

A HISTORICAL PERSPECTIVE TO *Simulium (Ectemnaspis)* AND *Simulium (Psilopelmia)* LIMITS

by

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Resumen

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Los límites de los subgéneros de la familia Simuliidae han cambiado a lo largo del siglo. Esos límites están basados en diferentes perspectivas sobre grupos, caracteres y marcos teóricos. Actualmente la dificultad para definir los límites de especies entre *Simulium (Ectemnaspis)* y *Simulium (Psilopelmia)* se genera a partir de dos propuestas: Coscarón (1984, 1987, 1990, 1991) y Crosskey (1987, 1990). Esta controversia puede ser resuelta al usar un enfoque filogenético para crear un marco de corroboración de los límites entre los subgéneros.

Palabras claves: Simuliidae - filogenia - *Ectemnaspis* - *Psilopelmia*.

Abstract

Taxonomic limits between subgenera of the Simuliidae have changed throughout this century. Some of the difficulties in defining the subgenera *Simulium (Ectemnaspis)* and *Simulium (Psilopelmia)* arise from differing perspectives about the groups, the use of different sets of characters, and/or the application of different theoretical frameworks to study them. Of particular importance in this connection are the opposing points of view presented by Coscarón (1984, 1987, 1990, 1991) and Crosskey (1987, 1990). The controversy can be resolved with the use of a phylogenetic approach which provides an effective method to clarify the limits between subgenera.

Key words: Simuliidae - phylogeny - *Ectemnaspis* - *Psilopelmia*.

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"It is the objective of phylogenetic systematics to discover these [supraspecific] taxa and either name them or make their presence immediately apparent."

Wiley (1981:70)

Introduction

Simuliidae is a well known family since some of its members are *Onchocerca / Mansonella* vectors or pests due to their biting activity (Crosskey, 1990) or interesting from an ecological perspective (Cummins, 1987). Their economic and scientific importance notwithstanding, the taxonomy of the family is not clearly understood and there remain many taxonomic problems to be solved at the generic, subgeneric and specific levels.

For the purposes of this study we have chosen *Simulium (Ectemnaspis)* and *Simulium (Psilopelmia)*, but this situation could be extended to all neotropical Simuliidae. The main difficulty arises from the existence of two opposite view points. Coscarón (1984, 1987, 1990, 1991) and Crosskey (1987, 1990) have each had different perspectives in their definition of species limits in these two subgenera. Kuhn (1970) says we see the world using a particular metaphor and, always, different metaphors come from dissimilar theoretical frameworks. Since we have to choose just one classification to carry out our systematic research, we must try for this choice to be, if not completely objective, at least testable (*sensu* Popper, 1959, 1963).

Generic concepts

The meaning of the word "genus" has been controversial since it was first proposed by Linnaeus (1735). The International Code of Zoological Nomenclature requires the use of this category as defined by Linnaeus. The "orthodox" school on the other hand, states that the species is the only valid or real taxonomic entity (see Mayr, 1969). The genus concept was originally used by Plato or maybe even before but its usefulness and value continue to be a matter of discussion (Radl, 1988; Papavero & Llorente, 1992; Papavero, Abe & Llorente, 1993a,b).

Plato (*circa* 370 b.c.) formulated the "diaeresis" method through which one could go bi-dissecting from general to particular to find the last indivisible particle. This "diaeretic" method is based on the "contradiction principle" which states that an object can not be included

simultaneously in being and not being. On this basis, first was the dicotomy {as a bi-section} guided by the affirmation - contradiction principle and second defining the object using the properties it has or lacks.

The effort to arrive at the classification of the last object (*eidos=species*) through "diaeresis", made Plato and his academy understand the species as a logical systematic concept as opposed to the "genus" concept (*genos=genus*), which was placed eventually above it (Jahn *et al.*, 1990). At the beginning of the scholastic period Porfirio (*circa* 260) reinitiated the controversy by asking if the "genus" (and species) was a real entity [*sive substant*] or only a conception of the mind [*sive in solis nudis intellectibus consistant*] (Radl, 1988).

Under Plato's view therefore, the species (*eidos*) is the logical unit in the strict sense while the genus facilitates the grouping of the *eidos* using a small set of characters (Papavero & Abe, 1992; Papavero & Llorente, 1992).

Current definitions of "genus"

Papavero & Llorente (1992) proposed two generic definitions:

1) The C-genus {catalog genus} is the result of the Aristotelian postulates about species, based on individual "types". Since the species are abstractions, the genus becomes a meta-abstraction [an abstraction of an abstraction], therefore not being a real space-time entity. Using this definition, a genus is a "class" (*sensu* Hull, 1976).

2) The F-genus {phylogenetic genus} is the result of the application of evolutionary theory. It is a set of three or more species that is monophyletic *sensu* Hennig (1966). According to this definition, the genus is neither a "class" nor an "individual", but a historical group (*sensu* Wiley, 1981; Brooks & Wiley, 1988).

Inclusion-exclusion test

Inclusion of a group in another, previously defined, group can be corroborated using the classical hypothetical-deductive scheme (Popper, 1959; 1963). The distribution of the sinapomorphies shows whether the group has at least one evolutionary novelty that covers all of its members, or if it is necessary to add additional taxa to obtain a monophyletic group. Such monophyly could also be tested by using the Topology Permutation Tail Probability Test [T-PTP] (Faith, 1991; Faith & Ballard, 1994).

