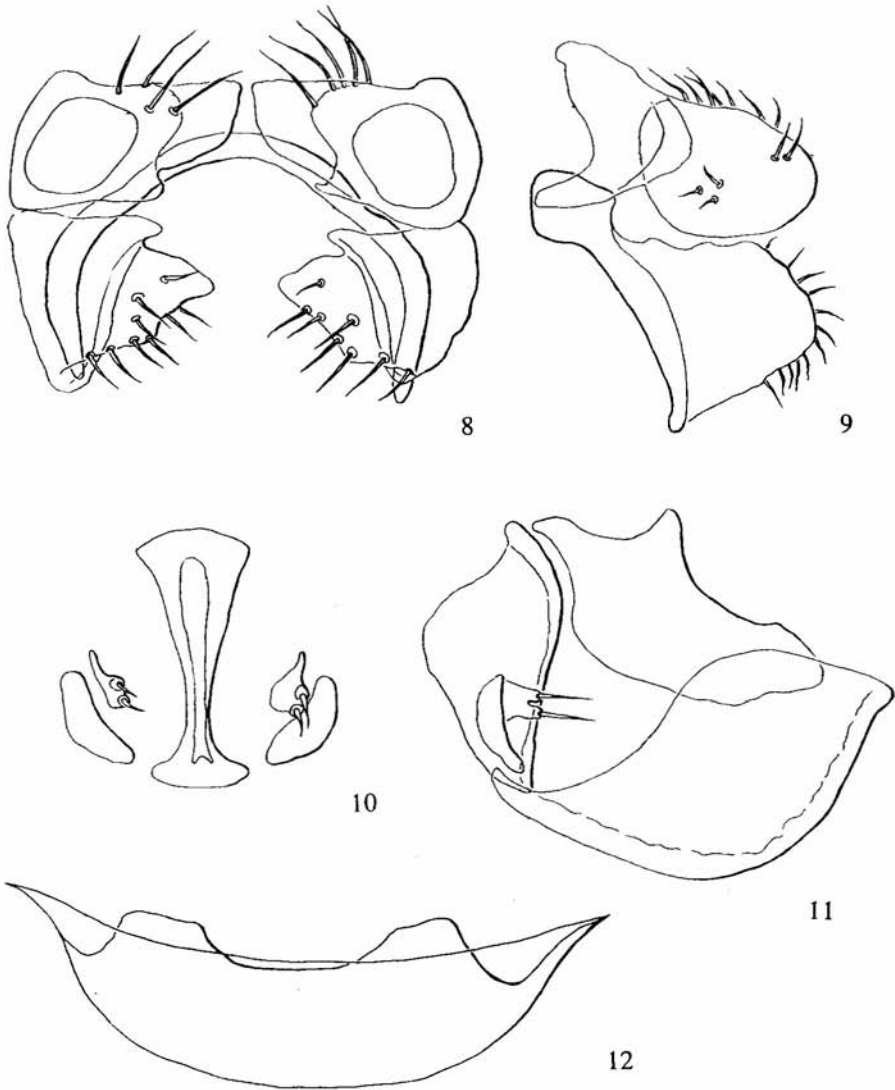
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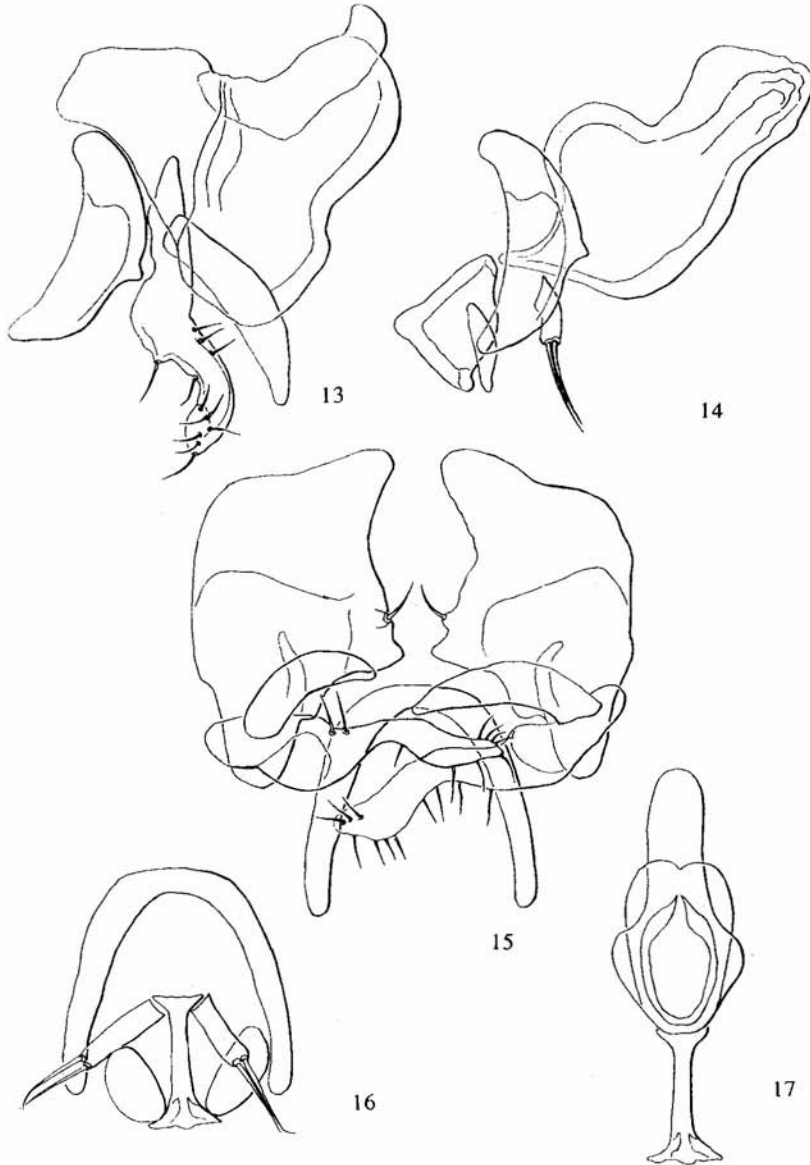
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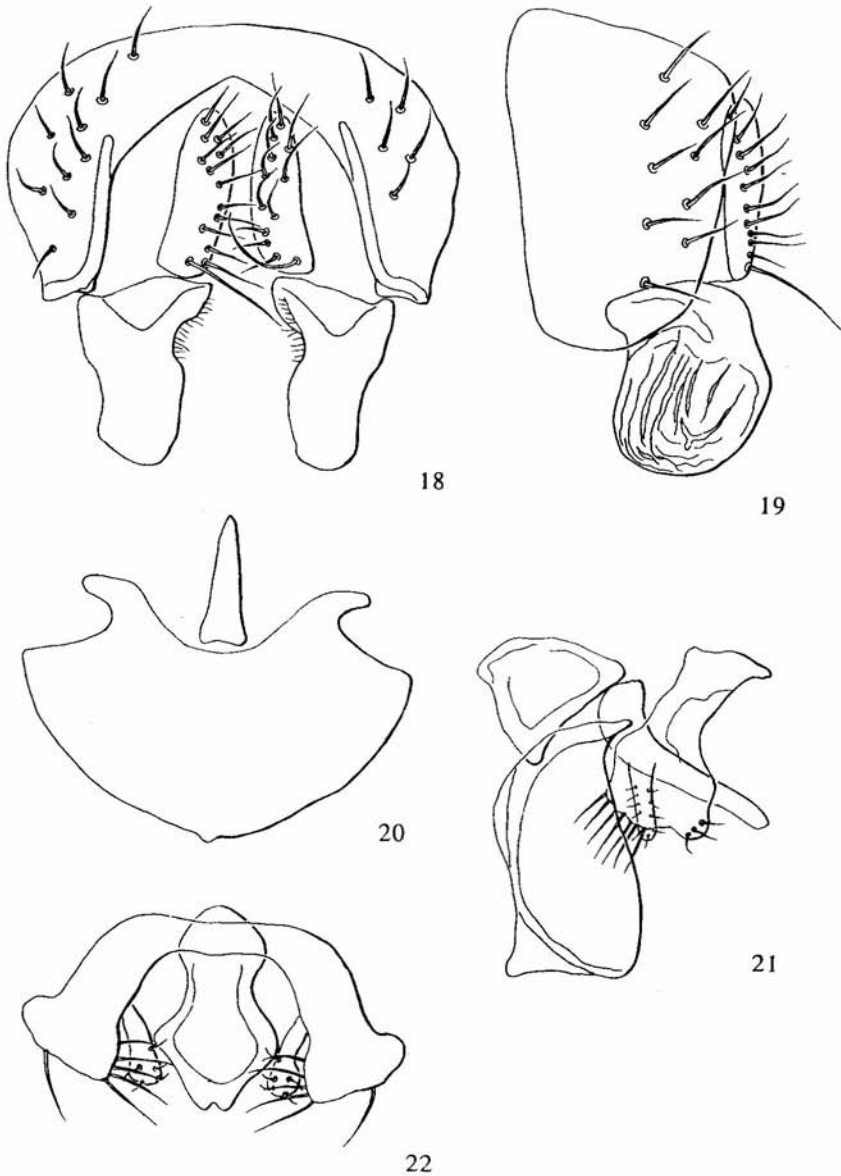
5-7. The ground plan scheme of the male genitalia in major shore-flies subfamily groups in anterior view: 5 - *Hydrelliinae* subfamily group, 6 - *Gymnomyzinae* subfamily group. 7 - Subepandrial plate, dististylus and claspers of *Diastata fuscula* (FALLÉN) from Piechowice, Poland, dorsal view



