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A CONTRIBUTION TO A GENERIC REVISION OF THE NEOTROPICAL MILESINAE (DIPTERA: SYRPHIDAE)

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ABSTRACT

A revised generic classification of the Neotropical Milesinae is proposed. Twelve tribes, six subtribes and forty-two genera are recognized and keys to these taxa are provided. Detailed descriptions of the tribes and genera, along with a discussion of the new characters used, are included. The male genitalia and some of the other principal characters for almost all the genera are figured.

One new genus (*Nollochellosia*, type-species *Chilosia nitescens* Shannon and Aubertin) is described. The following new synonymies are made: *Copestylum Macquart* (= *Apophysophora* Williston, = *Megametopon Giglio-Tos*, *Viereckomyia Curran*, = *Lepidopsis Curran*, = *Volosyrpha* Shannon and = *Volucellosia Curran*); *Dolichogyna Macquart* (= *Nosodepus* Spelser); *Habromyia* Williston (= *Edwardia* Hull, = *Lycopale* Hull and = *Crithrix* Hull); *Meromacrus* Rondani (= *Thalamopales* Hull); and *Sterphus Philippi* (= *Crepidomyia* Shannon, = *Tatuomyia* Shannon, = *Senoceria* Hull and = *Mutillimya* Hull). *Copestylum Macquart* is recognized for the New World species of *Volucella* Geoffroy. *Chromochellosia* Hull and Fluke is given full generic status and transferred from *Chellosia* (Chellosini) to the tribe *Chrysogasterini*. *Eristalis Latreille* is partitioned into *Eristalis*, s. s., *Eoseristalis* Kanervo and *Palpada* Macquart.

Zoogeography of the Neotropical milesine fauna is discussed. The gross statistics of the fauna are compared to those of other regions and these statistics indicate a long-isolated fauna. The distributional patterns and phylogenetic relationships of the Neotropical genera are also analyzed and these patterns and relationships support a Nearctic origin for almost all of the South American milesine flies. Continental Drift and its possible effect on the Neotropical fauna is also briefly reviewed. Finally the transition between the Nearctic and Neotropical milesine faunas is examined and this transition appears to consist of predominantly Neotropical groups that have moved northward, whereas only one Nearctic group has moved southward in the transitional zone.

INTRODUCTION

The family Syrphidae, commonly called "Flower or Hover flies", is a large group (over 5000 species) of rather conspicuous flies. Their sizes range from 4 mm to 25 mm and their colors from bright yellows and oranges to dull drab blacks and grays. Most syrphid adults are Batesian mimics of stinging Hymenoptera and are highly beneficial as pollinators. The economic importance of the larvae extends from the highly beneficial aphidophagous type of the subfamily Syrphinae to a few injurious pests of Narcissus bulbs (*Eumerus* spp. and *Merodon*

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equestris Linné). The vast majority are neither useful nor detrimental to man in the larval stage. Their medical importance is almost nil; a few cases of accidental intestinal myiasis have been caused by the drinking of putrid water containing the saprophagous larvae of *Eristalis* (see James, 1957, and Zumpt, 1965, for a general review).

Syrphid flies are worldwide in distribution, with their greatest diversity of forms in the New World tropics. Despite this interesting diversity and the critical zoogeographic importance of the Neotropical area, the South American forms are probably the most neglected of all syrphids taxonomically. Most of the research on the South American syrphids has been restricted to the simple description of new taxa with the majority of this having been done by Curran and Hull in the 1930's and 40's. Very little has been done to organize and synthesize all such descriptive studies. In the last seventy years only two keys to the Neotropical genera of the Syrphidae have been published. Both of these were written by Shannon in the later 1920's and early 1930's and thus do not include the more recent works of Curran and Hull. Hull (1949) has published a revision of the world genera, but his keys are difficult to use and his descriptions are incomplete and misleading. Considering the outdated nature of Shannon's work and the inadequacy of Hull's, a synopsis of the South American genera of Syrphidae is needed. This paper is intended as a contribution toward the filling of this void.

The approach I have used in this revision is three-fold. First, I will discuss and review the characters used for the groups of syrphid flies. Then from this base, the taxonomic interrelationships indicated by these characters will be discussed. Finally, the history of the syrphid distributions in South America will be deduced from an integration of syrphid phylogeny with the geological history of South America.

The methods of preparation and study of the specimens were the traditional ones: Flies were obtained and prepared for study by the standard techniques as described in various textbooks (Oldroyd, 1958; Ferris, 1928; and others); genitalic structures were prepared in the usual manner as discussed by Metcalf (1921), and were stored in microvials attached to the insect pin as described by Gurney *et al.* (1964); drawings were made with the aid of an ocular grid and graph paper (see Oldroyd, 1958).

The scope of this revision is restricted to the tribes and genera of the subfamily Milesinae that are found in the Neotropical region. This region is here considered as all of South America and all of Middle America south of the isthmus of Tehuantepec. The isthmus of Tehuantepec is the traditional boundary used for the Neotropical region by the zoogeographers. However, for practical reasons, the two catalogues covering the Nearctic and Neotropical Diptera have used the boundary between Mexico and the United States for the division of their coverage. Thus to make this revision correspond to the catalogue coverage, I have included the genera found in Mexico north of the isthmus of Tehuantepec in my keys, but I have not described them.

Although this revision is restricted to the Neotropical region, I have studied all available milesine taxa (about 80% of the genera) of the world for the purpose of improving my taxonomic perspective on the Neotropical fauna. For this reason I have included in my character tables and discussions all of the non-neotropical milesine genera that were available to me. With this information it was possible to work out preliminary schemes of generic phylogeny within various milesine tribes and, to a lesser extent, of tribal phylogeny of the Milesinae. It should be clearly realized that these phylogeny representations are only tentative, being based in many places on incomplete information about some of the non-neotropical taxa.