If the F-genus definition is accepted and if not all nodes in the phylogeny are named, as **Papavero, Lorente & Abe** (1992) suggested, the genus becomes a monophyletic group. There is however no standard categorization of the node and, as a result, not all nodes correspond to a Linnean category (**Liden & Oxelman**, 1989; **Green**, 1991).

When a group is defined according to a homology series, the assignation of a name can be tested against the cladogram and the position of the "type".

Given the species
1, 2, 3, 4, 5, 6, 7

and two possible supraespecific units
I II

where the type species are [eventually the "type" is only a name-bearing entity and does not define the group]:

I = 1 II = 2

it is possible to define two coherent supraespecific taxa if there is an arrangement such as the following:

I = { 1, 3, 4, 6 } II = { 2, 5, 7 }

or any other similar arrangement. If the monophyletic group is

I - II = { 1, 2, 3, 4, 5, 6, 7 }

this must be seen as only one supraespecific taxon which should be named according to the priority principle as established by the code.

Using the T-PTP test, the length of the different hypotheses is tested against the data and the shortest is selected. The two approaches must give the same result to define the genus as a monophyletic group (see *pro* PTP **Faith**, 1991, **Faith & Cranston**, 1992; but *against* **Bryant**, 1992).

Supraspecific taxa and categories and their importance

Supraspecific taxa are important not only from the nomenclatural point of view. They are part of our language and of the way we manipulate reality. A good example of the importance of supraespecific taxa is provided by the sugarbeet leafhopper, *Circulifer tenellus*, which was originally thought to be a member of the genus *Eutettix*; under this assumption, the search for a natural enemy in South America was unsuccessful. When it was shown that it belonged in reality to the European genus *Circulifer*,

the search for enemies in the Mediterranean was successful and it was then possible to introduce them to California (SA2000, 1994).

By the same token, in ecological/environmental research there is continuous reference to supraespecific taxa. However, because many traditional taxa are paraphyletic, it is necessary to carry out phylogenetic studies to establish the monophyly of the groups concerned (**Cranston**, 1990; **Farris**, 1979, 1980, 1983). When supraespecific categories are defined on the basis of a phylogeny, the information they contain makes it possible to undertake different types of research such as character mapping and adaptation studies.

The *Ectemnaspis* / *Psilopelmia* situation. A retrospective view and the state of the art.

Until 1914 all species of Simuliidae were assigned to *Simulium* (**Rubtsov**, 1974). **Malloch** (1914) adopted *Prosimulium* in a generic sense and proposed *Parasimulium* as a new genus. **Enderlein** (1921) recognized 17 genera and, later (**Enderlein**, 1930) increased that number to 30. **Edwards** (1931) considered only *Parasimulium* as a valid genus and assigned subgeneric rank to *Prosimulium*, *Morops*, *Gigantodax*, *Austrosimulium*, *Cnephia*, *Eusimulium* and *Simulium*.

Enderlein (1934) established the genera *Ectemnaspis* and *Psilopelmia* with *Simulium bicoloratum* and *S. escomeli*, respectively as types and included them in Nevermanniinae. Actually, subgenus *Nevermannia* is circumscribed to the holarctic and palaearctic regions and *Nevermannia* **Enderlein**, 1921 is a synonym of *Simuliini* **Newman**, 1834.

Twinn (1936) recognized only *Parasimulium* and *Simulium* as valid genera. He considered the other taxa as subgenera, implying that he saw no valid differences to accept these groups at the generic level.

Fairchild & Briceño-Iragorry (1943) placed their new species, *Simulium lutzianum*, in subgenus *Eusimulium* based on the presence of hairs on Rb, a conclusion that was agreed on by **Dampf** (1943).

Vargas (1945), in his first neotropical revision of Simuliidae placed *Eusimulium* in the synonymy of *Simulium*. **Vargas et al.** (1946) found the delimitation of genera and subgenera proposed by **Smart** (1945), **Enderlein** (1921 through 1937) and **Baranov** [cited by **Vargas**, 1945 and by **Crosskey & Peterson**, 1972], difficult to accept mainly because the characters they used

are of a secondary nature and cannot be used to show phylogenetic relationships.

Vargas *et al.* (1946) accepted, provisionally, Smart's (1945) genera *Austrosimulium*, *Cnephia*, *Gigantodax*, *Parasimulium*, *Prosimulium* and *Simulium*. They saw *Simulium* as a heterogeneous group that could be subdivided into subgenera. In *Simulium* (*Lanea*) [*S. (Psilopelmia)*] they included the following species: *S. beameri*, *S. callidum*, *S. dandrettai*, *S. downsi*, *S. dugesi*, *S. haematopotum*, *S. incrustatum*, *S. johannseni*, *S. mangabeirai*, *S. mediovittatum*, *S. ochoai*, *S. samboni*, *S. trivittatum*, *S. veracruzianum* and *S. zempoalense*.

S. ochraceum was placed by Vargas *et al.* (1946) and Iriarte (1947) in *Cnephia* (*Cnephia ochraceum*), but Vargas and Díaz-Nájera (1951) moved it back into *Simulium*. Actually, *Cnephia* is a member of Prosimulini with a holarctic - palearctic distribution (Crosskey, 1987).

In the description of *S. romanai*, Wygodzinsky (1951) put that species in *Simulium* according to Vargas *et al.* (1946) key, based on male genitalia.

Dalmat (1955) proposed a new classification of *Simulium* using mainly the dorsal pattern in male/female adults, the shape of the gonostilum and the chaetotaxia in pupa stage, and the anal escleritis and secondary subdivision of the first antennal segment in larvae.