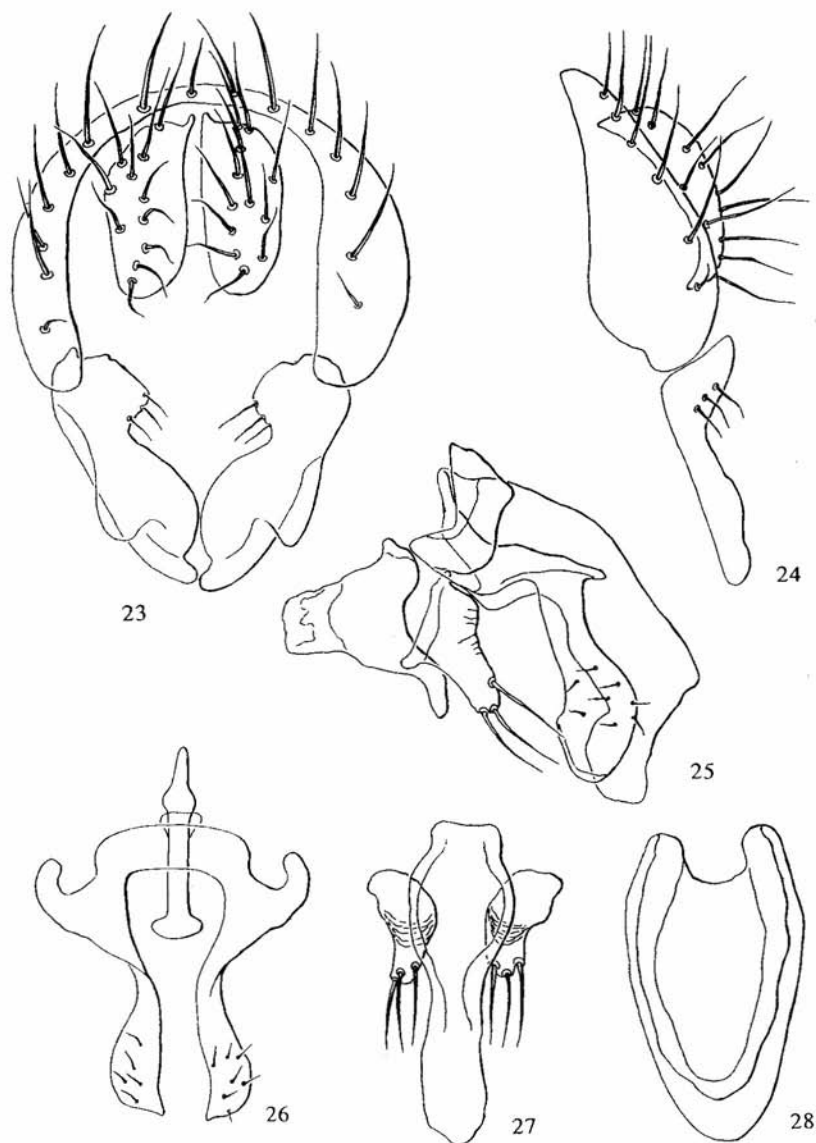
8-12. Male genitalia of *Hostis guamensis* CRESSON from Honolulu, Hawaii (tribe *Discomyzini*): 8 - Subepandrial plate, dististyli and clasper, dorsal view, 9 - Same, lateral view, 10 - Aedeagal apodeme, pre- and postgonites, dorsal view, 11 - Aedeagus, aedeagal apodeme, hypandrium, pre- and postgonite, lateral view, 12 - Hypandrium, dorsal view



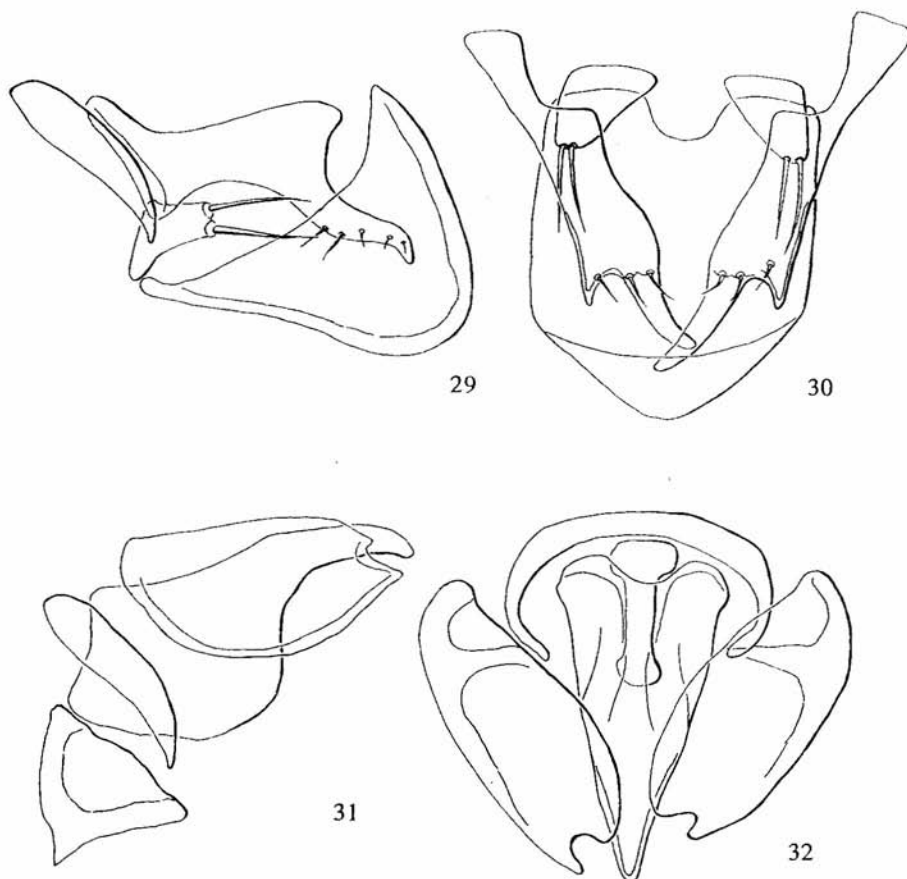
13-17. Male genitalia of *Mimapsilopa schildi* CRESSON from Finca Prusia, Mexico (tribe *Discomyzini*): 13 - Subepandrial plate; dististyli and clasper, lateral view, 14 - Subepandrial plate, aedeagus, aedeagal apodeme, pre- and postgonite, lateral view, 15 - Subepandrial plate, dististyli and clasper, dorsal view, 16 - Subepandrial plate, aedeagal apodeme, pre- and postgonites, dorsal view, 17 - Aedeagus and aedeagal apodeme, dorsal view



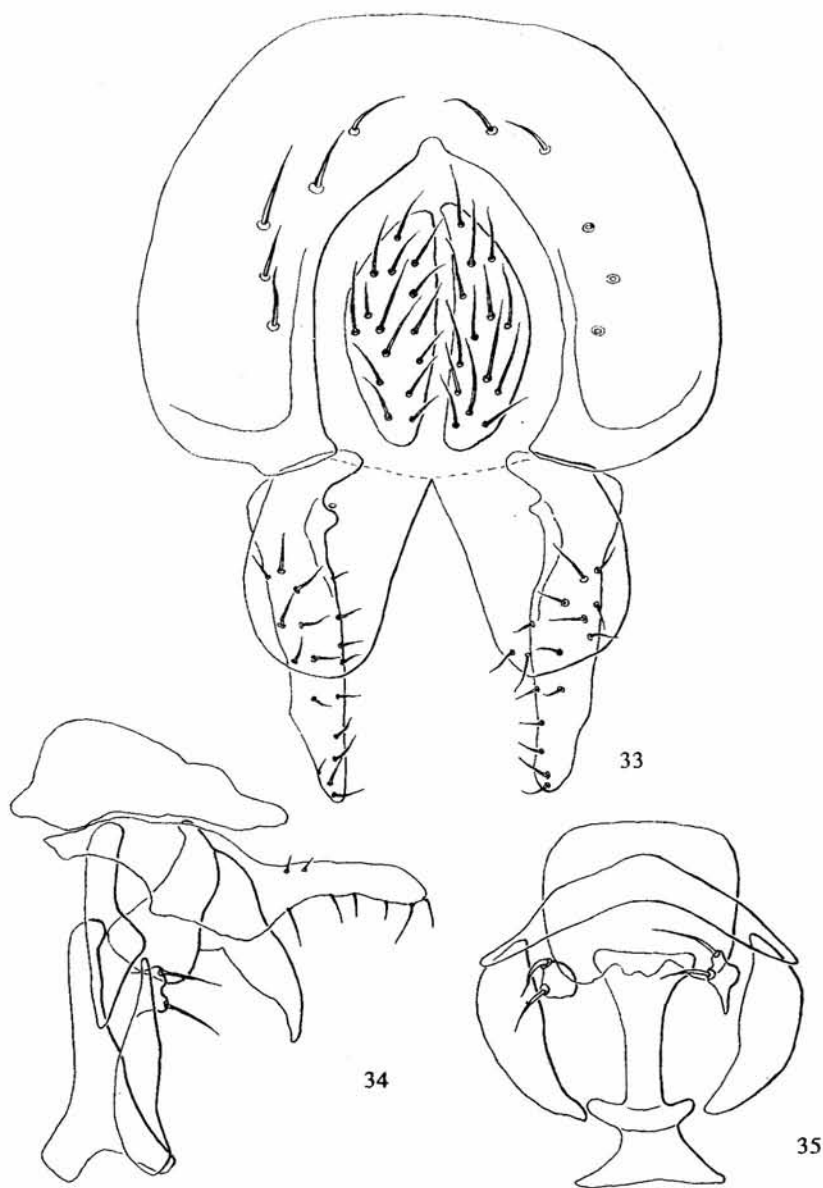
18-22. Male genitalia of *Helaeomyia petrolei* (COQUILLET) from Montebello, California (USA) (tribe *Discomyzini*): 18 - Cerci, epandrium and dististyli, dorsal view, 19 - Same, lateral view, 20 - Hypandrium and aedeagal apodeme, dorsal view, 21 - Subepandrial plate, gonites and aedeagus, dorsal view, 22 - Internal structures, lateral view