With over 3000 species and some 150 genera of known milesine syrphids in the world, of which over 500 species and about 50 genera and undoubtedly many more unknown forms are Neotropical, it is obviously not possible to study all the taxa, all the stages and all structures in one lifetime. Thus a sampling-type of approach to each genus must usually be used. A knowledge of the nature of the sample used for the basis of the study is necessary for the reader's proper evaluation of my conclusions. The sample has been limited, of course, to the Milesinae and to the Neotropical region, as indicated by the title. The nature of the taxonomic sample¹ is precisely indicated for each genus in a list of the species studied along with the approximate numbers of known world and Neotropical species. Being confined to external structure of the adult I may have missed some sources of possible characters of phylogenetic importance in the syrphids, such as immature stages and internal anatomy. However, it is not possible to investigate these other sources at present because too little material, suitable for study is available. In the immature stages, less than 10% of the Neotropical genera and less than 1% of Neotropical species have been described in the literature. Thus it has not been possible to include any meaningful data on the immature stages in this revision. Likewise, for the internal anatomy of these flies, there has been neither properly prepared material available for study nor any information available in the literature. Museum material has been available for the study of the male genitalia which I have used in this revision to help decipher the phylogeny of the milesine taxa and to assess the value of the external characters I have used. That is, I have checked to see that the male genitalia are consistent with interpretations based on external characters. I have figured the male genitalia of the type-species where possible and "typical" examples otherwise. The study of the full range of genitalic variation is beyond the scope of this revision as presently defined since it would involve many non-neotropical genera and species. Thus it is not possible now to indicate

(1) The format for these sample statements is as follows: Material examined: number of world species (number of Neotropical species); list of species examined. The asterisk indicates a Neotropical species and the (HT) or (PT) indicates that either the holotype or paratypes were examined.

what characters of the male genitalia are of tribal, generic, *etc.* importance.

The reasons given above for restricting myself to external adult characters are really only symptoms of a taxonomically confusing situation. The basic reason why immature stages have not been described, why internal anatomy has not been studied and why the range of variation in male genitalia has not been evaluated is that at the present time it is almost impossible to identify even the adults of the Neotropical species of syrphids. The first step toward the solution of the Neotropical species problem was made by Fluke whose catalogue (1956-57, being revised by Sedman, *in litt.*) provides an index to all the literature on the known Neotropical species and genera. This present revision provides the second step: a preliminary framework in which to place all the presently described species (and hopefully, new ones too!). In short, it is hoped that this contribution will provide a useful higher classification of the Neotropical milesines which will aid the study of the Neotropical fauna and the search for the answers to many of the unsolved questions it has revealed. Prerequisite to establishing such a framework is a concise working definition of a genus.

The *definition* of a *genus* generally accepted by taxonomists is: "a taxonomic category containing a single species or a monophyletic group of species, which is separated from other genera by a decided gap" (Mayr, 1969:92). Much generic synonymy is due to the fact that taxonomists do not always agree on the same interpretation of the words, "decided gap". Although Mayr has qualified the interpretation of "decided gap" by recommending "for practical reasons that the size of the gap be in inverse ratio to the size of the taxon", there still can be much latitude in interpretations as to what is a sufficient gap for the separation of two genera. Because of the latitude of opinions on the proper extent of the gap, the working standard used for genera in this revision is defined here. For practical purposes, a genus is here defined as a group of similar species in which: 1) a group of species is distinctly separable from all other related groups in all life stages, if known; and 2) *all* and *only* the species descendent from a unique common ancestor are included in a genus, so that all member species will be more closely related to one another than to species outside the genus concerned. The first qualification discourages the construction of genera on the basis of characters found only in one sex and encourages generic revision when the immature stages become known. Also by requiring genera to be distinctive in all stages, the genus will correspond more precisely with the ecological niches involved. The second qualification eliminates the use of paraphyletic groups (Hennig, 1965 and 1966).

The above operational definition places the emphasis on finding similarities, not differences between taxa. When the emphasis is placed on differences, the usual attitude of taxonomists, the tendency is to split groups, not to combine them. The result is a trend towards a

hodge podge of smaller and more numerous taxa with less and less distinctness. In some cases however, monotypic taxa are necessary since, for lack of sufficient evidence of similarities, certain species *can not* be placed in genera with other species.

TAXONOMY OF NEOTROPICAL GENERA OF THE MILESINAE

TAXONOMIC CHARACTERS OF GENERIC IMPORTANCE IN THE MILESINAE

Most of the characters used in this study are the well-known traditional ones (see Williston 1886:272-278; Lundbeck 1916:18-28; Shannon 1922:117-120; Curran 1924:14-16; Shannon 1926:6-7; and Hull 1949:259-268).

However, a few new characters and new interpretations of old characters have been used in this revision and an explanation of these with discussion of their distribution among the milesine syrphids has been included.

FACIAL SHAPE

Although the shape of the face is one of the traditional group characters in the syrphids, it is only recently (Hull 1945 and 1949) that the phylogenetic development of the various types of faces has been studied. In the conclusion of Hull's revision of fossil syrphids (1945) he discusses and diagrams the probable evolution of the facial region. He hypothesized that all the types of faces evolved from a straight type and diverged from this in four different lines — concave epistomal thrust type; convex type; tubercle type; and frontal thrust type (Hull 1945: Fig. 2). Later, Hull (1949) reversed himself on the starting point of the character phylogeny and stated that the convex type of face was the most primitive. This seems reasonable since the convex face is the type found in the primitive related Microdontidae (and also in the related primitive Pipunculidae). One alteration should be made of Hull's arrangement of facial types. My studies indicate that the tuberculate face is not a "dead-end" development but leads from the simple type of face to all the other facial types (Fig. 1).

In the Pipizini, the most primitive tribe of the Milesinae, as based on wing venation, pilosity, *etc.*, one can see a transition from the convex type of face to the tuberculate type. The pipizines have a convex face except for some species of *Trichopsomyia* which show traces of the development of a tubercle. *Trichopsomyia* is the most highly specialized member of the Pipizini (see text discussion, p. 93). In all the groups with frontal thrust types of faces there are still traces of the tubercle. The same is true of those groups with a downward thrust type of face and most of those groups with an epistomal thrust type. The concave type of face is a direct development from the tuberculate type. If the tubercle were removed from a face

the result would be a slightly concave face. In some genera of Chrysogasterini and Milesini, where the males have tuberculate faces, the females have a slightly concave, non-tuberculate face.