Díaz-Nájera & Vulcano (1961), in the description of *S. longithallum*, stated that *Psilopelmia* is composed of *S. mediovittatum*, *S. veracruzianum*, *S. ochoai*, *S. trivittatum*, *S. dugesi*, *S. haematopotum* and *S. longithallum*.

According to Díaz-Nájera (1961), the analysis of 13 yellow-colored species allowed him to recognize *S. (P.) antillarum* as a new species, and to conclude that *S. (P.) antillarum*, *S. (P.) dinellii*, *S. (Simulium) wolcotti* and *S. (S.) ochraceum* can be recognized as a homogeneous group, even though these four species had been previously placed in two different subgenera.

Stone (1963) considered *S. bicoloratum* as related to *S. flavifemur* which is the type of *Chirostilbia*, therefore placing *Ectemnaspis* in the synonymy of *Chirostilbia*.

Díaz-Nájera (1969) described six new species that he included in *Psilopelmia* because of their similarity in pupae form and adult color to *Simulium* (*Psilopelmia*) *trivittatum*.

Wygodzinsky (1971) revived *Chirostilbia rubiginosa*, a name that he applied to the southern Southamerica form

of *S. ignescens*, while keeping this name for the northern South American form. He redescribed *S. bicoloratum* and compared it with *S. (Chirostilbia) pertinax*. He did not agree however, with Stone's point of view (Stone, 1963), because there are differences between *S. bicoloratum* and *S. (C.) pertinax* in the uniform black color of the thorax of *S. (C.) pertinax*, the presence of plates in the scutellum, the shape of the ventral plate, the basimerus-distimerus length, and the cocoon shape. Wygodzinsky therefore, kept *Ectemnaspis* as a valid name because "these characters are on the level of those possibly indicating subgeneric difference."

According to Rubtsov & García-Avila (1972), the subdivision of genera and subgenera proposed by Enderlein (1930, 1933) and others was accepted by Dalmat (1955) without a critical analysis. As a result, whole groups of species were assigned to various genera and subgenera without explanation. According to these authors no revisions had been made until that time of the contents, size, taxonomic meaning or nomenclature of these names, or of the groups of species that actually exist in nature.

In addition to the species included by Dalmat (1955) in *Psilopelmia*, Rubtsov and García Avila also listed *S. callidum*, *S. jacobsi*, *S. samboni*, *S. haematopotum*, *S. dugessi*, *S. downsi*, *S. veracruzianum*, *S. colvini*, *S. dinellii*, *S. wolffhuegeli*, *S. jujuyense*, *S. opaliniformis*, *S. ignescens*, *S. romanai*, *S. adolfolutzii*, *S. paraguayense*, *S. bicoloratum*, *S. escomeli*, *S. riveti*, *S. limay*, *S. waltermittmeri*, *S. paynei*, *S. incrustatum* and *Chirostilbia*. If we follow this classification, then neither *Ectemnaspis* nor *Psilopelmia* are valid subgenera because the types of three different subgenera coexist in them. Using the priority principle, the correct name must be *Chirostilbia* (it comes first in Enderlein work). This subgenus definition, however, says nothing about phylogenetic relationships and does not permit the recognition of natural groups in a classification.

The phylogenetic approach was first proposed by Coscarón & Wygodzinsky (1972), who considered that *S. perflavum* should be induced in *Ectemnaspis*. They presented only an intuitive idea of *Ectemnaspis*, showing that the closest relationship is between *S. perflavum*, *S. dinellii*, *S. rubiginosum*, *S. ignescens*, *S. romanai* and *S. adolfolutzii*. This classification is quite similar to current opinion where *S. ignescens* and *S. rubiginosum* belong to the *bicoloratum* group while, *S. perflavum*, *S. romanai* and *S. dinellii* represent the other three groups in *Ectemnaspis*.

Coscarón (1984, 1987) recognized 37 species in subgenus *Ectemnaspis* which he distributed in 4 groups:

bicoloratum, *romanai*, *perflavum* and *dinellii* (Appendix 1). In his revision of neotropical *Simulium* (Coscarón, 1987) he also recognized subgenus *Psilopelmia* with 24 species with no additional subdivisions (Appendix 2). Subgenera *Psilopelmia* and *Ectemnaspis* are, along with the *S. oviedoii* group, monophyletic taxa with *Ectemnaspis* and *Psilopelmia* being sister groups.

According to Duque *et al.* (1988), Coscarón's (1987) classification is supported by chromosomal data, because extensive chromosomal homologies have been found to exist not only between *S. ignescens* and *Simulium* "C" [*S. tunja*], but also between *S. ignescens* and other *Ectemnaspis sensu* Coscarón (1984), including *S. ochraceum*.

Crosskey (1987), on the other hand, recognized only 14 species in *Ectemnaspis* (Appendix 1), almost as many as Coscarón (1984) had included in his *bicoloratum* group. Crosskey further recognized *Psilopelmia* as being composed of 50 species that include *Psilopelmia sensu stricto* plus Coscarón's *romanai*, *perflavum* and *dinellii* groups (Appendix 2). In Crosskey's view (personal communication) many of Coscarón's *Ectemnaspis* [*dinellii*, *perflavum* and *romanai* groups] are more related to *S. escomeli* (*Psilopelmia* type) than to *S. bicoloratum* (*Ectemnaspis* type). In some instances this is difficult to see because even though *S. romanai* and *S. lewisi* are closely related, Crosskey placed them in two different subgenera.