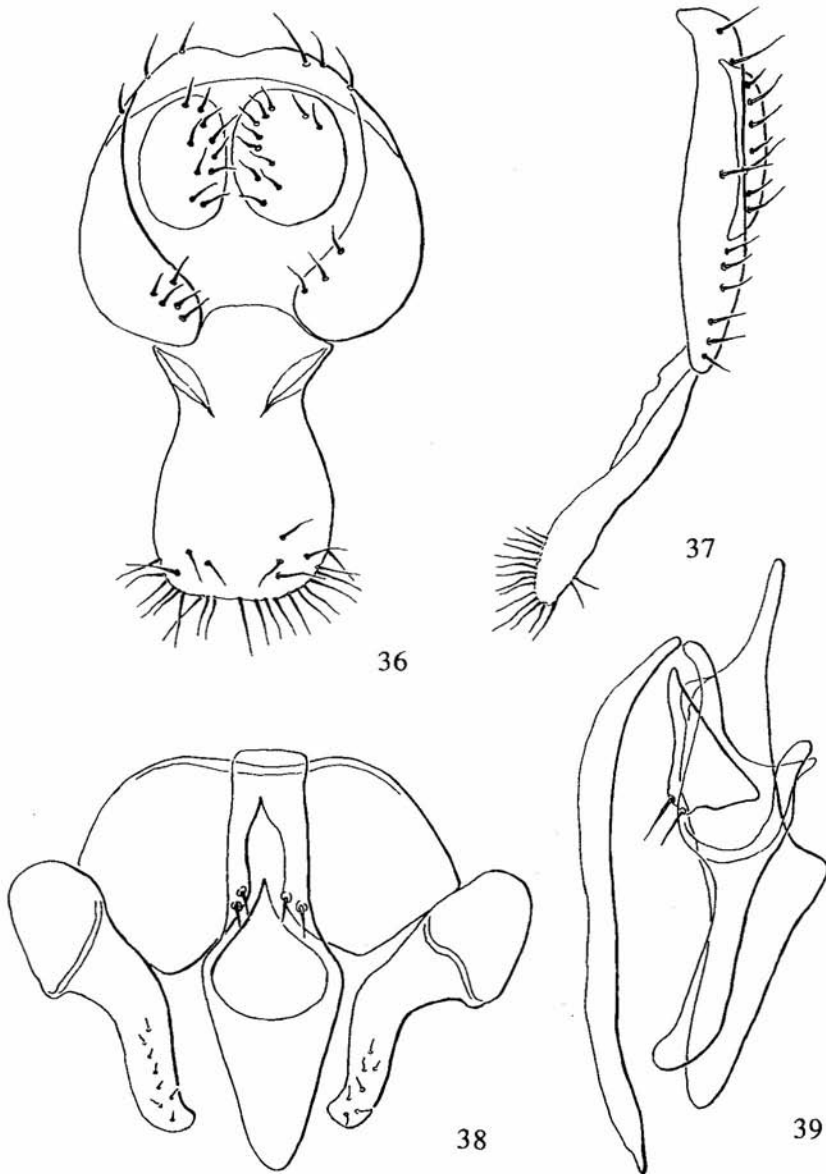
23-28. Male genitalia of *Cressonomyia nitidifrons* (CRESSON) from Peralta, Costa Rica (tribe *Psilopini*): 23 - Cerci, epandrium and dististyli, dorsal view, 24 - Same, lateral view, 25 - Internal structures without hypandrium, lateral view, 26 - Subepandrial plate, claspers and aedeagal apodeme, dorsal view, 27 - Aedeagus and gonites, dorsal view, 28 - Hypandrium, dorsal view



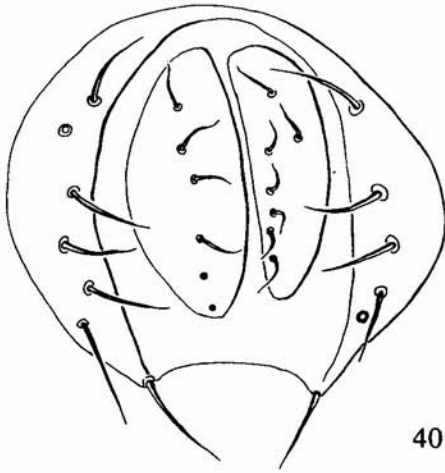
29-32. Male genitalia of *Leptopsilopa nigrimana* (WILLISTON) from Manati, Puerto Rico (tribe *Psilopini*):
 29. Subepandrial plate, clasper, gonite, and hypandrium; lateral view, 30 - Clasper, gonites and
 hypandrium, dorsal view, 31 - Subepandrial plate, dististylus, aedeagal apodeme and aedeagus, lateral
 view, 32 - Subepandrial plate, dististyli, aedeagal apodeme and aedeagus, dorsal view



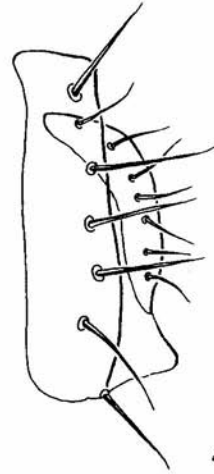
33-35. Male genitalia of *Eleleides chloris* CRESSON from Melbourne, Australia (tribe *Typopsilopini*): 33 - Cerci, epandrium, dististyli and claspers, dorsal view, 34 - Dististylus and internal structures without hypandrium, lateral view, 35 - Internal structures without hypandrium and clasper, dorsal view



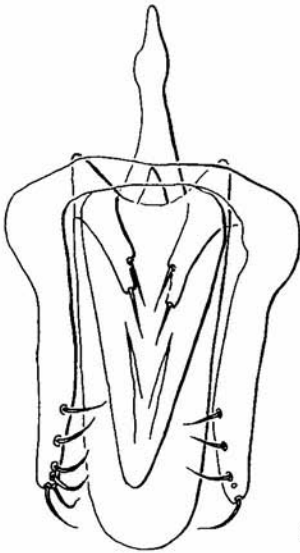
36-39. Male genitalia of *Isgamera globicornis* GIORDANI SOIKA from Ngomeni, Kenya (tribe *Atissini*): 36 - Cerci, epanthrium and fused dististyli, dorsal view, 37 - Same, lateral view, 38 - Claspers, gonites and aedeagal apodeme fused with aedeagus, dorsal view, 39 - Claspers, gonites, hypandrium and aedeagal apodeme fused with aedeagus, lateral view



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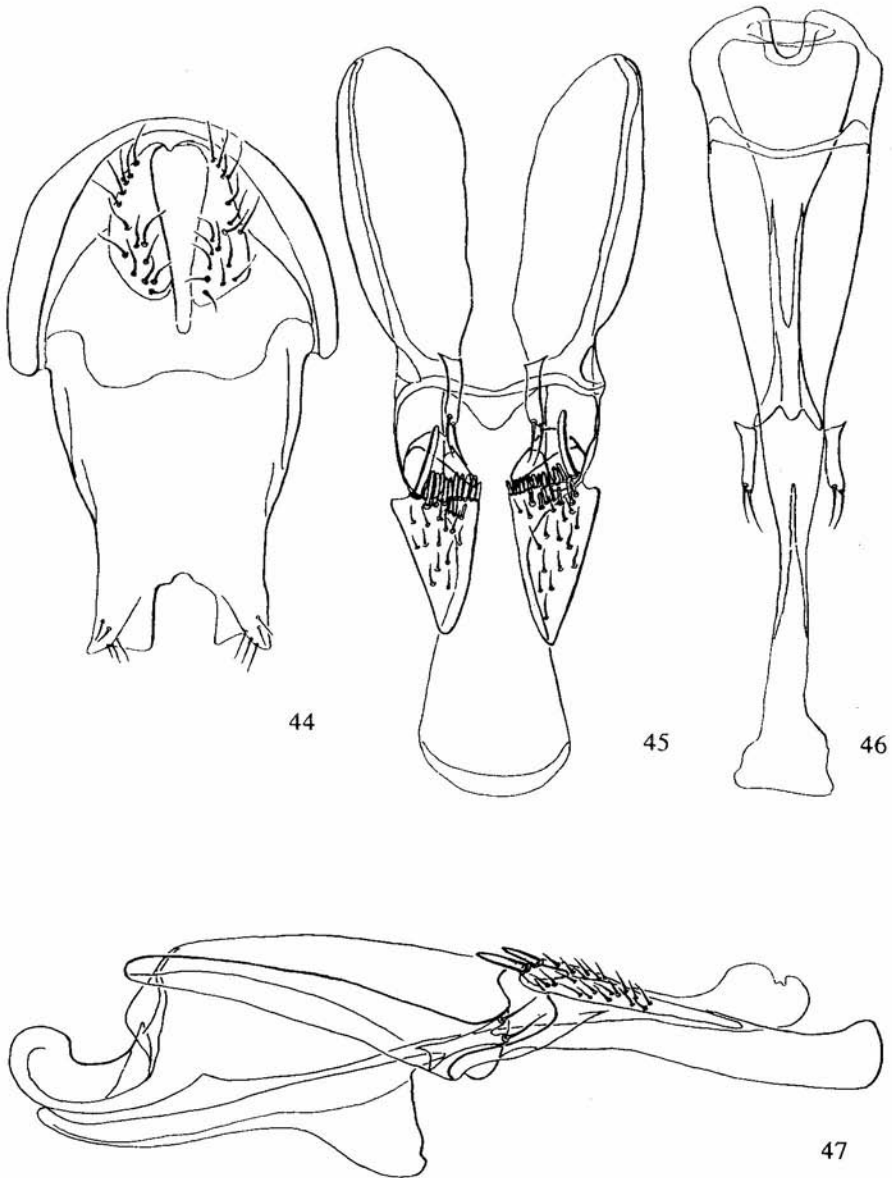