METASTERNAL DEVELOPMENT

The extent of sclerotization and shape of the metasterna varies within the Syrphidae. The different forms of the metasterna have been arranged into a linear morphocline (Fig. 2). At one extreme of the cline the metasternal sclerites are just a thin sclerotic band stretching from one coxal articulation to the other; at the other end of the cline the metasternal sclerites are strongly produced ventrally and their medial areas are sclerotized. I have designated the former

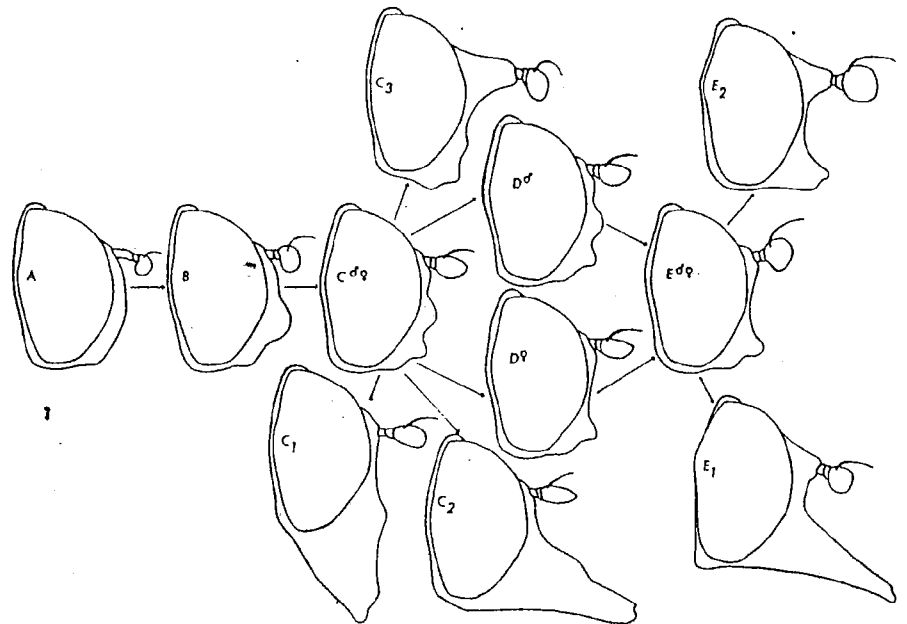


Fig. 1. Interrelationships between various milesine facial types. A, convex type; B, tuberculate type without notched oral margin; C, tuberculate types — C, normal tuberculate type; C₁, downward thrust type; C₂, epistomal thrust type; C₃, frontal thrust type; D, sexually dimorphic type; E, concave types — E, normal concave type; E₁, epistomal thrust type; E₂, frontal-epistomal thrust type.

as underdeveloped, the other extreme as well developed. The pipizines display the typical underdeveloped metasterna, whereas *Milesia* shows a good example of the well developed condition. The underdeveloped condition of the metasterna is found in pipunculids and microdontids and is therefore considered primitive.

FIRST ABDOMINAL SPIRACLE

The first abdominal spiracle is usually embedded in the metathoracic epimeron (Fig. 3). However, in two groups, Pipizini and Eumerini, the spiracle lies free of the epimeral plate in the membrane between the abdominal tergites and sternites (Fig. 3, 4).

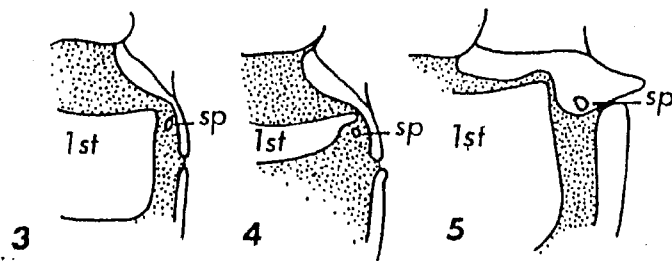
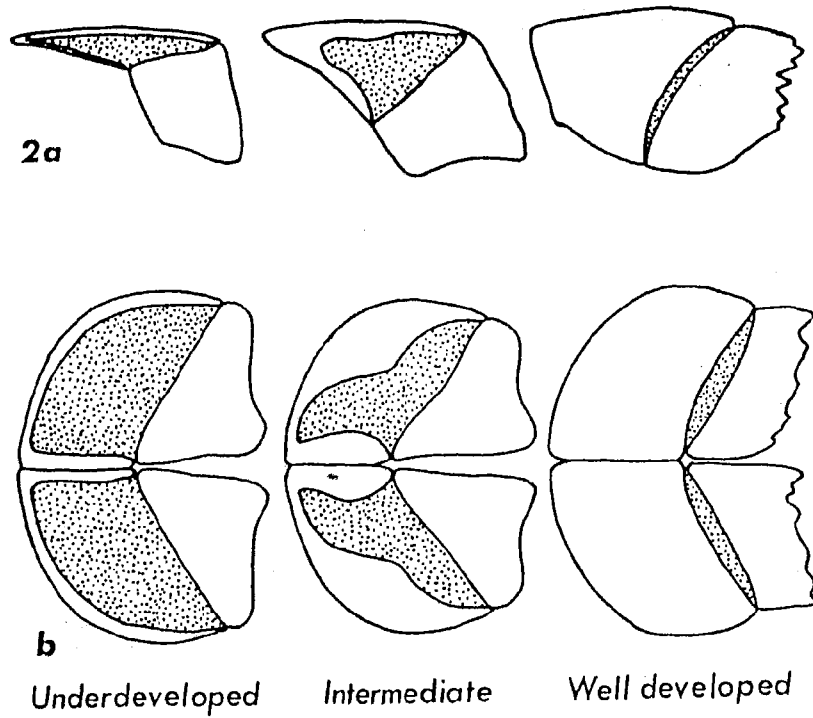


Fig. 2. Metasternal development: a, lateral view; b, ventral view. Figs. 3-5, first abdominal spiracle, ventral view: 3, Pipizine type; 4, Eumerine type; 5, normal type.

In the pipizines the "free" spiracle is probably a primitive condition since: 1) this is the condition of the spiracle in related primitive families (Microdontidae and Pipunculidae), and 2) many other characters show the pipizines to be primitive. This condition in the eumerines is probably a secondary specialization because 1) all the intermediate ancestral groups between the pipizines and the eumerines have the spiracle embedded in the epimeron; and 2) the first abdominal sternite has been reduced and modified to fit around the spiracle in eumerines whereas the pipizines have a normal first sternite as in other groups of the Milesinae.