Shelley *et al.* (1989), in their study of onchocerciasis in Ecuador, included four species (*S. bipunctatum*, *S. lewisi*, *S. escomeli*, *S. quadrivittatum*) in *Psilopelmia sensu* Crosskey (1987), and questioned the validity of the two subgenera indicating that a decision on whether they should be maintained awaits further integrated morphological and cytological studies.

Using Coscarón's classification as their framework and using chromosomal banding patterns, Miranda & Muñoz de Hoyos (1993) defined the phylogenetic relationships within the *bicoloratum* group.

The systematic context

This brief overview of the history of taxonomic studies on Simuliidae shows that the development of a classification of the family has been complicated by the different sets of characters being used as well as by the different perspectives with which authors have looked at them. Those perspectives depend on the sensorial perception and the conceptual scheme given a historical / social / personal moment. The representation of the hu-

man figure, for example is not the same in Dali's than in Leonardo's eye; the same analogy is valid for systematics [cf. Feyerabend (1987), his "Science as art"].

It is often not so easy to find a character that serves to define a group, not because this character does not exist, but because the researcher fails to recognize it as important or valid. As a result, some species move from one subgenus/genus to another following a particular researcher's views of supraspecific taxa. Genera and subgenera are defined according to that personal view, and species go in or out of them depending on whether some characters of the proposed member agree with those of a previous member of that group or not. This way, taxa are not under test; here we have C-genus impossible to corroborate.

When there are difficulties in defining limits between taxa the level of the character is of the utmost importance because different researchers assign different weights to the same character. These differences are not due to ignorance (in the colloquial sense) or lack of understanding. They are the result of the fact that each researcher is a product of his or her time and of the particular frameworks used to understand and manipulate nature. Different times produce different frameworks and dissimilar limits. Indeed, this is true not only of simuliids or even of insects. Recent hominid taxonomy shows a similar situation, and Wood's (1994) questions are valid not only to fossils: given a new specimen does the material belong to an existing species group? If not, can it be assigned to existing genera?, must the new species *aramis* be placed in *Australopithecus* or in *Pan*?, is it necessary to create a new genus?

White *et al.* (1994) suggested to include the new *Aramis* in *Australopithecus*. Wood (1994), on the other hand, stated: "My own prejudice is that, even on the present evidence, the differences between the *Aramis* species and *A. afarensis* are more profound, and are more likely to reflect the sorts of grade distinction that is most usefully reflected in generic distinctions, then the differences between, say, *A. afarensis* and *A. africanus*". With a quite different approach, Simon & Rasmussen (1994) described not only a new species, *Plesiopithecus teras*, but a new genus, family and superfamily as well.

Earlier Simuliid classifications were typological in nature (Dampf, 1943; Edwards, 1931; Enderlein, 1921, 1930, 1933; Fairchild & Briceño-Iragorry, 1943; Malloch, 1914; Twinn, 1936), as they tried to get to the essence (*eidos*) based on a small set of characters. At the beginning of this century evolution was seen from a different perspective than it is today.

By the middle of the century Darwin's ideas about evolution were commonplace so, while the context changed, such changes were relatively minor. Between 1943 and 1958 Vargas and collaborators (Vargas, 1943, 1945; Vargas & Díaz-Nájera, 1951, 1953, 1958; Vargas *et al.*, 1946) gave a connotation of importance to the male / female genitalia. Theirs was a typological view (to define the group on the basis of a few characters) but in a Darwinian sense (reproductive importance).

Wygodzinsky and Coscarón (Coscarón, 1984, 1987, 1990, 1991; Coscarón & Wygodzinsky, 1972; Wygodzinsky, 1951, 1953, 1958, 1971; Wygodzinsky & Coscarón, 1982), using a completely different approach, recognized synapomorphies as the only way to test or create a classification. Indeed Wygodzinsky was one of the earlier translators of Hennig's work (Farris & Platnick, 1989; Crow, 1992). But the transition to a truly phylogenetic approach is slow, as can be seen in some of their papers (Wygodzinsky, 1971; Coscarón & Wygodzinsky, 1972) where the darwinian context, based on the level or in the importance of characters is obvious.

Crosskey (1987, 1990) and Shelley *et al.* (1989), as apposed to Coscarón saw the species as the focal point of classification and did not concern themselves with the definitions or limits of genera and/or subgenera.

Crosskey's and Coscarón's views are not alternative theories (*sensu* Feyerabend, 1980) because each uses different statements based on different approaches. *Sensu lato*, these are incommensurable points. Crosskey does not deny phylogeny but his work is at the species level and does not include phylogenetic statements, while Coscarón is based mainly on phylogeny.

The possible solution

Working with Prosimuliinae Py-Daniel (1990, 1994) has proposed to elevate subgenera to generic status and to redefine the current subfamily/tribe limits and groups. This problem is similar to the *Ectemnaspis* - *Psilopelmia* situation. It does not matter if a monophyletic group is recognized at the generic or subgeneric level. The real problem is that the solution must be coherent with data alongside sister groups in order to keep sister groups at the same hierarchical level. Whether the groups are recognized as genera or subgenera will depend on the context in relation to their sister supraspecific taxon. This situation could and must be modified in the future when new data (cytological, DNA) are available or when the way we see the characters change. If we include phylogeny in our perspective we can get a classification that could be

tested against data and not against a researcher's individual point of view. But we have to accept that today's classification is only a hypothesis that links an earlier classification with a later one.