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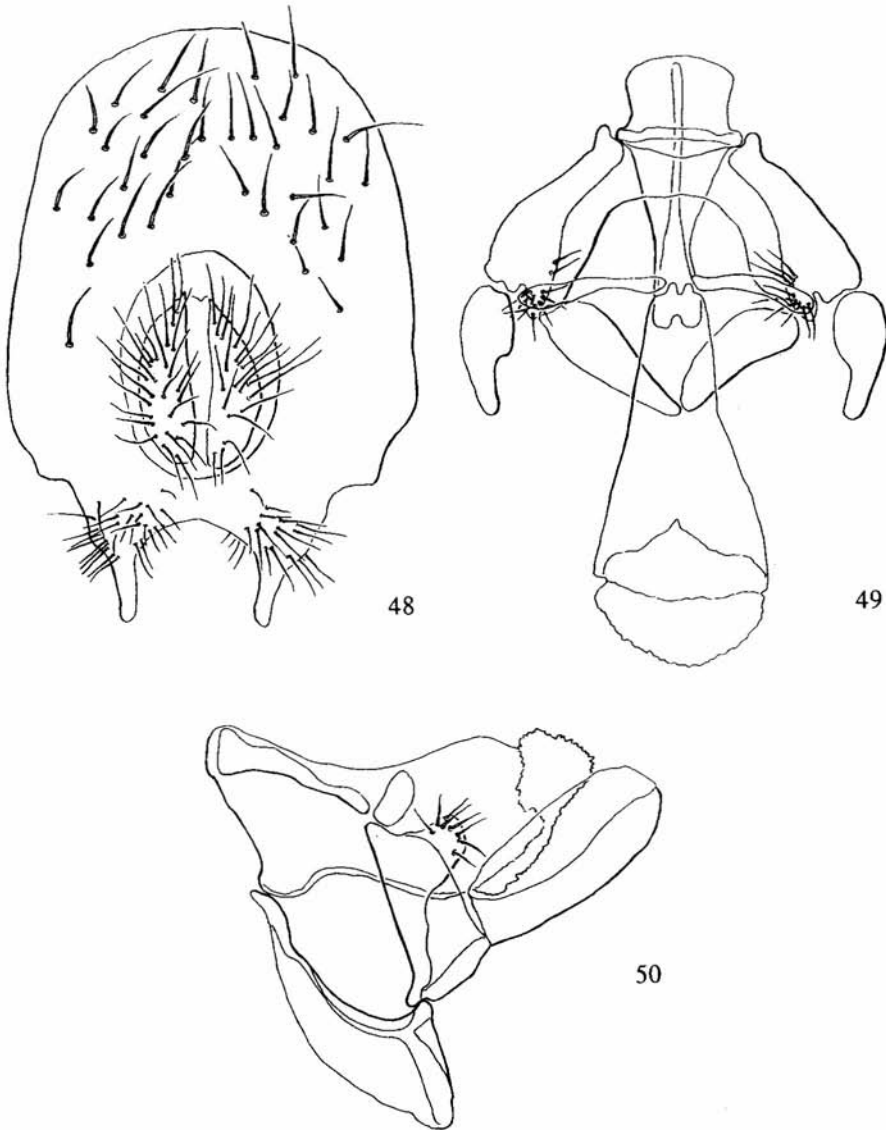


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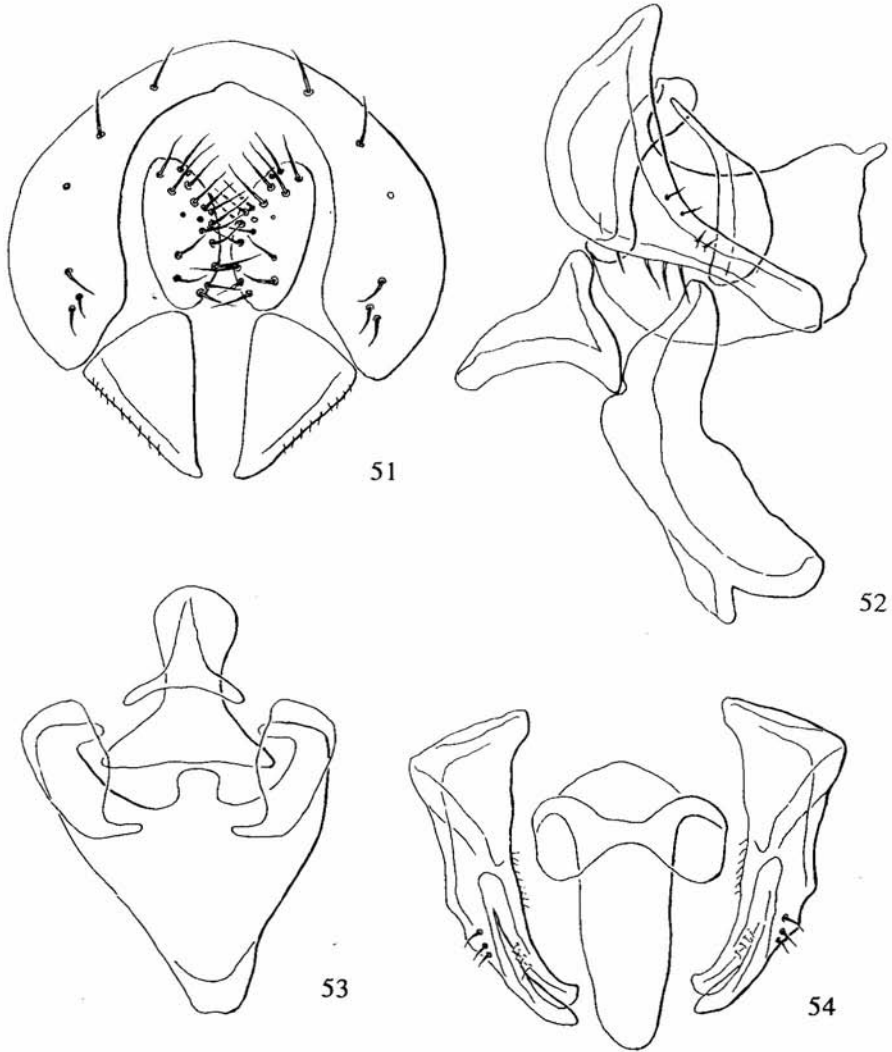
40-43. Male genitalia of *Ptilomyia setulosa* (CRESSON) from Cartago, Costa Rica (tribe *Atissini*): 40 - Cerci, epanthrium and fused dististyli, dorsal view, 41 - Same, lateral view, 42 - Claspers, gonites, hypandrium and aedeagal apodeme fused with aedeagus, dorsal view, 43 - Same, lateral view



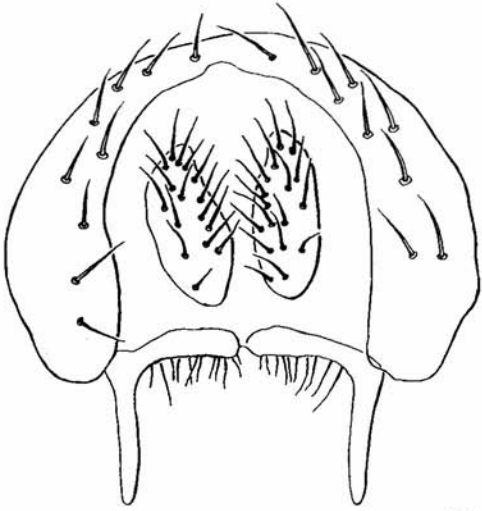
44-47. Male genitalia of *Hydrellia otteliae* SÉGUY from Tsimbagaga, Madagascar (tribe *Hydrelliini*): 44 - Cerci, epanthrium and fused dististyli, dorsal view, 45 - Claspers, gonites, hypandrium and 5th sternite, dorsal view, 46 - Gonites, aedeagal apodeme and aedeagus, dorsal view, 47 - Internal structures and 5th sternite, lateral view