THORACIC PILE PATTERNS

The taxonomic use of arrangement of pile on the thorax is a rather new development in syrphid classification and has not yet gained wide acceptance. Shannon was perhaps the first to recognize the great importance of pile patterns for generic characters. In a series of generic revisions (1921, 1922, 1926 and 1927) Shannon pointed out where the presence or absence of pile on particular parts of the thorax could be used to separate some groups. Although Shannon's work was accepted by most other syrphid workers, no other investigations for new thoracic pile characters were conducted until recently. Only Collin (1952a, b), Vockeroth (1969 and *in litt.*) and Thompson (1969) have extended this work. They found pleural thoracic pile patterns of great value for working out difficult groups like the Microdontidae (Thompson), the Pipizini (Collin) and the Syrphini (Vockeroth). Perhaps the use of thoracic pile patterns in combination with the more traditional characters will help to remove the enigma long associated with syrphid classification and characterized by Willinston's famous quote, "While, as a general rule, the *Syrphidae* present excellent specific characters, there is a remarkable dearth of generic or group characters." (1886: xiii).

The following discussion of thoracic pile patterns is restricted to the subfamily Milesinae. Vockeroth (1964 and 1969) has studied the pile patterns of the Syrphini and other syrphine groups.

Four conditions relating to hairs are usually recognized in the study of syrphids: 1) *Bare* — without pile but sometimes with either pubescence or pollinosity; 2) *Pollinosity* — opaque material which looks like fine powder or dust; 3) *Pubescence* — very short fine hairs, closely set together, much like velvet; 4) *Pilosity* — long scattered hairs, in some genera broadly flattened into *scales* (i.e., *Lepidomyia*, etc.), in other genera (i.e., *Meromacrus*, etc.) very thick and opaque and called *tomentum*; frequently in those genera and species which are wasp mimics there is a tendency for the thoracic pile to be composed of relatively small and appressed hairs. In the species of *Ceriana*, *Spheginobaccha*, *Neplas*, and other wasp mimics the normally long hairs of those sclerites which are pilose are very short and appressed to the exoskeleton.

Of the three types of modified hairs, the pilose condition is now considered to be primitive (Collin, 1952a; Chillcott, 1961:19). Hull (1949) considered the pilose condition to be derivative. He stated that there is a tendency toward the acquisition of pile on the metasterna, eyes and face. However, it is more logical to assume that primitive syrphids displayed the pilose condition since the pilose state is the usual condition found in Brachycerous and lower Cyclorrhaphous groups of Diptera (also in some higher Cyclorrhaphous groups).

Prothoracic Pile Patterns:

Pronotum, anepisternum, katespisternum, anepimeron and basisternum are the only distinct sclerotic areas of the prothorax, due to its reduction in size in the Diptera.

Pronotum or humerus: Shannon (1921-22) noted that the presence or absence of pile on the humerus could be used to distinguish most of the aphidophagous forms from other syrphids. This character correlates with the reduction of the pregenital segments in the males. All syrphids with five pregenital segments have the humerus bare and those with four pregenital segments have it pilose. Either one of these two characters will separate the subfamilies of Syrphidae. The subfamily placement of the Pipizini is somewhat in doubt. Even though they have a pilose humerus and four pregenital segments in the male, like the milesine flies, they are aphidophagous like the syrphines. Hopefully a study of the larvae will eventually elucidate their relationships. In *Alipumilio* the humeral hairs are greatly reduced in size and number, perhaps due to chafing against the close fitting head, but close examination will reveal a few hairs always to be present.

The *anepisternum* is usually strongly pilose. *Cerogaster*, all the Pipizini except *Pipiza*, and some species of *Ceriana* have the anepisternum bare. In *Spheginobaccha* the anepisternum is enlarged and swollen and has a vertical row of long stiff hairs in contrast to the normal, short, soft, scattered hairs.

The *katespisternum* is always bare on the posterior portion and frequently is completely bare. Most cristaline genera, and some species of the genera *Cheilisia* and *Copestylum* have the anterior portion pilose (usually not visible with the head attached).

The *anepimeron* has the pilosity ranging from completely absent through short and scattered to densely pilose. The majority of the Milesinae have the anepimera strongly pilose. A few short and scattered hairs can be found on this sclerite in *Valdivia*, *Chamaesphegina*, *Portevinia*, *Lepidomyia*, *Cerogaster*, *Neplas* and some species of *Sterphus*. It is bare in *Hammerschmidtia*, *Neoascia*, *Spheginobaccha* and *Alipumilio*. The whole spectrum of pilosity can be found in the genera *Ceriana* and *Brachyopa*.

The *basisternum* is usually pilose but the pile is generally represented by only a few hairs. In a few species the basisternum is bare but there appears to be no generic significance to this loss of pile.

The pilosity of this sclerite is either present or absent in each of the following genera: *Graptomyza*, *Trichopsomyia*, *Neocnemodon*, *Sphegina* and *Hemixylota*. In *Neoascia* it is always bare.

Mesothoracic Pile Patterns:

Of the three principal areas of the mesothorax, only the pleuron was found to display pile patterns of generic importance. The notum, except for the ventral portion of the scutellum, is always pilose and the sternal areas have been completely obliterated by the extension of the pleuron in Diptera. The sclerites of the pleuron that were examined for pile characters are: anepisternum; katepisternum; anepimeron; and meropleuron.

The *anepisternum*, frequently referred to as the mesopleuron, should, for the convenience of studying the pile, be considered as composed of two separate areas, a flat anterior portion and a convex raised posterior portion. Only in *Alipumilio* and *Nausigaster* is this distinction between the two portions lost and in these genera one finds a uniformly raised pilose anepisternum. The condition of the pile on the *anterior* part being variable amongst species, is of value for generic taxonomy. The *posterior* portion of the anepisternum is always pilose. The presence of some long hairs on the anterior anepisternal area was used by Collin (1952b) to separate his *Parapenium* from all other British Pipizini. Collin (1952a) also noted this character for a number of species in the genus *Syrphus*. His work appears to have been the first recognition of the importance of the pile of this particular sclerite. Very few of the milesine syrphids have the anterior anepisternum pilose and those that do are mainly limited to two principle taxa, Eumerini and Volucellina. These have the anterior anepisterna strongly pilose. *Spilomyia*, *Hardimyia*, *Odyneromyia* and a few species of *Temnostoma* also have the anterior part of the sclerite pilose. *Ceriana* has the upper half of the anterior anepisternum pilose. There are also traces of anterior anepisternal pile in a few other groups. In *Lepidomyia*, *Orthonevra* and some species of *Myolepta* there are a few hairs on the upper posterior corner of the anterior anepisternal area and *Valdivia* has a patch of a few hairs in the middle of the posterior edge of this area.