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Literature cited

- Brooks, D.R & E.O. Wiley. 1988. Evolution as entropy. University of Chicago press. Chicago.
- Bryant, H.N. 1992. The role of permutation tail probability test in phylogenetic systematics. *Systematic Zoology* 41:258-263.
- Coscarón, S. 1984. Revisión del Género *Simulium* (*Ectemnaspis*) Enderlein (Simuliidae: Diptera: Insecta). *Revista de la Sociedad Entomológica Argentina* 43:283-325.
- . 1987. El género *Simulium* Latreille en la Región neotropical: Análisis de los grupos supraespecíficos, especies que lo integran y distribución geográfica (Simuliidae: Diptera). Museo Paraense Emilio Goeldi. Belem
- . 1990. Taxonomía y distribución del subgénero *Simulium* (*Ectemnaspis*) Enderlein (Simuliidae, Diptera, Insecta). *IHERINGIA. Serie Zoología. Porto Alegre* (70):109-170.
- . 1991. Insecta. Diptera. Simuliidae. Fascículo 2. Fauna de Agua dulce de la república de Argentina XXXVIII:1-304.
- & P. Wygodzinsky. 1972. Notas sobre simúlidos neotropicales III. Sobre tres especies de jejenos con hembras de color claro, del SE del Paraguay y del NE de la Argentina. *Revista del Museo de La Plata. Sección Zoología*. XI:209-231.
- Cranston, P.S. 1990. Biomonitoring and invertebrate taxonomy. *Environmental and Monitory Asses.* 14:265-273.
- Crow, R. 1992. Margins of cladistics: identity, difference and place in the emergence of phylogenetics systematics 1864-1975. pp. 65-107. In: Griffiths, P. (Ed.) *Essays on the Philosophy of Biology*. Kluger, Dordrecht, The Netherlands.
- Crosskey, R. 1987. An annotated checklist of the world black flies (Diptera:Simuliidae), pp. 425-520. In: Kim, K.C. & R.W. Merritt (Eds), *Black flies: ecology, population management and annotated word list*. The Pennsylvania State University Press. London.
- . 1990. *The natural history of Black flies*. Jhon Wiley & Sons. London.
- & B.V. Peterson. 1972. The simuliidae described by N. Baranov and their types (Diptera). *Bulletin British Museum. Entomology* 27:189-214.
- Cummins, K. 1987. The functional role of the black flies in stream ecosystems. pp. 1-10. In: Kim, K.C. & R.W. Merritt (Eds), *Black*