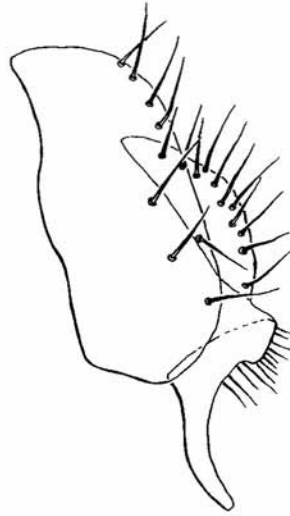
48-50. Male genitalia of *Notiphila major* STENHAMMAR from Abisko, Sweden (tribe *Notiphilini*): 48 - Cerci, epandrium with fused dististyli, dorsal view, 49 - Internal structures, dorsal view, 50 - Same, lateral view



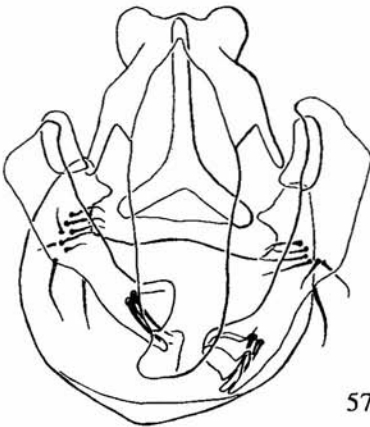
51-54. Male genitalia of *Oedenops nudus* (COQUILLET) from Layou River mouth, Dominica (tribe *Dryxini*):
 51 - Cerci, epandrium and dististyli, dorsal view, 52 - Internal structures, lateral view, 53 - Divided
 subepandrial plate, aedeagal apodeme and hypandrium, dorsal view, 54 - Aedeagus and claspers, dorsal
 view



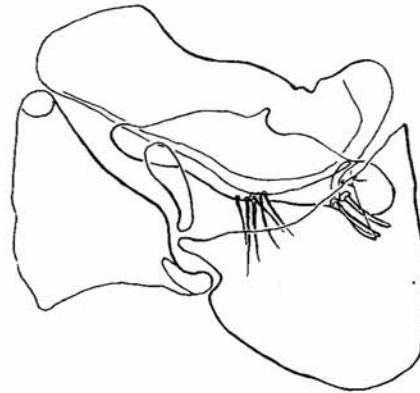
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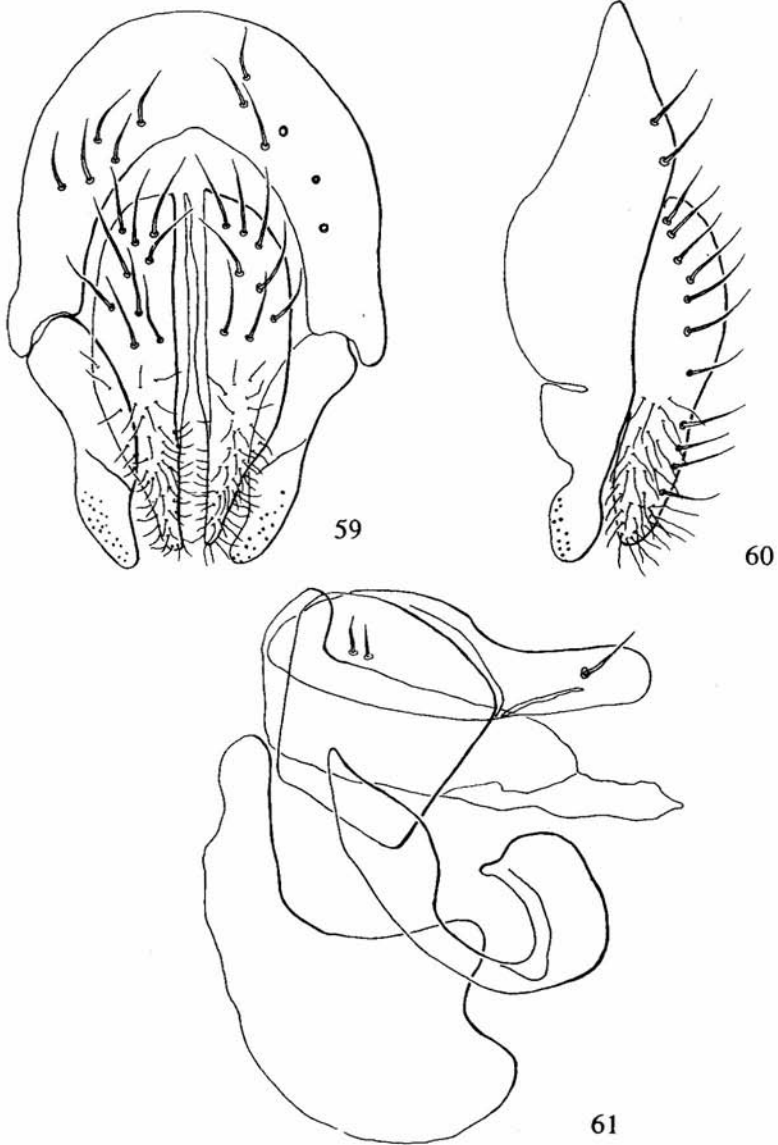


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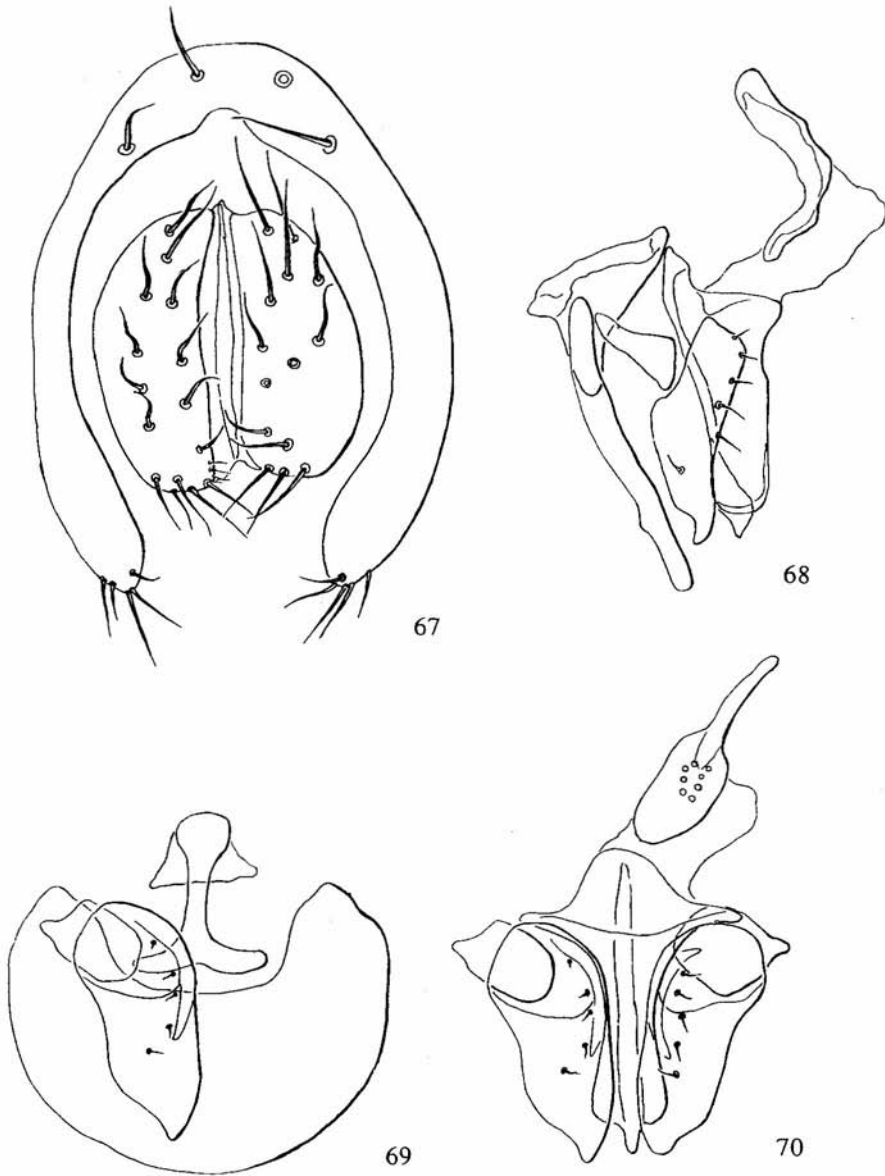
55-58. Male genitalia of *Paralimna spona* GIORDANI SOIKA from Kanyabayongo, Zaire (tribe *Dryxini*): 55 - Cerci, epandrium and dististyli, dorsal view, 56 - Same, lateral view, 57 - Internal structures, dorsal view, 58 - Same, lateral view



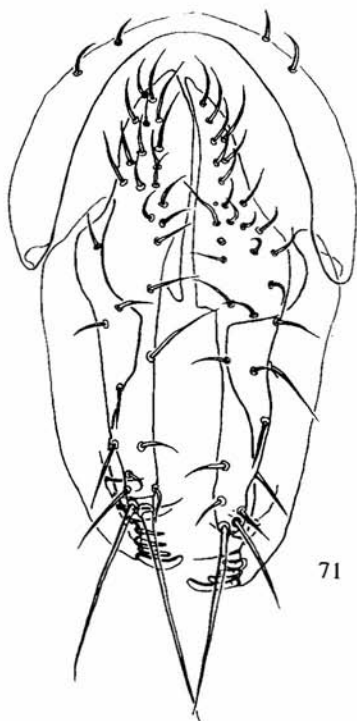
59-61. Male genitalia of *Cerometopon mosilloides* CRESSON from Colonia Benites, Chaco, Argentina (tribe *Gymnomyzini*): 59 - Cerci, epandrium and dististyli, dorsal view, 60 - Same, lateral view, 61 - Internal structures, lateral view