Katepisternum: Malloch (in Shannon 1922) pointed out that *Sphegina* could be separated from *Neoascia* by its completely bare sternopleuron (katepisternum). Except for this particular case, the presence or absence of katepisternal pile was found to be of little use in the generic taxonomy of the Milesinae. In the majority of the species examined there are two patches of pile on the katepisternum: a dorsal patch on the upper portion of the sclerite and a ventral patch between the pro- and mesocoxae, usually separated by a broad bare area. In a few scattered species one or the other of these patches is absent and in some other species these patches are broadly connected. Although the katepisternal pile patches appear to have no value as generic

characters, they may be useful as species or species group characters. It should be noted that, whereas in the milesines no generic value for the pilosity of the katepisternum is apparent, Vockeroth (1969) has found the character very helpful with syrphine genera.

The *anepimeron*, frequently referred to as the pteropleuron, should, for convenience of studying the pile, be divided by an imaginary line from the large cleft on its dorsal edge to the ventral edge into an anterior and posterior portion. The anterior portion is always pilose. The posterior portion is commonly bare but in a few groups this part of the anepimeron is pilose. In *Spilomyia*, *Korinchia*, *Ornidia*, *Pseudovolucella*, *Pyritis*, *Arctophila* and many eristaline genera there is some pile on the posterior portion.

The *meropleuron* is always bare except for two restricted areas, along the barrete and in front of the metathoracic spiracle.

The barrette, the upper edge (usually convex) of the meropleuron, is bare in most milesine syrphids. It is pilose in all Pipizini except *Pipiza*. *Chromocheilosia bicolor* and *Myolepta luteola* are the only chrysogasterines I have seen with pilose barrettes. In the volucellines all species of *Volucella* and *Ornidia* and a large group of *Copestylum* have the barrette pilose. In the milesines only *Merapioidus*, *Deineches*, and some species of *Criorhina* have the barrette pilose. *Criorhina* can be divided into two species groups based on the presence or absence of pile on the barrette (Vockeroth, *in litt.*). In the Eristalini, *Mesembrius*, *Megaspis*, *Eristalodes*, *Eristalis*, *Palpada*, *Lycastirrhyncha*, *Simioides*, and *Dolichomerus* have the barrette pilose.

The presence of a *metathoracic spiracular pile patch*, a patch of long hairs in front of the metathoracic spiracle, is a primitive trait found in only a few groups of syrphids. Among the non-syrphine groups I have found this character state in only the volucellines, some eristalines, *Psilota*, *Notiocheilosia*, *Lepidomyia*, most species of *Myolepta*, and some species of *Rhingia*. In *Rhingia* some species (*nasica* and *campestris*) have a distinct patch, others like *harrisi* have a few hairs only, and still others (*rostrata*) are completely bare in some individuals and have a few hairs in others. The patch is reduced to a narrow row of hairs in the eristaline genera which have the spiracular patch. Only *Megaspis*, *Simioides*, *Meromacrus*, *Eristalodes*, *Palpada*, and *Lycastirrhyncha* among the eristaline genera have the spiracular hair patch.

The *scutellar fringe* frequently is present on the ventral apical portion of the scutellum. This fringe was first noted by Lundbeck (1916) and its condition was described by him for all the Danish syrphid genera. Shannon (1922) discussed this character in relationship to the various cheilosine groups. He noted: 1) that all the Cheilosini had an "abundant fringe"; 2) *Chrysogaster* and *Apicomomyia* (= *Cynorrhinella*) had a fringe reduced to a single row of hairs; and 3) all the rest of the groups of Cheilosinae lacked the fringe altogether. Goffe (1952), in his reclassification of the syrphids, used this character to define his third key dichotomy. I have noted a distinct

subscutellar fringe in the following tribes and genera: Pipizini; Cheilosini; most Milesini except *Spilomyia*, *Chrysosomidia*, *Merapiooidus*, some species of *Criorhina*, and *Temnostoma*; *Notiocheilosia*; *Chromocheilosia*; *Psilota*; *Azpeytia*; and some *Copestylum*.

Metathoracic Pile Patterns:

Like the prothorax, the metathorax in Diptera is greatly reduced and only three distinct areas are identifiable on the metathorax: episternum, epimeron and basisternum. The episternum is pilose only in *Spilomyia*, *Syritta*, *Senogaster* and *Mesembrius*. The epimeron is bare in all groups of milesine syrphids except *Nausigaster*. In *Nausigaster* this small sclerite is sparsely punctate and pilose.

The pair of sclerites between the meso- and metacoxae have been called by various terms such as, antecoxal piece, metasternum, and basisternum. Shannon in 1921-22 first used the presence or absence of pile on the antecoxal piece as a taxonomic character to separate some of the genera of his subfamily Xylotinae. Later Shannon (1922) discussed the value and distribution of the various states of this character in the Cheilosinae. He made the undefended statement that the character is only of "specific importance" in the Cheilosinae as is the case in the Xylotinae. Then in his revision of the xylotine flies (1926) he used the character for the main division of his key and also described two new genera based on metasternal pile. In his two keys to the South American genera (1927) and (1933) he continued to follow his 1926 use of the character in the xylotine groups. Hull (1949) in his revision of the world genera also placed strong emphasis on metasternal pile, describing it for all the genera.