- flies: ecology, population management and annotated word list. The Pennsylvania State University Press. London.
- Dalmat, H.T.** 1955. The black flies (Diptera, Simuliidae) of Guatemala and their role as vectors of onchocerciasis. *Smithsonian Miscellaneous Collection* **125**:1-425.
- Dampf, A.** 1943. La crisálida de *Eusimulium ochraceum* (Walker 1860) (Insecta, Diptera). *Revista de la sociedad Mexicana de Historia Natural* **IV**:33-42.
- Díaz-Nájera, A.** 1961. Nota acerca de *Simulium (Psilopelmia) antillarum* Jennings, 1915, nueva especie para México. *Revista Instituto Salubridad y Enfermedades Tropicales (Méx.)* **21**:79-92.
- _____. 1969. Simúlidos de Aguascalientes y zacatecas. Descripción de seis especies del subgénero *Psilopelmia* y datos de dimorfismo. *Revista Instituto Salubridad y Enfermedades Tropicales (Méx.)* **29**:21-63.
- _____ & **M.A. Vulcano.** 1961. Descripción de *Simulium (Psilopelmia) longithalum* n.sp. (Diptera: Simuliidae). *Revista Instituto Salubridad y Enfermedades Tropicales (Méx.)* **21**:221-235.
- Duque, S., Muñoz de Hoyos, P. & K. Rothfels.** 1988. The polytene chromosomes of *Simulium (Ectemnaspis) ignescens* Roubaud and the related species *Simulium "C"*, both from Colombia. *Canadian Journal of Zoology* **66**:300-309.
- Edwards, F.W.** 1931. Simuliidae. In: *British Museum (Natural History): Diptera of Patagonia and South Chile* **2**:121-154.
- Enderlein, G.** 1921. Das System Kriebelmücken (Simuliidae). *Deutsch. Tierärztl. Wochenschr.* **29**:197-200.
- _____. 1922. Weitere Beiträge zur Kenntniss der Simuliiden *Konowia* **1**:67-76.
- _____. 1930. Der heutige Stand der Klassifikation der Simuliiden. *Arch. Klassif. Phylogen. Ent.* **1**:77-97.
- _____. 1934. Weiterer Ausban des Systems der Simuliiden. *Deutsch. Ent. Zeitschr (1933)*. **I/II**:273-292.
- _____. 1935. Auëereuropaische Simuliiden aus dem Wiener Museum. *Sitzungsberichte der Gessellschaft naturforschender Freunde (1934)*:190-195.
- _____. 1937. Simuliologica I. *Sitzungsber. Gessell. Naturf. Fr.* pp. 113-130.
- Fairchild, G.B. & L. Briceño-Iragorrry.** 1943. Notas sobre *Simulium lutzianus*. *Boletín del Laboratorio Clínica Luis Razzeti* **3**:187-188.
- Faith, D. P.** 1991. Cladistic permutation test for Monophyly and non-monophyly. *Systematic Zoology* **40**:366-375.
- _____ & **J.W.O. Ballard.** 1991. Length differences and topology-dependent tests: a response to Källersjö *et al.* *Cladistics* **10**:57-64.
- _____ & **P.S. Cranston.** 1992. Probability, Parsimony and Popper. *Systematic Zoology* **41**:252-257.
- Farris, J.S.** 1979. On the naturalness of phylogenetic classification. *Systematic Zoology* **28**:200-214.
- _____. 1980. The information content of the phylogenetic system. *Systematic Zoology* **29**:483-519.
- _____. 1983. The logical basis of phylogenetic analysis. pp. 1-47 In: **Platnick, N.I. and V. A. Funk.** (Eds.) *Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society.* Columbia University Press, New York.
- _____ & **N. Platnick.** 1989. Lord of the flies: the sistematist as study animal. *Cladistics* **5**:295-310.
- Feyerabend, P.K.** 1980. How to be a good empiricist - A plea for tolerance in matters epistemological. pp. 164-195. In: **Morick, H.** (Comp.) *Challenges to empiricism.* Methuen Co.
- _____. 1987. *Farewell to reason.* Verso. London.
- Green, D. M.** 1991. Chaos, Fráctals and Nonlinear Dynamics in Evolution and Phylogeny. *Trends in Ecology and Evolution* **6**:333-337.
- Hennig, W.** 1966. *Phylogenetic Systematics.* Univ. of Illinois press. Urbana.
- Hull, D.L.** 1976. Are species really individuals? *Systematic Zoology* **25**:174-191.
- Iriarte, D.R.** 1947. Nueva especie de simúlido para Venezuela. *Boletín del Laboratorio de la clínica Luis Razzeti.* **15**:509-511.
- Jahn, I., Lother R. & K. Senglaub.** 1990. *Historia de la Biología. Teorías, Métodos, Instituciones y Biografías breves.* Labor. Barcelona.
- Kuhn, T.S.** 1970. *The structure of scientific revolutions.* Univ. Chicago press. Chicago.
- Liden, M. & M. Oxelman.** 1989. Species Concept - Pattern or Process? *Taxon* **38**:228-232.
- Linnaeus, C.** 1735. *Systema Naturea, sive regna tria naturae systematice proposita per classes, ordines, genera & species.* Haak, Lugduni Batavorum (Leiden).
- Malloch, J.R.** 1914. American black flies or Buffalo gnats. U.S. department of agriculture. Bureau of Entomology. technical series (**26**):28-75.
- Mayr, E.** 1969. *Principles of systematic zoology.* McGraw Hill, New York.
- Miranda, D.R. & P. Muñoz de Hoyos.** 1993. Relaciones filogenéticas del género *Simulium* subgénero *Ectemnaspis* subgrupo *bicoloratum*. *Revista de la Academia de Ciencias.* **18**:571-577.
- Papavero, N. & J.M. Abe.** 1992. Funciones que preservan orden y categorías lineanas. *Publicaciones especiales del Museo de Zoología UNAM* **5**:39-74.
- _____ & **J. Llorente.** 1992. El uso equivoco del concepto género en sistemáticas filogenética. *Publicaciones especiales del Museo de Zoología* **5**:31-37.
- _____, **Abe, J.M. & J. Llorente.** 1993a. Propuesta de un nuevo sistema de nomenclatura para la sistemática filogenética. V: Las categorías supraespecíficas. *Publicaciones especiales del Museo de Zoología UNAM* **7**:1-45.
- _____, **Abe, J.M. & J. Llorente.** 1993b. Propuesta de un nuevo sistema de nomenclatura para la sistemática filogenética. VI: La cuestión de los 'subgéneros'. *Publicaciones especiales del Museo de Zoología UNAM* **7**:47-62.
- _____, **Llorente J. & J.M. Abe.** 1992. Propuesta de un nuevo sistema de nomenclatura para la sistemática filogenética I. *Publicaciones especiales del Museo de Zoología UNAM* **5**:1-20.
- Peterson, B.V.** 1993. The black flies of the genus *Simulium* subgenus *Psilopelmia* (Diptera: Simuliidae), in the contiguous United States. *Journal of the New York Entomological Society* **101**:301-390.
- Popper, K.** 1959. *The logic of the scientific discovery.* Hutchinson. London.
- _____. 1963. *Conjetures and refutations: the growth of Scientific Knowledge.* Harper & Row. New York.