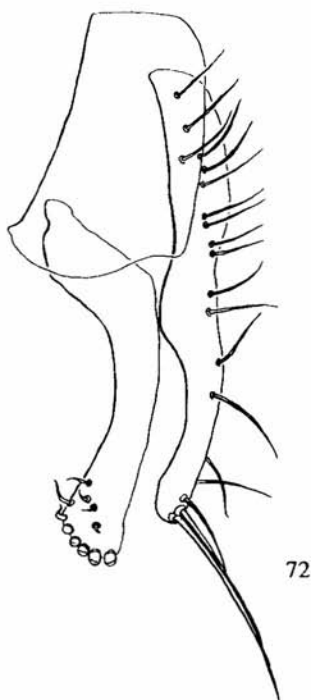
62-66. Structures of the male genitalia: 62-63. *Stratiothyrea femorata* CRESSON from Rennell Niupani, Solomon Is. (tribe *Gymnomyzini*): 62 - Aedeagal apodeme, hypandrium, pre- and postgonite, dorsal view, 63 - Same, lateral view. 64-66. *Pectinifer aeneus* CRESSON from Antrim, Dominica (tribe *Discocerini*): 64 - Gonites and hypandrium, dorsal view, 65 - Aedeagus and aedeagal apodeme, dorsal view, 66 - Internal structures, lateral view



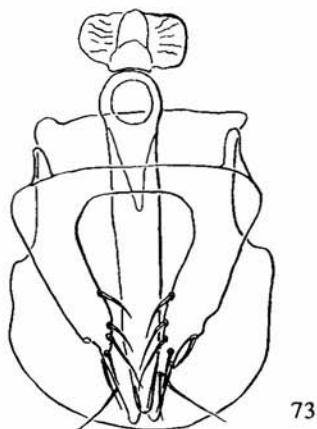
67-70. Male genitalia of *Gymnoclastiopa aurivillii* (BECKER) from Bv. Veggli, Norway (tribe *Discocerini*):
 67 - Cerci and epandrium, dorsal view, 68 - Internal structures, lateral view, 69 - Hypandrium, aedeagal
 apodeme, left pre- and postgonite, dorsal view, 70 - Pre- and postgonites, aedeagus and ejaculatory
 apodeme, dorsal view



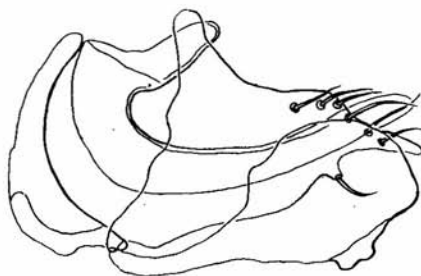
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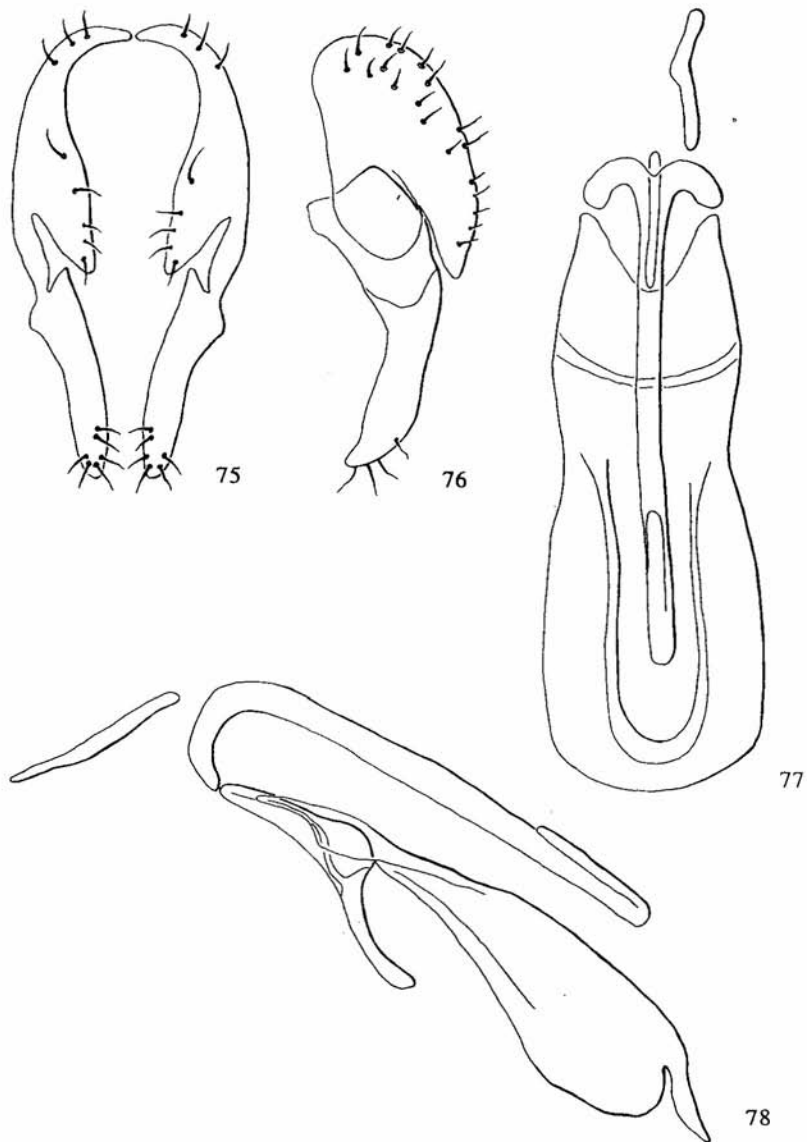


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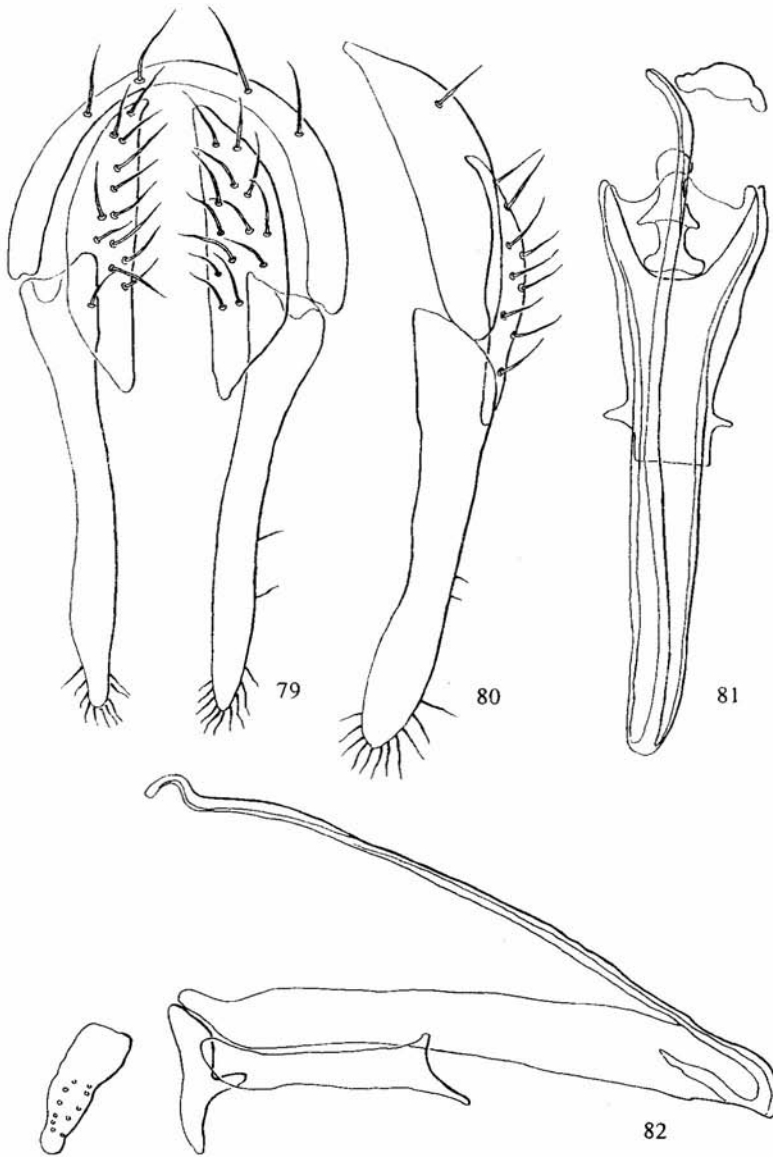