I have found the metasterna bare in the following taxa: Pipizini, Cheilosini (Pelecocerina), all Chrysogasterini except some species of *Myolepta*, Cerioidini, *Nausigaster* of Eumerini, and some Milesini (*Blera* group; *Xylota* group except *Xylotomina*, *Neplas* and *Chalcosyrphus*; *Temnostoma* group except *Takaomyia*, *Teuchnemis* and some species of *Temnostoma*; and *Korinchia*, *Pseudozettsetdia*, *Palumbia* and *Hemixylota* of *Milesia* group). The following taxa have the metasterna pilose: Cheilosini (Cheilosina), some species of *Myolepta* of Chrysogasterini, Eristalini, all Eumerini except *Nausigaster*, and some Milesini (*Criorhina* group; *Tropidia* group; *Milesia* group except *Korinchia*, *Pseudozettsetdia*, *Palumbia* and *Hemixylota*; *Takaomyia*, *Teuchnemis* and some species of *Temnostoma* of *Temnostoma* group; and *Xylotomina*, *Neplas* and *Chalcosyrphus* of *Xylota* group). The metasternal pile character is intragenerically variable in only two genera, *Myolepta* and *Temnostoma*. However, it should be noted that this may be only an artifact of the present classification, and thus a more thorough investigation of these two genera from a worldwide basis might show the state of the character to be constant in each genus.

CLASSIFICATION OF NEOTROPICAL GENERA OF THE MILESINAE

CHARACTERIZATION OF THE FAMILY SYRPHIDAE

The syrphids can be easily separated from most dipterous groups by the following wing venational characters: 1) presence of long basal and anal cells; 2) apical and discal cells present and closed; 3) presence of a spurious vein between the radial and medial veins; and 4) radial sector only two-branched. The only family with which the Syrphidae may be confused is the Microdontidae, which was until recently included in the Syrphidae (Thompson, in preparation). However, the following key will separate the two families and summarize the main differences.

1. Hind femora, and usually tibiae, with pronounced scars or cicatricies; postmetacoxal bridge always complete; face always convex in profile, uniformly pilose, with oral margin not notched; antennae usually long, longer than face, with first segment usually much longer than broad. Male genitalia with: ejaculatory duct strongly sclerotized on posterior part, with a swollen and spherical portion partially enclosed by base of aedeagus, with apical portion elongate and completely ensheathed by aedeagus; aedeagus elongate, swollen basally, unsegmented, tubular, never with lateral or dorsal processes although frequently divided apically into two parallel tubes; aedeagal apodeme double or absent; posterior dorsal surface of ninth sternite infolded
..... Microdontidae

Hind femora and tibiae never with scars or cicatricies; postmetacoxal bridge usually incomplete, if complete, then face either distinctly concave or tuberculate; face usually either straight, concave, or tuberculate, rarely convex, either pilose or bare, almost always with a distinct notch in the oral margin; antennae usually short, shorter than face, with first segment rarely longer than broad. Male genitalia radically different from the Microdontidae: ejaculatory duct membranous, never swollen or spherical, always a simple unmodified duct; aedeagus rarely elongate, frequently two-segmented, usually with lateral or dorsal processes; aedeagal apodeme always present and single; posterior dorsal surface of ninth sternite not infolded Syrphidae

The subfamilies of the family Syrphidae can be separated by the following key:

1. Pronotum bare, with 5 pregenital segments in male
..... Syrphinae
- Pronotum pilose, with 4 pregenital segments in male
..... Milesinae

CHARACTERIZATION OF THE SUBFAMILY MILESINAE

Unlike the Syrphinae, the subfamily Milesinae is a very diverse group in both adult and larval forms, and at present is easily defined by two characters: 1) pronotum pilose; and 2) male with only four pregenital segments. The possession of only four pregenital segments in the males is the result of many complex peculiarities including such things as: reduction of fifth tergite and sternite, asymmetric modification of the fifth sternite, and 90° rotation of the sixth segment. This character complex is a derived condition found only in one other group of the Aschiza, the family Microdontidae. All other related families have five pregenital segments in the male (Platypezidae, Phoridae, Ironomyidae, Pipunculidae, Conopidae, and many groups of the Schizophora).

A major unsolved problem with the present subfamily groupings is the placement of the tribe Pipizini. The pipizines have a pilose pronotum and four pregenital segments in the male, like the rest of the Milesinae, but their larvae are aphidophagous, which is unique among the milesines. Various workers (such as Hartley, 1961, and Wirth *et al.*, 1965) have used the carnivorous type of larvae as the evidence for placing pipizines with all the rest of the aphidophagous syrphids in the subfamily Syrphinae, but as pointed out by Thompson (1969), this placement in the Syrphinae creates more problems than it solves. Also, it should be noted that our knowledge of the aphidophagous habits of the pipizines rests mainly on field work, and thus, until someone does a detailed morphological study of the mouthparts of the larval pipizines to show whether the carnivorous habit is convergent with the Syrphinae or not, the pipizines are best left in the Milesinae on the basis of adult structures. Another unsolved question which could affect the placement of the Pipizini is whether the aphidophagous types of larvae are derived from the supposed primitive saprophagous types or vice versa. The present evidence (Hartley, 1961 and 1963) is not conclusive for either option. Pending new evidence to the contrary, the Pipizini are placed in the Milesinae where most workers have placed them (Shannon, 1921-22; Curran, 1924; Sack, 1928-30, 1930; Shiraki, 1949 and 1968; Seguy, 1965; Hull, 1949; Coe, 1954; and Fluke, 1957-58).

The history of the suprageneric classification of the family Syrphidae is in a large part also the history of the classification of the Milesinae since the Syrphinae have remained the same since it was first recognized and almost all the major changes in the classification of the Syrphidae have occurred in what is here considered the Milesinae. Since Rondani (1856-1857) first divided the Syrphidae into suprageneric groups, there have been two separate trends in classifying the higher groups of the family. The earliest of these trends was to elevate gradually each distinctive group of genera to subfamily status. Starting with Rondani's five subfamilies, various workers have increased the number of subfamilies to a high of 21. Goffe (1952) has reviewed, except for Shiraki's work (1949 and 1968), the historical development

of the increase in syrphid subfamilies. Goffe (1952) was first to reverse the trend of increasing the number of subfamilies and suggested the use of two main groups only. Since Goffe's two subfamilies represent the two major phylogenetic lineages in the family, it is unfortunate that his oversimplified system of dividing the subfamilies results in obviously polyphyletic suprageneric groups and does not represent syrphid phylogeny. Whereas Goffe reduced the number of subfamilies to two, he increased the number of suprageneric groups to a new high of 32. Wirth *et al.* (1965) have slightly modified Goffe's two subfamily groups and have greatly improved the arrangement within each subfamily by reducing and incorporating Hull's 1949 classification into Goffe's two main groups. I have also followed Goffe's usage of two subfamilies except for considering one of his subtribes, the Microdontina, as a separate and distinct family (Thompson, in preparation) arrangement of tribes within the subfamily Milesinae (Sphixinae Goffe) is quite different from that of Goffe or Wirth.