- Py-Daniel, V.** 1990. Revisão da tribo Prosimuliini seg. Crosskey (Diptera, Culicomorpha, Simuliidae) nas regiões zoogeográficas neártica e neotropical (larvas e pupas). Ph. D. Thesis. Instituto Nacional de Pesquisas da Amazonia.
- _____ & **R. T. Moreira Sampaio**, 1994. *Jalacingomyia* gen. n. (Culicomorpha); a ressurreição de Gymnopauidinae; a eliminação do nível tribal; a apresentação dos novos caracteres e a redescrção dos estgios larval e pupal de *Simulium colombaschense* (Fabricius, 1787) (Diptera:Simuliidae). Memórias del CAICET IV (1,2):101-148.
- Radl, E.M.** 1988. Historia de las teorías biológicas. vol I. Madrid. Alianza Universidad.
- Rubtsov, I. A.** 1974. Ob evolyutsii, filogenii i klassifikatsii semeistva moshek (Simuliidae, Diptera) [English translation. Evolution, phylogeny and classification of the family simuliidae (Diptera)]. Trudy. Zool. Inst. AN USSR 53:230-281.
- _____ & **I. García-Avila**. 1972. Los simúlidos de Cuba (Diptera:Simuliidae). Poeyana. Instituto de Zoología. Academia de Ciencias de Cuba 96:1-39.
- Shelley, A.J., Arzube M. & C.A. Couch.** 1989. The Simuliidae (Diptera) of the Santiago onchocerciasis focus of Ecuador. Bulletin of the British Museum natural History 58:79-130.
- Simon, E.L. & D.T. Rasmussen**, 1994. A remarkable cranium of *Plesiothecus teras* (Primates, Prosimii) from the eocene of Egypt. Proceedings. of the National Academy of Science USA. 91:9946-9950.
- Smart, J.** 1945. The classification of simuliidae (Diptera). Royal Entomological Society Transactions 95:463-528.
- Stone, A.** 1963. An annotated list of genus-group names in the family Simuliidae (Diptera). Agricultural research service USDA. Technical bulletin 1284:1-28.
- Systematics Agenda 2000**, 1994. Charting the biosphere. Technical report. New York.
- Twinn, C.R.** 1936. The blackflies of Eastern Canada (Simuliidae, Diptera). Part I. Canadian Journal of Research 14:97-150.
- Vargas, L.** 1943. Nombres y datos nuevos sobre simúlidos del Nuevo mundo. Revista de la Sociedad Mexicana de Historia Natural 4:135-146.
- _____. 1945. Simúlidos del Nuevo Mundo. Monografías del Instituto de Salubridad y Enfermedades Tropicales (Méx.) 1:1-241.
- _____ & **A. Díaz-Nájera**. 1951. Nota sobre los simúlidos de México y su distribución geográfica (Diptera: Simuliidae). Revista Instituto de Salubridad y enfermedades tropicales (Méx.) 12:89-100.
- _____ & **A. Díaz-Nájera**. 1953. Nota sobre el examen de tipos de simúlidos descritos por el prof. G. Enderlein. (Méx.) Revista Instituto de Salubridad y enfermedades tropicales 13:137-152.
- _____ & **A. Díaz-Nájera**. 1958. Nota sobre *Simulium bivittatum* Malloch, 1914. Revista Instituto de Salubridad y enfermedades tropicales (Méx.) 18:13-30.
- _____, **Díaz-Nájera, A. & A. Martínez-Palacios**. 1946. Simúlidos de México. Datos sobre sistemática y morfología. Descripción de nuevos subgéneros y especies. Revista Instituto de Salubridad y enfermedades tropicales (Méx.) 7:101-192.
- White, T, Suwa, G. & B. Asfaw**. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature. 371:306-312.
- Wiley, E.O.** 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons, New York.
- Wood, B.** 1994. The oldest hominid yet. Nature. 371:280-281.
- Wygodzinsky, P.** 1951. Sobre *Simulium ignescens* Roubaud 1906, *Simulium romañai* sp. n. y *Simulium adolfolutzii* sp. n. (Simuliidae, Diptera). Anales del Instituto de Medicina Regional 32:221-236.
- _____. 1953. Sobre algunos Simúlidos de los países andinos. Anales del instituto de Medicina Tropical III:321-337.
- _____. 1958. Notas y descripciones de "Simuliidae" patagónicos y andinos (Diptera). Acta Zológica Lilloana 16:121-148.
- _____. 1971. Descriptions and redescrptions of species of the Black fly genus *Simulium* from the Northern Andes Simuliidae, Diptera). American Museum Novitates (2447):1-38.
- _____ & **S. Coscarón**. 1982. Description of three unusual species of the black fly subgenus *Simulium* (*Ectemnaspis*) from the Andes of Colombia (Diptera, Simuliidae). American Museum Novitates (2736):1-13.

Appendix 1. Species composition of subgenus *Ectemnaspis* Enderlein, 1934.**Sensu Coscarón (1990)*****Bicoloratum* group**

- S. antonii* Wygodzinsky, 1953
S. arcabucense Coscarón, 1990
S. bicoloratum Malloch, 1912
S. bicornutum Wygodzinsky & Coscarón, 1982
S. cormonsi Wygodzinsky, 1971
S. furcillatum Wygodzinsky & Coscarón, 1982
S. ignescens Roubaud, 1906
S. jaimeramirezi Wygodzinsky, 1971
S. pautense Coscarón & Takaoka 1989
S. pifanoi Ramírez-Pérez, 1971
S. roquemayu Coscarón, 1984
S. rubiginosum (Enderlein, 1934)
S. tolimaense Coscarón, 1984
S. tunja Coscarón, 1990

***Romanai* group**

- S. albanense* Coscarón, 1990
S. alirioi Ramírez-Pérez & Vulcano, 1973
S. gabaldoni Ramírez-Pérez, 1971
S. lewisi Ramírez-Pérez, 1971
S. lutzianum Pinto, 1931
S. mayuchuspi Coscarón, 1990
S. romanai Wygodzinsky, 1951
S. wolffhuegeli (Enderlein, 1922)

***Perflavum* group**

- S. kabanayense* Ramírez-Pérez & Vulcano, 1973
S. maroniense Floch & Abonnenc, 1946
S. perflavum Roubaud, 1906
S. rorotaense Floch & Abonnenc, 1946
S. suarezi Ramírez-Pérez, Rassi & Ramírez, 1977