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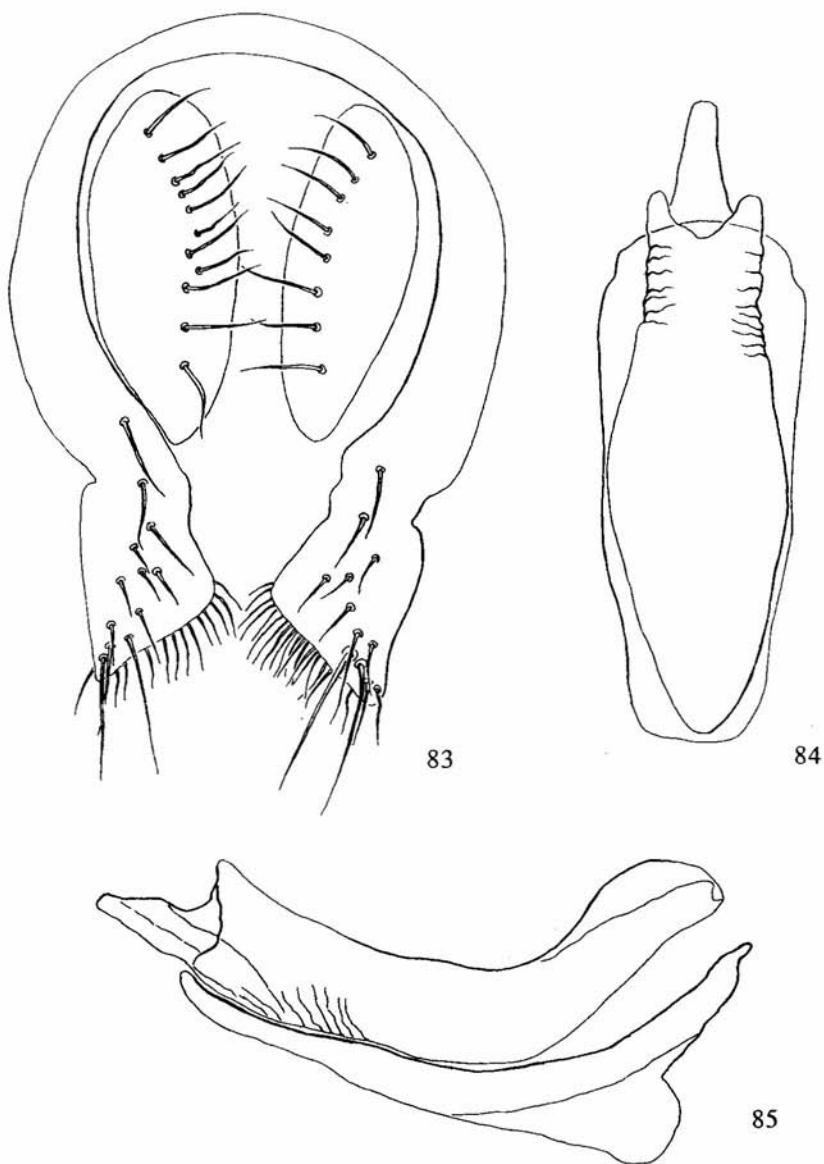
71-74. Male genitalia of *Hecamede albicans* (MEIGEN) from Burgas, Bulgaria (tribe *Hecamedini*): 71 - Cerci, epandrium and dististyli, dorsal view, 72 - Same, lateral view, 73 - Internal structures, dorsal view, 74 - Same, lateral view



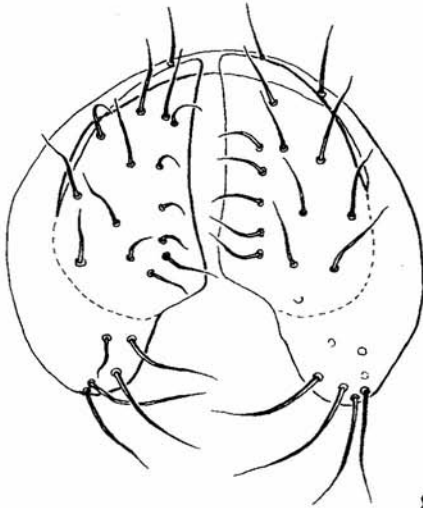
75-78. Male genitalia of *Lipochaeta slossonae* (COQUILLET) from Corona del Mar, California (USA) (tribe *Lipochaetini*): 75 - Cerci, epandrium and dististyli, dorsal view, 76 - Same, lateral view, 77 - Internal structures, dorsal view, 78 - Same, lateral view



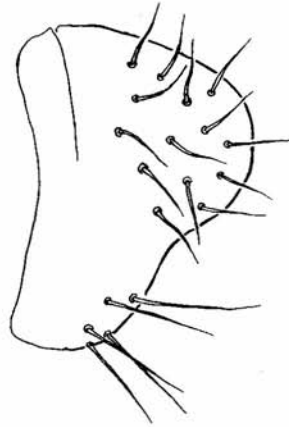
79-82. Male genitalia of *Paraglanthe bahamensis* WIRTH from Stann Creek, Belize (tribe *Lipochaetini*):
 79 - Cerci, epandrium and dististyli, dorsal view, 80 - Same, lateral view, 81 - Internal structures, dorsal
 view, 82 - Same, lateral view



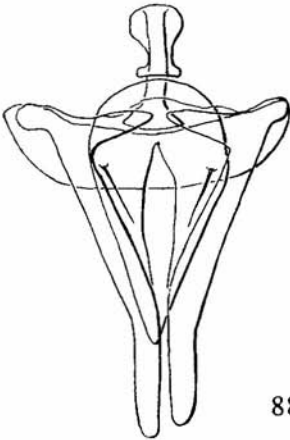
83-85. Male genitalia of *Zeros invenatus* (LAMB) from PNG, Zaire (tribe *Ilytheini*): 83 - Cerci and epandrium fused with dististyli, dorsal view, 84 - Internal structures, dorsal view, 85 - Same, lateral view



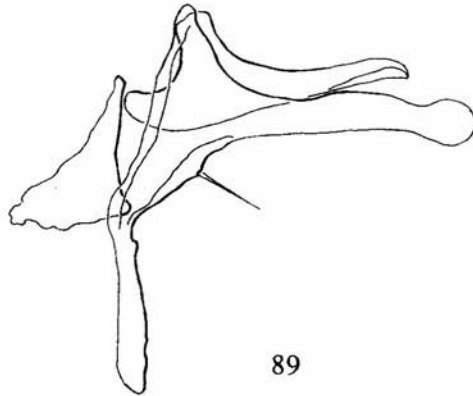
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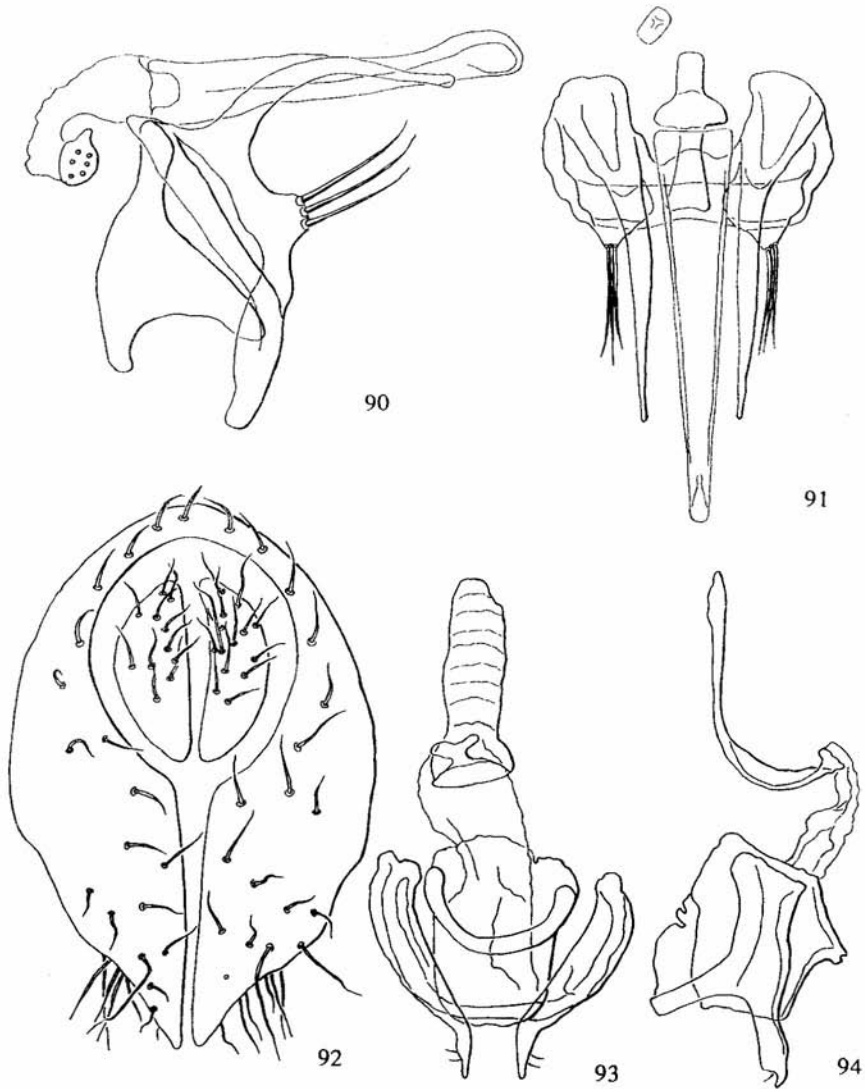


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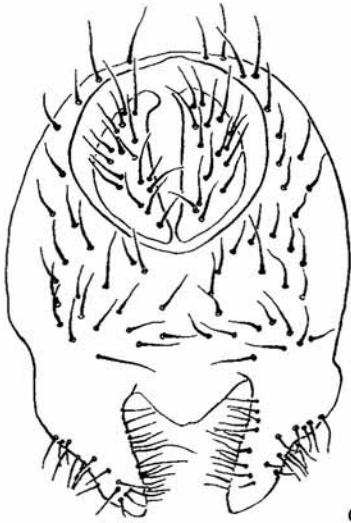