In this revision 12 tribes are recognized in the Milesinae. Hull (1949) recognized 12 subfamilies and 25 tribes (Table I) among the

Table I. The arrangement of suprageneric taxa used by Hull (1949) for the World milesine Syrphids

Subfamily Microdontinae	Subfamily Volucellinae
Tribe Ceratophyini	Tribe Graptomyzini
Microdontini	Volucellini
Subfamily Eumerinae	Subfamily Sericomyinae
Subfamily Nausigasterinae	Subfamily Xylotinae
Subfamily Cheilosinae	Tribe Xylotini
Tribe Rhingini	Temnostomini
Pipizini	Milesinae
Chrysogasterini	Criorhinini
Sphagini	Pocotini
Myioleptini	Tropidini
Cheilosini	Subfamily Psarinae
Subfamily Calliceratinae	Subfamily Cerioidinae
Subfamily Pelecoceratinae	Subfamily Eristalinae
	Tribe Helophilini
	Eristalini

group of flies equivalent to my usage of Milesinae. More recently Wirth *et al.* (1965) have reduced the status of many of Hull's tribes and subfamilies to incorporate them into a two subfamily arrangement (Table II). My arrangement of tribes and genera in the subfamily Milesinae follows that of Wirth *et al.* except for four major changes along with a number of minor changes in the placement of genera into the tribes. The first change, the placement of the Pipizini into the subfamily Milesinae, has been discussed above. The second change is in recognition of the fact that the Microdontini are not true syrphids but represent a separate family as outlined above under the family discussion. This will also be covered in more detail in a separate paper. The third major change is the combination of three small aberrant tribes (two are monotypic) into one. I have "lumped" the Eumerini, Nausigasterini, Merodontini, along with *Psilota* and *Alipumilio* of Chrysogasterini into one tribe, Eumerini. The previous recognition of these tribes as separate taxa has been due to the fact that taxonomists have em-

Table II. The arrangement of suprageneric taxa used by Wirth

& *al.* (1965) for the milesine syrphids found in

America north of Mexico

Subfamily Syrphinae

Tribe Pipizini

Subfamily Milesinae

Tribe Cheilosini

Myoleptini

Chrysogasterini

Callicerini

Pelecocerini

Nausigasterini

Eumerini

Microdontini

Volucellini

Sericomyini

Milesini

Certeroidini

Merodontini

Eristalini

phasized the unique characters of each taxa and did not look for similarities. For example, Wirth *et al.* separated *Merodon* from the Eristalini to form a separate tribe because *Merodon* has a phytophagous larva whereas the rest of the eristalines have saprophagous larvae. It is surprising to me that they did not compare *Merodon* with the *only* other phytophagous milesine syrphid group, the eumerines. As a matter of fact, both *Merodon* and *Eumerus* have the same common English generic name, Narcissus Bulb Flies. The detailed reasons for combining these tribes and genera together has been discussed under the tribe Eumerini in the text.

Finally, I have reduced the Pelecocerini to a subtribe in Cheilosini. The traditional reason for considering the pelecocerines as a separate tribe or subfamily has been their unusual arista. However, I do not feel that the unusual arista alone is sufficient ground for tribal recognition. Sedman (1955) has shown that the pelecocerines have the typical and unique two-segmented aedeagus of the cheilosines. The nature of the aedeagus, along with the presence of thoracic bristles and non-dimorphic tuberculate faces, indicates that the pelecocerines are nothing more than cheilosines with atypical arista. Thus I have reduced the tribe to subtribal status (also see page 101).

Presently it is not possible to draw a detailed phylogenetic arrangement for the milesine tribes because too little is known about the primitive or derived nature of various character states. However, it is possible to present a general picture of the phylogenetic position of the tribes from the information provided by a few wellknown morphoclines.

The best known morphocline among the syrphids is the change in the shape and position of the anterior crossvein relative to the discal cell. The anterior crossvein ranges from being straight and located almost at the base of the discal cell to being strongly oblique and almost at the outer extreme of the discal cell, with almost every intermediate stage represented by some living species. Schiner (1862) was, I believe, the first to recognize the taxonomic importance of the anterior crossvein and since then it has been almost universally accepted by syrphid workers that the basal position represents the primitive end of the cline. The primitive nature of the basal position is supported by the fact that this is the condition found in the most closely related primitive families (Microdontidae and Pipunculidae) in addition to the reasons given by Hull for example (1949:274). The second morphocline of importance relates to the facial shape, evolving from a pilose convex condition to a bare concave condition. The facial morphocline has been illustrated and discussed in the character section. It should be noted that the extremes of the anterior crossvein cline and the facial cline correlate well with each other. The change in development of the metasterna from the very underdeveloped condition to the greatly enlarged condition (see character section) forms another morphocline which also corresponds in evolutionary direction with the facial and anterior crossvein clines.

Another major trend in the syrphids is the loss of pile on various parts of the body. This has not occurred in a uniform fashion, but generally the metathoracic sclerites, meropleurae, and anterior meso-anepisterna appear to have been the first areas to lose their pile. The loss of pile appears to be irreversible. The arrangement of thoracic pile has been discussed in the character section as well as the reasons for considering the bare condition as being derivative. Other tendencies of value in determining the phylogeny of the syrphids are: 1) bases of femora acquire basal setal patches; 2) hind femora acquire ventral spines; 3) third vein acquires a loop or kink. All of these trends have been discussed in detail by Hull (1949:262-268, 273-274).

With the above morphoclines the phylogenetic positions of the milesine tribes can be characterized as follows:

Pipizines are clearly the most primitive of the milesine syrphids because they have: 1) strongly basal and straight anterior crossvein; 2) pilose convex faces; 3) underdeveloped metasterna; 4) no hind femoral spines; 5) no basal setal patches on any femora; 6) third vein always straight; and 7) subscutellar fringe. In short, the pipizines display the primitive extremes of all the morphoclines studied.