***Dinellii* group**

- S. antillarum* Jennings, 1915
S. bipunctatum Malloch, 1912
S. dinellii Joan, 1912
S. nuneztovari Ramírez-Pérez, Rassi & Ramírez, 1977
S. ochraceum Walker, 1861
S. pseudoantillarum Ramírez-Pérez & Vulcano, 1973
S. scutellatum Lane & Porto, 1940
S. shewellianum Coscarón, 1984
S. wolcotti Fox, 1953
S. wuayaraka Ortiz, 1957

Sensu Crosskey (1987)

- S. adolfolutzii* Wygodzinsky, 1951
S. antonii Wygodzinsky, 1953
S. bicoloratum Malloch, 1912
S. bicornutum Wygodzinsky & Coscarón, 1982
S. cormonsi Wygodzinsky, 1971
S. furcillatum Wygodzinsky & Coscarón, 1982
S. ignescens Roubaud, 1906
S. jaimeramirezi Wygodzinsky, 1971
S. pifanoi Ramírez-Pérez, 1971
S. romanai Wygodzinsky, 1951
S. roquemayu Coscarón, 1985
S. rubiginosum (Enderlein, 1934)
S. sicuani Smart, 1944
S. tolimaense Coscarón, 1985

New species described after 1990 (Placed in the **romanai** group).

- S. anaimense* Coscarón & Muñoz de Hoyos, 1995

Apéndice 2. Species composition of subgenus *Psilopelmia* Enderlein, 1934.

Sensu Coscarón (1987)

- S. bivittatum* Malloch, 1914
S. callidum (Dyar & Shannon, 1927)
S. dandrettai Vargas, Martínez Palacios & Díaz Nájera, 1946
S. downsi Vargas, Martínez Palacios & Díaz Nájera, 1946
S. dugesi Vargas, Martínez Palacios & Díaz Nájera, 1946
S. escomeli Roubaud, 1909
S. gonzalezherrejoni Díaz Nájera, 1969
S. haematopotum Malloch, 1914
S. iracouboense Floch & Abonnenc, 1946
S. jacobsi Dalmat, 1953
S. jerezense Díaz Nájera, 1969
S. letrasense Díaz Nájera, 1969
S. longithallum Díaz Nájera & Vulcano, 1962
S. mangabeirai Vargas, 1945
S. mediovittatum Knab, 1969
S. netтели Díaz Nájera, 1969
S. ochoai Vargas, Martínez Palacios & Díaz Nájera, 1946
S. olimpicum Díaz Nájera, 1969
S. pseudocallidum Díaz Nájera, 1965
S. samboni Jennings, 1915
S. trivittatum Malloch, 1914
S. veracruzianum Vargas, Martínez Palacios & Díaz Nájera, 1946
S. vulcanoe Díaz Nájera, 1969
S. zenpoalense Vargas, Martínez Palacios & Díaz Nájera, 1946

Sensu Crosskey (1987)

- S. alirioi* Ramírez-Pérez & Vulcano, 1973
S. antunesi Lane & Porto, 1940
S. bipunctatum Malloch, 1912
S. bivittatum Malloch, 1914
S. callidum (Dyar & Shannon, 1927)
S. dandrettai Vargas, Martínez Palacios & Díaz Nájera, 1946
S. dinellii (Joan, 1912)
S. downsi Vargas, Martínez Palacios & Díaz Nájera, 1946
S. dugesi Vargas, Martínez Palacios & Díaz Nájera, 1946
S. escomeli Roubaud, 1909
S. gabaldoni Ramírez-Pérez, 1971
S. gonzalezherrejoni Díaz Nájera, 1969
S. griseum Coquillett, 1898

- S. haematopotum* Malloch, 1914
S. iracouboense Floch & Abonnenc, 1946
S. jacobsi Dalmat, 1953
S. jerezense Díaz Nájera, 1969
S. kabanayense Ramírez-Pérez & Vulcano, 1973
S. letrasense Díaz Nájera, 1969
S. lewisi Ramírez-Pérez, 1971
S. longithallum Díaz Nájera & Vulcano, 1962
S. lutzianum Pinto, 1932
S. mangabeirai Vargas, 1945
S. mauense Nunes de Mello, 1974
S. mazzottii Díaz Nájera, 1981
S. mediovittatum Knab, 1969
S. netтели Díaz Nájera, 1969
S. nilési Rambajan, 1979
S. notatum Adams, 1904
S. nuneztovari Ramírez-Pérez, Rassi & Ramírez, 1977
S. ochoai Vargas, Martínez Palacios & Díaz Nájera, 1946
S. ochraceum Walker, 1861
S. olimpicum Díaz Nájera, 1969
S. panamense Fairchild, 1940
S. perflavum Roubaud, 1906
S. pseudoantillarum Ramírez-Pérez & Vulcano, 1973
S. pseudocallidum Díaz Nájera, 1965
S. quadrivittatum Loew, 1862
S. rorotaense Floch & Abonnenc, 1946
S. samboni Jennings, 1915
S. shewellianum Coscarón, 1985
S. spinifer Knab, 1914
S. suarezi Ramírez-Pérez, Rassi & Ramírez, 1977
S. sucamense Nunes de Mello, 1974
S. trivittatum Malloch, 1914
S. venator Dyar & Shannon, 1927
S. veracruzianum Vargas, Martínez Palacios & Díaz Nájera, 1946
S. vulcanoe Díaz Nájera, 1969
S. wolffhuegeli Enderlein, 1922
S. zenpoalense Vargas, Martínez Palacios & Díaz Nájera, 1946
 New species described after 1990
S. labellei Peterson, 1993
S. robynae Peterson, 1993