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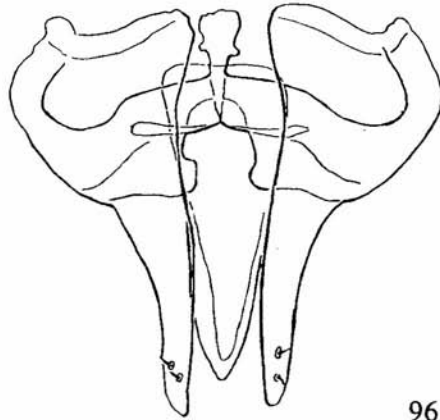
86-89. Male genitalia of *Nostima picta* (FALLÉN) from Praha-Holešovice, Czechoslovakia (tribe *Philygriini*):
 86 - Cerci and epandrium, dorsal view, 87 - Same, lateral view, 88 - Internal structures, dorsal view, 89
 - Same, lateral view



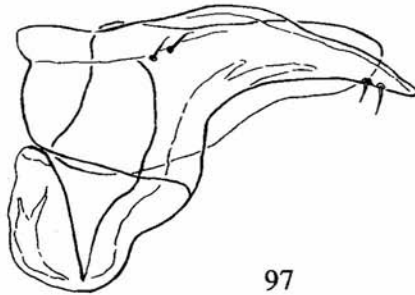
90-94. Male genitalia: 90-91. *Parydroptera discomyzina* COLLIN from Southwold, United Kingdom (tribe Hyadinini), 92-94. *Scatella subguttata* (MEIGEN) from Tipperne, Denmark (tribe Scatellini), 91, 93 - Internal structures, dorsal view, 90, 94 - Same, lateral view, 92 - Cerci and epandrium, dorsal view



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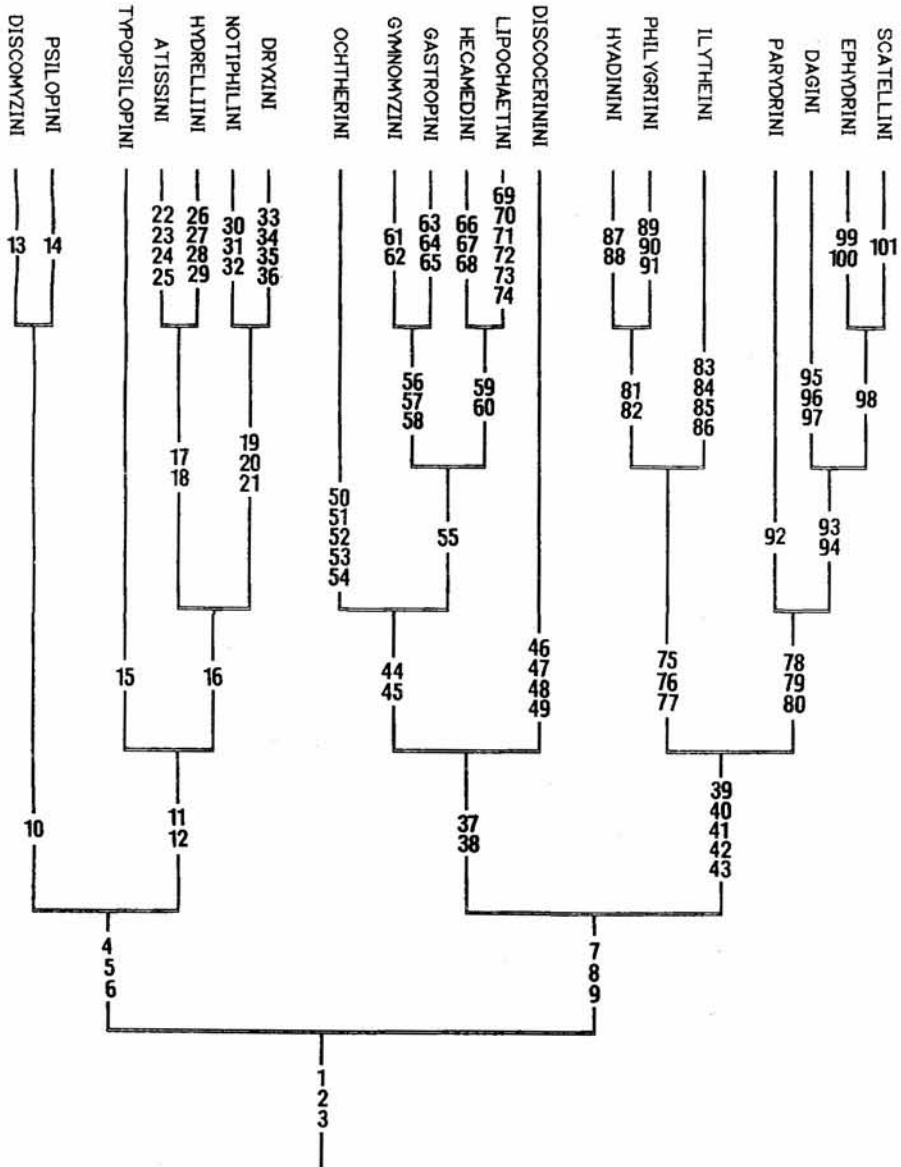


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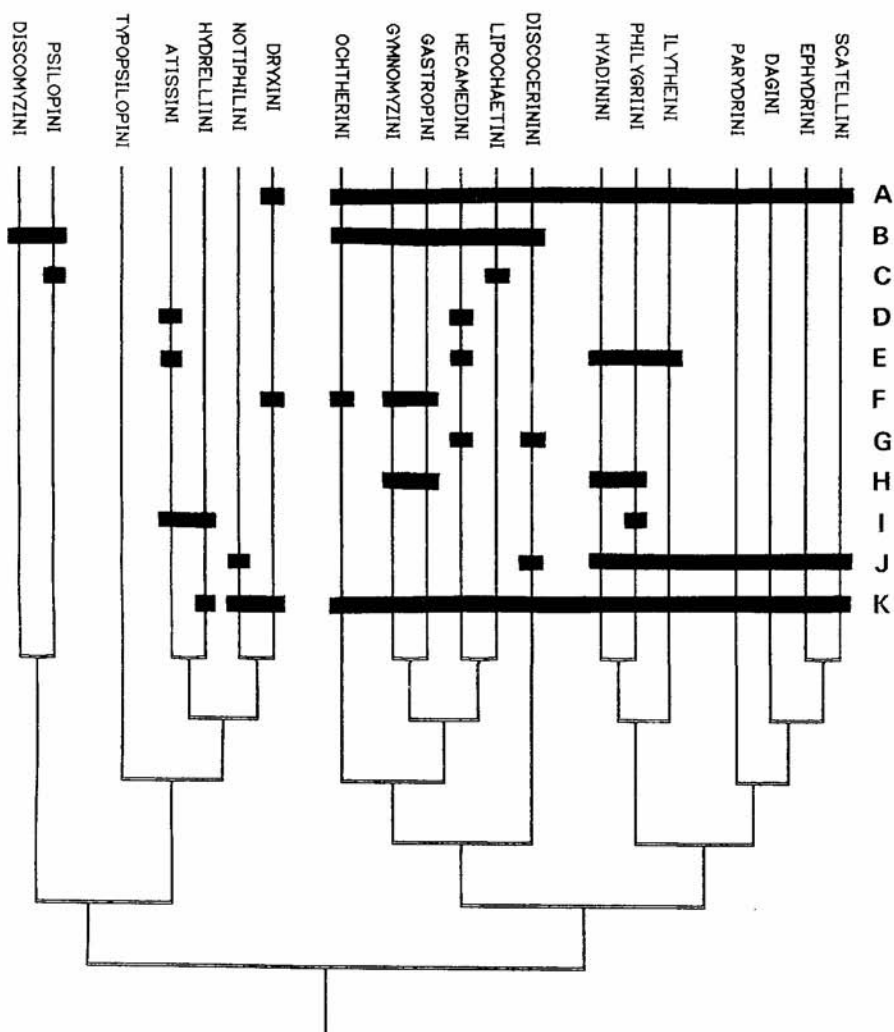


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95-97. Male genitalia of *Thiomyia quatei* WIRTH from Santa Paula, California (USA) (tribe *Ephydrini*): 95 - Cerci and epandrium, dorsal view, 96 - Internal structures, dorsal view, 97 - Same, lateral view



98. Hypothetical phylogeny of tribes of the *Ephydriidae*, based on the character evidence outlined in the chapter "Character analysis"



99. Homoplasies on the tribal level of the *Ephyridae*. Letters indicate the following kinds of characters (the numbers in parentheses correspond with those used in the chapter "Character analysis" and the cladogram): A - face projected (7, 33); B - postsutural dorsocentral seta reduced (10, 37); C - pseudo-postocellar seta reduced (14, 71); D - fronto-orbital seta anterior to ocellar seta (24, 66); E - upturned posterior notopleural seta (25, 60, 77); F - spine on pedicel weak (36, 51, 57); G - ocellar seta anterior to the ocellus (47, 67); H - prescutellar acrostichal seta reduced (56, 82); I - eye hairy (18, 91); J - dististyli reduced (30, 41, 49); K - subepandrial plate reduced (8, 21, 28)