Callicerini, *Volucellini*, and *Cheilosini* represent a group of primitive flies characterized by possession of the following common features: 1) pilose and non-dimorphic (sexual) tuberculate faces; 2) pilose and underdeveloped metasterna; 3) anterior crossvein basal in position and straight; 4) thoracic bristles and subscutellar fringe usually present; and 5) absence of hind femoral spines. *Cheilosini*, with their highly specialized two-segmented aedeagi, are perhaps more recently derived than either *Callicerini* or *Volucellini*, which both have unsegmented aedeagi.

The *chrysogasterines* are intermediate between the more primitive milesine tribes mentioned above and the more advanced ones mentioned below. The intermediate conditions found in the *chrysogasterines* are: 1) anterior crossvein usually at the middle of the discal cell or slightly before it; 2) faces concave in both sexes or concave in females and tuberculate in males and usually bare; 3) metasterna bare but underdeveloped; 4) subscutellar fringe usually absent but scutellar or thoracic bristles frequently present.

The position of the *Sericomyini* is certainly phylogenetically intermediate and may be closely related to the *Volucellini*. The intermediate and specialized conditions found in the *sericomyines* are: 1) faces usually bare; 2) anterior crossvein at or beyond the middle of the discal cell; and 3) thoracic bristles absent. The primitive conditions of the *sericomyines* are: 1) faces non-dimorphic tuberculate; 2) femoral spines absent; and 3) metasterna pilose and underdeveloped. The tuberculate faces, position of anterior crossvein, lack of femoral spines, and particularly the plumose arista suggest a close relationship to the *volucellines*.

The exact phylogenetic position of *Spheginobacchini* is rather problematic. The straight and basal position of the anterior crossvein

along with the underdeveloped metasterna and tuberculate or convex faces are indicative of the primitive nature of the spheginobacchines but the presences of femoral spines strongly suggests that Spheginobacchini has an intermediate position in the phylogeny of Milesinae.

The *eumerines*, like the chrysogasterines, are intermediate. The possession of concave but pilose faces is a curious intermediate condition apparently restricted to the eumerines and *Milesia*. The ventral femoral spines and usually developed metasterna are derived conditions in the Eumerini, whereas the pilose anterior meso-anepisterna is a primitive trait. The anterior crossvein is in the middle area of the discal cell.

The *eristalines* are a recently derived milesine tribe because they are the only tribe with basal setal patches on all femora and always have a looped third vein. They also have hind femoral spines, an advanced feature. However, the pilose and tuberculate faces, pilose metasterna, and anterior crossvein at or only slightly beyond the middle of discal cell indicate that the eristalines are not as highly advanced as either the Milesini or Cerioidini.

The *cerioidines* and *milesines* are apparently the most highly advanced of the milesine tribes since they are generally essentially bare flies with the anterior crossvein located well beyond the middle of discal cell. Whether the cerioidines are more recently derived than the milesines is difficult to determine because both tribes are evolving along different lines. The cerioidines have retained the primitive tuberculate face and terminal style on the antennae, but they have greatly developed metasterna. On the other hand, while the Milesini includes, undoubtedly, the most recently derived genera (such as *Milesia*, which has a strongly concave face, greatly reduced pile, well-developed metasterna, and highly specialized wing venation), some of the milesine genera are much more primitive (such as *Hemixyloa*, which has a basal anterior crossvein). In short, Cerioidini are a small homogeneous taxon with many derived traits but a few very primitive ones, and the Milesini are a large heterogeneous tribe with many highly derived genera but with a few intermediate genera.

In general, the milesine tribes can be grouped as primitive, intermediate, or advanced on the basis of facial development, position of anterior crossvein, and presence or absence of hind femoral spines. The primitive tribes have basal anterior crossveins, convex or tuberculate faces in both sexes, and lack hind femoral spines, whereas advanced tribes have apical anterior crossveins, hind femoral spines, and usually have concave faces. The intermediate tribes have a mixture of primitive and derived character states, but usually have the recently derived hind femoral spines.

KEY TO THE TRIBES OF THE SUBFAMILY MILESINAE

1. Hind femur with well-developed anterior, basal patch of setulae;
anterior meso-anepisterna bare Eristalini

- Hind femora without basal patches of setulae; if with basal patch of setulae, then anterior meso-anepisterna pilose. 2
2. Anterior crossvein (r-m) usually perpendicular, usually before the middle of the discal cell, never greatly slanted nor extending to the outer third or more of discal cell; if located at the middle area of the discal cell, then either with bristles on the thorax or with ventral spines on anterior four femora, or with basal patch of setulae on hind femora; and usually with underdeveloped metasterna 3
- Anterior crossvein always slanted, usually beyond the middle of the discal cell, frequently greatly slanted and extending to the outer third or more of the discal cell; if located at the middle area of the discal cell, then with neither bristles on the thorax nor ventral spines on anterior four femora nor basal patches of setulae on hind femora and usually with developed metasterna 10
3. Oral margin evenly rounded, not notched apically; eyes and face pilose; subscutellar fringe present; facial grooves reduced to pits; hind femora unarmed Pipizini
- Oral margin notched anteriorly; never with all the above characters together in combination 4
4. Pro-anepisternum greatly swollen and produced dorsoventrally, with a vertical row of long stiff hairs ... Spheginobacchini
- Pro-anepisternum not greatly swollen nor produced, without a row of hair 5
5. Apical crossvein (upper turned portion of R4+5) either strongly recessive or straight; arista usually plumose; with a distinct patch of hairs in front of metathoracic spiracle .. Volucellini
- Apical crossvein usually not recessive or straight; if recessive or straight, then without the metathoracic spiracular hair patch 6
6. Anterior meso-anepisternum pilose; frequently with a notal wing shield; scutellum with apical rim Eumerini
- Anterior meso-anepisterna bare; never with notal wing shield; scutellum without apical rim 7
7. Antennae on short frontal pedicel; 1st abdominal spiracle free. Psarini
- Antennae not on a pedicel; 1st abdominal spiracle in meta-epimeron 8
8. Subscutellar fringe usually absent; if present, then hind tarsi with ventral longitudinal combs; hind femora always armed with ventral spines Chrysogasterini